DOES IMMIGRATION “RESCUE” POPULATIONS FROM EXTINCTION?

by

MICHAEL CLINCHY

B.Sc., University of Toronto, 1988

M.Sc., Queen’s University, 1990

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES

(Department of Zoology)

We accept this thesis as conforming

to the required standard:

THE UNIVERSITY OF BRISTISH COLUMBIA

July 1999

ABSTRACT

I measured the rate of immigration by female common brushtail possums (*Trichosurus vulpecula*) in response to the removal of resident breeding females, in a landscape with no physical barriers to dispersal. I removed 10 residents from one 36 ha study grid and 9 from another, and monitored immigration over the next two years. Only one immigrant settled in one of the two removal areas. Sixteen breeding females resident on the periphery of the removal areas expanded their ranges into the removal areas. The one immigrant was a subadult that did not give birth in the breeding season following her arrival. Parentage analysis using microsatellite DNA indicated that the immigrant had moved only one home range away from her putative mother's home range (≅ 200 m).

All of the known daughters of resident females settled beside their mothers. Parentage analysis indicated that 39 % of adjacent pairs of resident females were putatively mother and daughter, which is close to the 42 % expected if daughters always settle beside their mothers. The sex ratio of pouch-young was significantly male-biased, as predicted by the 'local resource competition' hypothesis, if most males disperse and most females settle beside their mothers.

A deterministic, stage-based model of demography indicated that the birth rate was insufficient to balance the death rate ($r = - 0.1$), suggesting that the site was a 'dispersal sink'. However, even with immigration, the projection was that density would decline by 84 %. Neither 'old age', starvation, predation or disease could explain 11 of the 24 deaths among resident females. Most of these females demonstrated prior symptoms of stress. Females that were captured and handled more frequently had a significantly lower probability of survival, and the estimated adult survival rate was significantly lower than that expected from the observed age distribution. I suggest apparent 'dispersal sinks' may often be of our own making.

Deaths due to capture and handling are analogous to removals. Consequently, since there were evidently more than 19 'removals', I conclude that the results of the experiment likely *over*estimate the importance of immigration in replacing losses among breeding females.

TABLE OF CONTENTS

Abstract ii

Table of Contents iii

List of Tables vi

List of Figures x

Preface xiii

Acknowledgements xiv

CHAPTER 1: Does immigration "rescue" populations from extinction?

General introduction 1
References 8

CHAPTER 2: Does immigration "rescue" populations from extinction? Implications regarding movement corridors and the conservation of mammals

Introduction 11
Alternative hypotheses 12
Behavioural data 13
Conclusions 17
References 18

CHAPTER 3: Methodological problems in the study of immigration and extinction

Introduction 25
The correlational-survey approach 25
Identifying immigrants in open populations in the field 27
An integrated approach 30
References 33

CHAPTER 4: Does immigration "rescue" populations from extinction? Evidence from a large-scale field experiment on common brushtail possums

Introduction 40

Methods

Study species 46
Study site 48
Detection, capture, and handling 50
Definitions and experimental design 52
Radio telemetry and den mapping 56
Live-trapping 58
Spotlighting and darting 59
Complete enumeration 60
Adequacy of location data from radio telemetry 71
Collection of tissue samples and analysis of microsatellite DNA 73

Results
- Female immigration following removals 74
- The vacuum effect and breeding dispersal 76
- Potential immigrants captured in the core 77
- Adverse effects of capture and handling and the measured rate of immigration 79
- Locations of known mothers and daughters 82
- Locations of mothers and daughters identified using microsatellite DNA 83
- Direct observations of restricted movements between the grids 84
- Restricted movements between the grids identified using microsatellite DNA 85
- Sex ratios of pouch-young 85

Discussion 86
References 93

CHAPTER 5: Connectivity or carnivory: what's more important to the demography of common brushtail possum populations?

Introduction 139
Methods 142
- Age estimates from cementum annuli 142
- Date of birth of pouch-young 143

Results
- Seasonality of births 144
- Sex ratios of dependent young 145
- Stages in the weaning of young 146
- Pre-weaning survival of young 147
- Pre-weaning loss of young as a result of capture and handling 149
- Pre-weaning loss of young as a result of predator chases 154
- Pre-weaning loss of young as a result of infanticide 154
- Pre-weaning loss of young as a result of food shortage 155
- Post-weaning survival of young 160
- Age at first breeding 168
- Reproductive success of first-time breeders 169

Discussion 174
References 179

CHAPTER 6: Dispersal sinks and handling effects: interpreting the role of immigration in common brushtail possum populations

Introduction 212
Methods 215
Results
- Adult female survival 217
- A model of possum demography 220
- Wobbly possums 224
- Other indices of poor condition 229
- Weight loss associated with trapping, among apparently healthy animals 231
- Deaths due to predation 232
- Necropsies 234
- Age at death 240
- Survival and the frequency of handling 243
- Population growth rates and "censored" survival estimates 246

Discussion 247
References 253

CHAPTER 7: Conclusions and implications for conservation

General discussion 282
References 288

APPENDIX 1: Assumptions underlying the analysis of microsatellite DNA

Introduction 290
Linkage disequilibrium and deviations from Hardy-Weinberg equilibrium (HWE) 290
Parentage analysis 292
Absolute likelihoods 298
References 300

APPENDIX 2: Estimating the date of birth of pouch-young

Introduction 304
Derivation of methods 304
Protocols adopted 307
References 309

LIST OF TABLES

Table 2.1 Summary of results of examining populations illustrated in Figure 2.2 and asking the question "do both populations persist from time 1 to time 2?" 21

Table 2.2 Contingency table for analysis of relationship between proximity and persistence using evidence from Table 2.1 and Figure 2.2. 22

Table 3.1 Distance to the nearest occupied patch at time 1, as compared between populations found to be extinct or extant at time 2, based on results from four surveys of the Bodie, California, pika metapopulation, as reported in Smith and Gilpin (1997, their Fig. 2) 37

Table 4.1 Number and date of, and level of effort associated with, full-grid trapping sessions on the West grid. 102

Table 4.2 Number and date of, and level of effort associated with, full-grid trapping sessions on the East grid. 103

Table 4.3 Level of effort associated with, and number of animals seen during spotlight transects in the core areas of the two study grids. 104

Table 4.4 Level of effort associated with, and number of animals seen during spotlight transects on the periphery of the two study grids. 105

Table 4.5 Population size estimates regarding all adult and subadult females on the West grid. 106

Table 4.6 Population size estimates regarding all adult and subadult females on the East grid. 107

Table 4.7 Population size estimates regarding all adult and subadult males on the West grid. 108

Table 4.8 Population size estimates regarding all adult and subadult males on the East grid. 109

Table 4.9 Allele frequencies observed at six microsatellite loci. 110

Table 4.10 Putative mother-daughter relationships identified among adult (and subadult) females on the West grid. 111

Table 4.11 Putative mother-daughter relationships identified among adult (and subadult) females on the East grid. 112

Table 4.12 Differences in mean likelihood scores, as shown in Tables 4.10 and 4.11, between adjacent and non-adjacent putative parent-offspring pairs of adult (and subadult) females. 113

Table 4.13 Reported sex ratios of pouch-young. 114

Table 5.1	Differences in the reproductive biology of common brushtail possums in disturbed and undisturbed populations.	185
Table 5.2	Number of resident adult females producing a primary young in either autumn or winter, compared to the number of females that did not reproduce.	186
Table 5.3	Sex ratios (F:M) of dependent young, categorized by study area and breeding season.	187
Table 5.4	Pre-weaning survival of primary young.	188
Table 5.5	Mean interval, in days, between occasions on which females were handled, while they were carrying a pouch-young, prior to 175 days after the birth of their young, as compared between instances where the young was known to have survived to the onset of weaning (at 175 days), and where it did not.	189
Table 5.6	Pre-weaning loss of young in relation to ear-tagging.	190
Table 5.7	Survival of young to October-November, 1996, as compared between mothers subject to repeated capture and handling (On-grid) and others that had not been previously trapped and handled (Off-grid).	191
Table 5.8	Predator activity during the pre-weaning phase of development of primary young, from mid-March to mid-December, in 1995 and 1996, based on sightings, sounds, signs, and diagnoses of the proximate cause of death of adult possums.	192
Table 5.9	Survival of primary young to August 1, in both 1995 and 1996, on both principal study grids.	193
Table 5.10	Survival of pouch-young to the onset of weaning (175 days) in 1995 and 1996, among females demonstrating any or all of four symptoms of poor condition.	194
Table 5.11	Changes in the status of individual adult female possums examined in a given season in 1995 for evidence of rump wear as compared to the same individual's status in the same season in 1996.	195
Table 5.12	Median difference in mean weight (g) of individual adult possums measured in a given season in 1996 as compared to the same individual's mean weight in the same season in 1995.	196
Table 5.13	Weight (g) of adult females weighed with or without a young in the pouch, in October-November, 1996, as compared between On-grid and Off-grid locations.	197
Table 5.14	Number of young tagged as pouch-young in the year indicated, that were later seen as subadults, independent of their mothers.	198
Table 5.15	Mean, median, and other summary statistics, regarding the distribution of mean autumn body weights (g), among known-aged animals.	199

Table 5.16 New individuals detected during grid trapping from the beginning of spring 1995 onwards. 200

Table 5.17 Birth dates of pouch-young (expressed as the number of days from the beginning of autumn) among first-time breeders and females that had given birth at least once before (repeat breeders). 201

Table 5.18 Birth dates of pouch-young (expressed as the number of days from the beginning of autumn) in relation to the pre-weaning survival of primary young (see Table 5.4) on each of the two principal study grids in each of the two complete years for which data were available. 202

Table 6.1 Definitions regarding the parameters used in the model of possum demography illustrated in Figure 6.4. 259

Table 6.2 Sources of parameter values for the Paddys Land population, used in the model of possum demography illustrated in Figure 6.4. 260

Table 6.3 Sources of parameter values for the Orongorongo Valley population, used in the model of possum demography illustrated in Figure 6.4. 261

Table 6.4 Population growth rate (*r*) predicted using the model illustrated in Figure 6.4, as regards possums at the Paddys Land site, given three sets of assumptions regarding their breeding biology, and as compared to the predicted *r* at the Orongorongo Valley site. 262

Table 6.5 Total number of trap-captures per season, in each year, on the two principal study grids. 263

Table 6.6 Number of times animals were observed to have either lost weight or not lost weight between successive occasions on which they were weighed. 264

Table 6.7 Total number of times females were trapped and handled per season, in each year, on the two principal study grids. 265

Table 6.8 Potential predators of common brushtail possums recorded at the Paddys Land site over the three years of the study. 266

Table 6.9 Relationship between the results of tests conducted to determine whether the bandaging wrapped around an individual's radio-collar was inundated with blood, and the condition of the individual's carcass, in 21 of the 22 cases where a radio signal was tracked to a dead female. 267

Table 6.10 Prevalence and intensity of parasitic infections among the 23 possums from the Paddys Land site that were necropsied, categorized by the fate of the host. 268

Table 6.11 Prevalence and intensity of ectoparasitic infections compared between adult females observed with symptoms of rump wear on at least one occasion, versus females never observed with symptoms of rump wear. 269

Table 6.12 Prevalence and intensity of *Parastrongyloides trichosuri* infections, categorized by the fate and condition of the host. 270

Table 6.13 Mean (and S.E.) age in years, as determined from cementum annuli, among the 23 possums that were necropsied, categorized by fate (Died versus Killed) and sex. 271

Table 6.14 Observed number of individuals in each of two age classes, among 38 possums aged from cementum annuli, as compared to the expected number in each class if survival is assumed to be 81.3 % per annum. 272

Table 6.15 Seasonal survival of radio-collared adult females (1997 data excluded), under four scenarios regarding the treatment of censored data, and the effects on the value of *r* predicted by the model of possum demography (assuming 'Typical' parameter values for the Paddy Land site). 273

Table A1.1 Observed (H_O) end expected (H_E) heterozygosity at each of the six microsatellite loci described in Table 4.9, as calculated using genotypic frequency data from both grids, both combined and separately. 301

Table A1.2 Known mother-young pairs where both mother and young were successfully typed at one or more of the microsatellite loci described in Table 4.9. 302

Table A1.3 Average exclusion probabilities based on allelic frequencies on each grid, of each of the six microsatellite loci listed in Table 4.9. 303

LIST OF FIGURES

Figure 2.1 Conventional portrayal of relationship between proximity and persistence. 23

Figure 2.2 Environmentally induced synchrony of population dynamics signified by clustering of populations. 24

Figure 3.1 Steps in delineating a peripheral “buffer strip” for use in the unambiguous identification of “true” immigrants. 38

Figure 3.2 Example of how immigration may be overestimated if handling has a significantly adverse effect on resident reproduction or survival. 39

Figure 4.1 Schematic map of the study site showing the relative position of the two principal study grids. 115

Figure 4.2 Schematic map of the West grid. 116

Figure 4.3 Schematic map of the East grid. 117

Figure 4.4 Location of all females captured on the West grid prior to August 1, 1995. 118

Figure 4.5 Location of all females captured, or known to be present, on the West grid, between August 1, and September 15, 1995. 119

Figure 4.6 Location of all females captured, or known to be present, on the West grid, between September 15, 1995, and March 15, 1996. 120

Figure 4.7 Location of all females captured, or known to be present, on the West grid, between March 15, 1996, and August 1, 1996. 121

Figure 4.8 Location of all females captured, or known to be present, on the West grid, between August 1, 1996, and March 15, 1997. 122

Figure 4.9 Location of all females captured, or known to be present, on the West grid, between March 15, and August 1, 1997. 123

Figure 4.10 Location of all females captured on the East grid prior to August 1, 1995. 124

Figure 4.11 Location of all females captured, or known to be present, on the East grid, between August 1, and September 15, 1995. 125

Figure 4.12 Location of all females captured, or known to be present, on the East grid, between September 15, 1995, and March 15, 1996. 126

Figure 4.13 Location of all females captured, or known to be present, on the East grid, between March 15, 1996, and August 1, 1996. 127

Figure 4.14 Location of all females captured, or known to be present, on the East grid, between August 1, 1996, and March 15, 1997. 128

Figure 4.15 Location of all females captured, or known to be present, on the East grid, between March 15, and August 1, 1997. 129

Figure 4.16 Cumulative number of newly-identified females initially captured in the core of one of the two study grids, from the start of spring 1994, until the end of the study in July 1997. 130

Figure 4.17 Cumulative number of newly-identified females initially captured on the periphery of one of the two study grids, from the start of spring 1994, until the end of the study in July 1997. 131

Figure 4.18 Cumulative number of newly-identified males initially captured in the core of one of the two study grids, from the start of spring 1994, until the end of the study in July 1997. 132

Figure 4.19 Cumulative number of newly-identified males initially captured on the periphery of one of the two study grids, from the start of spring 1994, until the end of the study in July 1997. 133

Figure 4.20 Plot of the minimum number of females known to be alive on a grid (MNA-Grid), in a given trapping session, versus the Jolly-Seber estimate of the number (N) of females present. 134

Figure 4.21 Proportion of full-grid trapping sessions during which radio-collared females were captured. 135

Figure 4.22 Total number of dens used by a given female as compared to the total number of radio fixes for that female. 136

Figure 4.23 Total denning range length (the maximum distance between any two dens, in m) calculated for a given female, as compared to the total number of radio fixes for that female. 137

Figure 4.24 Mean (+/- S.E.) proportion of radio fixes tracked to each of the array of dens used by a given female, among females located a minimum of 15 times. 138

Figure 5.1 Deviation, in years, between age estimates, based on cementum annuli, made using two teeth (PM1 and M3) from the same individual. 203

Figure 5.2 Number of births per week during autumn and winter in each of the three years of the study. 204

Figure 5.3 Number of observations concerning the three stages in the weaning of young, vs. the age of the young. 205

Figure 5.4 Percentage of adult possums seen feeding upon being released from a trap, in each season, among animals that were known to have survived to the end of the season. 206

Figure 5.5 Percentage of adult female possums demonstrating symptoms or behaviours potentially indicative of poor condition, in each season, among animals that were known to have survived to the end of the season. 207

Figure 5.6 Mean (+ S.E.) body weight (g) of adult possums, categorized by season. 208

Figure 5.7 Total monthly rainfall (solid black line) recorded at the Kookabookra weather station (20 km from the Paddys Land site) over the course of the study. 209

Figure 5.8 Body weight (g) of known-age pouch-young plotted against age in days. 210

Figure 5.9 Mean autumn body weight (g) of known-age adults and subadults, plotted against age in years. 211

Figure 6.1 Number of radio-collared adult females at risk, from the beginning of autumn 1995, until the end of the study in July 1997. 274

Figure 6.2 Cumulative probability of survival of radio-collared adult females, based on the Kaplan-Meier estimator, modified for staggered entry. 275

Figure 6.3 Thirteen-week seasonal survival of radio-collared adult females, based on the Kaplan-Meier estimator, modified for staggered entry. 276

Figure 6.4 Structure of the model of possum demography . 277

Figure 6.5 Number of individuals demonstrating a given rate of proportionate weight loss, measured as the percentage of body weight lost within 5 days, among: possums found moribund or dead in a trap (in grey) and apparently healthy animals (in black). 278

Figure 6.6 Number of individuals (N = 38) aged 2 to 14 years (open bars), as determined from cementum annuli, compared to the expected frequency distributions (given 38 individuals) if survival is assumed to be either 81.3 % (black line), or 89.9 % (grey line), per annum. 279

Figure 6.7 Cumulative probability of survival of radio-collared adult females categorized by median handling interval, based on the Kaplan-Meier estimator, modified for staggered entry. 280

Figure 6.8 Change in population size with time (in years) predicted given five different population growth rates (*r*). 281

Figure A2.1 Head length (in mm) of pouch-young versus known minimum (grey circles) and maximum (open circles) age (in days) based on trapping records. 310

PREFACE

Publications

Chapter 2 of this thesis has already been published as:

Clinchy, M. 1997. Does immigration “rescue” populations from extinction? Implications regarding movement corridors and the conservation of mammals. Oikos, 80: 618-622.

ACKNOWLEDGEMENTS

All research is collaborative research. In initial drafts, I used “we” instead of “I” to reflect the fact that this is a collaborative effort, and I only reluctantly changed this to conform with the required use of “I” in a thesis. I had four principal collaborators whose help was indispensable: Liana Zanette, Beryl Clinchy, and Win and Len Perry. It was Liana’s scholarship that put food on the table for the four years we were in Australia, and it was Liana’s scholarship that allowed me to obtain a visa to work in Australia. It was mostly mom’s money that paid for the research. God forbid that the scum-sucking capitalists that run this country should have to pay taxes to provide funding, far better that working people should have to bankrupt themselves! Viva la Revolution!!! Aside from material support both Liana and mom provided an inexhaustible supply of love and unfailing faith in me. Win and Len Perry’s generosity was truly astounding. Not only did they let me disturb their solitude, they provided me with a place to stay, on the spot data collection, and truck repairs. More importantly, they gave me infinite cups of tea and hundreds of hours of great (and sometimes heated) conversation. I miss them very much. Special thanks as well to Bert Jenkins for saving my sanity (and ruining my waistline).

I wanted to work with Charley Krebs because I greatly admired the clarity and rigour of his research. As a born cynic and skeptic the highest praise I can offer is that I admire Charley even more now. Charley’s advice has been invaluable, because I knew if I could convince Charley, the idea must be right. Peter Jarman acted as my unofficial co-supervisor in Australia. Peter was immensely generous and always supportive of my research. I had hoped that the continuation of the research at Paddys Land would partly repay my debt to Peter and my biggest regret is that this did not come to pass. Hopefully my thesis will provide an impetus for some more inspired student of Peter’s to restart the research there. I would also like to thank the members of my research committee: Judy Myers, Dolph Schluter, Tony Sinclair and Jamie Smith.

I first met Andrea Taylor at the Australian Mammal Society meeting in September, 1995. I knew what information I wanted to obtain from genetics data when I first spoke to Andrea, but I am still occasionally struck with disbelief that it actually all worked out. Andrea not only accomplished the mammoth task of

conducting all the typing, but also undertook the even greater task of patiently answering my endless questions about genetics.

Dave Spratt and Pete Haycock undertook the unenviable task of poking through all the dead possums. I long ago concluded that wading through rotting carcasses all day was what was responsible for the bizarre sense of humour shared by most parasitologists. David Obendorf conducted the histopathology. I am delighted that my collaboration with Dave, Pete and David has produced results of interest to all concerned. Steve Hum and Bob Coverdale, formerly of the now defunct Armidale Regional Vet Lab, generously provided assistance, advice and facilities in which to conduct the necropsies. The N.S.W. government's decision to close the Lab was another triumph of economic rationalism.

Murray Efford kindly provided me with a stack of invaluable reports regarding the Orongorongo Valley population.

Paul (Dickson) Forest and Claudia Frosch were both outstanding field assistants and good friends. Paul's unceasing optimism was an excellent foil to my unending cynicism. Claudia was the polar opposite, always on the lookout to protect herself from having a single optimistic thought cross her mind.

Over the years many people at UBC have provided assistance and advice, thanks especially to: Lance Barrett-Lennard, Alistair Blanshard, Cole Burton, Andrea Byrom, Dennis Chitty, Dan Haydon, Karen Hodges, Greg Hood, Tim Karels, Alice Kenney, Andy Kliskey, Don Reid, Christoph Rohner, Karl Vernes, Irene Wingate and Deb Wilson.

Stuart Green deserves special commendation for spending so many hours in the middle of the night in the middle of nowhere staring up at tranquilized possums hanging by their tails. I would also like to thank: Nihal Agar, John Duggin, Frank Dyer, Kate MacGregor, Annette McLeod and Sally Radford.

Christa Clinchy, Andy Collins, Georgia de Biasi, Lindsay Fulloon, Nicole Gammie, Peter Hancock, Rick James, Robyn Martin, Natasha Noble, Josh Rapp, Lyndal Redman, Brit Rollo, Rebecca Scrivener, Michael Stanford, Piers Thomas, Steve Tremont, Jeanette van der Lee, Will Weir, Susan Wright and Gilly Young all provided valuable assistance in the field.

For hospitality and friendship, thanks to: Chris Johnson, Allen McIlwee and Richard Rowe, in Townsville; Elsie Krebs and David Green, in Canberra; and Murray Evans, for making Armidale a little more bearable

CHAPTER 1

DOES IMMIGRATION “RESCUE” POPULATIONS FROM EXTINCTION?

The focus of my research has been on the question: does immigration “rescue” populations from extinction? Despite the fact that dispersal is the process underlying metapopulation dynamics, this question has received scant attention in the literature on metapopulations, evidently because the answer is always assumed to be “yes”. On the other hand, researchers interested in cyclic species of small mammals might not only answer “no”, but may also suggest that immigration can induce local population extinctions. I will begin by briefly sketching the historical origins of these different attitudes to the role of immigration in animal population dynamics. Ultimately, I think the difference in attitude derives from both: 1) an artificial separation of the ideas of distribution and abundance; and 2) a preponderance of generalizations regarding the role of dispersal in local and global extinctions, in contexts in which there is little or no direct evidence.

In 1954, Andrewartha and Birch proposed a “General theory of the number of animals in natural populations”, which was a challenge to the then dominant paradigm of population regulation by “density-dependent factors”. Andrewartha and Birch contrasted the empirical evidence that most natural populations demonstrate large and erratic fluctuations in size, with the density-dependent paradigm’s theoretical expectation of “balance” or “steady-density”. Andrewartha and Birch’s theory emphasized the importance of stochastic factors (catastrophes) and environmental heterogeneity as determinants of population size. Stochastic fluctuations in population size must logically include the possibility of population extinction. Andrewartha and Birch proposed a patch-occupancy model of local population dynamics to account for this possibility. Andrewartha and Birch argued that most natural populations are composed of a series of local populations inhabiting “favourable localities” (patches), among which local extinctions are commonplace, while the aggregate population remains extant, because local extinction in a given locality is eventually followed by colonization by immigrants from other localities. While Andrewartha and Birch’s patch-occupancy model encompasses all of what is now referred to as metapopulation dynamics theory, their model was only one facet of a broader theory. Andrewartha and Birch (1954, p. 5) stressed that “it has become customary to separate distribution [between-patch dynamics] and abundance [within-patch dynamics]”, however, “the separation should never be allowed to persist in the final synthesis, for distribution and abundance are but the obverse and reverse of the same problem”.

Unfortunately, Andrewartha and Birch’s patch-occupancy model “remained little developed in the mainstream population dynamics literature”, apparently because their work “became identified as the losing side in the controversy” about the role of density-dependent factors in local population dynamics (Hanski and Gilpin 1991, p. 4). Consequently, the term “metapopulation”, as used to describe “a population of populations”, derives from work by Richard Levins in the late 1960’s, rather than the earlier work by Andrewartha and Birch (Hanski and Gilpin 1991). Levins’ patch-occupancy model consists of just three components: 1) the proportion of occupied patches; 2) the extinction rate; and 3) the colonization rate. Levins’ model is often described as a two-state model because populations are either present or absent. The Levins model can be treated as analogous to a single-species version of MacArthur and Wilson’s (1967) model of the equilibrium theory of island biogeography, if the probability of local population extinction in the Levins model is made to be a function of local population size (Hanski and Gilpin 1991).

When the Levins model is extended to include the effects of local population size on the probability of local population extinction, a positive feedback relationship is apparent between the proportion of occupied patches and metapopulation persistence (Hanski 1991). A greater proportion of occupied patches entails a greater exchange of immigrants between occupied patches, which is assumed to increase the population size in each occupied patch, and thereby reduce the probability of both local *and* global extinction. Brown and Kodric-Brown (1977, p. 445) described this as the “rescue effect”, whereby the “demographic and genetic contributions of immigrants” are assumed to “rescue” recipient populations from extinction.

Andrewartha and Birch’s (1954, p. 644) patch-occupancy model also included the idea that the probability of local population extinction was a function of local population size, an idea which they cited as originating with Darwin. In addition, Andrewartha and Birch (1954, p. 13) emphasized the importance of differences between individuals, stressing that “every individual in a population of animals is part of the environment of other individuals”. According to Andrewartha and Birch, persistence within each patch is not simply a function of population size, but also depends on the sex, age, and genotype of the individuals composing the population.

While ignored in some quarters, Andrewartha and Birch's (1954) emphasis on the importance of dispersal between patches, in conjunction with socially-mediated interactions among different types of individuals, has been influential among researchers interested in population cycles in small mammals (Chitty 1996, p. 119). In a recent review, Krebs (1996, p. 21) concluded that "spacing behaviour in voles and lemmings produces dispersal, which is necessary for population regulation [and] breeding females appear to be the key".

Researchers working on population cycles in small mammals have generally not concerned themselves with measuring the pattern of patch occupancy, but rather the number and nature of individuals moving in and out of patches, and the effects on residents within the patch (Stenseth and Lidicker 1992). In contrast to expectations from Levins-type patch-occupancy models, small mammal ecologists have reported adverse effects of immigration on the demography of recipient populations associated with acts of infanticide perpetrated by adult immigrant females against resident juveniles (Sherman 1981, Lambin and Krebs 1993, Wolff et al. 1997). The "sociobiological hypothesis", which is one of several general explanations proposed to explain population cycles (Krebs 1996, Boonstra et al. 1998), suggests that population declines are actually induced by an influx of unrelated immigrants. Wolff (1997) proposed that defence against infanticide is a key factor in the evolution of mechanisms of population regulation among mammals in general.

In a recent review, Noss (1999, p. 115) credited the development of "modern conservation biology" in the mid-1970's to the "explosion of interest" in the potential application of MacArthur and Wilson's (1967) theory of island biogeography, and associated ideas regarding metapopulations, to the design of nature reserves. Noss (1999, p. 116) argued that there are nine general principles of conservation biology that have become "sufficiently well established" in the intervening 25 years, to guide conservation policy in particular cases. Two of these nine general principles are based of the idea that the exchange of immigrants helps "rescue" populations from extinction. One principle is that blocks of habitat that are closer together are better than blocks that are far apart, and the other is that blocks of habitat connected by "movement corridors" are better than isolated blocks.

Unfortunately, there has been little attention given in the literature on conservation biology to the results of research on population cycles. In part, this is because applied research on cyclic species has more often focussed on eradication of perceived “pests” than on the conservation of these species (Hansson 1992). Efforts have been made to use small mammals in “experimental model systems” (EMSs; Ims et al. 1993, Wolff et al. 1997) to test the effects of habitat fragmentation and the use of corridors on demographic parameters. However, these have been criticized as being so artificial as to be of “little relevance to real conservation problems and decisions” (Beier and Noss 1998, p. 1246).

In Chapter 2, I argue that the idea that immigration necessarily “rescues” populations from extinction can be challenged on the grounds that there may be adverse effects on the dynamics of recipient populations resulting from an influx of immigrants. The direct evidence in support of this contention largely comes from the research on population cycles in small mammals described above. It may be that small mammals behave differently from other species. However, small mammals and large mammals alike share a common characteristic with respect to dispersal, insofar as most dispersers are male. The fact that almost all Levins-type metapopulation models fail to distinguish between the sexes appears to be a consequence of the artificial separation of the ideas of distribution and abundance that Andrewartha and Birch (1954) cautioned against. Demographic models of abundance within a patch always account for sex and often also account for age-structure (Beissinger and Westphal 1998), and it only seems logical that this should also be the case when considering distribution between patches. In a recent review, Reed (1999) presented similar arguments with respect to birds to those I present regarding mammals.

Andrewartha and Birch (1954, p. 5) noted that part of the reason for the artificial separation of distribution and abundance involves methodological problems. In Chapter 3, I argue that this appears to be just as true today. Researchers interested in Levins-type metapopulation dynamics tend to conduct presence/absence surveys of a series of “favourable localities”. Such studies rarely actually measure whether dispersal is even occurring, but instead, draw inferences regarding dispersal from the pattern of patch-occupancy. By contrast, researchers working on small mammals have considered the problems associated with the direct measurement of dispersal in great detail (Lidicker and Stenseth 1992), and have developed an array of techniques for doing so (Stenseth and Lidicker 1992). Andrewartha and Birch (1954, p. 89) recognized that it is of foremost importance to be able to distinguish between “movement associated with the ordinary activities of searching for food, a mate, and other requirements from movement which leads to finding a new place to live". One aspect concerning the direct measurement of dispersal, which has not received much attention, is the degree to which rigorous measurement may itself produce inaccurate results. This potential source of error can be evaluated by comparison between direct and indirect measurements of the relative importance of dispersal.

In Chapter 4, I report the results of a large-scale field experiment conducted on common brushtail possums (*Trichosurus vulpecula*) in old-growth Eucalypt forest in south-eastern Australia, which was designed to address the question: does immigration "rescue" populations from extinction? I chose to study the common brushtail possum as a "model" medium-sized (1-3 kg), herbivorous, marsupial, in a "real landscape". The decline of medium-sized mammals in Australia clearly represents a "real conservation problem". Short and Smith (1994) reported that 47 % of all mammalian species extinctions in the past two centuries have occurred in Australia. Of the 245 species of mammals present in Australia at the start of European settlement in the 1780's, 16 are now extinct and a further 26 now occupy less than 20 % of their former ranges (Short and Smith 1994). The majority of these extinctions and declines have involved medium-sized (35-5500 g), herbivorous, marsupials (Burbidge and McKenzie 1989). The common brushtail possum had the largest geographic range of any Australian marsupial at the time of European settlement, but now occupies only 37 % of its historical range (How and Kerle 1995).

Numerous causes have been suggested to explain the declines and extinctions among medium-sized mammals in Australia. These include: the introduction of exotic herbivores (sheep, cattle and rabbits) and predators (foxes and cats); clearing of land for agriculture; and changed fire regimes (Burbidge and McKenzie 1989, Recher and Lim 1990, Short and Smith 1994). However, no single cause is sufficient to explain the decline of all of the affected species, and in many cases no single cause is sufficient to explain the decline of a given species across the affected range (Morton 1990, Recher and Lim 1990). Morton (1990) proposed that the natural distribution of native mammalian herbivores was particularly patchy, as these species were restricted to areas of high plant productivity on fertile soils, which in Australia are relatively scarce. According to Morton (1990), these same areas of high plant productivity acted as focal points of disturbance. Graziers naturally stocked their sheep and cattle at highest densities on these fertile patches, the invading rabbits would also congregate in these patches, and the introduced predators would then be attracted to these patches because of the rabbits. Morton (1990) argued that it was the medium-sized mammals that suffered more extinctions and declines because: 1) they were more likely to be locally extirpated than smaller mammals because of their lower rates of natural increase; and 2) they were less likely than larger mammals to be “rescued” by immigration because of their poorer dispersal abilities.

As part of the process of European settlement, state governments in many parts of Australia implemented a policy of retaining narrow strips of Crown land between adjacent blocks of freehold land. These narrow strips were retained as “travelling stock routes” (TSRs), to permit farmers to transport their products to market without having to cross privately held land. In most cases TSRs were not cleared and retained some natural features, while the surrounding freehold land was extensively cleared to create paddocks or cropland. TSRs appear to be ideal movement corridors for wildlife, although they were not designed for that purpose. A large number of studies have been conducted on these apparent movement corridors, primarily involving surveys for the presence or absence of native and introduced mammals. Consequently, Australian mammals feature prominently in the literature on movement corridors. In a recent review, Beier and Noss (1998) found 16 studies on mammals suggestive of a positive role for conservation corridors, of which, 6 involved Australian marsupial possums and gliders. Similarly, Laurance and Gascon (1997) advocated the retention of corridors in association with logging operations, based in part on Laurance’s (1990) survey work in Australia on four species of possums, including the common brushtail possum.

Comparatively little is actually known about the role of dispersal in the population dynamics of medium-sized Australian mammals (Lee and Cockburn 1985, Johnson 1989). For the most part, what is known about dispersal in these species derives from research on common brushtail possums conducted in New Zealand. At the same time as common brushtail possums have disappeared from large parts of their former range in Australia they have become a significant pest species in New Zealand, where they were first introduced in the 1830’s (Cowan 1990). While there has been considerable interest in New Zealand concerning dispersal by common brushtail possums, the focus has been on the role of possums as vectors in the transmission of bovine tuberculosis to domestic livestock (Efford 1991). The importance of immigration in “rescuing” populations from extinction has been of little interest to New Zealanders as their goal since the late 1940’s has been the eradication of the species (Cowan 1990).

While Andrewartha and Birch (1954, p. 88) emphasized the importance of dispersal in population dynamics, they also stressed the importance of differences between species in their “innate tendency toward dispersal”. MacArthur and Wilson (1967, p.83) also emphasized the importance of life-history differences between “good” and “bad” colonizers, in the context of island biogeography, arguing that it is important to have a large intrinsic rate of increase to be a “good” colonizing species. Sinclair et al. (1998, their Table 1) reported per annum intrinsic rates of increase for two species of medium-sized Australian macropods (*Bettongia lesueur* and *Lagorchestes hirsutus*), and the common brushtail possum, as being, 0.932, 0.930 and 0.928, respectively. By way of comparison, Sinclair (1996, his Appendix 2) reported an intrinsic rate of increase of 2.190 for the snowshoe hare (*Lepus americanus*). Lee and Ward (1989) and Seebeck et al. (1989) both noted the relatively low fecundity of medium-sized, marsupial, herbivores in Australia, as compared to similar-sized species of mammals in other groups. In Chapter 5, I describe the reproductive biology of common brushtail possums at my study site and make comparisons with the reproductive biology of the species reported at other sites. Using the results of the experiment described in Chapter 4 in conjunction with the comparisons made in Chapter 5, I consider whether issues associated with connectivity and metapopulation dynamics, or factors such as “harvesting” by introduced predators, are more important to the demography, and likelihood of local population extinction, of common brushtail possums, and by extension, other medium-sized, marsupial, herbivores.

In Chapter 6, I present a deterministic, stage-based model of possum demography. Using the model, together with supplementary information regarding the proximate causes of adult deaths, I consider whether the rigorous methods used to accurately measure immigration, as described in Chapter 4, may confound the interpretation of the role of immigration, as suggested in Chapter 3. I argue that this is a particularly important issue to address before drawing conclusions about “dispersal sinks” (Pulliam 1988), as negative population growth rates may often be the consequence of adverse effects of repeated capture and handling.

In Chapter 7, I discuss the general implications of my results as regards the decline of medium-sized mammals in Australia, and strategies to conserve those species and populations that remain.

REFERENCES

Andrewartha, H. G., and Birch, L. C. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.

Beier. P., and Noss, R. F. 1998. Do habitat corridors provide connectivity? Conservation Biology, 12: 1241-1252.

Beissinger, S. R., and Westphal, M. I. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management, 62: 821-841.

Boonstra, R., Krebs, C. J., and Stenseth, N. C. 1998. Population cycles in small mammals: the problem of explaining the low phase. Ecology, 79: 1479-1488.

Brown, J. H., and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. Ecology, 58: 445-449.

Burbidge, A. A., and McKenzie, N. L. 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. Biological Conservation, 50: 143-198.

Chitty, D. 1996. Do lemmings commit suicide? Beautiful hypotheses and ugly facts. Oxford University Press, Oxford.

Cowan, P. E. 1990. Brushtail possum. *In* The handbook of New Zealand mammals. *Edited by* King, C. M. Oxford University Press, Auckland, New Zealand, pp. 68-98.

Efford, M. 1991. A review of possum dispersal. DSIR Land Resources Contract Report 91/73, DSIR Land Resources, Dunedin, New Zealand

Hanski, I., and Gilpin, M. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society, 42: 3-16.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society, 42: 17-38.

Hansson, L. 1992. Small mammal dispersal in pest management and conservation. *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 181-198.

How, R. A., and Kerle, J. A. 1995. Common brushtail possum. *In* The mammals of Australia. *Edited by* Strahan, R., Reed Books, Sydney, Australia, pp. 273-275.

Ims, R. A., Rolstad, J., and Wegge, P. 1993. Predicting space use responses to habitat fragmentation: can voles *Microtus oeconomus* serve as an experimental model system (EMS) for capercaillie grouse *Tetrao urogallus* in boreal forest? Biological Conservation, 63: 261-268.

Johnson, C. N. 1989. Dispersal and philopatry in the macropodoids. *In* Kangaroos, wallabies and rat-kangaroos. *Edited by* Grigg, G., Jarman, P., and Hume, I. Surrey Beatty and Sons, Sydney, Australia, pp. 593-601.

Krebs, C. J. 1996. Population cycles revisited. Journal of Mammalogy, 77: 8-24.

Lambin, X., and Krebs, C. J. 1993. Influence of female relatedness on the demography of Townsend's vole populations in spring. Journal of Animal Ecology, 62: 536-550.

Laurance, W. F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. Journal of Mammalogy, 71: 641-653.

Laurance, W. F., and Gascon, C. 1997. How to creatively fragment a landscape. Conservation Biology, 11: 577-579.

Lee, A. K., and Cockburn, A. 1985. Evolutionary ecology of marsupials. Cambridge University Press, Cambridge.

Lee, A. K., and Ward, S. J. 1989. Life histories of macropodoid marsupials. *In* Kangaroos, wallabies and rat-kangaroos. *Edited by* Grigg, G., Jarman, P., and Hume, I. Surrey Beatty and Sons, Sydney, Australia, pp. 105-115.

Lidicker, W. Z., Jr., and Stenseth, N. C. 1992. To disperse or not to disperse: who does it and why? *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 21-36.

MacArthur, R. H., and Wilson, E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Morton, S. R. 1990. The impact of European settlement on the vertebrate animals or arid Australia. Proceedings of the Ecological Society of Australia, 16: 201-213.

Noss, R. 1999. Is there a special conservation biology? Ecography, 22: 113-122.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist, 132: 652-661.

Recher, H. F., and Lim, L. 1990. A review of current ideas on the extinction, conservation and management of Australia's terrestrial vertebrate fauna. Proceedings of the Ecological Society of Australia, 16: 287-301.

Reed, J. M. 1999. The role of behaviour in recent avian extinctions and endangerments. Conservation Biology, 13: 232-241.

Seebeck, J. H., Bennett, A. F., and Scotts, D. J. 1989. Ecology of the Potoroidae: a review. *In* Kangaroos, wallabies and rat-kangaroos. *Edited by* Grigg, G., Jarman, P., and Hume, I. Surrey Beatty and Sons, Sydney, Australia, pp. 67-88.

Sherman, P. W. 1981. Reproductive competition and infanticide in Belding's ground squirrels and other animals. *In* Natural selection and social behaviour. *Edited by* Alexander, R. D., and Tinkle, D. W., Chiron Press, New York, pp. 311-331.

Short, J., and Smith, A. 1994. Mammal decline and recovery in Australia. Journal of Mammalogy, 75: 288-297.

Sinclair, A. R. E. 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. *In* Frontiers of population ecology. *Edited by* Floyd, R. B., Sheppard, A. W., and DeBarro, P. J., CSIRO Publishing, Melbourne, Australia, pp. 127-154.

Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D, Mahon, P., and Newsome, A. E. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology 12: 564-575.

Stenseth, N. C., and Lidicker, W. Z., Jr. 1992. Where do we stand methodologically about experimental design and methods of analysis in the study of dispersal? *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 295-318.

Wolff, J. O. 1997. Population regulation in mammals: an evolutionary perspective. Journal of Animal Ecology, 66: 1-13.

Wolff, J. O., Schauber, E. M., and Edge, W. D. 1997. Effects of habitat loss and fragmentation on the behaviour and demography of gray-tailed voles. Conservation Biology, 11: 945-956.

CHAPTER 2

DOES IMMIGRATION “RESCUE” POPULATIONS FROM EXTINCTION? IMPLICATIONS REGARDING MOVEMENT CORRIDORS AND THE CONSERVATION OF MAMMALS

The “rescue effect” is one of the principal rationales provided for “movement corridors for conservation” (Simberloff et al. 1992). The conventional conceptualization of the rescue effect may be paraphrased as follows: ‘the closer two “island” populations are to one another, the more likely they are to exchange immigrants, which will reduce the probability of extinction of either population, thanks to the “demographic and genetic contributions of immigrants” (Brown and Kodric-Brown 1977, p. 445) to recipient populations’. Insofar as corridors facilitate the exchange of immigrants, they will aid conservation by reducing the probability of local population extinctions.

The conventional conceptualization of the rescue effect masks two distinct components: 1) an empirical phenomenon involving a positive correlation between physical proximity and the persistence of populations in sequential surveys of “island” populations; and 2) the mechanism responsible for this positive correlation, which is hypothesized to be immigration.

Positive correlations between proximity and population persistence are well-documented in mammals (e.g., Smith 1980, van Apeldoorn et al. 1992), amphibians (e.g., Sjogren 1991), and vascular plants (e.g., Ouborg 1993), and I do not question the existence of this correlation. However, whether immigration is the mechanism underlying this correlation can be challenged on three grounds: 1) the absence of direct empirical evidence; 2) the failure to consider alternative hypotheses: and 3) the abundance of conflicting behavioural data.

Simberloff et al. (1992) commented on the absence of direct empirical evidence of a role for immigration, and this verdict still holds. Immigration is rarely measured directly (Simberloff et al. 1992), and almost never in a sufficiently rigorous fashion (Stenseth and Lidicker 1992). Despite the absence of direct empirical evidence, the idea that immigration is the mechanism responsible for the rescue effect is never challenged. The idea is accepted as dogma, as it is so “intuitively obvious” (Caughley and Gunn 1996). Unfortunately, intuitions may often be wrong (Caughley and Sinclair 1994).

In this Chapter, I will illustrate that alternative hypotheses can be readily formulated as regards the mechanism underlying the positive correlation between proximity and persistence. Moreover, I will argue that, for mammals at least, patterns regarding individual dispersal behaviour are well-established, and these patterns suggest that immigration may often *decrease* the probability of persistence of recipient populations.

Alternative hypotheses

The nearer any two populations are, the more likely they are to be subject to similar deterministic environmental effects, and hence, the more likely they are to fluctuate in synchrony (Harrison and Quinn 1989). It is not necessary to posit a role for immigration in inducing such synchrony. However, a correlation between proximity and synchrony in population fluctuations is as likely to lead to a negative correlation between proximity and persistence as it is to lead to a positive correlation. Yet the empirical phenomenon associated with the rescue effect involves a consistently positive correlation between proximity and persistence. I will demonstrate how a consistently positive relationship between proximity and persistence can result from: 1) environmentally induced synchrony; coupled with 2) the way in which we ask the question.

The correlation between proximity and persistence is conventionally described as follows (Fig. 2.1). Several “island” populations are surveyed for the presence/absence of a species at time 1, and then again at time 2. Persistence is defined as presence of the species in both surveys. Extinction is more likely to occur in “outlying” populations. All populations are assumed to demonstrate independent population dynamics which are modified solely by the exchange of immigrants.

As an alternative, we can envisage that populations occur in clusters, wherein there is complete independence of population dynamics between clusters, but perfect synchrony within clusters, as a result of exposure to similar deterministic environmental effects. The eight independent populations illustrated in Figure 2.1 are now arranged into four independent clusters containing two synchronous populations in each cluster (Fig. 2.2). To establish whether there is a relationship between proximity and persistence we first ask: “do both populations persist from time 1 to time 2?” We can arrange the results of this query as shown in Table 2.1. Using the evidence from Table 2.1 and Figure 2.2 we can establish a simple contingency table (Table 2.2), categorizing populations as to whether they persist from time 1 to time 2, and whether they are near of far from one another. Populations within clusters are categorized as near to one another, whereas populations in all other clusters are categorized as far. Sutcliffe et al. (1996) used contingency tables to analyze the relationship between proximity and population synchrony in various species of butterflies in England. Using a G-test, there is no evidence of a relationship ($G = 0.904$, $p > 0.05$). However, had we assumed there were five populations within each of four clusters, the result would reach statistical significance ($G = 4.706$, $p < 0.05$), demonstrating a significant positive relationship between proximity and persistence. Naturally, a greater number of populations within each cluster would lead to ever more statistically significant results.

What the above example demonstrates is that it is not necessary to posit a role for immigration in order to explain the empirically observed positive relationship between proximity and persistence, associated with the rescue effect. While immigration may be the mechanism responsible for the rescue effect, we cannot simply assume it is, just because it is "intuitively obvious" (Caughley and Gunn 1996).

Behavioural data

Part of the reason why it is conventionally believed that immigration must be the mechanism underlying the rescue effect, is because in almost all current metapopulation models, immigration is invariably assumed to contribute positively to the persistence of the recipient population.

There are two fundamental aspects to most models concerning the rescue effect (e.g., Hanski and Gyllenberg 1993): 1) population size, N, is assumed to be positively correlated with persistence; and 2) only "additive" models of demography are ever considered.

I do not wish to challenge the idea that population size is positively correlated with persistence, but it must be remembered that such demographic models apply to females only. Research scientists and managers alike often seem to forget this restriction (Caughley and Gunn 1996). To emphasize this point, we can bring the scale down to the level of individual behaviour, and recognize that the persistence of a population depends on the rate of "breeding replacement". Breeding replacement is here defined as the rate, in real time, at which individual, resident, reproductively active females that die or emigrate, are replaced by new reproductively active females, as a result of either immigration or local recruitment (after Watson and Moss 1970).

"Additive" models of demography are those familiar from any introductory textbook in ecology:

$N_{\text{time}} = (B + I) - (D + E)$

Most metapopulation models assume the only alternative, involving immigration, is what might be described as an "isolation" model of demography:

$N_{\text{time}} = (B) - (D + E)$

It follows that, all else being equal, the positive rate of increase in the population will necessarily be greater with immigration, and hence, persistence will necessarily be more probable with immigration. However, it is possible to conceive of at least a second alternative model of demography, one which allows for interactions between the fundamental demographic parameters:

$N_{\text{time}} = (B + I) - (D + E) - (IB + ID + IE)$

In this case, persistence is more probable with immigration, only if the positive contribution of immigration, I, is greater than the potential negative interactions between immigration and the other fundamental demographic parameters: IB, ID, and IE. Currently, the only example in the literature involving the recognition of interactive effects comes from work by Hess (1994), who considered the detrimental effects on persistence as a result of disease transmission by immigrants.

Whereas Hess (1994) suggested disease transmission as a "special case" whereby immigration decreases the probability of persistence, I argue that there is an abundance of behavioural data, at least as regards mammals, to suggest that immigration is normally irrelevant to, and may often decrease, the probability of persistence of recipient populations. The abundance of behavioural data indicating detrimental effects of immigration on recipient populations can be understood by recognizing the conflict between immigrants and residents in terms of intraspecific competition for physical and genetic resources. Intraspecific competition is a fundamental and inescapable aspect of population dynamics, and cannot be dismissed as a "special case". Competition for physical resources, such as food and shelter, has familiar consequences, most often modeled in the form of the logistic growth curve. Competition for genetic resources has markedly different consequences, and is described in detail below.

Several reviews of the literature (Greenwood 1980, Waser and Jones 1983, Johnson and Gaines 1990) have all concluded that in most mammalian species: 1) most dispersers are male; and 2) most females are philopatric, establishing home ranges near their mothers. As a result: 1) most immigrants are male; and 2) most populations consist of neighbourhoods of related females, with immigrant females entering a family's territory/range, rather than a lone individual's range.

Returning to the idea that persistence depends on the rate of breeding replacement, it becomes obvious that, as most immigrants are male, most immigration is irrelevant to the persistence of the recipient population. Further, if males and females compete for the same physical resources, the addition of immigrant males to a population may increase competitive pressure on resident females, potentially lowering the rate of reproduction, thereby reducing the rate of breeding replacement via local recruitment, and decreasing the probability of persistence of the population. Male immigration may be modeled as:

$N_{\text{time}} = (B) - (D + E) - (IB)$

Clearly, female immigration can contribute to breeding replacement, and hence increase the probability of persistence of the population. However, interactions between immigrants and residents must be acknowledged. What is important is the net rate of breeding replacement in the presence of immigrant females. As with males, immigrant females may compete with resident females for physical resources. In addition, immigrant females will compete with families of resident females for "genetic resources". The Darwinian fitness of an individual female does not depend on the absolute number of offspring she produces, but on the number relative to all other females in the population. Unlike competition for physical resources, competition for genetic resources is not necessarily a function of population size. Even if a population consists of only two unrelated females, they should both attempt to limit the other's contribution to the next generation. The effects of genetic competition have generally been overlooked in even the more sophisticated "structured" models of metapopulation dynamics (Hastings 1991), which assume logistic population growth (resulting from competition for physical resources) within each population composing the metapopulation.

Genetic competition among resident females will be mild, given that, as a result of female philopatry, adjacent residents are often relatives. Levels of aggression are lower among kin in most species

(Waldman 1988). Intrusion by immigrant females, on the other hand, can be expected to be fiercely resisted by the family of resident females (Lambin and Krebs 1991).

Infanticide can be seen as the extreme on the continuum of genetic competition, killing somebody else's offspring to create an "opening" for your own. Infanticide is well-documented in carnivores (Packer and Pusey 1984), primates (Quiatt and Reynolds 1993), rabbits (Kunkele 1992), and rodents (Cockburn 1988). Probably the best behavioural evidence of genetic competition between immigrant and resident females, leading to infanticide, comes from work by Sherman (1981) on Belding's ground squirrel. Sherman (1981) found: 1) infanticide was the largest single cause of resident juvenile mortality; 2) infanticide was never committed by resident females; 3) related resident females cooperated in defence against other individuals attempting to commit infanticide; 4) most infanticides were committed by immigrant adult females who did not eat their victims; and 5) 75 % of infanticidal adult females settled in territories adjacent to their victim's territory.

Individual behaviours do not necessarily have significant demographic consequences. Lambin and Krebs (1993) documented both behavioural and demographic consequences of infanticide by immigrant female Townsend's voles. They manipulated both: 1) the proximity of relatives of resident females; and 2) levels of female immigration. Lambin and Krebs (1993) observed: 1) six direct instances of infanticide; 2) lower mortality of adult resident females if their nearest neighbour was related, suggesting the operation of kin selection; and 3) higher resident juvenile mortality in the presence of immigrant females. Given Lambin and Krebs' (1993) results, female immigration ought to be modeled as:

$N_{\text{time}} = (B + I) - (D + E) - (ID)$

I began this section by emphasizing that in almost all current metapopulation models, immigration is invariably assumed to contribute positively to the persistence of the recipient population. By contrast, the abundance of behavioural data available, at least as regards mammals, suggests: 1) the bulk of immigration, as it involves males, is at best, irrelevant to the persistence of recipient populations; and 2) competition between immigrant females and families of resident females may often decrease the probability of persistence of the recipient population.

Conclusions

I have argued that the general acceptance of the idea that immigration is the mechanism responsible for the rescue effect can be seen to be a function of: 1) the failure to consider alternative hypotheses; and 2) the pre-eminence of certain demographic models. The problem underlying both these criticisms is the absence of direct empirical evidence. Simple presence/absence surveys are not enough. Only rigorous identification of immigrants, experiments directly manipulating immigration, and monitoring of effects on breeding replacement and/or persistence, are sufficient to establish that immigration is in fact the mechanism responsible for the rescue effect.

I have deliberately avoided any discussion of the “genetic contributions of immigrants” (Brown and Kodric-Brown 1977, p. 445) to recipient populations. Based on mathematical models and results from captive breeding, many authors (e.g., Soule 1987, Hedrick et al. 1996) have argued that a regular influx of new genetic material via immigration is absolutely crucial to the “health” of recipient populations. However, others (most notably Caughley 1994, and Caughley and Gunn 1996) have emphasized the absence of adequate evidence of inbreeding depression and like signs of genetic “ill-health” in any wildlife population. My arguments regarding the potentially negative “demographic contributions of immigrants” may or may not be ameliorated, depending upon your view of the importance of the “genetic contributions of immigrants”.

Simberloff and Cox (1987) questioned the values of movement corridors for conservation on the basis that there was no evidence that animals actually used corridors to move from one “island” population to another. Saunders and Hobbs (1991) presented limited evidence that animals do actually disperse through corridors. Simberloff et al. (1992) and Hess (1994) discussed negative “side effects” for conservation arising from the use of corridors. None of the authors have addressed the core issue, which concerns the nature of immigration. I have argued that, contrary to potential negative effects of immigration being a “special case”, conflict between immigrants and residents is an inescapable consequence of intraspecific competition for physical and genetic resources. Not only may movement corridors be a “poor investment” (Simberloff et al. 1992), they may be something we want to avoid.

REFERENCES

Brown, J. H., and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. Ecology, 58: 445-449.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology, 63: 215-244.

Caughley, G., and Gunn, A. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, Massachusetts.

Caughley, G., and Sinclair, A. R. E. 1994. Wildlife ecology and management. Blackwell Science, Cambridge, Massachusetts.

Cockburn, A. 1988. Social behaviour in fluctuating populations. Croom Helm, London.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour, 28: 1140-1162.

Hanski, I., and Gyllenberg, M. 1993. Two general metapopulation models and the core-satellite species hypothesis. American Naturalist, 142: 17-41.

Harrison, S., and Quinn, J. F. 1989. Correlated environments and the persistence of metapopulations. Oikos, 56: 293-298.

Hastings, A. 1991. Structured models of metapopulation dynamics. Biological Journal of the Linnean Society, 42: 57-71.

Hedrick, P. W., Lacy, R. C., Allendorf, F. W., and Soule, M. E. 1996. Directions in conservation biology: comments on Caughley. Conservation Biology, 10: 1312-1320.

Hess, G. R. 1994. Conservation corridors and contagious disease: a cautionary note. Conservation Biology, 8: 256-262.

Johnson, M. L., and Gaines, M. S. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics, 21: 449-480.

Kunkele, J. 1992. Infanticide in wild rabbits (*Oryctolagus cuniculus*). Journal of Mammalogy, 73: 317-320.

Lambin, X., and Krebs, C. J. 1991. Can changes in female relatedness influence microtine population dynamics? Oikos, 61: 126-132.

Lambin, X., and Krebs, C. J. 1993. Influence of female relatedness on the demography of Townsend's vole populations in spring. Journal of Animal Ecology, 62: 536-550.

Ouborg, N. J. 1993. Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine-system. Oikos, 66: 298-308.

Packer, C., and Pusey, A. E. 1984. Infanticide in carnivores. *In* Infanticide: comparative and evolutionary perspectives. *Edited by* Hausfater, G., and Hrdy, S. B., Aldine, New York, pp. 31-42.

Quiatt, D. D., and Reynolds, V. 1993. Primate behaviour: information, knowledge, and the evolution of culture. Cambridge University Press, Cambridge.

Saunders, D. A., and Hobbs, R. J. 1991. Nature conservation: the role of corridors. Surrey Beatty and Sons, Sydney, Australia.

Sherman, P. W. 1981. Reproductive competition and infanticide in Belding's ground squirrels and other animals. *In* Natural selection and social behaviour. *Edited by* Alexander, R. D., and Tinkle, D. W., Chiron Press, New York, pp. 311-331.

Simberloff, D., and Cox, J. 1987. Consequences and costs of conservation corridors. Conservation Biology, 1: 63-71.

Simberloff, D., Farr, J. A., Cox, J., and Mehlman, D. W. 1992. Movement corridors: conservation bargains or poor investments? Conservation Biology, 6: 493-504.

Sjogren, J. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biological Journal of the Linnean Society, 42: 135-147.

Smith, A. T. 1980. Temporal changes in insular populations of the pika (*Ochotona princeps*). Ecology, 61: 8-13.

Soule, M. E. 1987. Viable populations for conservation. Cambridge University Press, Cambridge.

Stenseth, N. C., and Lidicker, W. Z., Jr. 1992. Where do we stand methodologically about experimental design and methods of analysis in the study of dispersal? *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 295-318.

Sutcliffe, O. L., Thomas, C. D., and Moss, D. 1996. Spatial synchrony and asynchrony in butterfly population dynamics. Journal of Animal Ecology, 65: 85-95.

van Apeldoorn, R. C., Oostenbrink, W. T., van Winden, A., and van der Zee, F. F. 1992. Effects of habitat fragmentation on the bank vole, *Clethrionomys glareolus*, in an agricultural landscape. Oikos, 65: 265-274.

Waldman, B. 1988. The ecology of kin recognition. Annual Review of Ecology and Systematics, 19: 543-571.

Waser, P. M., and Jones, T. W. 1983. Natal philopatry among solitary animals. Quarterly Review of Biology, 58: 355-390.

Watson, A., and Moss, R. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. *In* Animal populations in relation to their food supply. *Edited by* Watson, A., Blackwell Scientific, Oxford, pp. 167-219.

Table 2.1. Summary of results of examining populations illustrated in Figure 2.2 and asking the question "do both populations persist from time 1 to time 2?"

	Populations						
	2	3	4	5	6	7	8
1	Yes	Yes	Yes	Yes	Yes	No	No
2		Yes	Yes	Yes	Yes	No	No
3			Yes	Yes	Yes	No	No
4				Yes	Yes	No	No
5					Yes	No	No
6						No	No
7							No

Table 2.2. Contingency table for analysis of relationship between proximity and persistence using evidence from Table 2.1 and Figure 2.2.

Distance	Do both populations persist from time 1 to time 2?	
	Yes	No
Near	3	1
Far	12	12

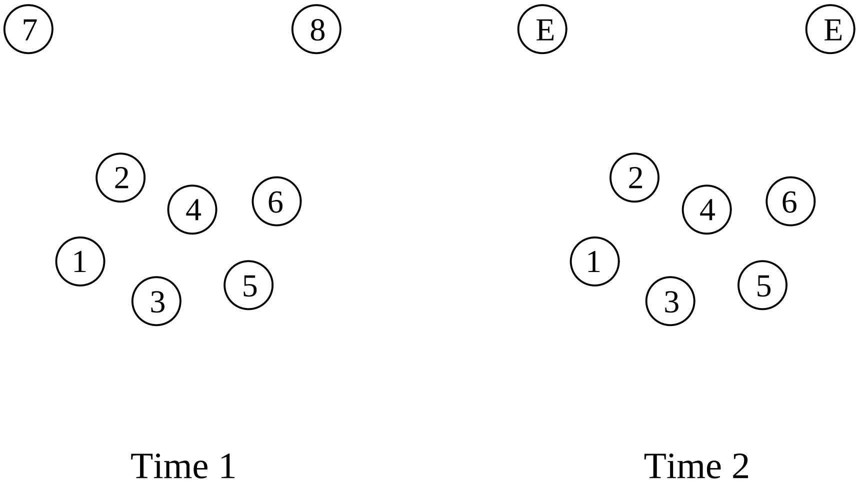

Figure 2.1. Conventional portrayal of relationship between proximity and persistence. Numerals signify individual "island" populations. The letter E signifies extinction of a population.

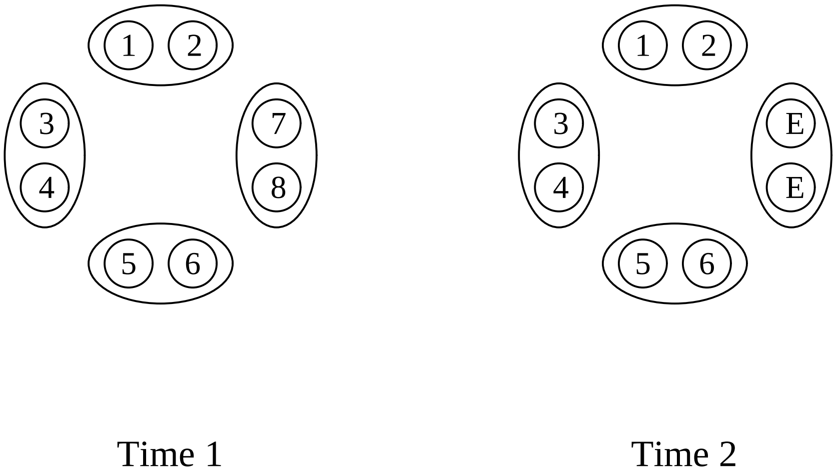

Figure 2.2. Environmentally induced synchrony of population dynamics signified by clustering of populations. Numerals signify individual "island" populations. The letter E signifies extinction of a population

CHAPTER 3

METHODOLOGICAL PROBLEMS IN THE STUDY OF IMMIGRATION AND EXTINCTION

The role of immigration in the dynamics of recipient populations has been the focus of attention of two groups of researchers, those interested in metapopulation dynamics, and those interested in population cycles. Within the metapopulation framework, immigration is viewed as a purely additive process (Clinchy 1997), whereby the "demographic and genetic contributions of immigrants" (Brown and Kodric-Brown 1977, p. 445) may help "rescue" recipient populations from extinction. By contrast, the potentially adverse effects of an influx of immigrants into a population has been suggested as the cause of the decline phase in cyclic populations of both birds (e.g., Watson et al. 1994) and mammals (e.g., Charnov and Finerty 1980, Hestbeck 1982, Lambin and Krebs 1991, Wolff et al. 1997). For various reasons, these two groups of researchers have adopted different methodological approaches to the study of immigration. Studies of metapopulation dynamics have tended to adopt what might be termed the "correlational-survey" approach, which draws inferences regarding immigration from patterns of patch occupancy, while studies on population cycles have generally involved direct attempts at measuring and manipulating immigration rates. As I will discuss, there are various difficulties associated with both these approaches to the study of immigration, and there has been little attempt to integrate the two approaches. I will focus primarily on mammals, both because mammals are more likely than other vertebrate taxa to demonstrate metapopulation dynamics (Lidicker and Koenig 1996), and because studies on small mammals dominate the literature on the potential role of dispersal in producing cyclic population dynamics (Stenseth and Lidicker 1992).

The correlational-survey approach

The correlational-survey approach requires the measurement of three variables: 1) the distance between a number of habitat patches which are all deemed to be "suitable" for the target species; 2) the presence or absence of the target species in each suitable patch; and 3) the density of the target species in each occupied patch. Immigration is judged to be important in "rescuing" populations from extinction, if: 1) among all suitable patches, isolated patches are more likely to be unoccupied;

and 2) among occupied patches, isolated patches have lower density populations. The argument that immigration must be the mechanism responsible, is as follows: the nearer two occupied patches are to one another the greater will be the rate of exchange of immigrants between them, which "props up" population size in both patches, and thereby reduces the probability of stochastic local extinction (Hanski and Gilpin 1997, p. 213). Conversely, more isolated patches receive fewer immigrants, and as a result have lower densities (pattern number 2 from above), and are therefore more likely to be unoccupied (pattern number 1 from above), because the resident populations have gone extinct.

While a large number of studies (e.g., Gottfried 1979, Fahrig and Merrian 1985, van Apeldoorn et al. 1992) have used the correlational-survey approach, the Bodie, California, "pika metapopulation is the best-known mammalian example" (Moilanen et al. 1998, p. 530), and it has been argued that the studies that have been done at this site (Smith 1974, Smith 1980, Smith and Gilpin 1997) "provide some of the best evidence available that [immigration] within mammalian metapopulations can … rescue local populations from extinction" (Stacey et al. 1997, p. 283). One of the strengths of the Bodie study is that, rather than the usual single survey of presence or absence and population density, a series of surveys have been conducted on the same habitat patches, over a number of years. In each of these several surveys it has been found that: 1) among all suitable patches, isolated patches are more likely to be unoccupied; and 2) among occupied patches, isolated patches generally have lower density populations.

The existence of a series of surveys at the Bodie site permits a further, more direct test of whether immigration likely "rescues" populations from extinction. If more isolated patches are more likely to go extinct because they receive fewer immigrants, then the spatial configuration of occupied patches in one survey ought to allow us to predict which populations (i.e., those more distant from their neighbours) will go extinct, and hence, which patches will be found to be unoccupied, in the next survey. I consider this a more direct test of the "rescue effect" because extinction is a dynamic process that occurs *over* time, in which case measurements made *over* time ought to be preferable to single survey "snapshots" of a given point in time. The spatial configuration, and history of patch occupancy, in each of the four surveys conducted at the Bodie site was reported in Smith and Gilpin (1997, their Fig. 2). When the distance to the nearest occupied patch (the measure of isolation used in Smith 1974, Smith 1980, and Smith and Gilpin 1997) in one survey was compared between populations that were found to be either extinct or extant in the next survey, there was no significant effect of nearest neighbour distance on the probability of extinction (Table 3.1). Consequently, while the pattern of patch occupancy *within* each survey of the Bodie site is consistent with that predicted by the "rescue effect" (Smith and Gilpin 1997, their Table 1), the pattern of *changes* in patch occupancy *between* surveys, is not.

Simulation models incorporating a large number of variables, including population densities within each patch and estimates of "typical" dispersal distances, have been more (Moilanen et al. 1998) or less (Smith and Gilpin 1997) successful in demonstrating that the observed pattern of patch occupancy at the Bodie site can be explained by metapopulation dynamics "in the presence of some regional stochasticity" (Moilanen et al. 1998, p. 539). But, "this is not to say that the observed pattern could not have other explanations" (Moilanen et al. 1998, p. 539).

As illustrated with respect to the Bodie study, difficulties can arise when interpreting the results of the correlational-survey approach because immigration is not actually measured, rather, its effects are simply inferred from the pattern of patch occupancy. Consequently, any number of alternative hypotheses (Clinchy 1997), such as localized effects of predation, or epidemic disease, could also explain the observed patterns of patch occupancy (Smith and Gilpin 1997).

Identifying immigrants in open populations in the field

Several very elegant experiments have been conducted in outdoor enclosures, which have measured and manipulated the rate of exchange of immigrants between habitat patches (e.g., Ims et al. 1993, Wolff et al. 1997, and Bjornstad et al. 1998). Enclosure experiments provide many advantages, the foremost, with respect to the study of immigration, being that the identity and origin of every individual is known with complete certainty, because they were put there by the experimenter. Unfortunately, some critics from among the ranks of those interested in metapopulation dynamics and associated conservation issues, have dismissed the results of enclosure experiments as being of "little relevance", because the experiments are conducted "in settings so dissimilar to [real] landscapes" (Beier and Noss 1998, p. 1246). Yet, at the same time, the level of certainty obtainable in enclosure studies seems indispensable, since "simulation models [of metapopulation dynamics] have shown that a surprisingly low number of immigrants per year … will allow individual populations to persist" indefinitely (Stacey et al. 1997, p. 268).

A number of steps need to be taken in order to measure immigration in open populations in "real landscapes", with anywhere near the degree of accuracy required to challenge the results from simulation studies. The central dilemma associated with measuring immigration in open populations in the field is that of how to identify who in fact is an immigrant. Immigration entails entering and settling in an occupied patch. The individuals, and their offspring, that already inhabit the patch, represent the resident population. Provided all the residents, and their offspring, have been completely enumerated, all newly-identified individuals must be immigrants. The problem here is that a proportion of the residents will almost certainly elude detection when only a single sampling technique (e.g., live-trapping) is employed (Krebs 1999). Consequently, any newly-identified individual may be an immigrant, or a resident that has previously eluded detection (Stenseth and Lidicker 1992). This problem can be substantially alleviated by employing at least two, fully independent sampling techniques (Fig. 3.1a). For example, Boonstra and Krebs (1978) used cage-trapping and pitfall-trapping to study voles and found a proportion of individuals susceptible to one, but not the other, trapping technique. Boutin (1980) used cage-trapping to monitor a population of snowshoe hares, coupled with repeated "hare-drives" involving the use of a line of volunteers acting as "beaters", who drove the hares into nets.

To avoid misidentifying local recruits, as immigrants, it is also necessary to completely enumerate all of the offspring of residents (Fig. 3.1a). In species with mobile, altricial young, such as marsupials, it is possible to capture and mark the mother and young at the same time (Efford 1998). In precocial species, complete enumeration of offspring often requires that extraordinary steps be taken. O'Donoghue (1994) held pregnant snowshoe hares in portable outdoor enclosures until they gave birth, and then radio-tagged the leverets. Another approach taken by Pugh and Tamarin (1991) was to inject pregnant voles with radionuclides which would pass from mother to young across the placental barrier, the limitation being that the offspring must be trapped and marked after birth by some other means, before the radionuclides become undetectable.

If the area of complete enumeration does not fully encompass the entire patch, newly-identified individuals may be neighbouring residents from just outside the area of complete enumeration that are either: 1) exploring beyond the boundaries of their normal home range (Lidicker and Stenseth 1992); or 2) are expanding their home range in response to vacancies created within the area of complete enumeration (Stenseth and Lidicker 1992). Neighbouring residents from just outside the area of complete enumeration are likely to be either related to, or familiar with, residents within the area of complete enumeration, and an influx of such individuals is not expected to have adverse effects on the residents within the area of complete enumeration (Hestbeck 1982, Lambin and Krebs 1991). In terms of metapopulation dynamics, excursions (or exploratory movements) and range expansion, represent forms of "quasi-dispersal" (Lidicker and Stenseth 1992, p. 23), which are distinct from the type of "true" dispersal that is assumed when discussing the exchange of immigrants between patches (see Krebs 1992, his Fig. 7.1). According to Lidicker and Stenseth (1992, p.23), "true" dispersal involves three phases, "leaving, travelling, and arriving", and the distance traveled must be such that "the new home range [is] disjunct from the abandoned one". Whether one is interested in the role of immigrants as unrelated and unfamiliar "intruders" that induce population declines, or as "rescuers" that prevent population extinction, it is necessary to distinguish between potential immigrants and neighbouring residents from just outside the area of complete enumeration.

To be able to distinguish between "true" immigrants and neighbouring residents from just outside the area of complete enumeration, the area of complete enumeration should include a "buffer strip" (or "border zone"; Stenseth and Lidicker 1992, p. 300), wherein newly-identified individuals detected in the "buffer strip" are not classified as immigrants. Once all of the residents, and their offspring, are completely enumerated within a given area (Fig. 3.1a), the area can be divided into a "core" area in which immigration will be measured, surrounded by a peripheral "buffer strip" (Fig. 3.1b). Following Lidicker and Stenseth's (1992, p. 23) definition of "true" dispersal, the "buffer strip" should be a minimum of one home range length across (Fig. 3.1b), in which case it can be said without ambiguity that newly-identified individuals that settle in the core of the area must have "traveled" across at least one home range, and their new home range is clearly "disjunct from the abandoned one". Subsequently (Fig. 3.1c): 1) if known adult residents that inhabit the "buffer strip" expand their ranges into the core of the area they can be readily distinguished from "true" immigrants (Lidicker and Stenseth 1992); similarly 2) if the offspring of residents that inhabit the "buffer strip" settle in the core area they too can be distinguished from "true" immigrants; but most importantly 3) newly-identified individuals entering and settling in the "buffer strip" are *not* classified as immigrants, as they are as likely to be neighbouring residents from just outside the area of complete enumeration. By this means, newly-identified individuals that do enter and settle in the core area can be classified as “true” immigrants, without ambiguity (Fig. 3.1c).

An integrated approach

As discussed, the problem of how to identify who in fact is an immigrant, in open populations in the field, can be solved by the use of a variety of sampling techniques aimed at achieving the complete enumeration of residents, and by delineating a peripheral “buffer strip” within the area of complete enumeration. However, solving the problem of unambiguous identification may create problems when it comes to interpreting the role of immigration in the dynamics of recipient populations. To completely enumerate all of the residents in an area, and their offspring, while at the same time making home range measurements to facilitate the delineation of a peripheral “buffer strip”, will in most cases require intensive handling and disturbance of the resident population. By contrast, immigrants have not been subjected to this intensive handling. Consequently, handling represents a treatment that residents receive but immigrants do not, at least not until they enter the study area. If the effect of handling is significant, then the measured rate of immigration may be incorrect.

In general, animals will suffer the greatest stress in response to their initial capture, and are then expected to habituate to repeated capture and handling (Harlow et al. 1992), such that they may even become “trap-addicted” (Krebs 1999). Assuming residents have “more to lose” from abandoning their normal home range than dispersers do from not establishing within a given home range, we can predict that dispersers are more likely to be “driven out” of an area in response to the stress associated with their initial capture, than residents, who are more likely to remain and be recaptured. Consequently, the rate of immigration is expected to be *under*estimated under these circumstances. Alternatively, if the repeated capture and handling of residents has adverse effects on their survival or reproduction, the rate of immigration may be *over*estimated. For example, if local recruitment normally preempts settlement by immigrants (Fig. 3.2a), and if the intensive handling of residents induces a significant loss of local young (Fig. 3.2b), then home ranges that would have been occupied by the offspring of residents are instead occupied by immigrants (Fig. 3.2b). In the latter case, if the handling-induced loss of local young is such that the rate of local recruitment is reduced to less than that required to “compensate” for adult losses ($\lambda < 1$), then the recipient resident population may appear to be a dispersal "sink" (Pulliam 1988), that would otherwise go extinct if it were not continually "rescued" by immigration.

Studies attempting to directly measure immigration in open populations in the field *must* include an evaluation of the potentially adverse effects of handling, *before* any interpretation is made regarding the role of immigration in the dynamics of the recipient population. Whether or not immigrants are often "driven out" of an area by the stress of their initial capture can be gauged by the likelihood of instantaneous trap-aversion. If animals are radio-collared at the time of their initial capture, or are marked in a way that allows individual identification if they are resighted, it will be possible to determine what percentage of residents are never recaptured, after initially being captured and handled. This approach can be augmented by using supplemental information regarding the characteristics of individuals that disappear after being captured on only one, or a few, occasions. Whether or not repeated capture and handling has an adverse effect on reproduction or survival can be evaluated by intentionally subjecting different groups to different handling regimes, or by determining whether reproduction or survival are correlated with the frequency of capture and handling.

The fact that the accurate measurement of immigration may often confound the interpretation of the role of immigration argues for an integrated approach to the question. As discussed, interpretations of the role of immigration in producing the patterns observed using the correlational-survey approach are ambiguous because immigration is not actually measured. On the other hand, the steps necessary to measure immigration in open populations in "real landscapes" may actually lead to ambiguities when interpreting the role of immigration. Consequently, the best approach would appear to be to supplement direct measurements of immigration with a less direct, but broader, "survey" of patterns expected to arise under different scenarios regarding the role of immigration (Eberhardt and Thomas 1991). In this respect, new genetic techniques may prove quite useful in providing a less invasive means of estimating rates of immigration (Ims and Yoccoz 1997). For example, Peacock and Smith (1997) measured DNA band-sharing scores among pikas at the Bodie study site and found evidence from parentage analysis (juveniles being found in a different patch from the one inhabited by their putative parent) to suggest that there was an exchange of immigrants between patches. Unfortunately, parentage analysis is not infallible, as it is sensitive to typing errors, and there is, at present, no agreed upon means of dealing with these errors

(SanCristobal and Chevalet 1997, Marshall et al. 1998; see also Appendix 1). Nonetheless, when used in conjunction with direct measurements of immigration, genetic techniques, and other sources of supplemental information, ought to allow us to answer with certainty as to whether immigrants should be viewed as “intruders” that induce population declines, or as “rescuers” that prevent population extinction.

REFERENCES

Beier. P., and Noss, R. F. 1998. Do habitat corridors provide connectivity? Conservation Biology, 12: 1241-1252.

Bjornstad, O. N., Andreassen, H. P., and Ims, R. A. 1998. Effects of habitat patchiness and connectivity on the spatial ecology of the root vole *Microtus oeconomus*. Journal of Animal Ecology, 67: 127-140.

Boonstra, R., and Krebs, C. J. 1978. Pitfall trapping of *Microtus townsendii*. Journal of Mammalogy, 59: 136-148.

Boutin, S. 1980. Effect of spring removal experiments on the spacing behaviour of female snowshoe hares. Canadian Journal of Zoology, 58: 2167-2174.

Brown, J. H., and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. Ecology, 58: 445-449.

Charnov, E. L., and Finerty, J. P. 1980. Vole population cycles: a case for kin selection. Oecologia, 45: 1-2.

Clinchy, M. 1997. Does immigration “rescue” populations from extinction? Implications regarding movement corridors and the conservation of mammals. Oikos, 80: 618-622.

Eberhardt, L. L., and Thomas, J. M. 1991. Designing environmental field studies. Ecological Monographs, 61: 53-73.

Efford, M. 1998. Demographic consequences of sex-biased dispersal in a population of brushtail possums. Journal of Animal Ecology, 67: 503-517.

Fahrig, L., and Merriam, G. 1985. Habitat patch connectivity and population survival. Ecology, 66: 1762-1768.

Gottfried, B. M. 1979. Small mammal populations in woodlot islands. American Midland Naturalist, 102: 105-112.

Hanski, I., and Gilpin, M. E. 1997. Metapopulation processes. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* Hanski, I., and Gilpin, M. E., Academic Press, San Diego, pp. 211-214.

Harlow, H. J., Lindzey, F. G., Van Sickle, W. D., and Gern, W. A. 1992. Stress response of cougars to nonlethal pursuit by hunters. Canadian Journal of Zoology, 70: 136-139.

Hestbeck, J. B. 1982. Population regulation of cyclic mammals: the social fence hypothesis. Oikos, 39: 157-163.

Ims, R. A., Rolstad, J., and Wegge, P. 1993. Predicting space use responses to habitat fragmentation: can voles *Microtus oeconomus* serve as an experimental model system (EMS) for capercaillie grouse *Tetrao urogallus* in boreal forest? Biological Conservation, 63: 261-268.

Ims, R. A., and Yoccoz, N. G. 1997. Studying transfer processes in metapopulations: emigration, migration, and colonization. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* Hanski, I., and Gilpin, M. E., Academic Press, San Diego, pp. 247-265.

Krebs, C. J. 1992. The role of dispersal in cyclic rodent populations. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 160-175.

Krebs, C. J. 1999. Ecological methodology, 2nd ed. Benjamin/Cummings, Menlo Park, California.

Lambin, X., and Krebs, C. J. 1991. Can changes in female relatedness influence microtine population dynamics? Oikos, 61: 126-132.

Lidicker, W. Z., Jr., and Koenig, W. D. 1996. Responses of terrestrial vertebrates to habitat edges and corridors. *In* Metapopulations and wildlife conservation. *Edited by* McCullough, D. R., Island Press, Washington, D.C., pp. 85-109.

Lidicker, W. Z., Jr., and Stenseth, N. C. 1992. To disperse or not to disperse: who does it and why? *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 21-36.

Marshall, T. C., Slate, J., Kruuk, L. E. B., and Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology, 7: 639-655.

Moilanen, A., Smith, A.T., and Hanski, I. 1998. Long-term dynamics in a metapopulation of the American pika. American Naturalist, 152: 530-542.

O'Donoghue, M. 1994. Early survival of juvenile snowshoe hares. Ecology, 75: 1582-1592.

Peacock, M. M., and Smith, A. T. 1997. The effect of habitat fragmentation on dispersal patterns, mating behaviour, and genetic variation in a pika (*Ochotona princeps*) metapopulation. Oecologia, 112: 524-533.

Pugh, S. R., and Tamarin, R. H. 1991. A comparison of population characteristics and reproductive success of resident and immigrant meadow voles. Canadian Journal of Zoology, 69: 2638-2643.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist, 132: 652-661.

SanCristobal, M., and Chevalet, C. 1997. Error tolerant parent identification from a finite set of individuals. Genetical Research, 70: 53-62.

Smith, A. T. 1974. The distribution and dispersal of pikas: consequences of insular population structure. Ecology, 55: 1112-1119.

Smith, A. T. 1980. Temporal changes in insular populations of the pika (*Ochotona princeps*). Ecology, 61: 8-13.

Smith, A. T., and Gilpin, M. 1997. Spatially correlated dynamics in a pika metapopulation. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* Hanski, I., and Gilpin, M. E., Academic Press, San Diego, pp. 407-428.

Stacey, P. B., Johnson, V. A., and Taper, M. L. 1997. Migration within metapopulations: the impact upon local population dynamics. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* Hanski, I., and Gilpin, M. E., Academic Press, San Diego, pp. 267-291.

Stenseth, N. C., and Lidicker, W. Z., Jr. 1992. Where do we stand methodologically about experimental design and methods of analysis in the study of dispersal? *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 295-318.

van Apeldoorn, R. C., Oostenbrink, W. T., van Winden, A., and van der Zee, F. F. 1992. Effects of habitat fragmentation on the bank vole, *Clethrionomys glareolus*, in an agricultural landscape. Oikos, 65: 265-274.

Watson, A., Moss, R., Parr, R., Mountford, M. D., and Rothery, P. 1994. Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. Journal of Animal Ecology, 63: 39-50.

Wolff, J. O., Schauber, E. M., and Edge, W. D. 1997. Effects of habitat loss and fragmentation on the behaviour and demography of gray-tailed voles. Conservation Biology, 11: 945-956.

Table 3.1. Distance to the nearest occupied patch at time 1, as compared between populations found to be extinct or extant at time 2, based on results from four surveys of the Bodie, California, pika metapopulation, as reported in Smith and Gilpin (1997, their Fig. 2). Distances were compared between groups using Mann-Whitney U tests.

