

REMOVING BROWN-HEADED COWBIRDS INCREASES SEASONAL FECUNDITY AND POPULATION GROWTH IN SONG SPARROWS

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Abstract. Parasitic Brown-headed Cowbirds may reduce the reproductive success of their songbird hosts and thus threaten rare and frequently parasitized host populations with extinction. The demographic impacts of cowbirds on hosts, however, have seldom been studied experimentally. We removed cowbirds to estimate how much they reduce the seasonal fecundity and population growth rates of a non-endangered cowbird host, the Song Sparrow. Over five control years, 61% of 515 sparrow nests were parasitized at three riparian study sites. When we removed female cowbirds from two of these sites, parasitism fell to 43% of 65 nests at Westham in 1996, to 30% of 117 nests at Westham in 1997, and 18% of 78 nests at Delta in 1998. The mean seasonal fecundity of sparrows increased from 1.67 fledglings per territory in controls to 3.40 fledglings per territory at Westham and from 1.23 to 3.16 fledglings per territory at Delta. At the third control site, Deas, seasonal fecundity averaged 2.07 fledglings per territory. The mean sizes of sparrow broods at fledging were increased in removal years from 0.53 to 0.95 young at Westham and from 0.47 to 1.15 young at Delta. Daily nest failure rates were reduced from 0.046 in control years to 0.030 during cowbird removals at Westham and from 0.049 to 0.035 at Delta. Survival over a 25-d nest cycle rose from an average of 0.32 in eight controls to 0.45 in three removals. Cowbird removals increased local population growth rates of song sparrows from well below replacement levels ($\lambda = 0.70\text{--}0.87$) to a stable condition ($\lambda = 0.93\text{--}1.06$). If cowbirds have similar or stronger effects on rarer and more vulnerable hosts, cowbird removal could improve the demographic performance of such hosts substantially.

Key words: brood parasitism; Brown-headed Cowbird; *Melospiza melodia*; *Molothrus ater*; nest predation; population growth rate; seasonal fecundity; Song Sparrow.

INTRODUCTION

Obligate brood parasitism, in which a species' reproduction takes place only via stealing parental care from foster parents, occurs in 100 species of birds worldwide (Davies 2000). Although few species have been studied in detail, avian brood parasites typically specialize on a few host species, and several species are adapted to parasitize a single preferred host by egg mimicry and other adaptations (Davies 2000). Host specialization results in most well-studied brood parasites, like the Common Cuckoo (*Cuculus canorus*), being uncommon compared to their principal hosts. They therefore parasitize a low percentage (typically <5%) of the host's nests on average (e.g., Davies and Brooke 1989, but see Nakamura et al. 1998) and probably have little demographic impact on hosts. Negative feedbacks between local host and parasite numbers are thought to dominate the population dynamics of such brood parasites (May and Robinson 1985), although larger scale spatial dynamics are known to affect populations of Common Cuckoos (Lindholm 1999).

Some species of avian brood parasite, however, de-

part from this typical pattern. The Brown-headed Cowbird (*Molothrus ater*) and the Shiny Cowbird (*M. bonariensis*) are extreme host generalists, which have been recorded to lay eggs in the nests of >200 host species (Davies 2000). Because they do not depend on any one host to maintain their own numbers, these generalist parasites are locally abundant when feeding habitat is readily available (Robinson 1999), and they commonly parasitize large fractions of nests per host across several co-occurring host species (Mason 1986, Trine et al. 1998). Brown-headed Cowbirds thus have large potential impacts on the population dynamics of host species (Trine et al. 1998).

Four negative effects of Brown-headed Cowbirds on the production of young from host nests have been well documented (Ortega 1998, Lorenzana and Sealy 1999; papers cited in Morrison et al. [1999] and Smith et al. [2000]). First, by removing host eggs, cowbirds reduce the size of host clutches (e.g., Arcese and Smith 1999). Second, egg removal (Rothstein 1982) and behavioral interactions at host nests (e.g., Hosoi and Rothstein 2000) can induce nest desertion by hosts. Third, female cowbirds may completely destroy whole clutches or broods of hosts (review in Arcese et al. [1996], but see McLaren and Sealy [2000]). Finally, cowbird young compete effectively with host young for parental care,

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particularly when the hosts are small relative to the size of the cowbird (Lorenzana and Sealy 1999).

While Brown-headed Cowbirds obviously lower the nesting success of their hosts by these activities, it is less clear how much they affect the demography of host populations. Mayfield (1977), Brittingham and Temple (1983), and Terborgh (1989) suggested that cowbird parasitism was to blame for population declines in many forest songbirds. These ideas stimulated much research on cowbirds (summarized in Ortega 1998, Morrison et al. 1999, Smith et al. 2000). These recent studies have revealed that there is considerable variation in how much cowbirds affect their hosts, and researchers have disagreed about the demographic significance of these effects (e.g., Rothstein and Robinson 1994, Griffith and Griffith 2000).

Debate over how severely cowbirds affect populations of their hosts is difficult to resolve because of a shortage of the necessary data. In particular, nearly all cowbird hosts are multi-brooded or are capable of re-nesting after an initial failure. Thus, the impacts of cowbirds should be assessed by estimating the reduction in seasonal fecundity of host females caused by parasitism (Pease and Grzybowski 1995, Sedgwick and Iko 1999), and not, as is commonly done, by comparing samples of parasitized and unparasitized nests (reviewed by Lorenzana and Sealy 1999). Additionally, it is of interest to know how much cowbirds reduce the population growth rates of their hosts (Whitfield et al. 1999).

