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COWBIRD REMOVAL PROGRAMS AS ECOLOGICAL EXPERIMENTS: MEASURING COMMUNITY-WIDE IMPACTS OF NEST PARASITISM AND PREDATION

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Abstract. Removal of Brown-headed Cowbirds (*Molothrus ater*) has been increasingly employed as a management tool for the protection of songbirds. Removal programs are ecological experiments that can yield information on the population and community impacts of cowbird parasitism. We illustrate this point with two examples. First, we used an existing cowbird removal program in Michigan to test the hypothesis that cowbirds alter the composition of host communities through their parasitic activities. We compared songbird abundance and species composition in areas where cowbirds had been removed for 5–11 years to carefully matched habitats where there had been no recent cowbird removal. As expected, communities at cowbird removal sites had a higher percentage of suitable hosts in the community relative to control sites >5 km from cowbird traps. Second, we used cowbird removal to test the hypothesis that cowbirds behave as nest predators. We removed cowbirds over two years from a site in British Columbia where Song Sparrows (*Melospiza melodia*) had experienced intense cowbird parasitism and frequent nest failure. Failure rates of sparrow nests declined sharply after cowbird removal, but remained high at nearby reference sites without removals. Both approaches suggest that cowbirds have more profound effects on songbirds at the community and population levels than is currently recognized. Removal programs are a relatively untapped source for improving our understanding of cowbird biology.

Key Words: brood parasitism, cowbird removal, *Melospiza melodia, Molothrus ater*, nest predation, removal experiments, suitable hosts.

There has been considerable recent concern that the brood-parasitic activities of Brown-headed Cowbirds (*Molothrus ater*) are contributing to declines of endangered or threatened songbird populations (e.g., Robinson et al 1995a,b) and to poor health of songbird populations and communities in general (Terborgh 1989). Because cowbirds are abundant host generalists (Lowther 1993, 1995, Robinson et al. 1995a), they have the potential to generate strong impacts on preferred hosts and to threaten particular populations with extinction (Robinson et al. 1995a). Although the range expansion of the Brown-headed Cowbird has slowed (Lowther 1993, Rothstein 1994), and its numbers are actually declining in many areas (Peterjohn et al. in press, Wiedenfeld in press), Shiny (*M. bonariensis*) and Bronzed cowbirds (*M. aeneus*) are still extending their ranges and threatening new host populations and communities (Post et al. 1993, Lowther 1995). Finally, even constant or declining numbers of cowbirds might have strong ecological effects when combined with increasing habitat loss and degradation.

To make strong inferences about how cowbirds affect host populations and communities, it is desirable to do controlled experiments that are replicated across several geographical locations. Constraints on budgets and personnel have so far precluded research of this type. The two largest costs involved in such research are: (1) the removal of cowbirds so that large areas with fewer cowbirds may be compared with similar, but unmanipulated areas; and (2) the costs of monitoring the numbers and breeding success of songbirds on experimental and control areas.

There is, however, a potential solution to the high costs of experimental manipulation of cowbird abundance. Cowbird removal on a landscape scale is already in progress in the form of cowbird control programs. Cowbird control figures prominently in the management of four endangered taxa: the Kirtland's Warbler (*Dendroica kirtlandii*), the Least Bell's Vireo (*Vireo bellii pusillus*), the Southwestern Willow Flycatcher (*Empidonax traillii extimus*), and the Black-capped Vireo (*V. atricapillus*) (Robinson et al. 1995a).

As a result of concerns about impacts of cowbirds on other songbird populations, extensive cowbird removal programs are becoming an increasingly common management practice in the U.S. (Robinson et al. 1995a, Kepler et al. 1996). There is general agreement that cowbird removal has been an appropriate tool for protecting populations of endangered species (but see Robinson et al. 1995a). However, Rothstein and Cook (in press), have noted that some recent cowbird control operations are founded on the tenuous idea that, if cowbird removal works in specific cases, it is generally an appropriate management tool. It is far from clear that cowbird parasitism has been a major contributor to population declines in songbirds (Peterjohn et al. in press, Wiedenfeld in press), despite the publicity accorded such claims (Terborgh 1989, Holmes 1993). It is therefore important to test the assumption that cowbirds are a significant general conservation concern, as well as a potentially serious local concern.