Survey	Fate of population at time 2	N	Distance (m) to the nearest occupied patch at time 1		U	z	p
			Median	Range			
1972-77	Extinct	10	42	23-123	133.0	-1.15	0.2513
	Extant	35	56	21-162			
1977-89	Extinct	13	56	25-115	153.5	1.10	0.2720
	Extant	30	46	21-94			
1989-91	Extinct	9	48	27-137	107.5	-0.20	0.8451
	Extant	25	55	21-137			
Pooled	Extinct	32	47	23-137	1408.5	-0.18	0.8545
	Extant	90	52	21-162			

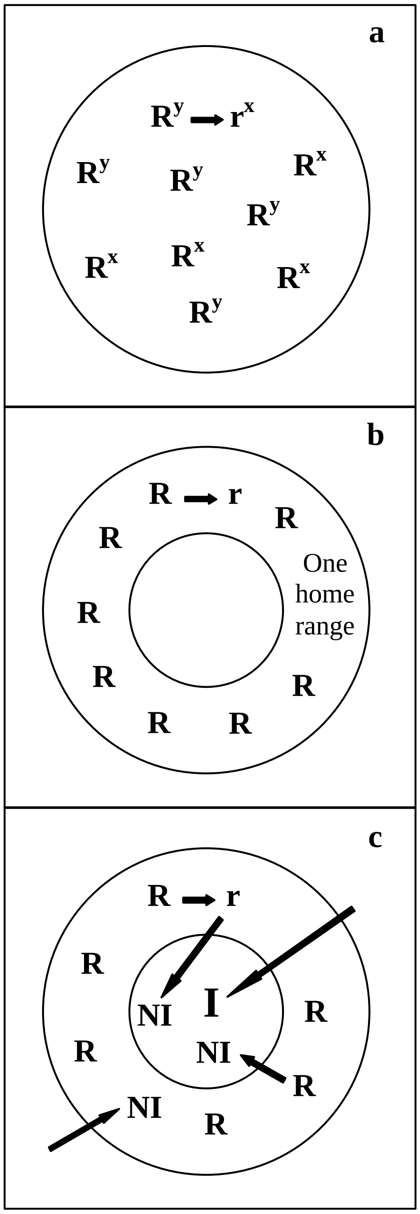

Figure 3.1. Steps in delineating a peripheral "buffer strip" for use in the unambiguous identification of "true" immigrants. Step one (a), completely enumerate all residents (R), and the offspring of residents (r), using at least two, fully independent sampling techniques (x and y). Step two (b), divide the area of complete enumeration into a "core" area surrounded by a peripheral "buffer strip" which is a minimum of one home range length across. Step three (c), distinguish between movements which can (I) and cannot (NI) be unambiguously classified as "true" immigration.

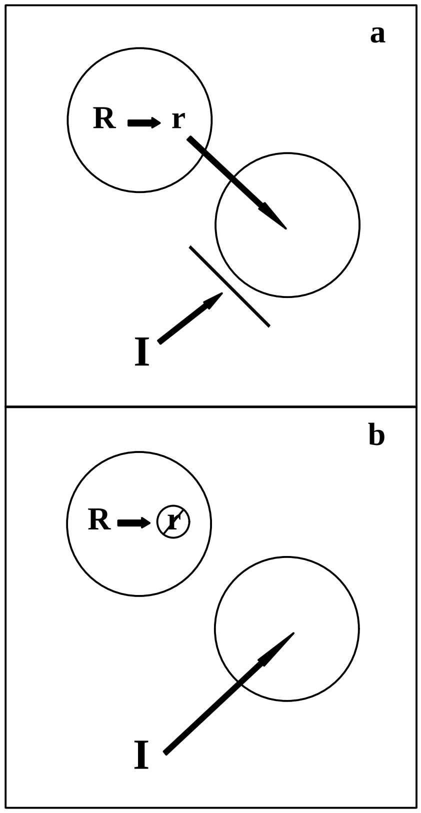

Figure 3.2. Example of how immigration may be overestimated if handling has a significantly adverse effect on resident reproduction or survival. In the absence of handling (a), assume that the offspring (r) of adult residents (R) normally settle in adjacent home ranges (open circle) and thereby preempt (solid line) settlement by immigrants (I). If handling (b) causes deaths (barred circle) among local young, then home ranges that would have been occupied by the offspring of residents are instead occupied by immigrants.

CHAPTER 4

DOES IMMIGRATION “RESCUE” POPULATIONS FROM EXTINCTION? EVIDENCE FROM A LARGE-SCALE FIELD EXPERIMENT ON COMMON BRUSHTAIL POSSUMS

According to metapopulation dynamics theory, landscapes are best viewed as “networks of idealized patches … in which species occur as discrete local populations” (Hanski 1998, p. 41). Patches become unoccupied as a result of local extinctions, but are eventually reoccupied by dispersers from other occupied patches. In some metapopulation models (Hanski 1985, 1991), the exchange of immigrants between occupied patches is expected to “rescue” recipient populations from extinction, thanks to the “demographic and genetic contributions of immigrants” (Brown and Kodric-Brown 1977, p. 445). Moreover, such “models … have shown that a surprisingly small number of immigrants per year (often between three and five adults, e.g., Stacey and Taper 1992 [Acorn Woodpeckers, *Melanerpes formicivorus*]) will allow individual populations to persist” indefinitely (Stacey et al. 1997, p. 268; see also Hanski 1991, Beier 1993 [cougars, *Felis concolor*], and Moilanen et al. 1998 [pikas, *Ochotona princeps*]). Although dispersal is the process underlying metapopulation dynamics, almost no attention is given to the nature of dispersal in most metapopulation models and applications (Clinchy 1997). In addition, studies of metapopulation dynamics rarely ever directly measure dispersal, but instead infer it from the pattern of patch occupancy (Clinchy 1997, Chapter 3). In this Chapter, I report the results of an experiment incorporating both direct and indirect measurements of dispersal, which was designed to test the role of immigration in “rescuing” populations of common brushtail possums (*Trichosurus vulpecula*) from extinction.

The only factor considered in most metapopulation models and applications which reflects some aspect of the dispersal process itself, is the size and structure of physical barriers to dispersal. In almost all metapopulation models, the rate of dispersal between patches is assumed to be a function of the physical distance across some “uniformly unsuitable habitat” (Hanski and Gilpin 1991; Hanski 1998, p. 41). In applications of metapopulation theory to conservation biology, the issue of physical barriers to dispersal manifests itself in discussions of “connectivity”, wherein “the best argument for corridors is that the original landscape was interconnected … [and] …corridors are simply an attempt to maintain or restore some of the natural landscape connectivity" (Noss 1987, p 162; Beier and Noss 1998). If the rate of exchange of immigrants is largely determined by physical barriers to dispersal (unsuitable habitat), it follows that the maximum rate of exchange of immigrants will be observed where there are no physical barriers to dispersal: in a uniformly suitable natural landscape.

In a recent review, Lidicker and Koenig (1996) concluded that mammals are more likely than other vertebrate taxa to demonstrate metapopulation dynamics. Well-established patterns are apparent with respect to dispersal among mammals that would seem to have significant implications regarding metapopulation dynamics. Wolff (1997) argued that, in territorial species, emigration is generally inversely density-dependent, because neighbouring territory owners act as a "social fence" (Hestbeck 1982), preventing movement through each other's home range. Resident territory owners can also be expected to attempt to preempt immigration into an area, because immigrants represent additional, unrelated, intraspecific competitors, and residents will generally benefit more by having their own offspring settle in local vacancies (Clinchy 1997). "Natal dispersal", involving young, pre-reproductive individuals, is the norm among most mammals, while "breeding dispersal" by reproductively-active adults is something of a rarity (Greenwood 1980, Waser and Jones 1983, Johnson and Gaines 1980). Because the frequency of natal dispersal depends on the rate of production of young, the role of dispersal in a species' ecology will depend in part on its fecundity. The importance of this aspect of dispersal was recognized early on in the development of metapopulation theory by MacArthur and Wilson (1967, p.83), who argued that it is important to have a large intrinsic rate of increase to be a "good" colonizing species, although this seems to have been frequently ignored in subsequent metapopulation models and applications. Finally, in the vast majority of mammals, most dispersers are males, while most females are philopatric, settling on or adjacent to their mother's home range (Greenwood 1980, Waser and Jones 1983, Johnson and Gaines 1980). This aspect of dispersal seems to have been completely ignored in metapopulation theory, even though it is of immense significance, as it is the rate of female dispersal only, that determines how often new populations are established, or how often existing populations are demographically "rescued" from extinction (Clinchy 1997).

Several authors have commented on the difficulties associated with the accurate measurement of emigration rates and distances (Stenseth and Lidicker 1992, Koenig et al. 1996, Ims and Yoccoz 1997). Measuring immigration in open populations in the field is a task fraught with as many, if not more, methodological problems (Chapter 3). At the same time, the modeling exercises that suggest that very few immigrants are required to "rescue" populations from extinction can only be refuted if one is able to: 1) demonstrate that immigration is almost non-existent; and 2) be able to do so with, as nearly as possible, complete certainty.

The foremost problem associated with the measurement of immigration is that a proportion of the existing residents will almost certainly elude detection when only a single sampling technique (e.g., live-trapping) is employed (Chapter 3). Consequently, any newly-identified individual may be an immigrant, or a resident that has previously eluded detection (Stenseth and Lidicker 1992). All attempts should be made (using multiple sampling techniques) to verify that the resident population has been completely enumerated, prior to classifying newly-identified individuals as immigrants (Chapter 3). At the same time, intensive efforts aimed at achieving complete enumeration may themselves generate errors (Chapter 3). If immigrants and residents respond differently to the stress of capture and handling, or if repeated capture and handling has adverse effects on reproduction or survival, the measured rate of immigration may be incorrect. The potentially adverse effects of capture and handling should be evaluated before drawing conclusions about the significance of immigration.

Another problem associated with the measurement of immigration arises when the area of complete enumeration does not fully encompass the entire patch. In such cases a "buffer strip" (or "border zone", Stenseth and Lidicker 1992) should be delineated, wherein newly-identified individuals detected in the buffer strip are not classified as immigrants, as they may be residents from just outside the area of complete enumeration that are either: 1) exploring beyond the boundaries of their normal home range (Lidicker and Stenseth 1992); or 2) are expanding their home range in response to vacancies created within the area of complete enumeration (Stenseth and Lidicker 1992, Chapter 3), a phenomenon sometimes referred to as the "vacuum effect" (Efford 1991). The vacuum effect is most commonly expected to occur in territorial species (Carpenter 1987, Mares and Lacher 1987, Schoener 1987). "True" immigration has the potential to "rescue" a recipient population from extinction by adding new individuals to an existing population, whereas the “reshuffling” of the existing population, associated with the vacuum effect, cannot be expected to “rescue” the population from extinction. Misidentifying the vacuum effect for “true” immigration will cause the rate and importance of immigration to be overestimated.

Given the many methodological problems associated with measuring immigration in open populations in the field, it ought not to be surprising that there have been very few such studies conducted on mammals (e.g., Boutin 1980, Lambin and Krebs 1993; see also Stenseth and Lidicker 1992), and they have all been relatively “short-term” (extending over 2 or 3 years). The short-term nature of these studies has allowed critics to claim that the results are not representative of processes occurring over the long term (Beier and Noss 1998). The frequency of dispersal over the longer term can be indirectly gauged by the magnitude of genetic differences between populations (Ims and Yoccoz 1997). However, this approach cannot distinguish between male and female dispersal, and as mentioned above, only the latter is of relevance with respect to the rate of establishment of new populations, or the demographic “rescue” of existing populations.

The likely frequency of female dispersal, over the longer term, can be indirectly gauged by the strength of female philopatry. If most females do not disperse, but instead settle on or adjacent to their mother’s home range, this should be discernible from the spatial pattern of female relatedness. For example, Ishibashi et al. (1997) used estimates of relatedness derived from microsatellite DNA to compare whether adjacent pairs of female grey-sided voles (*Clethrionomys rufocanus*) were more closely related than would be expected from a random dispersal pattern.

The strength of female philopatry may also be judged by deviations from parity in the primary sex ratio (Johnson 1988, 1989). If most daughters settle on or adjacent to their mother’s home range, while most sons disperse, there will be competition for local resources between mothers and daughters, that does not exist between mothers and sons. To reduce the level of local resource competition with their philopatric daughters, mothers should reduce the number of daughters they produce, resulting in a male-biased primary sex ratio. Male-biased dispersal *per se* is not sufficient to produce the biased sex ratio. If both sons and daughters disperse, but males disperse farther, dispersal is said to be male-biased, but in this case mothers and daughters are not in contact with one another, and are therefore not competing with one another, so there is no reason to reduce the number of daughters produced.

Consequently, a significantly male-biased primary sex ratio not only suggests that sons move farther, but also that most daughters generally do not disperse at all. An underlying assumption of the "local resource competition" hypothesis is that sons and daughters are equally "costly" to produce (Johnson 1988), and this must be evaluated prior to drawing inferences regarding female philopatry from deviations in the primary sex ratio.

The disruption of immigration between remnant populations has been identified as a key factor underlying the many declines (26 spp.) and extinctions (16 spp.) that have occurred among medium-sized (35-5500 g) mammals in Australia, in the 200 years since European settlement (Morton 1990). Correspondingly, Australian mammals feature prominently in the literature on connectivity. In a recent review, Beier and Noss (1998) found 16 studies on mammals suggestive of a positive role for conservation corridors, of which, 6 involved Australian marsupial possums and gliders (Families Burramyidae, Petauridae and Phalangeridae). Similarly, Laurance and Gascon (1997) advocated the retention of corridors in association with logging in tropical rainforests throughout the world, based in part on Laurance's (1990) survey work in Australian tropical rainforests on three species of ringtail possum (Family Petauridae) and the common brushtail possum (Family Phalangeridae).

At the time of European settlement, the common brushtail possum had the largest geographic range of any Australian marsupial, encompassing approximately 94 % of the continent (How and Kerle 1995). Although considered to be "relatively adaptable to anthropogenic habitats" (Beier and Noss 1998, p. 1248) because they frequently occur in urban areas, common brushtail possums (along with most other medium-sized mammals; Burbidge and McKenzie 1989, Short and Smith 1994) have been almost entirely extirpated from the center of the continent (Finlayson 1961, Kerle et al. 1992), and presently occupy only about 37 % of their historical range in Australia (How and Kerle 1995).

While both rodents and insectivorous marsupials are included among those species of Australian mammals that have suffered declines since European settlement, medium-sized, herbivorous, marsupials were more adversely affected than other groups (Burbidge and McKenzie 1989, Short and Smith 1994). I chose to study the common brushtail possum as a "model" medium-sized, herbivorous, marsupial. Common brushtail possums are similar in most respects to most of the other species of medium-sized, herbivorous, marsupials that have suffered declines. These species are all included in the suborder

Phalangeriformes (possums and kangaroos, Szalay 1994). Alpin and Archer (1987, p. liii) commented that "in terms of ecological diversity, [Phalangeriformes] is comprised predominantly of very generalized animals showing only minor variations in basic body plan, body size and lifestyle". Caughley and Gunn (1996, p. 61) concluded that those species that have suffered declines are all "ecologically similar enough to be considered a set". In this group, female age at first breeding ranges from 6 months to 2 years, and between 1-3 young are born each year (Lee and Cockburn 1985, Lee and Ward 1989). Calculated intrinsic rates of increase are comparable (Sinclair et al. 1998). Most of the species concerned are generally solitary, weakly territorial, have a promiscuous mating system, and demonstrate male-biased dispersal (Lee and Cockburn 1985, Croft 1989, Johnson 1989, Seebeck et al. 1989).

Despite the frequency with which research on medium-sized Australian mammals appears in the literature on movement corridors and connectivity, and the prominence of place given to dispersal in Morton's (1990) explanation of the decline of medium-sized mammals in Australia, relatively little is known about the importance of dispersal in the population dynamics of these species (Lee and Cockburn 1985, Johnson 1989). Accordingly, there has been no prior attempt to experimentally quantify the role of immigration in these species.

I measured the rate of immigration by female common brushtail possums in response to a spatially and temporally replicated, large-scale, field experiment involving the "pulsed" removal of resident females. The experiment was conducted in a vast (121,000 ha), uniformly suitable, natural landscape of old-growth Eucalypt forest in south-eastern Australia. I chose the seemingly counterintuitive approach of studying metapopulation dynamics in a continuous landscape under the assumption that if immigration plays little role in "rescuing" populations from extinction in a continuous landscape, it is likely to play an even smaller part where there are physical barriers to dispersal, as in fragmented or patchy landscapes. To determine if the results of my relatively "short-term" (2 year) experiment corresponded with the likely frequency of female dispersal, over the longer term, I used two methods to gauge the strength of female philopatry. I conducted parentage analysis using microsatellite DNA, and compared the frequency with which adjacent females were identified as being putative mothers and daughters, with that expected if daughters always settle on or adjacent to their mother's home range. In addition, I examined whether the sex ratio of pouch-young was significantly male-biased, as predicted by the "local resource competition" hypothesis, under conditions of strong female philopatry. Contrary to inferences drawn from surveys assessing connectivity, my results suggest that immigration likely plays little part in “rescuing” common brushtail possum populations from extinction. I discuss the implications of this result in terms of the ecology of medium-sized, herbivorous, marsupials, and caution against overgeneralizations regarding the role of dispersal in mediating local and global extinctions.

METHODS

Study species

The common brushtail possum (hereafter simply “possum”), is a solitary, nocturnal, medium-sized (1-3 kg), herbivorous, marsupial, endemic to Australia (Kerle et al. 1991, How and Kerle 1995). While having declined in Australia, possums are considered to be a significant pest species in New Zealand, where they were first introduced in 1837 (Cowan 1990). Although possums have been the subject of intensive research in New Zealand (Cowan 1990), comparatively little research has been conducted on the population ecology of possums in Australia (Green 1984, Kerle 1984).

The demography of possum populations in south-eastern Australia closely resembles that observed in New Zealand (Chapters 5 and 6). Almost all adult females give birth to a single young in April or May (antipodean autumn). The young first emerges from the pouch at around 175 days of age (Sept.-Oct.), and then rides on its mother’s back for another month or two. Back-young are referred to as “juveniles” by some researchers (Crawley 1973), in distinction to “subadults”, which are independent (weaned) young, that have not yet become reproductively-active. Subadult females are readily distinguished from adult (reproductively-active) females by the condition of the pouch (Clout and Efford 1984). In subadults, the pouch is little more than a shallow indentation on the abdomen. When a female first becomes reproductively-active the pouch enlarges and invaginates, and undergoes a variety of other characteristic changes (Bolliger and Carrodus 1938, 1940). Age at first reproduction varies from 1-3 years (Chapter 5). Subadult males may be distinguished from adult males by the length of the testes (Clout and Efford 1984). Tyndale-Biscoe (1955) reported that males with testes < 18 mm in length were never observed to have spermatozoa present in the epididymides, while males with larger testes were always found with spermatozoa present, independent of season.

Adults in undisturbed areas may live up to 14 years (Chapter 6). While adult survival is generally thought to be about 80 % per annum, I present evidence in Chapter 6 that suggests that adult survival is adversely affected by handling, and the “true” rate of adult survival is more likely about 90 % per annum. Survival of pouch-young to the onset of weaning (at 175 days of age) may vary significantly from one year to the next, ranging from 33-90 % (Chapter 5). Less variation is apparent in the survival of young from the onset of weaning, to their first birthday (365 days of age), with estimates ranging from 43-60 % (Dunnet 1964, Efford 1998, Chapter 5). Survival of yearling females (from 1-2 years) is not significantly different from that of older females, according to results from a 15-year study in New Zealand (Efford 1998).

In wooded areas, possums typically spend the day in a den in the hollow branch of a tree, and emerge at night to feed on leaves, grass, herbs, flowers and fruit (Kerle 1984). An animal’s foraging range is often considerably larger than its “denning range”. I define the latter as the minimum convex polygon connecting all dens used by an individual (see also Lindenmayer et al. 1997). While there is general agreement that male and female ranges overlap extensively, there is some disagreement as to whether individuals are territorial with respect to others of the same sex (Green 1984). The disagreement stems in part from the different methods used to measure range size. Male ranges are always found to be larger than female ranges, regardless of the method used (Green 1984). Both male and female ranges increase and decrease in size, depending on the season. Several studies (Crawley 1973, Ward 1978, Green and Coleman 1986) have found that male ranges are largest during the autumn breeding season. Shifts in female range size do not appear to be as consistent. Crawley (1973) reported that female ranges expanded in autumn and winter, while Green and Coleman (1986) found that females had larger ranges in summer. Green and Coleman (1986) suggested that changes in female range size reflected seasonal changes in food abundance, which may be expected to show different patterns at different sites. Seasonal changes are also observed in the composition of pairs of individuals found sharing dens. During the breeding season, females in oestrous are often followed by one or more male “consorts” (Clout and Efford 1984), that may share the female’s den (Caley et al. 1998). In the rare instances where den sharing is observed outside the breeding season, the animals are generally both females, that are assumed to be related (Caley et al. 1998).

Clout and Efford (1984) reviewed the results of studies conducted in both Australia and New Zealand and concluded that possums, like most other mammals, demonstrate male-biased dispersal (see also Efford 1991, 1998). Clout and Efford (1984) argued that movements in excess of 2 km ought to be considered long-distance dispersal, given that both male and female home ranges in continuously forested habitats are usually less than 500 m in length. Female home range lengths up to 1800 m have been recorded, but only under unusual circumstances where individuals were "commuting" from forest-interior den sites to an agricultural field, and back again, on a nightly basis (Green and Coleman 1986). Efford (1991) compiled evidence from all available sources and found 68 reported cases of long-distance dispersal, 13 of which involved females. In the majority (78 %) of cases reviewed by Efford (1991), animals dispersed from their natal range prior to their first birthday, while the remainder all dispersed prior to their second birthday. There was no evidence of long-distance dispersal by reproductively-active females (i.e., breeding dispersal), among the cases reviewed by Efford (1991).

Study site

The study was conducted in the eastern arm of Paddys Land State Forest, which lies near the center of the 121,000 ha Guy Fawkes Wilderness Area (GFWA), in northeastern New South Wales (NSW), Australia. The GFWA encompasses a few small "peninsulas" of the New England Plateau (maximum elevation = 1300 m) and the surrounding eastern slopes of the Great Dividing Range (NPWS 1992). The rugged terrain has prevented substantial logging or land clearance, leaving the continuous old-growth Eucalypt forest cover largely intact (NPWS 1992). Consequently, when the GFWA was legally "identified" as wilderness by the NSW government it was judged to have met the criterion that "the area is, together with its plant and animal communities, in a state that has not been substantially modified by humans and their works" (NPWS 1992, p. 6).

The GFWA is "unparalleled in south-eastern Australia" in being home to "every species of forest dependent marsupial" (in NSW; NPWS 1992, p. 35). In particular, the "high altitude open forests presently within State Forests contain the highest concentration of arboreal mammals found in NSW" (NPWS 1992, p. 20), and are "very important for arboreal mammals … at all scales (i.e., regional, state and continental)" (NPWS 1992, p. 35). The GFWA consists of "uniformly suitable habitat" for common brushtail possums, and possums are predicted to occur at moderate to high densities throughout the GFWA, based on a regional species distribution model incorporating a large number of site variables, including latitude, temperature, moisture, geology, terrain and vegetation type (NPWS 1994).

I established two 36 ha study grids in the eastern arm of Paddys Land State Forest in September, 1994 (Fig. 4.1). On each grid I marked out 49 permanent trap locations at roughly 100 m intervals in a 7 x 7 matrix (Figs. 4.2 and 4.3). The grids were established at roughly 2 km distance from one another to ensure that they were independent replicates with respect to dispersal, as any movement by an individual from one grid to another could be classified as long-distance dispersal (Clout and Efford 1984). The midpoint between the two study grids lies at latitude 30°06'00" S and longitude 152°10'20" E. The Paddys Land area is considered to be part of the New England Plateau (NPWS 1992), and the elevation on the grids ranged from 940-1040 m. The bottom corner of the East grid was within 100 m of the edge of the Plateau. A number of individuals captured on the East grid had dens to the south and east of the bottom corner of the grid (Fig. 4.3) which were located in trees growing on the steep sides of the Plateau. While measured slopes on the grids never exceeded 10.0 °, the mean (+/- S.E.) measured slope down the side of the Plateau was 18.1 ° (+/- 1.0), and the maximum slope I recorded was 32.0 °.

Chapman and Binns (1995) conducted flora surveys in May, 1993, at three sites in the vicinity of the study grids, one near (within a few hundred metres) the West grid, one near the East grid, and one near the midpoint between the two grids. Chapman and Binns (1995) described the soil as a sedimentary red podsolic. The general floristic community was classified as “grassy woodland”, with a very sparse shrub stratum largely composed of *Acacia filicifolia* and *Allocasuarina littoralis* (Chapman and Binns 1995). The area was lightly grazed by domestic livestock, and subject to infrequent, low intensity fires. Median annual rainfall is 837.8 mm (Range = 302.2-1247.4 mm; based on 64 years of data from the Kookabookra weather station, latitude 30°00'39" S, longitude 152°00"34" E, elevation 975 m).

Seven “forest types” (Forestry Commission of NSW 1989) were identifiable in the vicinity of the study grids based on aerial survey data available from the Walcha District offices of the Forestry Commission of NSW. The seven “forest types” include: No. 70, Spotted Gum (*Eucalyptus maculata*); No. 72, Spotted Gum - Grey Box (*E. maculata - E. moluccana*); No. 82, Grey Box (*E. moluccana*); No. 93, Eastern Red Gums (*E. amplifolia* dominant); No. 122, New England Stringybark (*E. caliginosa*); No. 161, Roundleaved

Gum (*E. deani*); and No. 163, New England Blackbutt (*E. andrewsii*). Chapman and Binns (1995) classified 2 of the 3 sites they surveyed as "forest type" No. 122, New England Stringybark, and the third was classified as "forest type" No. 70, Spotted Gum.

I measured the distance to, and height of, the nearest tree (defined as: > 20 cm DBH and > 2 m in height) in each of the four quadrants surrounding each permanent trap location on each grid (Figs. 4.2 and 4.3). Using program POINT QUARTER (Krebs 1999), I estimated that the mean (+/- S.E., and 95 % C.L.) density of trees was 137.0 per ha (+/- 0.4, 119.0 - 157.5) on the West grid, and 163.4 per ha (+/- 0.4, 141.8 - 187.8) on the East grid. Median tree height was 19.8 m (Range = 9.3 - 43.8 m) on the West grid, and 20.5 m (Range = 4.0 - 43.8 m) on the East grid.

Detection, capture, and handling

I used two, independent sampling techniques to detect the presence of possums on the study grids: 1) live-trapping; and 2) spotlighting. Trapping involves simultaneous detection and capture. To capture animals detected during spotlighting, I followed two procedures: 1) whenever feasible, I attempted to tranquilize the animal using a CO_2-powered dart-gun; otherwise 2) I set one or more traps at the base of the tree in which the animal was detected.

When captured for the first time, animals were weighed, tagged and sexed. Weight was recorded to the nearest 50 g using a spring scale. Aside from those individuals captured using the dart-gun, animals were generally not tranquilized prior to handling, but were instead immobilized using a variety of restraints. All animals (except pouch-young) were tagged in each ear with two types of Monel metal tags (National Band and Tag Co., Newport, Kentucky, U.S.A.). Individually numbered tags (size 1005-3) were located in a proximal and medial position. Smaller tags (size 1005-1) wrapped with coloured reflective tape were located in a distal and lateral position. Individuals were tagged in each ear with up to three coloured tags coded for sex, grid, and year of first capture. Pouch-young that were judged to have reached a sufficient size were tagged in each ear with smaller (size 1005-1), individually numbered tags, located in a proximal and medial position. The interior (non-numbered) edge of pouch-young tags were wrapped with coloured reflective tape, to ensure that surviving young were identifiable as being marked individuals, if they were later seen during spotlighting. Tags did not interfere with the development of the pinna of the ear.

When males were captured for the first time I measured testis length to the nearest 0.1 mm using vernier calipers. If the individual was judged to be an adult (testis length >= 18.0 mm), testis length was measured if and when it was next captured, to confirm that the animal was an adult, but was not measured on subsequent recaptures. If the individual was judged to be a subadult (testis length < 18.0 mm), testis length was measured on all subsequent occasions on which it was captured and handled, until such time as it was judged to have become an adult.

The condition of a female's pouch was checked on the first occasion on which she was captured, and on all subsequent occasions on which she was captured and handled. When a female was found to be bearing a pouch-young I attempted, whenever possible, to: 1) determine the sex of the young; and 2) measure the length of its head, to the nearest 0.1 mm, using vernier calipers. Head length is the most reliable trait to use in estimating the age of pouch-young (Chapter 5). It was not always possible to examine and measure the young because: 1) the pouch-young was judged to be too small to safely handle; or 2) the mother was struggling too much. As measurements were generally attempted by a single person, in the field, on animals that were not tranquilized, a judgement had to be made in each case on the trade-off between an accurate measurement and the possibility of harming the mother or causing her to eject the pouch-young. When the pouch-young was judged to be too small to handle safely, I attempted to estimate crown-rump length (Lyne and Verhagen, 1957, their Fig. 5), which can also be used to estimate the age of pouch-young. Crown-rump length was estimated to the nearest 5.0 mm by holding a ruler adjacent to the body of the pouch-young. For slightly larger pouch-young (head length <= 10.0 mm), and in instances where the mother was struggling too much, head length was estimated to the nearest 5.0 mm by holding a ruler adjacent to the head of the pouch-young.

A nursing mother may leave an older dependent young in a den, while she searches for food (Winter 1976, p. 246). Consequently, the survival of a young to the onset of weaning may be inferred even if the young itself is not seen, if the mother is found to be still nursing at the appropriate phase in the development of the young (Chapter 5). Females were classified as still nursing if: 1) they had an engorged mammary gland; and 2) they were still lactating. An engorged mammary gland was operationally defined as one that could be readily identified as a distinct oval shaped organ with minimum dimensions of 20.0 x 30.0 mm, when measured with vernier calipers (Dunnet 1964, Smith et al. 1969, Crawley 1973). Lactation was determined by squeezing the female's teat.

Whenever a female's pouch was examined I also noted if she was: 1) "rumpy"; or 2) "bony". "Rump wear" is a condition involving fur loss, lesions, and scab formation, generally on the lower back and base of the tail. The condition is typically observed in association with heavy infestations by the haematophagous, ectoparasitic mite, *Trichosurolaelaps crassipes* (Presidente 1984, Hemsley and Canfield 1993, Clark 1995, Chapter 6). To check a female's pouch it was necessary to restrain the female's hindlegs with one hand while examining the pouch with the other hand. Contrasts between females were apparent in the condition of their hindlegs. The majority of females' hindlegs felt muscular while some females' hindlegs felt like little more than skin and bone. Such contrasts have been used previously in evaluating the condition of adult possums (Humphreys et al. 1984). Females observed to be both "rumpy" and "bony" had a significantly lower probability of survival than females that were never seen to be so (Chapter 6).

Aside from those selected for removal, all animals were released at their point of capture, during the day. Upon release I attempted to follow the animal as it made its way to a den or some other refuge (Dunnet 1956). I noted all occasions on which an animal either stopped and began eating grass, or climbed a tree and began eating leaves, as feeding during the daytime has been interpreted as a sign of poor condition (Mackintosh et al. 1995). In addition, I noted all occasions on which an animal was seen to be "weak and wobbly" upon release. Symptoms of more or less severe ataxia (loss of motor control) have been reported in association with "wobbly possum syndrome" in New Zealand (Mackintosh et al. 1995). Survivorship among females observed to be "weak and wobbly" upon release was significantly poorer than among females that were never seen to be so (Chapter 6).

Definitions and experimental design

I began live-trapping on the study grids in November, 1994. Residency was defined with respect to a (somewhat) arbitrarily chosen date of August 1, 1995, such that any female captured prior to August 1, 1995, was defined as being a resident female, as was the daughter of any such female (Chapter 3). While the regional species distribution model mentioned above predicted that the GFWA was "uniformly suitable habitat" for possums, the spatial resolution of the model was not such that areas as small as an individual's home range could be judged to be “suitable” or not. Female immigrants would not be expected to settle on the study grids if, as a result of stupendous bad luck, the habitat on the study grids was somehow “unsuitable”. To ensure that the study grids were indeed “suitable” habitat, I defined residency with respect to the latest date (August 1) by which I expected all females to have given birth, if they were going to breed in that year (1995). I could then say without ambiguity that the study grids were “suitable” habitat for at least as many breeding females as were known to be present on August 1, 1995 (Boutin 1980). Subsequent records, over three breeding seasons, indicated that the August 1 cut-off was reasonable, as the latest date on which a female was known to have given birth to a primary young (defined on p. 144) was July 11 (Chapter 5). Among those resident females captured prior to, and known to be still alive on or after August 1, 1995, 31 of 33 on the West grid, and 27 of 29 on the East grid, were known to have given birth in the preceding breeding season. On each grid, there was one subadult female with a range interior to the periphery of the trapping grid (Figs. 4.2 and 4.3), that did not breed; and one adult female with a range exterior to the periphery of the trapping grid, that was first captured prior to the beginning of the 1995 breeding season, that may have given birth, and lost her young, before being recaptured after August 1, 1995. All four females in question occupied roughly the same ranges, and were known to have given birth, in the following breeding season (1996).

There were three components to the experimental design involving: 1) the complete enumeration of resident females; 2) the delineation of a peripheral “buffer strip”; and 3) the “pulsed” removal of resident females. The steps taken to ensure the complete enumeration of resident females are discussed in a subsequent section.

Each study grid was divided into arbitrarily defined “core” and “peripheral” areas (Figs. 4.2 and 4.3). Resident females with denning ranges to the interior of the inner dashed lines shown in Figures 4.2 and 4.3 were defined as “core” resident females, while those with denning ranges to the exterior of the inner dashed lines were defined as “peripheral” resident females. Females first identified after August 1, 1995, were defined as “potential immigrants”. Non-breeding potential immigrants that disappeared after a period of less than three months were classified as “transients” (Dunnet 1956, Crawley 1973). Any potential immigrant that was either found to be bearing a pouch-young, or was known to have been present for three or more months, was classified as a “settler”. I defined the “buffer strip” as being the roughly 100 m distance between the inner and outer dashed lines shown in Figures 4.2 and 4.3. Assuming I was successful in completely enumerating all resident females, any potential immigrant that settled in the core of one of the two study grids would have had to have: 1) come from outside the periphery of the trapping grid (shown by the outer dashed lines in Figs. 4.2 and 4.3); and 2) would therefore have had to have dispersed across the 100 m buffer strip to reach the core of the grid (shown by the inner dashed lines in Figs. 4.2 and 4.3). If, as I expected to be the case, the buffer strip was occupied by a more or less contiguous ring of peripheral resident females, it could also be concluded that any potential immigrant that settled in the core had dispersed across at least one home range (that of a peripheral resident female) in order to reach her destination. Lidicker and Stenseth (1992) argued that permanent movement across one home range length should be considered as a minimum criterion for any biologically meaningful definition of dispersal. Consequently, only potential immigrants that settled in the core were classified as “true immigrants”. Potential immigrants that settled in the buffer strip, or exterior to it, were not classified as “true immigrants”, as they were as likely to be females with home ranges just outside the initial area of complete enumeration (Chapter 3).

In order for immigration to “rescue” populations from extinction, female immigrants must enter and add to an existing population of resident females (Clinchy 1997). Most metapopulation models assume that immigrants replace residents lost as a result of stochastic processes, in which case, immigrants are more likely to “rescue” populations from extinction the more rapidly they replace lost residents (Clinchy 1997). To measure the rate at which immigrants replaced lost residents, I removed all of the core resident females from both study grids on August 1, 1995. If a female’s denning range straddled the dashed line defining the core of the study grid (Figs. 4.2 and 4.3), I determined the position of the arithmetic mean center of her denning range in order to judge whether she ought to be considered a core or peripheral resident female.

Range expansion in response to removals (the vacuum effect) is generally not considered to be part of dispersal (Lidicker and Stenseth 1992). Consequently, if peripheral resident females expanded their ranges into the core of the study grid following the removal of core resident females, I did not consider this to be immigration (Chapter 3). The question I was interested in was not whether peripheral females replace core females, but whether immigrants replace residents.

I monitored the rate at which female immigrants entered and settled in the core removal areas from August 1, 1995, to August 1, 1996. In order to recreate conditions on the grids as they had existed after the August 1, 1995, removals, and thereby temporally replicate the experiment, any female that had established her denning range in the core of either grid during the 1996 breeding season (March to June, Chapter 5) was removed on August 1, 1996. I chose to remove any and all “true immigrants”, as well as any originally peripheral resident female that had expanded her denning range into the core. The rate at which female immigrants entered and settled in the core removal areas was then monitored for a second year, from August 1, 1996, to August 1, 1997.

Over the course of the study, several of the originally peripheral resident females either died, or expanded their denning ranges into the core and were removed, leaving gaps in the ring of peripheral females. In such cases I generally made a pointed effort to try to capture any female with a range just exterior to that of the originally peripheral resident female. I classified females captured under such circumstances as “secondary” peripheral females. Part of my aim in following this protocol was to maintain a more or less contiguous ring of peripheral females, but I also wished to maintain adequate sample sizes in order to estimate demographic parameters (Chapter 6). Following from the definitions above, if any of the secondary peripheral females, or their daughters, shifted their denning ranges into the core they would be classified as “true immigrants”, as they would have dispersed across the formerly occupied range of the originally peripheral resident female.

Much of the data I present is in the form of maps showing the location of individuals on the study grids (Figs. 4.4-15). The location of each female is indicated by an uppercase letter, either by itself, or followed by a number, or preceded by either a lowercase or uppercase letter. Single uppercase letters identify adult or subadult resident females. Uppercase letters followed by a number identify daughters tagged when still with their mother (who is identified by the uppercase letters). Uppercase letters preceded by the lowercase letter “d” indicate resident females that died prior to August 1, 1995. Uppercase letters preceded by the lowercase letter “r” indicate core resident females removed on August 1, 1995. Uppercase letters preceded by the uppercase letter “A” indicate females first identified after August 1, 1995, which are by my definition all potential immigrants. Letters or symbols enclosed in a rectangle indicate the location at which an individual was captured, in those cases where the animal was not radio-collared. Single lowercase letters enclosed in a diamond symbol indicate where unmarked possums were seen during spotlighting. When referring to a given individual in the body of the text, the individual's identifier is preceded by an uppercase letter "W" or "E", to indicate which study grid I am discussing (e.g., "W-A" refers to resident female "A" on the West grid).

Radio telemetry and den mapping

All but four of the resident females known to be alive immediately prior to the August 1, 1995, removals, were radio-collared. The four exceptions included two subadult females (W-P1 and E-D, Figs. 4.4 and 4.10) and two adult females (W-B and W-U, Fig. 4.4). I did not radio-collar the subadults because I was concerned that I would lose the radios if these females dispersed off the study grids. The two adults in question were first captured prior to February, 1995, when I first began radio-collaring, and were not recaptured until after August 1, 1995. In addition to the 60 radio-collared resident females (30 per grid) known to be alive immediately prior to August 1, 1995 (Figs. 4.4 and 4.10), there were 3 radio-collared resident females on the East grid that had died prior to August 1 (E-dA, E-dB and E-dC; Fig. 4.10).

Following the August 1, 1995, removals, I managed to radio-collar 3 of the 4 residents that were not previously radio-collared (W-B, W-P1 and E-D). In addition, I radio-collared all but three newly-identified females (i.e., potential immigrants) that were judged to have settled (i.e., found possessing a pouch-young or known to be present for three or more months) on the study grids. In one of the three cases where a newly-identified settler was not radio-collared, the female in question (W-AI, Fig. 4.7) died during capture. In the other two cases, the individuals in question (W-AA and E-AA, Figs. 4.5 and 4.11) were the very first newly-identified females captured after August 1, 1995. Both females had pouch-young, and both were captured within two weeks of August 1. By too rigidly interpreting my own definitions, I categorized both females as potential immigrants (because they were captured after August 1), and judged that I ought not risk the expense of having "dispersers" run-off with a couple of expensive radios. I subsequently changed my protocols such that any newly-identified female captured on the study grids that was found to be bearing a pouch-young was given a radio-collar.

Each radio-collar (total weight = 35 g; Titley Electronics, Ballina, NSW, Australia) was equipped with a mortality sensor. In addition, each radio had a whip antenna, which I wrapped with coloured reflective tape, using individually-identifiable combinations of colours. I occasionally needed to locate a female at night so that I could attempt to dart her, in order to replace her radio, or tag her pouch-young. If the female's radio had already failed (18 cases) I could still identify her from the colour combinations on the antenna. Each female's radio signal was checked on a weekly basis, to ensure that she was still alive and her radio was still operational.

Radio-tracking principally involved homing in on a female's den during the day. Only daytime tracking was used in defining a female's denning range. Females were never located more than once in the same day, since daytime movements by possums are extremely rare (Mackintosh et al. 1995). The majority of radio-tracking "sessions" took place at the same time as "full-grid" trapping sessions (Tables 4.1 and 4.2), as I would generally be involved in trapping on one grid while an assistant radio-tracked on the other grid. When defining a female's denning range I excluded all cases where a female tracked during the day had been captured on the previous night. I used a female's denning range to describe her location on the study grid, in part because this ought to best reflect the core of her home range (Winter 1976). In addition, I was interested in determining whether females that entered the removal areas would use the same dens as had been used by the resident females, which would suggest that suitable dens are an important limiting resource (Caley et al. 1998).

All den sites were marked with individually numbered aluminum tags. I determined the position of each den site, relative to the nearest permanent trap location, by using a sighting compass and measuring the distance to the nearest 0.1 m using a tape line. When measurements were made up or down hillsides, the slope was recorded using a clinometer. The positions of the permanent trap locations were surveyed and mapped by Resource Engineering students from the University of New England (Armidale, NSW, Australia), using theodolites, sighting compasses and tape lines. All locations shown on the grid maps (Figs. 4.2, 4.3, and 4.4-4.15) are plotted using Euclidean coordinates (i.e., corrected for elevation).

Live-trapping

Possums were live-trapped using 30 x 30 x 60 cm, hook-operated, wire mesh cage traps (Mascot Wire Works, Sydney, Australia) set at the base of a tree and baited with apple. Animals trapped overnight were processed and released beginning at dawn the next day. In addition to live-trapping on the study grids (described below), I live-trapped along the vehicle trail running between and away from the two study grids (Fig. 4.1). In the latter case I positioned 40 traps at roughly 100 m intervals along the vehicle trail, which were baited and set for 13 nights (520 trap-nights), during October and November, 1996. My aim in trapping along the vehicle trail was to assess the reproductive success of females that had not been previously captured and handled (Chapter 5). Information was also gained regarding exploratory movements by animals normally trapped on the study grids.

I followed three procedures when live-trapping on the study grids, which I define as: 1) full-grid trapping; 2) target trapping; and 3) nighttime trapping. I define a full-grid trapping session as one in which traps were set at all 49 permanent trap locations on a grid (Figs. 4.2 and 4.3). During most full-grid trapping sessions traps were set for 3 consecutive nights, however, I also include in this category both 1-night and 4-night trapping sessions. Animals were weighed and handled on the first occasion on which they were captured during a trapping session and were thereafter simply released from the trap if they were recaptured during the same trapping session. Over the course of 32 months, from the beginning of December, 1994, to the end of July, 1997, I conducted 26 full-grid trapping sessions on the West grid (Table 4.1) and 24 full-grid trapping sessions on the East grid (Table 4.2). I conducted monthly full-grid trapping sessions on both grids during the autumn breeding seasons in each of the three years of the study (1995, 1996, 1997). During winter and spring I occasionally did not conduct a full-grid trapping session in a given month, but instead concentrated on “target trapping” (described below). I often did not trap in every month during summer because trapping success was poorer and there was less information to be gained. Instead, I concentrated on measuring den tree characteristics and other activities.

Target trapping involved three procedures: 1) setting traps at a den known to be presently occupied by a radio-collared female; 2) setting traps at dens formerly occupied by peripheral resident females, with the aim of capturing secondary peripheral females; and 3) setting traps at refuge sites (which were presumed to be dens) that were seen to be used by males upon release from capture (Dunnet 1956), in areas of the grid where no female had yet been caught. Being able to trap radio-collared females at their dens was very important for ensuring the complete enumeration of all resident pouch-young (Chapter 3). It was also extremely advantageous to be able to use the denning ranges of currently radio-collared females to identify areas on the grid where a female “ought” to be found, and then concentrate trapping effort in that area.

Nighttime trapping was that conducted in conjunction with spotlight transects. If an unmarked possum was detected during a spotlight transect, and the dart-gun was unavailable or unusable (because it was too windy, or the animal was too high in the canopy), I set as many traps as were readily available, at the base of the tree in which the animal was seen, or had run to.

Spotlighting and darting

Possums have a distinctive orange eye-shine which is readily detected at night with the use of a spotlight. I used 30-watt spotlights powered by 12-volt lead-acid batteries. With the aid of binoculars I was generally able to determine the colour of the reflective ear-tags born by marked possums, at distances of up to 50 m. I usually began spotlighting about an hour after dark and typically finished before midnight. To facilitate spotlighting I marked out transect lines between each permanent trap location on each grid (Figs. 4.2 and 4.3) using nails wrapped with reflective tape. I conducted four types of spotlight transects: 1) full-grid transects; 2) core transects; 3) peripheral transects; and 4) target transects. Full-grid transects involved starting at one corner of a study grid (Figs. 4.2 and 4.3), moving up a trapline, and then across and down the next, and so forth. Core transects involved moving between core traps only (Figs. 4.2 and 4.3), while following the same procedure as for full-grid transects. Peripheral transects involved circling around the periphery of the trapping grid (shown by the outer dashed lines in Figs. 4.2 and 4.3). A target transect, like target trapping, involved an intensive search in an area of the grid where a female “ought” to be found. Possums seen on transect lines connecting two core traps (Figs. 4.2 and 4.3) were categorized as having been seen in the core (Table 4.3), while possums seen on transect lines connecting core and peripheral traps, or two peripheral traps, were categorized as having been seen on the periphery of the study grid (Table 4.4).

I conducted spotlight transects on a regular basis, between late February (just prior to the beginning of the autumn breeding season) and August 1, in each of the three years of the study (1995, 1996, 1997).

I spent an average of 500 minutes (Range = 345-825) spotlighting each area (core vs. periphery), of each grid, in each year (Tables 4.3 and 4.4). The level of effort was comparable to similar spotlighting surveys, such as that by Laurance (1990), who spent an average of 481 minutes (Range = 175-740) spotlighting for possums at each of 20 sites in tropical rainforest in northeastern Australia. For various reasons, I conducted an additional 440 minutes worth of spotlighting in the core of the West grid in the late winter and early spring of 1995 (Table 4.3).

I used a Montech Model 2 CO_2-powered dart-gun (Montech Pty Ltd, Melbourne, Australia), whenever possible, to attempt to capture unmarked possums detected during spotlighting, or to recapture radio-collared females that were resistant to target trapping. The dart-gun fired a modified 0.5 ml insulin syringe, which was filled with "Zoletil 100" (active ingredients include Tiletamine and Zolazepam; Virbac Pty Ltd, Sydney, Australia), at a concentration of 30 mg per 0.15 ml.

Complete enumeration

I enumerated a total of 200 adult and subadult possums, 105 (47 females, 58 males) on the West grid, and 95 (48 females, 47 males) on the East grid. I also enumerated a total of 154 dependent young (pouch-young or juveniles), 82 on the West grid, and 72 on the East grid.

Trapping success (measured as the proportion of traps possessing possums during full-grid trapping sessions) was generally very good. Mean (+/- S.E.) trapping success was 40.2 % (+/- 2.0) on the West grid (Table 4.1), and 33.0 % (+/- 1.8) on the East grid (Table 4.2). Table 4.1 shows the number of captures during full-grid trapping, target trapping, and nighttime trapping, relative to the dates on which full-grid trapping sessions were conducted on the West grid. Table 4.2 shows the comparable data for the East grid. Tables 4.1 and 4.2 also show the number of times animals were either darted or resighted during spotlighting, relative to the dates on which full-grid trapping sessions were conducted. A resight refers to an animal detected during spotlighting, that was not captured, but whose identity could nonetheless be determined, either because it was a radio-collared female, or because it bore a unique combination of coloured reflective ear-tags.

I followed five steps in evaluating whether I had achieved my goal of completely enumerating all adult and subadult possums on the study grids, which is one of the necessary preconditions that has to be met in order to unambiguously identify immigrants (Chapter 3). The first step involved comparing between a total count of the population, such as that generated using the minimum-number-alive (MNA) method (Krebs 1999), and a mark-recapture estimate of population size, such as the Jolly-Seber estimate. If the population has been completely enumerated, the MNA and Jolly-Seber estimates should be nearly the same (Krebs 1999, p. 94). Deviations between the results generated by the two methods may arise, either because: 1) complete enumeration has not been achieved; or 2) some of the assumptions underpinning the population estimate have been violated. The Jolly-Seber estimate assumes that all animals marked at a given time are equally catchable, and that those not yet marked are as equally catchable as those already marked (Krebs 1999, p. 49). To evaluate the first of these two assumptions regarding equal catchability (step 2 in evaluating complete enumeration) I determined how often a radio-collared female, known to be present on a grid, was actually captured during full-grid trapping sessions on that grid. To evaluate the latter assumption regarding equal catchability (step 3 in evaluating complete enumeration) I plotted the cumulative number of newly-identified individuals captured over time, which ought to reach a more or less abrupt asymptote if animals that are not already marked are as equally catchable as those that are (Krebs 1999, p. 56). Animals that are completely *un*catchable using a given technique (e.g., live-trapping) can only be detected by using a different technique (e.g., spotlighting; Krebs 1999, p. 50). As the fourth step in evaluating the success of complete enumeration, I compared the proportion of marked and unmarked animals detected during spotlighting, with the expectation that the number of unmarked animals detected should be very nearly zero (except for transients or immigrants that have not yet been captured). As a final step I used all available information, such as the circumstances of capture, reproductive status, and likely relatedness to residents, to draw inferences regarding the potential origin of newly-identified individuals.

Table 4.5 lists MNA and Jolly-Seber estimates regarding the number of females on the West grid, over the course of the study. I present three MNA tallies, concerning the number of females known to be alive based solely on full-grid trapping (MNA-Grid), the number of radio-collared females (MNA-Radio), and the number of females known to be alive based on all available data (MNA-All). To permit comparisons with the Jolly-Seber estimate, only females that were at some point captured or resighted along or interior to the periphery of the trapping grid were included in the MNA-Radio and MNA-All tallies, as these females were all, at least potentially, “susceptible” to being caught during the full-grid trapping sessions, and thereby stood some chance of being included in the Jolly-Seber estimate. Table 4.6 lists MNA-Grid, MNA-Radio, MNA-All, and Jolly-Seber estimates, regarding the number of females on the East grid. Tables 4.7 and 4.8 list MNA-Grid, MNA-All, and Jolly-Seber estimates, regarding the number of males on the two study grids.

For the most part the MNA-Grid and Jolly-Seber estimates of population size were very nearly the same, regardless of sex or study grid (Tables 4.5-8). MNA-All was generally greater than the Jolly-Seber estimate of population size because newly-identified individuals were often first captured during target trapping (Tables 4.1 and 4.2) at peripheral den sites (Figs. 4.2 and 4.3), prior to being caught on the grid, which gave me some idea as to their (recent) point of origin. The Jolly-Seber B statistic reflects "additions" to the population (sampled by the trapping grid), composed of: 1) newly-identified animals whose origin is unknown; 2) animals from just off the grid that have been previously captured during target trapping; and 3) the surviving offspring of residents, that have begun to fend for themselves. In the latter case, the offspring of residents are included in the Jolly-Seber B statistic as newly-identified individuals, when in fact their identity is known (because they were tagged while still in the pouch). The Jolly-Seber B statistic should be compared to Figures 4.16-19, which plot the cumulative number of newly-identified individuals caught at core and peripheral locations on the grid. For purposes of comparison with the Jolly-Seber estimates of N and B, Figures 4.16-19 show what is equivalent to the cumulative number of MNA-All, insofar as only animals caught or detected on or interior to the periphery of both grids, are included. As with MNA-All, individuals are added to the cumulative tally shown in Figures 4.16-19 at the time at which they are detected. Because there was often some delay between the time at which individuals were first captured during target trapping, etc … (and thereby added to the MNA-All tally), and when they were later caught at one of the permanent trap locations (and thereby included among the "additions" reflected in the Jolly-Seber B statistic), the timing of increases in B may not correspond perfectly with the timing of increases in MNA-All, as shown in Figures 4.16-19. Nonetheless, the aggregate number of additions as tallied in Figures 4.16-19, and as estimated by the Jolly-Seber B statistic, were very nearly the same, regardless of sex or study grid (Tables 4.5-8).

Figure 4.20 shows the relationship between the MNA-Grid and Jolly-Seber estimates of female numbers, when the two estimates are plotted against one another. There should be a 1:1 relationship if attempts at complete enumeration have been successful (Krebs 1999, p. 94). If the two estimates are not equal, the Jolly-Seber estimate will always be the larger. The median deviation between the MNA-Grid and Jolly-Seber estimates was 0.6 on the West grid and 1.0 on the East grid. The largest single deviation between the estimates (5.7) occurred on the East grid in session 7 (Table 4.6), which was *prior* to the "deadline" (August 1, 1995) for achieving complete enumeration (Table 4.2). Moreover, the Jolly-Seber estimate of the number of females (30.7) present in session 7, was equivalent to the number of females (31) I eventually managed to capture and radio-collar prior to session 8. The number of radio-collared females shown in session 8 in Table 4.6 is 21, because one radio-collared female died and nine more were removed, in between sessions 7 and 8.

The Jolly-Seber estimate of population size will exceed the estimated MNA if marked animals become trap-averse, because the marked segment of the population will then be underestimated relative to the unmarked segment. I evaluated whether marked animals became trap-averse by determining the proportion of times radio-collared females that were known to be present on a grid were actually captured during full-grid trapping sessions on that grid. Figure 4.21 shows the relevant data as regards 77 of the total of 79 females, radio-collared over the course of the study. The two females not included in Figure 4.21 are E-dA (Fig. 4.10), who was first radio-collared in session 6 and died prior to session 7 (Table 4.2), and E-AJ (Fig. 4.15), who was first radio-collared during the last full-grid trapping session (24) on the East grid (Table 4.2). Most of the 77 radio-collared females for which data were available, were captured during full-grid trapping sessions, most of the time (Fig. 4.21). However, seven females (9 %) were not recaptured during full-grid trapping sessions, during the time that they were radio-collared. Several of the seven females in question occupied denning ranges outside the periphery of the trapping grids, and rather than being trap-averse, they simply may not have been captured during full-grid trapping sessions because they were not often in the vicinity of any of the permanent trap locations. Indeed, 4 of the 7 females in question were each trapped on repeated occasions when I attempted to trap them at their dens. The remaining three females (4 % of the total of 77) were never successfully re-trapped, even when I set traps at their dens. I set traps at the dens of the three females in question (E-rA, E-AF, and W-K) on 1, 5, and 18 occasions, respectively. Female W-K was unquestionably trap-averse. Fortunately, I was able to recapture W-K on three occasions using the dart-gun. Moreover, the presence of W-K would not have gone undetected, even if she had avoided being trapped in the first place, because she was also successfully resighted during spotlighting.

In a “closed” population (= no transients or immigrants, in this context), if unmarked animals are as equally catchable as marked animals, the cumulative number of newly-identified individuals should reach a more or less abrupt asymptote, and then level off (Krebs 1999, p. 56). In an “open” population (where some of the unmarked animals may be transients or immigrants), the level should increase more or less gradually after asymptoting. Figure 4.16 shows the cumulative number of newly-identified females first caught in core traps on both grids. On the East grid the number of newly-identified females asymptoted fairly abruptly and leveled-off, prior to the “deadline” for achieving complete enumeration (August 1, 1995). On the West grid, four females were first trapped in core traps following the August 1, 1995, “deadline”. Based on supplementary information (discussed later), I was able to classify 3 of the 4 females first identified after August 1, 1995 (W-AE, W-AF and W-AK), as new “recruits” (either transients or immigrants). Supplementary information (discussed later) indicated that W-AD (one from among the 30 non-“recruits” on both grids = 3 %) did appear to be a resident female that was initially resistant to being trapped. Notably, while W-AD may have initially been somewhat trap-averse, she was readily re-trapped on seven occasions over the subsequent 11-month period, prior to her death.

Figure 4.17 shows the cumulative number of newly-identified females first caught in peripheral traps on both grids. The cumulative number of newly-identified females reached an abrupt asymptote just after the August 1, 1995, “deadline” for complete enumeration. The four females (W-AA, W-AB, W-AC and E-AA) first trapped within the first two weeks of August, 1995, were all found to be bearing pouch-young. As suggested earlier, classifying the four females in question as potential immigrants because they were first captured after the (somewhat) arbitrary August 1 “deadline”, can be faulted for being too rigid, and it is more biologically meaningful to classify them as residents, given that they were carrying pouch-young when they were first captured, and were therefore known to have given birth within the vicinity of the study grid during the 1995 breeding season. All of the 10 females first captured after the second week of August, 1995 (Fig. 4.17), could be classified as secondary peripheral females. From the preceding, I interpret Figure 4.17 as indicating that among the originally peripheral resident females under consideration, previously unmarked females were no less catchable than those that had already been marked.

Figure 4.18 shows the cumulative number of newly-identified males first caught in core traps on both grids. Comparing Figures 4.16 and 4.18, it is clear from the gentler slope prior to the asymptote, in the latter figure, that previously unmarked males were less catchable than previously unmarked females. There are at least two reasons why males may be less catchable. One reason is that males have larger home ranges (Green 1984) and spend less time in the vicinity of the trapping grid. The other reason may be that males spend more time looking for females and less time looking for food. Consistent with the suggestion that males are less catchable is the fact that the cumulative number of newly-identified males shown in Figure 4.18 did not appear to reach an asymptote until the end of winter, in 1995, six weeks after the August 1 "deadline" for complete enumeration. In addition, while the male first caught in the autumn of 1996 on the West grid (Fig. 4.18) was clearly a new "recruit" (weight = 1333 g, testis length = 10.9 mm; likely less than 1 year old, Chapter 5), the male first caught on the East grid at roughly the same time was an adult, that subsequent trapping suggested, may have been resident all along, with a range in the vicinity of that of female E-X (Fig. 4.10). The two males first caught at the end of summer, in 1997 (Fig. 4.18), on the West grid, were an adult, and a large (2000 g) subadult, respectively. While I cannot rule out the possibility that these two males were residents that had eluded detection, it had been more than 17 months since a newly-identified resident male had been caught in the core of the West grid, and it seems safe to conclude that the two males in question were in fact new "recruits". The two newly-identified males first trapped in the autumn and winter of 1997 (Fig. 4.18) were both clearly new "recruits", as they were both likely less than (or were just barely) one year old (weight < 1750 g, testis length < 11.0 mm; Chapter 5).

The cumulative number of newly-identified males first caught in peripheral traps reached an asymptote on both grids by the middle of spring, 1995 (Fig. 4.19), and then began gradually increasing again, from the autumn of 1996 onwards. The pattern just described is congruent with that described regarding males first trapped in core traps (Fig. 4.18). Peripheral resident males (Fig. 4.19) appear to have been less catchable than peripheral resident females (Fig. 4.17), given the gentler slope, and greater delay before asymptoting, in Figure 4.19 as compared to Figure 4.17. Also as discussed with respect to males first caught in core traps (Fig. 4.18), the gradual increase in the number of newly-identified peripheral males (Fig. 4.19) from the autumn of 1996 onwards, in part reflects the addition of new male “recruits” (such as the three yearling, and two older males, described in relation to Fig. 4.18), as is to be expected, given that dispersal in possums is known to be male-biased (Clout and Efford 1984; Efford 1991, 1998).

From the preceding discussion I conclude that I was successful in enumerating all but one of the females resident on both study grids, by the end of the second week of August, 1995, and that with the capture of female W-AD at the end of November (late spring), 1995, I had achieved my goal of completely enumerating all of the resident females on both grids. As I will explain in a later section, I feel confident in classifying W-AD as a resident, based on the analysis of microsatellite DNA. My conclusion regarding the complete enumeration of resident females assumes that there are no *un*catchable females. As the fourth step in evaluating the success of complete enumeration, I compared the results from live-trapping with those obtained using a second, independent, sampling methodology (Chapter 3), namely spotlighting.

Table 4.3 shows the number of times both marked and unmarked possums were detected in the core areas of both grids during spotlight transects. Table 4.4 shows the comparable data as regards possums detected on the periphery of both grids. Possums were seen during spotlight transects on 302 occasions, of which 30.1 % (91) were resights (individually-identifiable, Tables 4.1 and 4.2). The last occasion on which an unmarked animal was seen in the core (Table 4.3) of the West grid, prior to the August 1, 1995, “deadline” for complete enumeration, was in early June, and the last occasion on which an unmarked animal was seen in the core of the East grid, prior to August 1, 1995, was in late February. These results are clearly congruent with those based on live-trapping (Figs. 4.16 and 4.18), that indicate that most of the animals present in the core areas of both grids had been captured and marked prior to August 1, 1995. Unmarked animals continued to be detected on the periphery of both grids (Table 4.4) up to the time of the August 1, 1995, removals. This too is in accordance with the live-trapping results (Figs. 4.17 and 4.19), wherein unmarked peripheral residents continued to be caught during the first few weeks of August, 1995. Seven of the unmarked animals detected on the periphery of the grids during spotlighting, prior to August 1, 1995, were successfully captured (Table 4.4). Six of the seven animals in question were first captured by darting, including: four peripheral resident females on the East grid (E-F, E-N, E-W and E-X; Fig. 4.10); one peripheral resident female on the West grid (W-I, Fig. 4.4); and one male. All six animals first captured by darting were eventually, and then repeatedly thereafter, caught in traps.

From August 1, 1995, until the end of the study in July, 1997, I detected possums in the core areas of the study grids during spotlight transects on 68 occasions, of which 3 occasions (4 %) involved unmarked animals (Table 4.3). I detected possums on the periphery of the grids, over the same period, on 90 occasions, of which 10 occasions (11 %) involved unmarked animals. I was able to capture the unmarked animals detected during spotlighting on 1 of the 3 occasions on which they were seen in the core (Table 4.3), and 2 of the 10 occasions on which they were seen on the periphery (Table 4.4).

Although I was unsuccessful at capturing several of the unmarked animals detected during spotlighting, at the time at they were first seen, I feel confident that most of the individuals in question were eventually trapped. The locations at which unmarked animals were detected, but not captured, during spotlight transects conducted after August 1, 1995, are all indicated on the appropriate range maps (Figs. 4.4-15) by lowercase letters enclosed in a diamond symbol. The sequence of letters (a, b, c, etc…) follows the sequence of occurrences. For example, W-a (Fig. 4.6) indicates the first occasion (after August 1, 1995) on which an unmarked animal was seen on the West grid, which was in late February, 1996. Secondary peripheral female W-AG (Fig 4.7) was first caught at this same location about 2 1/2 months later, in early May. W-b (Fig. 4.7) indicates the location at which a notably smaller unmarked animal was seen in early April, 1996. A small (1770 g, Chapter 5), adult male was first trapped at an adjacent trap in late April, who was thereafter repeatedly trapped in that vicinity. The arithmetic mean center (AMC) of the trapping range (based on N = 17 records) occupied by the male in question was 24.7 m northeast of the location of W-b, shown in Figure 4.7. Similarly, W-c (Fig. 4.8) was a notably smaller animal seen in late February, 1997, and a small (1717 g, Chapter 5), adult male was first trapped at an adjacent trap in late March, with an AMC (N = 12) 50.2 m northeast of the location of W-c, shown in Figure 4.8. W-d (Fig. 4.9) signifies a larger animal seen in late March, 1997, and a large (2525 g, Chapter 5) male was first trapped in an adjacent trap in early June, with an AMC (N = 3) 22.0 m northwest of the location of W-d, shown in Figure 4.9. Larger, unmarked animals were seen at locations W-e and W-f (Fig. 4.9) in May and July, 1997, respectively. No new animals were trapped in the vicinity of these two locations in the remaining three months of the study, although new animals continued to be trapped elsewhere on the periphery of the West grid (Figs. 4.17 and 4.19).

The first occasion (E-a, Fig. 4.13), after August 1, 1995, on which an unmarked animal was seen during spotlighting on the East grid, was in late May, 1996. Secondary peripheral female E-AE (Fig. 4.13) was first caught at this same location about a month later, in late June, and was re-trapped at this location over the next several months. The next occasion on which an unmarked animal was seen during spotlighting on the East grid (E-b, Fig. 4.15), involved a notably smaller animal seen in the core of the grid in mid-June, 1997. Only four days later, a small (1700 g, Chapter 5), subadult male was trapped at an adjacent trap (shown by the male symbol in Fig. 4.15). No unmarked animals had been seen during spotlight transects in the core of the East grid since February, 1995 (26 months earlier, Table 4.3), and no new animals had been trapped in the core of the East grid since mid-April, 1996 (14 months earlier, Figs. 4.16 and 4.18). Consequently, I am completely certain that the subadult male that was trapped was the same individual that was seen during spotlighting four days earlier. Larger, unmarked animals were seen at locations E-c and E-d (Fig. 4.15) in June and July, 1997, respectively. No new animals were trapped in the vicinity of these two locations in the remaining two months of the study, although new animals continued to be trapped elsewhere on the periphery of the East grid (Figs. 4.17 and 4.19).

From my review of the circumstances surrounding sightings of unmarked animals, I am confident that the unmarked animals detected during spotlighting transects were, on all but the last four occasions, eventually trapped. I infer from this that the unmarked animals detected on the periphery of both grids during spotlighting in the last three months of the study (occasions W-e, W-f, E-c and E-d; Table 4.4) would also have eventually been trapped, if the study had continued. Considering the ever-increasing number of newly-identified males captured on the periphery of the grids (Fig. 4.19), as compared to the small number of newly-identified females (Fig. 4.17), I conclude that the unmarked animals detected during spotlighting in the last three months of the study were most likely males.

Based on my evaluation of the evidence available from spotlighting, I conclude that there were no *un*catchable animals that would not have eventually been live-trapped, given that: 1) all of the individuals that were initially captured by darting were eventually trapped; 2) the large majority of animals seen during spotlighting were in fact marked and had, therefore, already been trapped (Tables 4.3 and 4.4); and 3) the fact that for most occasions on which an unmarked animal was seen during spotlighting, I was able to identify an individual of the same relative size, trapped in the same vicinity, a short time later.

Determining whether there were *un*catchable animals in the population was the fourth step in evaluating the success of complete enumeration. The final step involves using all available information to draw inferences regarding the potential origin of newly-identified individuals. All of the supplemental information, which I will describe later, reinforces the following two conclusions: 1) I was entirely successful in completely enumerating all adult and subadult possums present in the core areas of both study grids; and 2) I was successful in completely enumerating all adult and subadult possums present on the periphery of both grids over most of the duration of the study.

In addition to completely enumerating all adults and subadults, all of the offspring of resident females must also be accounted for, as a necessary precondition for the unambiguous identification of immigrants (Chapter 3). Including the females with pouch-young initially caught in the first two weeks of August (W-AA, W-AB and W-AC; Fig. 4.5), and female W-AD (Fig. 4.6), there were 26 adult resident females known to be alive and "present" (= MNA-All) on the West grid, immediately following the August 1, 1995, removals. In 21 of the 26 cases in question I was able to either tag the female's young while it was still in the pouch (18 cases), or I was certain that her young had died (3 cases). In 2 of the 3 cases where I was certain the young had died, the mother was found with no pouch-young, and was no longer nursing, 141 and 166 days, respectively, after the young had been born. Evidence presented in Chapter 5 indicates that surviving young never leave the pouch before 175 days, and are never completely weaned before 200 days of age. In the third case where I was certain the young had died, the young was found dead and rotting in the mother's pouch (the mother being apparently still healthy). There were five cases on the West grid, in 1995, where I could not account for the whereabouts of the offspring of a resident female. Females W-B and W-AD (Figs 4.4 and 4.6) were not caught during the 1995 breeding season and may or may not have given birth and produced a surviving young. Females W-I and W-O (Fig. 4.4) did produce young, but I was unable to recapture these females prior to the time at which their young may have weaned. Female W-U was resighted with a young on her back in late October (at the position indicated in Fig. 4.6), but I was unable to catch her. I collected tissue samples from 4 of the 5 females in question (the exception being W-U, Table 4.10), and was thus able to determine if any potential immigrants captured after August 1, 1995, were in fact the untagged offspring of the females in question, based on the analysis of microsatellite DNA.

There were 23 adult females known to be alive (= MNA-All) on the West grid immediately after the August 1, 1996, removals. Among the 23 females in question, one did not breed in 1996 (W-S, Fig. 4.7), and another died before its young could have weaned (W-K, Fig. 4.7). In 20 of the 21 remaining cases I was successful in tagging the young in the pouch. In the one case where the young was not tagged, the mother (W-AD, Fig. 4.7) was found with no young, and was no longer nursing, 115 days after the birth of the young. I conclude that there were no unaccounted for offspring of resident females on the West grid in 1996.

Including female E-AA (Fig. 4.11), who was found to possess a pouch-young when initially caught in the first two weeks of August, there were 22 adult resident females known to be alive (= MNA-All) on the East grid, immediately following the August 1, 1995, removals. Two of the females in question died before their young could have weaned (E-U and E-Y, Fig. 4.11). In three more cases I was certain that the young had died. In 2 of the 3 cases where I was certain the young had died, the mother was found with no pouch-young, and was no longer nursing, 135 and 143 days, respectively, after the young had been born. In the third case, the mother had ejected the pouch-young when she was trapped and it was found dead on the floor of the trap. In 15 of the remaining 17 cases I successfully tagged the young while it was still in the pouch. In two cases, involving females E-K and E-M (Fig. 4.11), I could not account for the whereabouts of the offspring, but I had collected tissue samples from the two mothers in question (Table 4.11), and was thus able to evaluate whether any “potential immigrants” were in fact the untagged offspring of these two females, based on the analysis of microsatellite DNA.

There were 19 adult females known to be alive (= MNA-All) on the East grid immediately after the August 1, 1996, removals. Three of the females in question died before their young could have weaned (E-A, E-N and E-O; Fig. 4.14). In three more cases I was certain that the young had died because the mother was found with no pouch-young, and was no longer nursing, 102, 118, and 162 days, respectively, after the young had been born. I was successful in tagging the young in the pouch in all of the remaining 13 cases. I conclude that there were no unaccounted for offspring of resident females on the East grid in 1996.

From the preceding discussion I feel confident in stating that there was only one case (involving female W-U, Fig. 4.6), in a total of 83 cases (1.2 %), where originally peripheral resident females were known to have given birth (and were still alive on August 1, in either 1995, or 1996, or both), in which the offspring of a resident female could have been misidentified as being an immigrant, if it was later recaptured. In addition, I was not at a complete loss as regards the untagged offspring of female W-U, because I at least knew its (approximate) age, given that it was already riding on its mother's back (Chapter 5) when it was resighted in late October, 1995. I have not discussed the enumeration of young during the 1997 breeding season because the study ended at the end of July, 1997, well before any of the young produced in that year would have begun to emerge from the pouch (Chapter 5).

I have examined the evidence for complete enumeration in great detail because I wish it to be understood that when I present the results of the experiment, what I am discussing are (as nearly as possible) total censuses of the female population. Consequently, I have (or am as nearly as possible to having) the capacity to distinguish "true immigrants", without ambiguity (Chapter 3).

Adequacy of location data from radio telemetry

I radio-collared 1 subadult, and 78 adult (37 West, 41 East) females, over the course of the study. Females were tracked to their dens on 3,109 occasions. Deciding whether a female has settled in the core of one of the two study grids, and should thereby be classified as a "true immigrant", requires an accurate means of assessing her location. The adequacy with which radio-tracking data can be said to describe the extent on an animal's movements can be gauged by plotting the number of radio-fixes against some measure of the animal's movements. The point at which the plot reaches an asymptote provides an indication of the minimum number of fixes required to adequately describe the animal's movements (Lindenmayer et al. 1996). Figure 4.22 plots the number of fixes recorded for a given female against the total number of dens used by that female. There was a significant correlation between the total number of fixes and total number of dens used, on both the West grid ($N = 38$, Spearman's $r = 0.46$, $t = 3.15$, $p = 0.0033$) and the East grid ($N = 41$, Spearman's $r = 0.75$, $t = 6.99$, $p < 0.0001$). I conclude that there was no minimum number of fixes, below the maximum of 79 recorded for females on both grids (Fig. 4.22), that was adequate to describe the total number of dens used by a given female.

If a female uses ever more dens that are all within a circumscribed area, this will have no effect on the estimated size of her denning range, which was defined previously as being the minimum convex polygon connecting all dens used by an individual. Figure 4.23 plots the number of radio-fixes recorded for a given female against the female's total denning range length (the maximum distance between any two dens used by the same female). There was no significant correlation between the total number of fixes and the total denning range length of females on the West grid (N = 38, Spearman's r = 0.25, t = 1.54, p = 0.1327), but there was one on the East grid (N = 41, Spearman's r = 0.68, t = 5.84, p < 0.0001). On the West grid, as few as 8-10 fixes were as sufficient as up to 79 fixes, in order to adequately describe a female's denning range length (Fig. 4.23). The discrepancy between the grids derives in part from two differences in the data sets. On the East grid there were a number of females (5) for which there were very few fixes (< 8; Fig. 4.23). In addition, five of the females on the East grid (E-Q, E-R, E-S, E-T and E-AB; Figs. 4.10-4.15), that appeared to use a large number of dens, and had very large denning range lengths, had dens in trees growing on the steep sides of the Plateau on which the grids were located. These den trees on the side of the Plateau were significantly (t = 3.80, df = 187 p = 0.0002) taller (N = 41, mean height in m +/- S.E. = 27.5 +/- 1.1) than den trees elsewhere on the East grid (N = 148, 23.3 +/- 0.5). The rougher terrain and taller trees meant that it generally took much longer to locate the five females in question, and there was likely a correspondingly greater rate of misidentification of den trees, which may have inflated the estimated number of dens and total denning range lengths occupied by these females. I conclude that the number of radio-fixes recorded was sufficient to accurately determine the location of a female's denning range in all cases on the West grid, and in most cases on the East grid.

A very few fixes may be required to determine a female's general position if one den is used much more frequently than all others. The maximum number of dens used by any given female was 15, in which case, it is possible to establish the pattern of den tree preferences for all females for which there was a minimum of 15 fixes. If den trees were selected at random by a female, the proportion of times she was found in a given den would be equal across all dens. Figure 4.24 plots the mean proportion of fixes tracked to each of the array of dens used by a given female. Females on both the West grid and the East grid were located in their most preferred den about 50 % of the time. Consequently, there was a greater than 95 % probability that a female would be found in her principal den at least once, even if she was only located five times (probability = $1 - 0.5^n$, where n is the number of fixes). Only two females (E-dA, Fig. 4.10; and E-AJ, Fig. 4.15), from among the 79 (3 %) I radio-collared, were located fewer than five times.

I conclude that the number of radio-fixes recorded was sufficient to have included a female's principal den in all but these two cases on the East grid. In the various range maps used to describe the position of each female (Figs. 4.4-15), I have used "bubble plots" to indicate the frequency with which a female was located at a given den, and have drawn polygons to indicate each female's denning range.

Collection of tissue samples and analysis of microsatellite DNA

From October, 1995, onwards, I collected tissue samples from all adult and subadult possums captured on both study grids. Tissue samples were collected from pouch-young if they were judged to be large enough to be not too adversely affected. For various reasons, tissue samples were available from a small number of animals that had died or been removed before October, 1995. Tissue samples were collected from a total of 176 individuals (97 West, 79 East). In 27 cases (17 West, 10 East), samples were simultaneously collected from mothers and their dependent (known) young.

Tissue samples were generally obtained by cutting a small notch (< 5 mm on a side) in the distal part of an animal's ear. All samples were stored in 100 % ethanol (analytic reagent rate quality), and were then forwarded to Dr Andrea Taylor (Macquarie University, Sydney, Australia), for genetic analysis. Possums at the Paddys Land site were successfully typed at 6 microsatellite loci (Table 4.9), which are described in detail in Taylor and Cooper (1998).

I calculated allele frequencies, linkage disequilibrium among loci, allele frequency differences between grids, F_{ST}, Rho_{ST}, and deviations from Hardy-Weinberg equilibrium (HWE), using program GENEPOP, Version 3.1c (Raymond and Rousset 1995). I used Fisher's combined probabilities test (Sokal and Rohlf 1995, p. 794) to obtain a global probability value over all loci, when comparing allele frequencies between grids (Paetkau et al. 1995), and when testing deviations from HWE (Piertney et al. 1998). Mean number of alleles per locus, mean proportion of loci typed, and the estimated frequency of null alleles, were all calculated using program CERVUS, Version 1.0 (Marshall 1998). Results of tests regarding linkage disequilibrium and deviations from HWE are presented in Appendix 1.

I conducted parentage analysis using both program KINSHIP, Version 1.2 (Goodnight and Queller 1998), and program CERVUS, Version 1.0 (Marshall 1998). These programs differ in: 1) their sensitivity to deviations from Hardy-Weinberg equilibrium; and 2) their treatment of typing errors. Data from the 27 cases in which tissue samples were simultaneously collected from both mother and young were used to compare the two programs as to the accuracy with which the most likely mother chosen by each program correctly identified the true mother (Appendix 1). I used iterated runs to derive a typing error rate for program CERVUS that produced slightly more accurate results than program KINSHIP. When I used the method of estimating typing error rates recommended by the authors (Marshall et al. 1998) of program CERVUS, the program performed much more poorly than program KINSHIP. Since there is disagreement in the literature about the most appropriate method of treating typing errors (SanCristobal and Chevalet 1997, Marshall et al. 1998; see also Appendix 1), I report the most likely mother identified by both program CERVUS, using the iterated (empirically more accurate) error rate, and program KINSHIP, when considering parentage among adult (and subadult) females, of unknown relatedness.

To identify putative parent-offspring relationships among adult (and subadult) females, each adult (and subadult) female for which microsatellite typing data were available was compared against every other typed female on the same grid, and the candidate female with the highest likelihood score was judged to be the most likely "mother" of the female under consideration (SanCristobal and Chevalet 1997). Obviously, when comparing among adult females of unknown age, an individual identified as the most likely "mother", may in fact be the daughter of the female under consideration. Putative mother-daughter pairs were classified as being adjacent if: 1) their ranges overlapped; or 2) no other female's range was known to have separated the ranges of the putative mother and daughter.

RESULTS

Female immigration following removals

Figure 4.4 shows the location of all females captured on the West grid prior to August 1, 1995. On August 1, 1995, I removed the 10 center-most females from the core of the grid (Fig. 4.5). All 10 females removed on August 1 had pouch-young, indicating that the core of the West grid represented suitable habitat for at least 10 reproductively-active females.

Figure 4.10 shows the location of all females captured on the East grid prior to August 1, 1995. Three of the peripheral resident females shown in Figure 4.10 (E-dA, E-dB and E-dC) died during June and July. All three were known to have given birth earlier in the year. On August 1, 1995, I removed the nine center-most females from the core of the grid (Fig. 4.11). All nine females removed on August 1 had pouch-young, indicating that the core of the East grid represented suitable habitat for at least nine reproductively-active females.

Over the course of the year following the August 1, 1995, removals, only one newly-identified female (W-AE, Figs. 4.6 and 4.7) entered and settled in the core of one of the two study grids (Figs. 4.7 and 4.13), and thereby qualified as a “true immigrant”. Also over the course of the year, two originally peripheral resident females on each grid (W-J and W-Q, Fig. 4.7; E-D and E-P, Fig. 4.13), either largely or completely shifted their denning ranges into the core areas of the grids, consistent with the vacuum effect (see below).

On August 1, 1996, I removed W-J, W-Q and W-AE from the core of the West grid (Figs. 4.7 and 4.8), and E-D and E-P from the core of the East grid (Figs. 4.13 and 4.14), in order to recreate conditions on the grids similar to those existing on August 1, 1995 (Figs. 4.5 and 4.11), and thereby temporally replicate the experiment. No newly-identified females entered and settled in the core of either of the two study grids over the course of the year from August 1, 1996, until the end of the study in late July, 1997 (Figs. 4.9 and 4.15). Consequently, there was only one “true immigrant” female (W-AE, Figs. 4.6 and 4.7) that entered and settled in the core of one of the two study grids, over the course of the two years following the August 1, 1995, removal of 19 core resident females.

W-AE was first caught in early February, 1996 (Fig. 4.6). She was a small (1833 g, Chapter 5), subadult, that was between 1 and 2 years (circa 22 months) old when first captured (as determined from cementum annuli, Chapter 5). W-AE was judged to have settled in the core of the grid because she was present for more than three months (see Methods), but she did not breed during the 1996 breeding season, and was still a subadult on August 1, 1996. Given her age, W-AE could not have been the untagged offspring of female W-U (Fig. 4.6), described earlier. Parentage analysis using microsatellite DNA (Table 4.10) indicated that W-AE was almost certainly ($p < 0.01$, Appendix 1) the daughter of secondary peripheral female W-AG (Fig. 4.7).

Given that W-AE was the daughter of W-AG, she clearly met Lidicker and Stenseth’s (1992, p. 24) *minimum* criterion for “true” dispersal, by moving across at least one home range, occupied by peripheral resident female W-W (Fig. 4.7). Moreover, since W-AE was the only “true immigrant” female, and all known daughters settled adjacent to their mothers (see below), it can also be said that W-AE's movement across one home range represented the *maximum* female dispersal distance recorded in this study.

The vacuum effect and breeding dispersal

Over the course of the year following the initial August 1, 1995, removal of the 19 core resident females, four originally peripheral resident females (W-J and W-Q, Fig. 4.7; E-D and E-P, Fig. 4.13) shifted the centers of their denning ranges into the core areas of the grids, and six more peripheral residents each expanded part of their range into the core (W-C, W-P and W-S, Fig. 4.7; E-F, E-L and E-S, Fig. 4.13). In the year following the August 1, 1996, removals (involving: W-J, W-Q and W-AE, Fig. 4.7; and E-D and E-P, Fig. 4.13), one peripheral resident female further expanded her denning range into the core (W-C, Fig. 4.9), and six other females, that had not previously done so, each expanded part of their range into the core (W-E, W-P1, W-W and W-AC, Fig. 4.9; E-B and E-W, Fig. 4.15). In 36 of 48 cases (75 %), the core den sites occupied by the originally peripheral females, had been previously occupied by one of the 19 core resident females, removed on August 1, 1995.

In nine cases, the death or removal of an originally peripheral resident female was followed by the occupation of all or part of her range, by either an adjacent, originally peripheral resident female (W-J vs. W-K, Figs. 4.4-7; E-I vs. E-H, Figs. 4.10-15; E-N vs. E-M, Figs. 4.13-14; E-Y vs. E-W, Figs. 4.10-13), or a secondary peripheral female (W-K vs. W-AM, Figs. 4.8-9; E-K vs. E-AD, Figs. 4.11-13; E-L vs. E-AE, Figs. 4.13-15; E-O vs. E-AJ, Figs. 4.13-15; E-P vs. E-AC, Figs. 4.10-15). In 18 of 26 cases (69 %), the dens used by the "new" female, had been previously occupied by the female that had died or been removed.

As described in the introduction (see also Chapter 3), in the absence of rigorous protocols, apparent cases of breeding dispersal by reproductively-active adult females may in fact be instances of range expansion involving the usurpation of all or part of a neighbour's territory, i.e., the vacuum effect. I conclude that there is abundant evidence of the vacuum effect given the results presented in the previous two paragraphs. This does not mean that the possibility of breeding dispersal is precluded *per se*. By my protocols, if any of the newly-identified adult females first caught after the August 1, 1995, removals (see Figs. 4.16 and 4.17), had entered and settled in the core of either of the two study grids, she would have been classified as a "true immigrant", and this would represent unambiguous evidence of breeding dispersal. Four adult females first identified after August 1, 1995 (W-AC, W-AD, W-AF and W-AK; Figs. 4.6-9 and 4.16-7), were captured in the core of the West grid, but as I will discuss, none of them settled in the core. Consequently, there is no evidence of breeding dispersal in response to the experimental removals.