The most direct way to estimate the impact of any limiting factor on a population is to remove or ameliorate it experimentally. Whitfield (2000, Whitfield et al. 1999) and Stutchbury (1997) removed cowbirds to estimate their impacts on populations of songbird hosts. In both studies, reproductive success of the focal host was improved, but neither study had a strong grade 3 experimental design (sensu Newton 1998:183–184) with replication, contemporaneous controls, and/or reversal of treatments in different years. Cowbird removal programs have been associated with the recovery of populations of two small and endangered cowbird hosts, the Least Bell's Vireo (*Vireo belli pusillus*) and the Black-capped Vireo (*Vireo atricapillus*), but may have had little effect on two other endangered cowbird hosts (Hall and Rothstein 1999, Rothstein and Cook 2000).

In this study, we conducted a controlled field experiment at three sites over 5 yr to estimate the effects of cowbird removal on the seasonal fecundity, frequency of parasitism, rate of nest failure, and population growth rate in the Song Sparrow (*Melospiza melodia*). The Song Sparrow is one of the most frequently used cowbird hosts in North America (Smith and Myers-Smith 1998), and there is also much descriptive data available on the effects of parasitism on this species (e.g., Nice 1937, Smith 1981, Smith and Arcese 1994, Arcese et al. 1996, Rogers et al. 1997, Arcese

and Smith 1999). The reproductive success of Song Sparrows is negatively correlated with the frequency of cowbird parasitism on both local and geographic scales (Arcese and Smith 1999). We therefore expected cowbird removals to increase the seasonal fecundity of sparrows through decreased parasitism and reduced nest failure rates. We also expected cowbird removal to improve reproductive success and local population growth rates in the sparrow.

METHODS

We worked at three riparian study sites in the Fraser River Delta, British Columbia, Canada, which we term Westham, Deas, and Delta. At Westham, we studied 12 ha of Reifel Bird Sanctuary from 1995 to 1999 and an adjacent 6-ha part of the Alaksen National Wildlife Area, from 1995 to 1997. Rogers et al. (1997) describe the location and vegetation characteristics at this site. Deas (123°10' W, 49°10' N) is a managed park on the banks of the Fraser River. We studied a 25-ha area of the park. Habitats in the study area included thickets of blackberry (*Rubus discolor* and *R. laciniatus*) below a canopy of red alder (*Alnus rubra*) on river dikes, wet meadows dominated by reed canary grass (*Phalaris arundinacea*), and stands of horsetails (*Equisetum* sp.) below mature cottonwood trees (*Populus balsamifera*). The site at Delta Nature Reserve (123°00' W, 49°11' N) consisted of a 2 km × 100 m strip (20 ha) between 72nd Street and Nordel Way, Vancouver, along a small creek and railway line. Vegetation at Delta was dominated by blackberries, reed canary grass, hardhack (*Spirea douglasii*), and salmonberry (*Rubus spectabilis*), with an overstory of alder and willow (*Salix* sp.). Deas is located 8 km east of Westham, and Delta is 12 km east of Deas.

In the Fraser Delta, Song Sparrows begin to lay in the last week of March or first week of April (Rogers et al. 1997); they stop laying at the end of July. Territories of breeding pairs of Song Sparrows were located at the beginning of the season each year. Cowbirds generally arrive in the Fraser Delta in mid-April, and breeding females are readily detected by their conspicuous chatter calls (Rothstein et al. 2000). The first cowbird eggs are laid in the last week of April or the first week of May (Rogers et al. 1997). We trapped cowbirds at each site using two portable house traps 1.6 × 1.6 × 2.0 m in size. The traps were supplied with ample millet seed and water, and they contained five live cowbird decoys (De Groot et al. 1999). Adult females were held in outdoor aviaries until mid-July when they were released at the capture site. Trapped males were banded and released immediately, unless they were used as decoys in traps. The work was done under permits issued by the University of British Columbia Animal Care Committee and the Canadian Wildlife Service.

Our study ran from 1995 to 1999 and our experimental design (Table 1) involved removing female

TABLE 1. Experimental design and allocation of Brown-headed Cowbird removal treatments to study sites by year in the Fraser River Delta, British Columbia, Canada.

Site	1995†	1996†	1997	1998	1999
Westham	control	removal	removal	control	control
Delta	pilot work	control	control	removal	control
Deas	pilot work	control	control	control	not used

† We were unable to estimate seasonal fecundity reliably at all three sites in these years.

cowbirds from one site per year over 3 yr. Overall, the first parasitized Song Sparrow nests of the season were found on 20 April at Westham, 29 April at Delta, and 2 May at Deas (averaging over control years only). Removals began on 16 May 1996 and 10 April 1997 at Westham and 2 May 1998 at Delta.

We checked the contents of Song Sparrow nests regularly, usually every 4 d. Checks were made at most nests up to fledging (i.e., when nestlings were 9–11 d of age). While we did not find all nests on each territory, we did find 90% of all nests at the egg stage, and this frequency varied little by site or year. Egg and nestling identity (sparrow or cowbird) was assessed as described by Smith and Arcese (1994). Ages of nestlings were estimated by inspection. Hatching date was estimated to ± 1 d by backdating from the estimated age of nestlings at the first check after hatching. Numbers of Song Sparrows and cowbirds reared were counted by visual inspection in the nest at 9–11 d of age. During these late checks, we took care not to disturb the vegetation around the nest to avoid inducing premature fledging. Cowbird and Song Sparrow fledglings are readily distinguished by their begging calls (Smith and Merkt 1980).