Over one million dollars of federal and state funds is spent annually on cowbird control programs in California alone (S. I. Rothstein pers. comm.). Therefore, it is likely that several million dollars are spent annually on cowbird control across the U.S. With such a significant allotment of conservation dollars to cowbird control, we believe that managers and researchers have a duty to collaborate to gain as much information as possible from a management action that can absorb much of a regional conservation budget.

Viewing cowbird removal programs as ecological experiments permits fruitful investigation into several areas of cowbird biology. Our aim in this paper is to illustrate the use of removal programs through two examples that explore (1) the effects of cowbirds on host communities, and (2) the mechanisms of parasite/host interactions. Although these two studies were conducted at different spatial and temporal scales, they both employed cowbird removal as an experimental tool. Hereafter, we refer to cowbird trapping as "cowbird removal" and restrict use of the term "control" to the experimental sense, i.e., reference sites that do not receive the experimental treatment (cowbird removal).

I. EFFECTS OF LONG-TERM COWBIRD REMOVAL ON HOST COMMUNITY COMPOSITION

Cowbird pressure on suitable host species may reduce abundance of suitable host populations relative to the abundance of host species with which the cowbird does not interact strongly, e.g., species that have evolved egg ejection (Rothstein 1975a). As cowbirds are host generalists, they can have strong effects on a number of preferred hosts without negative feedback on their own numbers (Robinson et al. 1995a). If several host species are affected, cowbird pressure may eventually change the composition of entire songbird communities. One prediction of the hypothesis that cowbirds have significant effects on host communities is that suitable hosts will make up a larger percentage of songbird individuals in areas where cowbirds have been removed on a long-term basis compared to areas in similar habitat where cowbird densities are unmanipulated. Few studies of cowbird biology to date have examined the host community as a whole (but see Peck and James 1987, Strausberger and Ashley 1997) and none, to our knowledge, have conducted a search for such patterns. We now use a cowbird removal program as a treatment in a community-wide experiment to test this prediction.

EFFECTS OF COWBIRD REMOVAL ON SONGBIRD COMMUNITIES IN JACK-PINE HABITAT

One of us (KD) conducted a study in the jack-pine (*Pinus banksiana*) ecosystem of northern lower Michigan, where cowbirds have been removed since 1972 in an effort to protect the Kirtland's Warbler. Cowbird traps are patchily distributed across a 19,200 km^2 region near breeding sites used by the warblers. Since the distribution of the warblers is dynamic, the location of traps shifts over periods of a few years. However, many local areas have been trapped consistently for 5–11 years. Details of cowbird removal procedures on the breeding grounds of the Kirtland's Warbler are given in DeCapita (in press) and Kelly and DeCapita (1982).

Unlimited radius point counts of 8 min duration were performed in 1996 at ten cowbird removal sites where cowbird trapping had been conducted for 5–11 years, and at ten control sites in similar-aged jack pine habitat that were >5 km from cowbird traps (total number of sites censused = 20). Control sites were in areas that had not experienced cowbird removal for at least five years. All control areas were chosen according to detailed survey maps followed by extensive ground-truthing to match the early successional jack pine forests of removal sites. Further detailed habitat measurements confirmed that density and composition of vegetation were similar at removal and control sites (K. De Groot, unpubl. data).

Point counts and habitat measurements were performed similarly in 1997 with the following changes. (1) Eight removal sites and eight control sites between 5 and 10 km from cowbird traps were used. (2) An additional eight control sites >10 km from cowbird traps were censused (total number of sites censused = 24). (3) Point counts were extended to ten min. (4) Five min of playback of cowbird female chatter call was added after each point count. Thus, counts of cowbirds and other songbirds are not directly comparable from 1996 to 1997. Cowbird playback was implemented to improve the likelihood of detecting cowbirds, following very low cowbird detection rates in 1996. Counts were performed twice in 1996 and three times in 1997 between mid-May and early July.