Clout and Efford (1984) argued that movements by possums in excess of 2 km can be unambiguously classified as dispersal. None of the 78 radio-collared adult females in this study made movements of anywhere near this magnitude. The maximum recorded denning range length (the maximum distance between any two dens used by the same female) was 550 m (Fig. 4.23), which is comparable to the figure of 500 m cited by Clout and Efford (1984) as regards normal range lengths among possums in continuously forested habitats. The frequency of long-distance dispersal is often difficult to determine because it cannot be established whether animals that have disappeared have either died or emigrated (Stenseth and Lidicker 1992, Koenig et al. 1996, Ims and Yoccoz 1997). I can say with certainty that none of the 78 radio-collared adult females in this study dispersed because none of the radios were lost, and I was able to determine the fate (alive or dead) of all of the radio-collared females, up to the end of the study (Chapter 6). I conclude that there is no evidence of breeding dispersal, based on Clout and Efford's (1984) criterion.

Potential immigrants captured in the core

Newly-identified females first caught anytime after the August 1, 1995, removals, represented potential immigrants (see Methods). In addition to the one "true immigrant", W-AE (Figs. 4.6 and 4.7), there were four potential immigrants, that were either originally (W-AD, W-AF and W-AK; Fig. 4.16) or eventually (W-AC, Fig. 4.9) captured in the core of the West grid. As noted above, these four females were all adults. In addition to the evidence against breeding dispersal by adult females (Efford 1991, see above), I will present other details regarding each of these four females that reinforces my conclusion that W-AE was the only "true immigrant". None of the 10 potential immigrants caught on the East grid (Figs. 4.16 and 4.17), were ever captured in the core of that grid (Figs. 4.10-4.15).

W-AC was initially captured during the first two weeks of August, 1995, after the August 1 "deadline" for the complete enumeration of resident females. I decided to classify W-AC as a peripheral resident (along with W-AA and W-AB, Figs. 4.5 and 4.17), given that she was found to be bearing a pouch-young, and had therefore been both, present on the grid, and reproductively-active during the 1995 breeding season (see Methods). Results from one of the two programs used to evaluate parentage from microsatellite DNA (Table 4.10), suggested that W-AC was most likely the mother or daughter of the adjacent peripheral resident female, W-I (Fig. 4.5), apparently confirming W-AC's status as an originally peripheral resident female. However, the DNA data cannot be taken as being conclusive, given the disagreement between the two programs (Table 4.10). If I had rigidly stuck to the August 1 definition of who is, or is not, a resident, W-AC would be classified as a potential immigrant, and the expansion of her denning range into the core (Fig. 4.9) might then constitute "true immigration". However, W-AC was only tracked to the core den site shown in Figure 4.9 on five occasions, and then returned to her most frequently used den (as shown in Fig. 4.7), which was located in the peripheral buffer strip surrounding the core of the grid. W-AC was found dead in late June, 1997, near the latter location. The arithmetic mean center of W-AC's denning range during the 1997 breeding season was located within the peripheral buffer strip, 26.8 m to the southwest of the innermost den used by female W-AM (Fig. 4.9). I conclude that W-AC's movements (Figs. 4.5, and 4.7-9) cannot be classified as "true immigration", under either interpretation as to her status.

W-AD was initially captured in late November, 1995, at a core trap location (Figs. 4.6 and 4.16). When first trapped, W-AD had an enlarged pouch, and had clearly given birth on one or more occasions (Bolliger and Carrodus 1938, 1940), but she was not nursing and did not have a pouch-young. She was fitted with a radio-collar, and was thereafter repeatedly tracked to just two den sites, both of which were located in the peripheral buffer strip (Fig. 4.7). According to my definitions (see Methods), W-AD represented a potential immigrant that had settled in the peripheral buffer strip, and was therefore not a "true immigrant". Parentage analysis using microsatellite DNA (Table 4.10) indicated that W-AD was almost certainly ($p < 0.01$, Appendix 1) the mother or daughter of the adjacent peripheral resident female, W-P (Fig. 4.7). Consequently, I conclude that W-AD was most likely a peripheral resident female that had eluded capture until November, 1995. As previously discussed (see Methods), I am confident that, with the capture of female W-AD, I had achieved my goal of completely enumerating all of the resident females on both grids.

W-AF was initially captured in late April, 1996, at a core trap location (Figs. 4.7 and 4.16). She was re-trapped on two occasions in the first two weeks of May, and was then never seen again.

Similarly, W-AK was initially captured in late March, 1997, at a core trap location (Figs. 4.9 and 4.16), was re-trapped the next night, and was then never seen again. Both females were adults with enlarged pouches, that had clearly given birth on one or more occasions (Bolliger and Carrodus 1938, 1940), but neither was found to be carrying a pouch-young, either on the first or last occasion on which she was captured. According to my definitions (see Methods), both W-AF and W-AK represented potential immigrants that were transients on the grid, as they did not have pouch-young and were present less than three months. No putative mother or daughter of W-AF was found among those females on the West grid for which DNA typing data were available (Table 4.10). Results from one of the two programs used to evaluate parentage from microsatellite DNA (Table 4.10), suggested that W-AK may have been the mother or daughter of female W-K (Fig. 4.8). However, given that the number of loci compared was low (Table 4.10), that there was a "mismatch" at one of the few loci compared, and that the calculated likelihood was low, I conclude that the putative relationship is almost certainly spurious (Appendix 1).

While it is possible that both W-AF and W-AK stayed on the grid following their initial capture and thereafter managed to elude subsequent detection, I conclude that this is highly improbable. Arguably, W-AF and W-AK may have eluded subsequent detection because they became trap-averse. However, the three radio-collared females (out of the 77 considered, Fig. 4.21; see Methods) that I suspect had, in fact, become trap-averse, were each only trapped on a single occasion, suggesting that trap-aversion was a response to the stress of initial capture (Humphreys et al. 1984, Harlow et al. 1992). W-AF and W-AK, on the other hand, were each trapped more than once. W-AF was trapped on 3 of the 4 nights on which traps were set, during the period she was known to be present, and W-AK was trapped on 2 of the 3 nights on which traps were set, during the period she was known to be present. Even if W-AF and W-AK had become trap-averse, both had unique sets of coloured ear-tags, and would have been recognized if resighted during spotlighting (Tables 4.1 and 4.3), which they never were.

Adverse effects of capture and handling and the measured rate of immigration

It is possible that the two transient females discussed in the previous section, W-AF and W-AK (Figs. 4.7, 4.9 and 4.16), did not settle on the West grid because of an adverse reaction to the stress of capture and handling (Chapter 3). At the time she was first caught, W-AF only weighed 1750 g, which is exceptionally low for an adult female (Chapter 5). In addition, W-AF demonstrated rapid weight loss in between the second to last, and last occasion on which she was trapped (when she weighed only 1600 g, Chapter 5), and was "weak and wobbly" upon release, when last seen. Females seen to be "weak and wobbly" upon release had a lower probability of survival (Chapter 6), and W-AF may have disappeared because she was dead. W-AK, on the other hand, was in good condition, and of above average weight (2250 g, Chapter 5), and it seems very unlikely that she disappeared because she was dead (Chapter 6). While W-AF was already in poor condition when she was first trapped, it is possible she may have died *because* she was repeatedly trapped and handled (Chapter 6). Moreover, while it seems unlikely, given that she was trapped more than once, it is at least conceivable that the stress of being captured and handled may have "driven off" female W-AK.

If the stress of capture and handling inhibited either W-AF or W-AK from settling on the West grid, this might cause me to *under*estimate the rate of female immigration. However, even if W-AF and W-AK had settled on the grid, there is no guarantee that they would have settled in the core, and if they settled on the periphery, there would be no effect on the estimated rate of female immigration. Notably, W-AF (Fig. 4.7) and W-AK (Fig. 4.9) both appeared in evident gaps in the otherwise contiguous ring of peripheral resident females. Given that they were adults, and that there was abundant evidence of the vacuum effect, and no evidence of breeding dispersal, I conclude that, W-AF and W-AK were most likely residents from just outside the area sampled by the grid, in the process of making "exploratory movements" (Lidicker and Stenseth 1992) into the peripheral buffer strip.

While the eventual fate of W-AF and W-AK was uncertain, one potential immigrant, W-AI (Fig. 4.7), was known to have died as a *direct* result of capture and handling, and this also could have caused me to *under*estimate the rate of female immigration. However, I am confident that W-AI would not have entered and settled in the core of the grid, and thereby become a "true immigrant", if she had lived. W-AI died during her initial capture, in late July, 1996 (Fig. 4.17). She was a very large (2575 g, Chapter 5), very old (aged 14 years, as determined from cementum annuli; Chapter 5), adult female that was carrying a large pouch-young. No putative mother or daughter of W-AI was found among those females on the West grid for which DNA typing data were available (Table 4.10). However, a small (1900 g, Chapter 5), adult male, first caught in October, 1996, at a trap site adjacent to where W-AI had been captured, was almost certainly

($p < 0.01$, Appendix 1) the son of W-AI. Based on her age, the presence of a pouch-young, and the location of her putative son, W-AI was assuredly a resident from just outside the area sampled by the grid.

In 1997, I found the remains of one unidentifiable young of the year (< 1 year old, as determined from cementum annuli; Chapter 5), on the East grid, in late summer (indicated by the "?" enclosed in a rectangle in Fig. 4.14), and another, on the West grid, in mid-autumn (Fig. 4.9). In both cases, I was unable to find the animal's ears or its abdomen, so I could not identify the individual, or its sex. There were no newly-identified young of the year females captured on either grid following the 1996 breeding season. Consequently, if the unidentifiable remains were those of potential immigrant females, these individuals did not die *because* of capture and handling. Since there were at least 17 resident offspring that disappeared following weaning in the spring of 1996 (Chapter 5), and the measured rate of female immigration was so low, I conclude that the remains in question were most likely those of either, resident offspring, or male immigrants.

I conclude that adverse effects of capture and handling had the potential to disrupt female immigration in only three cases, and as all three cases involved older adult females, it is unlikely that any of the three were in fact in the process of dispersing. Consequently, there is little reason for supposing that the rate of female immigration was *under*estimated, as a result of adverse effects of capture and handling, on potential immigrants (Chapter 3).

As discussed in Chapter 3 (see Fig. 3.2), adverse effects of capture and handling on resident reproduction or survival has the potential to cause immigration to be *over*estimated, if local recruitment or range expansion by adults normally preempts settlement by immigrants. Evidence presented in Chapter 5 suggests that the survival of the pouch-young of resident females may have been adversely affected by repeated capture and handling, and evidence presented in Chapter 6 indicates that the survival of the resident females themselves was almost certainly adversely affected by repeated capture and handling. Consequently, there are good reasons for supposing that the rate of female immigration was, if anything, *over*estimated.

In Chapter 6, I report that, over the course of the study, there may have been as many as 13 deaths among the 78 radio-collared adult females, that appeared to be either directly (2) of indirectly (11) associated with capture and handling. Such "unnatural" deaths are analogous to removals. Taking these 13 “unintentional” removals together with the 19 intentional removals, it could be argued that I created a total of 32 adult home range vacancies.

Considering *both* core and peripheral areas of both grids, I captured only two newly-identified subadult females, over the course of the two years following the August 1, 1995, removals. Other subadult females were captured, but these were all identifiable because they had been tagged while still with their mothers. One of the two newly-identified subadult females was the one “true immigrant” female, W-AE. The other was E-AH (Figs. 4.14, 4.15 and 4.17). E-AH was first trapped in September, 1996 (Fig. 4.17). When first captured (Fig. 4.14), she was a very small (1100 g, Chapter 5), subadult. She was later recaptured in mid-May, 1997, at which time she was found to be bearing a pouch-young. E-AH was fitted with a radio-collar on the latter occasion, and was thereafter tracked to a total of two den sites, both of which were also used by the adjacent adult female, E-AE (Figs. 4.13-15). Parentage analysis using microsatellite DNA (Table 4.11) indicated that E-AH was most probably ($p < 0.05$, Appendix 1) the daughter of E-AE. I conclude that female E-AH was not a disperser, but rather a philopatric female that settled and bred within her mother’s home range.

Assuming that breeding dispersal does not exist (or very rarely occurs; Efford 1991, see above), “true” immigration must only involve subadult females (as a consequence of natal dispersal). Again considering *both* core and peripheral areas of both grids, there may have been as many as 32 adult home range vacancies created as direct or indirect consequence of the experimental protocols. At the same time, only one subadult female, W-AE (Fig. 4.7), was known to have dispersed away from her mother’s (W-AG, Fig. 4.7) home range, and immigrated into one of these 32 adult home range vacancies. Consequently, I conclude that the estimated rate of one female immigrant per 19 vacancies every two years, given earlier, is almost certainly an *over*estimate of the importance of female immigration in replacing losses among breeding females.

Locations of known mothers and daughters

There were a total of eight cases where daughters, first tagged while still with their mothers, were later recaptured, by themselves. In every case the daughters were recaptured at a location adjacent to their mother’s denning range (Figs. 4.4-15). In 2 of the 8 cases (involving W-P1 and W-L2, Figs. 4.7 and 4.9), the daughter, in turn, was known to have given birth. Female W-P1 was fitted with a radio-collar, and she and her mother, W-P, were generally found to be together in the same den tree, while both of them bore pouch-young, both in 1996 (Fig. 4.7) and in 1997 (Fig. 4.9). Female W-L2 was recaptured at a location adjacent to her mother's (W-L) denning range (Fig. 4.9), on the last day of the study, in July, 1997, and was found to be bearing a pouch-young.

Locations of mothers and daughters identified using microsatellite DNA

Putative mother-daughter relationships among the adult (and subadult) females on each grid, based on microsatellite DNA, are reported in Tables 4.10 and 4.11. Putative mother-daughter pairs judged to have adjacent ranges are shown in bold letters in Tables 4.10 and 4.11 for comparison with the appropriate range maps (Figs 4.4-15).

If females generally settle adjacent to their mothers, putative mother-daughter relationships involving adjacent females are most likely true mother-daughter relationships while those involving non-adjacent females are most likely "false positives". Parentage analysis may generate "false positives" when the true parent has been falsely excluded, as a result of typing errors, or when individuals are compared at only a few loci and the probability of exclusion is correspondingly low (Marshall et al. 1998). In both cases, likelihood scores associated with "false positives" will generally be lower than likelihood scores identifying true parent-offspring relationships. It follows that likelihood scores among adjacent putative mother-daughter pairs ought to be substantially greater than among non-adjacent putative mother-daughter pairs (Ishibashi et al. 1997). I conducted a series of t-tests comparing likelihood scores between adjacent and non-adjacent putative mother-daughter pairs. If a given relationship was reciprocal (e.g., A was the most likely mother/daughter of B, and B was the most likely mother/daughter of A), the likelihood score was only included once in the statistical comparisons. In addition, the lone immigrant female, W-AE, was not included, as her status (as an immigrant) was already established. Adjacent putative mother-daughter pairs had significantly higher likelihood scores than non-adjacent pairs, on both grids, and regardless of which program (KINSHIP or CERVUS) was used to generate the likelihood scores (Table 4.12).
I conclude that adjacent putative mother-daughter pairs are most likely true mothers and daughters, and because the same inference was arrived at using both program KINSHIP and program CERVUS, I also

conclude that the result is robust with respect to assumptions regarding deviations from Hardy-Weinberg equilibrium, and the treatment of typing errors (Appendix 1).

Given that the adjacent putative mother-daughter pairs identified in Tables 4.10 and 4.11 are most likely true mothers and daughters, 14 (CERVUS) or 15 (KINSHIP) of the 35 females under consideration on the West grid (40-43 %), and 11 (KINSHIP) or 13 (CERVUS) of the 33 females under consideration on the East grid (33-39 %), were philopatric. If all females are philopatric, and all females everywhere are sampled, then the mother or daughter of a given female would always (100 % of the time) be found to be one of the several females occupying the adjacent home ranges surrounding the home range of the female under consideration. In the present case, not all females were sampled. Because tissue sampling did not begin until early October, 1995, which was after the core females had been removed, what I sampled was a more or less contiguous ring of females. Figures 4.5 and 4.11 illustrate the configuration of females at about the time I began collecting tissue samples. Since what I sampled was a ring, or circular chain of females, I generally only sampled 2 females (from either side), from among the likely 4 to 6 females (depending on home range shape), that had home ranges adjacent to a given female. Consequently, even if almost all females are philopatric, I would only expect to find adjacent mothers and daughters in about one-third (sampling 2 of 6 adjacent females = 33 %) to one-half (sampling 2 of 4 adjacent females = 50 %) of the cases I examined, given the manner in which females were sampled. I conclude that the observed frequency with which females were found to be adjacent to their likely mother or daughter (33-43 %) is consistent with the expected frequency (33-50 %), given the hypothesis that almost all female possums at the Paddys Land site settle on or adjacent to their mother’s home range.

Direct observations of restricted movements between the grids

There was no evidence of long-distance dispersal (> 2 km) between the grids, as animals tagged on one grid were never recaptured on the other grid. However, one male was known to have undertaken a long-distance “excursion” (or “exploratory movement”), within the area between the grids. The male in question was regularly caught in the same trap in the southeast sector of the West grid (as indicated by the male symbol in Fig. 4.8), from December, 1994, onwards. In October, 1996, he was caught at vehicle trail trap-site Vt6 (Fig. 4.1), some 1263.0 m from his normal location. When he was next recaptured, in February, 1997, he was back in his usual trap.

Only two other animals were caught at vehicle trail trap-sites in Oct.-Nov., 1996, that were normally caught on the grids. Female W-B (Fig. 4.7) was trapped at vehicle trail trap-site Vt16 (Fig. 4.1), and female E-AI (Fig. 4.15) was trapped at vehicle trail trap-site Vt1 (Fig. 4.1). In these two cases the vehicle trail trap-sites were 138.1 and 163.2 m, respectively, from the normal positions at which these females were trapped on the grids.

Restricted movements between the grids identified using microsatellite DNA

Allele frequencies differed significantly between the two study grids (Table 4.9). There were significant differences as regards each of 3 of the 6 loci considered, and the combined probabilities test across all loci was highly significant. However, the magnitude of genetic subdivision between the grids was slight ($F_{ST} = 0.0062$, $Rho_{ST} = 0.0078$), accounting for less than 1 % of the total genetic variation among individuals (Hartl 1988). Restricted “migration” between the grids is consistent with, but not the only possible explanation for, the observed allele frequency differences (Hartl 1988).

Sex ratios of pouch-young

Strong female philopatry is expected to select for a significantly male-biased primary sex ratio, according to the “local resource competition” (LRC) hypothesis (Johnson 1988, 1989). The LRC hypothesis assumes that there is male-biased dispersal in the species, and that males and females are equally “costly” to produce. As discussed previously (see Methods), possums are known to demonstrate male-biased dispersal, and this also appears to be the case at the Paddys Land site (comparing Figs. 4.16 vs. 4.18, and 4.17 vs. 4.19).

There was no evidence that male and female pouch-young developed at different rates, or weaned at different weights at the Paddys Land site (Chapter 5), nor has this been reported in the literature (Lyne and Verhagen 1957, Kerle and Howe 1992). Kerle and Howe (1992) measured eight morphometrics and concluded that adult body weight showed the most significant level of sexual dimorphism, with males being heavier than females. Crawley (1973) also reported that adult males were significantly heavier than adult females, when data were pooled across seasons, but differences were more apparent in some seasons (summer and autumn) than others (winter and spring). In contrast to both Crawley (1973), and Kerle and Howe (1992), Cowan (1990) concluded that there was little evidence of sexual size dimorphism in the species, based on a review of nine separate studies, with adult female body weight being on average 98.6 % of that of adult male body weight. Similarly, I found few noteworthy differences in adult body weights between the sexes at the Paddys Land site (Chapter 5). I conclude that there is little evidence that either sex is more “costly” to produce than the other.

Table 4.13 shows the total number of male and female pouch-young recorded in this study, as well as that recorded in all available published studies, that have reported on the breeding biology of common brushtail possums. In each of the 10 studies considered in Table 4.13, the reported number of male pouch-young was greater than the number of female pouch-young. The numbers reported in three studies, including this one, were significantly different from parity. While the numbers reported in the remaining seven studies were not significantly different from parity, there was no significant difference in the ratios reported across all 10 studies (Table 4.13). Considering the results from all 10 studies, taken together, a significantly male-biased sex ratio of pouch-young is clearly the norm for the species (Table 4.13). Since males and females are equally “costly” to produce, I conclude that the strongly male-biased sex ratio of pouch-young at both the Paddys Land site and across all 10 studies, can be interpreted as indicating that most females do not disperse, but instead settle on or adjacent to their mother’s home range, both at the Paddys Land site, and in most other populations.

DISCUSSION

Only one female immigrant (W-AE, Fig. 4.7) entered and settled in the core of one of the two study grids, over the course of the two years following the removal of 19 core resident females. I conclude that female immigration was almost non-existent, and having dealt with the issue of complete enumeration at length, I feel confident in saying that my measurement of female immigration was, as nearly as possible, made *without error*. If the strict definitions and protocols followed in the design and interpretation of the experiment are relaxed, it would appear that there were as many as 32 adult female “removals”, at the same time as there was still only the one female immigrant. In this case, the estimated rate of one female immigrant per 19 vacancies every two years, is almost certainly an *over*estimate of the importance of female immigration in replacing losses among breeding females.

Critics may claim that my experiment was too “short-term”, and the near absence of female immigration was just the result of “a couple of bad years”. The survival of young to the onset of weaning (175 days of age) was indeed very poor (33 %) in 1995, apparently as a result of very low rainfall during autumn and winter (Chapter 5), and the absence of immigration by female young of the year (born in 1995) in 1996 (W-AE was born in 1994) could be explained as a result of there being too few surviving young in the region as a whole, for there to be all that many dispersers. However, 1996 was a very wet year, adults measured in both years (1995 and 1996) were significantly heavier in 1996, and survival of young to the onset of weaning was significantly better in 1996 (81 %) than in 1995 (Chapter 5). Yet, there was still no immigration by female young of the year (born in 1996), in 1997. Efford (1991) concluded from a review of all available studies that most (78 %) dispersers are young of the year. Nonetheless, it is conceivable that young animals at the Paddys Land site generally delay dispersal until they are yearlings (1-2 years old), in which case there may not have been an influx of young born in 1996 until 1998, after the end of the study. Three of the four subadult males (75 %) first captured in the core of one of the two study grids, following the August 1, 1995 removals (Fig. 4.18), were young of the year (from both 1995 and 1996), which suggests that the typical age of dispersers at the Paddys Land site is similar to that at other sites. Efford (1991) found no significant difference between males and females with respect to age at dispersal, and it is unlikely, on theoretical grounds, that subadult females would disperse at a later age than subadult males, as they have “more to lose” from delaying breeding, than males do (Johnson 1986). Nonetheless, as the only female immigrant I observed (W-AE), was a yearling, I cannot rule out the possibility that there may have been an influx of yearling females (born in 1996) in 1998, after the end of the study.

Female immigration may have been next to non-existent over the two years of the experiment because these were “a couple of bad years”, or because female immigration is next to non-existent in most years, because most females do not disperse, but instead settle on or adjacent to their mother’s home range. Three lines of evidence indicate that strong female philopatry is clearly the norm at the Paddys Land site. Firstly, in the two cases where daughters tagged as pouch-young were later known to have given birth, the daughter either shared a den with her mother (W-P1, Figs. 4.7 and 4.9), or was captured at a location adjacent to her mother's denning range (W-L2, Fig. 4.9). Secondly, parentage analysis using microsatellite DNA (Table 4.10 and 4.11) indicated that: 1) adjacent putative mothers and daughters were significantly more likely to be "true" mothers and daughters than non-adjacent putative mothers and daughters (Table 4,12); and 2) the observed frequency with which adjacent pairs of females were putatively identified as being mother and daughter (33-43 %), was close to that expected (33-50 %), if daughters almost invariably settle on or adjacent to their mother's home range. Thirdly, the significantly male-biased sex ratio of pouch-young at the Paddys Land site (Table 4.13) is consistent with the predictions of the "local resource competition" hypothesis, again suggesting that most females settle on or adjacent to their mother's home range. I conclude that strong female philopatry is the norm at the Paddys Land site, and infer that the near absence of female immigration over the two years of the experiment *is* representative of what would be found in most years, and was not merely the product of "a couple of bad years". Moreover, the fact that a significantly male-biased primary sex ratio appears to be the norm for the species (Table 4.13), suggests that strong female philopatry, and the resulting near absence of female immigration, will also be found to be the norm in most other populations of common brushtail possums.

I have suggested, based on the results of the experiment, the location of known mothers and daughters, the location of putative mothers and daughters identified using microsatellite DNA, and the sex ratio of pouch-young, that female immigration will generally be "almost" non-existent. But I did of course observe an instance of female immigration. Perhaps the addition of a single subadult female, every second year, is somehow sufficient to "rescue" a population from extinction. Qualitatively, the one female immigrant, W-AE, did not "replace" any of the reproductively-active, core resident females, because she did not herself become reproductively-active (Clinchy 1997). Quantitatively, W-AE's probability of surviving and breeding in the following year was > 80 % (Chapters 5 and 6). In the latter case, it could be argued that the results of the experiment confirm that immigration has the potential to "rescue" recipient populations from extinction, provided that: 1) the populations are no more than one home range apart, as this was the extent of the distance traveled by W-AE; and 2) the populations are completely interconnected by "uniformly suitable habitat", as was the case at the Paddys Land site. Assuming that physical barriers attenuate dispersal, I conclude that the results of the experiment indicate that immigration will rarely ever "rescue" common brushtail possum populations from extinction, in cases where the populations are separated by larger distances (more than one home range length), and/or “uniformly *un*suitable habitat”.

I chose to conduct the experiment in a “uniformly suitable habitat” in view of the fact that metapopulation theory predicts that the maximum rate of exchange of immigrants ought to be observed where there are no physical barriers to dispersal. However, dispersal might also be impeded by social barriers. Hestbeck (1982, p. 157) proposed the “social fence” hypothesis, whereby emigration will be lower at higher densities, because of the increasing “social impermeability of neighbouring groups”. Female possums at the Paddys Land site demonstrated evidence of territoriality, insofar as they generally occupied exclusive, non-overlapping denning ranges (Green 1984), and many of them expanded their ranges in response to the removal of neighbouring, core resident females (i.e., the vacuum effect; Carpenter 1987, Mares and Lacher 1987, Schoener 1987). Nonetheless, I suggest that it is unlikely that territoriality acts as a barrier to emigration in possums, although it may act as a barrier to immigration.

Hestbeck (1982, p. 158) suggested that where a social fence exists, one would not expect to see individuals making “brief exploratory jaunts into the neighbouring areas”. I recorded one such “exploratory jaunt” during the vehicle trail trapping session, and I interpret the appearance and disappearance of females W-AF (Fig. 4.7) and W-AK (Fig. 4.9), and the ever-increasing cumulative number of newly-identified males caught on the periphery of the grids (Fig. 4.19), as further evidence of other such “exploratory jaunts”. Moreover, the fact that several new males, and a new female (W-AE), were caught in the cores of the grids, following the August 1, 1995 removals (Figs. 4.16 and 4.18), suggests that the contiguous ring of peripheral resident females (Figs. 4.5 and 4.11) was quite permeable. Similarly, none of the females tagged as pouch-young that were later caught by themselves apparently dispersed into the core of either grid, despite the *absence* of core resident females. Female W-P1 (Fig. 4.9), did show some expansion of her range into the core, but this was almost two years after the initial removals, and even at that she was still generally (80 % of the time) found in the same den as her mother, and continued to be found there up to the end of the study. The significant difference in allelic frequencies between the grids (Table 4.9) suggests that travel between the grids was unusual, and I did not observe any instances of animals from one grid showing up on the other grid, but the very low level of genetic subdivision (< 1 %) indicates that there was no significant barrier to gene flow between the grids

(Hartl 1988). Finally, it is difficult to see how a territory owner could patrol an area of one or two hectares (being the approximate size of most denning ranges), on a sufficiently frequent basis to actually prevent travel *through* the territory. As I will discuss, suitable den sites appear to be an important resource, but even in this respect, each female's denning range generally contained several den sites and it is unlikely she could adequately patrol all of them, so as to prevent travel through the territory.

As the "typical" female's denning range was about 1 hectare in size, it likely encompassed about 150 trees (see Methods), of which 10 % might be used as den sites, and several more might be used as refuge sites. Yet, most females were tracked to just a single den tree about half of the time (Fig. 4.24). Moreover, where females expanded their denning ranges into a previously occupied range (the vacuum effect), they almost always used the same den(s) as had been used by the previous occupant. I infer from this that while there is clearly a surplus of "shelter sites", there is evidently competition for the few "prime" den sites (see also Caley et al. 1998). There may be a barrier to immigration insofar as dispersers will not settle, but instead continue moving, if they find that the prime den site in an area is occupied by a resident animal (Chapter 3). Alternatively, if immigrants enter an area and occupy a prime den site before the offspring of a resident is able to do so, this may limit local recruitment (Clinchy 1997). Given that males and females presumably compete for the same prime den sites (Caley et al. 1998), the addition of more males to an area will result in increased competition for den sites. On four occasions, I successfully followed one of the newly-identified males first caught in a core trap, after August 1, 1995 (Fig. 4.18), to a den tree, and in 3 of 4 cases, it was a den that had been previously occupied by one of the core resident females removed on August 1, 1995. Since female immigration was found to be next to non-existent, the effects of (male) immigration on the demography of recipient populations will most likely be negative (e.g., Mansergh and Scotts 1989; Clinchy 1997), and I suggest that this will largely be a consequence of adverse effects on local recruitment resulting from increased competition for prime den sites.

My conclusion is that female immigration is generally next to non-existent at the Paddys Land site, despite there being no apparent physical or social barriers to dispersal (emigration), and I infer that immigration is likely to play an even smaller part in "rescuing" populations from extinction, where there are physical barriers to dispersal, as in fragmented or patchy landscapes. Logically, female dispersal must play some part in the ecology of common brushtail possums, otherwise the species could not have come to occupy 94 % of Australia (How and Kerle 1995). The one female immigrant, W-AE, dispersed about 200 m. If female possums spread from a point of origin at a rate of 200 m every two years, it would take roughly 40,000 years for them to distribute themselves from one side of Australia to the other. I propose this simply as a ballpark figure indicating order of magnitude. My point is that an infinitesimally slow rate of expansion is not contradicted by a wide geographic range given infinite time, and 40,000 years is not all that long in the history of most mammalian species (Simpson 1983).

It may be objected that it should have taken 14,000 years for possums to colonize all of New Zealand, at a rate of expansion of 200 m every 2 years, whereas it only took about 140 years. However, the current distribution of possums in New Zealand is largely the result of “assisted dispersal” (Cowan 1990, p. 76). Possums were introduced to New Zealand beginning in the 1830’s as part of a government policy to establish a fur industry. Numerous introductions from Australia were followed by hundreds of translocations of New Zealand-bred progeny, particularly between 1890-1940. Possums were even introduced to 17 offshore islands. Although government policy shifted towards eradication in the 1940’s, the possum fur industry still exists and illegal translocations by trappers still occur (Cowan 1990).

Given the similarities between common brushtail possums and other species of medium-sized, herbivorous, marsupials, I suggest that immigration does not often “rescue” populations of any of these species from extinction. Like common brushtail possums, many of the other medium-sized, herbivorous, marsupials that have declined had very large geographic ranges prior to European settlement, and also like common brushtail possums, I suggest it probably took tens of thousands of years to establish such broad distributions. All of these species demonstrate a pattern of life history involving low fecundity and high survivorship (Chapters 5 and 6) generally considered to be characteristic of larger mammals (Lee and Cockburn 1985, Sinclair 1996), particularly large ungulates (Gaillard et al. 1998). Whatever the reasons were for the evolution of this type of life history, it is clearly not one suited to being a “good” colonizer (MacArthur and Wilson 1967, p.83).

Since life history theory would predict that medium-sized, herbivorous, marsupials will be “bad” colonizers, and the results of my study appear to confirm this, how is it that these species feature prominently in the literature on connectivity and conservation corridors (Laurance and Gascon 1997, Beier and Noss 1998), and that the disruption of dispersal should be suggested as a key factor in their decline (Morton 1990)? I suggest that the “intuitively obvious” consequences of metapopulation models may often distract attention from the nature and details of dispersal in real animals. This raises the related question of just what is being measured in studies of connectivity and conservation corridors, such as the one by Laurance (1990), and those cited by Beier and Noss (1998), that have focussed on Australian marsupial possums and gliders? In the absence of female immigration, animals detected in corridors during presence/absence surveys of the type conducted by Laurance (1990), must either be: 1) individuals that are resident in the corridor (Beier and Noss 1998); or 2) males that are dispersing through the corridor. In already fragmented landscapes, the corridor will likely be one of only a few remaining pieces of remnant habitat, and the fact that it might sustain a resident population ought to be justification enough for its retention. However, there is no basis for suggesting that it is possible to somehow “creatively fragment” (Laurance and Gascon 1997) a continuous, natural landscape (such as that at the Paddys Land site), and still maintain connectivity through the retention of movement corridors, because the only individuals that are likely to move through the corridors will all be males, and these are as likely as not to have adverse effects on the populations they move into (e.g., Mansergh and Scotts 1989; Clinchy 1997).

REFERENCES

Alpin, K. P., and Archer, M. 1987. Recent advances in marsupial systematics with a new syncretic classification. *In* Possums and opossums: studies in evolution. *Edited by* Archer, M. Surrey Beatty and Sons Limited, Sydney, Australia, pp. xv-lxxii.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology, 7: 94-108.

Beier. P., and Noss, R. F. 1998. Do habitat corridors provide connectivity? Conservation Biology, 12: 1241-1252.

Bolliger, A., and Carrodus, A. L. 1938. Changes in and around the pouch of *Trichosurus vulpecula*, as occurring naturally and as the result of the administration of oestrone. Journal and Proceedings of the Royal Society of New South Wales, 71: 615-622.

Bolliger, A., and Carrodus, A. L. 1940. The effects of oestrogens on the pouch of the marsupial *Trichosurus vulpecula*. Journal and Proceedings of the Royal Society of New South Wales, 73: 218-227.

Boutin, S. 1980. Effect of spring removal experiments on the spacing behaviour of female snowshoe hares. Canadian Journal of Zoology, 58: 2167-2174.

Brown, J. H., and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. Ecology, 58: 445-449.

Burbidge, A. A., and McKenzie, N. L. 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. Biological Conservation, 50: 143-198.

Caley, P., Spencer, N. J., Cole, R. A., and Efford, M. G. 1998. The effect of manipulating population density on the probability of den-sharing among common brushtail possums, and the implications for transmission of bovine tuberculosis. Wildlife Research, 25: 383-392.

Carpenter, F. L. 1987. The study of territoriality: complexities and future directions. American Zoologist, 27: 401-409.

Caughley, G., and Gunn, A. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, Massachusetts.

Caughley, G., and Kean, R. I. 1964. Sex ratios in marsupial pouch young. Nature (London), 204: 491.

Chapman, B., and Binns, D. 1995. Flora survey of the Walcha/Nundle and Styx River Management Areas. Walcha/Nundle and Styx River Management Areas EIS, Supporting Document No. 2. Forestry Commission of New South Wales, Sydney, Australia.

Clark, J. M. 1995. The diet of the parasitic mite *Trichosurolaelaps crassipes* Womersley, 1956, and its potential to act a disease vector. New Zealand Veterinary Journal, 43: 215-218.

Clinchy, M. 1997. Does immigration "rescue" populations from extinction? Implications regarding movement corridors and the conservation of mammals. Oikos, 80: 618-622.

Clout, M. N., and Efford, M. G. 1984. Sex differences in the dispersal and settlement of brushtail possums (*Trichosurus vulpecula*). Journal of Animal Ecology, 53: 737-749.

Coleman, J. D., and Green, W. Q. 1984. Variations in the sex and age distributions of brush-tailed possum populations. New Zealand Journal of Zoology, 11: 313-318.

Cowan, P. E. 1990. Brushtail possum. *In* The handbook of New Zealand mammals. *Edited by* King, C. M. Oxford University Press, Auckland, New Zealand, pp. 68-98.

Crawley, M. C. 1973. A live-trapping study of Australian brush-tailed possums, *Trichosurus vulpecula* (Kerr), in the Orongorongo Valley, Wellington, New Zealand. Australian Journal of Zoology, 21: 75-90.

Croft, D. B. 1989. Social organization of the Macropodoidea. *In* Kangaroos, wallabies and rat-kangaroos. *Edited by* Grigg, G., Jarman, P., and Hume, I. Surrey Beatty and Sons Limited, Sydney, Australia, pp. 505-625.

Dunnet, G. M. 1956. A live-trapping study of the brush-tailed possum *Trichosurus vulpecula* Kerr (Marsupialia). CSIRO Wildlife Research, 1: 1-18.

Dunnet, G. M. 1964. A field study of local populations of the brush-tailed possum *Trichosurus vulpecula* in eastern Australia. Proceedings of the Zoological Society of London, 142: 665-695.

Efford, M. 1991. A review of possum dispersal. DSIR Land Resources Contract Report 91/73, DSIR Land Resources, Dunedin, New Zealand.

Efford, M. 1998. Demographic consequences of sex-biased dispersal in a population of brushtail possums. Journal of Animal Ecology, 67: 503-517.

Finlayson, H. H. 1961. On central Australian mammals. Part IV. The distribution and status of central Australian species. Records of the South Australian Museum, 14: 141-191.

Forestry Commission of N.S.W. 1989. Research Note No. 17. Forest types in N.S.W. Forestry Commission of N.S.W., Sydney, Australia.

Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N. G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution, 13: 58-63.

Goodnight, K. F., and Queller, D. C. 1998. KINSHIP Version 1.2. Goodnight software, Rice University, Houston, Texas, U.S.A. Available at [http://www.bioc.rice.edu/~kfg/Gsoft.html].

Green, W. Q. 1984. A review of ecological studies relevant to the management of the common brushtail possum. *In* Possums and gliders. *Edited by* Smith, A. P., and Hume, I. D. Australian Mammal Society, Sydney, Australia, pp. 483-499.

Green, W. Q., and Coleman, J. D. 1986. Movement of possums (*Trichosurus vulpecula*) between forest and pasture in Westland, New Zealand: implications for Bovine Tuberculosis transmission. New Zealand Journal of Ecology, 9: 57-69.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour, 28: 1140-1162.

Hanski, I. 1985. Single-species spatial dynamics may contribute to long-term rarity and commonness. Ecology, 66: 335-343.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society, 42: 17-38.

Hanski, I. 1998. Metapopulation dynamics. Nature (London), 396: 41-49.

Hanski, I., and Gilpin, M. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society, 42: 3-16.

Harlow, H. J., Lindzey, F. G., Van Sickle, W. D., and Gern, W. A. 1992. Stress response of cougars to nonlethal pursuit by hunters. Canadian Journal of Zoology, 70: 136-139.

Hartl, D. L. 1988. A primer of population genetics, 2nd ed. Sinauer Associates, Inc., Sunderland, Massachusetts.

Hemsley, S., and Canfield, P. 1993. Dermatitis in brushtail possums (*Trichosurus vulpecula*). Proceedings of the Annual Meeting of the Australasian section of the Wildlife Disease Association, Wildlife Disease Association, Sydney, Australia, pp. 23-24.

Hestbeck, J. B. 1982. Population regulation of cyclic mammals: the social fence hypothesis. Oikos, 39: 157-163.

Hintze, J. 1996. NCSS Statistical Software. NCSS, Kaysville, Utah, U.S.A. Information available at [http://www.ncss.com].

Hope, R. M. 1972. Observations on the sex ratio and the position of the lactating mammary gland in the brush-tailed possum, *Trichosurus vulpecula* (Kerr) (Marsupialia). Australian Journal of Zoology, 20: 131-137.

How, R. A., and Kerle, J. A. 1995. Common brushtail possum. *In* The mammals of Australia. *Edited by* Strahan, R. Reed Books, Sydney, Australia, pp. 273-275.

Humphreys, W. F., Bradley, A. J., How, R. A., and Barnett, J. L. 1984. Indices of condition of Phalanger populations: a review. *In* Possums and gliders. *Edited by* Smith, A. P., and Hume, I. D. Australian Mammal Society, Sydney, Australia, pp. 59-77.

Ims, R. A., and Yoccoz, N. G. 1997. Studying transfer processes in metapopulations: emigration, migration, and colonization. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* Hanski, I., and Gilpin, M. E., Academic Press, San Diego, pp. 247-265.

Ishibashi, Y., Saitoh, T., Abe, S., and Yoshida, M. C. 1997. Sex-related spatial kin structure in a spring population of grey-sided voles *Clethrionomys rufocanus* as revealed by mitochondrial and microsatellite DNA analyses. Molecular Ecology, 6: 63-71.

Johnson, C. N. 1986. Sex-biased philopatry and dispersal in mammals. Oecologia, 69: 626-627.

Johnson, C. N. 1988. Dispersal and sex ratio at birth in primates. Nature (London), 332: 726-728.

Johnson, C. N. 1989. Dispersal and philopatry in the Macropodoids. *In* Kangaroos, wallabies and rat-kangaroos. *Edited by* Grigg, G, Jarman, P, and Hume, I. Surrey Beatty and Sons Pty Limited, Sydney, Australia, pp. 593-601.

Johnson, M. L., and Gaines, M. S. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics, 21: 449-480.

Kerle, J. A. 1984. Variation in the ecology of *Trichosurus*: its adaptive significance. *In* Possums and gliders. *Edited by* A. P. Smith and I. D. Hume. Australian Mammal Society, Sydney, Australia, pp. 115-127.

Kerle, J. A., Foulkes, J. N., Kimber, R. G., and Papenfus, D. 1992. The decline of the brushtail possum, *Trichosurus vulpecula* (Kerr 1778), in arid Australia. Rangelands Journal, 14: 107-127.

Kerle, J. A., and Howe, C. J. 1992. The breeding biology of a tropical possum, *Trichosurus vulpecula arnhemensis* (Phalangeridae : Marsupialia). Australian Journal of Zoology, 40: 663-665.

Kerle, J. A., McKay, G. M., and Sharman, G. B. 1991. A systematic analysis of the brushtail possum, *Trichosurus vulpecula* (Kerr, 1792) (Marsupiala : Phalangeridae). Australian Journal of Zoology, 39: 313-331.

Koenig, W. D., Van Vuren, D., and Hooge, P. N. 1996. Detectability, philopatry, and the distribution of dispersal distance in vertebrates. Trends in Ecology and Evolution, 11: 514-517.

Krebs, C. J. 1999. Ecological methodology, 2nd ed. Benjamin/Cummings, Menlo Park, California.

Lambin, X., and Krebs, C. J. 1993. Influence of female relatedness on the demography of Townsend's vole populations in spring. Journal of Animal Ecology, 62: 536-550.

Laurance, W. F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. Journal of Mammalogy, 71: 641-653.

Laurance, W. F., and Gascon, C. 1997. How to creatively fragment a landscape. Conservation Biology, 11: 577-579.

Lee, A. K., and Cockburn, A. 1985. Evolutionary ecology of marsupials. Cambridge University Press, Cambridge.

Lee, A. K., and Ward, S. J. 1989. Life histories of macropodoid marsupials. *In* Kangaroos, wallabies and rat-kangaroos. *Edited by* Grigg, G., Jarman, P., and Hume, I. Surrey Beatty and Sons, Sydney, Australia, pp. 105-115.

Lidicker, W. Z., Jr., and Koenig, W. D. 1996. Responses of terrestrial vertebrates to habitat edges and corridors. *In* Metapopulations and wildlife conservation. *Edited by* McCullough, D. R., Island Press, Washington, D.C., pp. 85-109.

Lidicker, W. Z., Jr., and Stenseth, N. C. 1992. To disperse or not to disperse: who does it and why? *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 21-36.

Lindenmayer, D. B., Welsh, A., Donnelly, C. F., and Meggs, R. A. 1996. Use of nest trees by the mountain brushtail possum (*Trichosurus caninus*) (Phalangeridae : Marsupialia). I. Number of occupied trees and frequency of tree use. Wildlife Research, 23: 343-361.

Lindenmayer, D. B., Welsh, A., and Donnelly, C. F. 1997. Use of nest trees by the mountain brushtail possum (Trichosurus caninus) (Phalangeridae : Marsupialia). III. Spatial configuration and co-occupancy of nest trees. Wildlife Research, 24: 661-677.

Lyne, A. G., and Verhagen, A. M. W. 1957. Growth of the marsupial *Trichosurus vulpecula* and a comparison with some higher mammals. Growth, 21: 167-195.

MacArthur, R. H., and Wilson, E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Mackintosh, C. G., Crawford, J. L., Thompson, E. G., McLeod, B. J., Gill, J. M., and O'Keefe, J. S. 1995. A newly discovered disease of the brushtail possum: Wobbly possum syndrome. New Zealand Veterinary Journal, 43: 126.

Mansergh, I. M., and Scotts, D. J. 1989. Habitat continuity and social organization of the mountain pygmy-possum restored by tunnel. Journal of Wildlife Management, 53: 701-707.

Mares, M. A., and Lacher, T. E., Jr. 1987. Social spacing in small mammals: patterns of individual variation. American Zoologist, 27: 293-306.

Marshall, T. C. 1998. CERVUS Version 1.0. University of Edinburgh, Edinburgh, Scotland. Available at [http://helios.bto.ed.ac.uk/evolgen].

Marshall, T. C., Slate, J., Kruuk, L. E. B., and Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology, 7: 639-655.

Moilanen, A., Smith, A.T., and Hanski, I. 1998. Long-term dynamics in a metapopulation of the American pika. American Naturalist, 152: 530-542.

Morton, S. R. 1990. The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. Proceedings of the Ecological Society of Australia, 16: 201-213.

Noss, R. F. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology, 1: 159-164.

NPWS. 1992. Guy Fawkes River Wilderness assessment report. N.S.W. National Parks and Wildlife Service, Sydney, Australia.

NPWS. 1994. Fauna of northeast N.S.W. forests. Northeast forests biodiversity study. N.S.W. National Parks and Wildlife Service, Sydney, Australia.

Paetkau, D., Calvert, W., Stirling, I., and Strobeck, C. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology, 4: 347-354.

Piertney, S. B., MacColl, A. D. C., Bacon, P. J., and Dallas, J. F. 1998. Local genetic structure in red grouse (*Lagopus lagopus scoticus*): evidence from microsatellite DNA markers. Molecular Ecology, 7: 1645-1654.

Presidente, P. J. A. 1984. Parasites and diseases of brushtail possums (*Trichosurus* spp): occurrence and significance. *In* Possums and gliders. *Edited by* A. P. Smith and I. D. Hume. Australian Mammal Society, Sydney, pp. 171-190.

Raymond, M., and Rousset, F. 1995. GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity, 86: 248-249. Available at [http://www.cefe.cnrs-mop.fr].

SanCristobal, M., and Chevalet, C. 1997. Error tolerant parent identification from a finite set of individuals. Genetical Research, 70: 53-62.

Schoener, T. W. 1987. Time budgets and territory size: some simultaneous optimization models for energy maximizers. American Zoologist, 27: 259-291.

Seebeck, J. H., Bennett, A. F., and Scotts, D. J. 1989. Ecology of the Potoroidae: a review. *In* Kangaroos, wallabies and rat-kangaroos. *Edited by* Grigg, G., Jarman, P., and Hume, I. Surrey Beatty and Sons, Sydney, Australia, pp. 67-88.

Short, J., and Smith, A. 1994. Mammal decline and recovery in Australia. Journal of Mammalogy, 75: 288-297.

Simpson, G. G. 1983. Fossils and the history of life. Scientific American Books, Inc., New York.

Sinclair, A. R. E. 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. *In* Frontiers of population ecology. *Edited by* Floyd, R. B., Sheppard, A. W., and DeBarro, P. J., CSIRO Publishing, Melbourne, Australia, pp. 127-154.

Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D, Mahon, P., and Newsome, A. E. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology 12: 564-575.

Smith, M. J., Brown, B. K., and Frith, H. J. 1969. Breeding of the brush-tailed possum, *Trichosurus vulpecula* (Kerr) in New South Wales. CSIRO Wildlife Research, 14: 181-193.

Sokal, R. R., and Rohlf, F. J. 1995. Biometry, 3rd ed. W. H. Freeman and Co., New York.

Stacey, P. B., and Taper, M. 1992. Environmental variation and the persistence of small populations. Ecological Applications, 2: 18-29.

Stacey, P. B., Johnson, V. A., and Taper, M. L. 1997. Migration within metapopulations: the impact upon local population dynamics. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* Hanski, I., and Gilpin, M. E., Academic Press, San Diego, pp. 267-291.

StatSoft, Inc. 1995. STATISTICA for Windows. StatSoft, Inc., Tulsa, Oklahoma, U.S.A. Information available at [http://www.statsoftinc.com].

Stenseth, N. C., and Lidicker, W. Z., Jr. 1992. Where do we stand methodologically about experimental design and methods of analysis in the study of dispersal? *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 295-318.

Szalay, F. S. 1994. Evolutionary history of the marsupials and an analysis of osteological characters. Cambridge University Press, Cambridge.

Taylor, A. C., and Cooper, D. W. 1998. Microsatellite markers for the Phalangerid marsupial, the common brushtail possum (*Trichosurus vulpecula*). Molecular Ecology, 7: 1780-1782.

Tyndale-Biscoe, C. H. 1955. Observations on the breeding and ecology of the brushtailed possum, *Trichosurus vulpecula* Kerr (Marsupialia) in New Zealand. Australian Journal of Zoology, 3: 162-184.

Ward, G. D. 1978. Habitat use and home range of radio-tagged opossums Trichosurus vulpecula (Kerr) in New Zealand lowland forest. In The ecology of arboreal folivores. Edited by Montgomery, G. G. Smithsonian Institute Press, Washington, D.C., pp. 267-287.

Waser, P. M., and Jones, T. W. 1983. Natal philopatry among solitary animals. Quarterly Review of Biology, 58: 355-390.

Winter, J. 1976. The behaviour and social organization of the brush tailed possum *Trichosurus vulpecula* (Kerr). Ph.D. Thesis, University of Queensland, Brisbane, Australia.

Wolff, J. O. 1997. Population regulation in mammals: an evolutionary perspective. Journal of Animal Ecology, 66: 1-13.

Zar. J. H. 1996. Biostatistical analysis, 3rd ed. Prentice Hall, Upper Saddle River, New Jersey.

Table 4.1. Number and date of, and level of effort associated with, full-grid trapping sessions on the West grid. Also shown are the number of captures during full-grid trapping, target trapping, and nighttime trapping, as well as the number of times animals were either darted or resighted during spotlighting, relative to the dates on which full-grid trapping sessions were conducted.

	Full-grid trapping sessions			Trap captures		Spotlighting	
Session	Date	Trap-nights	Full-grid	Target	Nighttime	Darted	Resighted
1	04/12/94	147	17	1	4		
2	11/12/94	147	36		1		
3	19/12/94	147	58				
4	20/03/95	147	43	7			1
5	16/04/95	147	58				1
6	28/05/95	147	82				2
7	25/06/95	147	81	2			3
8	13/08/95	147	64	59	1	1	12
9	17/09/95	147	54	13			2
10	03/11/95	49	25	1		3	1
11	21/11/95	49	22				
12	28/11/95	147	52	1			
13	11/01/96	147	47	3			
14	11/02/96	147	53	2			
15	31/03/96	147	57	23			4
16	28/04/96	49	20	4			4
17	12/05/96	147	87	4		2	
18	23/06/96	147	82	29	1		5
19	03/08/96	147	65	8			12
20	21/10/96	147	64	95		2	1
21	18/02/97	196	62	22			
22	28/03/97	147	59				
23	21/04/97	147	50				
24	19/05/97	147	52	47			6
25	13/06/97	147	63	3			1
26	20/07/97	147	65	48			3
Total		3577	1418	372	7	8	58

Table 4.2. Number and date of, and level of effort associated with, full-grid trapping sessions on the East grid. Also shown are the number of captures during full-grid trapping, target trapping, and nighttime trapping, as well as the number of times animals were either darted or resighted during spotlighting, relative to the dates on which full-grid trapping sessions were conducted.

	Full-grid trapping sessions			Trap captures		Spotlighting	
Session	Date	Trap-nights	Full-grid	Target	Nighttime	Darted	Resighted
1	05/01/95	147	10				
2	14/01/95	147	33				
3	05/02/95	147	48				
4	13/03/95	147	42				
5	06/04/95	147	64				
6	21/05/95	147	58	13			3
7	18/06/95	147	57	1			1
8	06/08/95	147	59	79	1	5	6
9	10/09/95	147	52	10		2	
10	05/12/95	147	45	1			
11	18/01/96	147	61	4			
12	18/02/96	147	38	4			5
13	24/03/96	147	36	4			
14	14/04/96	147	58	4			1
15	19/05/96	147	64	8			1
16	30/06/96	147	63	31			8
17	28/07/96	147	65	4	1		4
18	13/10/96	147	57	62			
19	02/03/97	147	35	13			
20	24/03/97	147	50				
21	24/04/97	147	34	19			
22	16/05/97	147	44	7			
23	16/06/97	147	49	45			1
24	17/07/97	147	43				3
Total		3528	1165	309	2	7	33

Table 4.3. Level of effort associated with, and number of animals seen during spotlight transects in the core areas of the two study grids. The identity (if female) of individuals captured in conjunction with spotlighting is shown, if the animal was first captured after August 1, 1995. In cases where unmarked animals were detected, but not captured, following August 1, 1995, the occasion was assigned a lowercase letter, and the location at which the animal was seen was plotted on the appropriate range map (Figs. 4.4-15), as shown by a diamond symbol enclosing the relevant lowercase letter.

		1995		1996	1997
		Prior to August 1	After August 1	Prior to August 1	Prior to August 1
West	Effort (minutes)	505	440	415	475
	Marked	24	16	25	14
	Unmarked				
	Captured	0	Male	0	0
	Not captured	6	0	W-b	0
East	Effort (minutes)	410	---	420	345
	Marked	18	---	5	5
	Unmarked				
	Captured	0	---	0	0
	Not captured	1	---	0	E-b

Table 4.4. Level of effort associated with, and number of animals seen during spotlight transects on the periphery of the two study grids. See caption to Table 4.3 for details.

		1995	1996	1997
West	Effort (min)	775	415	515
	Marked	35	25	21
	Unmarked			
	Captured	1	W-AI	0
	Not captured	7	W-a	W-c,d,e,f
East	Effort (min)	825	560	345
	Marked	33	24	10
	Unmarked			
	Captured	6	Male	0
	Not captured	13	E-a	E-c,d

Table 4.5. Population size estimates regarding all adult and subadult females on the West grid. MNA-Grid and Jolly-Seber estimates are based solely on full-grid trapping sessions. The number of radio-collared females "present on the grid" at the time of each trapping session is also shown. MNA-All includes all females tallied in the MNA-Grid estimate, as well as all those females initially captured using procedures other than full-grid trapping (target trapping, etc …), that were known to be "present on the grid", at the time of each trapping session. Females W-AH (Fig. 4.7) and W-AJ (Fig. 4.8) were never captured or resighted along or interior to the periphery of the trapping grid (shown by the outer dashed line in Fig. 4.2), and were not considered to be "present on the grid", for the purposes of these comparisons. The Jolly-Seber estimates of population size (N) and the number of new animals joining the population (B) were calculated using program JOLLY-SEBER (Krebs 1999).

Session		MNA		Jolly-Seber Model A			
	Grid	Radio	All	N	S.E.(N)	B	S.E.(B)
1	5		7				
2	13		15	13.0	2.3	13.3	2.8
3	24		26	25.5	2.8	3.5	2.8
4	25	5	28	26.7	2.9	-1.7	2.0
5	25	9	28	25.0	2.1	3.3	0.7
6	28	25	31	28.4	2.2	0.7	0.7
7	28	27	32	28.6	2.4	3.4	0.9
8	21	20	26	21.6	3.1	-0.4	0.9
9	20	20	25	20.0	2.9	0.0	0.0
10	20	20	24	20.0	2.9	0.0	0.0
11	20	20	24	20.0	2.9	3.1	1.5
12	22	20	25	23.1	3.3	-1.1	1.5
13	22	20	25	22.0	2.9	1.4	0.8
14	23	21	26	23.4	3.1	2.3	1.4
15	25	22	27	25.7	3.2	2.4	3.2
16	26	22	28	28.1	4.2	-0.9	3.1
17	27	25	29	27.9	3.1	-0.2	0.6
18	24	26	26	24.6	3.2	0.0	0.0
19	22	26	27	24.0	3.8	0.0	0.0
20	19	22	22	19.5	3.3	0.0	0.0
21	18	20	20	18.2	3.2	2.7	1.2
22	19	20	22	20.0	3.4	-0.7	1.1
23	18	19	20	19.1	3.5	1.3	0.7
24	17	18	19	17.9	3.4	-0.2	0.6
25	15	18	19	15.1	3.1		
26	15	16	17				

Table 4.6. Population size estimates regarding all adult and subadult females on the East grid. See caption to Table 4.5 for details. Females E-AF (Fig. 4.13) and E-AG (Fig. 4.14) were never captured or resighted along or interior to the periphery of the trapping grid (shown by the outer dashed line in Fig. 4.3), and were not considered to be "present on the grid", for the purposes of these comparisons.

Session	MNA			Jolly-Seber Model A			
	Grid	Radio	All	N	S.E.(N)	B	S.E.(B)
1	5		5				
2	14		14	14.2	1.7	10.5	3.3
3	21		21	23.8	3.1	1.3	3.0
4	23	3	23	24.1	1.9	4.2	1.8
5	26	5	26	27.2	2.2	2.0	2.0
6	27	20	27	30.0	3.0	2.3	2.1
7	25	24	28	30.7	4.7	5.9	2.3
8	22	21	23	24.0	3.6	-1.7	2.1
9	20	19	21	22.2	3.9	1.7	1.3
10	19	18	19	20.4	3.5	0.6	1.4
11	19	17	19	19.3	3.1	-0.3	0.7
12	19	17	19	19.0	3.0	0.0	0.0
13	19	17	19	19.0	3.0	0.0	0.0
14	19	17	19	19.0	3.0	0.0	0.0
15	19	19	19	19.0	3.0	1.3	0.7
16	20	22	22	20.6	3.2	-0.3	0.8
17	19	21	21	22.1	4.2	1.0	0.3
18	13	15	16	13.2	2.9	1.4	1.1
19	12	14	16	12.9	3.1	1.1	1.5
20	12	14	16	13.7	3.5	2.1	2.8
21	11	14	16	12.5	3.7	-1.6	2.8
22	11	15	16	11.6	2.9	1.1	0.5
23	11	15	17	11.6	3.1		
24	10	14	15				

Table 4.7. Population size estimates regarding all adult and subadult males on the West grid. See caption to Table 4.5 for details.

Session	MNA		Jolly-Seber Model A			
	Grid	All	N	S.E.(N)	B	S.E.(B)
1	10	11				
2	19	19	22.6	3.7	4.6	3.0
3	23	24	23.1	1.7	2.6	1.2
4	24	25	24.6	2.1	4.5	1.8
5	28	29	29.4	2.4	-1.1	1.4
6	27	28	27.2	2.0	3.8	1.2
7	29	31	30.7	2.7	1.8	1.5
8	28	32	29.2	2.9	-0.5	0.9
9	24	26	24.5	3.0	0.0	0.0
10	23	24	23.0	2.9	0.0	0.0
11	23	24	23.0	2.9	1.3	0.7
12	24	24	24.3	3.0	-0.3	0.7
13	24	24	24.0	2.9	0.0	0.0
14	24	24	24.4	3.0	1.3	0.7
15	24	25	24.3	3.0	1.7	1.7
16	25	26	26.0	3.4	1.2	1.7
17	27	28	27.2	3.0	1.0	0.7
18	28	30	28.5	3.1	1.0	0.7
19	27	29	27.7	3.2	5.4	1.1
20	29	32	29.9	3.4	2.7	1.9
21	28	30	30.4	4.0	1.4	1.7
22	28	29	28.5	3.5	1.2	1.6
23	29	30	31.2	4.0	-0.7	1.2
24	27	28	27.8	3.6	2.4	0.8
25	25	25	26.3	4.4		
26	21	24				

Table 4.8. Population size estimates regarding all adult and subadult males on the East grid. See caption to Table 4.5 for details.

Session	MNA		Jolly-Seber Model A			
	Grid	All	N	S.E.(N)	B	S.E.(B)
1	3	3				
2	13	13	9.3	1.4	6.9	0.0
3	16	16	16.3	1.7	1.2	1.3
4	17	17	17.5	1.7	5.3	1.6
5	22	22	22.9	2.0	-0.7	1.2
6	21	22	21.5	1.8	1.0	0.3
7	20	21	20.2	2.1	3.8	0.0
8	20	26	19.8	2.4	3.8	1.1
9	20	25	20.6	2.8	0.6	1.3
10	21	25	21.6	2.8	2.0	0.9
11	22	26	22.4	2.8	1.2	1.2
12	22	25	23.5	3.2	-0.4	0.8
13	20	23	20.0	2.8	4.0	0.5
14	24	27	24.2	2.9	0.0	0.5
15	20	23	20.1	3.0	0.0	0.0
16	19	22	19.4	3.1	1.1	0.5
17	19	23	19.3	3.1	2.0	0.7
18	20	23	20.2	3.1	1.3	1.0
19	20	25	20.8	3.3	1.8	1.0
20	21	23	21.4	3.1	1.2	1.0
21	20	24	20.4	3.2	-0.4	0.8
22	20	24	20.0	3.1	3.1	0.6
23	22	24	22.7	3.8		
24	15	15				

Table 4.9. Allele frequencies observed at six microsatellite loci. Mean number of alleles per locus was 16.3 on the West grid and 15.7 on the East grid. DNA was extracted from tissue samples from N = 176 individuals (97 West, 79 East). As is generally the case, not all individuals were successfully typed at each locus. The mean proportion of loci typed was 0.855 on the West grid and 0.749 on the East grid, which is comparable to other studies (Marshall et al. 1998). Allele frequency differences were compared between the grids, at each locus, using program GENEPOP (Raymond and Rousset 1995). Pooling across loci (using Fisher's combined probabilities test), the global probability of allele frequency differences between the grids was highly significant (χ^2 = 39.03, df = 12, p = 0.0001).

Locus	Population	N typed at locus	Alleles (named by size in terms of number of base pairs) and their frequencies																								Allele frequency differences between grids	
																											p	S.E.
Tv16			**118**	**120**	**122**	**124**	**126**	**128**	**130**	**132**	**134**	**136**	**138**	**140**	**142**	**144**	**146**											
	Total	165	0.10	0.04	0.02	0.00	0.11	0.02	0.06	0.07	0.14	0.11	0.15	0.06	0.05	0.02	0.05										0.0252	0.0016
	West	91	0.08	0.04	0.01	0.00	0.05	0.02	0.05	0.07	0.18	0.14	0.18	0.07	0.06	0.02	0.04											
	East	74	0.12	0.05	0.03	0.01	0.17	0.01	0.06	0.07	0.09	0.08	0.13	0.05	0.05	0.03	0.06											
Tv19			**254**	**256**	**258**	**260**	**262**	**264**	**266**	**268**	**270**	**272**	**276**	**278**	**280**	**282**	**284**	**286**	**288**	**290**	**294**							
	Total	107	0.01	0.00	0.04	0.11	0.04	0.13	0.06	0.11	0.04	0.05	0.03	0.08	0.12	0.03	0.07	0.06	0.00	0.01	0.00						0.2174	0.0053
	West	70	0.02	0.01	0.05	0.09	0.03	0.10	0.04	0.14	0.04	0.04	0.04	0.08	0.11	0.04	0.08	0.09	0.00	0.01	0.01							
	East	37	0.00	0.00	0.03	0.14	0.05	0.18	0.11	0.07	0.03	0.07	0.03	0.08	0.12	0.01	0.05	0.01	0.01	0.01	0.00							
Tv27			**169**	**171**	**173**	**175**	**177**	**179**	**181**	**183**	**185**	**187**	**189**	**191**	**195**													
	Total	157	0.02	0.10	0.14	0.11	0.22	0.12	0.09	0.05	0.09	0.02	0.01	0.04	0.01												0.1473	0.0044
	West	85	0.03	0.09	0.16	0.08	0.26	0.13	0.06	0.04	0.08	0.02	0.01	0.03	0.01													
	East	72	0.00	0.10	0.11	0.14	0.18	0.10	0.12	0.06	0.10	0.02	0.01	0.06	0.01													
Tv53			**222**	**224**	**234**	**236**	**238**	**240**	**242**	**244**	**246**	**248**	**250**	**252**	**254**	**256**	**258**	**260**	**262**	**264**	**266**	**270**						
	Total	119	0.05	0.00	0.01	0.00	0.03	0.01	0.05	0.12	0.04	0.06	0.07	0.08	0.18	0.15	0.04	0.02	0.03	0.04	0.01	0.00					0.0014	0.0003
	West	74	0.02	0.00	0.01	0.01	0.04	0.00	0.03	0.15	0.06	0.07	0.05	0.11	0.18	0.11	0.05	0.03	0.02	0.05	0.01	0.01						
	East	45	0.09	0.01	0.02	0.00	0.02	0.03	0.07	0.08	0.01	0.04	0.10	0.03	0.17	0.21	0.01	0.00	0.04	0.03	0.02	0.00						
Tv58			**124**	**126**	**133**	**134**	**136**	**138**	**140**	**142**	**144**	**146**	**148**	**150**	**152**	**154**	**156**	**158**										
	Total	168	0.01	0.01	0.06	0.01	0.02	0.00	0.10	0.02	0.14	0.01	0.09	0.21	0.13	0.11	0.05	0.02									0.1244	0.0047
	West	96	0.01	0.02	0.08	0.00	0.02	0.01	0.11	0.03	0.09	0.02	0.08	0.24	0.16	0.08	0.05	0.02										
	East	72	0.00	0.01	0.04	0.01	0.02	0.00	0.09	0.02	0.19	0.01	0.11	0.17	0.10	0.14	0.05	0.02										
Tv64			**138**	**146**	**149**	**151**	**153**	**155**	**157**	**159**	**161**	**163**	**173**	**175**	**177**	**179**	**181**	**183**	**185**	**187**	**189**	**191**	**193**	**195**	**197**	**199**		
	Total	142	0.02	0.01	0.01	0.04	0.01	0.00	0.01	0.08	0.01	0.02	0.05	0.05	0.11	0.06	0.05	0.04	0.13	0.10	0.07	0.01	0.08	0.00	0.02	0.01	0.0232	0.0019
	West	87	0.00	0.02	0.02	0.05	0.02	0.01	0.01	0.07	0.00	0.03	0.06	0.06	0.10	0.07	0.06	0.04	0.11	0.09	0.07	0.01	0.09	0.00	0.02	0.00		
	East	55	0.06	0.00	0.00	0.03	0.00	0.00	0.02	0.08	0.02	0.02	0.03	0.04	0.11	0.05	0.03	0.05	0.15	0.11	0.07	0.01	0.06	0.01	0.04	0.03		

Table 4.10. Putative mother-daughter relationships identified among adult (and subadult) females on the West grid. Letters refer to females whose ranges are plotted in Figures 4.4-9. Dashed lines signify cases where no putative "mother" was identified from among the available candidates. Numerals followed by an equal sign indicate instances where more than one putative "mother" had the same likelihood score. Letters in bold indicate instances in which the putative mother and daughter had adjacent ranges.

"Daughter"	"Mother"						
	Program KINSHIP			Program CERVUS (error rate = 0.00008)			
	ID	Loci compared	Score	ID	Loci compared	Loci mismatch	Score
rA	---			---			
rB	---			---			
A	**B**	5	2.812	**B**	5		5.887
B	**A**	5	2.812	**A**	5		5.887
C	---			---			
D	**E**	6	3.554	**E**	6		7.089
E	**D**	6	3.554	**D**	6		7.089
F	---			---			
G	---			---			
I	O	6	2.383	O	6		4.799
J	---			---			
K	---			AK	3	1	1.861
L	AH	4	1.711	AH	4		3.534
M	---			---			
N	**O**	6	4.281	**O**	6		7.950
O	**N**	6	4.281	**N**	6		7.950
P	**Q**	6	4.568	**Q**	6		9.061
Q	**P**	6	4.568	**P**	6		9.061
R	**S**	6	2.762	**S**	6		5.613
S	**R**	6	2.762	**R**	6		5.613
V	AH	4	0.583	AH	4		1.159
W	**X**	6	4.414	**X**	6		8.661
X	**W**	6	4.414	**W**	6		8.661
AB	---			---			
AC	**AJ**	3	1.399	**I**	6	1	3.271
AD	**P**	6	4.487	**P**	6		8.300
AE	AG	5	4.169	AG	5		7.804
AF	---			---			
AG	AE	5	4.169	AE	5		7.804
AH	L	4	1.711	L	4		3.534
AI	---			---			
AJ	**AC**	3	1.399	I	3		2.933
AK	---			K	3	1	1.861
AL	---			---			
AM	4 =	1	1.195	AJ	1		2.332

Table 4.11. Putative mother-daughter relationships identified among adult (and subadult) females on the East grid. Letters refer to females whose ranges are plotted in Figures 4.10-15. Dashed lines signify cases where no putative "mother" was identified from among the available candidates. Letters in bold indicate instances in which the putative mother and daughter had adjacent ranges.

"Daughter"	"Mother"						
	Program KINSHIP			Program CERVUS (error rate = 0.00631)			
	ID	Loci	Score	ID	Loci		Score
		compared			compared	mismatch	
dB	D	3	1.544	D	3		1.703
dC	**X**	3	1.599	**X**	3		2.282
A	**B**	5	2.616	**B**	5		3.144
B	**A**	5	2.616	**A**	5		3.144
D	dB	3	1.544	dB	3		1.703
F	Y	3	1.626	Y	3		2.323
H	---			T	5	2	1.498
I	---			Y	3	1	1.240
J	---			L	4	1	0.985
K	AG	3	1.842	AG	3		1.726
L	---			F	5	1	1.991
M	**AG**	3	2.281	**AG**	3		2.487
N	---			W	5	2	2.208
O	D	3	1.103	**dB**	4	1	1.390
P	**Y**	3	1.621	**Y**	3		2.287
Q	---			AE	4	2	1.384
R	M	3	1.09	AH	4	1	1.565
S	---			AB	3	1	1.224
T	**AB**	4	1.771	**AB**	4		2.443
U	AG	2	1.117	AG	2		1.539
W	---			**X**	5	1	2.264
X	**dC**	3	1.599	**dC**	3		2.282
Y	F	3	1.626	F	3		2.323
Z	---			AG	3	1	1.357
AB	**T**	4	1.771	**T**	4		2.443
AC	M	4	1.814	M	4		2.195
AD	---			F	4	1	2.242
AE	**AH**	4	2.146	**AH**	4		1.817
AF	---			dC	3	1	1.889
AG	**M**	3	2.281	**M**	3		2.487
AH	**AE**	4	2.146	**AE**	4		1.817
AI	---			AC	4	1	1.138
AJ	---			K	4	1	0.506

Table 4.12. Differences in mean likelihood scores, as shown in Tables 4.10 and 4.11, between adjacent and non-adjacent putative parent-offspring pairs of adult (and subadult) females. If a given relationship was reciprocal (e.g., A was the most likely mother or daugter of B, and *vice versa*), the likelihood score was only counted once in the tallies shown. In addition, W-AE was not included in the tallies shown, because her status (as an immigrant) was already established. Differences were compared using t-tests on untransformed likelihood scores. Assumptions regarding normality and homogeneity of variances were tested using program STATISTICA (StatSoft, Inc. 1995).

Program	Grid	Location	N	Likelihood scores		t	df	p
				Mean	S.E.			
KINSHIP	West	Adjacent	8	3.535	0.401	2.68	9	0.0250
		Non-adjacent	3	1.559	0.525			
	East	Adjacent	6	2.006	0.167	2.69	11	0.0209
		Non-adjacent	7	1.448	0.128			
CERVUS	West	Adjacent	8	6.979	0.690	4.56	12	0.0007
		Non-adjacent	6	2.770	0.527			
	East	Adjacent	8	2.264	0.180	3.17	24	0.0041
		Non-adjacent	18	1.595	0.116			

Table 4.13. Reported sex ratios of pouch-young. Deviation of the observed sex ratio from parity was analyzed at each site, by means of an exact binomial test (Zar 1996, p. 466), using program NCSS (Hintze 1996). Deviation of the observed sex ratio from parity, across all 10 sites, was tested by means of a log-linear analysis of sex ratio by site[1], using program STATISTICA (StatSoft, Inc. 1995).

Reference	Percentage	Number		p
	Female	Female	Male	
Tyndale-Biscoe (1955)	46.1	59	69	0.426
Dunnet (1956)	35.3	6	11	0.332
Lyne and Verhagen (1957)	48.2	66	71	0.733
Caughley and Kean (1964)	47.0	294	332	0.139
Smith et al. (1969)	47.7	74	81	0.630
Hope (1972)	45.4	94	113	0.211
Coleman and Green (1984)	46.3	354	410	0.047
Kerle and Howe (1992)	45.6	41	49	0.461
Efford (1998)	43.9	293	374	0.002
This study	35.4	34	62	0.006

[1] The analysis indicated a significant marginal association with sex ($\chi^2 = 22.83$, $p < 0.0001$) and site, but no interaction ($p > 0.65$).

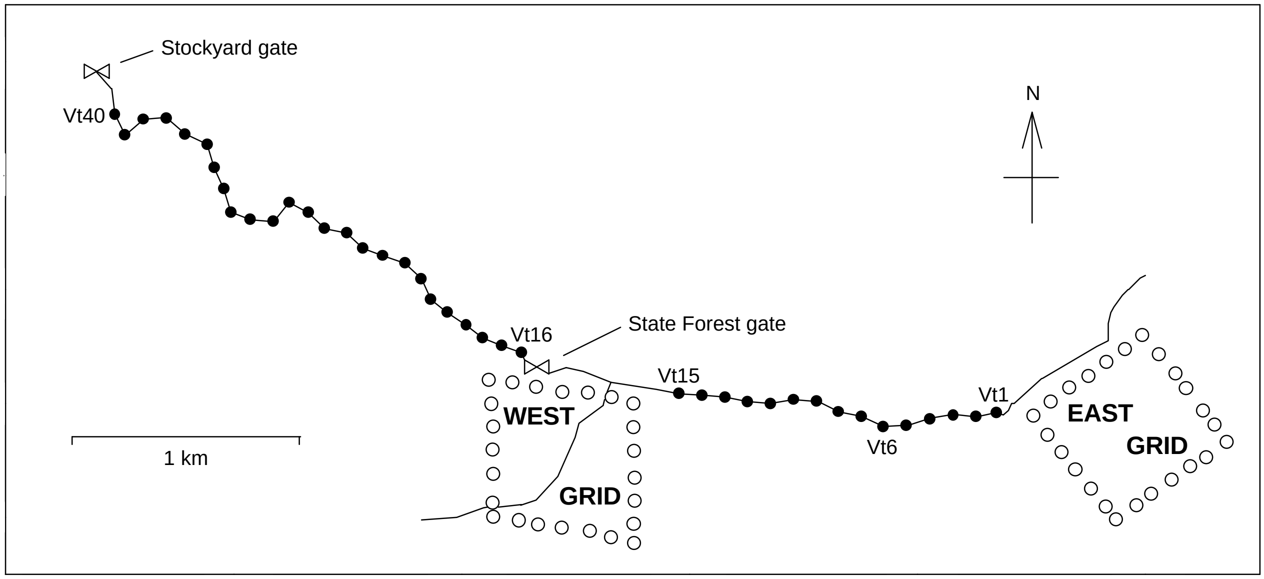

Figure 4.1. Schematic map of the study site showing the relative position of the two principal study grids. The vehicle trail trapline consisted of traps set 100 m apart (solid black circles) along the vehicle trail (Vt1 = the first vehicle trail trap) running between and away from the two principal study grids.

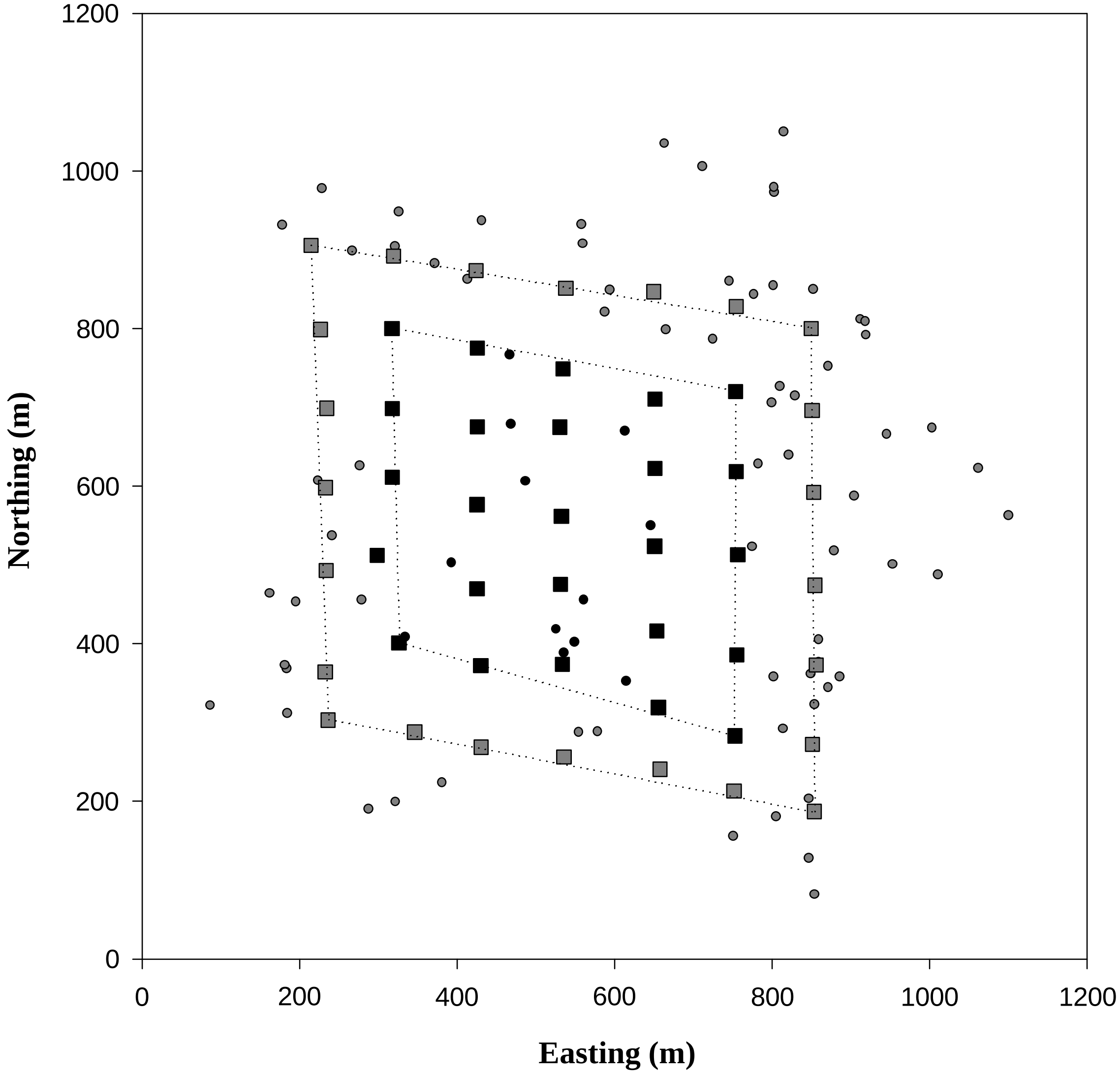

Figure 4.2. Schematic map of the West grid. Squares signify permanent trap locations, while circles indicate locations where animals were trapped at den trees. The inner dashed line delineates the "core" of the study grid, while the outer dashed line indicates the periphery of the trapping grid. Symbols in black represent "core" trap locations, while those in grey represent "peripheral" trap locations.

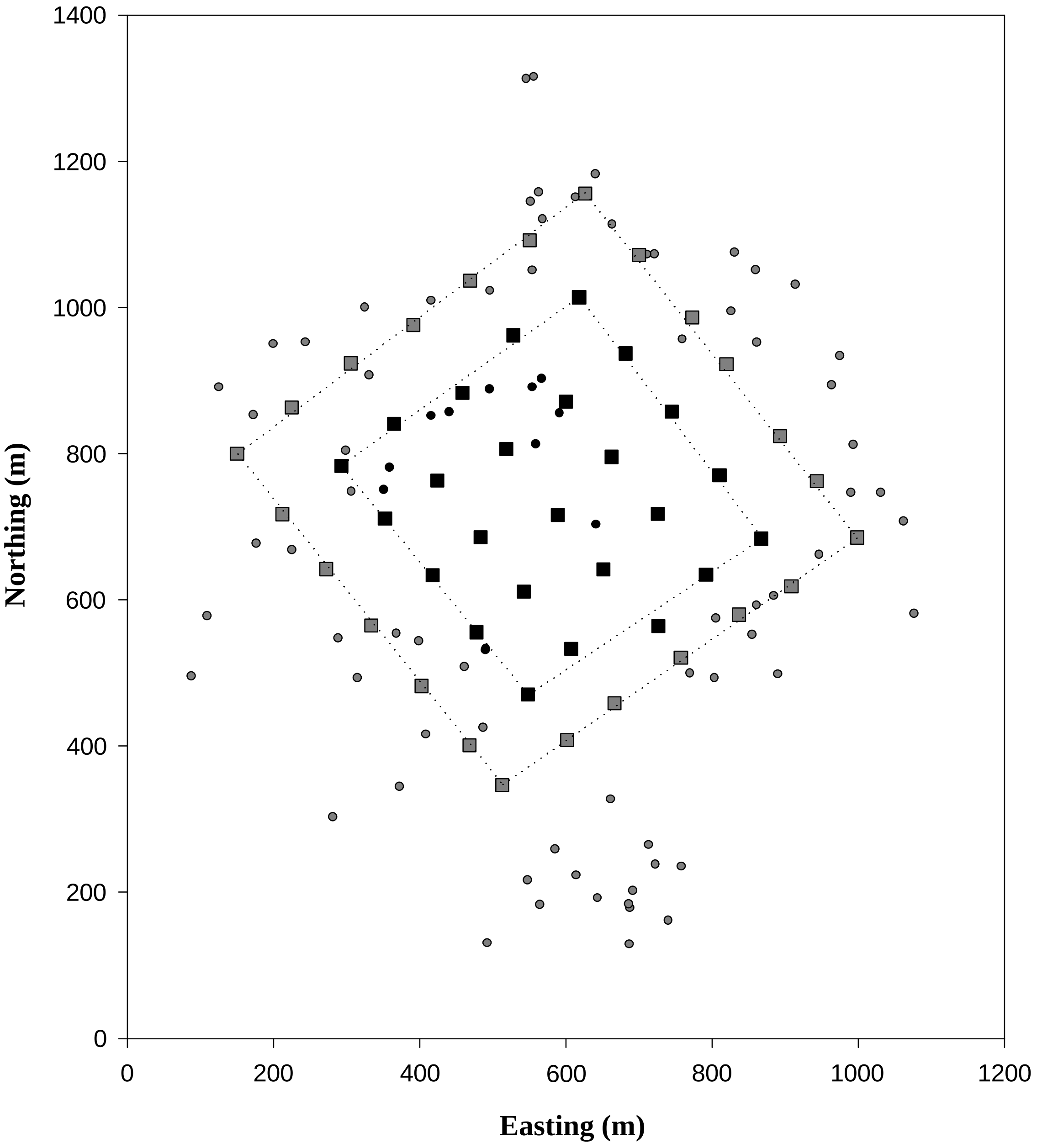

Figure 4.3. Schematic map of the East grid. Squares signify permanent trap locations, while circles indicate locations where animals were trapped at den trees. The inner dashed line delineates the "core" of the study grid, while the outer dashed line indicates the periphery of the trapping grid. Symbols in black represent "core" trap locations, while those in grey represent "peripheral" trap locations.