If the final check was made before young were 9 d old, the number of young fledged from that nest was scored as unknown, unless we confirmed the occurrence of one or both of two conditions. First, begging fledglings of the appropriate age were detected near the nest; second, the nest had abundant feces on the rim. The rationale for the latter condition is that, by the day before leaving the nest, young Song Sparrows often stand on the nest rim and feeding parents do not always remove their fecal pellets (Nice 1943). Thus, an accumulation of feces on the nest rim implies strongly that nestlings survived to our criterion age for successful fledging of 9 d. In both these cases, we assumed that all young present in the nest at the final check fledged successfully. Across the study, 8.7% of 969 nests were of uncertain outcome. The proportion of uncertain nests was higher in 1995–1996, while we were fine-tuning our field procedures, than in the three core years of the study, 1997–1999 (13.7% vs. 7.3%, $\chi^2 = 8.18$, $df = 1$, $P < 0.01$).

Seasonal fecundity (also commonly known as seasonal reproductive success) was estimated on 11–37 territories per site from 1997 to 1999 by summing the numbers of young reared from all nests on the territory that year (Table 1). If the outcome of a nest on any

territory was scored as uncertain, or if the number of young fledged from a nest was uncertain, we did not use that territory to estimate seasonal fecundity. We also did not estimate seasonal fecundity from any territories where young fledged from nests whose success we did not monitor, as estimates here could be biased by post-fledging mortality. We analyzed data on per territory production of Song Sparrows and cowbirds in 1997–1998 with fully factorial ANOVAs. Data for cowbird production were first log transformed to improve homogeneity of variances. All results are presented on their original scales.

Sample sizes here vary between analyses for three reasons. First, some nests were known to have failed, but their contents were unknown. In others, we knew the contents of a nest, but not the numbers of young fledged from it, because of the timing of the last nest check. Third, some nests were known to be parasitized because they contained cowbird eggs, fragments of cowbird eggshell, or cowbird nestlings when they were discovered, but they could not be assessed for clutch size.

Part of the adult sparrow population (10–40%) was individually color-banded at Westham each year and at Delta from 1997 to 1999. Banded birds of both sexes, like others previously studied at Westham (Rogers et al. 1997), were highly sedentary within a season. Thus, although we measured seasonal fecundity per territory, this quantity is very similar here to seasonal fecundity per female.

Daily nest survival rates and their standard errors were calculated following Bart and Robson (1982) and Krebs (1999); estimates of total nest survival were calculated using a 25-d nest period. Approximately 4% of nests were flooded by high tides or rain storms, trampled by cows, or contained infertile eggs. These nests were excluded from the analysis of survival rates, because their failure had nothing to do with cowbird activity. Thus, their inclusion would simply have added random errors to our experimental data. For nests with uncertain outcomes, we included data from these nests only up to the last check when they were still active. We compared daily nest survival rates among sites and treatments using chi-squared tests (Sauer and Williams 1989).

Estimates of the finite population growth rate (λ) for sparrows were calculated as

$$\lambda = S_f + (N_i \times S_j)$$

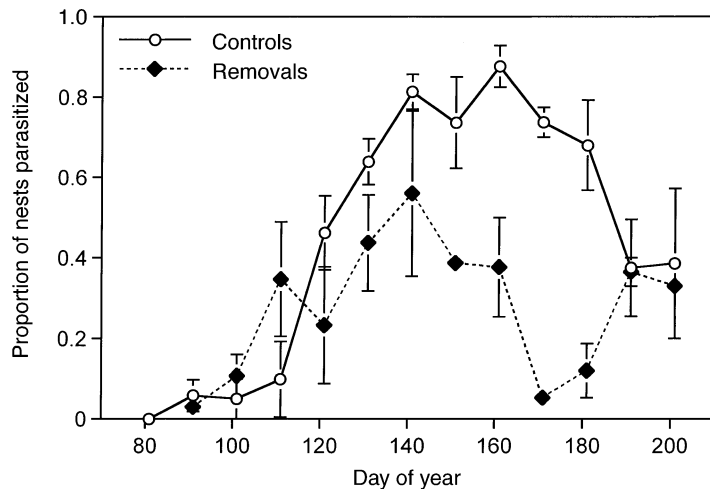


FIG. 1. Reductions in parasitism in Song Sparrow nests caused by removal of Brown-headed Cowbirds from two of three riparian study sites in the Fraser River Delta, British Columbia, Canada (means \pm 1 SE). Data from five control years and three removal years are pooled. Standard errors were calculated from data for each 10-d period for the three removal years and eight control years.

where S_f = annual survival of breeding females, N_i = number of female young fledged per female per year assuming that, on average, there is a 1:1 sex ratio of female : male offspring, and S_i = survival of fledglings from leaving the nest to breeding age (1 yr). Values of $\lambda < 1.0$ indicate that local production of yearlings is greater than the adult death rate, $\lambda = 1.0$ indicates a balance of birth and death rates, and $\lambda > 1.0$ indicates an increasing population. The survival rate for adult female sparrows, $S_f = 0.560 \pm 0.016$ (means \pm 1 SE), was estimated using 23 yr of data collected on nearby Mandarte Island from 1975 to 1999. A similar estimate ($S_f = 0.576 \pm 0.047$) was obtained for 4 yr of data gathered at Westham from 1988 to 1991 (Rogers et al. 1997). We also used a higher value for female survival ($S_f = 0.632 \pm 0.017$) for 21 yr at Mandarte without population crashes; such crashes have not been observed at Westham. Survival rates from fledging to 1 yr of age were also estimated using data from Mandarte; these were $S_i = 0.234 \pm 0.010$ for all years and 0.250 ± 0.011 for non-crash years (Arcese et al. 1992; P. Arcese and A. B. Marr, unpublished data). Both survival estimates had a binomial sampling distribution allowing us to calculate the sampling variance for each using the equation $S_p^2 = p(1 - p)/N_p - 1$, where p = the survival estimate. We estimated the sampling variance for λ by summing the variances of each random variable in the model (following Zanette 2000).

