

Does immigration “rescue” populations from extinction? Implications regarding movement corridors and the conservation of mammals

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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: 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: a) an empirical phenomenon involving a positive correlation between physical proximity and the persistence of populations in sequential surveys of “island” populations; and b) 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., Sjögren 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: a) the absence of direct empirical evidence; b) the failure to consider alternative hypotheses; and c) 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 paper, 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: a) environmentally induced synchrony; coupled with b) the way in which we ask the question.

The correlation between proximity and persistence is conventionally described as follows (Fig. 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

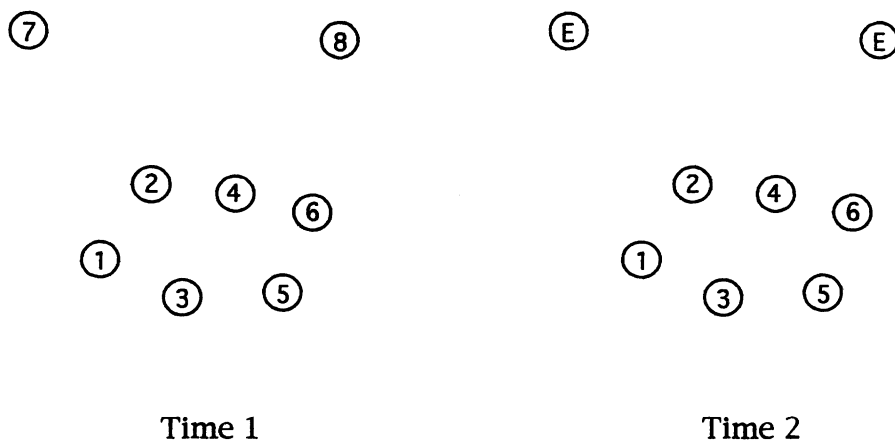


Fig. 1. Conventional portrayal of relationship between proximity and persistence. Numerals signify individual "island" populations. The letter E signifies extinction of a population.

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 Fig. 1 are now arranged into four independent clusters containing two synchronous populations in each cluster (Fig. 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 1. Using the evidence from Table 1 and Fig. 2 we can establish a simple contingency table (Table 2), categorizing populations as to whether they persist from time 1 to time 2, and whether they are near or 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 analyse 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 our 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

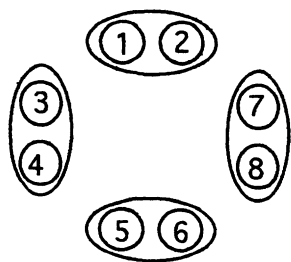
Part of the reason why it is conventionally believed that immigration must be the mechanism underlying the rescue effect, is because in almost all current metapopulation models, immigration is invariably assumed to contribute positively to the persistence of the recipient population.

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

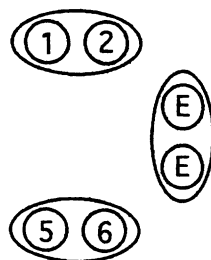
I do not wish to challenge the idea that population size is positively correlated with persistence, but it must be remembered that such demographic models apply to females only. Research scientists and managers alike often seem to forget this restriction (Caughley and Gunn 1996). To emphasize this point, 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 of ecology:

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



Time 1



Time 2

Fig. 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.

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 modelled 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: a) most dispersers are male; and b) most females are philopatric, establishing home ranges near their mothers. As a result: a) most immigrants are male; and b) 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

Table 1. Summary of results of examining populations illustrated in Fig. 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. Contingency table for analysis of relationship between proximity and persistence using evidence from Table 1 and Fig. 2.

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

persistence of the population. Male immigration may be modelled 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). Intrusions 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 (Künkele 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: a) infanticide was the largest single cause of resident juvenile mortality; b) infanticide was never committed by resident females; c) related resident females cooperated in defence against other individuals attempting to commit infanticide; d) most infanticides were committed by immigrant adult females who did not eat their victims; and e) 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: a) the proximity of relatives of resident females; and b) levels of female immigration. Lambin and Krebs (1993) observed: a) six direct instances of infanticide; b) lower mortality of adult resident females if their nearest neighbour was related, suggesting the operation of kin selection; and c) higher resident juvenile mortality in the presence of immigrant females.

Given Lambin and Krebs' (1993) results, female immigration ought to be modelled 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: a) the bulk of immigration, as it involves males, is at best, irrelevant to the persistence of recipient populations; and b) 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: a) the failure to consider alternative hypotheses; and b) 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: 445) to recipient populations. Based on mathematical models and results from captive breeding, many authors (e.g., Soulé 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 amelio-

rated, depending upon your view of the importance of the “genetic contributions of immigrants”.

Simberloff and Cox (1987) questioned the value 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 these 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.

Acknowledgements – Thanks to Charles J. Krebs, Joop Ouborg, Dolph Schluter, James N. M. Smith and Liana Zanette for comments on earlier drafts of this paper. Thanks also to Peter Jarman and the Ecology Discussion Group, Univ. of New England, Armidale, N.S.W., Australia, for helpful responses when I first presented these ideas in public. I would not have been able to accomplish anything without the love and support of Beryl and John Clinchy.

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