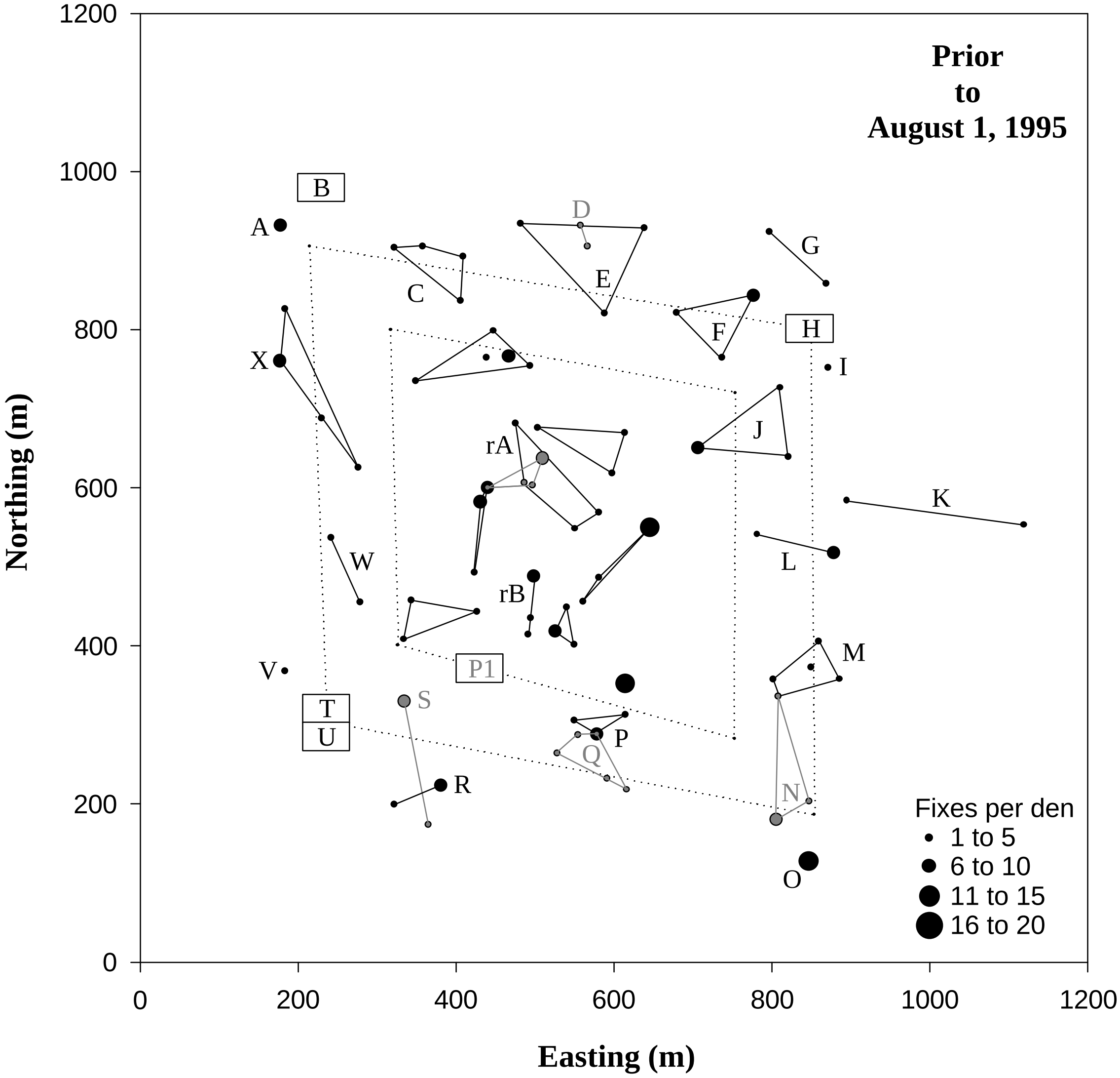

Figure 4.4. Location of all females captured on the West grid prior to August 1, 1995. Polygons show the denning ranges of radio-collared females. Rectangles indicate where females were captured, but not radio-collared. Uppercase letters identify individual females (see text for details). Polygons not accompanied by uppercase letters represent the denning ranges of core resident females removed on August 1, 1995.

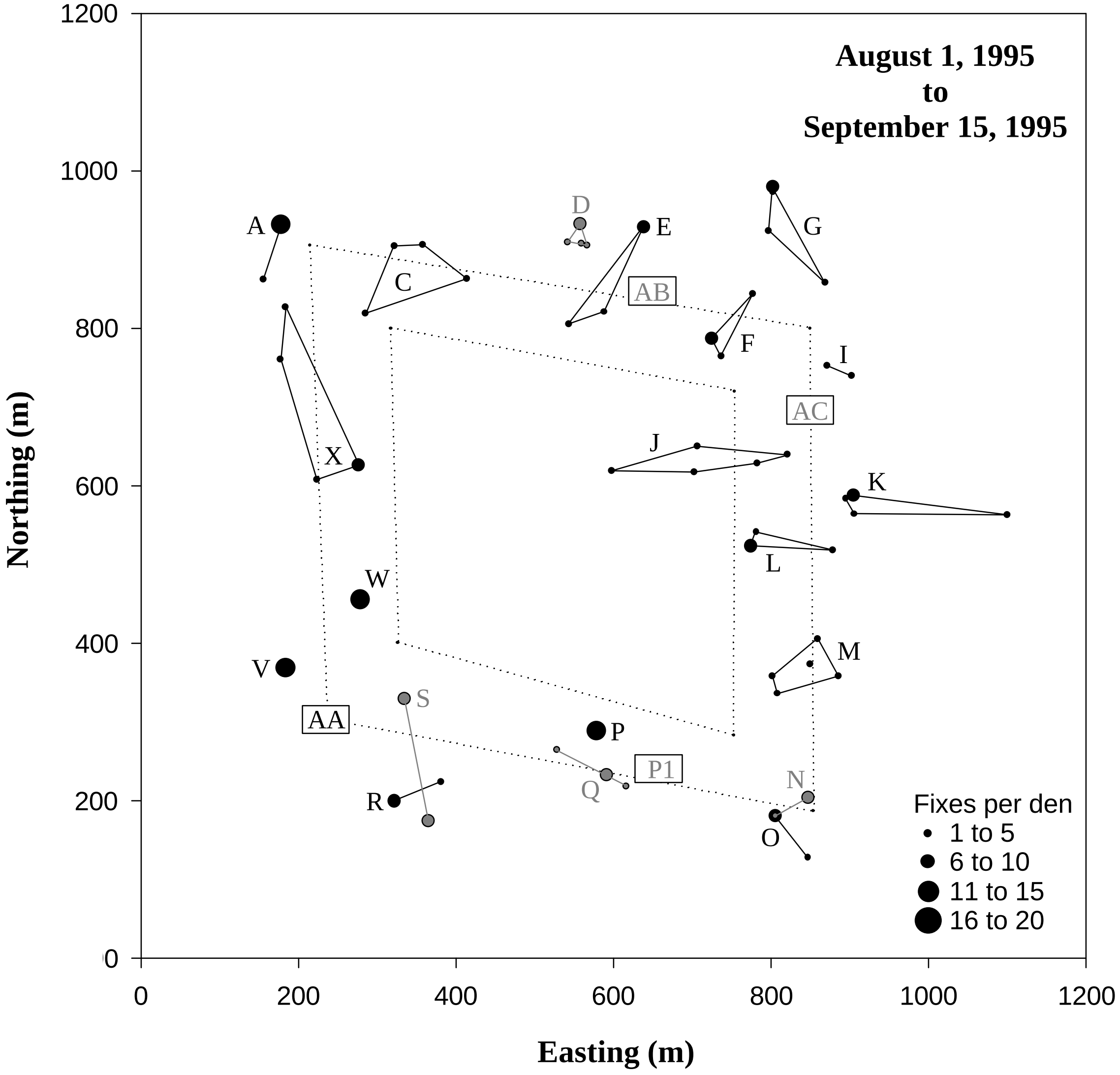

Figure 4.5. Location of all females captured, or known to be present, on the West grid, between August 1, and September 15, 1995. Polygons show the denning ranges of radio-collared females. Rectangles indicate where females were captured, but not radio-collared. Uppercase letters identify individual females (see text for details).

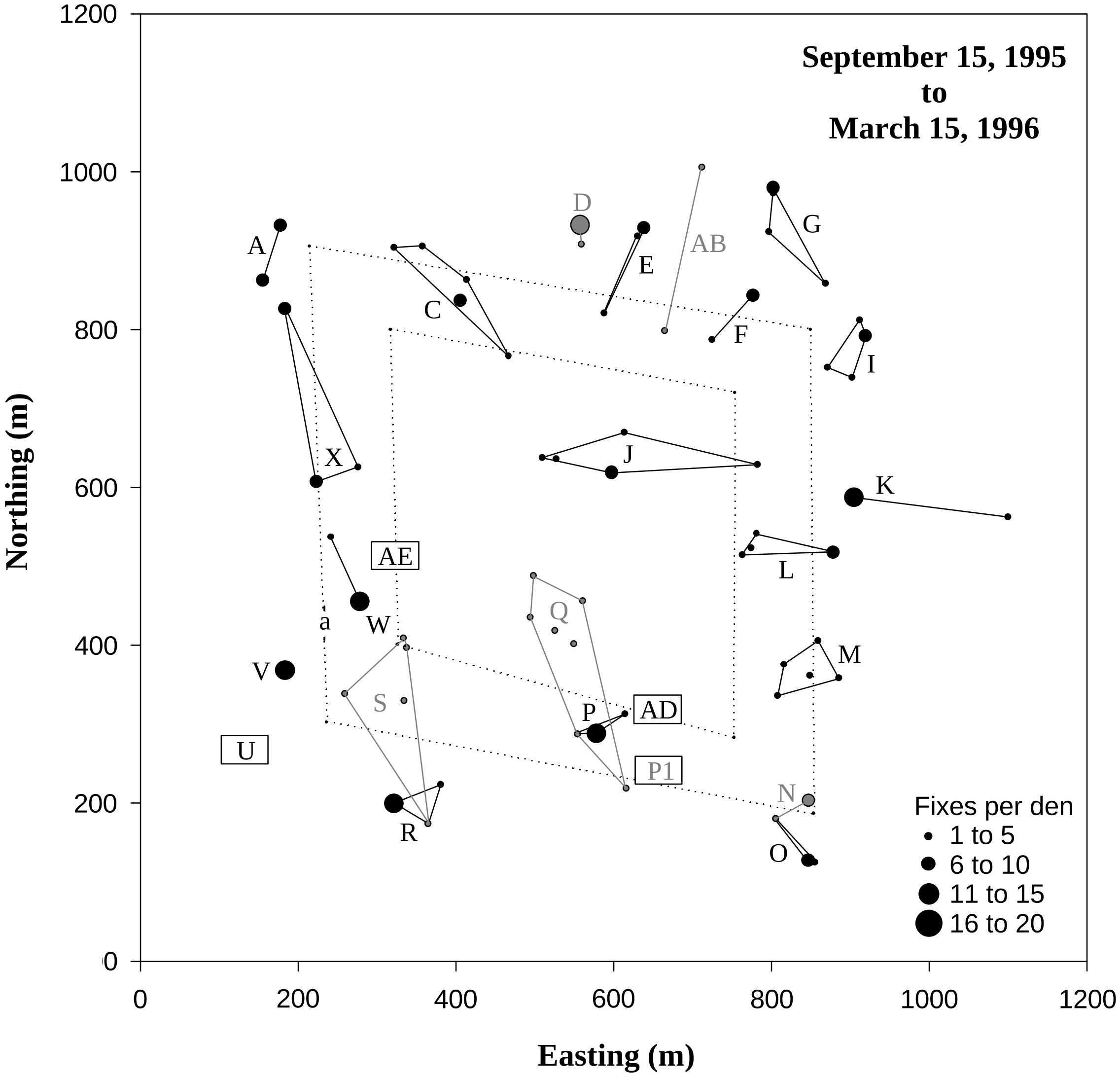

Figure 4.6. Location of all females captured, or known to be present, on the West grid, between September 15, 1995, and March 15, 1996. Polygons show the denning ranges of radio-collared females. Rectangles indicate where females were captured, but not radio-collared. Uppercase letters identify individual females (see text for details). Diamond symbols enclosing single lowercase letters indicate where unmarked possums where seen during spotlight transects.

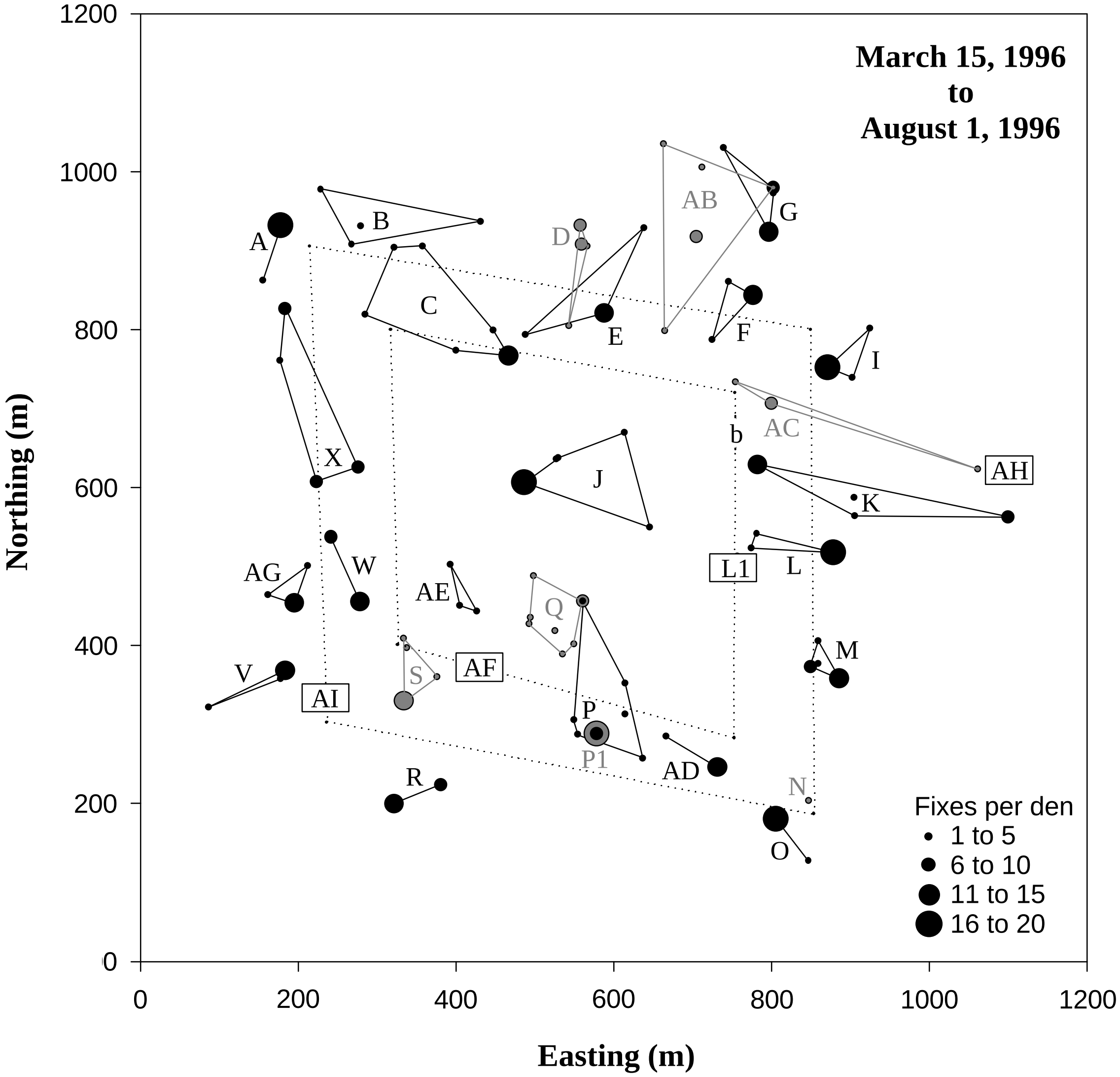

Figure 4.7. Location of all females captured, or known to be present, on the West grid, between March 15, 1996, and August 1, 1996. Polygons show the denning ranges of radio-collared females. Rectangles indicate where females were captured, but not radio-collared. Uppercase letters identify individual females (see text for details). Diamond symbols enclosing single lowercase letters indicate where unmarked possums where seen during spotlight transects.

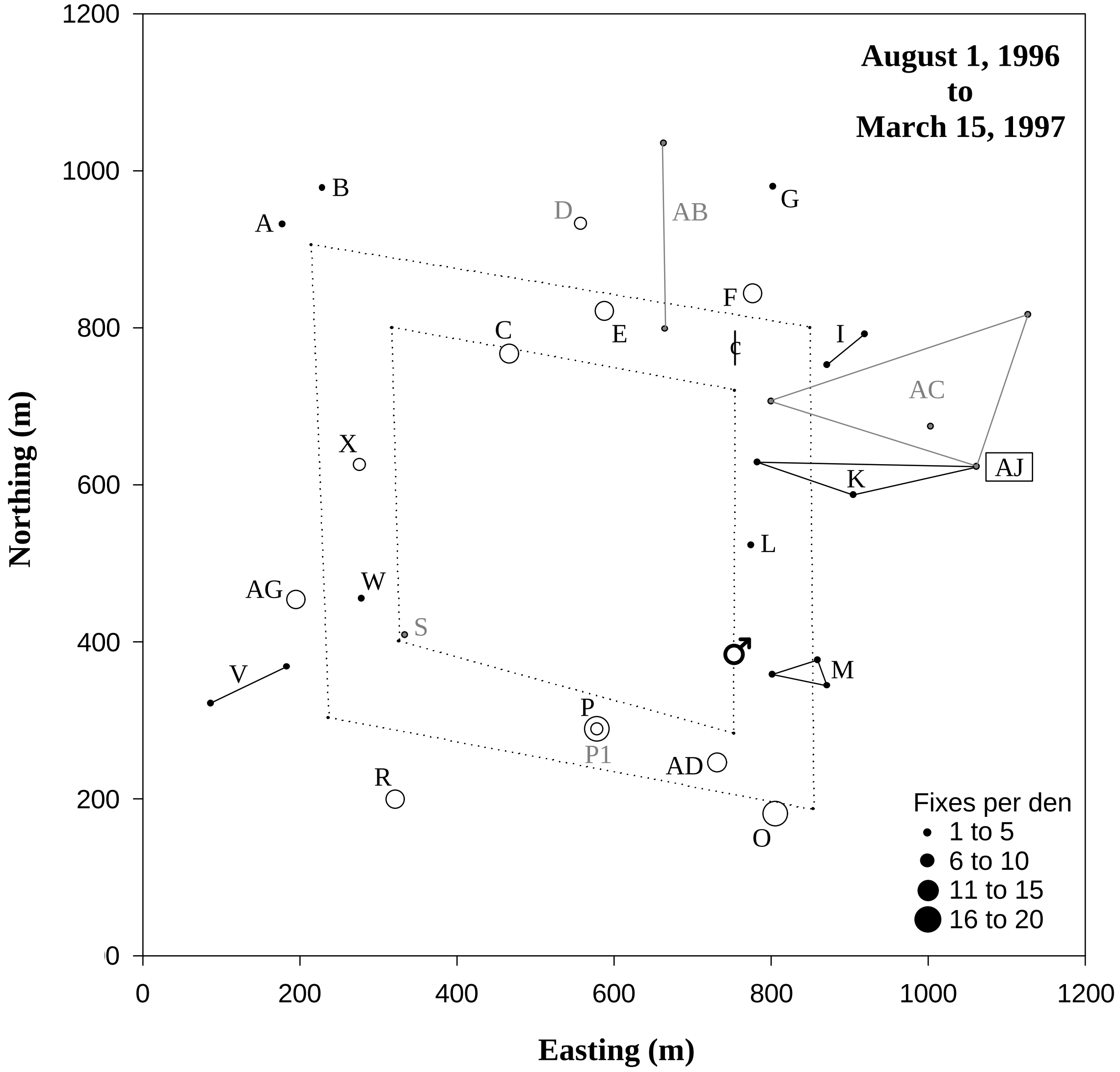

Figure 4.8. Location of all females captured, or known to be present, on the West grid, between August 1, 1996, and March 15, 1997. See caption to Fig. 4.7 for details. Open circles indicate the locations of the most frequently used dens (based on data presented in Fig. 4.7) of females that were not radio-tracked, but were known to be alive throughout part or all of the period from August 1, 1996, to March 15, 1997. The relevance of the male symbol is explained in the text.

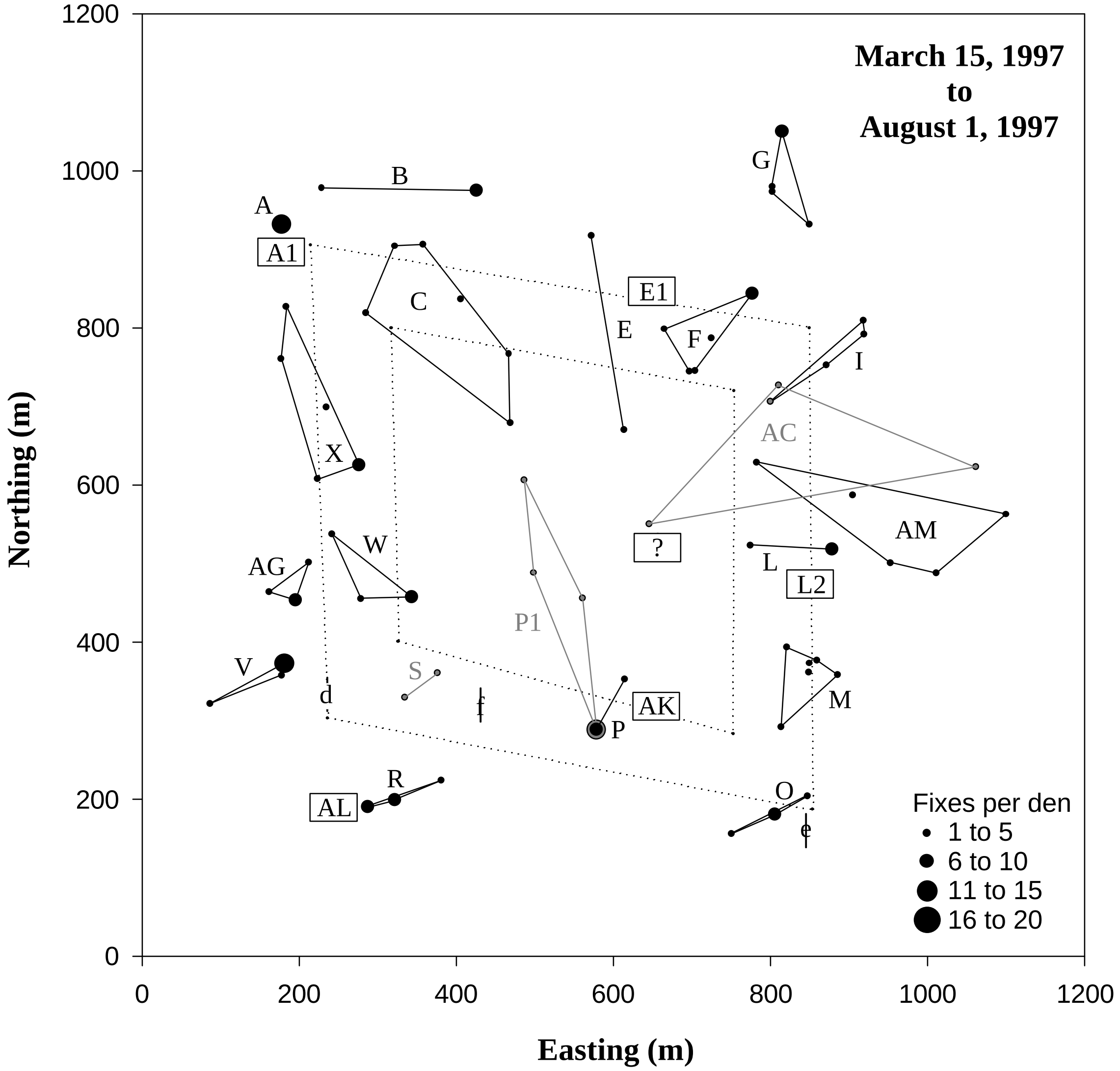

Figure 4.9. Location of all females captured, or known to be present, on the West grid, between March 15, and August 1, 1997. See caption to Fig. 4.7 for details. The rectangle enclosing a question mark indicates the location at which remains were found of an unidentifiable young of the year.

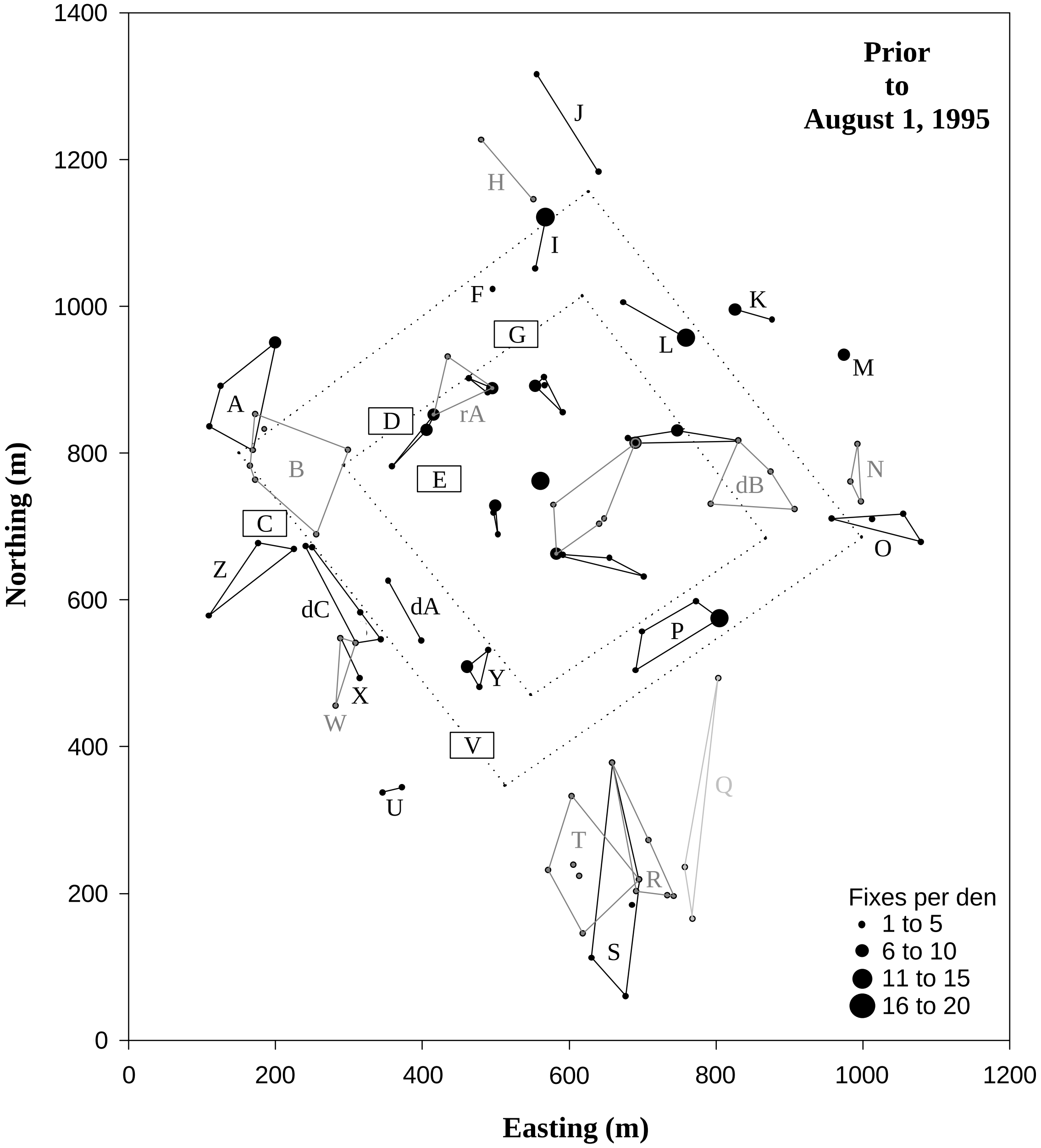

Figure 4.10. Location of all females captured on the East grid prior to August 1, 1995. Polygons show the denning ranges of radio-collared females. Rectangles indicate where females were captured, but not radio-collared. Uppercase letters identify individual females (see text for details). Polygons not accompanied by uppercase letters represent the denning ranges of core resident females removed on August 1, 1995.

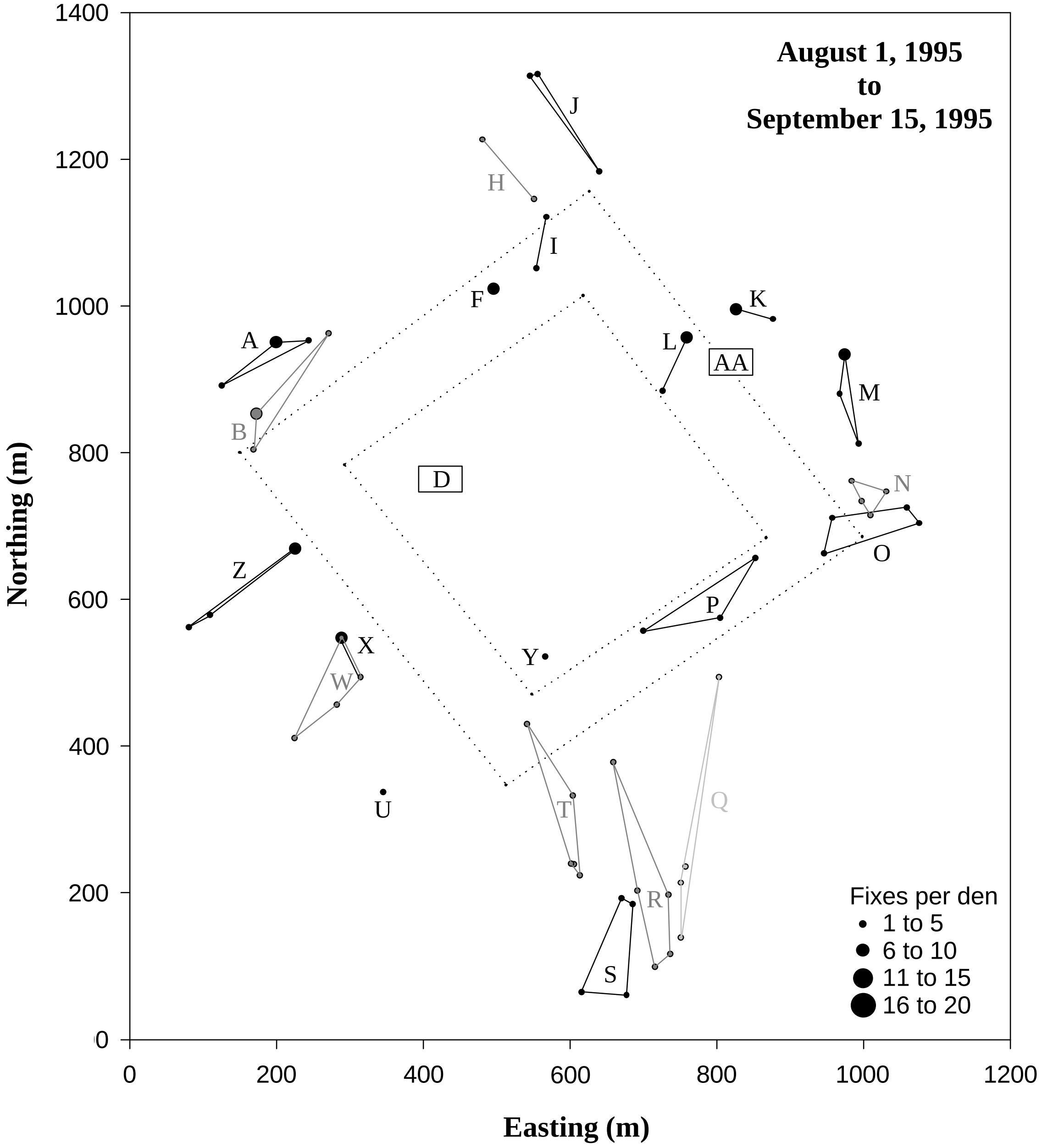

Figure 4.11. Location of all females captured, or known to be present, on the East grid, between August 1, and September 15, 1995. Polygons show the denning ranges of radio-collared females. Rectangles indicate where females were captured, but not radio-collared. Uppercase letters identify individual females (see text for details).

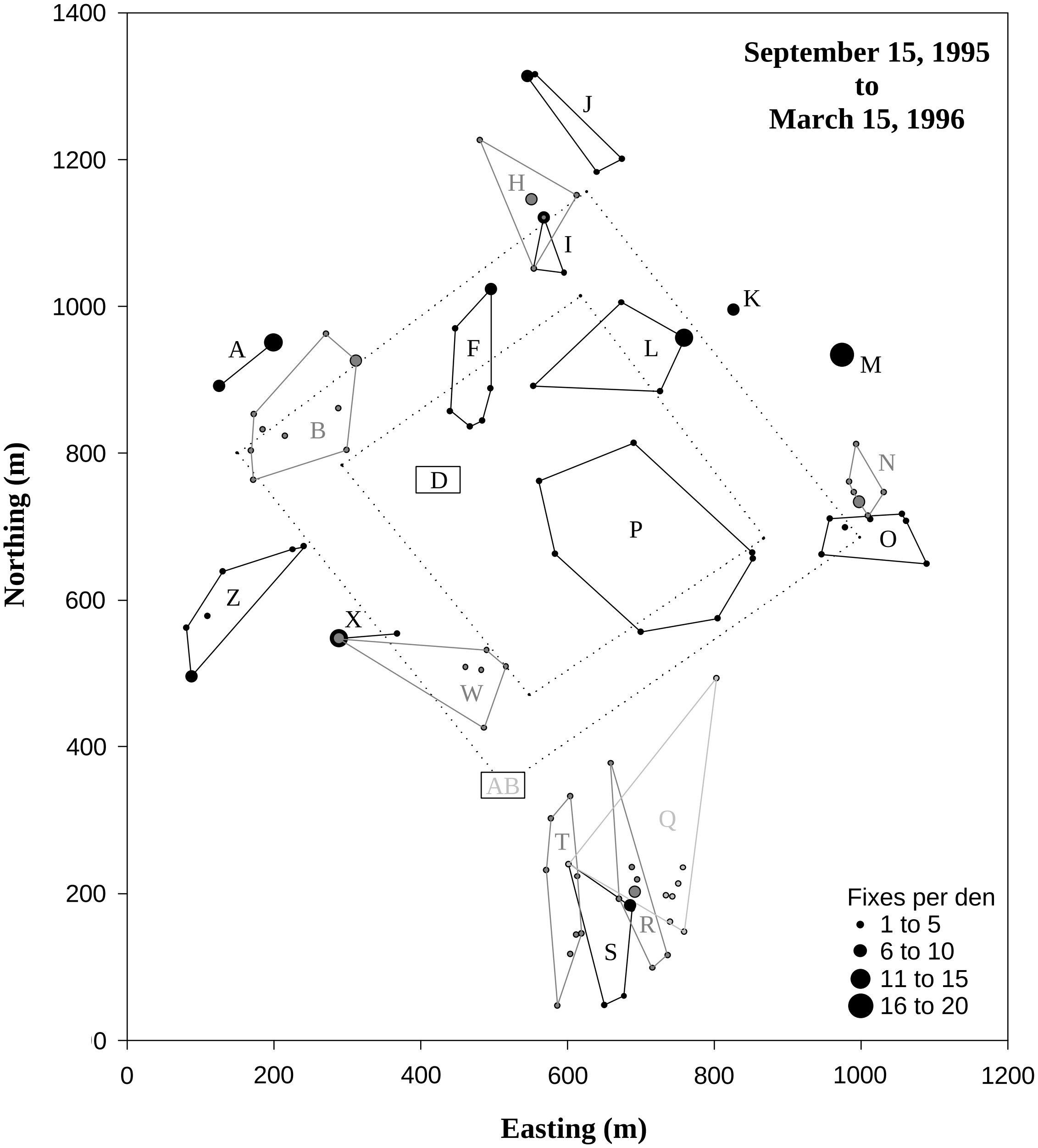

Figure 4.12. Location of all females captured, or known to be present, on the East grid, between September 15, 1995, and March 15, 1996. Polygons show the denning ranges of radio-collared females. Rectangles indicate where females were captured, but not radio-collared. Uppercase letters identify individual females (see text for details).

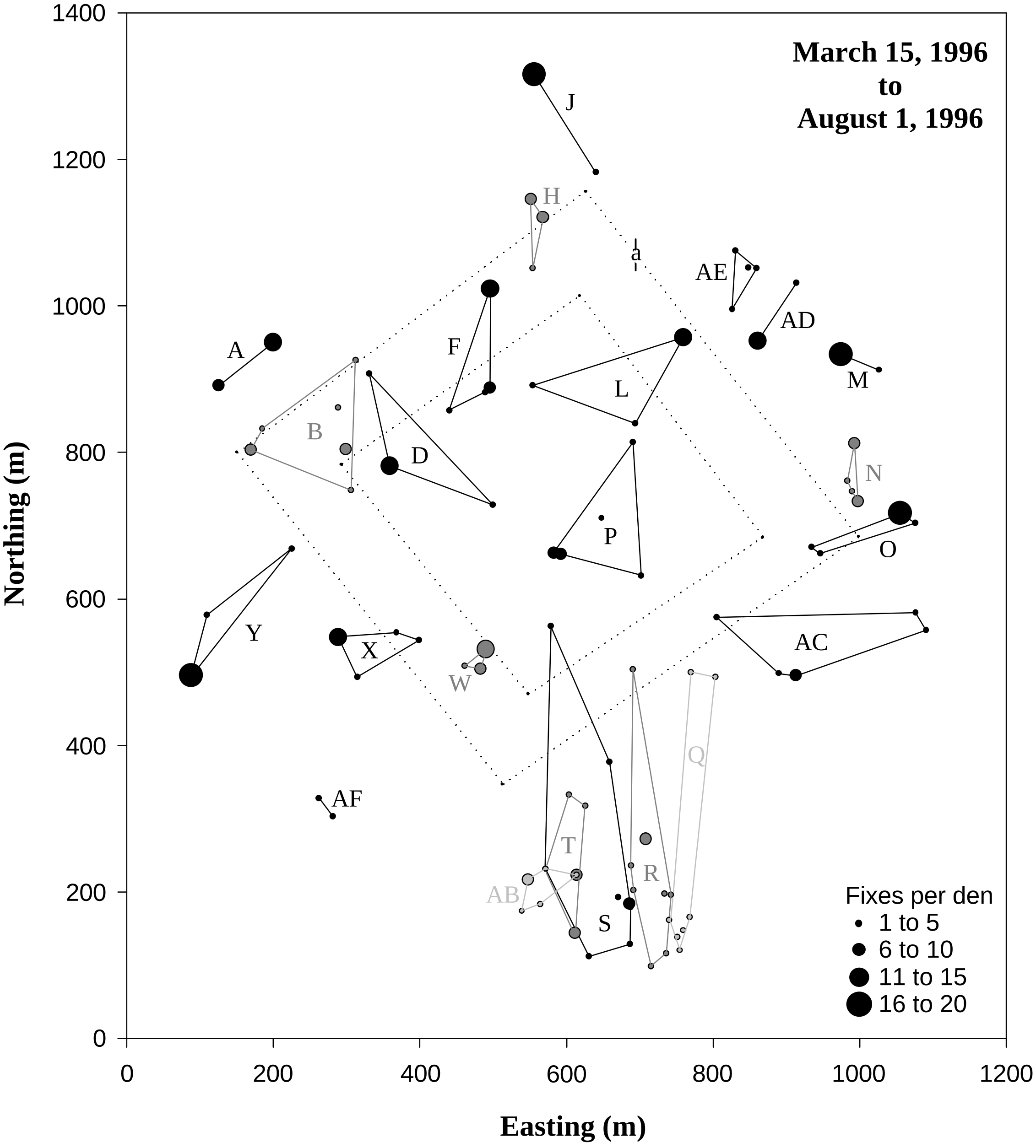

Figure 4.13. Location of all females captured, or known to be present, on the East grid, between March 15, 1996, and August 1, 1996. Polygons show the denning ranges of radio-collared females. Rectangles indicate where females were captured, but not radio-collared. Uppercase letters identify individual females (see text for details). Diamond symbols enclosing single lowercase letters indicate where unmarked possums where seen during spotlight transects.

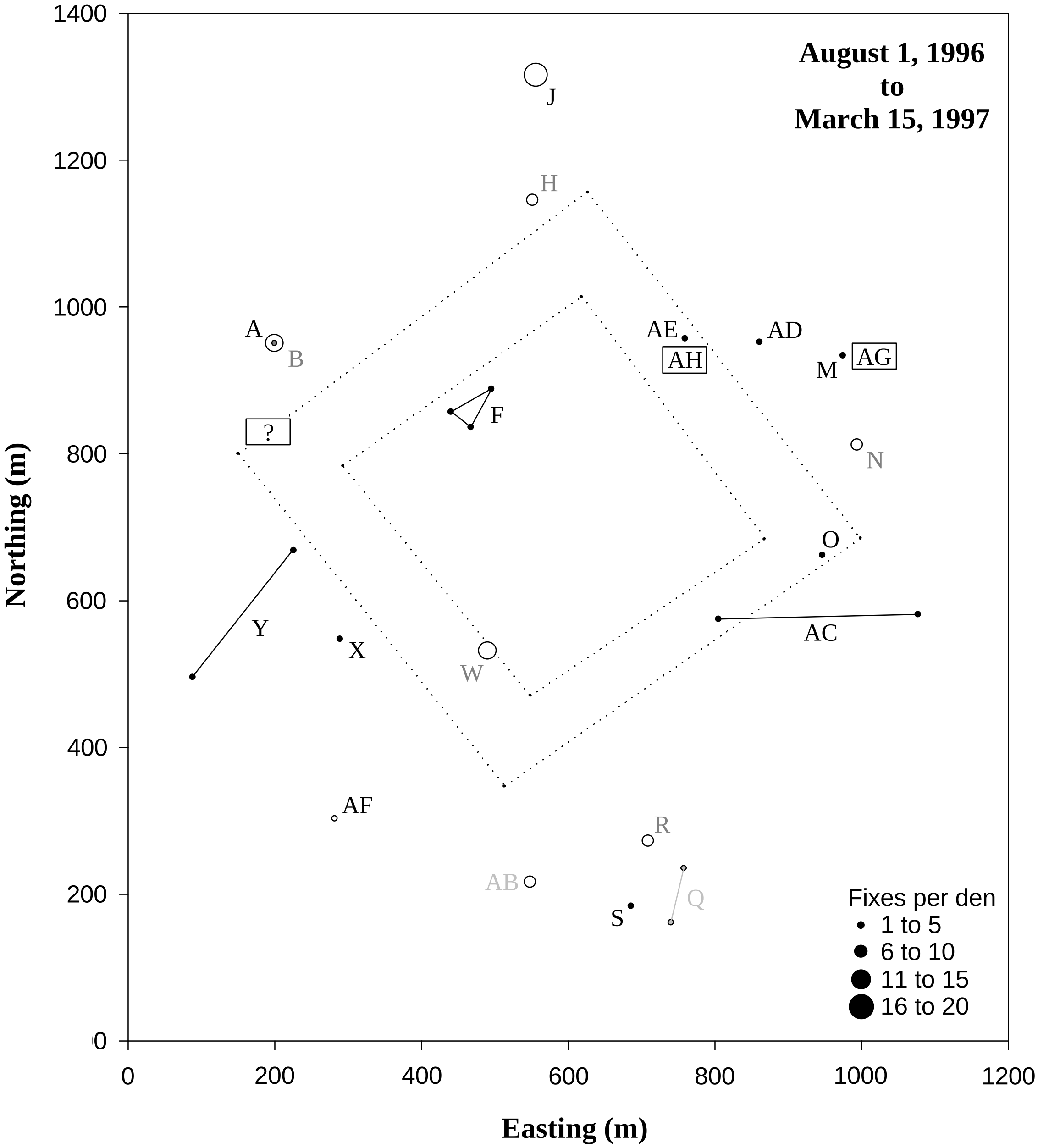

Figure 4.14. Location of all females captured, or known to be present, on the East grid, between August 1, 1996, and March 15, 1997. See caption to Fig. 4.13 for details. The caption to Fig. 4.8 explains the signficance of the open circles, and their locations are based on data presented in Fig. 4.13. The rectangle enclosing the question mark indicates the location at which remains were found of an unidentifiable young of the year.

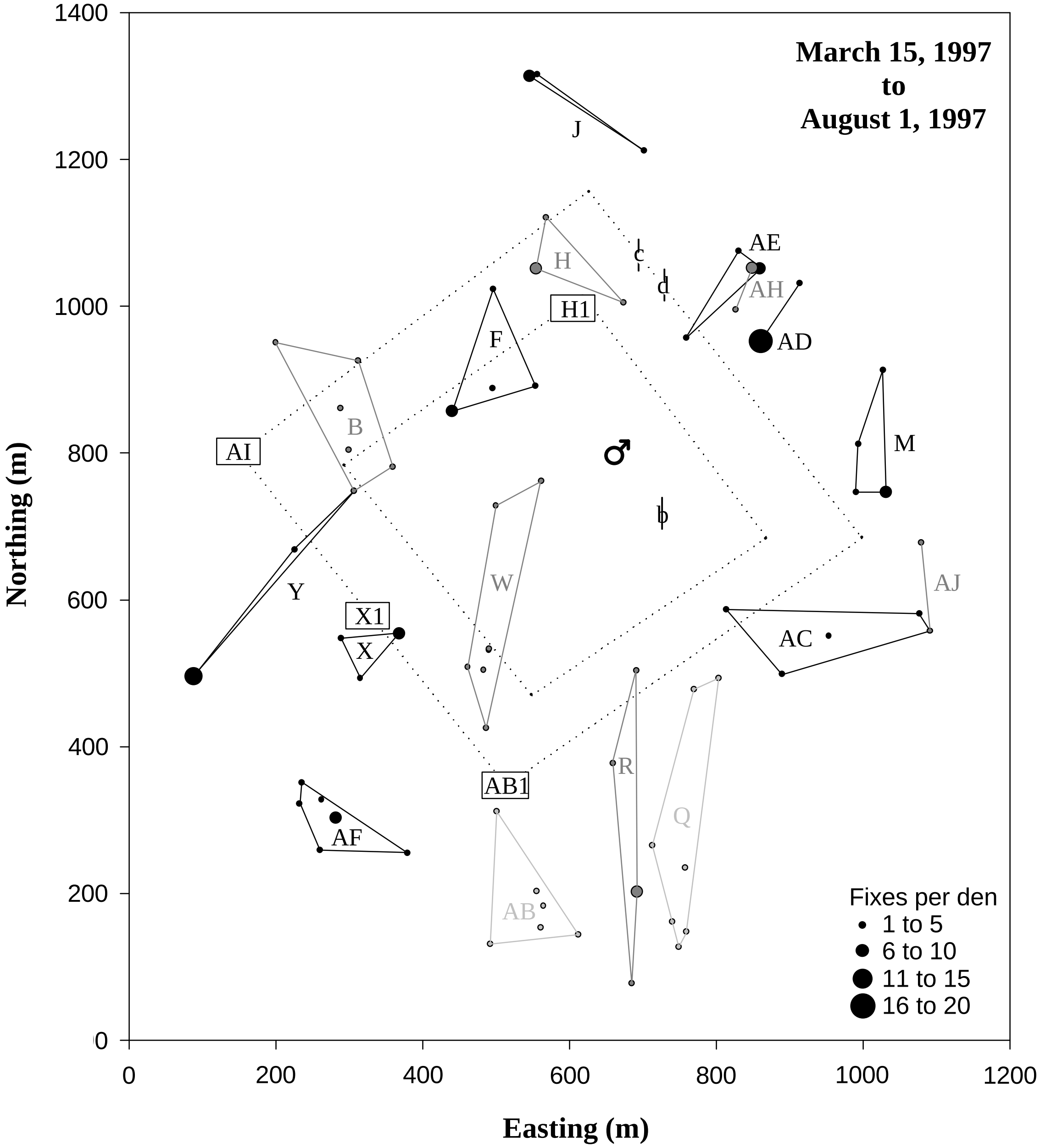

Figure 4.15. Location of all females captured, or known to be present, on the East grid, between March 15, and August 1, 1997. See caption to Fig. 4.13 for details. The relevance of the male symbol is explained in the text.

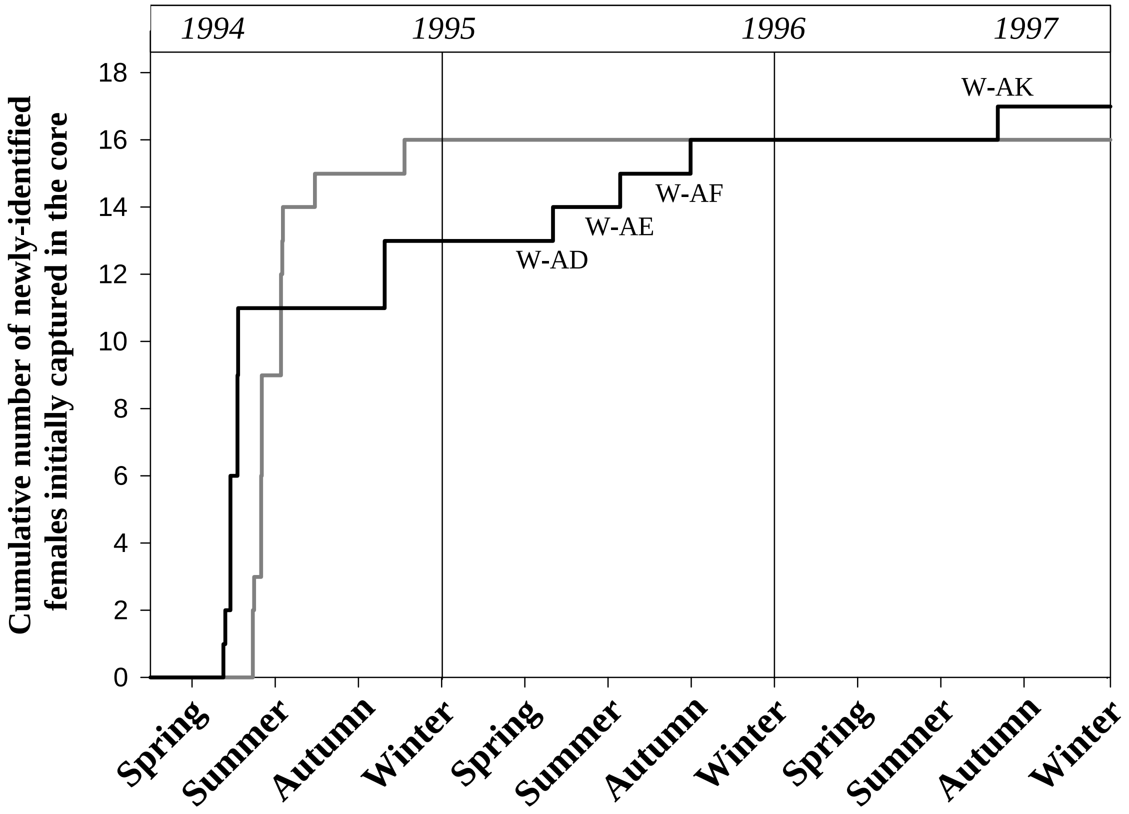

Figure 4.16. Cumulative number of newly-identified females initially captured in the core of one of the two study grids, from the start of spring 1994, until the end of the study in July 1997. The solid black line represents the number caught on the West grid, while the grey line indicates the number caught on the East grid. Letters identify individual females (see text for details). The vertical lines signify the August 1 removal of core females.

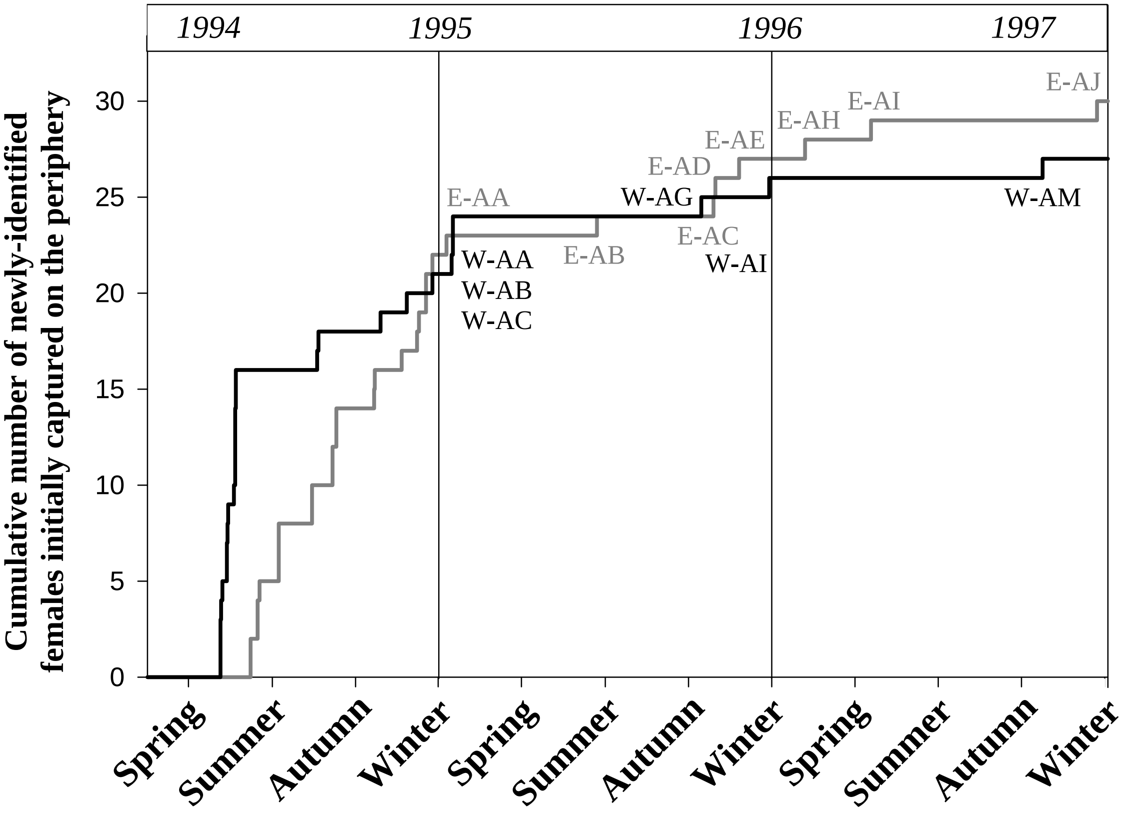

Figure 4.17. Cumulative number of newly-identified females initially captured on the periphery of one of the two study grids, from the start of spring 1994, until the end of the study in July 1997. The solid black line represents the number caught on the West grid, while the grey line indicates the number caught on the East grid. Letters identify individual females (see text for details). The vertical lines signify the August 1 removal of core females.

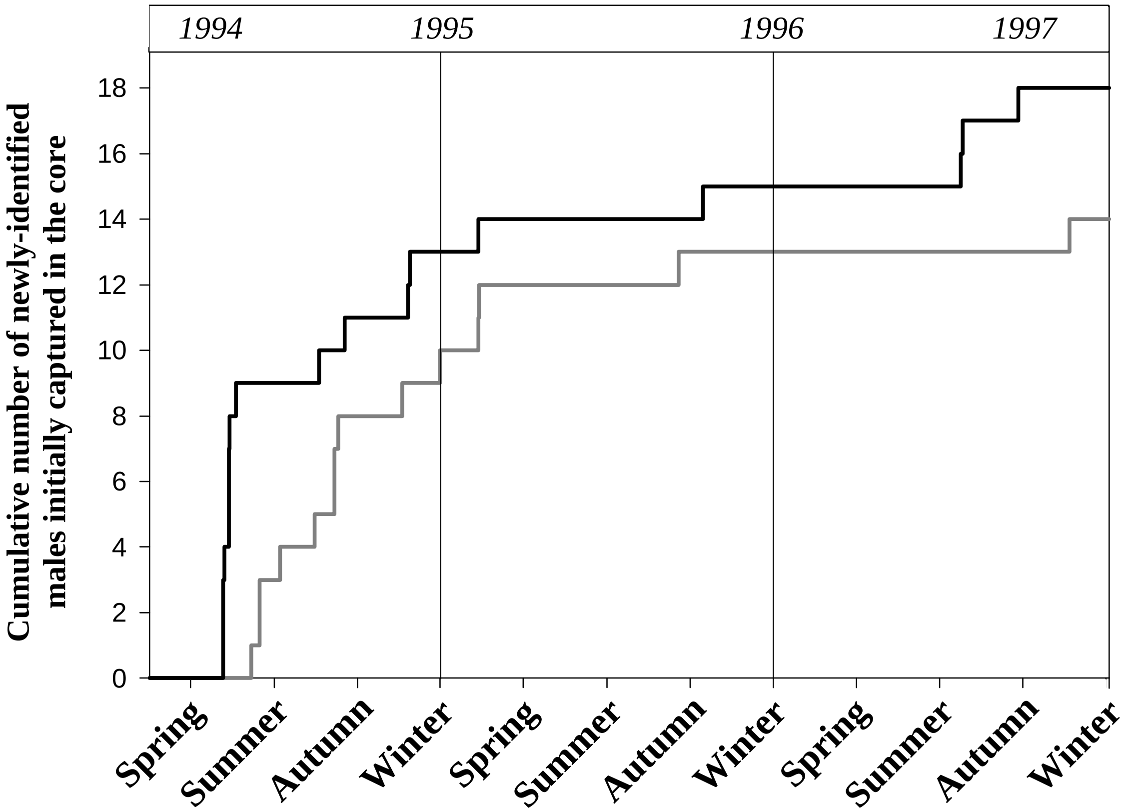

Figure 4.18. Cumulative number of newly-identified males initially captured in the core of one of the two study grids, from the start of spring 1994, until the end of the study in July 1997. The solid black line represents the number caught on the West grid, while the grey line indicates the number caught on the East grid. The vertical lines signify the August 1 removal of core females.

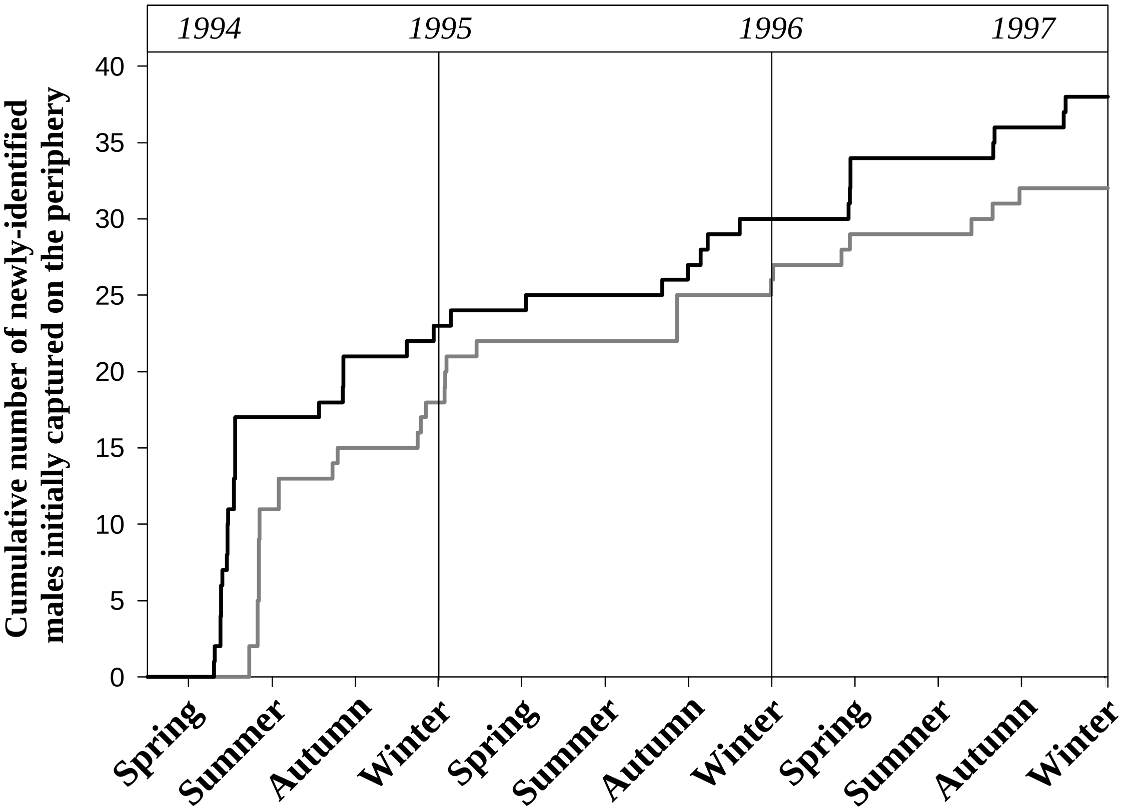

Figure 4.19. Cumulative number of newly-identified males initially captured on the periphery of one of the two study grids, from the start of spring 1994, until the end of the study in July 1997. The solid black line represents the number caught on the West grid, while the grey line indicates the number caught on the East grid. The vertical lines signify the August 1 removal of core females.

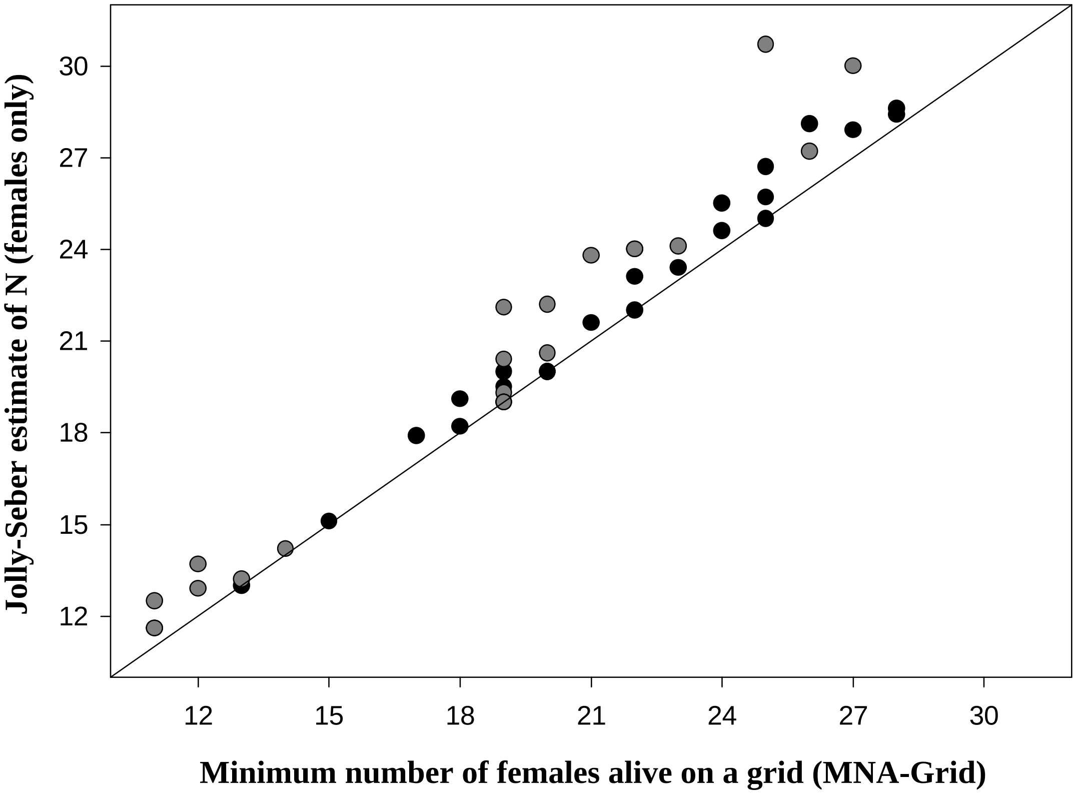

Figure 4.20. Plot of the minimum number of females known to be alive on a grid (MNA-Grid), in a given trapping session, versus the Jolly-Seber estimate of the number (N) of females present. Symbols in black signify data from the West grid, while those in grey represent data from the East grid. The diagonal line shows the expected 1:1 relationship if attempts at complete enumeration have been successful.

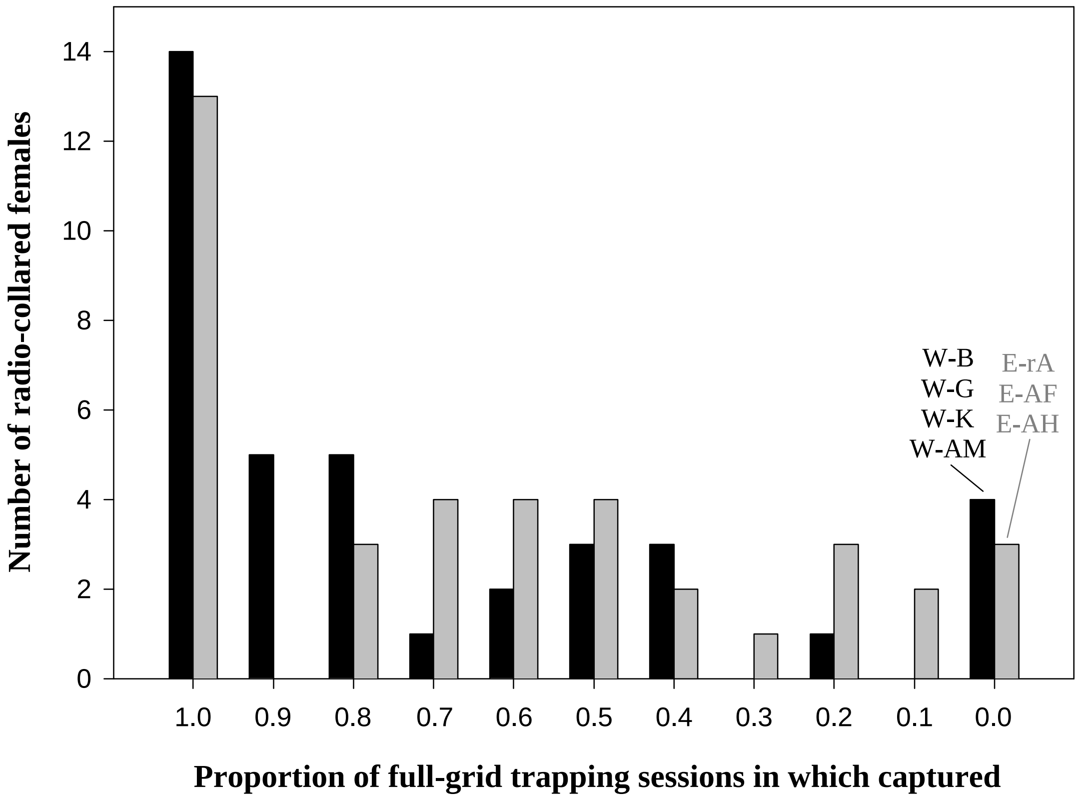

Figure 4.21. Proportion of full-grid trapping sessions during which radio-collared females were captured. Black bars signify data from the West grid, while grey bars represent data from the East grid. Letters identify individual females (see text for details).

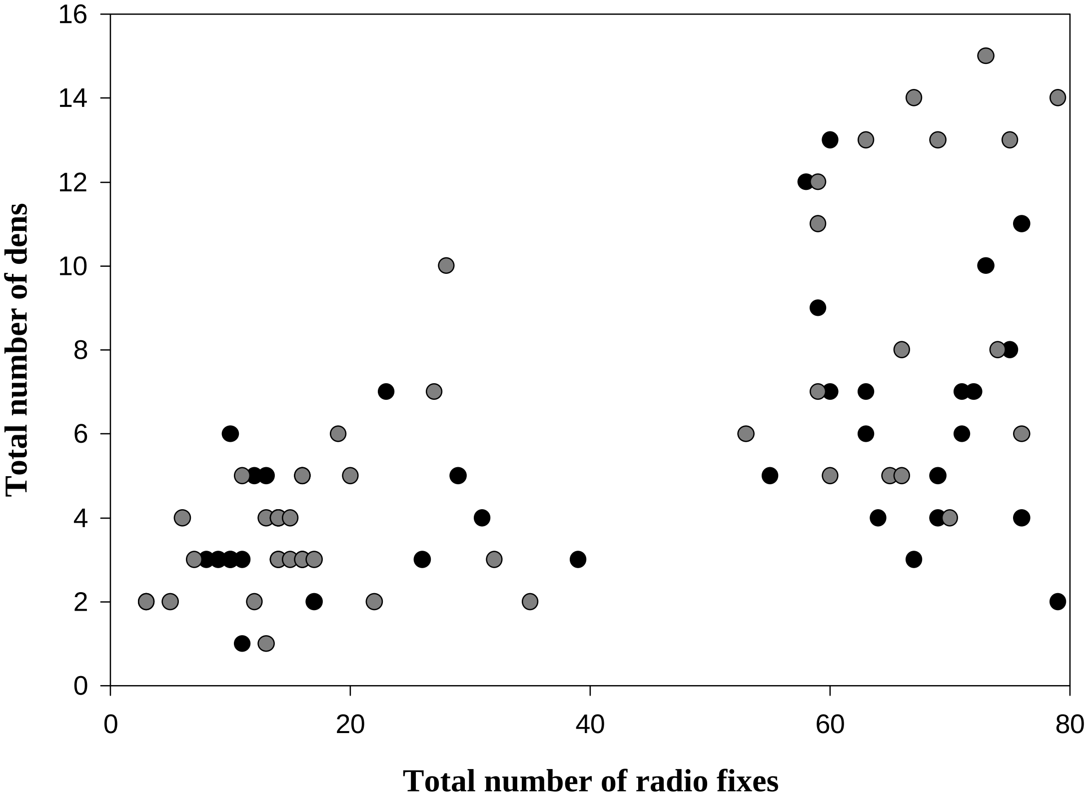

Figure 4.22. Total number of dens used by a given female as compared to the total number of radio fixes for that female. Symbols in black signify data regarding females from the West grid (N = 38), while those in grey indicate data regarding females from the East grid (N = 41).

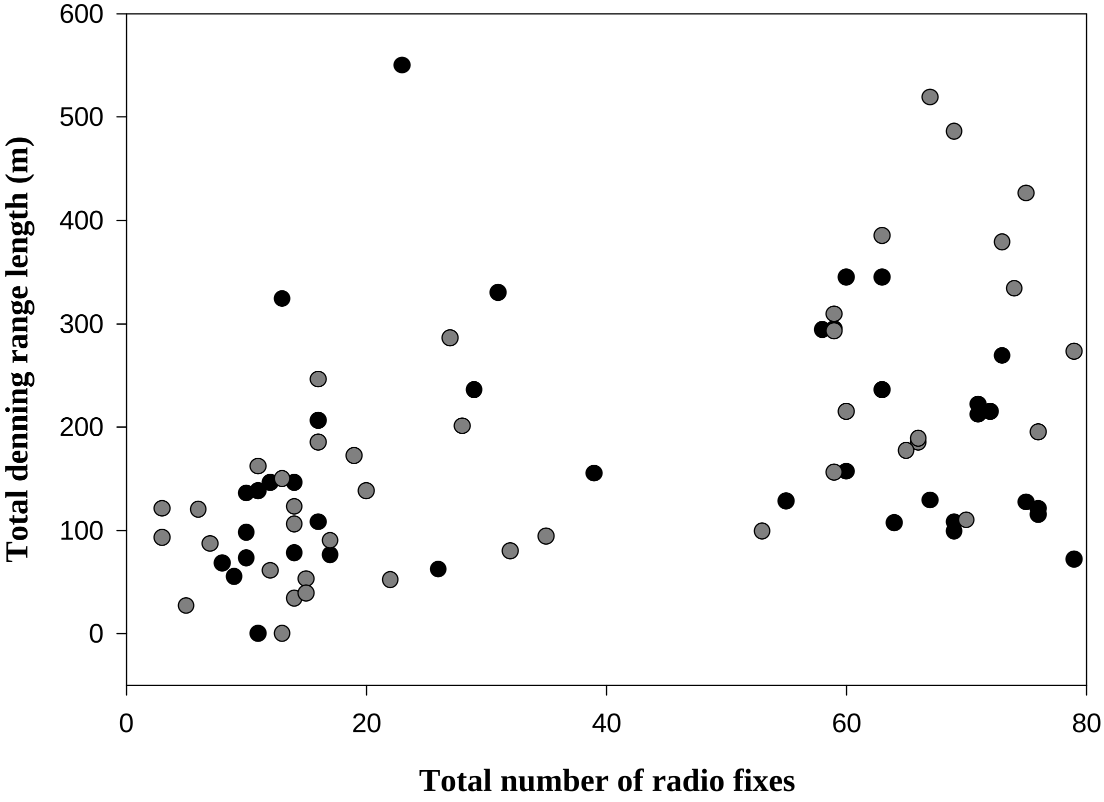

Figure 4.23. Total denning range length (the maximum distance between any two dens, in m) calculated for a given female, as compared to the total number of radio fixes for that female. Symbols in black signify data regarding females from the West grid (N = 38), while those in grey indicate data regarding females from the East grid (N = 41).

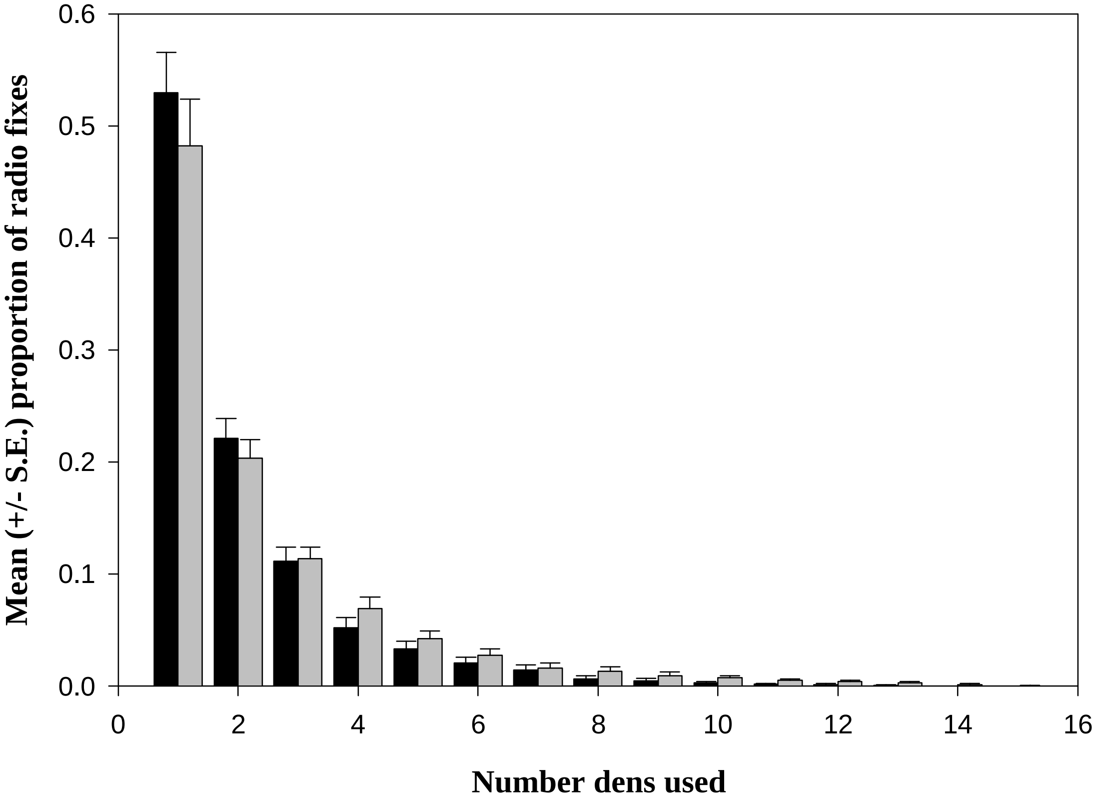

Figure 4.24. Mean (+/- S.E.) proportion of radio fixes tracked to each of the array of dens used by a given female, among females located a minimum of 15 times. Black bars signify data from the West grid (N = 27 females; minimum number of fixes for a given female was 16, maximum = 79, mean +/- S.E. = 55 +/- 4.08), while grey bars represent data from the East grid (N = 29 females; minimum number of fixes for a given female was 15, maximum = 79, mean +/- S.E. = 48 +/- 4.37).

CHAPTER 5

CONNECTIVITY OR CARNIVORY: WHAT'S MORE IMPORTANT TO THE DEMOGRAPHY OF COMMON BRUSHTAIL POSSUM POPULATIONS?

Habitat fragmentation has three major consequences: 1) habitat loss; 2) loss of connectivity; and 3) "edge effects" (Wilcove et al. 1986, Andren 1994). Species will be lost as a consequence of habitat loss if the amount of remaining habitat is less than the species' minimum area requirements. Loss of connectivity will affect movements between populations, and is thus of greatest relevance to the metapopulation dynamics of a species (Hanski 1998). Edge effects may include: greater penetration of generalist predators into remnant habitat patches; decreases in food availability within patches; and changes in habitat structure. Edge effects may affect both movements between populations, and dynamics within populations (Lidicker and Koenig 1996).

Loss of connectivity has been identified as a key factor in the decline (Morton 1990), and future conservation (Laurance 1990, Laurance and Gascon 1997, Beier and Noss 1998), of medium-sized, herbivorous, marsupials, in Australia, a group which has suffered more extinctions and declines than any other mammalian taxa (Short and Smith 1994). Others (Catling and Burt 1995, Sinclair et al. 1998) have emphasized the importance of introduced terrestrial carnivores (foxes, *Vulpes vulpes*; cats, *Felis catus*; and dingos, *Canis familiaris*), in the decline and future conservation of medium-sized Australian mammals. Morton (1990) proposed a "conceptual model" that attempted to integrate issues regarding connectivity and edge effects, as a way of explaining the precipitous decline of medium-sized Australian mammals. To address these issues, I chose to study the common brushtail possum (*Trichosurus vulpecula*) as a "model" medium-sized, herbivorous, marsupial, for reasons explained in Chapter 4.

I conducted a large-scale field experiment on common brushtail possums in old-growth Eucalypt forest in south-eastern Australia, which was designed to address the question: does immigration "rescue" populations from extinction? The study was conducted near the center of a vast (121,000 ha), largely undisturbed, wilderness area, where, it could be argued, connectivity was at a maximum, and edge effects were at a minimum (Chapter 4). In Chapter 4, I reported on the rate of female immigration recorded in response to the “pulsed” removal of resident females. Based on the results of the experiment, in conjunction with supplementary information regarding relatedness among resident females, and the primary sex ratio of pouch-young, I concluded that female immigration is generally next to non-existent in this environment. I inferred that since my study was conducted in an environment where connectivity was at a maximum, the rate of female immigration would be even lower where there were physical barriers to dispersal, as in fragmented or disturbed landscapes. My results indicate that the degree of connectivity is unlikely to have much influence on the demography of common brushtail possum populations in fragmented or disturbed landscapes. Consequently, any differences between the demography of the population I studied, in an unfragmented and largely undisturbed environment, and other populations in fragmented and disturbed environments, can be primarily ascribed to differences in the level of edge effects. From the preceding paragraph, the edge effects of most relevance will likely be those influencing the density and behaviour of introduced terrestrial carnivores.

While having declined in Australia (How and Kerle 1995, Chapter 4), common brushtail possums are considered to be a significant pest species in New Zealand, where they were introduced in the 19th century, in order to establish a fur industry (Cowan 1990). For the purposes of the fur industry, and because they are thought to have detrimental effects on forestry and agriculture, common brushtail possums have been the subject of intensive research in New Zealand (Cowan 1990), whereas there has been comparatively little research conducted on their ecology in Australia (Green 1984, Kerle 1984).

Several authors (Tyndale-Biscoe 1974, Green 1984, Cowan 1990) have reported that “disturbed” and “undisturbed” common brushtail possum populations in New Zealand demonstrate a largely consistent set of demographic differences, which I have listed in Table 5.1. The most well-studied undisturbed population in New Zealand occurs in mixed native forest in the Orongorongo Valley, near Wellington, North Island. The Orongorongo Valley population has been the subject of a live-trapping study that has continued without interruption since its initiation in 1966 (Crawley 1973, Fitzgerald 1976, Fitzgerald and Karl 1979, Humphreys et al. 1984, Efford 1998). Although no food addition experiments have been conducted, correlations between inter-annual variation in reproductive success, condition, and food supply (Humphreys et al. 1984), suggest that common brushtail possums in undisturbed populations in New Zealand are primarily food limited (Green 1984, Cowan 1990). This interpretation is supported by the fact that the effect of introduced terrestrial carnivores (cats, *Felis catus*; and dogs, *Canis familiaris*) on these populations appears to be very slight (Fitzgerald and Karl 1979, Efford 1998).

A “disturbed” population in New Zealand is, for the most part, a euphemism for a hunted population. Human hunting can be seen as analogous to a predator addition or removal experiment. According to Cowan (1990, p. 88), the low fecundity and delayed maturation characteristic of the reproductive biology of undisturbed possum populations (Table 5.1), shifts to the pattern of high fecundity and early maturation typical of disturbed populations (Table 5.1), following the onset of hunting in an area, and then shifts back to the earlier pattern of low fecundity and delayed maturation, following the cessation of hunting. Increased reproductive output in response to hunting pressure is the expected outcome in all wildlife harvesting operations (Caughley and Sinclair 1994, p. 281).

Green (1984) reviewed the results of seven studies conducted on common brushtail possum populations distributed over a wide geographic range in south-eastern Australia. The studies were conducted on farms (Smith et al. 1969, Winter 1976), in forestry plantations (Hocking 1981, cited in Humphreys et al. 1984; How 1981), or in city suburbs (Lyne and Verhagen 1957, Pilton and Sharman 1962, Dunnet 1964). The results from all seven studies indicated that the reproductive biology of common brushtail possums in south-eastern Australia most closely resembles that of disturbed populations in New Zealand (Table 5.1). Green inferred from this that the demography of undisturbed populations in New Zealand was, in a sense, “unnatural”. Cowan (1990, p. 95) reiterated Green’s argument, in stating that “density in Australia is controlled largely by social behaviour (e.g., residents commanding key resources, such as dens, and expelling transients and immatures; Winter 1976), whereas [undisturbed] New Zealand populations are limited more by food than by behaviour”. Green’s hypothesis was that the open Eucalypt forests of Australia, in which common brushtail possums evolved, are effectively a “2-dimensional habitat” (Green’s term), in which it is possible to defend exclusive areas, whereas spacing behaviour becomes ineffective in the more complex, “3-dimensional”, native forests of New Zealand, and population densities increase to the point at which they are food limited.