RESULTS

Numbers of cowbirds removed

We trapped a total of 238 female cowbirds over the three removal years; 51 at Westham in 1996, 163 at Westham in 1997, and 24 at Delta in 1998. Cowbird females at all sites gave frequent chatter calls and interacted conspicuously with males and with host Song Sparrows near their nests. When we removed the first females from Delta during May 1998, there was usually a day or two when we saw and heard only the banded

resident males, but these males were joined by chattering females within 3–4 d. The females we removed at Westham were replaced rapidly and without obvious gaps. Two cowbird females that were color-banded at Westham in 1995 avoided our traps in 1996, and one did so in 1997. These birds remained resident throughout the removal period in those 2 yr and presumably continued to lay eggs. Few of the banded cowbird females that we trapped, held in captivity, and released between 1996 and 1998 returned to breed in subsequent years, while several females that we marked at Westham in 1995 did return in 1996.

Cowbird removal and parasitism

Sixty-one percent of 515 sparrow nests were parasitized over all three sites in all control years. The proportions of nests containing cowbird eggs in each 10-d interval in control years rose steeply in early May (day of year: 120), remained $>70\%$ from late May to early July, and declined in mid-July (day of year: 190; Fig. 1). Cowbird removal reduced the proportion of parasitized nests slightly during May (days of year: 120–150) and considerably thereafter (Fig. 1). The proportion of parasitized nests in removal years, however, rose again to control levels after day 180. The proportion of parasitized nests in control years did not vary significantly by site or by year at Deas or Delta (Table 2, contingency table analyses, χ^2 tests, $df = 2$, $P > 0.05$). There was, however, variation across control years at Westham ($\chi^2 = 8.14$, $df = 2$, $P < 0.025$); parasitism was more frequent in 1995 than in 1998 or 1999, which were similar to each other ($\chi^2 = 1.39$, $df = 1$, $P > 0.2$; Table 2). This variation was due mainly to a low sample of nests ($n = 3$) in March and April 1995, a time when frequencies of parasitism were low (Fig. 1). There was also variation in the frequency of parasitism across the three removal years (contingency table analysis, $\chi^2 = 10.75$, $df = 2$, $P < 0.01$). The proportion of parasitized nests was highest at Westham

TABLE 2. Frequency and intensity of Brown-headed Cowbird parasitism in Song Sparrow nests at three sites from 1995 to 1999.

Site	No. nests	No. parasitized	Proportion parasitized	No. cowbird eggs per parasitized nest (SE)
1995				
Westham	48	39	0.81	1.73 (0.13)
1996				
Westham	65	28	0.43	1.33 (0.11)
Delta	34	24	0.71	1.40 (0.15)
Deas	18	13	0.72	1.50 (0.20)
1997				
Westham	117	35	0.30	1.16 (0.08)
Delta	61	28	0.46	1.35 (0.10)
Deas	45	31	0.69	1.20 (0.09)
1998				
Westham	109	63	0.58	1.32 (0.07)
Delta	78	14	0.18	1.14 (0.10)
Deas	77	48	0.62	1.42 (0.14)
1999				
Westham	80	53	0.66	1.31 (0.07)
Delta	53	27	0.51	1.41 (0.16)
All controls				
Westham	237	155	0.65	1.41 (0.05)
Delta	148	79	0.53	1.41 (0.08)
Deas	140	92	0.66	1.35 (0.08)
All removals				
Westham	182	63	0.35	1.24 (0.07)
Delta	78	14	0.18	1.14 (0.10)

Note: Cowbird females were removed in 1996 and 1997 at Westham and in 1998 at Delta.

in 1996 and lowest at Delta in 1998. Because of this variation among control and removal sites, we compared each removal year separately to the pooled controls for that site, but we omitted the atypical data of 1995 from the pooled controls at Westham.

When we compared pooled controls to removals at each site, removal reduced the proportions of parasitized nests from 0.65 to 0.43 at Westham in 1996 ($\chi^2 = 6.60$, $df = 1$, $P < 0.02$), from 0.65 to 0.30 at Westham in 1997 ($\chi^2 = 28.62$, $df = 1$, $P < 0.001$), and from 0.53 to 0.18 at Delta ($\chi^2 = 26.46$, $df = 1$, $P < 0.001$; Table 2). Proportions of parasitized nests per 10-d interval at the removal sites fell below that at the control sites soon after cowbird removals began in late April and early May and reached low levels by mid-June (day of year: 170; Fig. 1). In addition to reducing the proportion of parasitized nests, cowbird removal also lowered the mean number of cowbird eggs per parasitized nest from 1.41 ± 0.07 to 1.24 ± 0.07 eggs/nest at Westham and from 1.41 ± 0.08 to 1.14 ± 0.16 eggs/nest at Delta (Table 2).

Parasitic effects due to egg removal and reduced brood sizes at fledging were strong in our study. In control years for all sites pooled, 263 parasitized sparrow clutches contained 0.7 fewer sparrow eggs than

213 unparasitized nests (2.50 ± 0.07 vs. 3.20 ± 0.07 eggs). At all control sites, successful parasitized nests fledged only about half as many sparrows (1.24 ± 0.11 sparrows, $n = 90$) as successful unparasitized nests (2.45 ± 0.13 sparrows, $n = 60$). Considering all clutches and broods at the two removal sites, cowbird removals increased sparrow clutch sizes by an average of 0.26 eggs per nest at Westham and by 0.19 eggs per nest at Delta (Table 3). At Westham, the mean number of sparrow young fledged from all nests increased from 0.53 ± 0.06 sparrows in control years to 0.95 ± 0.09 sparrows in removal years. At Delta, the mean number of sparrows fledged per nest more than doubled after removals, increasing from 0.47 ± 0.08 to 1.15 ± 0.16 sparrows.