Songbirds (excluding cowbirds) detected during counts were placed into two categories: suitable hosts, i.e., species that accept cowbird eggs and feed their young a largely animal diet, and unsuitable hosts, such as cavity nesters, species that feed a mainly plant diet to their young, corvids, and species that reject cowbird eggs

TABLE 1. THE NUMBER OF COWBIRDS DETECTED IN THE SONGBIRD COMMUNITIES OF REMOVAL SITES, CONTROL SITES 5–10 KM FROM COWBIRD TRAPS AND >10 KM FROM COWBIRD TRAPS IN JACK-PINE FORESTS OF NORTHERN LOWER MICHIGAN

		Number of cowbirds detected per count station					
		1996		1997			
		8-min point counts		10-min point counts		5-min playback	
		females	males	females	males	females	males
Removal sites	Mean	0	0.025	0	0.063	0.021	0.028
	SE	0	0.018	0	0.034	0.015	0.015
Control sites	Mean	0	0.167	0.069	0.326	0.056	0.257
5–10 km	SE	0	0.069	0.025	0.062	0.021	0.035
Control sites	Mean	n/a	n/a	0.174	0.583	0.222	0.576
>10 km	SE	n/a	n/a	0.062	0.081	0.047	0.103

from their nests (Rothstein 1975a). The proportion of suitable cowbird hosts in the songbird communities was then analyzed using repeated measures analysis of variance (Kuehl 1994). Differences in cowbird numbers among removal sites, control sites 5–10 km from traps and control sites >10 km from traps were tested using Mann-Whitney U (1996) or Kruskall-Wallis (1997) non-parametric analyses, followed by Dunnett T3 multiple comparison tests (1997).

COWBIRD DENSITIES AS A FUNCTION OF DISTANCE FROM COWBIRD TRAPS

Cowbird removals were highly effective at reducing cowbird abundance at removal sites. In 1996, 0.025 male cowbirds were detected per count station at removal sites and no female cowbirds were counted on removal or control sites (Table 1). Male cowbird numbers increased over six-fold at control sites >5 km from cowbird traps compared to cowbird removal sites (Table 1; $Z = 2.171$, $P = 0.03$).

In 1997, the mean number of female cowbirds detected on removal sites ranged from zero during the 10-min point count to 0.021 per count station during the 5-min cowbird playback (Table 1). Mean numbers of male cowbirds ranged from 0.063–0.028 per count station on removal sites (Table 1). Both female and male cowbird abundances differed significantly among removal and all control sites (females $\chi_{0.05} = 11.015$, df = 2, $P = 0.004$; males $\chi_{0.05} = 18.795$, df = 2, $P < 0.001$). Mean number of female cowbird detections more than doubled when distance from removal sites increased to 5–10 km. However multiple comparison tests reveal that this difference is not statistically significant ($P > 0.05$). Female cowbird numbers at control sites >10 km from cowbird trap were more than three times higher than at sites 5–10 km from cowbird traps ($P = 0.025$) and more than ten-fold higher than at removal sites ($P = 0.01$). Male cowbirds were five times more abundant when distance from traps increased from removal sites (0 km) to control sites 5–10 km from cowbird traps ($P = 0.001$). Nine times more male cowbirds were counted at sites >10 km from traps compared to removal sites ($P = 0.003$). Male cowbird numbers were also significantly higher at sites >10 km from cowbird traps compared to sites 5–10 km from traps ($P = 0.046$).

IMPACTS ON SONGBIRD COMMUNITY COMPOSITION

The percentage of suitable host individuals in cowbird removal areas was 4–9% higher than in control sites (Fig. 1). This difference was significant at the 5% level in 1996 ($F_{1,18} = 11.762$, $P = 0.003$) but not in 1997, where it was significant at the 10% level only ($F_{2,21} = 2.859$, $P = 0.08$). No individual species accounted for a large part of the difference in proportions of suitable hosts. Rather, the shift in community composition was a result of small positive shifts in the abundance of suitable host individuals in cowbird removal sites, compared to control sites.

II. COWBIRDS ACT AS PREDATORS TO INDUCE NEST FAILURE IN SONG SPARROWS

It is widely agreed that nest predation (total nest failure) is one of the principal limiting factors in songbird populations (e.g., Martin 1993, Robinson et al. 1995b). Cowbirds can cause total nest failure in several ways. (1) Hosts may desert clutches when harassed by laying cowbirds or when a parasitic egg appears in the nest (Burhans in press). (2) Egg removal may reduce host clutches below a desertion threshold (Rothstein 1982). (3) Cowbirds may damage or puncture eggs and induce hatching failure (Post and Wiley 1977, Smith and Arcese 1994). (4) Cowbirds may prey on clutches or broods of host young (Arcese et al. 1992, 1996).