In this Chapter, I report on the reproductive biology of common brushtail possums at my study site (Paddys Land), in south-eastern Australia. Contrary to the results of previous studies in south-eastern Australia, the reproductive biology of common brushtail possums at the Paddys Land site demonstrated all of the patterns characteristic of undisturbed populations in New Zealand (Table 5.1). Moreover, there was a remarkably close correspondence between the values of the various measurements I recorded, and those reported for the Orongorongo Valley population. I evaluate the likely causes of inter-annual variation in reproductive success, and suggest that common brushtail possums at the Paddys Land site, like those at the Orongorongo Valley site, are primarily food limited. I propose that the principal reason for the different demography of common brushtail possums at the Paddys Land site, as compared to other sites in south-eastern Australia, is that possums at other sites are subject to a greater rate of "harvesting" by introduced terrestrial carnivores. I discuss the implications of this for the conservation of medium-sized, herbivorous, marsupials, in general.

METHODS

Details regarding the study species, study site and general methodology were discussed in Chapter 4. Animals that were captured and released were either trapped or darted. Handling, as regards females, is here defined as making a visual inspection of the interior of the pouch. Females that were trapped more than once during a standard, full-grid trapping session, were generally only handled on the first occasion. On subsequent occasions during the trapping session the individual's ear-tag numbers were read through the bars of the trap and the animal was released without further processing. On all occasions when females were captured by darting, they were handled, held until the tranquilizer had worn off, and then released.

I recorded the date, location and circumstances, in all instances where I either saw, heard or observed signs of potential predators. I also attempted to identify the predator involved in all cases where possums were attacked in traps, or where they were apparently killed by a predator (Chapter 6).

Age estimates from cementum annuli

In all cases where animals were found dead, I attempted to retrieve the teeth from the animal's lower jaw. Previous studies on common brushtail possums (Pekelharing 1970, Clout 1982), using known-age samples, have shown that the number of layers in the cementum cushion between the roots of each tooth can be used to determine the animal's age, in years. As it is well-established that new cementum layers are deposited on a yearly basis, these can be justifiably referred to as cementum annuli (Pekelharing 1970, Clout 1982).

I retrieved teeth from a total of 40 animals. I removed the first premolar (PM1) and third molar (M3) from the right lower mandible. Each tooth was assigned a randomly-selected number, and then all of the teeth collected (80 in total) were sent to Matson's Laboratory (Milltown, Montana, U.S.A.; [http://www.matsonslab.com]) for microscopic examination of the number of cementum annuli. Two serial sections were made of each tooth in this initial batch. Matson's Laboratory was not informed as to which two teeth belonged to the same animal, allowing me to conduct a blind test of the reliability of the results. The age estimates were highly correlated ($r^2 = 0.81$, $t = 12.61$, $df = 40$, $p < 0.0001$). In the majority of cases (80 %), the age estimates were either the same, or they differed by as little as one year (Fig. 5.1). In four cases (10 %) there was a discrepancy between the age estimates of three or more years (Fig. 5.1).

A second batch of teeth (12 in total) was sent to Matson's Laboratory, consisting of the first premolar (PM1) and third molar (M3) removed from the left lower mandible of each of the four animals for which there was a discrepancy between age estimates of three or more years in the first batch, along with teeth from two other animals. Six serial sections were made of each of the teeth in the second batch to ensure greater accuracy (Clout 1982), given the initial discrepancies. As with the first batch of teeth, Matson's Laboratory was not informed as to which two teeth belonged to the same animal. The previous discrepancies were either eliminated or greatly reduced in the results from the second batch (Fig. 5.1).

I used the following protocols to assign a single age to each of the 40 animals whose teeth were examined: 1) I ignored estimates from the first batch of teeth examined if age estimates were also available from the second batch; and 2) where discrepancies existed within a batch, I used the higher of the two estimates, under the assumption that cementum layers are more likely to be overlooked than they are to be misidentified (Clout 1982).

Date of birth of pouch-young

To evaluate the seasonality of births, and survival of young, it was necessary to assign a date of birth to each pouch-young observed during the study. For very small pouch-young, age in days was estimated from crown-rump length (mm), using the nomogram developed by Lyne and Verhagen (1957, their Fig. 7). For larger young, age in days was estimated from head length (mm), using Equation 1:

$$\text{Days} = -\,2.50757 + 1.99855\ (\text{Head}) + 0.01216\ (\text{Head}^2)$$

Details regarding the derivation of Equation 1, and the protocols adopted, are presented in Appendix 2.

RESULTS

Seasonality of births

Of the 152 dependent young for which a date of birth was identified, 147 (96.7 %) were born in autumn, and 5 were born in winter (Fig. 5.2). This very closely resembles the situation in the Orongorongo Valley, where about 95 % of births occur in autumn (Efford 1998, his Fig. 1). Two of the 5 winter-born young at the Paddys Land site were “replacement” young (Fig. 5.2), as the mothers of these young had already produced a pouch-young in autumn, which was lost, and then “replaced” by the new, winter-born young. I use the term “primary” young, in contrast to “replacement” young, to refer to a pouch-young produced by a female that has not yet given birth within the calendar year in question. “Double breeding” refers to situations in which a female gives birth to a young in early autumn, successfully raises it to weaning, and then gives birth to a second young in the spring of the same year (Green 1984, Kerle 1984). There were no instances of “double breeding” observed at the Paddys Land site. Similarly, Crawley (1973, p. 88) reported that “double breeding” was never observed during the first few years of the Orongorongo Valley study, and this would also appear to be true of later years, as Efford (1998, p. 513) noted that the 0.8 % of births in the Orongorongo Valley that occurred as late as September (see also Cowan 1990, his Table 19) all involved “replacement” young.

There was a great deal of variation among females as to when they gave birth to their primary young (Fig. 5.2), with births being separated by up to 115 days (on the East grid in 1995). In contrast to the variation between females, there was very little variation in median birth dates (Fig. 5.2) across years (Kruskal-Wallis H = 1.20, N = 150, df = 2, p = 0.5495) or between study grids (Mann-Whitney U = 2642.0, z = 0.60, p = 0.5516). The median birth date of primary young at the Paddys Land site was around the third week of April, the exact date differing slightly depending on year and study grid (Fig. 5.2). Efford (1998,

p. 504; see also his Fig. 1) reported that that the annual median birth date in the Orongorongo Valley varied between April 18 and May 14.

Almost all adult females at the Paddys Land site produced a single pouch-young each year (Table 5.1). Among radio-collared, resident, adult females, there were 144 cases (96.0 %) where the female gave birth in either autumn or winter, and only 6 cases where she did not do so (Table 5.2). Four of the six non-breeding females died during the breeding season: one was killed by a predator, another died from a massive *Ophidascaris robertsi* infection (Chapter 6), the third was observed to be both “rumpy” and “bony”, and the fourth was observed to be “weak and wobbly”. As documented in Chapter 6, survival among females observed to be both “rumpy” and “bony”, and females observed to be “weak and wobbly”, was significantly poorer than among females that never demonstrated these symptoms of poor condition. Two females survived throughout the breeding season but apparently did not give birth. One of these two surviving females had been attacked by a predator in mid-February and was severely injured. The final “non-breeding” female may actually have given birth and lost her pouch-young before she was first captured in mid-June, as she was recorded at this time as having an engorged mammary gland, although she was not lactating. A different female was known to have given birth and lost her young prior to the end of June, indicating that the “true” autumn birth rate may be slightly underestimated if judged solely on the presence or absence of a pouch-young in late June. Efford (1998, p. 510) reported that 90.4 +/- 6.0 % (mean +/- S.D.) of adult females trapped in the latter half of June at the Orongorongo Valley site were found to possess pouch-young.

Sex ratios of dependent young

The sex of dependent young was identified whenever possible. As with measurements of head length it was not always possible to check the sex of the young because: 1) the pouch-young was judged to be too small to safely handle; or 2) the mother was struggling too much. The sex of young cannot be identified reliably prior to 14-21 days of age (Tyndale-Biscoe 1955). In most cases estimates of head length were easier to accomplish than examinations of sex because the head of the pouch-young generally lies adjacent to the opening of the pouch while the hind limbs are nestled in the folds of the pouch.

Sporadic examinations were sufficient to identify the sex of 94.0 % of young in 1996 and 1997 (Table 5.3). However, the unanticipated, poor survival of pouch-young in 1995 (described later) meant only a handful of young were examined for sex prior to their disappearance (Table 5.3). Fewer than half of the young seen during the vehicle trail trapping session in Oct.-Nov., 1996 (Fig. 4.1), were sexed (Table 5.3), because my objective was simply to check for the presence or absence of young. My aim in trapping along the vehicle trail was to assess the reproductive success of females that had not been previously captured and handled, and I wanted to minimize the level of stress experienced by these animals, in case I decided to trap along the vehicle trail trapline at some later date.

A log-linear analysis of the sex ratio of primary young, by study grid (West, East) and year (1995, 1996, 1997), revealed a significantly male-biased sex ratio, independent of study grid or year (Table 5.3; see also Table 5.1). Hope (1972) reported differential mortality between the sexes during pouch life, with the proportion of males decreasing significantly with increasing age. The sex of many of the dependent young at the Paddys Land site was not identified until late in pouch life, or when they were already back-young. If the phenomenon Hope (1972) described applied at the Paddys Land site, then the magnitude of the male bias in the sex ratio reported in Table 5.3 is potentially an underestimate. Efford (1998, p. 510) reported a significantly male-biased sex ratio of pouch-young in late June at the Orongorongo Valley site.

Stages in the weaning of young

Young possums can potentially breed when they are a year old (Green 1984). Whether the young survives to this age is in part a function of the mother's survival, at least until the young is weaned. Unfortunately, differentiating between pre-weaning and post-weaning survival is not straightforward. Young in the pouch can be classified as pre-weaning (Kerle and Howe 1992). Young that have permanently left the pouch and begun riding on their mother's back may or may not be weaned. Kerle and Howe (1992) suggested that the initiation of weaning begins no earlier than 175 days of age, about 25 days after the young has begun riding on its mother's back. It is not clear from the literature what the minimum age is at which weaning can be said to have been completed, and the young could survive on its own. Kerle and Howe (1992) stated that the young is weaned between 175-240 days of age, whereas Smith et al.

(1969) suggested that young are weaned completely between 220-290 days of age. If a back-young is present and the mother is still nursing, then it is likely the young is still largely dependent on its mother.

Another complication is that nursing mothers may leave their older dependent young in the den while they forage (Winter 1976, p. 246). In addition, Winter (1976, p. 250) reported that young began to be seen at night independent of their mothers, while still sharing their mother's den, once the young was 200 days of age. Consequently, a stage will be reached when mothers may be seen to be nursing, in the absence of their young being present. Only when the young is seen after the mother is known to be no longer nursing can the young be truly classified as having survived to the post-weaning phase of development.

Figure 5.3 illustrates all relevant observations made at the Paddys Land site concerning the timing of the three stages in the weaning of young: 1) together with the mother and still nursing; 2) separate from the mother but still nursing; and 3) separate from the mother and no longer nursing. The earliest a dependent young was first seen out of the pouch and riding on its mother's back was at 172 days of age. The earliest a nursing mother was seen without her young was when the young was 183 days old. The latest a mother was seen to be still nursing was when the young was 287 days old. The earliest a surviving young was known to have been completely weaned was at 202 days of age, however, the next earliest, among the other 14 young known to have survived to independence, was at 271 days.

Pre-weaning survival of young

Pre-weaning survival depends in part on the mother's survival, which could be checked on a weekly basis simply by tuning into her radio frequency. To evaluate the fate of the young required that the mother be captured and examined. Given the irregularities in the frequency of captures the most sensible way to deal with data concerning the pre-weaning survival of the young itself was to judge whether or not the young had survived to some threshold age.

Smith et al.'s (1969) suggestion that young are completely weaned (stage 3 in the process of weaning) between 220 and 290 days of age is clearly an overestimate as regards at least some of the young at the Paddys Land site (Fig. 5.3). At the same time, Kerle and Howe's (1992) suggestion that the process of weaning begins at 175 days, 25 days after the young leaves the pouch and begins riding on its mother's back, may be overly conservative, as young at the Paddys Land site were only just emerging from the pouch at 175 days (Fig. 5.3). Given these alternatives, I decided to err on the side of caution and set the minimum threshold for pre-weaning survival at 175 days. Females observed to be without a young and no longer nursing prior to 175 days after the birth of their young were judged to have lost their young prior to weaning.

Results regarding pre-weaning survival in the two complete years for which data were available are presented in Table 5.4. The longer a young survived the more likely it was to be seen alive. Once seen, the young's survival could then be "back-dated". A young seen on day 200 obviously survived to day 175. Since young generally survived longer in 1996, more of them were seen alive. Consequently, there were fewer young for which it was unknown (the "?" column in Table 5.4) whether they survived to 175 days. The survival of such "back-dated" young is a function of both the likelihood of pre-weaning survival as well as survival during and after weaning. Pre-weaning survival, in and of itself, can only be evaluated by limiting consideration to those young known to have been lost prior to 175 days of age (the "No" column in Table 5.4). Pre-weaning survival was significantly poorer in 1995 than in 1996 (Table 5.4, see also Table 5.1). There was an almost significant three-way interaction in the relevant log-linear analysis, with the difference between years being much more dramatic on the West grid than the East grid (Table 5.4). However, as just discussed, this test is conservative in only using data from the "No" column in Table 5.4. If the proportion of failed young in the unknown sample (the "?" column in Table 5.4) was the same as in the known sample ("No" vs. "Yes" columns in Table 5.4) the effect of year would be more pronounced and the difference between grids less so.

In a later section of the present Chapter, I report on evidence indicating that survival of pouch-young to the onset of weaning is significantly poorer among first-time breeders. Considering only females that were known or presumed to have given birth at least once before, I estimate that survival to the onset of weaning was 33.3 % in 1995, and 81.3 % in 1996. Efford (1998, p. 510) reported that the estimated survival of pouch-young from June to September at the Orongorongo Valley site was 82.4 +/- 17.6 % (mean +/- S.D.), very close to the estimated rate of survival at the Paddys Land site in 1996. Efford (1998, pp. 504 and 513) cited several pieces of evidence which suggest that the sample of females used to generate the estimated survival of pouch-young at the Orongorongo Valley site likely included only those females that had given birth at least once before. The estimated 33.3 % survival of pouch-young to the onset of weaning at the

Paddys Land site in 1995 is below the lower 95 % confidence limit for survival at the Orongorongo Valley site (= 47.9 % = 82.4 - [1.96 x 17.6]). Efford (1998, p. 513) noted that survival to the onset of weaning at the Orongorongo Valley site was estimated to be only 52 % during the early years of the study (1966-1975). Efford suggested that the poorer survival of pouch-young during the early years of the Orongorongo Valley study may have been attributable to the greater frequency with which mothers with pouch-young were captured and handled in the earlier years of the study as compared to later years (1980-1994).

A difference in the frequency of capture and handling is one of at least four proximate causes that may explain the significant difference between 1995 and 1996 as regards the pre-weaning loss of pouch-young at the Paddys Land site. Other potential causes include: 1) a difference in the frequency with which mothers were chased by predators; 2) a difference in the frequency of infanticide; and 3) a difference in food availability.

Pre-weaning loss of young as a result of capture and handling

Two pouch-young were lost as a direct result of the mother being captured, one case involved trapping and the other involved darting. Neither of these two pouch-young are included in the tallies presented in Table 5.4. In the case where the young was lost as a direct result of trapping, the 90-day-old young was found dead, lying on the floor of the trap beside its mother. The mother had been trapped previously with her pouch-young, was apparently unharmed, and showed no signs of having been harassed by a predator while in the trap. In only one other instance was a young ejected from the pouch when the mother was trapped. In the latter instance, the 149-day-old young was, however, evidently unharmed, as its mother was trapped the very next day with the young securely back in the pouch. Moreover, this particular young was known to have survived to independence. These two cases of young being ejected in response to trapping were clearly exceptional. Females were trapped with pouch-young less than 175 days of age on 624 occasions, and in 622 cases the mother did not eject the young. There were a total of three instances where the young had not been ejected in the trap, but after having been processed, the young was not securely back in the mother’s pouch upon her release. In two instances the young was out of the pouch but was seen to be securely attached to the mother’s back as the mother was followed back to her den. In the third instance the young did become separated from its mother, but she evidently returned and retrieved the young within the space of an hour.

There were nine occasions when females with pouch-young less than 175 days of age were darted. On two of these occasions the young fell out of the pouch. In both instances the young was put back in the pouch. In one case the pouch-young was alive and well and securely in the mother's pouch when she was released the next morning. In the other case the young was found lying dead, beside its mother, even though the mother was evidently unharmed. It is likely the tranquilizer had the effect of relaxing the pouch muscles. In the instance where the young had fallen out but survived, the pouch had been loosely sealed with surgical tape (which was removed before releasing the mother), after the young was put back in the pouch. This precaution was not taken in the case where the young was later found dead.

Although there were only two direct observations of young being lost in response to trapping or darting, there may have been less obvious effects of handling animals such that the poorer survival of pouch-young in 1995 was, nonetheless, the consequence of experimenter-induced loss of young.
I undertook three analyses to evaluate the importance of experimenter-induced loss of young, I tested:
1) whether the fate of young was associated with the frequency with which the mother was handled (Table 5.5); 2) whether losses were induced by ear-tagging (Table 5.6); and 3) whether the survival of young was greater among a group of females that had not been trapped previously, as compared to females that had been trapped and handled repeatedly (Table 5.7).

For each of the 63 pouch-young shown in Table 5.4, whose fate was known for certain (excluding those in the "?" column), I identified each occasion on which the mother was handled while the young was in the pouch, up to the time the young was 175 days of age. I then calculated the interval, in days, between each successive occasion on which the mother was handled. There were 9 young whose mother's were only handled once during the period in question, 4 of which survived to the onset of weaning, while the remaining 5 did not. For each of the remaining 54 young whose mother's were handled on more than one occasion, I calculated the mean, and median, interval (in days) between occasions on which the mother was handled. I calculated both the mean and median handling interval for each female because I had no *a priori* way of knowing what the shape of the distribution of handling intervals would be. If a distribution is symmetrical there will be little difference between the mean and the median value (Sokal and Rohlf 1995,

p. 46). To evaluate the shape of the distribution of handling intervals, I compared the mean and median handling intervals for each female using Wilcoxon's signed-ranks test. As there was no significant difference between mean and median handling intervals (T = 44.0, z = 0.53, p = 0.5936), I conclude that the mean handling interval is representative of the "typical" frequency with which the mother was handled. Mean handling intervals were compared between young that died prior to, and those that survived to, the onset of weaning (175 days), in both years, on both grids, using a three-way ANOVA (Table 5.5). The mean interval between handling occasions was significantly shorter among young that died, than those that survived. The mothers of young that died were generally handled about once a month, while the mothers of surviving young were generally handled about once every second month (Table 5.5), suggesting that mothers that were handled more frequently were more likely to lose their young.

The interval between occasions on which a mother was handled while the young was in the pouch, prior to 175 days after the birth of her young, will be a function of the number of times she was handled, and the total time over which the young survived. If a pouch-young died only a few days after its birth, its mother would likely have been handled on fewer occasions while the young was alive, than the mother of a young that survived to 175 days of age, which may confound the interpretation of just what the mean interval between handling occasions represents. However, as regards the 54 pouch-young under consideration in Table 5.5, there was no significant difference in the number of times the mother was handled (Mann-Whitney U = 317.5, z = 0.73, p = 0.4644) between young that died, and those that did not, suggesting that the interval between handling occasions is not confounded by the number of times the mother was handled. Young that survived a shorter period of time had mothers that were handled as often as young that survived a longer period of time, indicating that the *interval* between handling occasions was what was different between the two groups.

I interpret the results of Table 5.5 as suggesting that handling may have had an adverse effect on the survival of pouch-young. Tagging the young was clearly the most invasive procedure I undertook while the young was still in the pouch. Thirty-five of the 63 known-fate pouch-young shown in Table 5.4 were known to have survived after being ear-tagged. Yet it was quite often the case that a young would be ear-tagged on one occasion, and the next time its mother was seen, the young had been lost. However, among the 28 pouch-young shown in Table 5.4 that were known to have died prior to 175 days of age, there was no significant association between when the young was lost and whether it had been ear-tagged (Table 5.6). About as many young died before being ear-tagged (13) as died after being ear-tagged (15).

The most rigorous means of testing the importance of experimenter-induced loss of young is to compare the survival of young between females that have not been trapped previously as against females that have been captured and handled repeatedly. In October-November, 1996, I attempted to capture every radio-collared female on the two principal study grids (which I will refer to as "On-grid" females), to determine whether their young had survived to 175 days of age. At the same time I attempted to capture as many previously untrapped adult females as possible along the vehicle trail trapline, illustrated in Figure 4.1. The 40 vehicle trail traps were baited and set for 13 nights (520 trap-nights) between October 12 and November 15. There were a total of 98 captures (18.8 % trap success) over the 13 nights. I caught 49 previously untrapped adult and subadult possums, of which 16 were adult females (which I will refer to as "Off-grid" females).

Table 5.7 summarizes the fate of young of both On-grid and Off-grid mothers. The tallies regarding the On-grid mothers include the 34 pouch-young shown in Table 5.4, whose fate was known for certain in 1996 (excluding those in the "?" column), as well as the single young known to have been lost in response to darting, given that I was interested in evaluating the adverse effects of capture and handling (the single instance when a young was lost after its mother ejected it, in response to trapping, occurred in 1995). Among On-grid females, 22 were seen with dependent young, 6 were not seen with young but were clearly still nursing more than 175 days after the birth of their young, 9 were known to have lost their young, and 2 did not have young and showed no signs of nursing (Table 5.7). Among Off-grid females, 8 were seen with dependent young, 6 were not seen with young but were clearly still nursing, and 2 did not have young and showed no signs of nursing (Table 5.7). I assume that both Off-grid females that did not have young and were no longer nursing, had in fact given birth earlier in the year ($p > 0.95$, Table 5.2). Both females had large pouches, indicating that they had clearly given birth on at least one or more occasions (Bolliger and Carrodus 1938, 1940), neither showed signs of being in poor condition, and both were within the range of normal body weights (2000 g or more) for adult females at this time of year (Fig. 5.6)

The two On-grid females trapped in the October-November period that did not have dependent young and were no longer nursing (Table 5.7), were trapped 189, and 197 days, respectively, after the birth of their young. The two Off-grid females that did not have young with them and were not nursing were trapped 183, and 207 days, respectively, after the median birth date of young on the trapping grids (April 20, Fig. 5.2). If these two Off-grid females had young that were born on March 18, the earliest known birth date in 1996, the young would have been 216, and 240 days old, respectively, when their mothers were first trapped. The earliest a surviving young was known to have been completely weaned was at 202 days of age, and the next earliest, among the other 14 young known to have survived to independence, was at 271 days (Fig. 5.3). It is therefore almost certain that both of the On-grid females and at least one of the two Off-grid females had lost their young prior to the completion of weaning. Assuming that females seen without young and showing no signs of nursing had lost their young, the proportion of young surviving to the onset of weaning that were born to On-grid mothers (70.3 %), was not significantly from that among Off-grid mothers (87.5 %, Table 5.7). Only if both of the two Off-grid females, had in reality, already weaned their young, would the difference be significant.

The results from Table 5.5 regarding differences in the frequency of handling among On-grid females suggest that handling may have had an adverse effect on the survival of pouch-young, while the results from Table 5.6 regarding the consequences of ear-tagging suggest that this is not the case. Assuming that the frequency of handling influences survival, but ear-tagging does not, this is not a sufficient explanation of the difference in the survival of pouch-young between 1995 and 1996 because there was no significant difference in the frequency with which females were captured and handled, between these two years (Chapter 6). However, as will be demonstrated in a later section, there was evidence of food shortage in 1995 as compared to 1996, and there may have been an interaction such that the same level of handling nonetheless resulted in poorer survival in 1995, because mothers were already in poorer condition. Unfortunately, because I did not conduct Off-grid trapping in 1995, as I did in 1996 (Table 5.7), I cannot rule out the possibility that the decreased survival of pouch-young in 1995 was the result of an interaction between food shortage and the frequency of capture and handling.

Pre-weaning loss of young as a result of predator chases

Marsupial mothers have the distinct advantage of being able to eject their young from the pouch when being chased by a predator, thereby sacrificing the young to the predator in order to save themselves. If the greater pre-weaning loss of pouch-young in 1995 was a response to predators I would expect to have evidence of greater rates of predator activity in 1995 than in 1996. Table 5.8 summarizes the available evidence of predator sightings, sounds, and signs, as well as the number of adult possums apparently killed or scavenged by a given predator, during the pre-weaning phase of development of young in 1995 and 1996. Since I spent comparable amounts of time in the field during this period in both 1995 and 1996 (Tables 4.1 and 4.2), differences in the number of incidental observations can be attributed to differences in the level of predator activity rather than differences in the amount of sampling.

While there was a trend towards greater predator activity in 1995 (Table 5.8), notably as regards dingos, the numbers are too small to provide an adequate test of the relationship to the pre-weaning loss of pouch-young. Nonetheless, it seems unlikely that the occasional pursuit by a predator could be responsible for the dramatic difference in survival between 1995 and 1996. When possums were released from traps, every attempt was made to try to follow them back to their dens. Excluding instances when the animal was not followed or when it disappeared from view, there were 502 cases where females with pouch-young were followed until they came to rest. Often this would involve running after the animal at (the experimenter's) top speed. In no case did the mothers respond to this pursuit by ejecting their young. Overall it seems females were extraordinarily reticent to give up their young. The most salient example of this was a female trapped and released 110 days after the birth of her young, who was observed to still have her young in the pouch, even though it was dead and rotting. Crawley (1973, p. 82) also reported instances of young being found dead in the pouch at the Orongorongo Valley site.

Pre-weaning loss of young as a result of infanticide

While it cannot be said that the activity of predators differed dramatically between 1995 and 1996, the density of female conspecifics certainly did. As documented in Chapter 4, the center-most, resident, adult females were removed from both principal study grids on August 1, 1995. A total of 10 females were removed from the West grid, while 9 were removed from the East grid, a reduction in the density of adult females by about one-third (Tables 4.5 and 4.6; Figs. 4.4 vs. 4.5, and 4.10 vs. 4.11). No new adult females settled in the vacancies created, over the course of the next two years. Consequently, the density of adult females in 1996 was about one-third less than the density in July, 1995 (Tables 4.5 and 4.6; Figs. 4.4 vs. 4.7, and 4.10 vs. 4.13). Wolff (1997) argued that infanticide committed by adult females against one another is a principal driving force in the evolution of social systems in many mammalian lineages. If aggressive encounters between female possums were responsible for the loss of young (direct infanticide as opposed to resource-depletion), I would expect better survival of young in 1996, as was observed, given the lower density of females.

Wolff (1997) argued that marsupials are unlikely to demonstrate infanticide since their otherwise vulnerable altricial young are protected in the mother's pouch. Wolff (1997) was apparently not aware that marsupials demonstrate behaviours such as mothers leaving their dependent young in the den while they forage, which he suggests is the phase of development when infanticide occurs in prosimian primates. In the present context I am addressing pre-weaning survival to 175 days, when most young are still in the pouch (Fig. 5.3). Hence, Wolff (1997) would predict that infanticide is not a significant threat to survival at this stage of development. Nonetheless, it is at least possible that possums can cause each other to eject their young. If infanticidal aggression between females was the principal cause of the loss of pouch-young I would expect more pre-weaning loss of young before August 1, 1995, when the reduction in female density was undertaken, than after. Moreover, I would expect poorer survival prior to August 1 in 1995 than in 1996. In both 1995 and 1996 the "typical" pouch-young was about 100 days old as of August 1, given that the median birth date of primary young in both years was around April 21 (Fig. 5.2). As is shown in Table 5.9, at most, a single pouch-young was lost prior to August 1 on a particular trapping grid in a given year. Obviously, the majority of cases of pre-weaning loss of pouch-young in 1995 occurred after the August 1 reduction in adult female densities, and not before (compare Tables 5.4 and 5.9). Similarly, there was no difference between 1995 and 1996 as to survival prior to August 1 (Table 5.9).

Pre-weaning loss of young as a result of food shortage

Since the majority of cases of pre-weaning loss of pouch-young occurred after August 1 (Table 5.9), this implies that most young were lost sometime after they were about 100 days old (given a median birth date of April 21, Fig. 5.2). The weight of pouch-young increases very gradually from 0-100 days of age and then increases very dramatically from 100 days onwards (Fig. 5.8; see also Lyne and Verhagen 1957, their Fig. 8). The evidence that the timing of the loss of young (sometime after August 1, Table 5.9) corresponds to the period of growth during which the young is putting the greatest energetic demands on the mother (after 100 days of age, Fig. 5.8) suggests that the survival of young to the onset of weaning at the Paddys Land site is most likely governed by the availability of food. Similarly, Humphreys et al. (1984, p. 64) noted that the average median date on which pouch-young were lost at the Orongorongo Valley site was August 19. Moreover, Humphreys et al. (1984, their Table 2) reported a significantly positive relationship between the survival of pouch-young and adult female body weight in winter, which in turn showed a significantly positive relationship to the size of the annual crop of Hinau fruit.

To evaluate the possibility that the loss of pouch-young at the Paddys Land site was a function of food shortage I examined evidence regarding four potential indices of condition, as well as changes in adult body weights. The four indices of condition were, whether or not an individual: 1) was seen to stop and feed on grass or leaves, following their release from a trap during the day; 2) was observed to be “weak and wobbly” upon release; 3) felt “bony”; or 4) was noticeably “rumpy”. Survival was significantly poorer among females observed to be “weak and wobbly” upon release, and among those observed to be both “rumpy” and “bony”, as compared to females that never demonstrated these symptoms of poor condition (Chapter 6). Naturally, if the mother dies, so too will the pouch-young. In the present context I am interested in factors that might influence the survival of pouch-young possessed by surviving females. Table 5.10 shows the proportion of young that survived to the onset of weaning in 1995 and 1996 whose mothers demonstrated any or all of the four symptoms of poor condition under consideration. The observed proportions reported in Table 5.10 were compared to those expected in each of 1995 and 1996 (33.3 and 81.3 % survival respectively) based on the data presented in Table 5.4. Sample sizes were too small to conduct statistical tests except in the case of “rumpy” females. Mothers that were noticeably “rumpy” were significantly less likely ($\chi^2 = 7.96$, df = 3, $p = 0.0468$) to have a pouch-young that survived to the onset of weaning, as compared to other females.

Figure 5.4 shows the percentage of surviving individuals of both sexes seen feeding on grass or leaves, following their release from a trap, in each season, over the course of the study. The percentage of surviving adult females that were either observed to be “weak and wobbly” upon release, felt “bony”, or were noticeably “rumpy”, in each season, over the course of the study, is shown in Figure 5.5. In all cases the proportion of individuals showing symptoms of poor condition was greater during the 1996 breeding season than during the 1995 breeding season. This is the opposite pattern to that expected if the four symptoms of poor condition under consideration were causally related to the poorer survival of pouch-young in 1995.

The most direct way of examining contrasts between the 1995 and 1996 breeding seasons is to compare changes in the status of the same individual. Whether or not an individual demonstrated any of the four symptoms of poor condition in a given season in 1995 was compared to whether or not it demonstrated symptoms in the same season in 1996. The proportion of individuals demonstrating a change in symptoms was evaluated using a repeated measures “exact” binomial test (Sokal and Rohlf 1995, p. 784). Pooling data across grids, there was a strong trend towards being more likely to be diagnosed as being “rumpy”, in the autumn of 1996 as compared to the autumn of 1995, although the trend is not significant if the p-value is interpreted conservatively (Table 5.11). Nonetheless, the direction of the trend is the opposite to that expected if the likelihood of being diagnosed as being “rumpy” were causally related to the poorer survival of pouch-young in 1995. There were no other significant effects or noteworthy trends regarding any of the other symptoms of poor condition under consideration.

While the survival of a pouch-young within a year appeared to be related to whether or not its mother was noticeably “rumpy” (Table 5.10), the difference in the proportion of young surviving between years (1995 vs. 1996) did not appear to be associated with inter-annual differences in the proportion (Fig. 5.5) and frequency (Table 5.11) with which females were diagnosed as being “rumpy”. This might suggest that the significant difference between 1995 and 1996 in the proportion of young surviving to the onset of weaning (Table 5.4) was not a function of food shortage, if food shortage were the only factor influencing the severity of “rump wear”. However, the cause of “rump wear” is probably multifactorial and contributing factors include behavioural stress, immunosuppression, and underlying disease (Hemsley and Canfield 1993, Viggers and Spratt 1995), all of which may be exacerbated by food shortage. That food shortage by itself is not sufficient to explain the underlying cause of “rump wear” is demonstrated by the fact that the condition has been reported in captive animals (Presidente 1984, Clark 1995). Nonetheless, as food shortage can be expected to exacerbate the underlying causes of “rump wear”, the argument that food shortage was responsible for the poorer survival of pouch-young in 1995 is not supported by the evidence regarding “rump wear”, nor by the evidence regarding the other three indices of condition under consideration.

Figure 5.6 illustrates the pattern of seasonal changes in mean body weights of adult females and males, over the course of the study. Body weights of adult females shown in Figure 5.6 are the aggregate of the mother’s weight and the weight of her pouch-young. No attempt was made to remove the young from the pouch in order to get a separate measurement for mother and young. During the pre-weaning phase of development the aggregate weight of mother and young is wholly dependent on the mother’s ability to find food, as the young has not yet begun to forage on its own. In essence the young at this time represents an enlargement of female reproductive tissue. The mother’s weight taken alone may not reflect difficulties in finding food as accurately as the aggregate weight if the mother “chooses” to invest the bulk of her energy into the growth of her young at the expense of her own condition.

In 1996 the mean weight of females, being for the most part the aggregate weight of mothers and young, as most females had surviving young (Table 5.4), increased steadily from autumn to spring on both grids (Fig. 5.6). By contrast, aggregate weights declined from autumn to spring on both grids in the 1995 breeding season. As the majority of females in 1995 had lost their young by the middle of spring (Table 5.4), weights taken at this time primarily reflect the mother’s weight by itself. Given that the weight of the pouch-young in autumn is negligible (the oldest young at the end of autumn would be 90 days of age, corresponding to a weight of 60 g, according to Lyne and Verhagen 1957; see also Fig. 5.8), the decrease in weight between autumn and spring suggests that the mother’s own weight was declining during this period.

Interpreting changes in adult male body weights is more straightforward. Mean male body weights on both grids declined between autumn and winter in both 1995 and 1996 (Fig. 5.6). In 1995 mean weights on both grids continued to decline between winter and spring, whereas mean weights increased from winter to spring on both grids in 1996.

Changes in mean body weight could reflect either changes in the weight of the same individuals measured over time or a change in the composition of the population being measured. For example, there may have been an influx of fat males in the spring of 1996. To avoid potentially confounding factors associated with a change in the composition of the population, I restricted the analysis to an examination of the change in weight of the same individuals measured over time. Table 5.12 summarizes the median difference in the mean weight of individual adult possums of both sexes (female weights representing the aggregate weight of mother and young) measured in a given season in 1996 as compared to the same individual's mean weight in the same season in 1995. There were no clear differences between the two years regarding comparative weights in autumn or winter. However, an individual measured in the spring of 1996 was generally about 200 g heavier than it had been in the spring of 1995, regardless of sex. The difference in spring weights was statistically significant for males on both grids. The difference was statistically significant for females on the West grid, and all six females, for which data were available, on the East grid, were also heavier.

The significant difference in spring weights between 1995 and 1996 may have been a consequence of the one-third reduction in the density of adult females associated with the removal of the center-most, resident, adult females undertaken on August 1, 1995 (Chapter 4). In this case, the reduction in intraspecific competitors is of importance as regards resource-depletion, rather than direct behavioural interactions such as would be involved in instances of infanticide. If the one-third reduction in the density of adult females were the only factor associated with the greater survival of pouch-young in 1996, I would predict poorer survival of pouch-young, and lower body weights among Off-grid females, as compared to On-grid females in 1996 (post-removal), under the assumption that Off-grid densities were similar to pre-removal On-grid densities in 1995. I have already discussed the fact that the proportion of young surviving to the onset of weaning was, if anything, slightly greater among Off-grid females (Table 5.7). Similarly, there were no significant differences in spring (Oct.-Nov.) body weights between On-grid and Off-grid females (Table 5.13).

While the one-third reduction in the density of adult females does not appear to be a sufficient explanation for the differences in the survival of pouch-young, and adult body weights, between 1995 and 1996, another, non-exclusive, explanation would be a change in environmental conditions between the two years. Total monthly rainfall in autumn and winter was dramatically different between the two years (Fig. 5.7). Total rainfall in August, 1995, fell below the 5 th percentile, based on 68 years of records, while total rainfall in May, 1996, was above the 97.5 th percentile (data are from the Kookabookra weather station, 30^{o}00’39”S 152^{o}00’34”E, elevation 975 m; approximately 20 km from the Paddys Land site). I did not attempt to measure food availability directly at the Paddys Land site because possums are “opportunistic herbivores” (Kerle 1984, Cowan 1990), so I was unable to identify a specific food item that might act as an index of overall food availability, such as was done at the Orongorongo Valley site, as regards the size of the annual crop of Hinau fruit (Humphreys et al. 1984). Humphreys et al. (1984) were able to use the availability of Hinau fruit as an index of food availability because an extensive dietary analysis had been conducted earlier on during the Orongorongo Valley study (Fitzgerald 1976). On the other hand, the fact that possums are “opportunistic herbivores” suggests that they will almost certainly benefit from a general increase in the amount of vegetation, resulting from increased rainfall.

In summary, three lines of evidence suggest that the poorer survival of pouch-young in 1995 was a function of food shortage: 1) the fact that most young were lost during the growth phase when they were putting the greatest energetic demands on the mother; 2) the fact that both males and females had significantly lower body weights in 1995; and 3) the fact that rainfall in the autumn and winter of 1995 was exceptionally low. Since none of the four indices of condition indicated that animals were in poorer shape in 1995, this clearly weakens the argument regarding food shortage, but it must be noted that it is not clear to what degree these indices of condition reflect nutritional state, as opposed to immunocompetence, stress level, or other components of general health.

Post-weaning survival of young

In total for the 1995 and 1996 breeding seasons combined, there were 14 primary young tagged in the pouch that were later seen as subadults, independent of their mothers (Table 5.14). One male subadult born in 1995 on the East grid was seen in January of 1996 and never again. The remaining 13 subadults were seen sometime after the beginning (mid-March) of the breeding season in the year following the year in which they were born.

More than twice as many young survived to the beginning of the breeding season in the year following their birth in 1996, than in 1995 (Table 5.14). The difference between the two breeding seasons could have been a function of differences in pre-weaning (to 175 days) survival (Table 5.4) or survival after the onset of weaning. Extrapolating the proportion of young known to have survived to the onset of weaning

(Yes/[Yes + No], Table 5.4) to the subset of young whose fate was unknown (the “?” column in Table 5.4), the total number of primary young surviving to the onset of weaning (Yes + [[Yes/[Yes + No]] x [?]]), in 1995, was most likely 13 . Similarly, the total number in 1996 was most likely 29. Survival after the onset of weaning to the beginning on the next breeding season was evaluated by calculating the proportion of young that survived to the beginning of the breeding season in the year following their birth (Table 5.14) from among the total number that likely survived to the onset of weaning (Table 5.4). Estimated survival from the onset of weaning to the beginning of the next breeding season was 30.8 % (4/13) in 1995, and 31.0 % (9/29) in 1996. Consequently, the difference between years in the number of young surviving to the beginning of the breeding season in the year following their birth would appear to be largely a function of pre-weaning survival (Table 5.4).

Since young were not radio-collared, it is not possible to conclusively differentiate between survival and disappearance due to emigration. Previous studies suggest that subadults begin to emigrate at 9-10 months of age (Clout and Efford 1984, Efford 1991). Differences in survival from the onset of weaning to the beginning of the next breeding season in 1995 and 1996 may have been masked if there was a corresponding difference in emigration rates. I have no direct way of evaluating this possibility, but indirect evidence (described below) suggests there was no difference in emigration rates between the two years in question.

Confounding survival with disappearance due to emigration causes survival to be underestimated. Pooling across years, survival from the onset of weaning to the beginning of the next breeding season is estimated to be 31.0 %. It is important to remember that this is a minimum estimate. Emigration rates in possums are often observed to be male-biased, although significant differences between the sexes are demonstrable only when large samples are generated by pooling across years or between sites (Clout and Efford 1984, Efford 1991). If my estimate of survival from the onset of weaning was confounded with disappearance due to emigration I would expect more females than males among the young surviving to the next breeding season, given male-biased emigration. I did in fact find that more females (7) than males (6) survived to the next breeding season, however, the proportion of survivors that were female did not differ significantly (χ^2 = 1.93, df = 1, p = 0.1643) from the number expected (4.6) given a primary sex ratio of 35.4 % female for the Paddys Land site (Table 4.13).

Another way of evaluating the frequency of emigration is to quantify the level of immigration. It is the level of immigration by 1-year-olds that is of most relevance with respect to post-weaning survival. To identify instances of immigration by 1-year-olds I needed to establish: 1) when it is appropriate to classify newly-identified individuals as potential immigrants (Chapters 3 and 4); 2) where they were detected relative to their potential point of departure (Chapters 3 and 4); and 3) what age they were. As discussed in Chapter 4, there was only one instance (on the West grid in 1995) in a total of 83 cases (1.2 %) where the offspring of a resident female could have been misidentified as being an immigrant (because I were unable to tag it while it was still in its mother's pouch), if it was later recaptured. As I will show, this potential source of error is only of relevance to the estimated rate of immigration by 1-year-old males. Where newly-identified individuals are first captured is of relevance because individuals caught in traps on the periphery of the trapping grids may be residents from just off the grid undertaking a long distance "excursion", rather than "true" dispersal (Lidicker and Stenseth 1992, Chapters 3 and 4). The closer to the interior of a trapping grid a newly-identified individual is caught, the more likely it is that this individual is actually in the process of emigrating from its original home range.

I used five types of evidence to evaluate the likely age of newly-identified individuals first captured any time after the beginning of spring, 1995 (Chapter 4): 1) whether they were sexually active (adult vs. subadult); 2) how much they weighed; 3) the condition of their pouch (if female); 4) the length of their testes (if male); and 5) their estimated age from cementum annuli (if available). Sexual maturity, by itself, is not a sufficiently accurate indicator of age. One female young tagged while still in the pouch was known to have given birth in the autumn of the year after the year in which she was born (Fig. 5.8). On the other hand, based on my sample of 40 animals aged from cementum annuli, the earliest at which all individuals are certain to be adults is at 4 years of age (Fig. 5.9). Sexual immaturity is at least a starting point in helping me sort out the age of potential immigrants, as I could be sure that subadults were all less than 4 years old. Efford (1994, p. 6) noted that this was also true of the Orongorongo Valley population.

Gilmore (1969) and Crawley (1973) both used body weight to aid in estimating the age of young possums. Adult body weights range from 1-3 kg depending upon location (Cowan 1990, Kerle et al. 1991, How and Kerle 1995), and growth rates of young vary accordingly (Efford 1991, p. 29; Appendix 2).

Consequently, it was necessary to determine the observed variation in adult body weight, and rate of growth of young at the Paddys Land site, prior to using body weight as an indication of age.

Gilmore (1969) classified as immature any animal weighing less than 2000 g. Crawley (1973, p. 78) reported that, among known-age young at the Orongorongo Valley site, 1-year-olds never weighed more than 1450 g, while 2-year-olds never weighed less than 1700 g. Figure 5.8 illustrates the pattern of increase in body weight with age among known-age young tagged in the pouch at the Paddys Land site. I have not attempted to fit a regression line to these data because they include repeated measures from the same individual, as well as data from different individuals. The overall pattern of growth illustrated in Figure 5.8 would appear to be similar to that observed among captive animals by Lyne and Verhagen (1957, their Fig. 8): 1) weight increases slowly up to 90-110 days of age; 2) the most rapid phase of weight gain occurs between 100 and 200 days of age; and 3) weight continues to increase, but at a slower rate, from 200 days of age onwards. While the weight of known-age 1- and 2-year-olds at the Paddys Land site (Table 5.15) generally corresponded to those described by Crawley (1973) as regards the Orongorongo Valley site, at least one 1-year-old at the Paddys Land site was known to have weighed as much as 1700 g during the autumn of the year after the year in which it was born (Fig. 5.8). Moreover, the sole 1-year-old female known to have given birth likely also weighed as much as 1700 g during the autumn of the year after the year in which she was born. This latter female was not trapped during autumn but was trapped with her pouch-young during mid-winter, when this new mother was 457 days old, at which time mother and young together weighed 1850 g. Based on my estimate of the age of the pouch-young, and using the pattern of weight gain among very young (< 150 days) possums described by Lyne and Verhagen (1957, their Fig. 8), I determined that the pouch-young by itself should have increased by 30 g in between the end of autumn and the time at which the mother and young were first trapped. Consequently, the aggregate weight of mother and young at the end of autumn was likely 1820 g.

In addition to evaluating the weights of known-age young tagged in the pouch I was able to determine the relationship between autumn body weight and age in years using three additional sources of information: 1) weights from two individuals, one male and one female, which I was certain were born in the autumn of 1994 (Fig. 5.9); 2) weights from individuals aged from cementum annuli (Fig. 5.9); and 3) weights from adults known to be a minimum age based on trapping records (Table 5.15). Intensive trapping was first begun on the West grid in late November, 1994. Among the animals trapped at this time was a mother who still had a back-young. The back-young must have been born in the autumn of 1994. The female back-young was trapped again, still with her mother, in mid-December, weighing 740 g, and having a head length of 73.9 mm. On the very same day, a subadult male was trapped weighing 710 g and also having a head length of 73.9 mm. I conclude that the subadult male in question must also have been born in the autumn of 1994. The relationship between weight and age could be categorized from trapping records insofar as individuals that were adult when first trapped that had been trapped over more than one year could be assigned a minimum age of “2 +” years, while those trapped over more than two years could be assigned a minimum age of “3 +” years. If the same individual was weighed more than once during autumn, I determined its mean weight for the season, and then used the latter value when plotting Figure 5.9 and calculating the summary statistics presented in Table 5.15.

Efford (1994, p. 6) reported that possums at the Orongorongo Valley site stop growing at about 4 years of age. This also appears to be true at the Paddys Land site. Figure 5.9 illustrates the relationship between autumn body weight and age among all known-age individuals from the Paddys Land site, for which data were available. As was the case with the data presented in Figure 5.8, I did not attempt to fit a regression line to the data shown in Figure 5.9 because the data include repeated measures from the same individual, as well as measurements from different individuals. Nonetheless, the overall pattern evident in Figure 5.9 is one involving a steady increase in body weight from 1 to 4 years of age, at which time the increase in body weight with age appears to asymptote. Average adult body weight in autumn at the Paddys Land site among adults known to be 4 years of age or older, and those known to be “2 +” and “3 +” years of age from trapping records, vary from about 2100 to 2400 g, depending on sex and age category (Table 5.15). Crawley (1973, his Table 4) reported that mean adult female body weight at the Orongorongo Valley site was 2200 g, and similar estimates of between 2200 to 2300 g have been made regarding data from later years, at the same site (Humphreys et al. 1984, their Table 1 and Fig. 2; Efford 1994, his Fig. 5 and Appendix 4).

Among adults at the Paddys Land site aged from cementum annuli, there were no cases of animals 4 years of age or older ever weighing as little as 1850 g in autumn (Fig. 5.9, Table 5.15). Among adults assigned a minimum age from trapping records there were instances of individuals weighing as little as 1700 g in autumn (see “2 +” Females, Table 5.15), but the probability of weighing 1825 g or less was less than 2.5 % (Table 5.15). Among known-age young that were weighed during autumn as 1-year-olds, the probability of weighing more than 1785 g was less than 2.5 % (Table 5.15). As stated above, the sole 1-year-old female that was known to have given birth was not captured and weighed in autumn, but was estimated to have weighed 1820 g (together with her pouch-young), on her first birthday. Taken together, it would appear from the preceding results that an autumn body weight of 1850 g represents a reasonable threshold weight, whereby individuals weighing less than this are unlikely to be more than 1 year old, and *vice versa*.

To identify potential 1-year-old immigrants I classified all newly-identified individuals first captured after the beginning of spring, 1995 (Chapter 4), as to whether they were subadult, and whether they weighed 1850 g or less, on any occasion (Table 5.16). Individuals first trapped as adults that consistently weighed more than 1850 g were assumed to be 2 years of age or older, and will not be discussed further. The initial step (Table 5.16) in identifying the number of potential 1-year-old immigrants indicated there was a maximum of 3 females, and 7 males. Supplementary evidence regarding each of these 10 individuals was used to exclude all but those I could be certain were 1-year-old immigrants.

Supplementary evidence indicated that none of the three females identified in the initial classification (Table 5.16) could be legitimately categorized as 1-year-old immigrants. Examination of cementum annuli revealed that the subadult female first trapped on the West grid (W-AE, Fig. 4.6) after the spring of 1995 (Table 5.16) was 2 years of age when she was first trapped. The subadult female first trapped on the East grid (E-AH, Fig. 4.14) after the spring of 1995 (Table 5.16) weighed an average of 1125 g (well below the known or probable weight range for 2-year-olds, Table 5.15), and was unquestionably a 1-year-old. However, additional evidence clearly indicated she was not an immigrant. The 1-year-old’s putative mother (E-AE, Fig. 4.14) was identified using microsatellite DNA (Table 4.11). During the following breeding season (1997) both the putative mother and daughter were radio-collared. The daughter used two den trees in total during the breeding season, which were 2 of the 5 known to be used by the putative mother (Fig. 4.15). Hence, the daughter was clearly not an immigrant given that she evidently had not left her natal range.

There was one adult female first trapped after the spring of 1995 that weighed less than 1850 g (Table 5.16). None of the 11 other newly trapped adult females weighed less than 2000 g. The one adult female weighing less than 1850 g was trapped near the center of the West grid (W-AF, Fig. 4.7) on three occasions over the course of 16 days between April 28 and the middle of May, during which time her weight dropped from 1800 to 1600 g. The probability that a 1-year-old would weigh as much as 1800 g is very low (Table 5.15). In addition, I am quite certain this female was more than 1 year old because: 1) the condition of her pouch was characteristic of females that have bred repeatedly; and 2) her low body weight could be explained as being a consequence of ill-health. When she was first trapped on April 28, it was noted that her pouch was large (even for an adult), it was lined with hair, and her nipples were small. She had obviously undergone an oestrus cycle but was not pregnant at the time (Bolliger and Carrodus 1938, 1940; Dunnet 1956), and the large size of her pouch indicated that she had in fact given birth repeatedly, and was therefore, several years old (Bolliger and Carrodus 1940, Tyndale-Biscoe and Renfree 1987; Hugh Tyndale-Biscoe, pers. comm.). Two lines of evidence indicate that this female was in poor condition: 1) her rapid loss of 200 g in body weight (more than 10 % of her total body weight); and 2) the fact that she was observed to be "weak and wobbly" upon release, on the last occasion on which she was seen. Survival among females observed to be "weak and wobbly" upon release was significantly poorer than among females never seen to be so, and death was almost always imminent in cases where appearing "weak and wobbly" was accompanied by rapid weight loss (Chapter 6).

There were three adult males first trapped after the spring of 1995 that weighed 1850 g or less (Table 5.16). One of these three, trapped on the West grid between the spring of 1995 and the winter of 1996, was later found to be 2 years of age, as determined from cementum annuli. One of the two apparently lightweight adult males trapped on the West grid between the spring of 1996 and the winter of 1997 was certainly not a 1-year-old, for while he did weigh 1850 g when first trapped in late February, 1997, he weighed an average of 2250 g during the subsequent autumn. The remaining lightweight adult male was first trapped at the end of March weighing 1850 g, and was trapped repeatedly thereafter, during which time his weight dropped to 1550 g. While males normally lose weight from autumn to winter (Fig. 5.6) the absolute and relative magnitude of the weight loss in this case was unusual. As with the female discussed in the previous paragraph, this would appear to be another case of an older animal (based on the initial weight) demonstrating an abnormally low body weight because it is in poor condition.

There was one subadult male trapped on the West grid after the spring of 1996 that weighed 2000 g (Table 5.16). Based on his body weight he was likely 2 or 3 years old (Fig. 5.9, Table 5.15), but this was not conclusive. While there was no apparent relationship between age and testis length in autumn among adult males (N = 11, Spearman's r = - 0.14, t = - 0.42, p = 0.6830) I found that there was a significant relationship among subadult males. Over the course of the study there were eight known-age subadult males that were measured for testis length in autumn: five 1-year-olds; and three others, known (from trapping records or cementum annuli) to be at least 2 years of age. Testis length among 1-year-olds (mean +/- S.D. = 10.4 +/- 2.0) was significantly smaller (Mann-Whitney U = 0.0, z = 2.24, p = 0.0254) than among older, subadult males (15.6 +/- 1.5). Efford (1998, p. 510 and his Fig. 4) also used testis length to discriminate between 1-year-old, and older, subadult males at the Orongorongo Valley site. The subadult male first seen after the spring of 1996 weighing 2000 g (Table 5.16) had testes that measured 16.5 mm, clearly indicating he was at least 2 years of age.

There were three subadult males trapped for the first time from the spring of 1995 onwards that weighed between 1333 and 1700 g (Table 5.16). None of the three had testes measuring more than 10.9 mm in length. Moreover, all three were caught at interior sites on the trapping grids. Consequently, I conclude that there is unambiguous evidence of emigration by 1-year-old males. Since there were twice as many potential immigrants (N = 2) following the 1996 breeding season as there had been following the 1995 breeding season (N = 1), this suggests that emigration rates did not differ between the two years as there were twice as many young surviving to the onset of weaning in 1996 as in 1995 (Table 5.4). As described above, there was no unambiguous evidence of emigration by 1-year-old females.

The fact that emigration by 1-year-olds was occurring clearly indicates that the estimates of survival from the onset of weaning to the beginning of the next breeding season are confounded by disappearances due to emigration. My minimum estimate that survival during this period is 31.0 %, pooled across years, is clearly too low. Given that there was no clear evidence of emigration by 1-year-old females, estimating survival using only females ought to provide me with a more accurate picture. Pooling across years, there were most likely 42 (13 + 29) young that survived to the onset of weaning (Table 5.4), of which 15

(35.4 %, Table 4.13) were probably female. As there were seven females that survived from the onset of weaning to the beginning of the next breeding season, survival during this period is likely 46.7 % (7/15). Considering the 1996 breeding season by itself, survival during this period could be as high as 60.0 % (6 surviving females / [29 x 0.354]), in some years. However, as there were no apparent differences between 1995 and 1996 in either post-weaning survival or emigration rates, I conclude that the estimate based on pooled data from both years (46.7 %) is likely typical of most years (see Table 5.1). Efford (1998, his Table 4) estimated that female survival from the onset of weaning to the beginning of the next breeding season at the Orongorongo Valley site is 43.3 %.

Age at first breeding

Previous studies (Tyndale-Biscoe 1955, Gilmore 1969, Smith et al. 1969) have reported that males generally become sexually mature at a later age than females. In most cases, males rarely become reproductively active before they are two years old, although this is not universal, as males of *T. v. arnhemensis,* from Australia's Northern Territory, do appear to become sexually active within their first year (Kerle and Howe 1992).

While there were only a handful of known-age males at the Paddys Land site, upon which to judge, the age at first breeding among females (discussed below), and the few direct observations regarding males, both indicate that males at the site rarely become sexually mature (testis length > 18 mm, Tyndale-Biscoe 1955) before they are two years old. There were no cases (0 %) where known-age males were known to have become sexually mature in their first year. Among the six known-age males tagged in the pouch that were known to have survived to their first birthday (Table 5.14), four were trapped in the winter following the first breeding season in which they could have potentially become reproductively-active, and all four were still subadult. The sole known-age male from 1994, discussed previously, was also still subadult until at least two years of age (Fig. 5.9). There were two known-age 2-year-old males (Fig. 5.9), one of which (50 %) was sexually mature in the autumn of his second year, while the other was not. So too were there two known-age 3-year-old males (Fig. 5.9), one of which (50 %) was sexually mature in the autumn of his third year, while the other was not. All males 4 years of age or older (100 %) were sexually mature (Fig. 5.9). A similar pattern is apparent at the Orongorongo Valley site, where < 1 % of 1-year-old males, 27.5 % of 2-year-olds, 74.3 % of 3-year-olds, and 92 % of 4-year-olds, were reported as having testes > 18 mm in length (Efford 1998, his Fig. 4).

Only one female was known to have given birth in the autumn of her first year (see Table 5.1). Among the seven known-age females tagged in the pouch that were known to have survived to their first birthday (Table 5.14), six were trapped in the winter following the first breeding season in which they could have potentially become reproductively-active: four were still subadult; one was subadult when trapped in autumn but had a fully invaginated pouch, but no pouch-young, when next trapped in early winter (she had become sexually mature, as indicated by the lower of the two black circles in Fig. 5.8, but was not yet reproductively-active); and the last was the sole 1-year-old female known to have given birth in autumn (indicated by the higher of the two black circles in Fig. 5.8). There were six known-age 2-year-old females: the sole female back-young from 1994, discussed previously; and five more, aged from cementum annuli (Fig. 5.9). All six known-age 2-year-olds were still subadult at the beginning of the autumn of their second year, so none of them could have bred as 1-year-olds. Pooling data from young tagged in the pouch, the 1994 back-young, and those aged from cementum annuli, I estimate that only 8.3 % of 1-year-old females generally give birth. Four of the six known-age 2-year-olds (66 %) gave birth in the autumn or early winter of their second year, while the remaining two were still subadult (Fig. 5.9). As previously discussed (Table 5.2), almost all females 3 years of age or older gave birth (Fig. 5.9). The pattern of delayed female maturation apparent at the Paddys Land site is very similar to that reported regarding the Orongorongo Valley site, where 5.5 % of 1-year-old females, 80.4 % of 2-year-olds, and all (100 %) 3-year-olds give birth (Efford 1994, 1980-1993 data from his Appendix 5; Efford 1998).

Reproductive success of first-time breeders

Humphreys et al. (1984, p. 64) reported results from over 10 years worth of demographic data from the Orongorongo Valley site, suggesting that females that bred in their first year rarely produced surviving young. At the Paddys Land site there were nine females first seen as subadults that were known to have later given birth. Among the 9 known first-time breeders, 7 gave birth in autumn, while 2 gave birth in winter. As discussed previously, winter births of primary young were unusual (Fig. 5.2). Humphreys et al. (1984, their Table 1) reported that females that gave birth later in the breeding season at the Orongorongo

Valley site had a significantly lower probability of successfully rearing their pouch-young. One of the two first-time breeders giving birth in winter at the Paddys Land site was known to be 2 years old. Assuming birth date within a season is related to reproductive success, this suggests that not just 1-year-old, but also 2- and 3-year-old first-time breeders are less likely than experienced females to successfully rear their young to weaning. I evaluated the reproductive success of first-time breeders by determining: 1) whether first-time breeders gave birth later in the breeding season than females that were known to have already given birth at least once before (repeat breeders); 2) whether the probability that a pouch-young survived to the onset of weaning (175 days) was a function of whether it was born earlier or later in the breeding season; and 3) whether the proportion of young surviving to the onset of weaning among first-time breeders differed from that among repeat breeders.

The ages of 7 of the 9 first-time breeders could be identified from trapping records or cementum annuli. There was one 1-year-old, five 2-year-olds, and one 3-year-old. There was no significant correlation between birth date and age among the seven known-age first-time breeders (N = 7, Spearman's r = - 0.20, t = - 0.46, p = 0.6636). Consequently, I used pooled data from all nine first-time breeders in the following analyses.

I compared birth dates of pouch-young produced by first-time breeders against the birth dates of pouch-young produced by females that were known to have already given birth at least once before (repeat breeders). Only females known from trapping records to have given birth in the previous year, or females known from cementum annuli to be four years of age or older, were included in the category of repeat breeders. As all 3-year-old females were reproductively active (Fig. 5.9), all females four years of age or older can be assumed to have already produced at least one pouch-young. Birth dates were standardized across years by determining the number of days from the beginning of autumn in each year. If a given female survived and bred throughout the study, up to three birth dates (assuming she gave birth in 1995, 1996, and 1997) would be attributable to her. In the present analyses the birth dates in 1996 and 1997 could be utilized as she was known to be a repeat breeder given that she produced a pouch-young in 1995. To avoid inflating sample sizes in the comparison with first-time breeders I calculated a single mean birth date for each female possessing multiple records. Prior to calculating mean birth dates I took steps to ensure that there were no systematic differences between years. There were 33 cases where there were multiple birth dates attributable to females known to be repeat breeders. There was no significant correlation between birth date in one year versus the next (N = 33, Spearman's r = 0.10, t = 0.55, p = 0.5833). Treating all births among repeat breeders as independent events, there were no significant differences in median birth dates across years (Kruskal-Wallis H = 0.38, N = 84, df = 2, p = 0.8258) or between trapping grids (Mann-Whitney U = 849.0, *z* = 0.14, p = 0.8921). Consequently, I felt confident in generating mean values across years for females with multiple records, as well pooling results across grids. By definition, only a single birth date was attributable to each first-time breeder. Among first-time breeders there was no significant difference in median birth dates across years (Kruskal-Wallis H = 2.48, N = 9, df = 2, p = 0.2893), but there was an almost significant difference between the two trapping grids (Mann-Whitney U = 2.0, *z* = 1.81, p = 0.0695), wherein births tended to occur later on the East grid (Table 5.17).

On both trapping grids the median birth date among first-time breeders was later than among repeat breeders (Table 5.17). Overall (Table 5.17), first-time breeders gave birth significantly later (median birth date = May 5) than did females that had given birth at least once before (median birth date = April 17). The difference between first-time and repeat breeders was significant when considering the East grid by itself, but the difference was not significant when the West grid was considered by itself, although the number of first-time breeders in the latter sample was very small (Table 5.17).

To evaluate whether the probability of surviving to the onset of weaning (175 days) was a function of birth date, I used the set of females described in Table 5.4 and identified the birth dates of all young that either did (the "Yes" column in Table 5.4) or did not (the "No" column in Table 5.4) survive. Table 5.18 presents details on the mean birth dates (and S.E.) of young that did or did not survive to the onset of weaning on each of the two principal trapping grids in 1995 and 1996. Young born earlier in the breeding season were more likely to survive to the onset of weaning, although there was a significant difference between the two trapping grids in the magnitude of this effect, such that, the effect was much more pronounced on the East grid (Table 5.18).

To evaluate whether the proportion of young surviving to the onset of weaning among first-time breeders differed from that among repeat breeders I once again used the set of females described in Table 5.4, identifying within this set the subset consisting of only first-time breeders and females known to have given birth at least once before. There were four first-time breeders among the females described in Table 5.4, there being one first-time breeder on each grid in each year, consisting of three 2-year-olds and one 3-year-old. All four first time breeders lost their young prior to the onset of weaning. There were 43 young born to repeat breeders among the females described in Table 5.4, 12 of the young being lost prior to the onset of weaning. There were four females among the repeat breeders described in Table 5.4 that gave birth in both 1995 and 1996: two females that lost their young in 1995, but had surviving young in 1996; one female that had a surviving young in 1995 but lost her young in 1996; and a fourth female that had surviving young in both years. Whereas the identity of the mother was unimportant in the previous analysis of the data presented in Table 5.4, as my goal was solely to establish a pattern between years or across trapping grids, in the present analysis I am directly concerned with whether the characteristics of an individual (whether it is a first-time or repeat breeder) influence the likelihood that its young will survive, and it is therefore inappropriate to count some individuals twice and others only once. As a “mean fate” makes little sense, I chose to exclude the four females that gave birth in both years from the subsequent analyses, leaving me with a set of 35 repeat breeders each of which was counted only once, thereby generating a set of 35 young, of which 9 were lost prior to the onset of weaning.

I compared the set of 4 first-time, and 35 repeat, breeders by conducting a log-linear analysis identical in form to the one described in Table 5.4, with the addition of a term identifying status (first-time versus repeat). As expected, given this is a subset of the data presented in Table 5.4, the best fit to the data was provided by a model incorporating a survival by year interaction with significant partial ($\chi^2 = 4.41$, $p = 0.0357$) and marginal ($\chi^2 = 6.71$, $p = 0.0096$) associations. Also as in Table 5.4, there were indications of differences in survival between the grids as the survival by grid terms were almost significant (partial $\chi^2 = 2.98$, $p = 0.0845$; marginal $\chi^2 = 3.46$, $p = 0.0628$). For the present purposes what is most important is that the survival by status terms were significant (partial $\chi^2 = 4.86$, $p = 0.0275$; marginal $\chi^2 = 6.11$, $p = 0.0134$) indicating that the proportion of young surviving to the onset of weaning among first-time breeders was significantly different from that among repeat breeders (see Table 5.1). As none of the higher order interaction terms in the model were significant ($p > 0.15$ in all cases), the differences attributable to status were not a function of year or trapping grid.

Thus far in this section I have demonstrated that: 1) first-time breeders give birth later in the breeding season (the effect being more pronounced on one of the two trapping grids); 2) females giving birth later in the breeding season are less likely to successfully rear their young to the onset of weaning (the effect being more pronounced on one of the two trapping grids); and 3) first-time breeders are less likely to successfully rear their young to the onset of weaning than are repeat breeders, independent of year or trapping grid. The observation that late breeders are less likely to successfully rear their young (result number 2), which was also reported by Humphreys et al. (1984, their Table 1) as regards the Orongorongo Valley site, could be a byproduct of the combination of results (1) and (3), whereby first-time breeders are later and less successful, and the latter relationship is the primary cause of the overall pattern between birth date and breeding success. In the previous analysis of the overall relationship between birth date and breeding success (result number 2), I did not consider the status of the individuals involved. First-time breeders (N = 4) were considered along with known repeat breeders and other females who may or may not have given birth before. It is not clear from Humphreys et al. (1984) whether they considered the status of individuals among the females they reported on.

Is there evidence of a relationship between birth date and breeding success when only repeat breeders are considered? In the following analysis I used the same set of 35 repeat breeders described in the analysis of the relationship between status and breeding success. I identified the birth dates of all young that either did (N = 20) or did not (N = 9) survive. Birth dates were pooled across years (Mann-Whitney U = 57.0, z = 0.17, p = 0.8624) and between trapping grids (Mann-Whitney U = 101.5, z = 0.11, p = 0.9126). There was no significant difference (Mann-Whitney U = 65.5, z = 1.16, p = 0.2478) concerning the timing of breeding within a season between repeat breeders that had surviving young (median birth date = April 17) as compared to those that lost their young prior to the onset of weaning (median birth date = April 23).

I conclude that the overall effect of birth date on breeding success reported by Humphreys et al. (1984) is a consequence of the fact that first-time breeders give birth significantly later in the season and are significantly less likely to successfully rear their young to weaning. If the fact that females generally do not give birth at the Paddys Land site until they are 2 or 3 years old, is taken together with the present results suggesting that first-time breeders are bad mothers, it follows that most females are unlikely to produce a surviving pouch-young until they are at least 3 or 4 years old. This is in dramatic contrast to

Green's (1984, p. 487) estimate that "if the effect of double breeding is ignored, 3-year-old females in Australia will have weaned, on average, 2.5 young".

DISCUSSION

I observed the following with respect to the reproductive biology of possums at the Paddys Land site (compare to Table 5.1). Females generally do not give birth until they are 2 or 3 years old and are generally unsuccessful in their first attempt, likely because they give birth too late in the season. Almost all older adult females give birth to a single young in autumn every year. Those few births that occur in winter generally involve "replacement" young, and there is no "double breeding" in spring. There is a large and consistent male-bias in the sex ratio of pouch-young. Survival of pouch-young to the onset of weaning can be highly variable (33-81 %). Inter-annual variation is most likely a function of food supply. Survival of pouch-young may be adversely affected by handling, and this may be a more significant problem in years when there is a shortage of food. Estimates of post-weaning survival must account for the fact that a certain proportion of males emigrate from their natal range at this time. Post-weaning survival of females does not appear to vary as much between years (47-60 %) as does pre-weaning survival (33-81 %), suggesting that inter-annual variation in recruitment is largely determined by inter-annual variation in pre-weaning survival, which in turn is largely determined by food supply. I conclude that the reproductive biology of common brushtail possums at the Paddys Land site clearly corresponds more closely to that of undisturbed populations in New Zealand (Table 5.1) than it does to either disturbed populations in New Zealand (Table 5.1) or other populations in south-eastern Australia (Green 1984).

As I have indicated throughout this Chapter, the reproductive biology of possums at the Paddys Land site is almost identical to that described regarding the Orongorongo Valley site. According to Cowan (1990, p. 93), "possums in New Zealand have adapted to new diets and habitats, and have fewer parasites, predators and competitors than those in Australia". As reported in Chapter 6, both the Paddys Land and Orongorongo Valley possum populations appear to share a similar suite of parasites as well as demonstrating a similar prevalence and intensity of parasitic infections. Moreover, there also appears to be a similar relationship between the intensity of nematode infections and poor condition. As regards predators, only 8 of 24 (33.3 %) “natural” deaths among radio-collared adult females at the Paddys Land site were attributable to predation, and in 6 of these 8 cases, the predators involved appeared to be feral cats and dogs (or dingos), both of which occur in the Orongorongo Valley (Fitzgerald and Karl 1979, Anderson 1990).

What is truly remarkable about the virtually identical demography of possums at the Paddys Land and Orongorongo Valley sites is that, in terms of folivory at least, possums in New Zealand have no competitors, other than phytophagous insects, because there were no non-volant, terrestrial mammals there prior to 1000 years ago (King 1990). The islands of New Zealand became separated from Australia in the late Cretaceous, about 90-65 million years ago, before the evolutionary radiation of mammals that followed the disappearance of the dinosaurs. Consequently, the majority of native plants in New Zealand are endemics that evolved in the absence of mammalian herbivores (King 1990). In contrast, Eucalypts in Australia have coevolved with a suite of arboreal marsupial folivores (including possums), and as a result, have numerous chemical defences against mammalian herbivory (Freeland and Winter 1975; White 1993, pp. 181-189; Foley and McArthur 1994). The continuous forest cover at the Paddys Land site is composed entirely of Eucalypts (Chapter 4). Moreover, the area is estimated to contain “the highest concentration or arboreal mammals found in New South Wales” (NPWS 1992, p. 20). Thus, in terms of vegetation and the abundance of interspecific competitors, there is no similarity whatsoever between the Paddys Land and Orongorongo Valley sites.

How is that the reproductive biology of possums at the Paddys Land site could be so similar to that at the Orongorongo Valley site, in New Zealand, while being so different from that at other sites in south-eastern Australia (Green 1984)? The 121,000 ha Guy Fawkes Wilderness Area (GFWA), of which Paddys Land is a part (Chapter 4), was legally “identified” as wilderness by the New South Wales government because it was judged to have met the criterion that “the area is, together with its plant and animal communities, in a state that has not been substantially modified by humans and their works” (NPWS 1992, p. 6). Given this, I conclude that the reproductive biology of possums at the Paddys Land site is representative of the “natural” pattern of demography in south-eastern Australia. In contrast to the Paddys Land site, I suggest that the farms, forestry plantations and city suburbs, that were the sites of previous studies on the reproductive biology of possums in south-eastern Australia (Green 1984), are all clearly fragmented or disturbed sites. As I argued in the introduction, I conclude from the results of the experiment discussed in Chapter 4 that connectivity likely plays little role in the demography of common brushtail possum populations, and that contrasts between the Paddys Land site and other sites in south-eastern Australia can therefore be attributed entirely to edge effects.

The high fecundity and early maturation characteristic of the reproductive biology of, what I will now refer to as, "disturbed" populations in south-eastern Australia (those reviewed by Green 1984), is in contrast to the low fecundity and delayed maturation apparent at the "undisturbed" Paddys Land site (Table 5.1). The greater reproductive output of disturbed populations could be attributable to greater food availability at disturbed sites. However, if disturbed populations are primarily food limited they should increase to a density at which food is limiting, and the demography should come to resemble that at the Paddys Land site, albeit at a higher density. But this is not the case. Moreover, the density of possums at the Paddys Land site (Chapter 4) is higher than the density of possums recorded at any of the disturbed sites considered in Green's (1984, his Table 1; see also Kerle 1984, her Table 3) review.

An alternative explanation for the greater reproductive output, and lower density, of disturbed populations in south-eastern Australia, is that these are "harvested" populations (Caughley and Sinclair 1994, p. 281). As described in the introduction, the level of human harvesting of possum populations in New Zealand largely determines which of the two patterns of reproductive biology (Table 5.1) is observed (Cowan 1990). Green (1984) noted that none of the south-eastern Australian studies he reviewed contained data on the likely causes of adult and (and subadult) deaths. Nonetheless, differences in the likely number, type and behaviour of introduced terrestrial carnivores, between the Paddys Land site and disturbed sites in south-eastern Australia, are congruent with the suggestion that disturbed populations are subject to a greater rate of "harvesting" by introduced terrestrial carnivores.

The density of introduced terrestrial carnivores (feral cats and dogs/dingos) at the Paddys Land site was low (Tables 5.8 and 6.8) in comparison with other areas in south-eastern Australia (Wilson et al. 1992), and as noted above, the effect of these predators on the demography of the population appeared to be minimal (Chapter 6). In addition, a salient feature of the ecology of the Paddys Land site is the apparent absence of foxes (which may be associated with the apparent absence of rabbits, *Oryctolagus cuniculus*; Morton 1990). The reports of the presence of foxes, listed in Tables 5.8 and 6.8, were made by field assistants, who themselves were not confident in their appraisal. As noted in Tables 5.8 and 6.8, foxes have never been seen by residents of the area, nor were foxes detected in predator surveys conducted in another part of the GFWA (Chaelundi State Forest) by Catling and Burt (1995). Catling and Burt's (1995, their Table 2 and Fig. 1) results are of particular note because there were only two sites they surveyed, other than those in the GFWA, where foxes were apparently absent, from among a total of 29 survey sites located in Eucalypt forests throughout eastern New South Wales. According to Catling and Burt (1995, p. 544), "severe disturbance such as clearing for grazing or agriculture, intensive logging or frequent prescribed burning appear to play some part in the distribution and abundance of the red fox and the demise of … medium-sized *ground-dwelling* mammals" (Catling and Burt 1995, p. 544; italics added). I conclude that disturbed sites in south-eastern Australia will generally posses both, more species (3 vs. 2), and greater densities, of introduced terrestrial carnivores than undisturbed areas, such as at the Paddys Land site.

Catling and Burt's (1995) emphasis on the relation between the abundance of foxes and the demise of *ground-dwelling* mammals is of note with respect to the fact that edge effects may not only involve changes in the density of predators but also changes in the vulnerability of prey. The mediating influence of cover, or some other refuge from predation, is demonstrated in the present distribution of common brushtail possums. Possums are now primarily restricted to the wooded margins of the Australian continent (How and Kerle 1995). In forests and woodlands, possums can readily escape from an introduced terrestrial carnivore by climbing a tree. In central Australia possums inhabited largely treeless landscapes and it is these regions from which they have disappeared (Kerle et al. 1992). All of the other medium-sized, herbivorous, marsupials that have suffered declines in central Australia are (were) strictly terrestrial (Morton 1990). That the importance of trees is largely as a refuge from predation is demonstrated by the fact that even in the wooded margins of the continent where possums still persist, most of the strictly terrestrial species of medium-sized, herbivorous, marsupials, have disappeared (Strahan 1995). If as I have suggested, the importance of trees is as a refuge from predation, then the fragmentation (Smith et al. 1969, Dunnet 1964) and thinning (Winter 1976; Hocking 1981, cited in Humphreys et al. 1984; How 1981) of the formerly continuous forest cover at disturbed sites in south-eastern Australia, will likely cause possums to spend more time on the ground away from cover, making them more vulnerable to "harvesting" by the greater number of introduced terrestrial carnivores.

Catling and Burt (1995, see also Short and Smith 1994) emphasized the importance of introduced terrestrial carnivores in the decline of *ground-dwelling*, medium-sized Australian mammals. I chose to study common brushtail possums as a “model”, medium-sized, herbivorous, marsupial, in order to address issues regarding the decline of medium-sized Australian mammals. It may be argued that possums are unrepresentative of this group because they are not strictly ground-dwelling, and persist in areas where other medium-sized mammals have disappeared. However, I interpret the contrasts between disturbed and undisturbed possum populations in south-eastern Australia which I have discussed, as reflecting the same phenomenon that have caused the complete disappearance of other species: possums at disturbed sites are heavily “harvested” by introduced terrestrial carnivores leading to a dramatically different pattern of demography than at undisturbed sites; whereas, other species that could not find refuge from predator attacks by climbing trees were “harvested” to extinction. In Chapter 4, I argued that the results of my experiment regarding the rate of female immigration in common brushtail possum populations suggest that immigration does not often “rescue” populations of any species of medium-sized, herbivorous, marsupial, from extinction. I conclude that carnivory is much more important than connectivity to the demography of common brushtail possum populations, and that this conclusion likely also applies to most other medium-sized, herbivorous, marsupials.

REFERENCES

Anderson, A. J. 1990. Kuri, Maori dog. *In* The handbook of New Zealand mammals. *Edited by* King, C. M. Oxford University Press, Auckland, New Zealand, pp. 281-287.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos, 71: 355-356.

Beier. P., and Noss, R. F. 1998. Do habitat corridors provide connectivity? Conservation Biology, 12: 1241-1252.

Bolliger, A., and Carrodus, A. L. 1938. Changes in and around the pouch of *Trichosurus vulpecula*, as occurring naturally and as the result of the administration of oestrone. Journal and Proceedings of the Royal Society of New South Wales, 71: 615-622.

Bolliger, A., and Carrodus, A. L. 1940. The effects of oestrogens on the pouch of the marsupial *Trichosurus vulpecula*. Journal and Proceedings of the Royal Society of New South Wales, 73: 218-227.

Catling, P. C., and Burt, R. J. 1995. Why are red foxes absent from some Eucalypt forests in eastern New South Wales? Wildlife Research, 22: 535-546.

Caughley, G., and Sinclair, A. R. E. 1994. Wildlife ecology and management. Blackwell Science, Cambridge, Massachusetts.

Clark, J. M. 1995. The diet of the parasitic mite *Trichosurolaelaps crassipes* Womersley, 1956, and its potential to act a disease vector. New Zealand Veterinary Journal, 43: 215-218.

Clout, M. N. 1982. Determination of age in the brushtail possum using decalcified molar teeth. New Zealand Journal of Zoology, 9: 405-408.

Clout, M. N., and Efford, M. G. 1984. Sex differences in the dispersal and settlement of brushtail possums (*Trichosurus vulpecula*). Journal of Animal Ecology, 53: 737-749.

Cowan, P. E. 1990. Brushtail possum. *In* The handbook of New Zealand mammals. *Edited by* King, C. M. Oxford University Press, Auckland, New Zealand, pp. 68-98.

Crawley, M. C. 1973. A live-trapping study of Australian brush-tailed possums, *Trichosurus vulpecula* (Kerr), in the Orongorongo Valley, Wellington, New Zealand. Australian Journal of Zoology, 21: 75-90.

Dunnet, G. M. 1956. A live-trapping study of the brush-tailed possum *Trichosurus vulpecula* Kerr (Marsupialia). CSIRO Wildlife Research, 1: 1-18.

Dunnet, G. M. 1964. A field study of local populations of the brush-tailed possum *Trichosurus vulpecula* in eastern Australia. Proceedings of the Zoological Society of London, 142: 665-695.

Efford, M. 1991. A review of possum dispersal. DSIR Land Resources Contract Report 91/73, DSIR Land Resources, Dunedin, New Zealand.

Efford, M. G. 1994. Long-term studies of the dynamics of a local population of brushtail possums. Live-trapping in the Orongorongo Valley in 1993/94. Manaaki Whenua - Landcare Research, Dunedin, New Zealand.

Efford, M. 1998. Demographic consequences of sex-biased dispersal in a population of brushtail possums. Journal of Animal Ecology, 67: 503-517.

Fitzgerald, A. E. 1976. Diet of the opossum *Trichosurus vulpecula* (Kerr) in the Orongorongo Valley, Wellington, New Zealand, in relation to food plant availability. New Zealand Journal of Zoology, 3: 399-419.

Fitzgerald, B. M., and Karl, B. J. 1979. Food of feral house cats (*Felis catus* L.) in forest of the Orongorongo Valley, Wellington. New Zealand Journal of Zoology, 6: 107-126.

Foley, W. J., and McArthur, C. 1994. The effects and costs of ingested allelochemicals in mammals: an ecological perspective. *In* The digestive system in mammals: food, form and function. *Edited by* Chivers, D. J., and Langer, P. Cambridge University Press, Cambridge, pp. 370-391.

Freeland, W. J., and Winter, J. W. 1975. Evolutionary consequences of eating: *Trichosurus vulpecula* (Marsupialia) and the genus *Eucalyptus*. Journal of Chemical Ecology, 1: 439-455.

Gilmore, D. P. 1969. Seasonal reproductive periodicity in the male Australian brush-tailed possum (*Trichosurus vulpecula*). Journal of Zoology (London), 157: 75-98.

Green, W. Q. 1984. A review of ecological studies relevant to the management of the common brushtail possum. *In* Possums and gliders. *Edited by* Smith, A. P., and Hume, I. D. Australian Mammal Society, Sydney, Australia, pp. 483-499.

Hanski, I. 1998. Metapopulation dynamics. Nature (London), 396: 41-49.

Hemsley, S., and Canfield, P. 1993. Dermatitis in brushtail possums (*Trichosurus vulpecula*). Proceedings of the Annual Meeting of the Australasian section of the Wildlife Disease Association, Wildlife Disease Association, Sydney, Australia, pp. 23-24.

Hintze, J. 1996. NCSS Statistical Software. NCSS, Kaysville, Utah, U.S.A. Information available at [http://www.ncss.com].

Hope, R. M. 1972. Observations on the sex ratio and the position of the lactating mammary gland in the brush-tailed possum, *Trichosurus vulpecula* (Kerr) (Marsupialia). Australian Journal of Zoology, 20: 131-137.

How, R. A. 1981. Population parameters of two congeneric possums, *Trichosurus* spp., in north-eastern New South Wales. Australian Journal of Zoology, 29: 205-215.

How, R. A., and Kerle, J. A. 1995. Common brushtail possum. *In* The mammals of Australia. *Edited by* Strahan, R. Reed Books, Sydney, Australia, pp. 273-275.

Humphreys, W. F., Bradley, A. J., How, R. A., and Barnett, J. L. 1984. Indices of condition of Phalanger populations: a review. *In* Possums and gliders. *Edited by* Smith, A. P., and Hume, I. D. Australian Mammal Society, Sydney, Australia, pp. 59-77.

Kerle, J. A. 1984. Variation in the ecology of *Trichosurus*: its adaptive significance. *In* Possums and gliders. *Edited by* Smith, A. P., and Hume, I. D. Australian Mammal Society, Sydney, Australia, pp. 115-127.

Kerle, J. A., Foulkes, J. N., Kimber, R. G., and Papenfus, D. 1992. The decline of the brushtail possum, *Trichosurus vulpecula* (Kerr 1778), in arid Australia. Rangelands Journal, 14: 107-127.