Daily nest survival rates over the season

For the controls, daily survival rates of sparrow nests per year were similar among sites within each year and among sites with all years combined (all P s > 0.25 , χ^2 tests). Survival rates were also homogeneous among removal years ($P > 0.25$, Table 4). Cowbird removals consistently increased survival rates (Table 4). When we compared all control years to all removal years, cowbird removals reduced average daily failure rates ($= 1 - \text{survival rates}$) from 0.460 to 0.300 at Westham ($\chi^2 = 11.94$, $df = 1$, $P = 0.006$) and from 0.049 to 0.035 at Delta ($\chi^2 = 3.94$, $df = 1$, $P = 0.047$). When the pooled removals at both removal sites were compared to all controls the overall decrease in failure rates during removals was highly significant ($\chi^2 = 16.18$, $df = 1$, $P < 0.001$). When these decreases in failure rates were scaled to a 25-d nest cycle, total nest survival rates after removals (Table 4) rose from a mean of 0.32 ± 0.03 in the eight control years to a mean of 0.45 ± 0.03 in the three removal years.

Seasonal fecundity

Data on seasonal fecundity were available for 1997–1999. Seasonal fecundity of sparrows at control sites varied from a low of 1.00 ± 0.35 fledglings per territory

TABLE 3. Clutch sizes for Song Sparrows and numbers of Song Sparrow fledglings produced per nest in relation to Brown-headed Cowbird removals (means ± 1 SE).

Treatment	No. clutches	No. eggs per nest	No. young fledged per nest	No. broods
Westham				
Controls	233	2.67 ± 0.07	0.53 ± 0.06	280
Removals	151	2.93 ± 0.07	0.95 ± 0.09	189
Delta				
Controls	136	3.01 ± 0.09	0.47 ± 0.08	154
Removals	84	3.20 ± 0.07	1.15 ± 0.16	88
Deas				
Controls	133	2.78 ± 0.10	0.57 ± 0.09	154

Note: The number of broods exceeds the number of nests because some nests were found after the young had hatched.

TABLE 4. Daily survival rates of Song Sparrow nests in relation to Brown-headed Cowbird removals in 1996–1997 at Westham and 1998 at Delta.

Site	Treatment	No. nests	Daily survival rate (SE)	Nest success†
1995				
Westham	control	50	0.948 (0.034)	0.260
1996				
Westham	removal	81	0.966 (0.006)	0.416
Delta	control	34	0.949 (0.011)	0.271
Deas	control	17	0.957 (0.013)	0.337
1997				
Westham	removal	90	0.973 (0.004)	0.503
Delta	control	66	0.952 (0.007)	0.292
Deas	control	46	0.964 (0.008)	0.399
1998				
Westham	control	123	0.956 (0.005)	0.320
Delta	removal	87	0.965 (0.005)	0.415
Deas	control	79	0.955 (0.006)	0.317
1999				
Westham	control	84	0.954 (0.005)	0.305
Delta	control	49	0.951 (0.008)	0.288
All controls				
Westham		257	0.954 (0.004)	0.303
Delta		236	0.951 (0.005)	0.286
Deas		142	0.958 (0.005)	0.344
Removals				
Westham		171	0.970 (0.003)	0.470
Delta		87	0.965 (0.005)	0.415
All removals		258	0.969 (0.003)	0.453

† Probability of nest success over 25 days.

at Delta in 1999 to a high of 2.64 ± 0.54 fledglings per territory at Deas in 1997 (one-factor ANOVA: site, $F = 7.32$, $df = 2$, 116 , $P = 0.296$; Fig. 2). For removals, seasonal fecundity was very similar between sites, ranging from a low of 3.16 ± 0.42 fledglings per territory at Delta in 1998 to a high of 3.40 ± 0.33 fledglings per territory at Westham in 1997 ($F = 0.19$, $df = 1$, 47 , $P = 0.666$). A two-factor ANOVA showed

that seasonal fecundity differed significantly with treatment (control vs. removal, $F = 21.52$, $df = 1$, 128 , $P < 0.001$), but not with year (1997 vs. 1998, $F = 0.70$, $df = 1$, 128 , $P = 0.604$), and there was no interaction ($F = 0.02$, $df = 1$, 182 , $P = 0.903$). In 1997, seasonal fecundity was increased from 2.00 ± 0.33 fledglings per territory in the pooled controls to 3.40 ± 0.36 fledglings per territory in the removal. In 1998, the increase was from 1.54 ± 0.23 fledglings per territory in the controls to 3.16 ± 0.41 fledglings per territory in the removal (Fig. 2).

The number of cowbird fledglings produced per territory was also reduced by removals. The reduction was from 0.52 ± 0.12 fledglings produced per territory in controls to 0.23 ± 0.08 fledglings produced per territory in removals in 1997 and from 0.28 ± 0.07 fledglings produced per territory in controls to 0.11 ± 0.07 fledglings produced per territory in removals in 1998 (two-factor ANOVA, year, $F = 4.05$, $df = 1$, 128 , $P = 0.046$; treatment, $F = 5.49$, $df = 1$, 128 , $P = 0.021$; year \times treatment, $F = 0.31$, $df = 1$, 128 , $P = 0.578$).