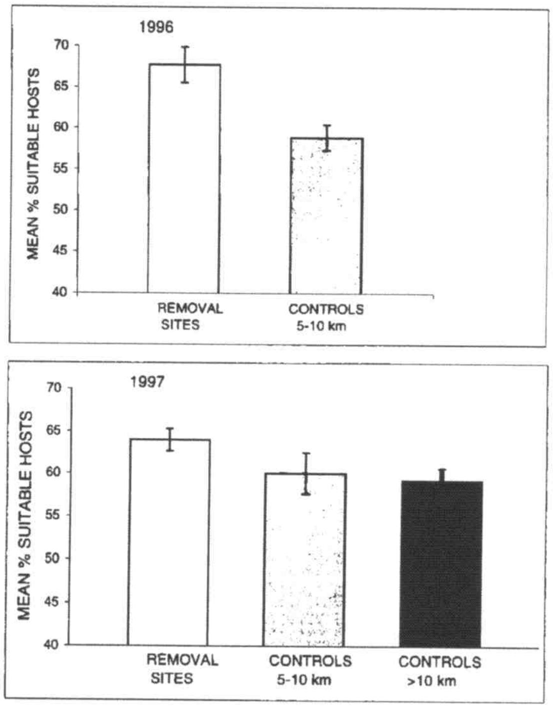

FIGURE 1. Mean percentages of suitable hosts detected during point counts in the songbird communities of jack-pine forests of northern lower Michigan at ten removal sites and ten control sites >5 km from cowbird traps in 1996 and eight removal sites, eight control sites 5–10 km from traps and control sites >10 km from cowbird traps in 1997. Bars represent one SE.

If cowbirds commonly exhibit such "predatory" activity, their effects on their hosts will be underestimated simply by monitoring their parasitic effects on hosts. Experimental removal of cowbirds is one way to estimate the extent to which cowbirds act as nest predators. If cowbirds commonly cause host nest failure, there should be a reduction in failure rates when cowbirds are removed from an area where they were abundant.

Local Cowbird Removals to Test the Strength of "Predatory" Behavior by Cowbirds

Cowbirds were removed from a study site on Westham Island in southwestern British Columbia, Canada. Cowbirds are abundant on Westham (5–10 % of the local songbird community), and parasitism of the Song Sparrow (*Melospiza melodia*) was frequent there during four years of previous work (Rogers et al. 1997). Two additional study sites in similar riparian habitat were established as experimental controls (i.e., no cowbird removal) in 1995. These sites were 8 km (Deas Island Regional Park) and 20 km (Delta Nature Reserve) from the removal site.

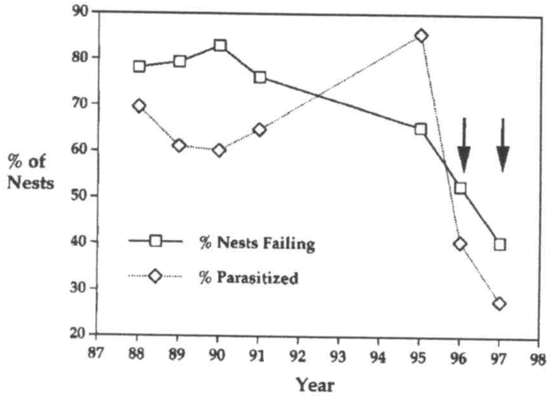

FIGURE 2. Annual percentages of nests parasitized by Brown-headed Cowbirds and daily nest failure rates in Song Sparrow nests on Westham Island, British Columbia, in relation to cowbird removals in 1996 and 1997. Arrows indicate cowbird removal.

Cowbirds were removed using modified portable Swedish Crow Traps supplied with three female and two male decoys (Griffith and Griffith in press), and by trapping at a feeding station on the study site. Removals began in mid-May 1996 and in mid-April 1997. Male cowbirds were released immediately, and females were held in captivity until the end of the cowbird breeding season (mid-July), when they too were released. Nests of Song Sparrows were monitored at the removal site from 1988 to 1991, and at removal and control sites from 1995 to 1997. Nests were found mainly by following incubating females back to their nests after foraging trips. Percentages of nests parasitized and failing at the three sites were compared using Chi-square tests of homogeneity.