Kerle, J. A., and Howe, C. J. 1992. The breeding biology of a tropical possum, *Trichosurus vulpecula arnhemensis* (Phalangeridae : Marsupialia). Australian Journal of Zoology, 40: 663-665.

Kerle, J. A., McKay, G. M., and Sharman, G. B. 1991. A systematic analysis of the brushtail possum, *Trichosurus vulpecula* (Kerr, 1792) (Marsupiala : Phalangeridae). Australian Journal of Zoology, 39: 313-331.

King, C. M. 1990. The mammals of New Zealand: general information. *In* The handbook of New Zealand mammals. *Edited by* King, C. M. Oxford University Press, Auckland, New Zealand, pp. 1-32.

Krebs, C. J. 1999. Ecological methodology, 2nd ed. Benjamin/Cummings, Menlo Park, California.

Laurance, W. F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. Journal of Mammalogy, 71: 641-653.

Laurance, W. F., and Gascon, C. 1997. How to creatively fragment a landscape. Conservation Biology, 11: 577-579.

Lidicker, W. Z., Jr., and Koenig, W. D. 1996. Responses of terrestrial vertebrates to habitat edges and corridors. *In* Metapopulations and wildlife conservation. *Edited by* McCullough, D. R., Island Press, Washington, D.C., pp. 85-109.

Lidicker, W. Z., Jr., and Stenseth, N. C. 1992. To disperse or not to disperse: who does it and why? *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 21-36.

Lyne, A. G., and Verhagen, A. M. W. 1957. Growth of the marsupial *Trichosurus vulpecula* and a comparison with some higher mammals. Growth, 21: 167-195.

Morton, S. R. 1990. The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. Proceedings of the Ecological Society of Australia, 16: 201-213.

NPWS. 1992. Guy Fawkes River Wilderness assessment report. N.S.W. National Parks and Wildlife Service, Sydney, Australia.

Pekelharing, C. J. 1970. Cementum deposition as an age indicator in the brush-tailed possum, *Trichosurus vulpecula* Kerr (Marsupialia). Australian Journal of Zoology, 18: 71-76.

Pilton, P. E., and Sharman, G. B. 1962. Reproduction in the marsupial *Trichosurus vulpecula*. Journal of Endocrinology, 25: 119-136.

Presidente, P. J. A. 1984. Parasites and diseases of brushtail possums (*Trichosurus* spp): occurrence and significance. *In* Possums and gliders. *Edited by* Smith, A. P., and Hume, I. D. Australian Mammal Society, Sydney, Australia, pp. 171-190.

Short, J., and Smith, A. 1994. Mammal decline and recovery in Australia. Journal of Mammalogy, 75: 288-297.

Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D, Mahon, P., and Newsome, A. E. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology 12: 564-575.

Smith, M. J., Brown, B. K., and Frith, H. J. 1969. Breeding of the brush-tailed possum, *Trichosurus vulpecula* (Kerr) in New South Wales. CSIRO Wildlife Research, 14: 181-193.

Sokal, R. R., and Rohlf, F. J. 1995. Biometry, 3rd ed. W. H. Freeman and Co., New York.

StatSoft, Inc. 1995. STATISTICA for Windows. StatSoft, Inc., Tulsa, Oklahoma, U.S.A. Information available at [http://www.statsoftinc.com].

Strahan, R. 1995. The mammals of Australia. Reed Books, Sydney, Australia.

Tyndale-Biscoe, C. H. 1955. Observations on the breeding and ecology of the brushtailed possum, *Trichosurus vulpecula* Kerr (Marsupialia) in New Zealand. Australian Journal of Zoology, 3: 162-184.

Tyndale-Biscoe, H. 1974. Life of marsupials. American Elsevier Publishing Company, Inc., New York.

Tyndale-Biscoe, H., and Renfree, M. 1987. Reproductive physiology of marsupials. Cambridge University Press, Cambridge.

Viggers, K. L., and Spratt, D. M. 1995. The parasites recorded from *Trichosurus* species (Marsupialia : Phalangeridae). Wildlife Research, 22: 311-332.

White, T. C. R. 1993. The inadequate environment: nitrogen and the abundance of animals. Springer-Verlag, Berlin.

Wilcove, D. S., McLellan, C. H., and Dobson, A. P. 1986. Habitat fragmentation in the temperate zone. *In* Conservation biology: the science of scarcity and diversity. *Edited by* Soule, M. E. Sinauer Associates, Sunderland, Massachusetts, pp. 237-256.

Wilson, G., Dexter, N, O’Brien, P, and Bomford, M. 1992. Pest animals in Australia: a survey of introduced wild mammals. Kangaroo Press, Sydney, Australia.

Winter, J. 1976. The behaviour and social organization of the brush tailed possum *Trichosurus vulpecula* (Kerr). Ph.D. Thesis, University of Queensland, Brisbane, QLD, Australia.

Wolff, J. O. 1997. Population regulation in mammals: an evolutionary perspective. Journal of Animal Ecology, 66: 1-13.

Table 5.1. Differences in the reproductive biology of common brushtail possums in disturbed and undisturbed populations.

	Disturbed	Undisturbed
Number of young born each year	2	1
Sex ratio of pouch-young	M > F	M >> F
Pre-weaning survival of young	consistently high	variable
Post-weaning survival of young	low	moderate
Age (years) at first breeding	1	3
Success of first-time breeders	high	low

Table 5.2. Number of resident adult females producing a primary young in either autumn or winter, compared to the number of females that did not reproduce. Values in parentheses indicate the number of weeks, out of the 13 in a season, during which the female in question was still alive.

		Breeding		Non-breeding		
		Autumn	Winter	Surviving	Dead	
					Autumn	Winter
1995	West	32	0	0	0	0
	East	29	3	1	0	0
1996	West	24	0	1	1 (9)	0
	East	21	0	0	0	2 (5,8)
1997	West	20	---	0	1 (9)	---
	East	15	---	0	0	---

Table 5.3. Sex ratios (F:M) of dependent young, categorized by study area and breeding season. Records for 1996 are divided into primary (A) and replacement (B) young. Numbers in bold were used in a log-linear analysis of the sex ratio of primary young on each of the two principal study grids in each of the three years of the study[1]. Empty cells indicate areas, or seasons, not sampled.

	1994	1995	1996 A	1996 B	1997
West	1 : 0	**2 : 3**	**10 : 15**	1 : 0	**5 : 12**
East		**0 : 4**	**9 : 13**	0 : 1	**4 : 11**
Vehicle trail			2 : 3		

[1] The analysis indicated a significant marginal association with sex ($\chi^2 = 8.47$, $p = 0.0036$), and no significant higher-order interactions.

Table 5.4. Pre-weaning survival of primary young. Values presented in the table were used in a log-linear analysis of the proportion of young that failed to survive to 175 days (No / [Yes + ?])[1].

		Survived to 175 days		
		No	Yes	?
1995	West	12	5	6
	East	8	4	8
1996	West	2	17	2
	East	6	9	2

[1] The analysis indicated that there was a significant partial ($\chi^2 = 5.51$, $p = 0.0189$) and marginal ($\chi^2 = 5.54$, $p = 0.0186$) association between survival and year. The three-way interaction term was, however, almost significant ($\chi^2 = 3.77$, $p = 0.0520$).

Table 5.5. Mean interval, in days, between occasions on which females were handled, while they were carrying a pouch-young, prior to 175 days after the birth of their young, as compared between instances where the young was known to have survived to the onset of weaning (at 175 days), and where it did not. A three-way ANOVA was conducted using transformed data[1]. The most appropriate transformation was selected using program BOXCOX (Krebs 1999). Assumptions regarding normality and homogeneity of variances were tested using program STATISTICA (StatSoft, Inc. 1995).

		Pouch-young survived to 175 days					
			No			Yes	
		N	Mean	S.E.	N	Mean	S.E.
1995	West	11	35.9	3.4	4	54.3	16.9
	East	6	38.4	8.0	4	54.3	19.3
1996	West	2	46.3	2.3	15	47.4	2.4
	East	4	32.4	5.9	8	58.8	9.5

[1] The analysis indicated a significant main effect of survival ($F_{1,46} = 5.50$, $p = 0.0234$), wherein the interval between occasions on which the mother was handled was greater among young that survived than those that didn't. There were no other significant main effects or interactions ($p > 0.20$ in all cases).

Table 5.6. Pre-weaning loss of young in relation to ear-tagging. Values presented in the table were used in a log-linear analysis of the number of pre-weaning pouch-young lost either before or after ear-tagging[1].

		Loss in relation to ear-tagging	
		Before	After
1995	West	4	8
	East	4	4
1996	West	1	1
	East	4	2

[1] The analysis indicated a significant marginal association with year ($\chi^2 = 6.61$, $p = 0.0318$), but no significant association with ear-tagging or study grid, and no significant higher-order interactions.

Table 5.7. Survival of young to October-November, 1996, as compared between mothers subject to repeated capture and handling (On-grid) and others that had not been previously trapped and handled (Off-grid)[1].

Survived to 175 days	Evidence	On-grid	Off-grid
Yes	Young known to be alive	22	8
	Mother still nursing	4	6
No	Young known to have died	9	---
	Mother no longer nursing	2	2

[1] The proportion of young known or presumed (because the mother still was nursing) to have survived to the onset of weaning (175 days) was not significantly different between the two groups (Fisher's exact test, p = 0.2986).

Table 5.8. Predator activity during the pre-weaning phase of development of primary young, from mid-March to mid-December, in 1995 and 1996, based on sightings, sounds, signs, and diagnoses of the proximate cause of death of adult possums.

Predator	Latin name	1995		1996	
		Presence detected	Possum eaten by	Presence detected	Possum eaten by
Wedge-tailed eagle	(*Aquila audax*)	14		8	
Dingo (or feral dog)	(*Canis familiaris*)	5	4	1	1
Feral cat	(*Felis catus*)			2	
Spotted-tailed quoll	(*Dasyurus maculatus*)	1			
European red fox[1]	(*Vulpes vulpes*)	1		1	
Powerful Owl	(*Ninox strenua*)	1	1		

[1] Unambiguous evidence of the presence of foxes was never obtained, and the animals reported here may have been feral dogs. Foxes have never been seen by residents of the area (Len and Winn Perry, pers. comm.). Nor are Foxes expected to be in the area based on survey results from the region (Catling and Burt 1995; their Table 2, regarding Chaelundi State Forest, which lies within the GFWA).

Table 5.9. Survival of primary young to August 1, in both 1995 and 1996, on both principal study grids.

		Survived to August 1		
		No	Yes	?
1995	West	1	27	3
	East	1	25	3
1996	West	0	22	1
	East	1	17	3

Table 5.10. Survival of pouch-young to the onset of weaning (175 days) in 1995 and 1996, among females demonstrating any or all of four symptoms of poor condition. See text for details.

Symptom	Breeding season	Pouch-young survived to 175 days	
		No	Yes
Feeding upon release	1995	1	0
	1996	0	2
"Weak and wobbly"	1995	2	0
	1996	0	1
"Bony"	1995	2	0
	1996	2	3
"Rumpy"	1995	10	0
	1996	4	6

Table 5.11. Changes in the status of individual adult female possums examined in a given season in 1995 for evidence of rump wear as compared to the same individual's status in the same season in 1996. The proportion of individuals demonstrating a change in status was analyzed by means of a repeated measures "exact" binomial test (Sokal and Rohlf 1995, p. 784), using program NCSS (Hintze 1996). The set of individuals used to compare between years in one season is not necessarily the same as the set used to make comparisons in the next season.

		Number of females examined	Rump wear Present 95 Absent 96	Absent 95 Present 96	Grid p^1	Pooled p^1
Autumn	West	16	0	4	0.1250	0.0313
	East	10	0	2	0.5000	
Winter	West	19	1	5	0.2188	0.0645
	East	17	1	4	0.3750	
Spring	West	16	3	1	0.6250	1.0000
	East	6	0	3	0.2500	

[1] As each group (e.g., females from the West grid) was tested three times, I should apply the Bonferroni method and set $p_{crit} = 0.017$. However, as the set of individuals used to compare between years in one season was not necessarily the same set used in the next season, applying the Bonferroni method may be overly conservative. If $0.05 > p > 0.017$, the result should be interpreted with caution.

Table 5.12. Median difference in mean weight (g) of individual adult possums measured in a given season in 1996 as compared to the same individual's mean weight in the same season in 1995. Changes in mean weight between years were analyzed using Wilcoxon's signed-ranks test. The set of individuals used to compare between years in one season is not necessarily the same as the set used to compare between years in the next season.

			Median difference in mean weight (g)	Number of individuals	T	z	p[1]
Autumn	Females	West	51	16	65.0	0.16	0.8767
		East	- 38	10	15.0	0.89	0.3743
	Males	West	33	15	56.0	0.23	0.8203
		East	113	7	1.0	2.20	0.0280
Winter	Females	West	50	19	75.5	0.78	0.4326
		East	- 75	17	61.0	0.73	0.4631
	Males	West	100	15	33.0	1.53	0.1252
		East	- 50	13	44.5	0.07	0.9443
Spring	Females	West	206	16	10.5	2.97	0.0030
		East	250	6	0.0	2.20	0.0277
	Males	West	221	16	3.0	3.36	0.0008
		East	150	10	0.0	2.67	0.0077

[1] As each group (e.g., females from the West grid) was tested three times, I should apply the Bonferroni method and set $p_{crit} = 0.017$. However, as the set of individuals used to compare between years in one season was not necessarily the same set used in the next season, applying the Bonferroni method may be overly conservative. If $0.05 > p > 0.017$, the result should be interpreted with caution.

Table 5.13. Weight (g) of adult females weighed with or without a young in the pouch, in October-November, 1996, as compared between On-grid and Off-grid locations. A two-way ANOVA was conducted using transformed data[1]. The most appropriate transformation was selected using program BOXCOX (Krebs 1999). Assumptions regarding normality and homogeneity of variances were tested using program STATISTICA (StatSoft, Inc. 1995).

	On-grid			Off-grid		
	N	Mean	S.E.	N	Mean	S.E.
Mother with young in pouch	8	2631	143	5	2810	113
Mother without young in pouch	24	2288	54	11	2245	72

[1] The analysis indicated a significant main effect of the presence or absence of a young in the pouch ($F_{1,44} = 20.16$, $p = 0.0001$), but no significant effect of location nor a significant interaction ($p > 0.25$ in both cases).

Table 5.14. Number of young tagged as pouch-young in the year indicated, that were later seen as subadults, independent of their mothers. The brackets signify an individual that was seen in summer, but never again, while numbers not in brackets signify individuals known to have survived to the beginning (mid-March) of the breeding season in the year following the year in which they were born.

	1995 Breeding Season		1996 Breeding Season	
	Females	Males	Females	Males
West	1	2	3	1
East	0	1 (1)	3	2

Table 5.15. Mean, median, and other summary statistics, regarding the distribution of mean autumn body weights (g), among known-aged animals. Ages "2 +" and "3 +" are composed of adult individuals known to be the minimum age specified, based on trapping records. Animals that were present in more than one year are included in each of the applicable age categories. Consequently, because individuals are included more than once, the tallies for each age category should not be interpreted as independent samples. S.D. = standard deviation. S.E. = standard error of the mean.

Age (years)	Sex	N	Mean -1.96 S.D.	Minimum	Mean	Median	Maximum	Mean +1.96 S.D.	S.E.
1	Pooled	9	847	925	1316	1300	1700	1785	80
2	Pooled	8	1428	1500	1810	1825	2150	2191	69
3	Pooled	6	1638	1683	2093	2154	2317	2548	95
4	Pooled	6	1878	1950	2135	2150	2300	2391	53
2 +	Females	31	1826	1700	2207	2250	2500	2589	35
	Males	42	1832	1850	2289	2267	2975	2747	36
3 +	Females	24	1975	1950	2314	2332	2550	2652	35
	Males	32	1965	2013	2387	2394	2800	2809	38

Table 5.16. New individuals detected during grid trapping from the beginning of spring 1995 onwards. For the purposes of this comparison individuals weighing 1850 g or less on any occasion were considered small, while those weighing more were considered large.

		Females				Males			
		Subadult		Adult		Subadult		Adult	
		Small	Large	Small	Large	Small	Large	Small	Large
Spring 1995 to	West	1	0	1	3	1	0	1	4
Winter 1996	East	1	0	0	3	0	0	0	6
Spring 1996 to	West	0	0	0	2	1	1	2	8
Winter 1997	East	0	0	0	3	1	0	0	5

Table 5.17. Birth dates of pouch-young (expressed as the number of days from the beginning of autumn) among first-time breeders and females that had given birth at least once before (repeat breeders). If a repeat breeder bred in more than one year, I calculated the mean birth date of her young, pooled across years, and used the derived value in the analyses presented below. Birth dates were compared between groups using Mann-Whitney U tests.

		N	Median	Minimum	Maximum	U	z	p
West	First time	3	47.0	9	52	32	0.50	0.6159
	Repeat	26	34.3	11	74			
East	First time	6	59.0	48	117	17	2.74	0.0061
	Repeat	22	36.3	17	80			
Pooled	First time	9	52.0	9	117	91	2.74	0.0062
	Repeat	48	34.8	11	80			

Table 5.18. Birth dates of pouch-young (expressed as the number of days from the beginning of autumn) in relation to the pre-weaning survival of primary young (see Table 5.4) on each of the two principal study grids in each of the two complete years for which data were available. A three-way ANOVA was conducted using untransformed data[1]. Assumptions regarding normality and homogeneity of variances were tested using program STATISTICA (StatSoft, Inc. 1995).

		Survived to 175 days					
			No			Yes	
		N	Mean	S.E.	N	Mean	S.E.
1995	West	12	28.6	5.0	5	39.2	9.5
	East	8	42.0	3.6	4	21.0	6.7
1996	West	2	44.5	2.5	17	35.4	3.6
	East	6	48.5	8.2	9	29.2	3.2

[1] The analysis indicated a significant main effect of survival ($F_{1,55} = 4.35$, $p = 0.0416$) and a significant two-way interaction between survival and trapping grid ($F_{1,55} = 5.07$, $p = 0.0284$), wherein young born earlier in the breeding season were more likely to survive, on the East grid. There were no other significant main effects or interactions ($p > 0.15$ in all cases).

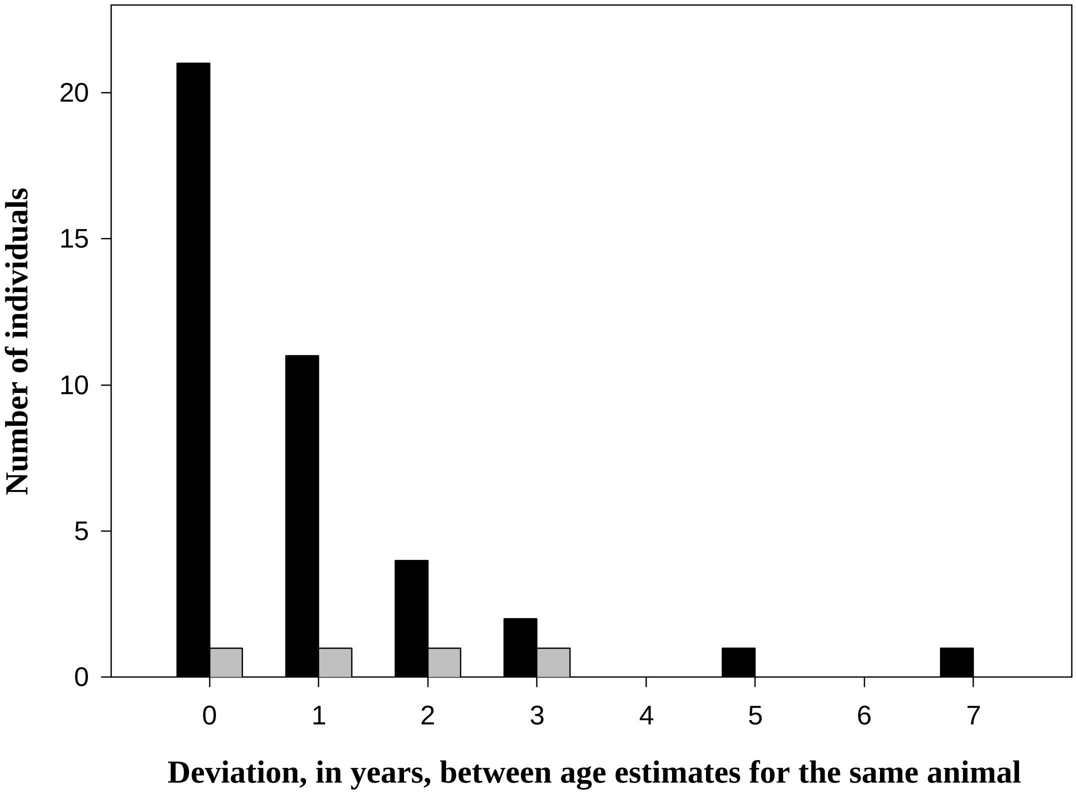

Figure 5.1. Deviation, in years, between age estimates, based on cementum annuli, made using two teeth (PM1 and M3) from the same individual. Black bars indicate data from the first batch of teeth examined for cementum annuli, while grey bars indicate data from a second batch that included a second set of two teeth from each the four individuals that demonstrated deviations of 3 or more years in the first batch.

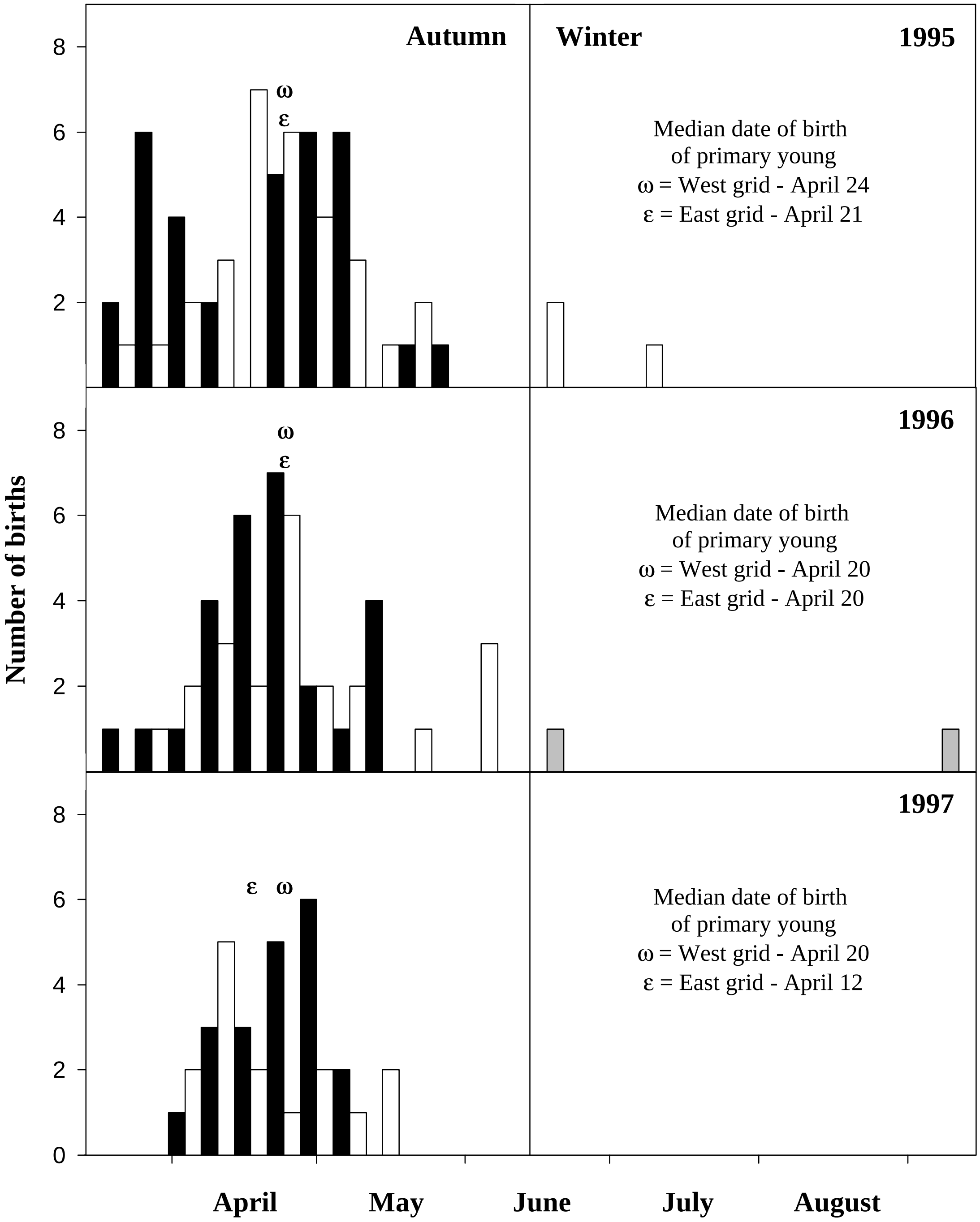

Figure 5.2. Number of births per week during autumn and winter in each of the three years of the study. Black bars signify primary young on the West grid, while open bars indicate primary young on the East grid. Grey bars indicate replacement young. The earlier replacement birth occurred on the West grid, while the later replacement birth occurred on the East grid.

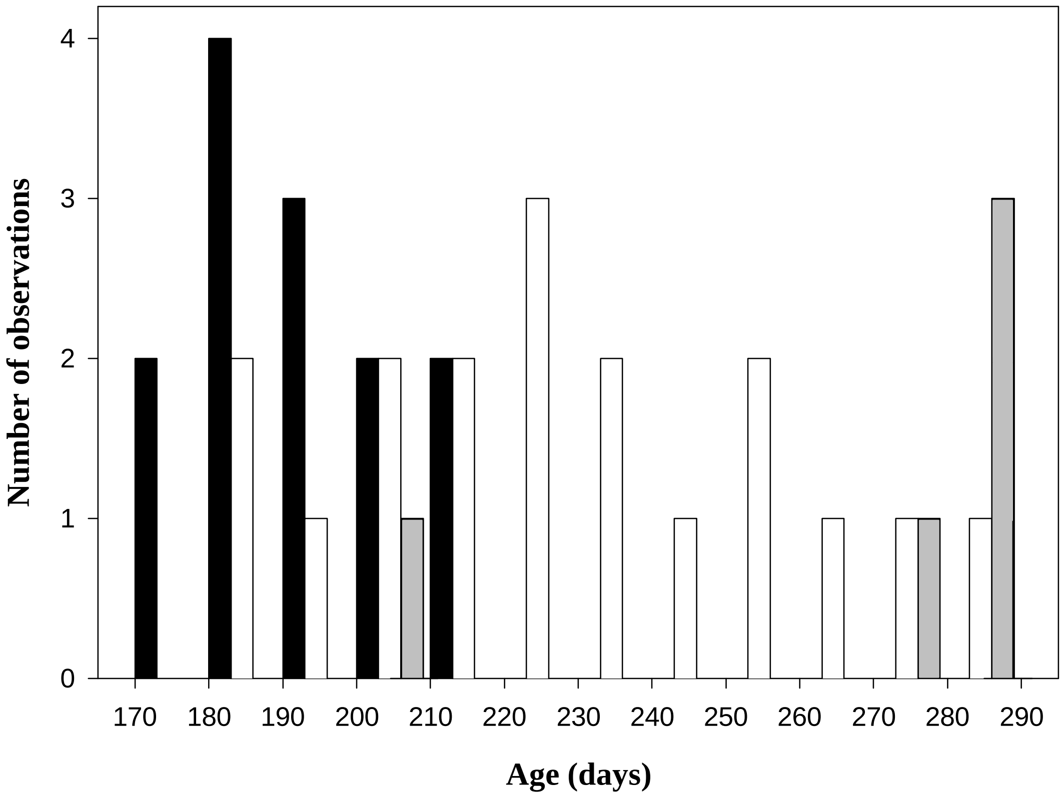

Figure 5.3. Number of observations concerning the three stages in the weaning of young, vs. the age of the young. Black bars indicate the earliest a young was seen riding on its mother's back. Open bars indicate nursing mothers seen in the absence of the young. Grey bars indicate the earliest a surviving young was known to have been completely weaned.

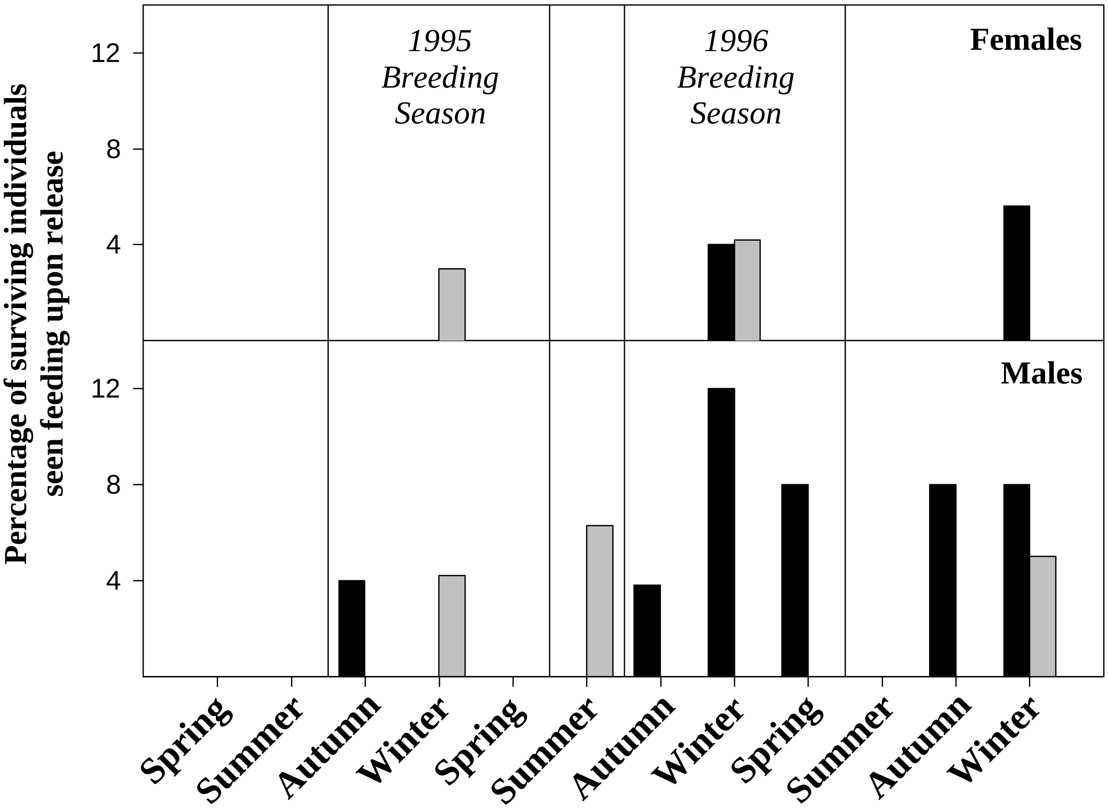

Figure 5.4. Percentage of adult possums seen feeding upon being released from a trap, in each season, among animals that were known to have survived to the end of the season. Black bars signify data from the West grid, while grey bars represent data from the East grid.

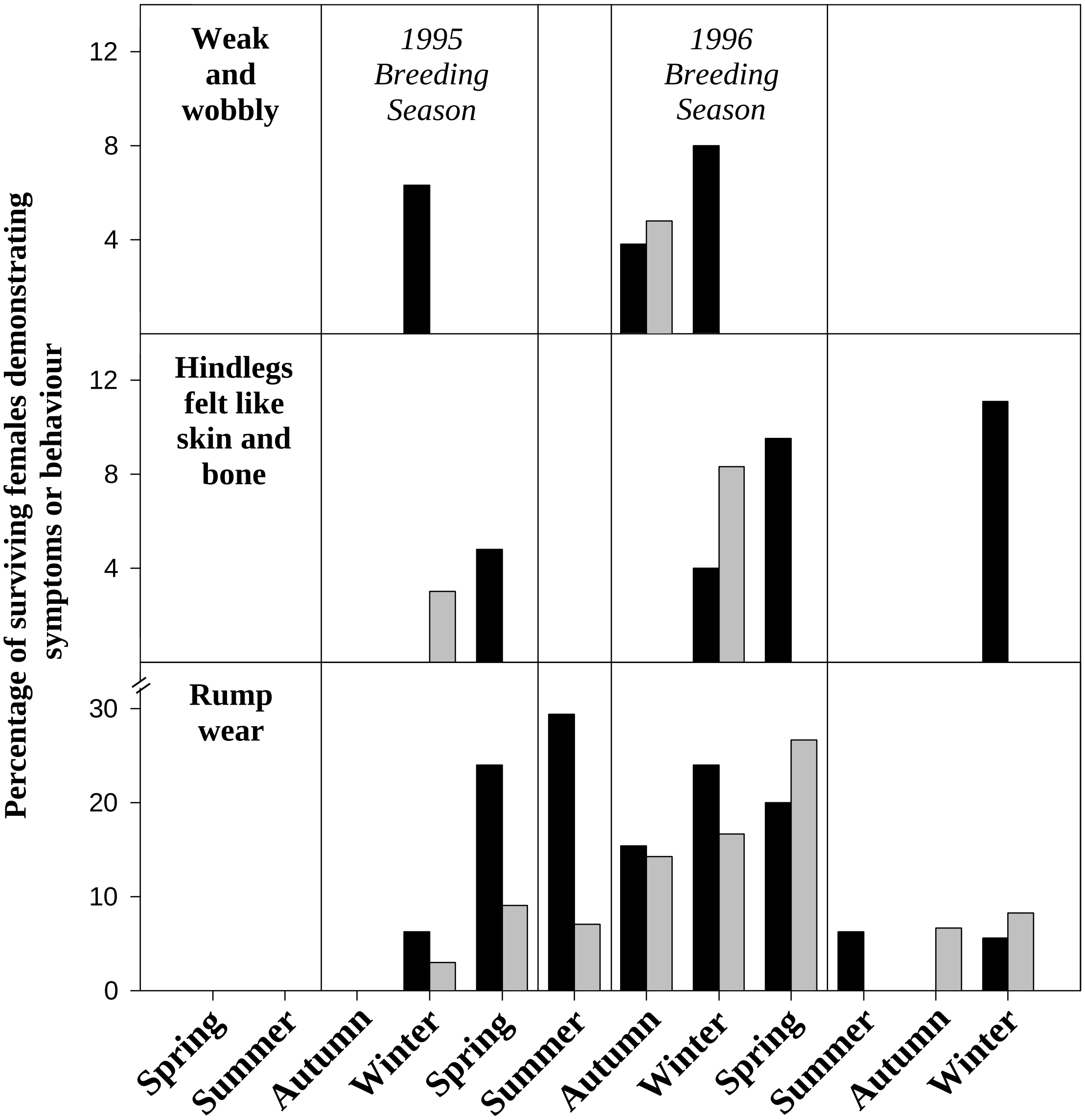

Figure 5.5. Percentage of adult female possums demonstrating symptoms or behaviours potentially indicative of poor condition, in each season, among animals that were known to have survived to the end of the season. Black bars signify data from the West grid, while grey bars represent data from the East grid.

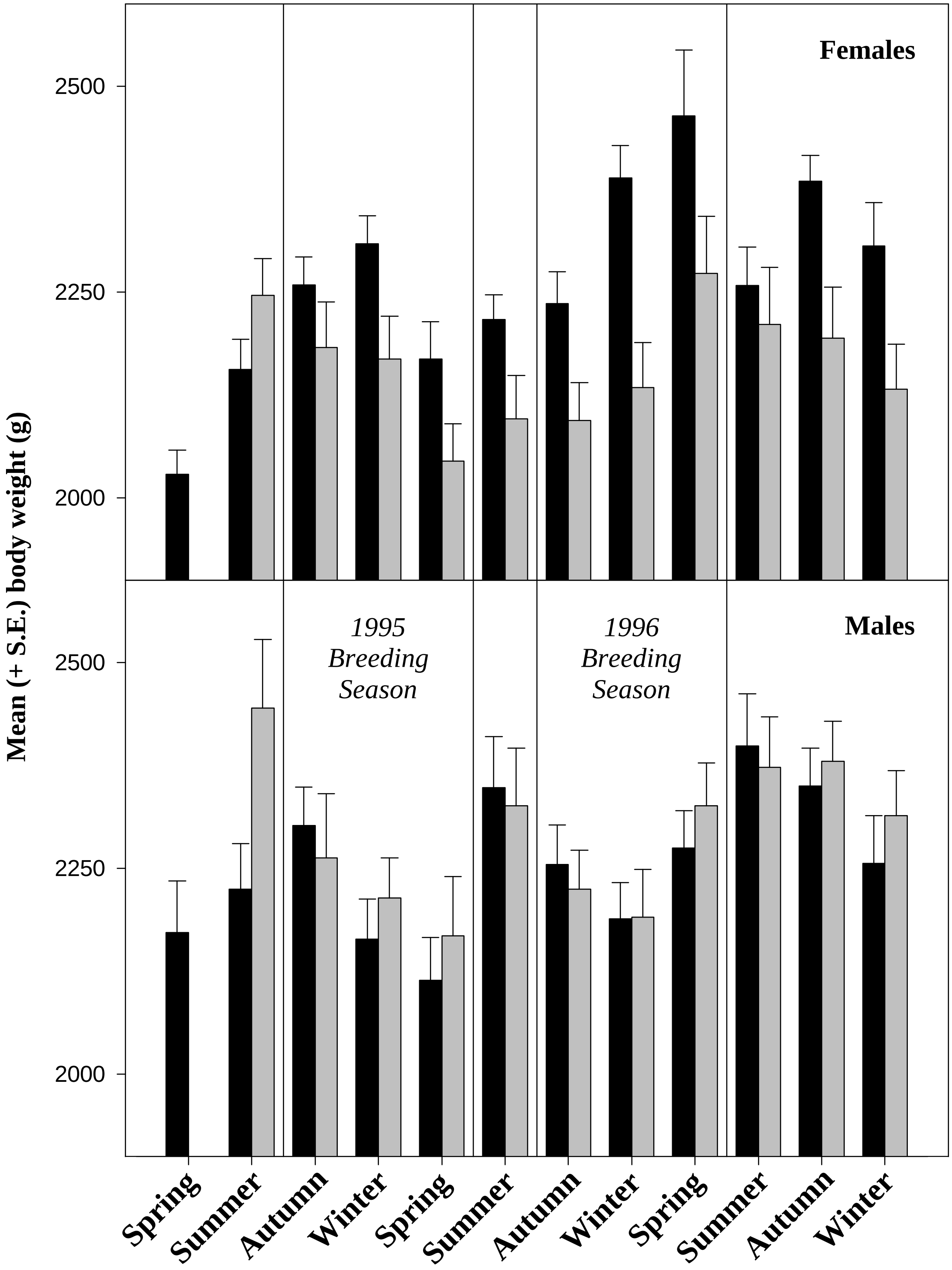

Figure 5.6. Mean (+ S.E.) body weight (g) of adult possums, categorized by season. Black bars signify data from the West grid, while grey bars represent data from the East grid.

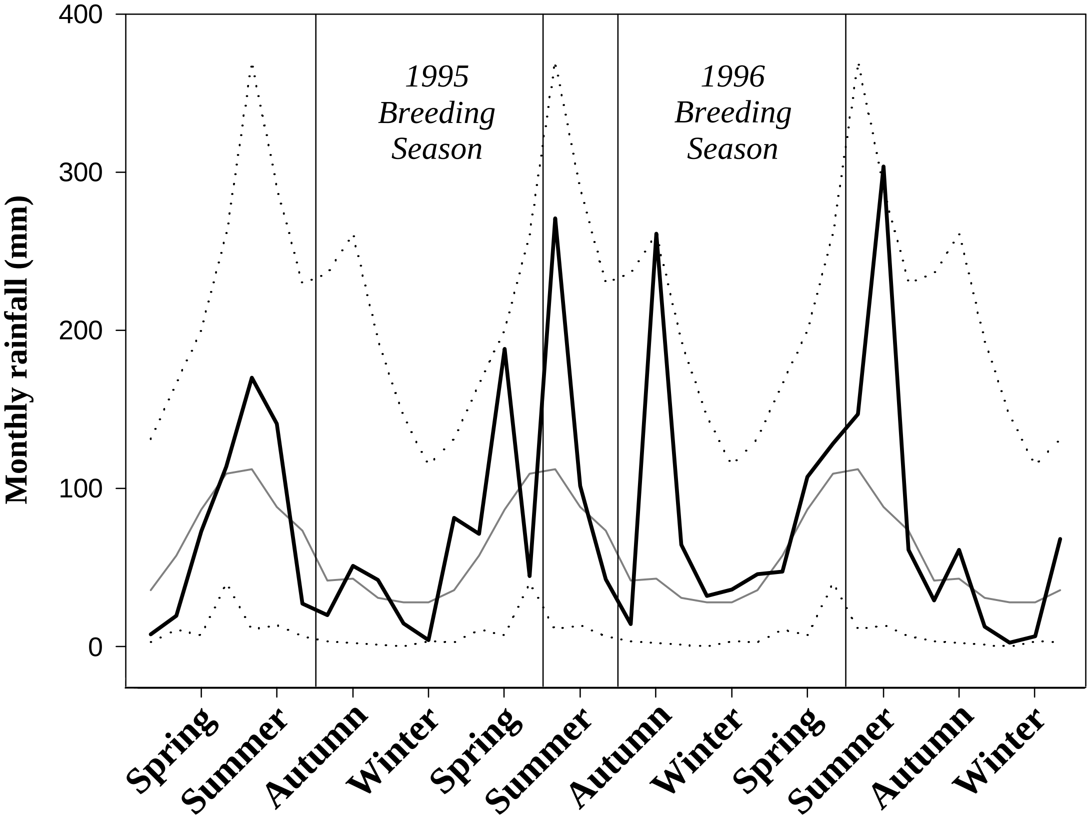

Figure 5.7. Total monthly rainfall (solid black line) recorded at the Kookabookra weather station (20 km from the Paddys Land site) over the course of the study. The solid grey line indicates the median monthly rainfall (over 68 years) while the dashed lines represent the 2.5 th and 97.5 th percentiles.

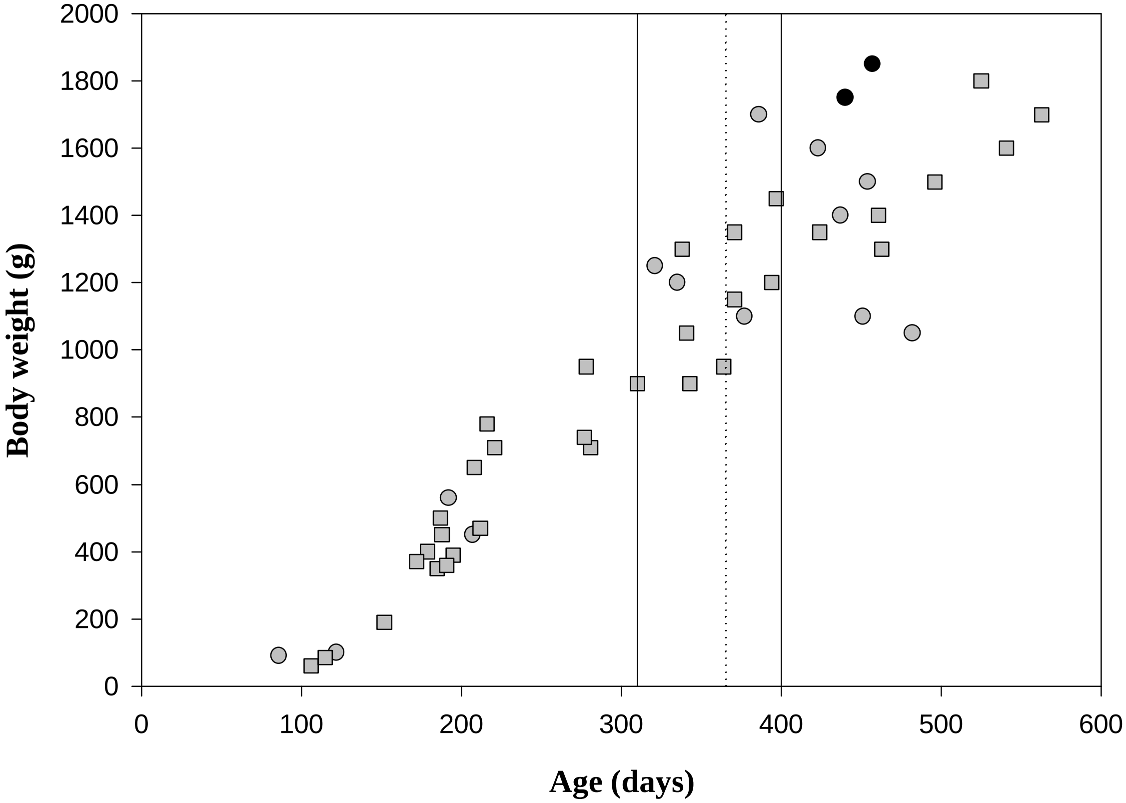

Figure 5.8. Body weight (g) of known-age pouch-young plotted against age in days. Circles represent females while squares signify males. Symbols in black indicate animals that had become sexually mature (adults), while those in grey were still subadult. The dashed vertical line indicates the first birthday (365 days). Solid vertical lines signify minimum (left) and maximum (right) potential age in the autumn of the year following the year in which the young was born.

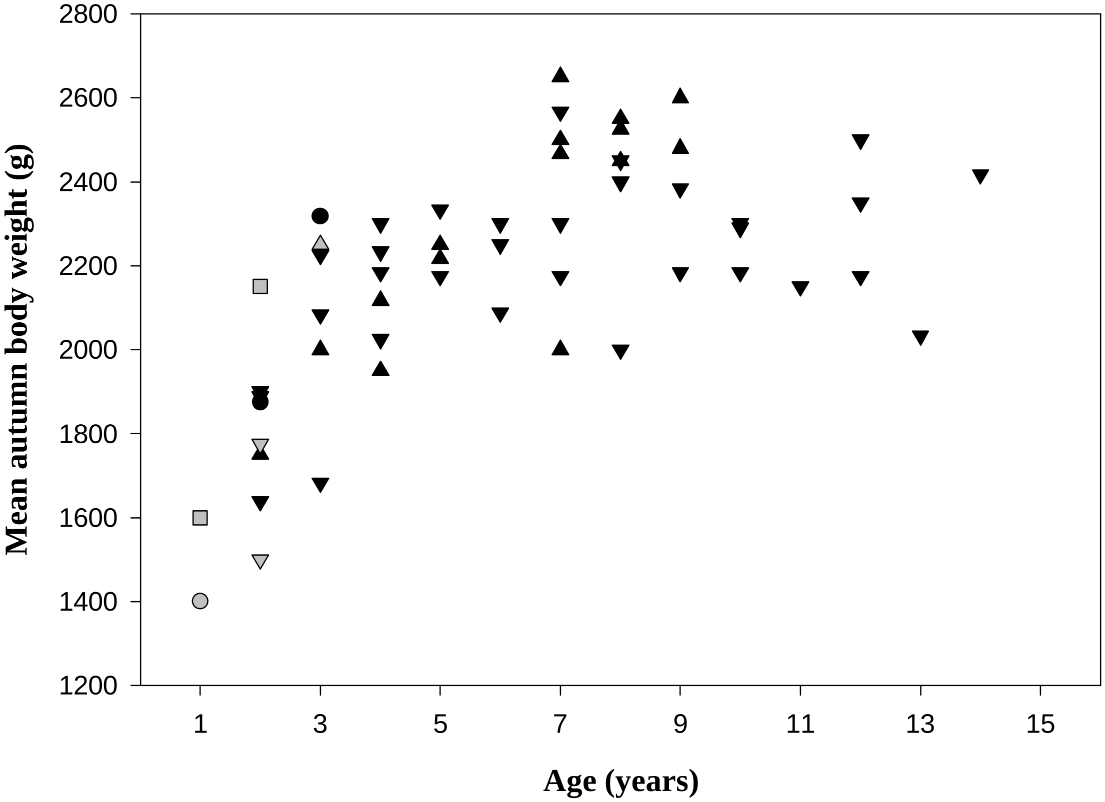

Figure 5.9. Mean autumn body weight (g) of known-age adults and subadults, plotted against age in years. Triangles indicate animals aged from cementum annuli, downwards triangles represent females, while upwards triangles indicate males. Circles represent values for the sole known-age female from 1994, while squares indicate values for the sole known-age male from 1994. Symbols in black indicate animals that had become sexually mature (adults), while those in grey were still subadult.

CHAPTER 6

DISPERSAL SINKS AND HANDLING EFFECTS: INTERPRETING THE ROLE OF IMMIGRATION IN COMMON BRUSHTAIL POSSUM POPULATIONS

A “dispersal sink” (Andrewartha and Birch 1954, Pulliam 1988, Stacey et al. 1997) may be defined as any habitat in which, in the absence of immigration, the resident population is expected to decline to extinction ($r < 0$), because local births are insufficient to compensate for local deaths (b < d). Dispersal sinks are cited in the literature on metapopulation dynamics as a case in which immigration is clearly important in “rescuing” populations from extinction (Stacey et al. 1997). Dispersal sinks are assumed to occur in sub-optimal habitat, whereas the “source” populations (b > d) from which the immigrants derive, are assumed to occur in optimal habitat.

Studies claiming to have demonstrated the existence of a dispersal sink were criticized by Watkinson and Sutherland (1995) on the grounds that: 1) inferences regarding the demography of the resident population were often made on the basis of measurements of either, birth rates, or death rates, in combination with assumptions regarding the other parameter, rather than on the basis of simultaneous measurements of both parameters; and 2) immigration was often not measured, and was rarely measured with sufficient rigour, in those cases in which it was. Only two studies on annual plants were judged by Watkinson and Sutherland (1995) to have adequately addressed these issues. In a more recent review, Diffendorfer (1998) added a third study on another annual plant to the list, but otherwise came to the same conclusions as Watkinson and Sutherland (1995).

I propose that a third criterion should be added to those suggested by Watkinson and Sutherland (1995), when considering animal studies, which is an evaluation of the effects of capture and handling on immigration, births and deaths. The rigorous measurement of immigration in open populations in the field will generally require intensive handling and disturbance of the resident population, much more so than would usually be the case in a study of demography (Chapter 3). If repeated capture and handling has an adverse effect on either the birth rate or death rate of residents, then what might be a stable (b = d), or even a source (b > d) population, in the absence of repeated capture and handling, may appear to be a declining population ($r < 0$), that will then need to be “rescued” from extinction by immigration. In addition, the artificial “removal” of residents resulting from deaths due to capture and handling, may actually induce an influx of immigrants (Stenseth and Lidicker 1992, Chapters 3 and 4), leading to the conclusion that the site is a dispersal sink. Despite the logical necessity of testing for biases in demographic parameters attributable to handling effects in this context, this is very rarely done in this or any other context (Haydon et al. 1999).

I conducted a large-scale field experiment on common brushtail possums (*Trichosurus vulpecula*) in “uniformly suitable” (NPWS 1994) old-growth Eucalypt forest in south-eastern Australia, which was designed to address the question: does immigration “rescue” populations from extinction? I took every possible step to ensure that my measurement of female immigration was, as nearly as possible, made *without error* (Chapter 4). In conjunction with measuring immigration, I also directly measured both, reproduction (Chapter 5), and survival (this Chapter), in the resident population. I suggest that my study meets the criteria proposed by Watkinson and Sutherland (1995), as being necessary to test for the existence of a dispersal sink. In Chapter 4, I concluded that there was no substantive reason for supposing that my measurement of female immigration was *under*estimated, as a result of the potentially adverse effects of capture and handling. In Chapter 5, I reported that one (Table 5.5) of three tests indicated that pre-weaning survival of the offspring of residents was adversely affected by repeated capture and handling. I evaluate the effects of capture and handling on adult resident survival in this Chapter.

In Chapter 5, I reported that the reproductive biology of common brushtail possums at my study site (Paddys Land) very closely resembles that of the “undisturbed” population in the Orongorongo Valley, New Zealand, which has been the subject of a long-term, live-trapping study, that was initiated in 1966 (Crawley 1973, Fitzgerald 1976, Fitzgerald and Karl 1979, Humphreys et al. 1984, Efford 1998). Efford (1991a, p. 43) reported that “local reproduction was inadequate to replace local mortality [$b < d$] and to maintain the population density” at the Orongorongo Valley site, leading him to conclude that “as the density remained stable [$r = 0$] and immigration exceeded emigration the local Orongorongo study area must be considered a ‘dispersal sink’”. Efford (1991a, p. 43) considered this “decidedly odd”, given that the mixed native forest in the Orongorongo Valley is “in some sense ‘optimal’ habitat for possums”.

The Orongorongo Valley study was not specifically designed to measure the rate of immigration (Chapters 3 and 4). Only a single sampling technique (cage-trapping) is employed, and less than two-thirds (62.7 %; Efford 1998, p. 510) of the offspring of residents are identifiable as such. Perhaps more importantly, there is no means of discriminating between “true” immigration, and instances when newly-identified individuals are in fact neighbouring residents from just outside the area sampled by the trapping grid, that are expanding their home range in response to vacancies created by the death of individuals on the trapping grid, a phenomenon Efford (1991a, p. 54) referred to as the “vacuum effect”. I reported direct evidence of just such a “vacuum effect” in response to removals at the Paddys Land site, in Chapter 4. Given these ambiguities surrounding the level of immigration at the Orongorongo Valley site, the study does not appear to satisfy Watkinson and Sutherland’s (1995) criteria for demonstrating the existence of a dispersal sink.

The Orongorongo Valley study does meet Watkinson and Sutherland’s (1995) criterion regarding the simultaneous measurement of both birth rates and deaths rates. Even if all instances of apparent immigration at the Orongorongo Valley site are simply cases of home range expansion (“quasi-dispersal”; Lidicker and Stenseth 1992, p. 23), this does not explain why the demography of the resident population is such that local reproduction is inadequate to replace local mortality ($b < d$), in what appears to be ‘optimal’ habitat. I suggest that the most parsimonious explanation is that repeated capture and handling is having an adverse effect on either the birth rate or death rate of residents.

In this Chapter, I report: 1) the *apparent* pattern of adult female survival at the Paddys Land site; and 2) the projected growth rate (r) of the resident population predicted using a deterministic, stage-based model of possum demography (I will hereafter refer to the projected growth rate predicted by the model, simply as the “predicted” growth rate). I compare the predicted growth rate of the resident population at the Paddys Land site, with that predicted for the resident population at the Orongorongo Valley site. Both sites would appear to have declining ($r < 0$) resident populations, despite both being in apparently ‘optimal’ habitat for possums. I show that the predicted growth rate is far more sensitive to changes in the rate of adult female survival, than to changes in any other parameter. I evaluate whether deaths among adult females at the Paddys Land site may have been due, in whole or in part, to the stress associated with repeated capture and handling, by: 1) ruling out other possible causes of death such as “old age”, starvation, predation or disease; 2) considering physiological and behavioural symptoms of stress; and 3) testing whether survival was correlated with the frequency of capture and handling. I demonstrate that the estimated per annum rate of adult female survival is 8.8 % higher if deaths that were most likely due to repeated capture and handling, are treated as "right-censored", and I show that this higher survival rate is more congruent with the observed age distribution. Moreover, when the higher survival rate is used in the model, the resident population at the Paddys Land site is predicted to be stable ($r = 0$), as is more congruent with the estimated "suitability" of the site (NPWS 1994). I report parallels between the causes of death and symptoms of stress observed at the Paddys Land site and those observed at the Orongorongo Valley site, and I show that if adult female survival at the Orongorongo Valley site were 8.8 % higher, the population would be predicted to be stable ($r = 0$). My results suggest that at both the Paddys Land and Orongorongo Valley sites, adult female survival was adversely effected by repeated capture and handling, causing what would otherwise be stable populations (b = d), to appear to be dispersal sinks, in need of an influx of immigrants to "rescue" them from extinction. I discuss whether it might often be that dispersal sinks are of our own making.

METHODS

Details regarding the study species, study site and general methodology were discussed in Chapter 4. As in Chapter 5, I define handling, as regards females, as making a visual inspection of the interior of the pouch. Females that were trapped more than once during a standard, full-grid trapping session, were generally handled on only the first occasion. For the most part, females that were trapped and handled were not tranquilized, but were instead immobilized using a variety of restraints. On all occasions when females were captured by darting, they were handled, held until the tranquilizer had worn off, and then released. In February, 1997, an independent study was begun by other researchers that involved taking extensive measurements of the size and condition of females trapped at their dens. Females that were trapped for the purposes of the other study were tranquilized on all occasions when they were handled. Basic data regarding the identity, weight and reproductive status of individuals trapped for the purposes of the other study were made available, and are included in the results of my study.

As noted in Chapter 5, I recorded the date, location and circumstances, in all instances where I either saw, heard or observed signs of potential predators. I also attempted to identify the predator involved in all cases where possums were attacked in traps, or where they were apparently killed by a predator. I report information regarding both males and females when discussing deaths in traps. Otherwise, my focus is on deaths among radio-collared adult females. Each female's radio signal was checked on a weekly basis, allowing me to generate weekly survival estimates. Survival estimates from radio-telemetry are more accurate than those obtainable from trapping data because the fate and time of death of each individual can be determined with certainty from radio-telemetry data, provided no radios are lost (Boutin and Krebs 1986, Krebs 1999). In addition, it is the rate of female survival, rather than male survival, that is of relevance when modeling the demography of mammal populations (Clinchy 1997, Beissinger and Westphal 1998).

Aside from cases where radio-collared females were found dead in traps or died during handling (N = 4), I was first alerted of possible deaths by the change in the signal rate of a female's radio, which resulted from the activation of the mortality switch. An individual was confirmed to be dead if: 1) the carcass was found (N = 20); or 2) the carcass was not found but the radio was found with the collar (a cable tie) still intact (N = 2). The only way an intact collar could have come off an animal was if the animal was decapitated. There were two instances when collars were found broken and the owners were later recaptured, alive and well. In a further nine instances the mortality switch had been activated, but when the radio signal was located, the owner was discovered to be alive and well. In addition, there were 18 cases when the radio itself failed, but I successfully recaptured the owner, alive and well. No radios were lost during the course of the study.

I wrapped each adult female's radio-collar with "Leukoplast" adhesive bandaging (BDF Beiersdorf AG, Hamburg, Germany), to assist in distinguishing between cases in which an animal was actually killed by a predator, as opposed to having been scavenged. My assumption was that the bandaging would become inundated with fresh blood in cases where an animal was attacked by predator, whereas the individual's blood would likely have already coagulated in cases where the animal was scavenged.
In all but one case where I was alerted to the death of a female by the activation of the mortality switch on her radio-collar (22 cases in total), I tested the bandaging for the presence or absence of blood. The

bandaging was removed from the radio-collar and placed in a vial containing a 0.9 % saline solution. The vial was shaken vigorously, allowed to stand for 1 hour, and then shaken a second time. A sample of liquid was then removed from the vial and tested for the presence of blood using the SKD Hemoccult II SENSA, Sensitive Serial Test for Enhanced Detection of Fecal Occult Blood (SmithKline Diagnostics, Inc., San Jose, California, U.S.A.).

In all cases where animals were found dead (both males and females), I attempted to retrieve the teeth from the animal's lower jaw. I successfully retrieved teeth from a total of 40 animals. As explained in Chapter 5, I used counts from the microscopic examination of the number of cementum annuli in serial sections of both the first premolar (PM1), and third molar (M3), to estimate each animal's age, in years.

Necropsies were conducted in all cases (23 in total) where animals were found dead in a trap, or died shortly after being found moribund in a trap, and whenever an individual's intact carcass was found soon after its death. Examinations for gross pathology, and the presence and intensity of parasitic infections were conducted in all 23 cases by Mr Peter Haycock and Dr Dave Spratt (CSIRO Wildlife and Ecology, Canberra, Australia). Animals from the Paddys Land site were included in a survey of the parasites and diseases of common brushtail possums in Australia, conducted on behalf of the New Zealand government (Obendorf et al. 1998). Details regarding methodologies are reported in Obendorf et al. (1998).

RESULTS

Adult female survival

In this section, I describe the pattern of adult female survival at the Paddys Land site under the assumption that all deaths that were not obviously caused by capture and handling were "natural" deaths. Two females were judged to have died as a direct result of capture and handling. One female was killed in a trap by a predator and the other died within a few minutes of being injected with a tranquilizer. These two females are treated as "right-censored" (Pollock et al. 1989) in the following analyses. There were a total of 24 deaths among radio-collared adult females that were not *apparently* the direct result of capture and handling.

Two general approaches can be taken when analyzing survivorship data: 1) comparing the shape of survivorship curves; and 2) comparing the proportion surviving to the end of a given time period, independent of the shape of the underlying survivorship curves (Pyke and Thompson 1986). Over the course of the study there were 10 “natural” deaths on the West grid and 14 “natural” deaths on the East grid. I compared the shapes of the survivorship curves from the two principal study grids using the time-dependent log-rank test described by Pollock et al. (1989). The time-dependent log-rank test is generally more applicable to wildlife studies than the time-independent log-rank test (Pollock et al. 1989). The latter test, which is typically used in medical studies, is biased by the fact that it assigns more weight to deaths in the tail of the survival curve (Lee 1992, p.117). The bias arises because the total number at risk decreases with each additional time interval considered (the denominator decreases), while equal weight is given to each death, regardless of the time interval in which it occurs (the numerator remains constant; Kleinbaum 1996, p. 65). Prentice and Marek (1979) suggested an alternative test (Peto’s generalized Wilcoxon statistic) which overcomes the problem in the time-independent log-rank test by weighting scores by the cumulative proportion of individuals at risk ($N_t/[N_t+1] \times N_{t+1}/[N_{t+1}+1] \times \ldots$). Weighting scores by the cumulative proportion at risk is not an applicable procedure in the case of the time-dependent log-rank test because the number at risk may in fact *increase* as individuals are added to the study (Bunck and Pollock 1993, p. 58). Indeed, Prentice and Marek’s (1979) alternative is redundant in the case of the time-dependent log-rank test described by Pollock et al. (1989), provided the total number at risk is kept relatively constant, which is precisely what Pollock et al.’s (1989) staggered entry design permits.

Figure 6.1 shows the total number of radio-collared adult females at risk at the Paddys Land site in each week, over the course of the study. If deaths had occurred very early on in the study they would have received a disproportionate weight in the following comparison between the two study grids. However, the first death did not occur until after 45 females had already been radio-collared. The maximum number at risk in a given week was 58, just prior to the removal of the core resident females from both grids on August 1, 1995 (Chapter 4). The number at risk in the last week of the study was 29. While the total number at risk varied over the course of the study, the proportion at risk on each grid was kept relatively constant, in which case the following comparison between the two study grids should be considered unbiased with respect to the number at risk (Fig. 6.1). The survivorship curves from the two principal study grids were not significantly different ($\chi^2 = 1.44$, df = 1, p = 0.2294; using the least conservative estimate of variance described by Pollock et al. 1989, as discussed by Cox and Oakes 1984, p. 104). Consequently, I pooled the data from both grids for use in subsequent analyses.

The solid black line in Figure 6.2 plots the cumulative probability of survival over the course of the study, based on the Kaplan-Meier estimator, modified for staggered entry (as described by Pollock et al. 1989), when all 24 “natural” deaths are included. Survival is plotted from the beginning of autumn, 1995, onwards. Two complete years of data were available, from the beginning of autumn, 1995, to the end of summer, 1996 (Fig. 6.2). In addition, data were available concerning all of autumn and the first six weeks of winter (19 weeks in total), in 1997 (Fig. 6.2). I examined for differences between the two complete years for which data were available by comparing the shape of the survivorship curve from the beginning of autumn to the end of summer, 1995, with the shape of the curve from the beginning of autumn to the end of summer, 1996 (Fig. 6.2). There was no significant difference in the shape of the survivorship curve in 1995 vs. 1996 ($\chi^2 = 0.03$, df = 1, p = 0.8656; using the least conservative estimate of variance described by Pollock et al. 1989). There were 8 deaths in 1995 and 9 in 1996. In both years, most deaths occurred in winter, with a few additional deaths occurring in late spring and early summer (Fig. 6.2). Aside from the first 11 weeks of autumn, the proportion at risk in each week was relatively constant between the two years, with the number at risk in either year in a given week being never more than 55 % of the total number at risk.

To compare the 19 weeks of autumn and winter data from 1997 with the relevant periods in 1995 and 1996 (Fig 6.2), I extended the two-sample time-dependent log-rank test described by Pollock et al. (1989) to comparisons between three groups by use of the formulas provided by Kleinbaum (1996, p. 82). Kleinbaum’s (1996) formulas combine the calculations for the variance-covariance matrix given by Mantel and Haenszal (1959, p. 744), with the necessary matrix algebra explained by Kalbfleisch and Prentice (1980, p. 18; see also Sauer and Williams 1989). There were 4 deaths in 1995 during autumn and the first six weeks of winter, 2 in 1996 during the same period, and 7 in 1997. There was a strong trend towards a difference in survivorship between the three years ($\chi^2 = 4.69$, df = 2, p = 0.0957). The variances calculated in Kleinbaum’s (1996) formulas correspond to the least conservative variance calculation described by Pollock et al. (1989). Kleinbaum (1996, p. 63) suggests an approximate formula that corresponds to the most conservative variance calculation described by Pollock et al. (1989; see also Cox and Oakes 1984, p. 105). Using the most conservative variance calculation makes little difference to the final value of the test statistic ($\chi^2 = 4.62$, df = 2, p = 0.0994). Pairwise comparisons of survival over the 19 week period in question, between each of the three years, indicated no significant difference between 1995 and 1996 (least conservative $\chi^2 = 0.03$, df = 1, p = 0.8656), nor was there a significant difference between 1995 and 1997 (least conservative $\chi^2 = 1.15$, df = 1, p = 0.2867), but there was a significant difference between 1996 and 1997 (least conservative $\chi^2 = 4.53$, df = 1, p = 0.0332; most conservative $\chi^2 = 4.44$, df = 1, p = 0.0351). The difference between 1996 and 1997 is not significant if *alpha* is corrected for the number of comparisons made using the Bonferroni method ($p_{crit} = 0.05/3 = 0.0167$; Sokal and Rohlf 1995, p. 240). Nonetheless, I will treat survivorship data from 1997 separately from that for 1995 and 1996 in most subsequent analyses because the strong trend towards poorer survival in 1997 is concurrent with a significant increase in the frequency of capture and handling, as described in a later section.

Fourteen of the 24 “natural” deaths recorded among radio-collared adult females occurred in winter. Figure 6.3 illustrates the 13-week seasonal survival for all four seasons, based on pooled data from 1995 and 1996, as well as seasonal survival for autumn and winter using data from 1995, 1996 and 1997 combined. I calculated 95 % confidence limits using Equation 3 from Pollock et al. (1989). While there was a strong trend towards poorer overwinter survival, the differences between seasons are not significant, in view of the overlapping confidence limits. The seasonal survival rates illustrated in Figure 6.3 are those used in the model of possum demography, as discussed in the next section.

A model of possum demography

Figure 6.4 illustrates the structure of the model developed to simulate the demography of possums at the Paddys Land site. Model parameters are defined in Table 6.1. As is conventionally the case when modeling demography (Beissinger and Westphal 1998), both the parameters, and the results produced by the model, concern females only. Embedded in the structure of the model are seven assumptions regarding possum demography: 1) the survival of pouch-young is a function of their own survival and that of their mother; 2) births are restricted to autumn and winter (Fig. 5.2); 3) winter-born young do not breed until at least their second year (Fig. 5.8); 4) young females (1-year-olds, 2-year-olds, and 3-year-olds) that give birth for the first time in one year, but lose their young (failed breeders), are automatically treated as adults in the next year (Chapter 5, p. 170); 5) all females aged 3 years or older give birth (Fig. 5.9); 6) the success of first-time breeders relative to adult females, as regards rearing a young to the onset of weaning, is independent of the age at which a female first gives birth (Chapter 5, pp. 169-174); and 7) all females aged 2 years or older have the same probability of survival (Efford 1998, p. 510). The evidence regarding most of these assumptions was discussed in Chapter 5. Additional evidence is discussed below. As will be shown, the model appears to be equally applicable to the Orongorongo Valley possum population.

Table 6.2 indicates the source of parameter values for the Paddys Land population. While most of the information in Table 6.2 is self-explanatory, there are four points I feel require added clarification. Firstly, I have excluded data from 1997 in calculating adult survival, for reasons discussed in the previous section. Secondly, I have assumed that the survival of 1-year-olds is equivalent to that of adults. While Efford (1998, his Table 4) reports separate survival estimates regarding adults and 1-year-olds, he notes that (p. 510) “the survival rate of adult females did not differ significantly from that of yearling [1-year-old] females”. Thirdly, I made no attempt to make separate measurements of the survival of autumn-born young to the end of their first spring (PAP in Table 6.2) and summer (PAU in Table 6.2). Instead, I estimated the survival of autumn-born young from the onset of weaning (at the end of winter) to the beginning of the next (autumn) breeding season (Chapter 5, p. 168), which includes both spring and summer. As separate estimates of spring (PAP) and summer (PAU) survival were required for use in the model, I used the square root of survival from the onset of weaning to the beginning of the next breeding season. When spring (PAP) and summer (PAU) survival are multiplied together, the product is equal to survival from the onset of weaning to the beginning of the next breeding season. Finally, the survival of winter-born young from birth to the beginning of the next (autumn) breeding season was assumed to be equivalent to the survival of autumn-born young from birth to the beginning of the next breeding season (PWW x PWP x PWU = PAA x PAW x PAP x PAU). I have no data on whether the survival of winter-born young differs from that of autumn-born young. Given the fact that almost all females give birth in autumn (Fig. 5.2), there must be some “penalty” for giving birth in winter. In the model (Fig. 6.4) the “penalty” paid by winter-born young is that they are unable to breed until at least their second year. Table 6.3 indicates the source of parameter values for the Orongorongo Valley population.

I used the model illustrated in Figure 6.4 to predict the population growth rate ($r = \ln[N_{t+1}/N_t]$, where N is the number of adult females alive at the beginning of autumn, and r = a constant, once a stable age distribution is established; Krebs 1994) at the Paddys Land site given three scenarios regarding the reproductive biology of possums at the site (Table 6.4). The three scenarios differ in the values used regarding: 1) the survival of young during the latter half of their period in the pouch (PAW, PWP and RYP); 2) the survival of young from the onset of weaning to the beginning of the next (autumn) breeding season (PAP, PAU, PWU and RYU); and 3) the success of first-time breeders relative to adult females (STB). In Chapter 5 (p. 148), I reported that there was a significant difference between the survival of autumn-born young to the onset of weaning (PAW) in 1995 (33.3 %), as compared to 1996 (81.3 %). The 'Average' scenario in Table 6.4 indicates the predicted population growth rate using the estimate of PAW based on pooled data from 1995 and 1996. The 'Best' scenario in Table 6.4 uses the estimate of PAW from 1996 alone, as does the 'Typical' scenario. In the latter case, I feel the results from 1996 more likely represent a "typical" year, as opposed to 1995, when there was a severe mid-winter drought (Chapter 5, Fig. 5.7). In contrast to the results regarding survival to the onset of weaning (PAW), there was no significant difference between 1995 and 1996 (Chapter 5, p. 168) in survival from the onset of weaning to the beginning of the next breeding season (PAP x PAU). Consequently, the values for PAP and PAU used in the 'Typical' scenario in Table 6.4 are the same as those used in the 'Average' (pooled data from 1995 and 1996) scenario. The 'Best' scenario in Table 6.4 presents values for PAP and PAU from 1996 alone (Chapter 5, p. 168). In addition, the 'Best' scenario in Table 6.4 assumes the success of first-time breeders is equivalent to adult females (STB = 1.00), despite the fact that first-time breeders were shown to be less likely to successfully rear their young to weaning, in Chapter 5 (p. 172).

Given my estimates regarding the 'Typical' demography of possums at the Paddys Land site (Table 6.4), the population is predicted to *decline* at a rate of 9.5 % per year. Even under the 'Best' case scenario (Table 6.4), which is known to involve an *over*estimate as regards STB (the success of first-time breeders relative to adult females), the population is still predicted to decline, at a rate of 6.4 % per year. Aside from the values that differ between the 'Typical' and 'Best' case scenarios (PAP, PAU, PWU, RYU and STB; Table 6.4), all other parameter values used in the 'Typical' scenario are upper estimates. Consequently, compared to the prediction under the 'Typical' scenario, the population is predicted to decline *even more rapidly* if: 1) I use the values presented under the ‘Average’ scenario (Table 6.4); or 2) I include data from 1997 in my estimates of adult survival (Table 6.2); or 3) I assume the survival of winter-born young is poorer than that of autumn-born young (Table 6.2); or 4) I assume the survival of 1-year-olds is poorer than that of adults (Table 6.2).

In Chapter 5, I reported that the reproductive biology of possums at the Paddys Land site is nearly identical to that at the Orongorongo Valley site. As indicated in Table 6.4 (ASA, ASW, ASP and ASU), adult female survival at the two sites also appears to be nearly identical. Based on the values presented in Table 6.4, annual adult female survival at the Paddys Land site is estimated to be 81.3 %, as compared to 81.8 % at the Orongorongo Valley site. As was true of the Paddys Land population, the Orongorongo Valley population is also predicted to decline, and at a comparable rate (9.2 % per year). The prediction from the model confirms Efford’s (1991a, p. 43) conclusion that “local reproduction was inadequate to replace local mortality and to maintain the population density” at the Orongorongo Valley site.

The similarity in the rates of decline predicted regarding the Paddys Land and Orongorongo Valley populations appears to be largely a consequence of the similarity in the estimated rates of adult female survival (Table 6.4). The final column in Table 6.4 indicates the sensitivity of the value of *r*, predicted by the model, to changes in the value of each of the demographic parameters used in the model. The value of *r* is primarily determined by adult survival, and in particular, overwinter adult survival (ASW). Parameters of secondary importance in determining the value of *r* include: 1) the sex ratio at birth (SEX); and 2) those parameters concerned with the latter stages of survival of autumn-born young of the year (PAW, PAP and PAU). The value of *r* is relatively insensitive to changes in the earliest stage of survival of autumn-born young (PAA), because of the opportunity females have to produce a replacement young (BRY). The sensitivity analysis also indicated that the tenuous assumptions made regarding the relevant values for a number of parameters (PWP, PWU, RYP, RYU, BRY and BPW; see Tables 6.2 and 6.3) concerned parameters that are of very little importance in determining the value or *r* (Table 6.4).

How can it be that two sites consisting of ‘optimal’ habitat for possums should both appear to contain declining resident populations? There are two alternatives: 1) the predicted declines are “real”, in which case the populations at both sites will go extinct unless they are “rescued” by immigration (i.e., both sites are dispersal sinks; Efford 1991a); or 2) the predicted declines are an artifact, and some or all of the values used in the model are biased. Assuming the predicted declines are not "real", and are instead the results of biases in the values used in the model, there are in essence two possible scenarios regarding the principal source of these biases: 1) the estimates of adult survival are reasonably accurate, in which case the estimates concerning most other parameters are *highly* inaccurate, given the overwhelming importance of adult survival in determining the value of r (Table 6.4); or 2) there is a tendency at both sites to moderately underestimate adult survival. The latter alternative is clearly the more parsimonious explanation. Moreover, I will present evidence regarding both the Paddys Land and Orongorongo Valley populations that suggests that many apparently "natural" deaths among adult females are, in part, due to repeated capture and handling.

Assuming the Paddys Land study site is not a dispersal sink, and the local population is capable of replacing itself, the extent to which adult survival has likely been underestimated can be gauged by identifying the adult survival rate required to generate a value of $r = 0.0$ in the model of possum demography. I used the 'Typical' parameter values for the Paddys Land site (Tables 6.2 and 6.4) to generate the following estimates. An annual adult survival rate of 89.9 % is required to generate a value of $r = 0.0$ in the model, if all four seasonal estimates of survival (ASA, ASW, ASP and ASU) are assumed to be the same (0.9738, given there was no significant difference between the seasonal survival rates). Whereas, an annual adult survival rate of 90.2 % is required to generate a value of $r = 0.0$ in the model, if the differences in survival between the seasons are maintained, and a constant (0.0251) is simply added to each one. In either case, an underestimate, or reduction, in the annual adult survival rate by as little as 9.0 %, is sufficient to produce the observed rate of population decline ($r = -0.0998$, Table 6.4).

Wobbly possums

Efford (1994, his Appendix 3) reported that from 1980 to 1994 there were 64 possums that died in association with capture and handling at the Orongorongo Valley site, representing 0.6, 2.1, and 0.8 % of the total number of individuals trapped in each of June, September, and February, respectively. I was able to determine the specific fates of 17 of the 64 animals in question (Efford 1991b, Efford and Hearfield 1992, Efford 1994). Four of the 17 animals were judged to have died as a direct consequence of handling ("for example as a result of cardiac arrest under ether"; Efford 1994, p. 4) and Efford did not include these deaths when calculating survival. Similarly, I did not include the case in which a female died within a few minutes of being injected with a tranquilizer, in the estimates of adult female survival at the Paddys Land site, reported in Table 6.4.

The circumstances surrounding the deaths of 13 of the 17 possums at the Orongorongo Valley site that died in association with capture and handling, and whose fates were specified, were as follows: 8 were reported as being found “comatose in trap”; 2 were reported as being found “dead in trap”; (Efford and Hearfield 1992, their Appendix 3); and the remaining 3 were reported as being “found dead or comatose in traps” (Efford 1991b, p. 6). According to Efford (1994, p. 4), “most possums that died in traps were in poor bodily condition and would probably have died soon even if not trapped”. Consequently, instances when possums were found “comatose” or dead in a trap were judged to be “natural” deaths, and Efford chose to include these deaths when calculating survival. If, on the other hand, it is assumed that capture and handling was a contributing factor, and that these animals would have otherwise survived, then adult survival at the Orongorongo Valley site is clearly being underestimated.

I assumed that 76.5 % (13/17) of the 64 deaths associated with capture and handling at the Orongorongo Valley site were incorrectly judged to be “natural” deaths, in which case, adult (and yearling) survival is likely underestimated by 0.4, 1.6, and 0.6 %, in each of Efford’s (1998) Seasons 1, 2, and 3, respectively. When the estimates of adult (and yearling) survival at the Orongorongo Valley site were adjusted accordingly (Table 6.4), the model of possum demography predicted that $r = -0.0685$. Misclassification of observed deaths in traps is not sufficient to explain the predicted decline of the Orongorongo Valley population. However, evidence regarding the circumstances of adult deaths at the Paddys Land site suggests that animals that are released from traps apparently unharmed, may nonetheless suffer more deaths than would “naturally” be the case.

There were seven occasions at the Paddys Land site, on which adult possums were either found moribund (2 females, 4 males) or dead (1 male) in a trap, even though they had evidently not been attacked by a predator. The traps were found upright and unmoved and the animals showed no external signs of injury. All but one of the seven instances occurred in winter, the one exception being a female found moribund in a trap in late autumn (in 1996). Three of the seven instances (all moribund) occurred in 1995, three more (two moribund and one dead) occurred in 1996, and the last case occurred near the end of the study, in the winter of 1997. Moribund animals were put in a warm shelter and given food *ad libitum*, but none of them recovered.

Five of the seven animals found moribund or dead in a trap had been trapped on the previous day, as well as being trapped and weighed between 2 to 5 days prior to being found moribund or dead. All five had lost between 250 and 300 g of body weight, which represents about 10-15 % of the average body weight of an adult possum at the Paddys Land site (Table 5.15, Fig. 5.9). The remaining two individuals, both of whom were found moribund in traps at the beginning of August, 1995, weighed 1500 and 1850 g respectively, when removed from the trap. The former was a 2-year-old female and the latter was a 5-year-old male. Both animals were exceptionally lightweight for their ages (Table 5.15), at the time they were found moribund. In addition, the female had lost 400 g of body weight in between the beginning of August, when she was found moribund, and the end of June, when she was last weighed. While the male had only lost 150 g over the same time period, he had lost 500 g since late March, when his maximum recorded weight was observed. Surviving individuals also demonstrated fluctuations in body weight over the course of autumn and winter, although these were rarely as large as 400 or 500 g (Fig. 5.6). Moreover, while surviving individuals commonly lost as much as 250 g, this was generally only evident in comparisons between one year and the next (Table 5.12).

The apparent loss of 250 or 300 g of body weight within the span of only five days or less may have simply been the result of measurement error. To determine if the weight loss among animals found moribund or dead in a trap was greater than would be expected from the “normal” distribution of measurement errors, I identified a total of 71 surviving adult possums that were weighed twice, within five days or less, in either autumn or winter. Seventeen of the surviving individuals either maintained or increased their weight, while 54 lost weight. I calculated the maximum proportionate loss in body weight (Weight T_2 - Weight T_1 / Weight T_1), demonstrated by each of the 54 surviving individuals (28 females, 26 males), and the five moribund or dead animals (Fig. 6.5). The rate of proportionate weight loss among the 5 possums found moribund or dead in a trap (median = 13.5 % of body weight) was significantly greater (Mann-Whitney U = 15.0, z = 3.27, p = 0.0011) than that among the 54 surviving individuals (median = 6.7 % of body weight). Supplementary tests (not shown) indicated that this result was not due to biases attributable to grid, sex, season or year. I conclude that the rapid weight loss demonstrated by animals found moribund or dead in a trap was a real, and dramatic phenomenon, and not merely an artifact of measurement error.

The six individuals found moribund in traps all demonstrated severe ataxia (loss of motor control), being either completely unable to stand up, or unable to take more than a few steps without falling over. Severe ataxia is also characteristic of those possums at the Orongorongo Valley site described as being "comatose in trap" (Phil Cowan, pers. comm.). Possums in laboratory colonies in New Zealand have also been described as demonstrating symptoms of severe ataxia, in the context of "wobbly possum syndrome", which is thought to be the consequence of a viral infection (Mackintosh et al. 1995). However, it is not clear whether the aetiology is the same in both laboratory and field populations.

In addition to the six instances of severe ataxia described above, milder symptoms of ataxia were also apparent on 20 occasions when animals were released from traps at the Paddys Land site. Animals exiting traps were classified as demonstrating symptoms of ataxia if it was noted that they were "weak and wobbly" upon release. All instances of animals appearing "weak and wobbly" occurred in either autumn (6 instances: 5 in 1996, 1 in 1997) or winter (14 instances: 8 in 1995, 6 in 1996), although this could be an artifact of the greater trapping intensity, and trapping success, at this time of the year (Tables 4.1 and 4.2). I compared the frequency with which animals were observed demonstrating symptoms of ataxia (both moribund animals and animals exiting traps, N = 26), against the total number of trap-captures, on each grid, during each season, in each year of the study (Table 6.5). A log-linear analysis indicated that symptoms of ataxia were more often observed in autumn and winter, (partial $\chi^2 = 14.44$, $p = 0.0024$; marginal $\chi^2 = 14.10$, $p = 0.0028$), and more often in winter than in autumn (Maximum likelihood $\chi^2 = 4.77$, $p = 0.0289$; Pearson's $\chi^2 = 4.59$, $p = 0.0322$), than would be expected from the frequency of trap-captures. Supplementary tests (not shown) indicated that this result was not due to biases attributable to either study grid or year. As indicated above, Efford (1994, his Appendix 3) reported a greater proportion of deaths in association with capture and handling at the Orongorongo Valley site, in September (late winter), as compared to February (late summer) and June (late autumn).