Host population growth

Host population growth rates (λ) in control years at all three sites ranged from 0.704 at Delta to 0.876 at Deas (Table 5) and they fell significantly (>4 SE) below replacement levels, when we used the lower survival estimates. When we used the higher estimates of adult and juvenile survival from Mandarte Island, they still fell significantly (>2 SE) below replacement levels (Table 5). In removal years, λ ranged from 0.929 to 1.057 and never fell as much as two standard errors below replacement levels. Lambda exceeded 1.0 at both Westham and at Delta when we used the higher survival estimates (Table 5).

DISCUSSION

In our study, cowbird removal reduced nest parasitism in Song Sparrows and increased daily nest survival

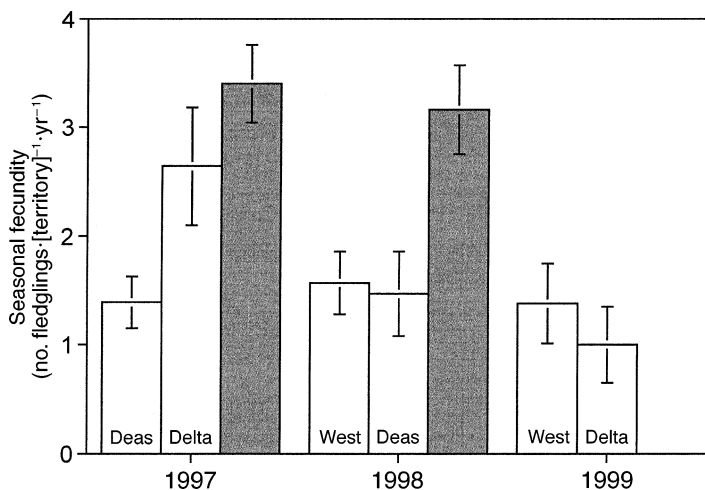


FIG. 2. Increases in seasonal fecundity of Song Sparrows in relation to experimental removal of female Brown-headed Cowbirds during 1997 and 1998 (means \pm 1 SE). Open bars represent control treatments; gray bars represent removal treatments. Within each year, control sites are labeled at the foot of the open bars (West = Westham). There are no data for Deas in 1999.

TABLE 5. Finite population growth rates (λ) of Song Sparrows in relation to Brown-headed Cowbird removals in 1997 at Westham and 1998 at Delta.

Treatment	Overall survival rate (SE)	Survival rate excluding crash years (SE)
Westham		
Controls	0.756 (0.033)	0.841 (0.035)
Removals	0.958 (0.048)	1.057 (0.051)
Delta		
Controls	0.704 (0.038)	0.786 (0.040)
Removals	0.929 (0.046)	1.027 (0.049)
Deas		
Controls	0.786 (0.043)	0.873 (0.046)
Delta and Westham		
Controls	0.739 (0.039)	0.823 (0.033)
Removals	0.947 (0.037)	1.045 (0.039)

Notes: The two columns of values of λ are for differing estimates of survival on nearby Mandarte Island. Overall survival rates are 0.560 for adult females and 0.234 for fledglings in 23 years; rates in 21 non-crash years are 0.632 for adults and 0.250 for fledglings.

rates. Moreover, when cowbirds were removed, the seasonal fecundity of Song Sparrows was approximately doubled. Our results were consistent among replicates in space and time, and reversing the experimental treatment at the two removal sites produced a corresponding reversal in the results. Our demographic calculations suggested that cowbird removals increased population growth in the Song Sparrow from well below replacement levels to a near stable condition. Our experiment confirms the results of many descriptive studies of the impacts of cowbirds on host reproduction (Lorenzana and Sealy 1999). Our work also adds to evidence from earlier experiments (Stutchbury 1997, Whitfield et al. 1999, Whitfield 2000) and cowbird management programs (Rothstein and Cook 2000) that cowbirds can lower the seasonal fecundity of hosts substantially and reduce local population growth rates. Finally, our experiment confirms a suggestion by Arcese et al. (1996) that nest failure induced by cowbirds can have a strong demographic impact on host reproduction.

Numbers of cowbirds removed

Nearly seven times as many female cowbirds were trapped at Westham in 1997 (163 cowbirds) compared to Delta in 1998 (24 cowbirds), while the numbers trapped at Westham in 1996 were intermediate (51 cowbirds). The difference in cowbird numbers trapped at Westham between 1996 and 1997 was mainly due to the earlier start of trapping in 1997. Trapping began on 16 May in 1996, ~1 mo after the first cowbird arrived at Westham, and on 10 April in 1997, two weeks after their arrival. The numbers of cowbirds caught after May 15 at Westham in the two removal years were similar (51 cowbirds in 1997 vs. 47 cowbirds in 1996).

The higher number of cowbird females removed at

Westham than at Delta was probably caused by the varying attractiveness of the two sites to feeding cowbirds. Westham lies at the mouth of the Fraser River Delta in a primarily agricultural landscape. A herd of cattle was grazed in adjacent fields each summer, and nearby arable lands provided further feeding opportunities to cowbirds. In addition, mixed seeds (provided daily at the bird sanctuary) attracted feeding flocks of cowbirds to Westham daily, even in the two removal years. At Delta, the adjoining landscape included suburban housing, industrial sites, and a 4000-ha wetland. Although cowbirds eat many invertebrates in the breeding season (Ortega 1998), Delta probably offered fewer feeding opportunities to cowbirds than did Westham.