In most instances (N = 16) where animals appeared "weak and wobbly" upon release from a trap (N = 20), the animal had lost weight in between when it was seen to be "weak and wobbly" and when it last weighed. There were not enough cases in which animals that were seen to be "weak and wobbly" were weighed within 5 days or less, prior to being seen to be “weak and wobbly”, to permit an evaluation of whether these individuals demonstrated the kind of rapid weight loss shown by animals found moribund or dead in a trap (Fig. 6.5). Instead, I conducted a log-linear analysis comparing the frequency with which “weak and wobbly” animals demonstrated weight loss, as against the frequency of instances of weight loss observed among all other adult possums that were weighed on successive occasions in either autumn or winter (Table 6.6). Instances of animals appearing “weak and wobbly” upon release from a trap were more likely to be preceded by a period of weight loss than would be expected (partial $\chi^2 = 8.83$, $p = 0.0030$; marginal $\chi^2 = 6.39$, $p = 0.0115$) given the general frequency of weight loss associated with trapping in autumn and winter. Supplementary tests (not shown) indicated that this result was not due to biases attributable to grid, sex, season or year.

Symptoms of severe ataxia (N = 6, involving those animals found moribund in traps) clearly signaled an animal’s imminent demise. To what extent did appearing “weak and wobbly” upon release from a trap also indicate an animal’s likely demise? The fate of 10 (9 radio-collared adult females, 1 male) of the 14 individuals that appeared “weak and wobbly” on at least one occasion (several individuals appeared “weak and wobbly” more than once) was known for certain: nine (8 females, 1 male) were known to have died, while the remaining individual was included in the experimental removal of core, resident females, described in Chapter 4. The earliest date on which a female, that was later seen to be “weak and wobbly”, was given a radio-collar, was April 6, 1995; and the last of the radio-collared “weak and wobbly” females to die, did so in mid-May, 1997. I compared the shapes of the survivorship curves between radio-collared adult females seen to be “weak and wobbly”, and those never seen to be “weak and wobbly”, for the 110-week period from early April, 1995, to mid-May, 1997. Survivorship among females seen to be “weak and wobbly” on at least one occasion was significantly poorer than that among females never seen to be “weak and wobbly” ($\chi^2 = 13.51$, df = 1, $p = 0.0002$; using the most conservative estimate of variance described by Pollock et al. 1989).

Only one female, from among the eight “weak and wobbly” radio-collared adult females that were known to have died, was apparently killed by a predator, 55 days after the last occasion on which she was seen to be “weak and wobbly”. In contrast, half (7/14) of all of the other “natural” deaths among radio-collared adult females were apparently due to predation, as will be described later. Consequently, it did not appear to be the case that survival was poorer among “weak and wobbly” females because they were more vulnerable to predation. One “weak and wobbly” female was eventually found moribund in a trap, and another died of a parasitic infection (described later). The remaining five “weak and wobbly” females were simply found dead on the ground, generally about 7 days (Range = 6-15) after the last occasion on which they were seen to be “weak and wobbly”.

There is a clear parallel between the circumstances surrounding cases in which animals were found moribund or dead in traps, and those in which animals died after being seen to be “weak and wobbly” upon release. Possums were found moribund in traps in autumn and winter, demonstrating symptoms of severe ataxia and rapid weight loss, that later died from causes not directly attributable to predation, starvation or disease (evidence regarding the latter two potentially proximate causes of death is presented in a later section). Similarly, possums were seen to be “weak and wobbly” upon release from a trap in autumn and winter, that demonstrated milder symptoms of ataxia, had generally lost weight prior to being seen with symptoms of ataxia, and, for the most part, died from causes not directly attributable to predation, starvation or disease (as described later). I conclude that the ultimate cause of death of animals found moribund or dead in traps, and those seen to be “weak and wobbly” upon release, must be one and the same thing, which I suggest is most likely the stress induced by repeated capture and handling. As noted above, possums at the Orongorongo Valley site were occasionally found moribund (“comatose”) in traps. Instances of animals appearing “weak and wobbly” upon release also occur at the Orongorongo Valley site (Phil Cowan, pers. comm.), although there are no reports of the frequency.

Other indices of poor condition

Whenever animals were released from traps I noted both whether they were “weak and wobbly”, and whether they either stopped and began eating grass, or climbed a tree and begin eating leaves, as feeding during the daytime has been interpreted as a sign of poor condition (Mackintosh et al. 1995). In addition, whenever a female’s pouch was examined I noted whether she was either: 1) “rumpy”; or 2) “bony” (Chapter 4). Occasions on which animals were seen feeding upon release, or were recorded as being either “rumpy” or “bony”, were as likely as not to be preceded by an instance of weight loss.

A log-linear analysis indicated that individuals were more likely to be observed feeding upon release in autumn and winter, (partial $\chi^2 = 15.00$, p = 0.0018; marginal $\chi^2 = 14.79$, p = 0.0020), and more often in winter than in autumn (partial $\chi^2 = 8.28$, p = 0.0040; marginal $\chi^2 = 7.55$, p = 0.0060), than would be expected from the frequency of trap-captures (Table 6.5). Supplementary tests (not shown) indicated that this result was not due to biases attributable to either study grid or year.

Only females were recorded as being either “rumpy” or “bony” because the relevant observations were made in association with the visual inspection of the interior of the female’s pouch (i.e., handling). I compared the frequency with which females were recorded as being either “rumpy” or “bony”, against the total number of times females were handled, on each grid, during each season, in each year of the study (Table 6.7). A log-linear analysis indicated that females were more likely to be recorded as being “bony” in winter, (partial $\chi^2 = 15.10$, p = 0.0017; marginal $\chi^2 = 14.76$, p = 0.0020), than would be expected from the frequency of handling. Supplementary tests (not shown) indicated that this result was not due to biases attributable to either study grid or year. The frequency with which females were recorded as being “rumpy” was idiosyncratic, varying significantly with season, study grid and year (analysis not shown).

Eight radio-collared adult females were seen feeding upon release, and while four of the eight eventually died, survivorship among females seen feeding upon release was not significantly different from survivorship among females never seen feeding upon release ($\chi^2 = 0.79$, df = 1, p = 0.3732; using the least conservative estimate of variance described by Pollock et al. 1989). Similarly, 11 of the 22 radio-collared females recorded as being “rumpy” on at least one occasion eventually died, and survivorship among females recorded as being “rumpy” was not significantly different from survivorship among females never recorded as being so ($\chi^2 = 0.60$, df = 1, p = 0.4367; using the least conservative estimate of variance described by Pollock et al. 1989). On the other hand, 9 of 14 radio-collared females recorded as being “bony” on at least one occasion eventually died, and the difference in survivorship between these females and those never recorded as being “bony” was very close to being significant ($\chi^2 = 3.13$, df = 1, p = 0.0770; using the least conservative estimate of variance described by Pollock et al. 1989)

Three of the four radio-collared females seen feeding upon release, that were known to have died, were also recorded as being “rumpy” on at least one occasion, and two of these were also recorded as being “bony”. While there was not enough data to statistically examine the survivorship of these few females, there were 12 radio-collared females that were recorded as being both “rumpy” and “bony”. Nine of the 12 females demonstrating this combination of symptoms eventually died. Survivorship among females recorded as being both “rumpy” and “bony” was significantly different from survivorship among females never recorded as being both “rumpy” and “bony” ($\chi^2 = 6.59$, df = 1, $p = 0.0103$; using the most conservative estimate of variance described by Pollock et al. 1989).

Notably, 7 of the 9 deaths among radio-collared females recorded as being both “rumpy” and “bony” involved females that were also seen to be “weak and wobbly” upon release from a trap. I have already discussed the circumstances surrounding the deaths of the seven “weak and wobbly” females. Neither of the remaining two females were evidently killed by a predator. In one case, all that was found was the female’s intact radio-collar, but there was no evidence of blood on the collar (results from blood tests are described below), so I concluded that she had most likely been scavenged after dying from some other cause. In the other case, the female in question only weighed 1900 g on the last occasion on which she was weighed, which was exceptionally low for a 7-year-old (Table 5.15, Fig. 5.9), as well as being dramatically less than her weight (2100 g)on the next to last occasion on which she was weighed (4 weeks earlier). In addition, she was found dead, only four days after the last occasion on which she was weighed, apparently unharmed, and hanging by her tail from the branch of a *Eucalyptus* tree. Given that most females observed to be both “rumpy” and “bony” were also “weak and wobbly”, and the similarities between the circumstances surrounding the deaths of “weak and wobbly” females and the two females that were seen to be both “rumpy” and “bony” but not “weak and wobbly”, I conclude that the ultimate cause of death of all of these animals is probably one and the same thing, which as I have suggested, is most likely the stress induced by repeated capture and handling.

Weight loss associated with trapping, among apparently healthy animals

I have discussed weight loss in association with trapping in the context of animals demonstrating apparent symptoms of poor condition. Efford (1994, p. 4) suggested that “most possums that died in traps [at the Orongorongo Valley site] were in poor bodily condition and would probably have died soon even if not trapped”. Efford’s statement implies that the weight loss that is evident when the same individual is trapped repeatedly is the consequence of the animal’s pre-existing poor condition, as opposed to the

weight loss, and poor condition, being the consequence of repeated trapping. To determine if otherwise apparently healthy animals also demonstrated weight loss in association with repeated trapping, I identified all occasions on which the same individual was weighed more than once during a single, full-grid (generally 3-night) trapping session (Tables 4.1 and 4.2). I determined the direction of change in weight (weight loss versus no weight loss) within a trapping session for 42 apparently healthy individuals.
A log-linear analysis indicated that apparently healthy animals were significantly more likely than not (30 of 42 cases) to lose weight over the course of a full-grid trapping session (partial $\chi^2 = 5.68$, $p = 0.0172$; marginal $\chi^2 = 5.68$, $p = 0.0172$). Supplementary tests (not shown) indicated that this result was not due to biases attributable to grid, sex, season or year. I conclude that repeated trapping causes stress to even apparently healthy possums.

Deaths due to predation

Two of the 24 apparently “natural” deaths among radio-collared adult females involved individuals found moribund in traps. In the remaining 22 cases, I was alerted to the death of the animal by the change in the signal rate of the radio resulting from the activation of the mortality switch. The animal’s remains were found lying on the ground in 19 cases, in 3 cases they were found in a tree, and in the remaining case the radio signal was tracked to a large bulge in the belly of a carpet python (Table 6.8).

In 21 cases, I was able to test whether the bandaging wrapped around the female’s radio-collar was inundated with blood (Table 6.9). On two occasions I found an intact radio-collar but no accompanying carcass, and in both cases, the tests for the presence of blood were negative (Table 6.9). As the animal had to have been decapitated for the intact collar to have become separated from the carcass, I do not see how this could be accomplished without getting blood on the collar, if the animal was freshly killed.
In another instance in which a female clearly had been killed by a predator (as her chest was ripped open), she had not been decapitated, nor did the skin and fur around her neck appear to have been damaged, yet two separate tests for the presence of blood on her collar were both (appropriately) positive. Moreover, positive results from the blood test are to be expected given its sensitivity (as demonstrated in the previous example), and its tendency towards a positive bias (described below). Consequently, I feel confident that

the negative results from the blood tests in the two cases where no carcass was found (Table 6.9) are sufficient evidence to conclude that these two females were not killed by predators.

In 19 cases, I was able to directly compare the results of the blood test with the condition of the carcass (Table 6.9). In 17 cases, the results of the blood test corresponded with the condition of the carcass (Table 6.9). In one case the female's carcass was found undamaged, yet three separate tests for the presence of blood were all positive (Table 6.9). Inspection during a necropsy conducted on the female in question did not reveal any puncture marks, or other discernible damage to the skin. The supporting documentation that accompanies the "SKD Hemoccult II SENSA" test kit cautions that the test is biased towards false positives, which appears to be the case in this instance. In another case, the female's carcass was found ripped apart and her bones had been picked clean, yet the results of four separate tests for the presence of blood on her collar were all negative (Table 6.9). Also of note was that this female's radio-collar was found separately from her carcass, yet it was covered in maggots. As the radio-collar by itself contains nothing organic that would induce flies to lay their eggs on it, the maggots must have come from the carcass itself, before the radio-collar became separated from the carcass. I conclude that this female was scavenged, rather than having been directly killed by a predator.

Based on the condition of the carcass, in combination with the results from the tests for the presence of blood, there were, at most, eight (7 from Table 6.9, plus 1 in the snake), radio-collared adult females directly killed by predators (not including the one killed in a trap). I conclude that only one-third (8/24) of all apparently "natural" deaths among radio-collared adult females at the Paddys Land site were attributable to predation.

A carpet python (Table 6.8) was known to be the predator involved in one attack, as was already noted. In another case, feathers and other evidence from the kill site suggested that the predator was a Powerful Owl (Debus and Chafer 1994; Steve Debus, pers. comm.). A feral cat was seen within 20 m of the kill site in another instance, and the remaining five cases all appeared to involve attacks by dingos (or feral dogs).

Three lines of evidence suggest that attacks by predators were infrequent at the Paddys Land site because the density of predators was low. Table 6.8 summarizes all available evidence of predator activity recorded at the Paddys Land site over the three years of the study. The encounter rates recorded are clearly indicative of low densities, based on the criteria suggested by Wilcove et al. (1992). In addition, while possums were caught in traps on 3,361 occasions, there were only nine instances (0.2 %) when a possum in a trap was attacked by a predator . Finally, in 8 of the 11 cases where I tracked a female's radio signal to her intact carcass (Table 6.9), the carcass was found lying on the ground (the other 3 were found in trees), and had evidently been there several days, without having been scavenged (Table 6.9). Since both feral cats and dogs eat carrion (Wilcove et al. 1992), I conclude that the carcasses were not scavenged because there were no scavengers about.

Necropsies

All seven animals (2 females, 5 males) found moribund or dead in a trap were necropsied. In addition, necropsies were conducted on 4 of the 11 females whose intact carcasses were located after the mortality switches on their radios had been activated (Table 6.9). I compared the results of these necropsies, with necropsies conducted on 12 possums (8 females, 4 males) that were directly killed, either as a result of being attacked in a trap by a predator, or as a result of other accidents. I will refer to the two groups as animals that "Died" versus those that were "Killed". Nineteen of the 23 animals that were necropsied had either Died or been Killed in winter. Two of the 11 animals that Died did so in autumn, and 2 of the 12 animals that were Killed, were killed in autumn. Among the 11 animals that Died, 6 died in 1995, 3 died in 1996, and 2 died in 1997. Among the 12 possums that were Killed, 1 was killed in 1995, 8 were killed in 1996, and 3 were killed in 1997.

Animals found moribund in a trap demonstrated symptoms of severe ataxia that were similar to the those described by Mackintosh et al. (1995) in association with "wobbly possum syndrome", as observed among laboratory animals in New Zealand. However, none of the 11 animals that Died demonstrated gross pathology congruent with that described by Mackintosh et al. (1995). I conclude that the aetiology of the symptoms of severe ataxia observed among possums at the Paddys Land site that Died was not the same as that found in laboratory animals in New Zealand (Obendorf et al. 1998).

None of the 11 animals that Died did so as a direct consequence of starvation. While most of the 11 individuals that Died had little or no subcutaneous or peritoneal fat, muscle mass was not noticeably poorer than in animals that were Killed, nor was there any gross pathology observable in the liver or kidneys that would indicate that starvation was the direct cause of death. In addition, every one of the 11 individuals that Died was found with food in its gut.

Histopathology was evaluated in 6 (4 females, 2 males) of the 11 individuals that Died. In 3 of the 6 cases where histopathology was evaluated, the spleen was not examined. However, in all three cases in which the spleen was examined (all females) the "white pulp" (lymphatic tissue) of the spleen (which plays a significant role in filtering the blood and launching an immune response, Junqueira et al. 1986) appeared diffuse and depleted (lymphoid follicular involution), which is suggestive of a response to stress (Obendorf et al. 1998). Two of the three individuals whose spleens were examined were among those animals found moribund in a trap, while the third was a female retrieved after the mortality switch on her radio had been activated, seven days after the last occasion on which she was trapped and released. No significant histopathology was observed in any other tissues taken from the six individuals examined (Obendorf et al. 1998).

I was able to obtain blood samples from only 2 of the 11 individuals that Died, and it was possible in only 1 of these 2 cases to have a biochemical analysis conducted on the blood. The individual in question was a male found moribund in a trap, who was taken alive to the N.S.W. Dept. of Agriculture, Regional Veterinary Laboratory, in Armidale (100 km from the Paddys Land site), for diagnosis, and it was there that the blood sample was taken. Biochemical analysis revealed a "stress haemogram", with elevated (> 6000 U/L) CPK levels (creatine phosphokinase, the enzyme responsible for liberating phosphate from creatine phosphate in the course of producing the ATP used in muscle contraction, Hainsworth 1981), which is consistent with a diagnosis of capture myopathy (David Obendorf, pers. comm.). However, I am unable to interpret whether the "stress haemogram" was more a reflection of being found moribund in a trap, or of being taken into captivity and transported to Armidale.

Serological evaluations were conducted on blood samples from six possums (one female that Died, and five females that were Killed). None of the six possums from the Paddys Land site tested positive for any of an array of antibodies. Tests were conducted for the presence of antibodies to the Eimeriid protozoan *Toxoplasma gondii*, the spirochaete bacterium *Leptospira interrogans* (serovar *hardjo* and serovar *pomona*), and five arboviruses: Ross River Virus, Murray Valley Encephalitis Virus, Kunjin Virus, Sindbis Virus and Barmah Forest Virus.

The prevalence and intensity of parasitic infections observed among the 23 animals that were necropsied are presented in Table 6.10. Overall, there were 8 types of endoparasites and 12 types of ectoparasites recorded. Gross pathology was evident in association with only one species of endoparasite, *Ophidascaris robertsi*. In the sole individual in which it occurred (a female), *O. robertsi* was clearly the proximate cause of death. A total of 267 *O. robertsi* larvae (which are 0.25-0.35 mm in diameter and may grow to a length of 93.0 mm in possums; Sprent 1963a, 1963b) were removed from the peritoneal cavity and lungs of the female in question, and several hundred more larvae were apparent in the liver, occupying approximately three-quarters of the volume of the liver. While gross pathology associated with *O. robertsi* infections has been reported previously (Presidente et al. 1982) in both common brushtail possums and mountain brushtail possums (*Trichosurus caninus*), *O. robertsi* has not previously been identified as a potential proximate cause of death in possums (Viggers and Spratt 1995). The magnitude of the infection seen in the Paddys Land female was certainly much greater than the maximum level of infection previously reported in possums, which involved a female mountain brushtail possum possessing 216 *O. robertsi* larvae, who was reported to be in "good condition", despite damage to one-third of her liver (Presidente et al. 1982, p. 38). Possums are an intermediate host of *O. robertsi*, the definitive host being the carpet python (Viggers and Spratt 1995). As noted in the previous section, carpet pythons were observed on several occasions at the Paddys Land site (Table 6.8), and one of the radio-collared adult females was eaten by a carpet python.

I compared the prevalence and intensity of parasitic infections between animals that Died and those that were Killed (Table 6.10). Prevalence refers to the proportion of infected hosts in the host population, while intensity refers to the number of individual parasites per infected host (Margolis et al. 1982). There was no significant difference ($p > 0.15$ in all cases) between the two groups with regard to the prevalence of any of the parasites observed (Table 6.10). There were sufficient data to compare the intensity of parasitic infections between possums that Died and those that were Killed, for 6 types of endoparasites and 5 types of ectoparasites (Table 6.10). Considering each type of parasite by itself, possums that Died demonstrated a significantly ($p < 0.05$) greater intensity of infection than possums that were Killed, with regard to both an endoparasite, *Parastrongyloides trichosuri*, and an ectoparasite, *Trichosurolaelaps crassipes* (Table 6.10). However, because I conducted 11 separate comparisons between the two groups, it was necessary to correct *alpha* for the number of comparisons made, which I did using the Bonferroni method (Sokal and Rohlf 1995, p. 240). While the difference between the groups in the intensity of *P. trichosuri* infections was statistically significant when evaluated using the Bonferroni-corrected value of *alpha*, the difference in *T. crassipes* infections was not (Table 6.10).

Supplementary evidence regarding the condition of each host suggests that the difference in the intensity of *T. crassipes* infections between animals that Died, and those that were Killed, did have an underlying biological significance. Since females observed to be both “rumpy” and “bony” were significantly more likely to die, it follows that they were more likely to necropsied. Indeed, 5 of the 6 females that Died (Table 6.10) were both “rumpy” and “bony”. In contrast, only 1 female was observed with rump wear, from among the 8 females that were Killed. Rump wear is typically observed in association with heavy infestations by *T. crassipes* (Presidente 1984, Hemsley and Canfield 1993, Clark 1995). When I compared the prevalence and intensity of the three types of ectoparasites, for which sufficient data were available, between females observed with rump wear, and those never observed with rump wear, the intensity of *T. crassipes* infections was significantly greater among females with rump wear (Table 6.11).

Three aspects of the biology of *Parastrongyloides trichosuri* are unusual for a nematode. *P. trichosuri* is a member of the family Strongyloididae (Table 6.10), which are noteworthy among nematodes for the rapid rate at which they reproduce (Noble et al. 1989, p. 292). Mackerras (1959) reported that *P. trichosuri* eggs removed from freshly passed possum faeces developed into third-stage infective larvae within three days. Adult *P. trichosuri* without eggs were found in the intestines of possums 14 days after experimental infections with third-stage larvae, and mature adults, with eggs, were found 28 days after infection (Heath et al. 1995). *P. trichosuri*, like other Strongyloididae (Noble et al. 1989, p. 294), is also unusual because it has both free-living and parasitic generations (Obendorf et al. 1998). Gruenberg and Bisset (1998, p. 10) suggested that the free-living generations of *P. trichosuri* “probably function as a multiplicative phase to increase the chances of transmission to new possum hosts”. Finally, infection occurs through the active penetration of the skin of the host by third-stage infective larvae, rather than by passive oral ingestion, as is more usually the case (Heath et al. 1998, p. 15). Evidence presented below suggests that the greater intensity of *P. trichosuri* infections in possums that Died is likely a function of both the rapid rate of reproduction and the active mode of transmission of this parasite.

Because of their rapid rate of reproduction, Strongyloidid infections tend to “track” changes in the immunocompetence of the host over a relatively short (weekly) time-scale (Noble et al. 1989). To evaluate the degree to which *Parastrongyloides trichosuri* infections reflected the condition, and likely immunocompetence, of the host, I categorized individuals by both fate *and* condition (Table 6.12). In previous sections I identified three groups of animals (1 **-** those found moribund or dead in a trap; 2 **-** those seen to be “weak and wobbly” upon release from a trap; and 3 **-** females observed to be both “rumpy” and “bony”) that demonstrated symptoms associated with a significantly lower probability of survival, and thus a greater likelihood of being necropsied. In addition, in this section, I identified the cause of death of one animal as being due to a massive *O. robertsi* infection, which must have severely challenged the individual’s immune system prior to its death. Consistent with the hypothesis that *P. trichosuri* infections “track” the immunocompetence of the host, the individual suffering from the massive *O. robertsi* infection possessed more *P. trichosuri* than any of the 12 animals that were Killed (Table 6.12). Notably, the median intensity of *P. trichosuri* infections among animals found moribund or dead in a trap was even greater than the intensity of infection demonstrated by the animal that died from the massive *O. robertsi* infection (Table 6.12). Individuals found moribund or dead in a trap demonstrated a significantly greater intensity of infection by *P. trichosuri* than was seen among all other animals combined ($t = 3.60$, $df = 21$, $p = 0.0019$).

The stress associated with capture and handling may impede an animal’s immunocompetence (Humphreys et al. 1984, Harlow et al. 1992). Three of the seven animals found moribund or dead in a trap were diagnosed with symptoms of stress (involving two of the three cases of lymphoid follicular involution observed in the spleen, and the one case of the “stress haemogram”), which suggests that there may be a link between the intensity of *Parastrongyloides trichosuri* infections and stress due to capture and handling. The third of the three cases of lymphoid follicular involution observed in the spleen, involved a female that was found dead on the ground, who had not previously shown symptoms of poor condition, and was found to possess only seven *P. trichosuri* (Table 6.12). This latter case does not disprove the possible association between capture, stress, and the intensity of *P. trichosuri* infections, because any such association will always depend on the level of exposure to infective stages of the parasite. The female in question died early on in the study, whereas the level of exposure may have increased over the course of the study as more and more faeces accumulated at permanent trap locations, which likely acted as foci for infection (Heath et al. 1998). As would be expected if the stress of repeated capture and handling, or the accumulation of faeces in traps, were contributing factors, Obendorf et al. (1998) reported that the prevalence and intensity of *P. trichosuri* infections was much greater at the Paddys Land site than at any of the other Australian sites they surveyed, where possums were not previously trapped and handled. Disentangling the effects of stress vs. exposure to infective larvae, ought to be readily achievable in future studies, as it is easy enough to manipulate the level of exposure by either cleaning traps or experimentally inoculating possums with infective larvae (Heath et al. 1998, p. 16).

Stankiewicz et al. (1998) reported that the prevalence of *Parastrongyloides trichosuri* infections, in two surveys of possums from the Orongorongo Valley site, was 60.4, and 97.0 %, respectively. The latter figure is greater than the prevalence observed at the Paddys Land site (Table 6.10). Stankiewicz et al. (1998, their Table 3) also reported that the mean (+/- S.D.) intensity of *P. trichosuri* infections in one of the two surveys of the Orongorongo Valley site was 95 (+/- 97), which is comparable to the mean intensity (149 +/- 267) observed at the Paddys Land site (Table 6.10). The prevalence and intensity of another intestinal nematode, *Paraustrostrongylus trichosuri*, also appears to be comparable between the two sites. Heath et al. (1998, p. 17) reported that possums at the Orongorongo Valley site that were in poorer condition (based on weight/length) had significantly more nematodes in their intestines, although the authors did not stipulate what proportion were *Parastrongyloides trichosuri* and what proportion were *Paraustrostrongylus trichosuri*. Except for *Adelonema trichosuri* (Table 6.10), all parasites observed at the Paddys Land site have also been recorded at the Orongorongo Valley site (Heath et al. 1998, Stankiewicz et al. 1998). The similarities between the parasitic fauna of possums at the Paddys Land and Orongorongo Valley sites is surprising given the differences between the Paddys Land site and other Australian sites noted by Obendorf et al. (1998). While it is not clear what the cause of these similarities might be, it is clear that if adverse effects of capture and handling are mediated through the action of parasites, the consequences will likely be the same at both the Paddys Land and Orongorongo Valley sites.

Diarrhea induced by heavy infections of *Parastrongyloides trichosuri* may have been part of the cause of the rapid loss of body weight observed among animals found moribund or dead in a trap at the Paddys Land site (Fig. 6.5). Profuse diarrhea generally accompanies “heavy” Strongyloidid infections (Noble et al. 1989, p. 295), and one of the moribund possums was diagnosed as suffering from severe dehydration, as would be expected to accompany a bout of profuse diarrhea. This could also explain the “poor bodily condition” (Efford 1994, p. 4) of possums found “comatose in trap” at the Orongorongo Valley site.

Age at death

I collected teeth from a total of 40 animals. The methods used to determine age, in years, from cementum annuli, were described in Chapter 5. Two of the 40 animals were less than 1 year old, having died sometime after weaning, and prior to the beginning of the autumn breeding season in the year following the year in which they were born. Survival of young animals during this period (PAP and PAU in Table 6.4) is significantly different from that among older animals (ASP and ASU in Table 6.4). In this section, I consider whether adult survival is a function of age, and whether the age distribution among the 38 adult possums (> 1 year old) aged from cementum annuli, is congruent with that expected, given the estimated annual adult survival rate, based on radio-telemetry (Fig. 6.3).

I collected teeth from all 23 animals that were necropsied (Table 6.13). As described in the previous section, necropsied animals were categorized as having either Died or been Killed. Eleven of the 15 other adult possums aged from cementum annuli could also be categorized by fate. Four animals were known to have been Killed, including a male and a female that were attacked in traps by predators, and two radio-collared females judged to have been killed by predators (Table 6.9). The remaining known-fate individuals were seven radio-collared females all categorized as having Died, as their carcasses were all found intact, and their collars tested negative for the presence of blood (Table 6.9).

There was no significant difference between the mean age of animals that Died and those that were Killed (Table 6.13). The result was the same whether or not all animals categorized by fate were included in the analysis, or only those that were necropsied. Supplementary tests (not shown) indicated that the result was not due to biases attributable to grid, season or year. I conclude that “old age” was not the proximate cause of death of animals that Died.

Since there were no significant differences in the age of individuals attributable to fate, sex, grid, season or year, I used data from all 38 adult possums aged from cementum annuli to test whether the observed age distribution (Fig. 6.6) was congruent with my estimates of adult survival (Fig. 6.3). The three 14-year-olds shown in Figure 6.6 were all females. Fourteen years is the maximum age that has been reported among free-living female possums (Cowan 1990). As one of the three 14-year-old females shown in Figure 6.6 had been Killed, it is possible that females at the Paddys Land site may live longer than 14 years.

The large number of long-lived animals shown in Figure 6.6 is unlikely if annual adult survival is 81.3 %, as was estimated from radio-telemetry (Fig. 6.3, Table 6.4). Figure 6.6 shows the expected age distribution (assuming $r = 0.0$; Krebs 1999, p. 506) among 38 individuals if survival is assumed to be either 81.3 %, or 89.9 %, per annum. The latter estimate is that required to generate a value of $r = 0.0$ in the model of possum demography, assuming equivalent rates of adult survival across all four seasons. The age distribution expected under an assumption of 89.9 % per annum adult survival clearly provides a better "fit" to the observed age distribution than that expected if survival is 81.3 % per annum (Fig. 6.6).

I conducted a series of goodness of fit tests comparing the observed age distribution with that expected if annual adult survival is 81.3 % (assuming $r = 0.0$), using: 1) data from all 38 animals (pooling across sex and fate, Fig. 6.6); 2) data from females only (N = 25); and 3) data from Killed females only (N = 11). Zar (1996, p. 466) recommended using the χ^2 test to evaluate goodness of fit if the number of groups, and the smallest expected cell frequency, are both > 2; while the exact binomial test should be used if there are only 2 groups. I pooled adjacent age classes to generate groups with minimum expected cell frequencies of > 2. I was able to generate four age classes using data from all 38 animals, three age classes using data from females only, and just two age classes using data from Killed females only. Table 6.14 presents the results of statistical comparisons between observed and expected cell frequencies when only two age classes (the maximum number as regards Killed females) are considered: individuals aged 2 to 8 years, and those aged 8 to 14 years (the number of 8-year-olds being divided equally between the two classes). Using data from all 38 animals, the observed age distribution was significantly different from that expected if survival is 81.3 % per annum, whether four age classes are considered ($\chi^2 = 8.47$, df = 3, p = 0.0372), or just two (Table 6.14). The same was true using data from females only, whether three age classes are considered ($\chi^2 = 7.83$, df = 2, $p = 0.0200$), or just two (Table 6.14). The observed age distribution was not significantly different from the expected one, using data from Killed females only (Table 6.14), although the power of this test is very poor ($1 - \beta > 0.62$; Zar 1996, pp. 536-537), as a consequence of the small sample size (N = 11). While a significant result, involving Killed females only, would permit me to conclusively rule out potential biases in the comparison of observed and expected age distributions, attributable to fate and sex, the previous analysis (Table 6.13) showed that there were no significant biases attributable to these factors. I conclude that the balance of evidence indicates that the observed age distribution among adult possums aged from cementum annuli is not congruent with that expected if annual adult survival is 81.3 % (assuming $r = 0.0$).

Table 6.14 should not be interpreted as demonstrating that the annual survival rate is not 81.3 % *per se*. The expected age distribution (n_x) is a function of both the survival rate (l_x) and the growth rate (r) of the population ($n_x = l_x / e^{rx}$; Krebs 1999, p. 507). In Table 6.14, I assumed $r = 0.0$, in which case the observed age distribution is not what would be expected given a per annum survival rate of 81.3 %. However, if it is assumed that $r = - 0.0998$ (from Table 6.4), and the survival rate is 81.3 % per annum, then the expected age distribution is equivalent to that if survival is 89.9 % and $r = 0.0$ (the gray line in Fig. 6.6). This is not so mysterious as it first may appear. In both cases I am generating values from the same model. In one case I am “fixing” the value of r and solving for l_x, while in the other case I am “fixing” l_x and solving for r. The point is that *both* curves illustrated in Figure 6.6 (the black line *and* the grey line) are congruent with a per annum survival rate of 81.3 %, given different assumptions regarding r. Hence, the observed age distribution can be interpreted in one of two ways, either: 1) the population is stable ($r = 0.0$), and the estimate of 81.3 % per annum survival is incorrect; or 2) the estimate of 81.3 % per annum survival is correct, and the population is in fact declining at a rate of 9.5 % per annum ($r = - 0.0998$), and has been declining at this rate *for at least 14 years*! Assuming the Paddys Land population had been declining at a rate of 9.5 % per annum for the 14 years prior to the start of my study, the predicted density of possums at the site in the early 1980’s would be around 5 animals per ha, which is higher than the highest recorded density of possums in Australia (4 per ha; Kerle 1984, her Table 3). I conclude that the most likely scenario is that the 81.3 % per annum annual survival rate, based on radio-telemetry, is a significant underestimate of the “true” rate of adult survival at the Paddys Land site.

While my interpretation of the relationship between the observed age distribution, and survival, requires an assumption regarding the population growth rate, the observed age distribution does suggest something conclusive as regards immigration and survival. If immigrants were continually "rescuing" the Paddys Land population and thereby maintaining the population density, as Efford (1991a, 1998) suggests is the case regarding the Orongorongo Valley population, then the aggregate growth rate of the population (population growth among residents = - 0.0998, Table 6.4; *plus* growth from the addition of immigrants) would be equal to 0.0. In this case, the observed age distribution illustrated in Figure 6.6 is clearly incongruent with an estimated per annum adult survival rate of 81.3 %, for the reasons discussed above.

Survival and the frequency of capture and handling

Radio-collared adult females were captured, handled, and released, on 695 occasions. The principal method of capture prior to handling involved trapping (682 cases). There were only 13 occasions when the method of capture involved darting. Nine females were darted during the course of the study. Four of the nine were darted on only one occasion, three were darted twice, and two were each darted three times. Only one of the nine darted females died during the course of the study, 13 months after the single occasion on which she was darted. Beginning from the date on which the first female was darted (July 7, 1995), I compared the post-darting survival of the nine darted females (starting from the first time the animal was darted if it was darted repeatedly), against the survival of females that were never darted. Females that had been darted had a slightly higher probability of survival, although the difference was not significant (least conservative $\chi^2 = 2.85$, df =1, p = 0.0914). As there was no significant effect of the method of capture on the probability of survival, I consider the frequency of handling, irrespective of the method of capture, in subsequent analyses.

For each radio-collared adult female, I calculated the interval (in days) between each successive occasion on which she was handled. There were 7 radio-collared females, out of the total of 78 adult females radio-collared during the course of the study (Chapter 4), for which it was not possible to determine the relationship between survival and the interval between handling occasions, because they were only handled once before being either removed (6 cases), or found dead (1 case). For each of the remaining 71 females, I calculated the mean, and median, interval (in days) between occasions on which she was handled. I calculated both the mean (mean of means = 49, median of means = 41, range = 14-161) and median (mean of medians = 42, median of medians = 37, range = 14-161) handling interval for each female because I had no *a priori* way of knowing what the shape of the distribution of handling intervals would be. If a distribution is asymmetrical, the median is a better indicator of the "typical" value, than the mean (Sokal and Rohlf 1995, p. 46). To evaluate the shape of the distribution of handling intervals, I compared the mean and median handling intervals for each female using Wilcoxon's signed-ranks test. The mean handling interval was significantly greater than the median interval ($T = 144.5$, $z = 5.15$, $p < 0.0001$), indicating that the mean interval was skewed upwards by unusually long intervals between handling occasions. I conclude that the median handling interval is more representative of the "typical" frequency with which a female was handled.

There was no significant difference in median handling intervals between the two study grids (Mann-Whitney $U = 616.0$, $z = 0.16$, $p = 0.8720$). Consequently, I pooled data from both grids for use in subsequent analyses. To examine for possible changes in handling frequency over the course of the study I identified all females that were handled in both of two time periods, and then compared the frequency of handling between time periods using Wilcoxon's signed-ranks test. There was no significant difference in median handling intervals between 1995 and 1996, among the 36 females handled in both years ($T = 330.5$, $z = 0.04$, $p = 0.9687$). As discussed previously, there were only 19 weeks of data from the autumn and winter of 1997 that could be compared against the equivalent periods in 1995 and 1996 (Fig. 6.2). The frequency of handling was significantly greater in the first 19 weeks of 1997, as compared to 1995, among the 12 females handled in both time periods ($T = 0.0$, $z = 2.93$, $p = 0.0033$). Similarly, the frequency of handling was significantly greater in 1997, as compared to 1996, among the 22 females handled in both years ($T = 39.0$, $z = 2.84$, $p = 0.0045$). I conclude that handling frequencies were comparable in 1995 and 1996, and then increased significantly in 1997. This is as expected given that a concurrent study was begun in February, 1997, that involved trapping and handling the same animals as were already being monitored in this study (see Methods). Data from 1997 are treated separately in the subsequent analyses, while data from 1995 and 1996 were pooled for use in the subsequent analyses.

I was able to calculate a median handling interval for each of 70 radio-collared females over the course of 1995 and 1996. To evaluate the relationship between survival and a particular "prognostic variable", Lee (1992, pp. 245-246) recommended dividing the group in question into subgroups, and then comparing the shape of the survivorship curve for one subgroup versus that for the other. I ranked the 70 radio-collared females in question according to median handling intervals. I created two equal sized subgroups (N = 35 in each). When ranked according to median handling interval, the division into subgroups consisted of females with a median handling interval of less than 42 days, and those with a median handling interval of more than 42 days. There were 10 deaths among the former, and 6 among the latter. The difference in survivorship between subgroups was significant (least conservative $\chi^2 = 6.79$, df = 1, $p = 0.0091$; most conservative $\chi^2 = 6.18$, df =1, $p = 0.0129$). When categorized by median handling interval, over the course of 1995 and 1996, females that were handled more frequently had a significantly lower probability of survival (Fig. 6.7).

There was a noticeable difference in the composition of the two subgroups illustrated in Figure 6.7. Many more females were “right-censored” (Pollock et al. 1989) in the frequently handled subgroup (18 cases) than in the infrequently handled subgroup (1 case). Under such circumstances the log-rank test will tend to generate an inflated χ^2 value, as was discussed previously. Consequently, the more conservative of the two χ^2 values reported above is likely more accurate.

The 18 right-censored females in the more frequently handled subgroup, illustrated in Figure 6.7, consisted of: 1 female killed in a trap by a predator in June, 1995; 12 females removed on August 1, 1995, as part of the experimental removal of core resident females (Chapter 4); and 5 females removed on August 1, 1996, also as part of the experimental removals. The one right-censored female in the infrequently handled subgroup was removed on August 1, 1995, as part of the experimental removals. Females removed in August, 1995, had been “at risk” for, at most, 20 weeks, before they were removed. If the median handling interval among females removed in August, 1995, was shorter simply because they were handled fewer times, then the composition of the subgroups would be an artifact of the removals. To determine whether the median handling interval was a function of the total number of times a female was handled, I analyzed the correlation between the two variables, using data from all 70 females for which I had calculated a median handling interval over the course of 1995 and 1996. There was no significant correlation between the median handling interval and the total number of times a female was handled ($N = 70$, Spearman’s $r = 0.10$, $t = 0.81$, $p = 0.4225$). Consequently, it does not appear that females were categorized as having been more frequently handled because they were removed. Instead, the division between the subgroups appears to reflect the fact that females were likely to be both, more frequently handled, and more likely to be removed, because they inhabited the center, rather than the periphery, of the study grid. I conclude that the difference in survivorship between the subgroups illustrated in Figure 6.7 is not an artifact of subgroup composition.

There were 31 females for which I was able to calculate a median handling interval over the course of the 19 weeks of autumn and winter data from 1997. As above, the 31 females were ranked according to median handling intervals. From the ranking I created two subgroups, composed of the first 16, and remaining 15, ranked females. When ranked according to median handling interval, the division into subgroups consisted of females with a median handling interval of less than 26 days, and those with a median handling interval of more than 26 days. There were 2 deaths in each subgroup. There was no significant difference in survivorship between the subgroups (least conservative $\chi^2 < 0.01$, df =1, p = 0.9612; most conservative $\chi^2 < 0.01$, df =1, p = 0.9616). I conclude that there was no apparent difference in survivorship between females handled more or less frequently during the autumn and winter of 1997. However, it is notable that the overall survival of radio-collared females was much poorer during the autumn and winter of 1997, at a time when all females were being handled significantly more often, as compared to the autumn and winter periods in 1995 and 1996 (Fig. 6.2).

Population growth rates and “censored” survival estimates

In Table 6.15, I list seasonal adult survival estimates, based on pooled data from 1995 and 1996, under four scenarios regarding the treatment of “censored” deaths. In the first scenario, only deaths that were obviously the result of capture and handling (the female killed in a trap by a predator) are treated as “right-censored”. This was the assumption underlying my original estimates of seasonal adult survival (Fig. 6.2), which when used in the model of possum demography together with ‘Typical’ parameter values for the Paddys Land site (Table 6.4), produced a predicted population growth rate of $r = -0.0998$ (Table 6.15). Figure 6.8 illustrates the pattern of change in population size over time given the predicted value of r under this scenario. Also illustrated in Figure 6.8 is the pattern of change in population size over time at the Orongorongo Valley site, predicted using the model of possum demography (Table 6.4).

In the second scenario listed in Table 6.15, animals found moribund or dead in traps are assumed to have died *because* of capture and handling, and these deaths are also treated as “right-censored”. Under this scenario the population growth rate at the Paddys Land site is predicted to be $r = - 0.0699$. The resulting pattern of change in population size over time is shown in Figure 6.8.

In a previous section, I noted the similarities between the symptoms shown by animals found moribund or dead in traps, and those seen to be “weak and wobbly” upon release. I concluded that the ultimate cause was the same, and suggested that it was the stress induced by repeated capture and handling. When otherwise inexplicable deaths (those not attributable to predation or parasitic infection) among females that were seen to be “weak and wobbly”, are treated as “right-censored”, along with cases where animals were found moribund or dead in traps, the Paddys Land population is still predicted to decline (Table 6.15), but at a much more gradual rate than in the previous scenarios (Fig. 6.8).

Finally, I argued that females recorded as being both “rumpy” and “bony” were on the same continuum of poor condition, resulting from the stress of repeated capture and handling, as were moribund, and “weak and wobbly” females. If otherwise inexplicable deaths (those not attributable to predation or parasitic infection) among females recorded as being both “rumpy” and “bony”, are treated as “right-censored”, along with cases involving moribund, and “weak and wobbly” females, the Paddys Land population is predicted to increase (Table 6.15), albeit ever so slightly (Fig. 6.8).

DISCUSSION

Adult possums at the Paddys Land site did not die of “old age” (Table 6.13). Nor did animals evidently starve to death, based on results from necropsies. If starvation had been a frequent cause of death I would have expected more deaths in 1995 than in 1996, since there was a severe mid-winter drought in 1995 (Fig. 5.7), and most animals weighed significantly less in 1995 than in 1996 (Table 5.12). However, there was no difference in adult female survivorship between the two years (Fig. 6.2). Only one-third (8/24) of all apparently “natural” deaths were due to predation (Table 6.9), and only 1 of 11 apparently “natural” deaths among animals not killed by predators, was directly attributable to a parasitic infection (Table 6.10). Consequently, more than half of all apparently “natural” deaths were inexplicable.

In almost half of all cases (11/24) of apparently “natural” deaths among radio-collared adult females, the female demonstrated one or more of a variety of symptoms of poor condition. These symptoms included ataxia (loss of motor control), weight loss, and being both “rumpy” and “bony”. In most cases (7/11) the female demonstrated the full spectrum of symptoms. Individuals showing symptoms of poor condition were burdened by significantly greater numbers of *Parastrongyloides trichosuri*, than apparently healthy individuals (Table 6.12), and diarrhea induced by *P. trichosuri* may have been partly responsible for the often dramatic weight loss demonstrated by those in poor condition (Fig 6.5). Heath et al. (1998, p. 16) reported that, in a laboratory study, “most” possums were able to resist *P. trichosuri* infections, following inoculation with 5000 infective larvae. Thus, while *P. trichosuri* infections may worsen the host’s condition by causing weight loss, sizeable *P. trichosuri* infections are a consequence of some other factor having compromised the host’s immunocompetence. Four lines of evidence suggest that these symptoms of poor condition, and the accompanying *P. trichosuri* infections, are ultimately caused by the stress induced by repeated capture and handling: 1) in 3 of the 4 cases where information was available, histopathology or blood biochemistry indicative of a response to stress was observed in individuals that showed symptoms of poor condition; 2) the prevalence and intensity of *P. trichosuri* infections at the Paddys Land site was much greater than at other Australian sites (Obendorf et al. 1998), where possums were not repeatedly trapped and handled; 3) even apparently healthy individuals showed symptoms of stress in association with repeated capture insofar as they were significantly more likely than not to lose weight over the course of a single, full-grid (generally 3-night) trapping session; and 4) radio-collared adult females that were handled more frequently, over the course of 1995 and 1996, had a significantly lower probability of survival (Fig. 6.7).

If a certain proportion of apparently “natural” deaths are actually due, in whole or in part, to the stress induced by repeated capture and handling, then the “true” rate of adult female survival will be greater than that estimated when only those deaths that are obviously caused by capture and handling (e.g., individuals attacked in a trap by a predator) are treated as “right-censored”. Two lines of evidence suggest that my initial estimates of adult female survival (Figs. 6.2 and 6.3), which were calculated under the assumption that all deaths that were not obviously caused by capture and handling were “natural” deaths, were in fact underestimates of the “true” survival rate. Firstly, the observed age distribution among adults aged from cementum annuli was significantly different from that expected based on my initial estimates of adult female survival (Table 6.14), and appeared to be more consistent with a higher survival rate (assuming $r = 0.0$, Fig. 6.6). Secondly, the predicted population growth rate of $r = - 0.0998$ for the Paddy Land site, which was generated when I used my initial estimates of adult female survival in the model of possum demography (Table 6.4), is inconsistent with the results of a regional species distribution model that predicts that the Paddys Land site is quite clearly 'optimal' habitat for possums (NPWS 1994).

In the last line of Table 6.15, I reported the seasonal adult female survival rates estimated when otherwise inexplicable deaths (those not attributable to predation or parasitic infection) among moribund, "weak and wobbly", and "rumpy" and "bony" females, were treated as "right-censored", along with those deaths that were obviously due to capture and handling. The 90.1 % per annum survival rate estimated under this scenario appears to provide a much better "fit" to the observed age distribution among adults aged from cementum annuli, as suggested by the grey line in Figure 6.6. In addition, when the seasonal survival estimates generated under this scenario are used in the model of possum demography (Fig. 6.4), the population growth rate at the Paddys Land site is predicted to be $r = 0.0015$ (Table 6.15), which is much more consistent with the assessment that the site represents 'optimal' habitat for possums (NPWS 1994). I conclude that otherwise inexplicable deaths among moribund, "weak and wobbly", and "rumpy" and "bony" possums, are the direct consequence of the stress induced by repeated capture and handling, and such deaths ought to be treated as "right-censored" when calculating survival estimates. The grey line in Figure 6.2 plots the resulting change in my estimate of the cumulative probability of survival of radio-collared females over the course of the study, and should be interpreted as more accurately portraying the "true" rate of adult female survival at the Paddys Land site.

The population growth rate at the Paddys Land site ($r = - 0.0998$), predicted using my initial estimates of adult female survival (illustrated by the solid black line in Fig. 6.2), was remarkably similar (Fig. 6.8) to the population growth rate at the Orongorongo Valley site ($r = - 0.0963$), predicted using Efford's (1998) estimates of adult female survival at that site. My initial estimates of adult female survival were very similar to Efford's, and a sensitivity analysis of the model of possum demography indicated that the similarity in survival estimates accounts for much of the overall similarity in predicted population growth rates, as the predicted growth rate is largely determined by the adult survival rate (Table 6.4). As is true of the Paddys Land site, the strongly negative growth rate predicted for the Orongorongo Valley site is inconsistent with the fact that the site is apparently ‘optimal’ habitat for possums.

Feral cats and dogs occur at both the Paddys Land (Table 6.8) and Orongorongo Valley sites (Fitzgerald and Karl 1979, Anderson 1990). According to Cowan (1990, p. 91), “the significance of natural predation in the population dynamics of possums [in New Zealand] is unknown”. Nonetheless, both Fitzgerald and Karl (1979), and Efford (1998, p. 513), concluded that the occurrence of adult possum remains in predator scats at the Orongorongo Valley site most likely represented “scavenging on the carcasses of possums that died from other causes”. I infer from this that, as is the case at the Paddys Land site (Table 6.9), few adult deaths at the Orongorongo Valley site are directly attributable to predation, and that most apparently “natural” deaths are inexplicable.

Possums at the Orongorongo Valley site are occasionally found “comatose or dead” in a trap. When all such deaths were treated as “right-censored”, the predicted population growth rate ($r = - 0.0685$) was very similar to that predicted for the Paddys Land site ($r = - 0.0699$), when all deaths among animals found “moribund or dead” in a trap were treated as “right-censored” (Table 6.15). Possums at the Orongorongo Valley site are occasionally observed to be “weak and wobbly” upon release, just as at the Paddys Land site. In addition, the prevalence and intensity of *Parastrongyloides trichosuri* infections appears to be very similar at the two sites, and there is some indication of an association between the intensity of *P. trichosuri* infections and poor condition at both sites. If the adult female survival estimates for the Paddys Land site, generated by “right-censoring” inexplicable deaths among females in poor condition (the last line in Table 6.15), are substituted for the adult female survival estimates for the Orongorongo Valley site shown in Table 6.4, the population growth rate at the Orongorongo Valley site is predicted to be $r = - 0.0099$ (i.e., $\cong 0.0$). I suggest that both the Paddys Land and Orongorongo Valley possum populations would be stable ($r = 0.0$), in the absence of repeated capture and handling. Efford (1998, p. 513) noted that the pre-weaning survival of pouch-young at the Orongorongo Valley site was poorer in the earlier years of the study (1966-1975) than in later years (1980-1994), and suggested that this may have been attributable to the greater frequency with which mothers with pouch-young were captured and handled in the earlier years of the study (see also Chapter 5). Efford and his colleagues do not appear to have evaluated the potentially adverse effects of capture and handling on the survival of adults at the Orongorongo Valley site, although this is probably not an oversight, but a reflection of the limitations of not having radio-telemetry data.

My results indicate that the predicted decline of the Paddys Land population is an artifact of repeated capture and handling. However, the adverse effects of handling are still real, and the population would likely have declined if the study had continued. I know from the results of the experiment described in Chapter 4 that the population would not be "rescued" by immigration. Following the removal of 19 resident adult females, only one female immigrant entered and settled in one of two removal areas, over the course of two years. The immigrant was a 2-year-old subadult, that did not breed in her second year. I modified the model of possum demography to simulate the addition of a 2-year-old subadult (Fig. 6.4), every second year. Using 'Typical' parameter values for the Paddys Land site (Table 6.4), and beginning with an initial population of 19 adult females (Fig. 6.4), the density is predicted to decline to a stable population of just 3 adult females. Thus, the measured rate of immigration was far from being sufficient to maintain a stable population density. Having rigorously measured immigration (Chapter 4), and after evaluating the demography of the resident population (this Chapter), I conclude that the Paddys Land site is definitely not a dispersal sink.

The fact that the model of possum demography predicted a declining growth rate for the resident population at the Orongorongo Valley site (Table 6.4) was not unexpected, as Efford (1991a, p. 43) reported that "local reproduction was inadequate to replace local mortality [$b < d$] and to maintain the population density". I have suggested that the reason for this may be poorer than "normal" adult survival resulting from the stress induced by repeated capture and handling. Yet the density of adult females at the Orongorongo Valley site is in fact stable (Efford 1998, his Fig. 3). It follows that females must be entering from outside the study area. The result from my "pulsed" removal experiment at the Paddys Land site was that only one "true" immigrant female entered and settled in one of two removal areas (Chapter 4). In addition, there were many adult females that were originally resident in the areas surrounding the removal areas, that responded to the removal of their neighbours by expanding their ranges into the removal areas (Chapter 4), thereby demonstrating the so-called "vacuum effect" referred to by Efford (1991a, p. 54). As discussed in Chapter 3, this type of range expansion represents "quasi-dispersal" (Lidicker and Stenseth 1992, p. 23), and is distinct from the type of "true" dispersal assumed when discussing the exchange of immigrants between patches. I propose that adults deaths due to repeated capture and handling are analogous to removals, in which case the Orongorongo Valley study may be viewed as a low-intensity, “press” (continuous) removal experiment (Stenseth and Lidicker 1992). Reproduction and survival will be higher outside the study grid because animals outside the study grid are not captured and handled. The creation of vacancies on the study grid, as a result of capture and handling, most likely draws in neighbours from just outside the study grid (i.e., the “vacuum effect”). Consequently, I suggest that it is the Orongorongo Valley study *itself* which has produced what appears to be a dispersal sink.

How often is it the case that handling effects actually generate apparent dispersal sinks? It might be objected that while repeated capture and handling evidently had adverse effects on two separate populations of common brushtail possums, this may just reflect some oddity with respect to common brushtail possums. It is difficult to respond to this objection because so few studies have tested for biases in demographic parameters attributable to handling effects (Haydon et al. 1999). Haydon et al. (1999) compared the predictions from a demographic model of snowshoe hare (*Lepus americanus*) dynamics with observed changes in population size, using data from two separate populations. Haydon et al. (1999) found that in both cases the model’s predictions underestimated the observed changes in population size, indicating that one or more of the demographic parameters was being underestimated. Haydon et al (1999) concluded that “true” adult and juvenile survival rates were each being underestimated by < 5 %, as a likely consequence of the stress of capture and handling. I suggest that snowshoes hares are sufficiently different in their ecology from common brushtail possums to make one suspect that biases in demographic parameters attributable to handling effects may be found to be quite a general problem. Consequently, I argue that the onus is on those who suspect they have evidence of the existence of a dispersal sink, to first demonstrate that it is not one of their own creation.

REFERENCES

Anderson, A. J. 1990. Kuri, Maori dog. *In* The handbook of New Zealand mammals. *Edited by* King, C. M. Oxford University Press, Auckland, New Zealand, pp. 281-287.

Andrewartha, H. G., and Birch, L. C. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.

Beissinger, S. R., and Westphal, M. I. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management, 62: 821-841.

Boutin, S., and Krebs, C. J. 1986. Estimating survival rates of snowshoe hares. Journal of Wildlife Management, 50: 592-594.

Bunck, C. M., and Pollock, K. H. 1993. Estimating survival of radio-tagged birds. *In* Marked individuals in the study of bird populations. *Edited by* Lebreton, J. -D., and North, P. M.. Birkhauser Verlag, Basel, Switzerland, pp. 51-63.

Catling, P. C., and Burt, R. J. 1995. Why are red foxes absent from some Eucalypt forests in eastern New South Wales? Wildlife Research, 22: 535-546.

Clark, J. M. 1995. The diet of the parasitic mite *Trichosurolaelaps crassipes* Womersley, 1956, and its potential to act a disease vector. New Zealand Veterinary Journal, 43: 215-218.

Clinchy, M. 1997. Does immigration “rescue” populations from extinction? Implications regarding movement corridors and the conservation of mammals. Oikos, 80: 618-622.

Cowan, P. E. 1990. Brushtail possum. *In* The handbook of New Zealand mammals. *Edited by* King, C. M. Oxford University Press, Auckland, New Zealand, pp. 68-98.

Cox, D. R., and Oakes, D. 1984. Analysis of survival data. Chapman and Hall, London.

Crawley, M. C. 1973. A live-trapping study of Australian brush-tailed possums, *Trichosurus vulpecula* (Kerr), in the Orongorongo Valley, Wellington, New Zealand. Australian Journal of Zoology, 21: 75-90.

Debus, S. J. S., and Chafer, C. J. 1994. The Powerful Owl (*Ninox strenua*) in New South Wales. Australian Birds, 28 (Supplement): 21-38.

Diffendorfer, J. E. 1998. Testing models of source-sink dynamics and balanced dispersal. Oikos, 81: 417-433.

Efford, M. 1991a. A review of possum dispersal. DSIR Land Resources Contract Report 91/73, DSIR Land Resources, Dunedin, New Zealand.

Efford, M. G. 1991b. Long-term studies of the dynamics of a local population of brushtail possums, *Trichosurus vulpecula*. Live-trapping in the Orongorongo Valley in 1990/91. DSIR Land Resources Technical Record 72, DSIR Land Resources, Lower Hut, New Zealand.

Efford, M. G. 1994. Long-term studies of the dynamics of a local population of brushtail possums. Live-trapping in the Orongorongo Valley in 1993/94. Manaaki Whenua - Landcare Research, Dunedin, New Zealand.

Efford, M. 1998. Demographic consequences of sex-biased dispersal in a population of brushtail possums. Journal of Animal Ecology, 67: 503-517.

Efford, M. G., and Hearfield, M. E. 1992. Long-term studies of the dynamics of a local population of brushtail possums. Live-trapping in the Orongorongo Valley in 1991/92. DSIR Land Resources Technical Record 111, DSIR Land Resources, Lower Hut, New Zealand.

Fitzgerald, A. E. 1976. Diet of the opossum *Trichosurus vulpecula* (Kerr) in the Orongorongo Valley, Wellington, New Zealand, in relation to food plant availability. New Zealand Journal of Zoology, 3: 399-419.

Fitzgerald, B. M., and Karl, B. J. 1979. Food of feral house cats (*Felis catus* L.) in forest of the Orongorongo Valley, Wellington. New Zealand Journal of Zoology, 6: 107-126.

Gruenberg, A., and Bisset, S. 1998. *Parastrongyloides trichosuri* as a potential vector for genes expressing proteins which could interfere with reproductive success, growth, or longevity of brushtailed possums. Royal Society of New Zealand Miscellaneous Series, 45: 10-12.

Hainsworth, F. R. 1981. Animal physiology: adaptations in function. Addison-Wesley Publishing Co., Reading, Massachusetts.

Harlow, H. J., Lindzey, F. G., Van Sickle, W. D., and Gern, W. A. 1992. Stress response of cougars to nonlethal pursuit by hunters. Canadian Journal of Zoology, 70: 136-139.

Haydon, D. T., Gillis, E. A., Stefan, C. I., and Krebs, C. J. 1999. Biases in the estimation of the demographic parameters of a snowshoe hare population. Journal of Animal Ecology, 68: 501-512.

Heath, D., Cowan, P., Stankiewicz, M., Clark, J., Hornerr, G., Tempero, J., Jowett, G., Flanagan, J., Shubber, A., Street, L., McElrea, G., Chilvers, L., Newton-Howse, J., Jowett, J., and Morrison, L. 1998. Possum biological control - parasites and bacteria. Royal Society of New Zealand Miscellaneous Series, 45: 13-19.

Heath, D. D., Jowett, G. H., and Stankiewicz, M. 1995. The life-cycle of *Parastrongyloides trichosuri*. New Zealand Journal of Zoology, 22: 185-186.

Hemsley, S., and Canfield, P. 1993. Dermatitis in brushtail possums (*Trichosurus vulpecula*). Proceedings of the Annual Meeting of the Australasian section of the Wildlife Disease Association, Wildlife Disease Association, Sydney, Australia, pp. 23-24.

Hintze, J. 1996. NCSS Statistical Software. NCSS, Kaysville, Utah, U.S.A. Information available at [http://www.ncss.com].

Humphreys, W. F., Bradley, A. J., How, R. A., and Barnett, J. L. 1984. Indices of condition of Phalanger populations: a review. *In* Possums and gliders. *Edited by* Smith, A. P., and Hume, I. D. Australian Mammal Society, Sydney, Australia, pp. 59-77.

Junqueira, L. C., Carneiro, J., and Long, J. A. 1986. Basic histology, 5th ed. Lange Medical Publications, Los Altos, California.

Kalbfleisch, J. D., and Prentice, R. L. 1980. The statistical analysis of failure time data. John Wiley and Sons, New York.

Kerle, J. A. 1984. Variation in the ecology of *Trichosurus*: its adaptive significance. *In* Possums and gliders. *Edited by* Smith, A. P., and Hume, I. D. Australian Mammal Society, Sydney, Australia, pp. 115-127.

Kleinbaum, D. G. 1996. Survival analysis: a self-learning text. Springer, New York.

Krebs, C. J. 1994. Ecology: the experimental analysis of distribution and abundance, 4th ed. Harper Collins, New York.

Krebs, C. J. 1999. Ecological methodology, 2nd ed. Benjamin/Cummings, Menlo Park, California.

Lidicker, W. Z., Jr., and Stenseth, N. C. 1992. To disperse or not to disperse: who does it and why? *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 21-36.

Lee, E. T. 1992. Statistical methods for survival data analysis, 2nd ed. John Wiley and Sons, Inc., New York.

Mackerras, M. J. 1959. *Strongyloides* and *Parastrongyloides* (Nematoda : Rhabditoidea) in Australian marsupials. Australian Journal of Zoology, 7: 87-104.

Mackintosh, C. G., Crawford, J. L., Thompson, E. G., McLeod, B. J., Gill, J. M., and O'Keefe, J. S. 1995. A newly discovered disease of the brushtail possum: Wobbly possum syndrome. New Zealand Veterinary Journal, 43: 126.

Mantel, N., and Haenszel, W. 1959. Statistical aspects of the analysis of data from retrospective studies of disease. Journal of the National Cancer Institute, 22: 719-748.

Margolis, L., Esch, G. W., Holmes, J. C., Kuris, A. M., and Schad, G. A. 1982. The use of ecological terms in parasitology (report of an *ad hoc* committee of the American Society of Parasitologists). Journal of Parasitology, 68: 131-133.

Noble, E. R., Noble, G. A., Schad, G. A., and MacInnes, A. J. 1989. Parasitology: the biology of animal parasites, 6th ed. Lea and Febiger, Philadelphia.

NPWS. 1994. Fauna of northeast N.S.W. forests. Northeast forests biodiversity study. N.S.W. National Parks and Wildlife Service, Sydney, Australia.

Obendorf, D., Spratt, D., Beveridge, I., Presidente, P., and Coman, B. 1998. Parasites and diseases in Australian brushtail possums, *Trichosurus* spp. Royal Society of New Zealand Miscellaneous Series, 45: 6-9.

Pollock, K. H., Winterstein, S. R., Bunck, C. M., and Curtis, P. D. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management, 53: 7-15.

Prentice, R. L., and Marek, P. 1979. A qualitative discrepancy between censored data rank tests. Biometrics, 35: 861-867.

Presidente, P. J. A. 1984. Parasites and diseases of brushtail possums (*Trichosurus* spp): occurrence and significance. *In* Possums and gliders. *Edited by* Smith, A. P., and Hume, I. D. Australian Mammal Society, Sydney, Australia, pp. 171-190.

Presidente, P. J. A., Barnett, J. L., How, R. A., and Humphreys, W. F. 1982. Effects of habitat, host sex and age on the parasites of *Trichosurus caninus* (Marsupialia : Phalangeridae) in north-eastern New South Wales. Australian Journal of Zoology, 30: 33-47.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist, 132: 652-661.

Pyke, D. A., and Thompson, J. N. 1986. Statistical analysis of survival and removal rate experiments. Ecology, 67: 240-245.

Sokal, R. R., and Rohlf, F. J. 1995. Biometry, 3rd ed. W. H. Freeman and Co., New York.

Sauer, J. R., and Williams, B. K. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management, 53: 137-142.

Sprent, J. F. A. 1963a. The life history and development of *Amplicaecum robertsi*, an ascaridoid nematode of the carpet python (*Morelia spilotes variegatus*). I. Morphology and functional significance of larval stages. Parasitology, 53: 7-38.

Sprent, J. F. A. 1963b. The life history and development of *Amplicaecum robertsi*, an ascaridoid nematode of the carpet python (*Morelia spilotes variegatus*). II. Growth and host specificity of larval stages in relation to the food chain. Parasitology, 53: 321-337.

Stacey, P. B., Johnson, V. A., and Taper, M. L. 1997. Migration within metapopulations: the impact upon local population dynamics. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* Hanski, I., and Gilpin, M. E., Academic Press, San Diego, pp. 267-291.

Stankiewicz, M., Cowan, P. E., and Heath, D. D. 1998. Endoparasites of possums from selected areas of North Island, New Zealand. New Zealand Journal of Zoology, 25: 91-97.

StatSoft, Inc. 1995. STATISTICA for Windows. StatSoft, Inc., Tulsa, Oklahoma, U.S.A. Information available at [http://www.statsoftinc.com].

Stenseth, N. C., and Lidicker, W. Z., Jr. 1992. Where do we stand methodologically about experimental design and methods of analysis in the study of dispersal? *In* Animal dispersal: small mammals as a model. *Edited by* Stenseth, N. C., and Lidicker, W. Z., Jr., Chapman and Hall, London, pp. 295-318.

Viggers, K. L., and Spratt, D. M. 1995. The parasites recorded from *Trichosurus* species (Marsupialia: Phalangeridae). Wildlife Research, 22: 311-332.

Watkinson, A. R., and Sutherland, W. J. 1995. Sources, sinks and pseudo-sinks. Journal of Animal Ecology, 64: 126-130.

Wilson, G., Dexter, N, O'Brien, P, and Bomford, M. 1992. Pest animals in Australia: a survey of introduced wild mammals. Kangaroo Press, Sydney, Australia.

Zar. J. H. 1996. Biostatistical analysis, 3rd ed. Prentice Hall, Upper Saddle River, New Jersey.

Table 6.1. Definitions regarding the parameters used in the model of possum demography illustrated in Figure 6.4. A primary young is defined as the first young born to a female within the year following the first day of autumn, while a replacement young is a young born to a female after the loss of her primary young, within the same year. Parameters concern females only.

Process	Parameter	Definition
SURVIVAL		
	ASA	Adult survival in autumn
	ASW	Adult survival in winter
	ASP	Adult survival in spring
	ASU	Adult survival in summer
	PAA	Survival of primary young born in autumn, to the end of autumn
	PAW	Survival of primary young born in autumn, to the end of winter
	PAP	Survival of primary young born in autumn, to the end of spring
	PAU	Survival of primary young born in autumn, to the end of summer
	PWW	Survival of primary young born in winter, to the end of winter
	PWP	Survival of primary young born in winter, to the end of spring
	PWU	Survival of primary young born in winter, to the end of summer
	RYW	Survival of replacement young born in winter, to the end of winter
	RYP	Survival of replacement young born in winter, to the end of spring
	RYU	Survival of replacement young born in winter, to the end of summer
	OSA	One-year-old survival in autumn
	OSW	One-year-old survival in winter
	OSP	One-year-old survival in spring
	OSU	One-year-old survival in summer
BIRTHS		
	FPA	Female primary young born in autumn = BPA x SEX
	FRY	Female replacement young born in winter = BPA x (1-PAA) x BRY x SEX
	FPW	Female primary young born in winter = (1-BPA) x BPW x SEX
	BPA	Proportion of adult females giving birth to a primary young in autumn
	BRY	Proportion of adult females giving birth to a replacement young in winter
	BPW	Proportion of adult females giving birth to a primary young in winter
	SEX	Sex ratio at birth = Proportion of pouch-young that are female
MATURATION		
	1RC	1-year-old recruits = MA1 x STB
	1FB	1-year-old failed breeders = MA1 x (1-STB)
	1IM	1-year-old subadults = (1-MA1)
	2RC	2-year-old recruits = MA2 x STB
	2FB	2-year-old failed breeders = MA2 x (1-STB)
	2IM	2-year-old subadults = (1-MA2)
	3RC	3-year-old recruits = STB
	3FB	3-year-old failed breeders = (1-STB)
	MA1	Maturity among 1-year-olds = Proportion of 1-year-olds that give birth
	MA2	Maturity among 2-year-olds = Proportion of 2-year-olds that give birth
	STB	Success of first-time breeders relative to adult females

Table 6.2. Sources of parameter values for the Paddys Land population, used in the model of possum demography illustrated in Figure 6.4. Parameters are defined in Table 6.1. Values concern females only.

Parameter	Source
ASA	Chapter 6, Fig. 6.3; data from 1995 and 1996, 1997 data excluded
ASW	Chapter 6, Fig. 6.3; data from 1995 and 1996, 1997 data excluded
ASP	Chapter 6, Fig. 6.3; data from 1995 and 1996
ASU	Chapter 6, Fig. 6.3; data from 1995 and 1996
PAA	Chapter 5, Table 5.9, Yes / (Yes + No); less 1 1st-time breeder
PAW	Chapter 5, Table 5.4, Yes / (Yes + No); less 4 1st-time breeders
PAP	Chapter 5, p. 168; square root of weaning-autumn survival [1]
PAU	Chapter 5, p. 168; square root of weaning-autumn survival [1]
PWW	Assumed = PAA; early survival of pouch-young unlikely to vary
PWP	Assumed = PAW; most likely PWP > PAW, no data available
PWU	Assumed = PAP x PAU = survival from weaning to autumn [2]
RYW	Assumed = PAA; early survival of pouch-young unlikely to vary
RYP	Assumed = PAW; most likely RYP > PAW, no data available
RYU	Assumed = PAP x PAU = survival from weaning to autumn [2]
OSA	Assumed = ASA; not significantly different, Efford (1998, p. 510)
OSW	Assumed = ASW; not significantly different, Efford (1998, p. 510)
OSP	Assumed = ASP; not significantly different, Efford (1998, p. 510)
OSU	Assumed = ASU; not significantly different, Efford (1998, p. 510)
BPA	Chapter 5, Table 5.2; less 9 1st-time breeders (Chapter 5, p. 169)
BRY	Assumed = BPA; two known cases, both had replacement young
BPW	Chapter 5, Table 5.2; less 9 1st-time breeders (Chapter 5, p. 169)
SEX	Chapter 4, Table 4.13
MA1	Chapter 5, p. 169
MA2	Chapter 5, p. 169
STB	Chapter 5, p. 172; 0 of 4 successful, assume maximum is 1 in 5

[1] The available estimate of concerns survival from the onset of weaning to the beginning of the next (autumn) breeding season, which includes both spring and summer. Separate values for spring and summer were required for use in the model. When the square root of survival from the onset of weaning to the beginning of the next breeding season is multiplied across spring and summer, the aggregate is correct (PAP x PAU = 0.6831 x 0.6831 = 0.4667).

[2] Winter-born primary and replacement young were assumed to have the same likelihood of surviving from the onset of weaning to the beginning of the next breeding season (PAP x PAU, see previous note) as were autumn-born young.

Table 6.3. Sources of parameter values for the Orongorongo Valley population, used in the model of possum demography illustrated in Figure 6.4. Parameters are defined in Table 6.1. Values concern females only.

Parameter	Source
ASA	Efford (1998) Table 4, Season 1
ASW	Efford (1998) Table 4, Season 2
ASP	Efford (1998) Table 4, square root of survival for Season 3 [1]
ASU	Efford (1998) Table 4, square root of survival for Season 3 [1]
PAA	Not measured for Orongorongo Valley population; from Table 6.2
PAW	Efford (1998) Table 4, Season 2
PAP	Efford (1998) Table 4, square root of survival for Season 3 [1]
PAU	Efford (1998) Table 4, square root of survival for Season 3 [1]
PWW	Assumed = PAA; see comments in Table 6.2
PWP	Assumed = PAW; see comments in Table 6.2
PWU	Assumed = PAP x PAU; see comments in Table 6.2
RYW	Assumed = PAA; see comments in Table 6.2
RYP	Assumed = PAW; see comments in Table 6.2
RYU	Assumed = PAP x PAU; see comments in Table 6.2
OSA	Efford (1998) Table 4, Season 1
OSW	Efford (1998) Table 4, Season 2
OSP	Efford (1998) Table 4, square root of survival for Season 3 [1]
OSU	Efford (1998) Table 4, square root of survival for Season 3 [1]
BPA	Efford (1998) p. 510; 0.9239 x 0.9785 [survival to June] = 0.9040
BRY	Efford (1998) p. 513, "0.8% of the September population" [2]
BPW	Efford (1998) Fig. 1, < 5 % of births after mid-June [in winter] [2]
SEX	Efford (1998) p. 510
MA1	Efford (1994) Appendix 5, 1980-1993
MA2	Efford (1994) Appendix 5, 1980-1993; % of 2-year-olds less MA1
STB	Humphreys et al. (1984) Table 1; 34 versus 62 % of p.y. reared

[1] Efford's (1998) Season 3 includes both spring and summer. Separate values for spring and summer were required for use in the model. When the square root of Efford's Season 3 survival is multiplied across spring and summer, the aggregate is correct (ASP x ASU = 0.9623 x 0.9623 = 0.9260).

[2] There were no direct estimates available for these parameters. Values were derived which produced the correct result (e.g., < 5 % of births in winter).

Table 6.4. Population growth rate (*r*) predicted using the model illustrated in Figure 6.4, as regards possums at the Paddys Land site, given three sets of assumptions regarding their breeding biology, and as compared to the predicted *r* at the Orongorongo Valley site. Parameters are defined in Table 6.1. Sources used to determine parameter values are indicated in Tables 6.2 and 6.3. Differences in the parameter values used in the different scenarios regarding the Paddys Land site are shown in bold. The sensitivity of *r* to changes in the value of a given parameter is shown in the final column. Sensitivity was evaluated by varying the parameter by 10 %, using the 'Typical' parameter values for the Paddys Land site as a starting point. Values and results concern females only.

Parameter	Parameter values				Δr given 10 % change in parameter
	Paddys Land			Orongorongo Valley	
		Assumptions regarding breeding biology			
	Average	Best	Typical		
ASA	0.9706	0.9706	0.9706	0.9680	0.1045
ASW	0.8957	0.8957	0.8957	0.9130	0.1118
ASP	0.9740	0.9740	0.9740	0.9623	0.0971
ASU	0.9600	0.9600	0.9600	0.9623	0.0973
PAA	0.9785	0.9785	0.9785	0.9785 [1]	0.0009
PAW	**0.5932**	0.8125	0.8125	0.8240	0.0102
PAP	0.6831	**0.7746**	0.6831	0.6580	0.0121
PAU	0.6831	**0.7746**	0.6831	0.6580	0.0121
PWW	0.9785	0.9785	0.9785	0.9785 [1]	0.0001
PWP	**0.5932**	0.8125	0.8125	0.8240	0.0001
PWU	0.4667	**0.6000**	0.4667	0.4330	0.0002
RYW	0.9785	0.9785	0.9785	0.9785 [1]	0.0002
RYP	**0.5932**	0.8125	0.8125	0.8240	0.0002
RYU	0.4667	**0.6000**	0.4667	0.4330	0.0003
OSA	0.9706	0.9706	0.9706	0.8490	----- [2]
OSW	0.8957	0.8957	0.8957	0.8600	----- [2]
OSP	0.9740	0.9740	0.9740	0.9439	----- [2]
OSU	0.9600	0.9600	0.9600	0.9439	----- [2]
BPA	0.9545	0.9545	0.9545	0.9239	0.0068
BRY	0.9545	0.9545	0.9545	0.3273	0.0002
BPW	0.2500	0.2500	0.2500	0.6000	0.0004
SEX	0.3542	0.3542	0.3542	0.4393	0.0241
MA1	0.0833	0.0833	0.0833	0.0545	0.0012
MA2	0.6667	0.6667	0.6667	0.7494	0.0006
STB	0.2000	**1.0000**	0.2000	0.5484	0.0009
r	-0.1240	-0.0658	-0.0998	-0.0963	

[1] This value was estimated using data from the Paddys Land site (see Table 6.3).

[2] Survival of one-year-olds was assumed to be equivalent to adult survival (e.g., OSA = ASA; see Table 6.2). The sensitivity of *r* to changes in adult survival was calculated by assuming simultaneous changes in the survival of one-year-olds, in which case reporting the sensitivity of *r* to the survival of one-year-olds is redundant.

Table 6.5. Total number of trap-captures per season, in each year, on the two principal study grids.

	Autumn	Winter	Spring	Summer
	1995, 96, 97	1995, 96, 97	1994, 95, 96	1994, 95, 96
West	183, 216, 211	217, 236, 176	59, 160, 100	65, 104, 68
East	135, 199, 177	259, 201, 114	0, 46, 68	133, 107, 37

Table 6.6. Number of times animals were observed to have either lost weight or not lost weight between successive occasions on which they were weighed.

			Autumn 1995, 96, 97	Winter 1995, 96, 97
Weight Loss	Females	West	18, 18, 18	12, 17, 20
		East	14, 16, 8	19, 15, 8
	Males	West	22, 21, 30	19, 34, 31
		East	18, 22, 28	25, 18, 17
No Wt Loss	Females	West	14, 14, 17	39, 38, 30
		East	12, 9, 11	38, 36, 11
	Males	West	17, 22, 16	16, 43, 22
		East	7, 10, 20	20, 28, 22

Table 6.7. Total number of times females were trapped and handled per season, in each year, on the two principal study grids.

	Autumn 1995, 96, 97	Winter 1995, 96, 97	Spring 1994, 95, 96	Summer 1994, 95, 96
West	62, 61, 57	59, 49, 46	19, 57, 23	25, 28, 19
East	52, 47, 35	63, 45, 25	0, 11, 18	68, 21, 10

Table 6.8. Potential predators of common brushtail possums recorded at the Paddys Land site over the three years of the study.

Predator	Latin name	Sightings	Sounds	Signs		
				Scats	Tracks	Other
Wedge-tailed Eagle	(*Aquila audax*)	42				
Dingo (or feral dog)	(*Canis familiaris*)	7	7	2	1	1[1]
Feral cat	(*Felis catus*)	7				
Carpet python	(*Morelia spilota*)	3				
Spotted-tailed quoll	(*Dasyurus maculatus*)	2				
European red fox[2]	(*Vulpes vulpes*)	2 (?)	1 (?)			
Powerful Owl	(*Ninox strenua*)	1				

[1] A juvenile spotted-tailed quoll carcass was found with the skin on the limbs peeled back, which suggests it was killed by a dingo.

[2] Unambiguous evidence of the presence of foxes was never obtained. The animals seen or heard may have been feral dogs. Foxes have never been seen by residents of the area (Len and Winn Perry, pers. comm.). Nor are foxes expected to be in the area based on survey results from the region (Catling and Burt 1995; their Table 2, regarding Chaelundi State Forest, which lies within the GFWA).

Table 6.9. Relationship between the results of tests conducted to determine whether the bandaging wrapped around an individual's radio-collar was inundated with blood, and the condition of the individual's carcass, in 21 of the 22 cases where a radio signal was tracked to a dead female.

Blood on the collar	Carcass Condition if found Intact	Eaten	Not found
Yes	1	7	0
No	10	1	2

Table 6.10. Prevalence and intensity of parasitic infections among the 23 possums from the Paddys Land site that were necropsied, categorized by the fate of the host. Parasite taxonomy and order of presentation follows Viggers and Spratt (1995, their Tables 1 and 3). Prevalence was compared using Fisher's exact test ($p > 0.15$ in all cases). Intensity was compared using a series of t-tests on transformed data. The most appropriate transformation was selected for each species using program BOXCOX (Krebs 1999). Assumptions regarding normality and homogeneity of variances were tested using program STATISTICA (StatSoft, Inc. 1995). I used the Bonferroni method (0.05 / the number of tests) to determine p_{crit}.

Parasite species	Died (6 females, 5 males)			Killed (8 females, 4 males)			Intensity compared between groups ($p_{crit} = 0.0045$)	
	Prevalence	Intensity		Prevalence	Intensity			
	(% of N)	Median	Range	(% of N)	Median	Range	t	p
Endoparasites								
Cestoda								
Anoplocephalidae								
Bertiella trichosuri	64	1	1-8	75	2	1-5	-0.58	0.5688
Nematoda								
Rhabditoidea								
Strongyloididae								
Parastrongyloides trichosuri	91	210	7-1183	92	9	2-146	3.47	0.0026
Trichostrongyloidea								
Herpetostrongylidae								
Paraustrostrongylus trichosuri	100	381	27-1462	100	457	18-4126	-0.62	0.5417
Trichostrongylidae								
Trichostrongylus retortaeformis	58	18	4-99	42	23	3-158	-0.02	0.9814
Female *Trichostrongylus* sp.	0	---	---	8	4	---		
Oxyuroidea								
Oxyuridae								
Adelonema trichosuri	58	2	1-35	75	8	1-246	-1.18	0.2590
Ascaridoidea								
Ascarididae								
Ophidascaris robertsi	8	> 500	---	0	---	---		
Spiruroidea								
Gongylonematidae								
Gongylonema sp.	100	15	4-39	100	14	5-38	0.16	0.8763
Ectoparasites								
Acari (ticks)								
Ixodoidea								
Ixodidae								
Haemaphysalis bancrofti	0	---	---	8	1	---		
Larval ticks	27	1	1-2	33	3	2-7	-2.51	0.0540
Acari (mites)								
Mesostigmata								
Laelapidae								
Trichosurolaelaps crassipes	100	71	7-225	83	15	1-34	3.07	0.0063
Haemolaelaps penelope	18	1	1-1	0	---	---		
Sarcoptiformes								
Atopomelidae								
Atellana papilio	45	14	13-185	67	44	1-500	-0.03	0.9763
Petrogalochirus dycei	27	2	1-3	58	7	1-18	-1.37	0.2086
Murichirus anabiotus	9	2	---	33	12	1-50		
Dasyurochirus longissimus	0	---	---	17	29	8-50		
Echimyopodidae								
Marsupiopus trichosuri	18	12	1-23	0	---	---		
Trombidiformes								
Trombiculidae								
Ascoschoengastia rattus	100	300	20-1155	100	258	35-1615	0.08	0.9409
Guntheria lappacea	9	2	---	0	---	---		
Unidentified Arachnida	36	3	1-12	8	3	---		

Table 6.11. Prevalence and intensity of ectoparasitic infections compared between adult females observed with symptoms of rump wear on at least one occasion, versus females never observed with symptoms of rump wear. Statistical comparisons between groups were undertaken as described in Table 6.10.

Ectoparasite	Rump wear						Intensity compared between groups (p_{crit} = 0.0167)	
	Present			Absent				
	Prevalence	Intensity		Prevalence	Intensity			
	(% of 5)	Median	Range	(% of 9)	Median	Range	t	p
Larval ticks	40	2	1-2	33	2	2-7	-1.81	0.1678
Trichosurolaelaps crassipes	100	153	21-225	89	14	1-73	3.41	0.0058
Ascoschoengastia rattus	100	300	20-895	100	155	35-1615	0.73	0.4788

Table 6.12. Prevalence and intensity of *Parastrongyloides trichosuri* infections, categorized by the fate and condition of the host. Statistical comparisons were undertaken as described in Table 6.10, and are reported in the text.

		Number of hosts	Prevalence (% of N)	Intensity Median	Range
Died	Moribund or dead in a trap	7	100	338	19-1183
	Massive *O. robertsi* infection[1, 2]	1	100	264	---
	"Weak and wobbly" upon release[2]	1	100	51	---
	No symptoms of poor condition	2	50	7	---
Killed	"Weak and wobbly" upon release	1	100	32	---
	No symptoms of poor condition	11	91	9	2-146

[1] This animal was also observed to be "weak and wobbly" upon release.

[2] These animals were also observed to be both "rumpy" and "bony".