The breeding female cowbirds that we removed were replaced rapidly during May and June, but more slowly thereafter. Replacement females could have occurred for at least three reasons. First, nonbreeding floater females may have been present in the cowbird population; this result was suggested by short gaps in sightings of females cowbirds at Delta in 1998 that were filled within a few days. Second, neighboring females may have expanded their ranges when breeding females were removed. Raim (2000) noted this pattern when females died or dispersed in Illinois, USA, but Whitfield (2000) found that neighboring females did not relocate in response to nearby removals in California, USA. Finally, females may have had overlapping ranges and the initial removals may merely have reduced local cowbird density (M. J. Whitfield, *personal communication*). This last explanation is plausible at Westham, where removals did not eliminate local sightings of female cowbirds and where parasitism remained between a half and two-thirds of control levels during removal years (Table 2). Because of our inability to reduce female densities to zero, cowbirds continued to lay in our removal treatments. Thus, the true effects of cowbirds on seasonal fecundity and population growth of Song Sparrows at our study sites were undoubtedly greater than those that we documented experimentally.

Perhaps the fact that we did not remove male cowbirds also contributed to the replacement of trapped females. Two management programs for cowbirds where males have been removed have reduced female cowbird numbers to near zero (DeCapita 2000, Griffith and Griffith 2000, De Groot and Smith 2001). In two other programs, only females were removed or male removals were less complete (Eckrich et al. 1999, Whitfield et al. 1999, Hayden et al. 2000, Whitfield 2000). In these programs, levels of parasitism in host nests remained well above zero after cowbird removals (Eckrich et al. 1999, Whitfield et al. 1999). Our data, and evidence from these management programs, show that even partial removal of cowbirds can reduce the demographic impacts of cowbirds substantially.

Why does cowbird removal increase seasonal fecundity?

The effects of brood parasites on the reproduction of their hosts can be divided into two general classes:

(1) those that reduce the number of fledglings produced per successful nest and (2) those that increase the rate of nest failure.

We first consider class 1 effects. The overall proportion of parasitized nests was reduced by cowbird removal from 0.61 to 0.30 (Table 2), although it rose again in removals at the end of the laying season (Fig. 1). The rise in proportion of nests parasitized in late July for the removals might have been caused by laying by the females that we released in mid-July. However, we searched for these color-banded birds on the removal sites after release, but observed none there. Reduced proportions of parasitized nests led to lower seasonal fecundity mainly because successful parasitized nests reared only half as many Song Sparrow fledglings as successful unparasitized nests (1.24 fledglings vs. 2.45 fledglings). Such results extend those of other cowbird removals (Stutchbury 1997, Whitfield et al. 1999, Whitfield 2000) and are consistent with nonexperimental estimates of costs to host species (review in Lorenzana and Sealy 1999). Our experiment demonstrates that the costs of parasitism contribute substantially to lowered seasonal fecundity here.

We now consider class 2 effects. Daily nest failure rates were reduced consistently in the three cowbird removal years, and the overall probability of nest success rose from 0.30 to 0.47 at Westham and from 0.29 to 0.42 at Delta (Table 4). Other studies (Arcese et al. 1996, Arcese and Smith 1999, Clotfelter and Yasukawa 1999) have documented that increased nest failure rates are correlated with high parasitic activity by cowbirds, but McLaren and Sealy (2000) did not find such a pattern in Yellow Warblers (*Dendroica petechia*). In another removal study, Whitfield et al. (1999) also found reduced nest failures in Willow Flycatchers (*Empidonax trailii*). These results, and the results of management programs, suggest that cowbird removals usually lower nest failure rates in heavily parasitized host species. Various mechanisms can generate elevated nest failures in cowbird hosts (Rothstein 1982, Arcese et al. 1996, Hosoi and Rothstein 2000, Nakamura and Cruz 2000). We will explore these mechanisms in detail in a future paper (J. N. M. Smith, M. J. Taitt, L. Zquette, and I. H. Myers-Smith, *unpublished manuscript*).

Other studies on a smaller host species, the Willow Flycatcher, have also found that the effects of cowbirds on seasonal fecundity of hosts can be large. Sedgwick and Iko (1999) found that seasonal fecundity increased from 0.80 fledglings in parasitized females to 2.11 fledglings in unparasitized ones. Whitfield et al. (1999) found that cowbird removals increased the seasonal fecundity of females from 1.04 to 1.74 fledglings.

In summary, both class 1 effects (reduced production of host young in parasitized nests) and class 2 effects (increased nest failure rates in the presence of cowbirds) contributed to increased seasonal fecundity after removals in our study. Class 1 effects of cowbirds on hosts are probably ubiquitous, although they range

widely in severity (Lorenzana and Sealy 1999). The extent to which class 2 effects are widespread remains uncertain. Our experiment confirms earlier suggestions (Arcese et al. 1992, 1996, Arcese and Smith 1999) that such effects are strong in Song Sparrows.

Effects of cowbird removal on host population growth

Previous demographic calculations for the Westham Island population were made using data collected between 1988 and 1991 (Rogers et al. 1997). These calculations suggested that class 1 effects of cowbirds alone would be insufficient to generate stable or growing populations of Song Sparrows at Westham, unless large class 2 effects were also operating as we have now demonstrated.

In this study, we confirm experimentally that local population growth rates of Song Sparrows can be improved by cowbird removals from below 0.8 to near to or above 1.0. Values of λ would presumably have exceeded 1.0 consistently, had we been able to trap and remove all breeding female cowbirds as soon as they settled. It is noteworthy that Song Sparrows at Westham can apparently maintain stable populations despite 30% of their nests being parasitized after cowbird removals. Some authors (e.g., Halterman et al. 1999) have considered 30% parasitism as the threshold value for expecting impacts of cowbirds on hosts to be severe. Although values of λ for the Song Sparrow population at Westham are well below 1.0 in the absence of cowbird removals, local numbers there have remained stable for 14 yr (M. J. Taitt and J. N. M. Smith, *unpublished data*), possibly because of net immigration (Rogers et al. 1997). In the case of isolated populations of endangered host species, demographic rescue via immigration would be unlikely.