Table 6.13. Mean (and S.E.) age in years, as determined from cementum annuli, among the 23 possums that were necropsied, categorized by fate (Died versus Killed) and sex. The mean age (and S.E.) among "Known fate" individuals was determined by pooling the age data for necropsied animals with age data concerning an additional 11 animals (10 females, 1 male) that could also be categorized by fate. I analyzed the data regarding necrospied and known fate samples separately, but in both cases I conducted a two-way ANOVA of the effects of fate and sex on transformed age data. The most appropriate transformation was selected using program BOXCOX (Krebs 1999). Assumptions regarding normality and homogeneity of variances were tested using program STATISTICA (StatSoft, Inc. 1995).

		Age (years)					
			Died			Killed	
		N	Mean	S.E.	N	Mean	S.E.
Necropsied [1]	Females	6	8.5	2.3	8	6.4	1.3
	Males	5	6.0	1.1	4	5.8	1.3
Known fate [2]	Females	13	8.4	1.1	11	6.2	1.1
	Males	5	6.0	1.1	5	5.6	1.0

[1, 2] The results of a two-way ANOVA indicated there were no main effects of fate or sex on age, and there was no significant interaction ($p > 0.50$ in all cases).

Table 6.14. Observed number of individuals in each of two age classes, among 38 possums aged from cementum annuli, as compared to the expected number in each class if survival is assumed to be 81.3 % per annum. The observed, or expected, number of 8-year-olds was divided equally between the two age classes. The observed and expected frequencies were compared using all available data from both sexes, using data from females only, and using data from Killed females only. Observed and expected cell frequencies were compared by means of a two-tailed binomial test (as recommended by Zar 1996, p. 466), using program NCSS (Hintze 1996).

		Age class (years)		p
		2 to 8	8 to 14	
Both sexes	Observed	25	13	0.0470
	Expected	30.1	7.9	
Females	Observed	15	10	0.0255
	Expected	19.8	5.2	
Killed females	Observed	8	3	0.7082
	Expected	8.7	2.3	

Table 6.15. Seasonal survival of radio-collared adult females (1997 data excluded), under four scenarios regarding the treatment of censored data, and the effects on the value of *r* predicted by the model of possum demography (assuming 'Typical' parameter values for the Paddy Land site).

Categories excluded	Censored		Dead	Seasonal survival				Predicted
	Category	Cumulative		Autumn	Winter	Spring	Summer	*r*
Killed in trap	1	1	17	0.9706	0.8957	0.9740	0.9600	-0.0998
Moribund/dead in trap	2	3	15	0.9889	0.9061	0.9740	0.9600	-0.0699
"Weak and wobbly"	4	7	11	0.9889	0.9510	0.9740	0.9600	-0.0207
"Rumpy" and "bony"	2	9	9	0.9889	0.9610	0.9740	0.9733	0.0015

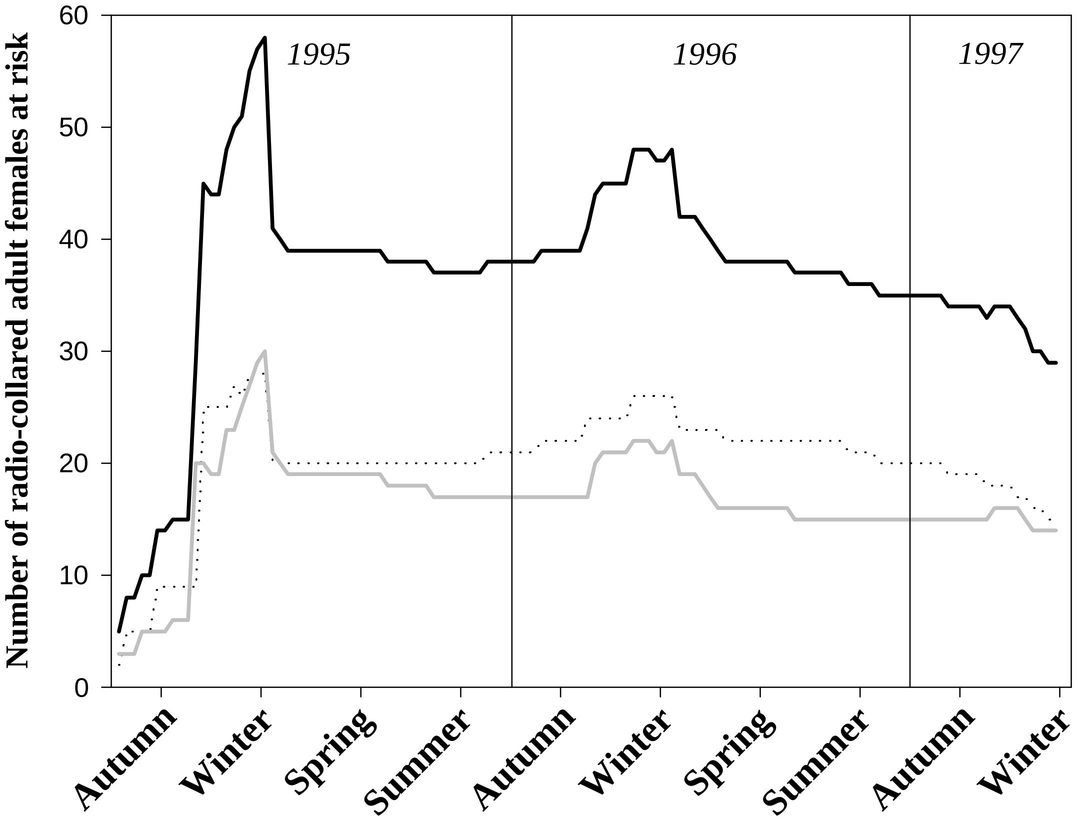

Figure 6.1. Number of radio-collared adult females at risk, from the beginning of autumn 1995, until the end of the study in July 1997. The solid black line indicates the total number at risk on both grids. The dotted line signifies the number at risk on the West grid, while the grey line represents the number at risk on the East grid.

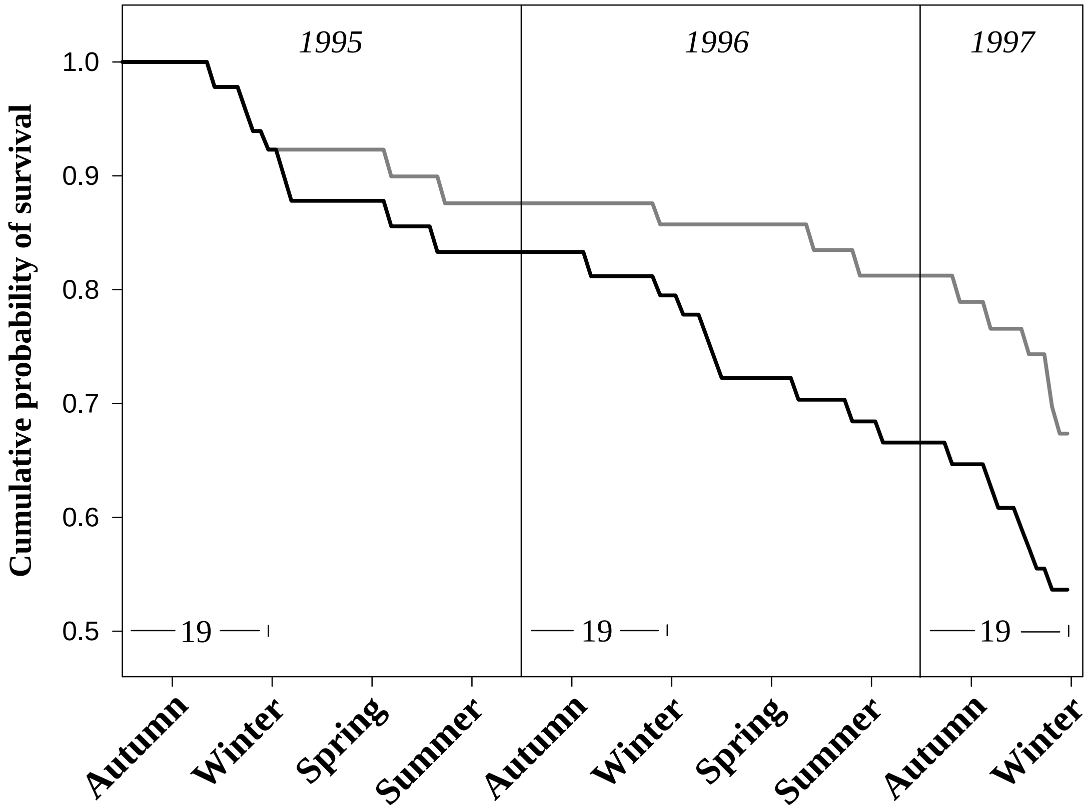

Figure 6.2. Cumulative probability of survival of radio-collared adult females, based on the Kaplan-Meier estimator, modified for staggered entry. The solid black line indicates survivorship when all apparently "natural" deaths (N = 24) are included, while the grey line signifies survivorship when otherwise inexplicable deaths (those not attributable to predation or parasitic infection) among moribund, "weak and wobbly", and "rumpy" and "bony" females (N = 9), are treated as "right-censored".

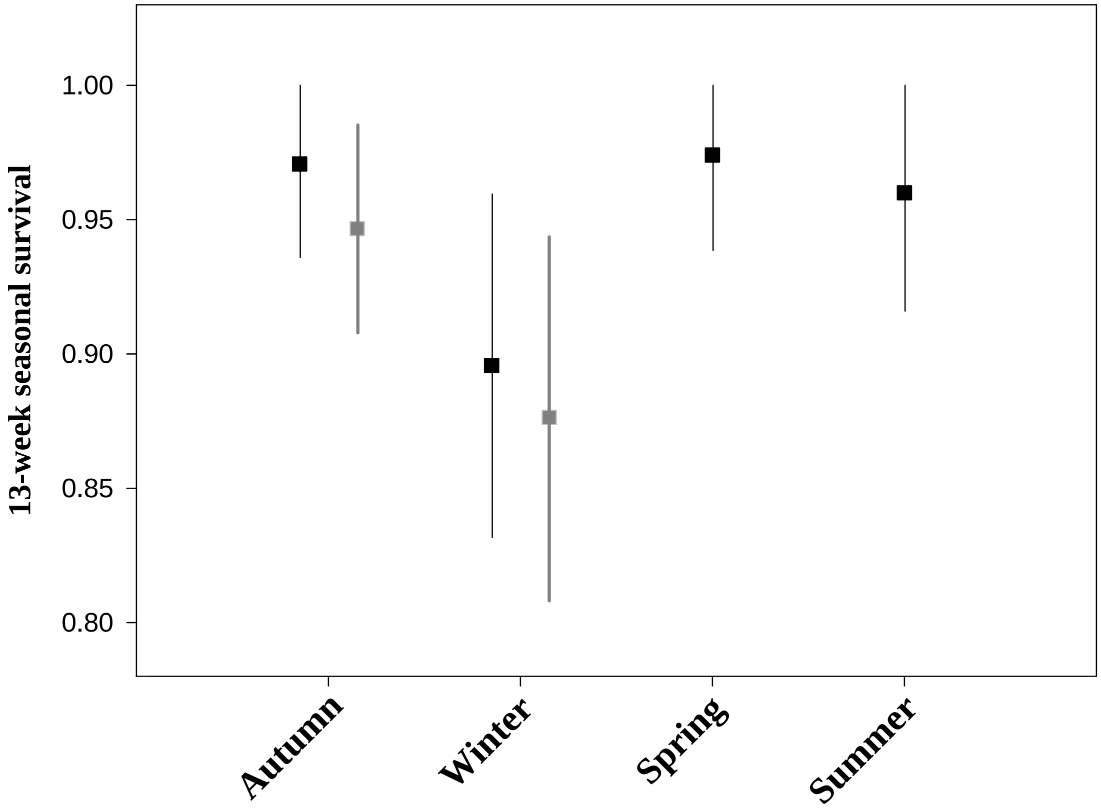

Figure 6.3. Thirteen-week seasonal survival of radio-collared adult females, based on the Kaplan-Meier estimator, modified for staggered entry. Squares indicate cumulative survival. Vertical lines signify 95 % confidence limits calculated using Equation 3 from Pollock et al. (1989). Values in black are based on pooled data from 1995 and 1996, while values in grey are based on pooled data from 1995, 1996 and 1997.

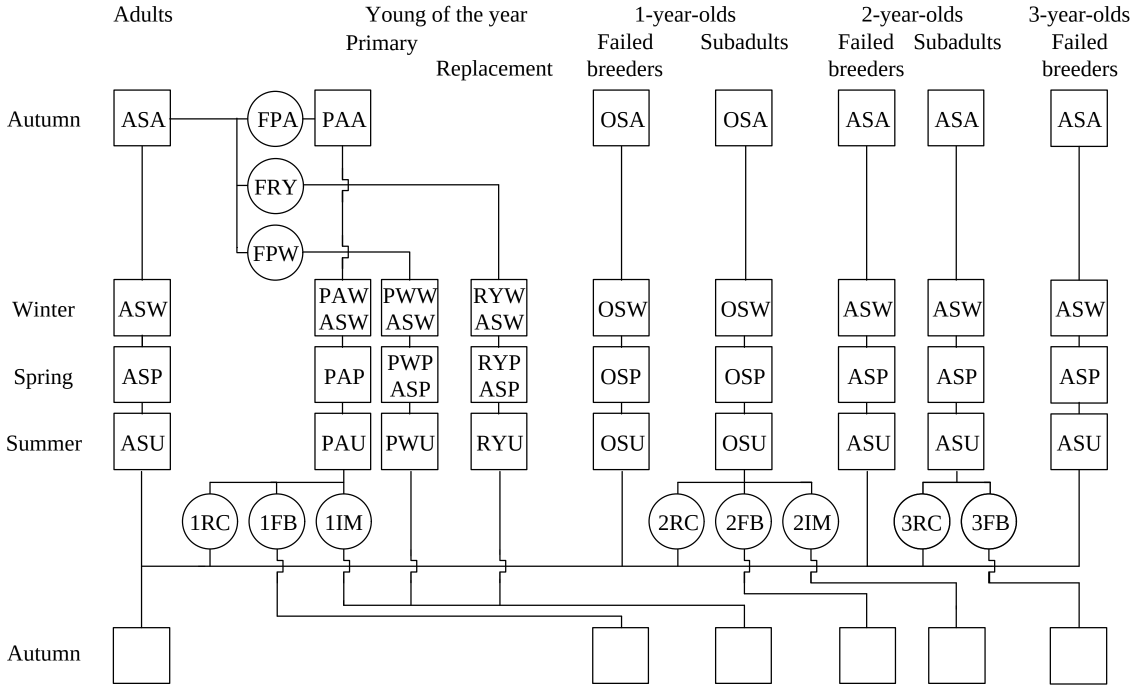

Figure 6.4. Structure of the model of possum demography. Boxes represent a given age-class in a given season subject to the survival probabilities indicated in the box. Circles represent decision-trees regarding births and maturation, with the probability of a given outcome indicated in each circle. Parameters are defined in Table 6.1. The population growth rate (*r*) is calculated based on the number of adult females alive at the beginning of autumn.

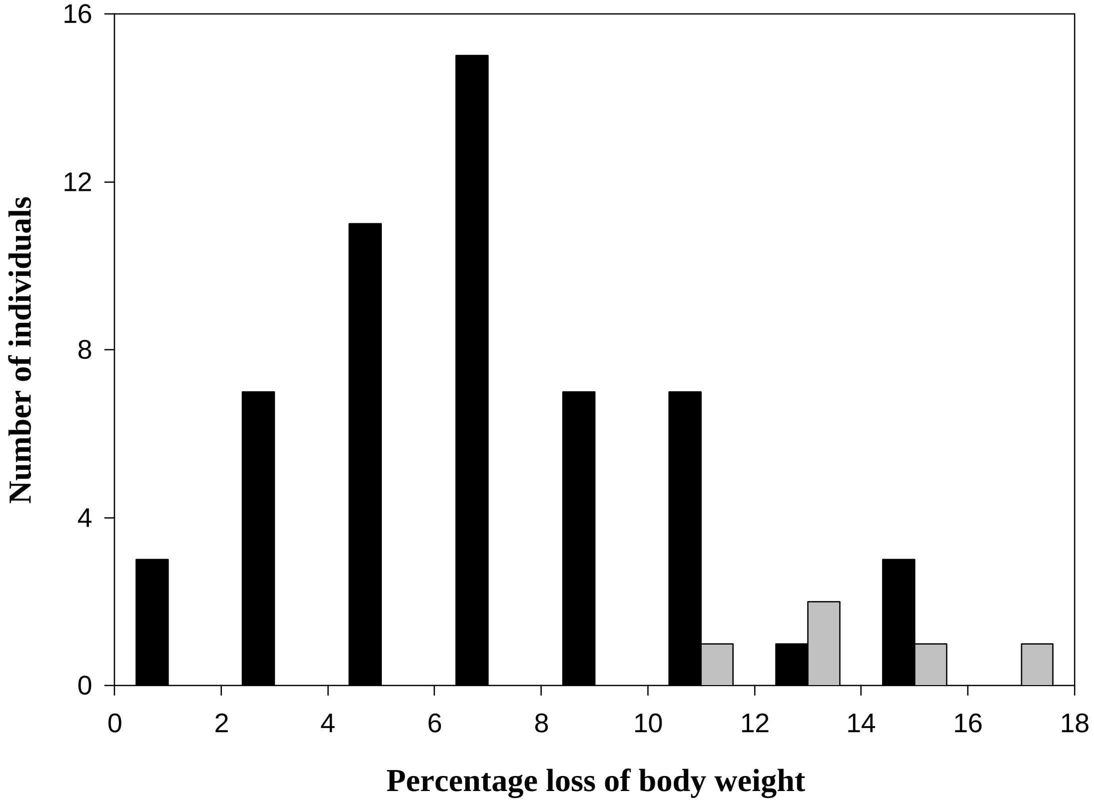

Figure 6.5. Number of individuals demonstrating a given rate of proportionate weight loss, measured as the percentage of body weight lost within 5 days, among: possums found moribund or dead in a trap (in grey) and apparently healthy animals (in black).

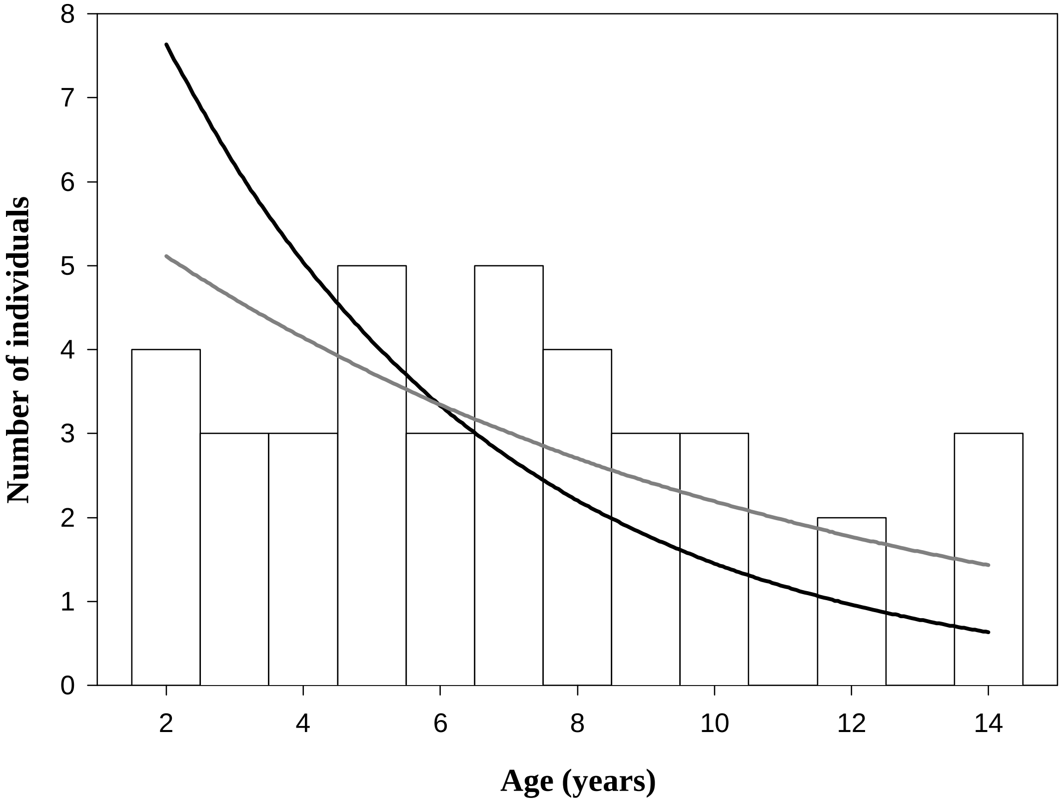

Figure 6.6. Number of individuals (N = 38) aged 2 to 14 years (open bars), as determined from cementum annuli, compared to the expected frequency distributions (given 38 individuals) if survival is assumed to be either 81.3 % (black line), or 89.9 % (grey line), per annum.

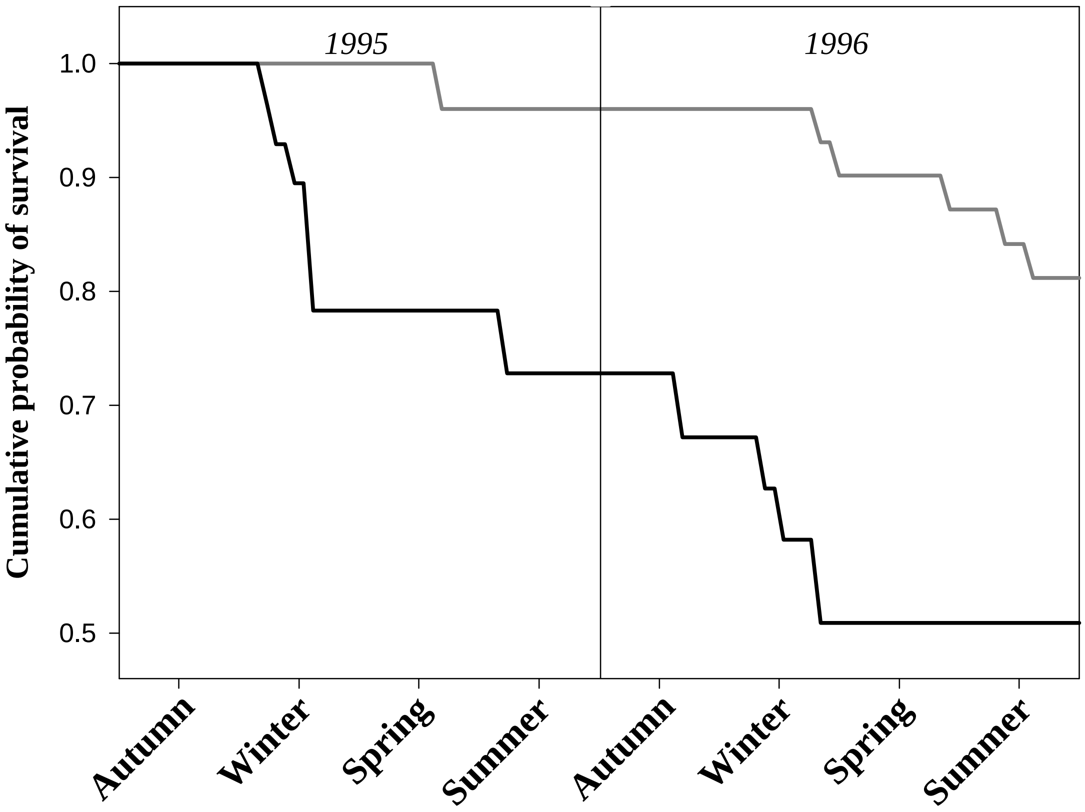

Figure 6.7. Cumulative probability of survival of radio-collared adult females categorized by median handling interval, based on the Kaplan-Meier estimator, modified for staggered entry. The solid black line indicates survivorship among females with a median handling interval of less than 42 days (N = 35), while the grey line signifies survivorship among females with a median handling interval of more than 42 days (N = 35).

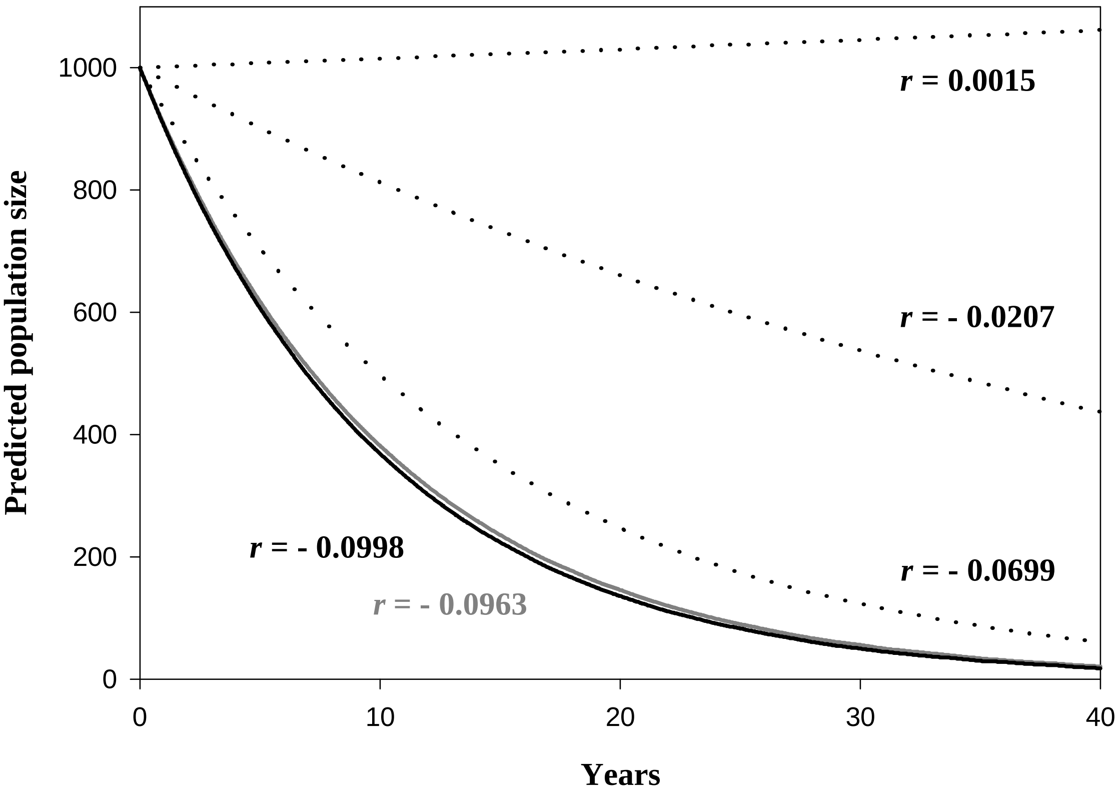

Figure 6.8. Change in population size with time (in years) predicted given five different population growth rates (*r*). The solid black line concerns the value of *r* predicted by the model of possum demography, given 'Typical' parameter values for the Paddys Land site, while the grey line indicates that for the Orongorongo Valley site (Table 6.4). The three dotted lines indicate outcomes under each of three scenarios regarding the treatment of "censored" deaths, as discussed in Table 6.15.

CHAPTER 7

CONCLUSIONS AND IMPLICATIONS FOR CONSERVATION

My conclusion is that immigration does not often “rescue” common brushtail possum populations from extinction. I argued in Chapter 4 that this likely also applies to other species of medium-sized, herbivorous, marsupials. In this Chapter, I discuss broader issues regarding the decline of medium-sized mammals in Australia, and the conservation of those that are left.

Morton (1990) proposed that mammalian herbivores in Australia had a naturally patchy distribution, and that declines and extinctions resulting from the disturbances associated with European settlement were more prevalent among medium-sized mammals because: 1) they were more likely to be locally extirpated than smaller mammals because of their lower rates of natural increase; and 2) they were less likely than larger mammals to be “rescued” by immigration because of their poorer dispersal abilities. I conclude that medium-sized mammals would take a very long time to re-occupy any patch from which they were extirpated (Chapter 4), and I suggest that this reinforces Morton’s (1990, p. 210) conclusion that active reintroductions will have to be an essential part of any recovery plan for these species.

Morton (1990, p. 206) used Hanski’s (1985, see also Hanski 1991) ideas about the importance of immigration in “rescuing” populations from extinction as a way of explaining the fact that many of the medium-sized mammals that declined disappeared very rapidly from large parts of their range. As noted in Chapter 1, in some Levins-type metapopulation models a positive feedback relationship is apparent between the proportion of occupied patches and metapopulation persistence because the greater proportion of occupied patches entails a greater exchange of immigrants between occupied patches, which assumedly “rescues” the recipient populations from extinction, and thereby lowers the global probability of extinction (Hanski 1991). As a corollary, if the proportion of occupied patches falls below a certain threshold, the metapopulation “collapses”, and all populations go to extinction. I conclude that since the exchange of immigrants between extant populations probably never played a significant role in “rescuing” populations of medium-sized, marsupial, herbivores from extinction (Chapter 4), Hanski’s (1991) metapopulation model cannot be used to explain the rapidity with which these species disappeared.

Morton's (1990) conceptual model regarding the decline of medium-sized mammals considers the effects of anthropogenic disturbances, such as the introduction of livestock, rabbits and foxes, in light of issues concerning life history and connectivity. My conclusion is that issues regarding dispersal and connectivity are of little relevance except when discussing very long time periods (Chapter 4). Instead, I suggest that issues regarding life history are of much greater relevance. Common brushtail possums, and other medium-sized, herbivorous, marsupials demonstrate a pattern of life history involving low fecundity and high survivorship (Chapters 5 and 6) generally considered to be characteristic of larger mammals (Lee and Cockburn 1985, Sinclair 1996), particularly large ungulates (Gaillard et al. 1998). I like to call this the "never say die" strategy. In response to a severe mid-winter drought at the Paddys Land site in 1995 (Fig. 5.7), most possum females lost their pouch-young (Table 5.4) and also lost about 10 % in body weight (Table 5.10), but there was no difference in female survivorship between 1995 and 1996 (Fig. 6.2), the latter being an extremely wet year (Fig. 5.7). Sinclair (1996, p. 131) proposed that this type of life history strategy centered on physiological adaptations to food supply. Part of the reason (Sinclair 1996, p. 129) for why this strategy appears to be more prevalent among medium-sized marsupials than among medium-sized eutherians may be because marsupials have lower metabolic rates (Lee and Cockburn 1985). The other reason is that a precondition for this strategy is that adult mortalities due to predation must be comparatively infrequent (Sinclair 1996, p. 137). This would appear to be the "natural" state of affairs in Australia, as prior to the introduction of the dingo 5,000 years ago (Strahan 1995), there was only one species of large terrestrial predator that was present throughout Australia, which was the wolf-like *Thylacinus cynocephalus*, and this species was probably never very numerous (Guiler 1991).

Morton (1990) argued that the introduction of cats (*Felis catus*) and foxes (*Vulpes vulpes*) to Australia is not a sufficient explanation for the decline of medium-sized mammals. Instead, Morton emphasized the interaction between introduced herbivores and predators. Aside from the wholesale habitat destruction accompanying the introduction of domestic livestock, Morton proposed that native mammals were made more vulnerable to predation by the removal of cover as a result of overgrazing by livestock. Overgrazing by introduced rabbits (*Oryctolagus cuniculus*) would have the same effect. More importantly, the great abundance of rabbits, together with carrion from domestic livestock, provided abundant food to sustain large numbers of cats, foxes, and probably dingos as well. Because medium-sized, herbivorous, marsupials have intrinsic rates of increase that are so much lower ($r_m \cong 0.9$, Sinclair et al. 1998) than that of the rabbit ($r_m \cong 2.2$, Sinclair 1996) they cannot sustain the same rate of "harvest" by predators (Caughley and Sinclair 1994) as rabbits can, and predator-prey theory predicts that they will be driven to extinction by predators that rely primarily on eating rabbits (Sinclair et al. 1998). As the model of possum demography presented in Chapter 6 demonstrates (Table 6.4), even comparatively small increases in adult mortality are sufficient to put populations of medium-sized, herbivorous, marsupials into a tailspin (Fig. 6.8). In Chapter 5, I reported that the demography of possum populations in formerly forested areas of Australia, that have been fragmented and disturbed, most closely resembles that of possum populations in New Zealand that are subject to human harvesting, and I argued that this is most likely because possums in fragmented and disturbed areas are being "harvested" by cats and foxes and dingos.

I propose that the ecology of common brushtail possums in undisturbed wilderness areas, such as at the Paddys Land site, most closely resembles that which existed prior to the European settlement of Australia. Population characteristics under these conditions include: 1) > 90 % per annum adult survival (Chapter 6); 2) low fecundity; and 3) delayed maturation (Table 5.1). Moving out from wilderness areas into the formerly forested, but now fragmented and disturbed areas that surround the few remaining wilderness areas, the resident possum populations are subject to a greater rate of harvesting by introduced predators. As is typical of harvested populations (Caughley and Sinclair 1994) poor survivorship is compensated for by increased reproduction (Table 5.1). Since these populations are subject to harvesting, densities will be lower (Caughley and Sinclair 1994) than in wilderness areas (Chapter 5), but the populations are not extirpated because the animals are still able to find refuge from predators in the remaining trees. Moving inland into regions where possums existed in treeless landscapes, in which there was no refuge from introduced predators, the resident populations would be overharvested and eventually extirpated, as was the case.

I predict that predator removal experiments in wilderness areas would have little or no effect on survivorship (Chapter 6) and resulting densities of common brushtail possums, while food addition experiments in wilderness areas would increase adult fecundity, lower the age at first breeding, and lead to higher densities (Chapter 5). On the other hand, I predict that predator removal experiments in fragmented and disturbed areas should increase survivorship and thereby increase densities, while food addition experiments in these areas would have little effect on reproduction, and resulting densities. If possums are primarily food limited in wilderness areas and primarily predator limited in fragmented and disturbed areas, adults in wilderness areas are likely to be in poorer condition. The fact that possums at the Paddys Land site had more parasites than possums at any of the other sites surveyed by Obendorf et al. (1998, Chapter 6) is consistent with the prediction that possums in wilderness areas are in poorer condition, as the Paddys Land site was the only site in a wilderness area among those sites surveyed by Obendorf et al. (1998). Food limited, energetically stressed possums in poor condition will likely be more adversely affected by cold and wet weather, leading to a premium being placed on finding suitable shelter. The competition for prime den sites evident at the Paddys Land site (Chapter 4) is consistent with this suggestion. I predict that the provision of artificial nest boxes would increase both survivorship and reproduction, and lead to higher densities, in wilderness areas, while having little effect in fragmented and disturbed areas.

I propose that common brushtail possums can be used as an “indicator species” in conservation plans for other medium-sized, herbivorous, marsupials. Many unsuccessful attempts have been made to reintroduce medium-sized, herbivorous, marsupials to parts of their former range, and for the most part the cause of these failures has been attributed to introduced predators (Short et al. 1992, Sinclair et al. 1998). There are three reasons why I think possums would make a good indicator species. Firstly, as discussed in Chapter 4, the life history of all these species is all very similar. Secondly, since possums historically occupied 94 % of Australia (How and Kerle 1995), there are no presently threatened or endangered species of medium-sized mammal with which they did not co-occur. Thirdly, since possums can find refuge in trees while their terrestrial counterparts cannot, possums will always be more resistant to the adverse effects of harvesting by introduced predators (Chapter 5). If possums are flourishing at a site, this can be taken as necessary but not sufficient evidence that other species will also do well. In conjunction with the five protocols for experimental reintroductions proposed by Sinclair et al. (1998), I propose that: 1) if possums do not already exist at the chosen site, attempts should first be made to reintroduce possums; 2) sites at which possums have persisted should be chosen over those sites where both the target species and possums have been extirpated; and 3) sites where possums demonstrate the type of high survival - low fecundity characteristics as observed at the Paddys Land site (Chapter 5 and 6), should be chosen over sites where possums demonstrate low survival - high fecundity characteristics. I suggest that this last criterion is the most important. Once-off samples in autumn and spring, checking reproductive status and taking a single tooth for ageing, ought to suffice to establish the likely pattern of demography (Table 5.1, Fig. 6.6). As described above, I suspect that high survival - low fecundity possum populations will now generally only be found in wilderness areas. If this is so, then wilderness areas are the logical place to attempt reintroductions.

The principal value of wilderness areas as potential sites for reintroductions lies in the lower density of introduced terrestrial carnivores, as compared to fragmented and disturbed sites (Catling and Burt 1995, Sinclair et al. 1998). It is clear that, in Australia at least, fragmenting a previously undisturbed site leads to increased densities of predators, and a greater harvest of native prey by the introduced predators. As discussed in Chapter 5, strictly terrestrial species will be more vulnerable to predation, while species such as possums that can find refuge in the trees retained in wood lots and travelling stock routes (TSRs) will likely persist, although the demography of possum populations in these areas indicates that they too are subject to harvesting by introduced predators. The connectivity provided by TSRs, or other linear strips of habitat specifically designed to be movement corridors, may be of value, but only at time scales measured in decades and centuries (Chapter 4). If cats and foxes and dingos have eaten everything in sight by that time, connectivity will not much matter. As noted in Chapter 1, a large number of studies have been conducted involving presence/absence surveys of native Australian mammals in TSRs, and these feature prominently in the literature on connectivity (Beier and Noss 1998). I suggest that TSRs are where all the native mammals are found because this is the only place they have to hide from all the introduced terrestrial carnivores.

The idea that it is possible to “creatively fragment” (Laurance and Gascon 1997) an existing natural landscape in a way that is expected to attenuate the adverse effects of land clearance through the retention of movement corridors is, at best, an overgeneralization of metapopulation dynamics theory. On the one hand, this suggestion focuses on connectivity and ignores edge effects, such as those associated with increases in the density of predators, and greater vulnerability of prey. At least as important is the fact that such overgeneralizations of metapopulation dynamics theory ignore the life history of the affected species. The “never say die” type of life history typical of medium-sized, herbivorous, marsupials appears to be the antithesis of that expected of a “good” colonizing species (*sensu* McArthur and Wilson 1967). Medium-sized, herbivorous, marsupials appear to be much more well-adapted for tenacious persistence within suitable patches. Laurance and Gascon’s (1997) argument that it possible to “creatively fragment” previously undisturbed landscapes as part of logging operations, was based in part on Laurance’s (1990) survey work in Australia on four species of possums, including the common brushtail possum. From the preceding discussion, I conclude that this idea has no merit with respect to possums, or any other medium-sized, herbivorous, marsupial.

I chose to focus on the question: does immigration “rescue” populations from extinction? My reason for choosing this question is that I think dispersal is generally such an important process that more attention should be given to the details surrounding it. I chose to study dispersal in medium-sized, herbivorous, marsupials in the hope that my work might be of relevance to the conservation of this very threatened group of species, and because so little information existed about the role of dispersal in this group.
I find it ironic that my conclusion should be that dispersal is of little relevance to the population ecology of medium-sized, herbivorous, marsupials.

REFERENCES

Beier. P., and Noss, R. F. 1998. Do habitat corridors provide connectivity? Conservation Biology, 12: 1241-1252.

Catling, P. C., and Burt, R. J. 1995. Why are red foxes absent from some Eucalypt forests in eastern New South Wales? Wildlife Research, 22: 535-546.

Caughley, G., and Sinclair, A. R. E. 1994. Wildlife ecology and management. Blackwell Science, Cambridge, Massachusetts.

Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N. G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution, 13: 58-63.

Guiler, E. 1991. The Tasmanian tiger. St David's Park Publishing, Hobart, Australia.

Hanski, I. 1985. Single-species spatial dynamics may contribute to long-term rarity and commonness. Ecology, 66: 335-343.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society, 42: 17-38.

How, R. A., and Kerle, J. A. 1995. Common brushtail possum. *In* The mammals of Australia. *Edited by* Strahan, R. Reed Books, Sydney, Australia, pp. 273-275.

Laurance, W. F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. Journal of Mammalogy, 71: 641-653.

Laurance, W. F., and Gascon, C. 1997. How to creatively fragment a landscape. Conservation Biology, 11: 577-579.

Lee, A. K., and Cockburn, A. 1985. Evolutionary ecology of marsupials. Cambridge University Press, Cambridge.

MacArthur, R. H., and Wilson, E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Morton, S. R. 1990. The impact of European settlement on the vertebrate animals or arid Australia. Proceedings of the Ecological Society of Australia, 16: 201-213.

Obendorf, D., Spratt, D., Beveridge, I., Presidente, P., and Coman, B. 1998. Parasites and diseases in Australian brushtail possums, *Trichosurus* spp. Royal Society of New Zealand Miscellaneous Series, 45: 6-9.

Short, J., Bradshaw, S. D., Giles, J., Prince, R. I. T., and Wilson, G. R. 1992. Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia - a review. Biological Conservation, 1992: 189-204.

Sinclair, A. R. E. 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. *In* Frontiers of population ecology. *Edited by* Floyd, R. B., Sheppard, A. W., and DeBarro, P. J., CSIRO Publishing, Melbourne, Australia, pp. 127-154.

Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D, Mahon, P., and Newsome, A. E. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology 12: 564-575.

Strahan, R. 1995. The mammals of Australia. Reed Books, Sydney, Australia.

APPENDIX 1

ASSUMPTIONS UNDERLYING THE ANALYSIS OF MICROSATELLITE DNA

Introduction

In this Appendix, I report and discuss tests of assumptions underlying the results regarding the analysis of microsatellite DNA, reported in Chapter 4. Details regarding tissue samples, identification of microsatellites, and software used in the following analyses, were presented in Chapter 4.

Linkage disequilibrium and deviations from Hardy-Weinberg equilibrium (HWE)

Table 4.9 lists allele frequencies and the size of each allele at each locus. I conducted exact tests for genotypic linkage disequilibrium at each pair of loci, using frequency data from both grids, both combined and separately (Becher and Griffiths 1998, Piertney et al. 1998). There were no significant pairwise comparisons when data from both grids were combined (15 comparisons; $p > 0.05$ in all cases). Two pairwise comparisons (out of 15) were significant (Tv19 vs. Tv27, and Tv19 vs. Tv58; $0.05 > p > 0.01$) on the West grid, while none (out of 15) were significant on the East grid. Given that, the results regarding the West grid were not significant when corrected for the number of independent comparisons (Bonferroni-corrected value of *alpha* = 0.05/15 = 0.003; Sokal and Rohlf 1995, p. 240), and that there was no consistent result between the grids, I conclude that linkage equilibrium across all six loci could not be rejected (Becher and Griffiths 1998, Piertney et al. 1998). Consequently, each locus can be treated as an independent replicate when combining probabilities to test for differences in allelic frequencies between grids (Table 4.9), or when calculating the probability of exclusion between putative parents and offspring (Table A1.3).

I conducted exact tests for deviation from Hardy-Weinberg equilibrium (HWE) at each locus (Table A1.1), using genotypic frequency data from both grids, both combined and separately (Becher and Griffiths 1998, Piertney et al. 1998). Using pooled data from both grids, 2 of the 6 loci (Tv16 and Tv53) showed significant deviations from HWE, and the combined probabilities test across all loci was highly significant. When analyzed by grid, Tv16, Tv53, and the combined probabilities test, all showed significant deviations from HWE on the West grid, but not on the East grid (Table A1.1). Population subdivision is one of the many potential causes of deviation from HWE (Hartl 1988), and as reported in Chapter 4, there were significant allelic frequency differences between the grids (Table 4.9).

One of the many potential causes of deviations from HWE is the presence of null alleles (Hartl 1988, Pemberton et al. 1995). Null alleles are alleles which are not amplified during PCR, apparently because of nucleotide sequence variation in the primer annealing sites flanking the microsatellite (Van Treuren 1998). The likely presence of null alleles at a locus can be evaluated by: 1) a significant deviation from HWE resulting from an excess of homozygotes; and 2) mismatches between known parents and offspring at the locus in question (Pemberton et al. 1995, Van Treuren 1998). Positive values of the null allele frequency estimate shown in Table A1.1 indicate an excess of homozygotes at a locus, while negative values indicate an excess of heterozygotes (Marshall 1998). According to Marshall (1998), if the null allele frequency estimate is greater than 0.05, null alleles are likely present. The Tv16 locus showed both a significant deviation from HWE, and a null allele frequency estimate greater than 0.05, on the West grid, but not on the East grid (Table A1.1). If null alleles are present at a locus, deviations from HWE and null allele frequency estimates ought to be consistent across populations (Becher and Griffiths 1998, Van Treuren 1998). Moreover, the suspected presence of null alleles on the West grid did not correspond with the fact that there were no mismatches between mother and young from among the 16 known young on the West grid that were successfully typed at the Tv16 locus (the one known young, among the 17 on the West grid, that was not successfully typed at the Tv16 locus, was only typed at 2 of 6 loci). I conclude that there is no consistent and compelling reason to believe that there is a high incidence of null alleles at the Tv16 locus.

Deviations from HWE involving an excess of homozygotes are also to be expected if the population contains more closely-related relatives than would be predicted by chance (Hartl 1988). The tests for deviation from HWE shown in Table A1.1 include data from 27 known mother-young pairs. There were more known mother-young pairs included in the data from the West grid (17) than in the data from the East grid (9), which may explain the differences between the grids shown in Table A1.1. However, the presence of known mother-young pairs was not sufficient to explain the observed deviations from HWE, as significant deviations from HWE were still apparent when known young were excluded (not shown). On the one hand, the fact that there were still significant deviations from HWE when known young were excluded could be interpreted as evidence of strong female philopatry, given that an excess of homozygotes is to be expected if there are a greater number of mother-daughter pairs among the adult (and subadult) females than would be predicted by chance alone, because daughters always settle on or adjacent to their mother's home range. On the other hand, the presence of significant deviations from HWE violates one of the assumptions underlying the calculations used in one of the two programs (CERVUS) used to conduct parentage analysis, as described in the next section, making it more difficult to test the strength of female philopatry.

Parentage analysis

I conducted parentage analysis using both program KINSHIP, Version 1.2 (Goodnight and Queller 1998), and program CERVUS, Version 1.0 (Marshall 1998). Program KINSHIP analyses parentage based on: 1) the principle of exclusion; and 2) the likelihood of relatedness by descent. The principle of exclusion is based on the simple rules of Mendelian segregation, whereby in sexually-reproducing diploid organisms, parents and offspring must possess one allele in common at every locus (Hartl 1988). Any putative parent that does not share an allele with a putative offspring at any and all loci is excluded from being the true parent. If there is more than one non-excluded putative parent, the likelihood of relatedness of each putative parent, as compared to the putative offspring, is calculated as a function of the uniqueness (as compared to the allelic frequency in the population) of the putative parent's alleles, in comparison with that of the putative offspring's alleles. The relatedness calculations used in program KINSHIP are explained in Queller and Goodnight (1989). Blouin et al. (1996) confirmed the accuracy of Queller and Goodnight's (1989) relatedness estimates using lab-reared house mice (*Mus musculus*) with known pedigrees. Program CERVUS calculates parentage based solely on the likelihood of relatedness by descent as determined from genotypic frequencies. Program CERVUS was designed to try to circumvent the fundamental flaw in the principle of exclusion, which is that data are assumed to be error-free. Because errors do occur during typing (as well as during data input, etc …) true parents and offspring may not always share an allele in common, and the principle of exclusion would lead to the conclusion that such individuals were not in fact parent and offspring. Program CERVUS simulates the effects of typing errors on genotypic frequencies and then calculates the likelihood of relatedness by descent.

The calculations underlying program KINSHIP are based on allelic frequencies rather than genotypic frequencies and are therefore robust to the conventional causes of deviation from HWE associated with non-random mating, natural selection, etc… (Queller and Goodnight 1989, p. 260). However, deviations from HWE associated with null alleles are of concern because the presence of null alleles can lead to apparent mismatches (no allele in common) between true parents and offspring (Pemberton et al. 1995). Deviations from HWE associated with null alleles are not of concern when using program CERVUS, which treats null alleles like any other form of typing error (Marshall et al. 1998). However, since the calculations underlying program CERVUS are based on genotypic frequencies, program CERVUS is sensitive to the conventional causes of deviation from HWE associated with non-random mating, natural selection, etc… (Marshall et al. 1998). Only if non-random mating (or natural selection, etc …) were specifically associated with a null allele, would it be possible for similar biases to appear in both program KINSHIP and program CERVUS. Consequently, I conclude that if both approaches to parentage analysis lead to the same inference, the result ought to be considered robust with respect to the observed deviations from HWE (Table A1.1).

Table A1.2 lists the 27 known mother-young pairs of possums from the Paddys Land site that were successfully typed. Table A1.2 shows the known young, its true mother, the number of loci at which mother and young were compared, and the number of mismatches (no alleles in common) between mothers and young. On the West grid, 17 known young were compared against their mothers at a total of 87 loci (average number of loci typed per individual = 5.1), and there were 2 loci at which the known young and its mother did not share an allele. On the East grid, 10 known young were compared against their mothers at a total of 47 loci (average number of loci typed per individual = 4.7), and there were 3 loci at which the known young and its mother did not share an allele. The proportion of loci demonstrating mother-young mismatches was not significantly different between the two grids ($\chi^2 = 1.30$, df = 1, p = 0.2542). Marshall et al. (1998) provide equations for calculating an error rate as a function of the number of mismatches between known mothers and young, and the average probability of exclusion at each locus (Table A1.3). Using Marshall et al.’s (1998) method, the error rate was estimated to be 0.01311 on the West grid, and 0.04435 on the East grid. Marshall et al. (1998) suggest that a 1 % (= 0.01) error rate is likely typical in large-scale screening of microsatellites, and they conducted simulations under a “typical” range of typing errors of from 1 to 4 % (= 0.04). I conclude that the error rate observed at the Paddys Land site was in no way unusual.

The effect of errors is simulated in program CERVUS by choosing genotypes at random and replacing them with genotypes selected under Hardy-Weinberg assumptions, in which case rare genotypes tend to be replaced by common ones (Marshall et al. 1998, p. 650). Because the error simulation routine in program CERVUS acts to homogenize genotypes, Marshall et al. found that the ability to discriminate among putative parents was strongly influenced by the estimated error rate. In contrast, SanCristobal and Chevalet (1997) found that the accuracy of parentage analysis was relatively insensitive to the estimated error rate. Notably, SanCristobal and Chevalet's error simulation routine was substantially different from Marshall et al.'s. SanCristobal and Chevalet conducted simulations whereby they replaced randomly chosen alleles with other randomly chosen alleles, regardless of allelic frequencies. SanCristobal and Chevalet's error simulation routine does not rapidly homogenize genotypes in the way that Marshall et al.'s does. SanCristobal and Chevalet found that, while allowing for errors (i.e., any non-zero error rate) significantly improved the accuracy with which known parents were identified in comparison with a conventional exclusion analysis (i.e., assuming no errors), the actual value of the error rate could be varied over an order of magnitude with no effect on accuracy. SanCristobal and Chevalet (1997, p. 59) commented that a more realistic approach than the random substitution method they employed would be to assume that the rates of substitution between alleles are a function of their physical size. SanCristobal and Chevalet then argued that, since random substitution would lead to readily apparent errors, while size substitutions would be more likely to be overlooked, the random substitution simulation they employed was likely too conservative.

I compared the accuracy with which program KINSHIP and program CERVUS were able to identify the known mother-young relationships listed in Table A1.2. There were 34 adult females (not including the subadult immigrant female, W-AE) successfully typed on the West grid (listed in Table 4.10), and 33 adult females successfully typed on the East grid (listed in Table 4.11). Each known young was compared against all adult females from the same grid, and the adult female with the highest likelihood score was judged to be the most likely mother (SanCristobal and Chevalet 1997).

On the West grid, program KINSHIP correctly identified 15 of the 17 known mothers (Table A1.2). In the remaining two cases the known mother and young were mismatched at a single locus, and program KINSHIP consequently excluded the true mother. At the same time, program KINSHIP also excluded all of the other 33 adult females on the West grid (Table A1.2). Hence, while KINSHIP falsely rejected the known mothers this did not lead to “false positives”, where another female was incorrectly identified as the most likely mother. Excluding all individuals, including the true mother, is a form of Type II error (or error of underestimation), leading to the conclusion that there is no relatedness structure in the population, when there really is. On the other hand, “false positives” are not only: 1) a form of Type I error (or error of overestimation), leading to the conclusion that there is an abundance of evidence indicating relatedness structure in the population when there really is not; but they may also 2) generate false impressions regarding the nature of the putative relatedness structure.

On the East grid, program KINSHIP correctly identified only 4 of the 10 known mothers (Table A1.2). Three of the 10 known mother-young pairs on the East grid were mismatched at a single locus, causing program KINSHIP to exclude the true mother. In 2 of the 3 cases where program KINSHIP excluded the true mother it committed the additional error of generating “false positives” (Table A1.2). Three more “false positives” were generated in cases where the true mother was not excluded. In the latter three cases the known mother-young pairs were compared at only 1, 2 and 3 loci respectively (Table A1.2). The probability of generating a “false positive” (= $\prod_{l=1}^{n} [1 - P_l]$; Marshall et al. 1998) is a function of the average exclusion probability at each locus (P_l) and the number of loci examined (n). The average exclusion probabilities at each locus were calculated (using program CERVUS) for each grid separately, and are presented in Table A1.3. On the East grid, the probabilities of generating a “false positive” when only 1, 2 or 3 loci are typed are approximately 0.35, 0.12, and 0.04 respectively. Non-excluded putative parents and offspring that match at fewer loci will generally have lower likelihood scores than those that match at more loci, reflecting the greater probability of exclusion when more loci are examined. Putative parents and offspring that match for rare alleles at fewer loci can have higher likelihood scores than those that match for common alleles at more loci. However, the number of loci compared provides a rough guide to the likelihood of relatedness insofar as putative parents and offspring that match at 5 or 6 loci are unlikely to be “false positives” (see Tables A1.2 and A1.3).

I conducted parentage analysis on the known mother-young data set shown in Table A1.2 using program CERVUS, assuming all candidates were typed, and all adult females on the same grid were candidates. The proportion of loci typed was calculated for each grid separately using the allele frequency analysis routine of program CERVUS, and the values are reported in Table 4.9. As described above, error rates were calculated for each grid separately (West = 0.01311, East = 0.04435), using the formulas provided in Marshall et al. (1998). Program CERVUS performed much more poorly than program KINSHIP (Table A1.2). Program CERVUS correctly identified only 11 of the 17 known mother-young pairs on the West grid, and committed the additional error of generating "false positives" in each of the 6 cases where it had failed to identify the true mother. On the East grid, program CERVUS correctly identified only 4 of the 10 known mother-young pairs, which is no worse than program KINSHIP. However, program CERVUS generated "false positives" in each of the 6 cases where it had failed to identify the true mother, while program KINSHIP only generated 5 such "false positives".

Program CERVUS was designed to overcome the problem of false exclusions of true parents attributable to typing errors, by simulating the effects of typing errors on genotypic frequencies. My comparison of program KINSHIP and program CERVUS indicates that the "solution" provided by program CERVUS is worse than the problem. SanCristobal and Chevalet's (1997) results suggest that the error simulation routine used by program CERVUS grossly overestimates the degree to which errors homogenize genotypes. Consequently, I iteratively reduced the error rate in runs of program CERVUS until I maximized the proportion of accurate identifications of known mother-young relationships, using the largest possible error rate. By using the largest permissible error rate I hoped to avoid underestimating the "true" error rate. While this approach may not make a theoretician happy, the theoreticians do not appear to have arrived at a consensus, and my empirical results indicate that the use of an iterated error rate was justifiable. The iterated error rate arrived at was 0.00008 for the West grid, and 0.00631 for the East grid. Using the iterated error rate, program CERVUS correctly identified 16 of the 17 known mother-young pairs on the West grid (one more than program KINSHIP, Table A1.2), and it excluded all 34 adult females (no "false positives") in the one case where it failed to identify the true mother (as did program KINSHIP). If the error rate was increased, fewer known mothers were correctly identified and more false positives were generated, while reducing the error rate (below 0.00008) could not lead to the correct identification of the true mother in the one case where she was not identified because she had already been excluded. Using the iterated error rate of 0.00631 arrived at for the East grid, program CERVUS correctly identified 5 of the 10 known mother-young pairs (one more than program KINSHIP, Table A1.2), and it generated "false positives" in each of the 5 cases where it had failed to identify the true mother (as did program KINSHIP). While the accuracy achieved using program CERVUS with an iterated error rate was marginally better than that achieved by program KINSHIP, I chose to use both program CERVUS with the iterated error rates, and program KINSHIP, in subsequent analyses, for reasons addressed earlier, regarding potential biases arising from the known deviations from HWE (Table A1.1).

My goal in evaluating the accuracy with which program KINSHIP and program CERVUS identified known mother-young pairs was to establish the most robust means by which to identify putative parent-offspring relationships among the adult (and subadult) females on each grid. Program KINSHIP identified a single most likely mother/daughter for 21 of the 35 females under consideration on the West grid (Table 4.10), and 20 of the 33 females under consideration on the East grid (Table 4.11). In 19 of 21 cases on the West grid, and 18 of 20 cases on the East grid, the most likely mother/daughter identified by program KINSHIP was also identified as such by program CERVUS. On the West grid, program CERVUS identified 3 more putative parent-offspring relationships than program KINSHIP did, while on the East grid program CERVUS identified 13 more putative parent-offspring relationships than program KINSHIP did. The discrepancy between the grids is almost certainly a result of the higher error rate used with program CERVUS when evaluating the East grid data. As previously demonstrated, when the error rate used with program CERVUS is increased, the program excludes fewer candidates and generates more "false positives".

As noted in Chapter 4, if females generally settle adjacent to their mothers, putative mother-daughter relationships involving adjacent females are most likely true mother-daughter relationships while those involving non-adjacent females are most likely "false positives". I reported in Chapter 4 that, consistent with this prediction, adjacent putative mother-daughter pairs had significantly higher likelihood scores than non-adjacent pairs, on both grids, and regardless of which program (KINSHIP or CERVUS) was used to generate the likelihood scores (Table 4.12). In Chapter 4, I concluded that this result supported the hypothesis that most females do not disperse, but instead settle on or adjacent to their mother's home range.

This result can also be interpreted as confirming the accuracy of parentage analysis. If the inferences regarding parentage, based on my analysis of microsatellite DNA, were completely erroneous, putative mother-daughter pairs would be expected to occur randomly with respect to spatial location. I can conceive of no way in which null alleles, or deviations from HWE, might lead to the observed association between relatedness and spatial location.

Absolute likelihoods

Up to this point I have been discussing relative likelihoods among groups of individuals. Theoretically, it ought to be possible to ascribe an absolute likelihood to a given putative parent-offspring relationship. For example, the lone immigrant female, W-AE, and her putative mother, W-AG, shared an allele at each of five loci (Table 4.10, female W-AG was not typed at the Tv19 locus). The probability (= 0.0054) of any two individuals matching at the five loci in question, by chance alone, can be calculated from the average exclusion probabilities shown in Table A1.3. Of course, the commonness or rarity of shared alleles also influences the likelihood of relatedness.

Program KINSHIP uses the population allelic frequencies (Table 4.9) to assemble simulated pairs of unrelated individuals and thereby generate a distribution of likelihood scores expected by chance alone (Queller and Goodnight 1989). Program KINSHIP's simulations suggest that likelihood scores greater than 1.939 on the West grid (Table 4.10), and 2.281 on the East grid (Table 4.11), are expected to occur by chance alone at a probability of < 0.001. Program KINSHIP's simulations suggest that the absolute likelihood that the lone immigrant female, W-AE, is the daughter of W-AG, is greater than 99.9 % (Table 4.10).

Program CERVUS also assigns probabilities to putative parent-offspring relationships by simulating the distribution of likelihood scores expected by chance alone. Because the error simulation routine in program CERVUS that was used to calculate likelihoods between given pairs of individuals is also used in the construction of the simulated distribution (Marshall et al. 1998, p. 643), the resulting probability statements are strongly influenced by the estimated error rate. Program CERVUS ascribed an absolute likelihood to the putative mother-daughter relationship between W-AE and W-AG of greater than 99 % when the iterated error rate for the West grid (0.00008) was utilized, but the absolute likelihood could only be said to be greater than 90 % when I used the calculated error rate for the West grid (0.01311). While Marshall et al. (1998, p. 650) recommend using the calculated error rate to interpret parentage, they also note that “it is important to realize that paternities [relationships] assigned with 80 % confidence are more accurate than can be achieved in most species”.

In Chapter 4, I noted that I was confident that female W-AD was an originally peripheral resident female, despite being first captured after the August 1, 1995, “deadline” for complete enumeration (Fig. 4.16), in part because of W-AD’s putative relationship with female W-P (Fig. 4.7). The putative mother/daughter relationship between W-AD and W-P (Table 4.10) was ascribed an absolute likelihood of greater than 95 %, both by program CERVUS, regardless of which error rate was used, and by program KINSHIP. Similarly, I argued that I was confident that female W-AI (Fig. 4.7) was a secondary peripheral female because a male was captured at a location adjacent to where W-AI had been captured, that was almost certainly her son. The putative mother/son relationship between W-AI, and the male in question, was ascribed an absolute likelihood of greater than 95 %, both by program CERVUS, regardless of which error rate was used, and by program KINSHIP.

REFERENCES

Becher, S. A., and Griffiths, R. 1998. Genetic differentiation among local populations of the European hedgehog (*Erinaceus europaeus*) in mosaic habitats. Molecular Ecology, 7: 1599-1604.

Blouin, M. S., Parsons, M. Lacaille, V., and Lotz, S. 1996. Use of microsatellite loci to classify individuals by relatedness. Molecular Ecology, 5: 393-401.

Goodnight, K. F., and Queller, D. C. 1998. KINSHIP Version 1.2. Goodnight software, Rice University, Houston, Texas, U.S.A. Available at [http://www.bioc.rice.edu/~kfg/Gsoft.html].

Hartl, D. L. 1988. A primer of population genetics, 2nd ed. Sinauer Associates, Inc., Sunderland, Massachusetts.

Marshall, T. C. 1998. CERVUS Version 1.0. University of Edinburgh, Edinburgh, Scotland. Available at [http://helios.bto.ed.ac.uk/evolgen].

Marshall, T. C., Slate, J., Kruuk, L. E. B., and Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology, 7: 639-655.

Pemberton, J. M., Slate, J., Bancroft, D. R., and Barrett, J. A. 1995. Nonamplifying alleles at microsatellite loci: a caution for parentage and population studies. Molecular Ecology, 4: 249-252.

Piertney, S. B., MacColl, A. D. C., Bacon, P. J., and Dallas, J. F. 1998. Local genetic structure in red grouse (*Lagopus lagopus scoticus*): evidence from microsatellite DNA markers. Molecular Ecology, 7: 1645-1654.

Queller, D. C., and Goodnight, K. F. 1989. Estimating relatedness using genetic markers. Evolution, 43: 258-275.

Raymond, M., and Rousset, F. 1995. GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity, 86: 248-249. Available at [http://www.cefe.cnrs-mop.fr].

SanCristobal, M., and Chevalet, C. 1997. Error tolerant parent identification from a finite set of individuals. Genetical Research, 70: 53-62.

Sokal, R. R., and Rohlf, F. J. 1995. Biometry, 3rd ed. W. H. Freeman and Co., New York.

Van Treuren, R. 1998. Estimating null allele frequencies at a microsatellite locus in the oystercatcher (*Haematopus ostralegus*). Molecular Ecology, 7: 1413-1417.

Table A1.1. Observed (H_O) end expected (H_E) heterozygosity at each of the six microsatellite loci described in Table 4.9, as calculated using genotypic frequency data from both grids, both combined and separately. Also shown is the null allele frequency estimate for each locus. Deviations from Hardy-Weinberg Equilibrium (HWE) were tested at each locus using program GENEPOP (Raymond and Rousset 1995). Fisher's combined probabilities test was used to calculate the global probability of deviation from HWE over all six loci (df = 12).

	Locus	H_O	H_E	Null allele frequency estimate	Hardy-Weinberg Equilibrium			
					Exact test		Fisher's test	
					p	S.E.	χ^2	p
Total	Tv16	0.78	0.91	0.07	0.0004	0.0002	28.6	0.0045
	Tv19	0.94	0.92	-0.01	0.5935	0.0102		
	Tv27	0.87	0.88	0.00	0.9985	0.0102		
	Tv53	0.91	0.91	0.00	0.0497	0.0044		
	Tv58	0.85	0.88	0.02	0.2329	0.0082		
	Tv64	0.89	0.93	0.02	0.2241	0.0096		
West	Tv16	0.74	0.89	0.10	0.0006	0.0002	29.72	0.0031
	Tv19	0.94	0.93	-0.01	0.7353	0.0085		
	Tv27	0.91	0.87	-0.03	0.9265	0.0036		
	Tv53	0.85	0.91	0.03	0.0126	0.0022		
	Tv58	0.83	0.88	0.02	0.2458	0.0084		
	Tv64	0.89	0.93	0.02	0.2779	0.0096		
East	Tv16	0.84	0.91	0.04	0.1666	0.0063	5.40	0.9432
	Tv19	0.95	0.91	-0.02	0.8878	0.0057		
	Tv27	0.83	0.89	0.03	0.9067	0.0032		
	Tv53	1.00	0.90	-0.06	0.9598	0.0034		
	Tv58	0.88	0.88	0.00	0.7750	0.0070		
	Tv64	0.89	0.93	0.02	0.6735	0.0104		

Table A1.2. Known mother-young pairs where both mother and young were successfully typed at one or more of the microsatellite loci described in Table 4.9. The number of loci at which mother and young were compared is listed along with the number of loci at which there was a mismatch (no alleles in common) between the mother and her young. Also shown is the most likely mother, from among the candidates indicated in Tables 4.10 and 4.11, as identified using program KINSHIP (Goodnight and Queller 1998) and program CERVUS (Marshall 1998), along with the number of loci at which the putative mother and young were compared, the number of mismatches between the putative mother and young, and the calculated likelihood score. Dashed lines signify cases where no putative parent was identified from among the available candidates. Numerals followed by an equal sign indicate instances where more than one putative parent had the same likelihood score. Letters in bold indicate instances in which the putative parent was the correct one. Program CERVUS was run using both calculated error rates (West = 0.01311, East = 0.04435), and iterated error rates (West = 0.00008, East = 0.00631). See text for details regarding the derivations of the various error rates.

	Offspring	Known mother			Program KINSHIP			Program CERVUS (calculated error)				Program CERVUS (iterated error)			
		ID	Loci		ID	Loci	Score	ID	Loci		Score	ID	Loci		Score
			compared	mismatch		compared			compared	mismatch			compared	mismatch	
West	A1	A	2		**A**	2	0.956	M	2		0.812	**A**	2		1.969
	A2	A	6	1	---			**A**	6	1	2.181	**A**	6	1	1.770
	C1	C	5		**C**	5	1.742	E	5	1	1.566	**C**	5		3.534
	D1	D	6		**D**	6	4.741	**D**	6		3.312	**D**	6		9.550
	E1	E	3		**E**	3	1.689	R	3	1	1.159	**E**	3		3.369
	J1	J	6		**J**	6	3.252	**J**	6		2.312	**J**	6		6.255
	K1	K	6		**K**	6	4.629	**K**	6		2.264	**K**	6		9.001
	L1	L	5		**L**	5	5.851	**L**	5		2.246	**L**	5		5.615
	L2	L	3		**L**	3	1.446	rA	3	1	0.877	**L**	3		2.825
	O1	O	5		**O**	5	1.357	I	5	1	2.544	**O**	5		2.780
	P1	P	6		**P**	6	4.040	**P**	6		2.418	**P**	6		7.914
	Q1	Q	6		**Q**	6	2.267	**Q**	6		1.329	**Q**	6		4.581
	R1	R	6		**R**	6	4.876	**R**	6		3.771	**R**	6		9.731
	R2	R	6		**R**	6	3.476	**R**	6		2.746	**R**	6		7.141
	V1	V	4	1	---			C	4	1	1.101	---			
	AC1	AC	6		**AC**	6	4.664	**AC**	6		2.889	**AC**	6		8.904
	AI1	AI	6		**AI**	6	4.279	**AI**	6		4.376	**AI**	6		8.887
East	B1	B	5		**B**	5	1.447	R	5	2	0.640	**B**	5		1.663
	F1	F	4	1	D	3	1.146	B	4	1	0.462	D	2		1.325
	I1	I	6		**I**	6	3.152	**I**	6		0.777	**I**	6		3.871
	P1	P	6		**P**	6	3.900	**P**	6		1.017	**P**	6		4.624
	R1	R	5	1	M	4	1.036	AE	5	2	0.743	R	5	2	1.970
	W1	W	6		**W**	6	10.587	**W**	6		0.978	**W**	6		5.530
	X1	X	1		5 =	1	0.578	2 =	1		0.237	2 =	1		0.880
	AB1	AB	2		AD	2	1.580	AD	2		0.767	AD	2		2.391
	AC1	AC	6	1	---			**AC**	6	1	0.857	**AC**	6	1	2.825
	AD1	AD	3		I	4	1.751	I	4		0.688	I	4		2.608

Table A1.3. Average exclusion probabilities based on allelic frequencies on each grid, of each of the six microsatellite loci listed in Table 4.9.

Locus	West	East
Tv16	0.638	0.676
Tv19	0.719	0.664
Tv27	0.568	0.617
Tv53	0.667	0.643
Tv58	0.592	0.599
Tv64	0.748	0.727
Total	0.998	0.998

APPENDIX 2

ESTIMATING THE DATE OF BIRTH OF POUCH-YOUNG

Introduction

In this Appendix, I describe the derivation of the method used, and the protocols adopted, when estimating the date of birth of pouch-young. Assigning a date of birth to each pouch-young observed during the study was a necessary precursor to describing the seasonality of births, and evaluating the survival of young (Chapter 5).

Derivation of methods

Several papers have addressed the issue of estimating the age of young in common brushtail possums, based on repeated measures of known-age young held in captivity (Tyndale-Biscoe 1955, Lyne and Verhagen 1957, Green and Coleman 1984, Kerle and Howe 1992). According to all these authors, head length (in mm, to a maximum of 60.0) is the most reliable trait to use in estimating the age of young. Several studies have noted that age estimates from head lengths greater than 60.0 mm are generally unreliable because the rate of increase in the size of the young begins to asymptote at this point (Lyne and Verhagen 1957, Smith et al. 1969, Kerle and Howe 1992). While head lengths less than 60.0 mm can be used to predict age accurately, each study of this relationship has produced a different predictive equation. Lyne and Verhagen (1957) used a quadratic equation to describe the relationship, while the other studies each used linear equations. In part, the lack of agreement regarding the specifics of each predictive equation may reflect the different source populations from which samples were drawn, as growth rates of pouch-young are known to vary between sites (Cowan 1990). Tyndale-Biscoe (1955) and Green and Coleman (1984) studied possums in New Zealand, which are presumed to derive from possums introduced from the Australian states of Tasmania and Victoria (Green 1984). Lyne and Verhagen (1957) studied possums sampled from near Sydney, New South Wales. Kerle and Howe (1992) studied a distinct subspecies (*T. v. arnhemensis*) from the Arnhem Land region of Australia's Northern Territory. Body size and other morphological traits of common brushtail possums are known to demonstrate a distinct north-south latitudinal cline (Kerle et al. 1991).

As there were no known-age pouch-young in the Paddys Land sample, and only 18 pouch-young were measured twice before exceeding a head length of 60.0 mm, it was not possible to derive a predictive equation for the relationship between head length and age in days based on this data set alone. Given that Lyne and Verhagen's (1957) study animals were drawn from a population that was nearest in geographic proximity to Paddys Land, preliminary age estimates were made by fitting measured head lengths to the nomogram for head length developed by Lyne and Verhagen (1957, their Fig. 7). However, it was noted with respect to the 18 pouch-young that had been measured twice, that in most cases the predicted date of birth moved forward in time as the animal grew, indicating that Lyne and Verhagen's estimator underestimated age for older animals, a problem first identified by Smith et al. (1969).

I was able to assign minimum and maximum ages (less than 200 days = head lengths less than 60.0 mm, according to all published estimators) to pouch-young, based on trapping records (N = 217). To illustrate, if a pouch-young was measured on day 100, and the mother had been caught previously on day 30, with a pouch-young, and on day 10, without a pouch-young, then on day 100 the pouch-young must be a minimum of 70 (100-30) and a maximum of 90 (100-10) days old. The best predictor of age in days based on head length can be identified using this data set, being the one that least often predicts ages outside the known minimum and maximum. Quantitatively, the best predictor is the one with the minimum sum of squared deviations, as in conventional regression analysis (Sokal and Rohlf 1995, p. 461). Unlike conventional regression analysis, however, deviations are calculated only for predicted values falling outside the "boundary conditions" of known minimum and maximum age. Using the example of the pouch-young measured on day 100, a predicted age of 80 days would lie within the boundaries of known minimum (70) and maximum (90) age and the squared deviation would equal 0, whereas a predicted age of 65 days would yield a squared deviation of 25 ($[70-65]^2$), as would a predicted age of 95 days ($[90-95]^2$).

Among the four published methods for predicting age from head length, the linear equation of Kerle and Howe (1992) provided the best fit to the trapping data (sum of deviations^2 = 558.97), followed by the method of Lyne and Verhagen (1957, sum of deviations^2 = 1911.25), and the two linear equations derived from New Zealand possums (Tyndale-Biscoe 1955, sum of deviations^2 = 2689.30; Green and Coleman

1984, sum of deviations^2 = 8253.71). Kerle and Howe's (1992) predictions tended to overestimate the known maximum ages, whereas the other predictors tended to underestimate the known minimum ages. As mentioned previously, Lyne and Verhagen's (1957) method was suspected of producing underestimates (Smith et al. 1969). The fact that Kerle and Howe's (1992) predictions overestimated known age is congruent with the fact that possums from the Northern Territory, in contrast to south-eastern Australian animals, asymptote at a significantly smaller body size despite taking approximately the same length of time to mature. A given increment in head length takes longer in Northern Territory animals, producing a steeper slope when plotting age as the ordinate and head length on the abscissa. By the same logic, the fact that the equations derived from New Zealand possums underestimated known minimum ages even more than the method of Lyne and Verhagen (1957) is congruent with the fact that New Zealand animals are significantly larger on average than those from New South Wales (Kerle et al. 1991).

Rather than utilize a previously published predictor known to be biased, I chose to generate a predictive equation from the minimum and maximum age data set for Paddys Land possums. The overall best fit to the trapping data (sum of deviations^2 = 324.86, Fig. A2.1) was provided by a quadratic equation solved by iteration. Solving for the set of minimum squared deviations through iteration is mathematically indistinguishable from solving for the set by means of standard formulas (Sokal and Rohlf 1995, p. 460), which could not be applied in this case (fitting deviations to boundary conditions). The overall best fit to the trapping data is provided by Equation 1:

$$\text{Days} = -\,2.50757 + 1.99855\,(\text{Head}) + 0.01216\,(\text{Head}^2)$$

Equation 1 was generated using all available trapping data, pooled across years and between the two trapping grids. Year to year variation in growth rates of common brushtail possums, at a single study site, has been reported previously (Cowan 1990). Normally such potential biases could be investigated by examining residuals. However, once Equation 1 was fit to the data there were only 17 cases in which the predicted value lay outside the boundary conditions. As an alternative means of evaluating potential biases between years, or trapping grids, I chose instead to look at deviations inside the boundary conditions, specifically between the predicted age and the known maximum age (N = 70). The magnitude of this deviation will be a function of the average intensity of trapping and any potential biases in growth rates. To illustrate, imagine every individual is trapped every day, then the magnitude of the deviation between the predicted age and the maximum age could be no more than one day. Similarly the magnitude of the deviation could be no more than 10 days if animals were trapped every 10 days. Within that 10 day interval the average deviation between predicted age and known maximum age ought to be 5 days. Deviations would be less than 5 days in a year when animals grew faster than average, and greater than 5 days in a year when animals grew slower than average. The same logic could be applied to deviations from the known minimum age, however, I chose to use deviations from maximum ages, given the more regular pattern of variation in deviations from maximum ages, evident in Figure A2.1. There was a significant difference between years in the magnitude of the deviations between predicted age and known maximum age (Kruskal-Wallis H = 20.05, N = 70, df = 2, $p < 0.0001$). While the magnitude of deviations in 1995 (median = 15.27) and 1996 (median = 18.82) were not significantly different (Mann-Whitney U = 119, z = - 0.04, p = 0.9690), deviations in 1997 (median = 5.40) where significantly smaller. The frequency and intensity (targeting particular animals) of trapping was significantly greater in 1997 than in the other two years (Chapter 6), so the method of evaluating the magnitude of deviations was able to detect this known source of bias. The greater frequency and intensity of trapping in 1997 is certainly part of the reason for the difference in the magnitude of deviations between 1997 and the other two years, however, the possibility remains that growth rates in 1997 may have differed from growth rates in the other two years. The description of the seasonality of births, presented in Chapter 5, relies on data from all three years and may as a consequence be biased by the potential inter-annual variation in growth rates. However, the analyses of the survival of pouch-young, presented in Chapter 5, rely on data from 1995 and 1996 only, and should be unbiased, given that there was no significant difference in the magnitude of deviations between these two years. There were no significant differences (Mann-Whitney U = 505.0, z = - 0.81, p = 0.4154) in deviations between the two trapping grids (West, median = 8.93; East, median = 9.96).

Protocols adopted

A birth date was assigned to each pouch-young observed during the Paddys Land study by applying the following series of protocols. As a first step, a set of predicted ages was generated using all available measurements of head length, estimates of head length, and estimates of crown-rump length. For measurements and estimates of head length, age was predicted using Equation 1. For estimates of crown-rump length, age was assessed by fitting the observed value to the nomogram for crown-rump length developed by Lyne and Verhagen (1957, their Fig. 7). If one or more of the predicted ages based on measurements of head length fell within the known minimum and maximum age limits, the “true” age was taken to be the average of these predicted ages (N = 78, 51.32 % of young). If none of the predicted ages based on measurements of head length, but one or more of the predicted ages based on estimates of head length and estimates of crown-rump length fell within the known minimum and maximum age limits, the “true” age was taken to be the average of these predicted ages (N = 73, 48.03 % of young). To ensure there was no systematic difference between “true” ages predicted by measurements of head length as against “true” ages predicted from estimates of head length and crown-rump length, the two were compared using the subset of young (N = 59) for which both predictions could be made. While “true” ages predicted from estimates of head length and crown-rump length tended to be less than those predicted from measurements of head length (median difference in days = - 3.0) the predicted ages were not significantly different (Wilcoxon’s signed-ranks test, T = 696.5, z = 1.23, p = 0.2183). Finally, if none of the predicted ages based on measurements of head length, and none of the predicted ages based on estimates of head length or estimates of crown-rump length fell within the known minimum and maximum age limits, the “true” age was taken to be the average between the minimum and maximum ages, each weighted by the number of predicted ages falling outside that limit (N = 1, 0.66 %). To clarify this last protocol, assume the maximum age is 50 and the minimum age is 25, three estimates predict an age greater than 50 days, so the “true” age is: (50+50+50+25)/4 = 43.8 days.

REFERENCES

Cowan, P. E. 1990. Brushtail possum. *In* The handbook of New Zealand mammals. *Edited by* King, C. M. Oxford University Press, Auckland, New Zealand, pp. 68-98.

Green, W. Q., and Coleman, J. D. 1984. Response of a brush-tailed possum population to intensive trapping. New Zealand Journal of Zoology, 11: 319-328.

Kerle, J. A., McKay, G. M., and Sharman, G. B. 1991. A systematic analysis of the brushtail possum, *Trichosurus vulpecula* (Kerr, 1792) (Marsupialia : Phalangeridae). Australian Journal of Zoology, 39: 313-331.

Kerle, J. A., and Howe, C. J. 1992. The breeding biology of a tropical possum, *Trichosurus vulpecula arnhemensis* (Phalangeridae : Marsupialia). Australian Journal of Zoology, 40: 663-665.

Lyne, A. G., and Verhagen, A. M. W. 1957. Growth of the marsupial *Trichosurus vulpecula* and a comparison with some higher mammals. Growth, 21: 167-195.

Smith, M. J., Brown, B. K., and Frith, H. J. 1969. Breeding of the brush-tailed possum, *Trichosurus vulpecula* (Kerr) in New South Wales. CSIRO Wildlife Research, 14: 181-193.

Sokal, R. R., and Rohlf, F. J. 1995. Biometry, 3rd ed. W. H. Freeman and Co., New York.

Tyndale-Biscoe, C. H. 1955. Observations on the breeding and ecology of the brushtailed possum, *Trichosurus vulpecula* Kerr (Marsupialia) in New Zealand. Australian Journal of Zoology, 3: 162-184.

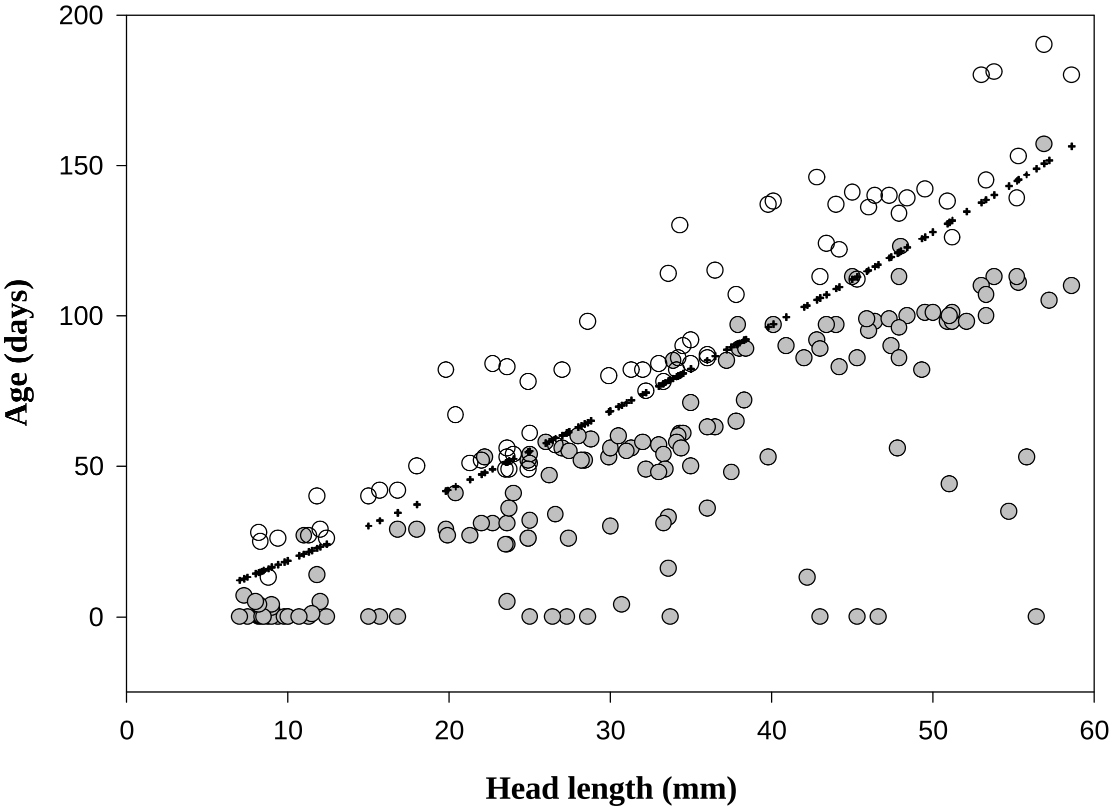

Figure A2.1. Head length (in mm) of pouch-young versus known minimum (grey circles) and maximum (open circles) age (in days) based on trapping records. The line of crosshairs indicates age predicted from head length, using Equation 1.