Our estimates of λ are not ideal, because only one of the three parameters involved, fledgling production per territory, was measured locally. The other parameter estimates were taken from the isolated Mandarte Island population. Local survival of both adults and fledglings can be estimated accurately on Mandarte (Arcese et al. 1992), and adult survival there was similar to that estimated at Westham (see *Methods* above). Successful natal dispersal, however, does occur from Mandarte (J. N. M. Smith, P. Arcese, L. F. Keller, and A. B. Marr, *unpublished data*), and such dispersal must bias local estimates of fledgling survival downward. While the magnitude of this bias is unknown, a sensitivity calculation shows that a 10% underestimate of fledgling survival would raise the estimates of λ for control sites from 0.756 to 0.775 at Westham, from 0.704 to 0.718 at Delta, and from 0.786 to 0.826 at Deas. A 25% underestimate of fledgling survival would raise values of λ at control sites to 0.804, 0.740, and 0.863, respectively. All of these values remain more than three standard errors below the break-even point ($\lambda = 1.0$). Applying the same corrections to estimates

of survival from non-crash years would raise λ to within two standard errors of 1.0 at Deas, but not at Westham or Delta. Thus, biases that underestimate fledgling survival would not readily have produced stable sparrow populations at our control sites, although they could have promoted population increases after cowbird removals.

Calculations of the effects of Brown-headed Cowbirds on population growth rates have also been made in Willow Flycatchers (Whitfield 2000) and Warbling Vireos (*Vireo gilvus*; Ward and Smith 2000). Woodworth (1999) calculated the effects of Shiny Cowbird parasitism on growth rates in Puerto Rican Vireos (*V. latimeri*). In all cases examined to date, such effects are potentially large.

How far can these results be generalized to other cowbird hosts?

Song Sparrows at our study sites have a long laying season (~20 March–1 August = ~130 d) during which they can make seven or more nesting attempts. In addition, many early nesting attempts are completed before cowbirds begin to breed (Smith and Arcese 1994, Rogers et al. 1997; Fig. 1). Also, the Song Sparrow is more effective than most smaller cowbird hosts at rearing its own young from parasitized nests (Lorenzana and Sealy 1999). Thus, Song Sparrows at our sites are tolerant to the effects of cowbird parasitism. Our experiment, therefore, will tend to underestimate the effects of cowbirds on the demography of less tolerant hosts and for hosts with laying seasons that overlap more with the laying season of cowbirds, if they experience equivalent levels of parasitism. For smaller hosts with shorter breeding seasons and greater overlap with the breeding season of the cowbird, demographic impacts of cowbirds are likely to be more severe, given equivalent levels of parasitism. Further cowbird removal studies focusing on heavily parasitized populations of such small host species would be valuable.

Parasitism levels in other studies sometimes exceed those seen here, particularly in parts of the Midwest U.S. (Trine et al. 1998, Robinson et al. 2000, Thompson et al. 2000, Trine 2000, Winslow et al. 2000). In studies like these, renesting after cowbird-induced failure is likely to be followed by further multiple parasitism, and demographic effects of cowbirds should be more severe than those we report here. In studies elsewhere, parasitism typically falls well below 60% of nests (papers cited in Morrison et al. [1999] and Smith et al. [2000]). With parasitism levels of below 35% of nests, cowbird impacts should be substantially lower than those demonstrated here.

Management of Brown-headed Cowbirds

Scientific opinion of the magnitude of the cowbird threat to host populations has oscillated over the past 25 yr. Early authors argued that the effects of cowbirds are severe enough to cause population declines in many

forest songbirds (Mayfield 1977, Brittingham and Temple 1983, Terborgh 1989). More recent research on cowbirds (summarized in Ortega [1998], Rothstein and Robinson [1998], Morrison et al. [1999], and Smith et al. [2000]) has revealed that effects on host populations are variable and difficult to assess from existing data (Smith 1999, Grzybowski 2001). Most authorities, however, agree that cowbirds can affect host populations strongly when they are abundant relative to hosts (e.g., Robinson et al. 2000) and when host populations are already in trouble because of habitat loss (Rothstein and Cook 2000). Furthermore, cowbird removal nearly always succeeds in increasing the production of host young and sometimes leads to spectacular recovery of host populations (Griffith and Griffith 2000). In addition, techniques for removing cowbirds locally are simple and reliable, and the financial and political costs of removals may be low compared to alternative options. Our experimental removals caused strong demographic responses in the Song Sparrow and are consistent with the view that similar, or even greater, benefits will follow from removal of cowbirds from heavily parasitized populations of endangered hosts.

Although our results suggest that cowbird removals will benefit threatened host populations, we echo the cautions of others (Ortega 1998, Hall and Rothstein 1999, Rothstein and Cook 2000) that cowbird removal programs should not be initiated lightly. First, before a management program is begun there should be evidence of both population declines and large parasitic effects for the target host(s). How severe such declines or parasitic effects should be is controversial (Smith 1999, Rothstein and Cook 2000). Second, because cowbird range expansion is thought to have occurred as a result of extensive land clearance and conversion to agriculture (Brittingham and Temple 1983, Rothstein 1994), removing cowbirds from specific locations can often only be a stop-gap measure. To alleviate parasitism pressure in the long term, politically demanding actions like increasing forest cover and the size of habitat reserves (Robinson and Smith 2000) and restricting cattle grazing near reserves (Goguen and Matthews 1999) may need to be implemented on a landscape scale. Otherwise, there must be a willingness to fund and continue removal programs for many years once they have begun (Rothstein and Cook 2000). Finally, there are ethical, political, and legal problems with cowbird removal (Hall and Rothstein 1999, Rothstein and Cook 2000).

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