We conducted longitudinal comparisons within one site (Westham) and horizontal comparisons across sites within each year. In each case, we predicted lower nest failure where cowbirds were removed. In longitudinal comparisons at the removal site across seven years, cowbird removals were associated with a sharp decline in rates of Song Sparrow nest failure and lower parasitism levels (Fig. 2). This occurred despite incomplete cowbird removal in both 1996 and 1997 (parasitism was never reduced below 29%). Proportions of nests failing at the two control sites were 18–58 % higher than at the removal site in 1996 and 1997 (Table 2). Daily nest failure rates were also higher at control sites than at the removal site in both 1996 and 1997 (Table 2).

Failures at Westham varied significantly across years ($\chi^2 = 6.22$, df = 2, $P < 0.05$), with lower values in the two removal years. Within years and across sites, failure rates were similar

TABLE 2. FREQUENCIES OF PARASITISM BY BROWN-HEADED COWBIRDS AND NEST FAILURE IN SONG SPARROWS AT THREE SITES IN SOUTHWESTERN BRITISH COLUMBIA, CANADA

Year/site	Number of nests	% parasitized	Proportion failing	Daily failure rate[a] (SE)
1995 Westham	55	76.4	0.654	0.037 (0.011)
1995 Delta	10	70.0	0.750	0.042 (0.036)
1995 Deas	5	100.0	0.600	0.036 (0.055)
1996 Westham[b]	85	40.7	0.528	0.037 (0.005)
1996 Delta	38	60.5	0.622	0.061 (0.022)
1996 Deas	19	70.6	0.684	0.050 (0.029)
1997 Westham[b]	132	29.4	0.454	0.030 (0.005)
1997 Delta	67	44.4	0.716	0.066 (0.012)
1997 Deas	44	64.6	0.574	0.041 (0.014)

[a] Daily failure rates (Hensler and Nichols 1981) were calculated from a slightly different sample of nests than those used to calculated the percentages of nests parasitized and the proportions of nests failing.
[b] Female Brown-headed Cowbirds were removed at this year and site.

in 1995 before the onset of cowbird removals (χ^2 = 0.15, df = 2, P > 0.10). In 1996, when cowbird removals began in mid-May, there was again no significant difference in failure rates across sites (χ^2 = 2.55, df = 2, P > 0.10). In 1997, when removals began a month earlier, there was a clear difference across sites (χ^2 = 12.40, df = 2, P = 0.002), with much lower failure rates at Westham (Table 2).

There were few data from the control sites in the pre-removal year (1995), precluding a strong test of the hypothesis that the three sites were not inherently different in their nest failure rates. Failure rates at the removal site in 1995, however, did not differ significantly from those at the control sites in 1996 and 1997 (χ^2 tests, P > 0.10). This result makes it unlikely that site effects, rather than cowbird removal, caused apparent temporal differences in failure rates at the removal site.

Parasitism levels did not differ significantly across sites in the pre-removal year (1995: χ^2 = 1.790, df = 2, P > 0.10), but were significantly lower at the removal site than at control sites in both 1996 (χ^2 =7.63, df = 2, P < 0.025) and 1997 (χ^2 = 16.902, df = 2, P = < 0.001). Thus, cowbird removals were associated with lower nest failure rates and sharply reduced parasitism levels both among sites within years and within one site across years.

DISCUSSION

COMMUNITY PATTERNS OF HOSTS IN RELATION TO COWBIRD ABUNDANCE

In the jack-pine forests of Michigan, cowbird removals greatly reduced the local density of cowbirds and were associated with a quantitative shift in the host community. Removal sites supported a higher percentage of suitable cowbird hosts compared to control sites at least 5 km from cowbird traps. While the magnitudes of these shifts were small, this region is heavily forested, and supports few cowbirds compared to other regions of the continent (Peterjohn et al. in press, Robinson et al. in press, Wiedenfeld in press, Whitfield in press). A marked shift in community composition would be much more likely in areas that support higher cowbird densities, and where cowbird removal is continuous at the same location over a longer period.

Similar comparisons at removal sites where cowbirds are much more abundant regionally would provide better tests of the idea that cowbirds have strong effects on host communities. Indeed, Griffith and Griffith (in press) have made precisely this claim for southern coastal California, but it has not yet been supported by survey data from a systematic study.

COWBIRDS AS CAUSES OF NEST FAILURE IN HOSTS

In the local cowbird removal study we conducted in British Columbia, cowbird removal reduced rates of nest failure in a common host, the Song Sparrow. Nest failure rates at the removal site in 1996 and 1997 were lower than in all five previous years of study at this site, although failure rates did vary somewhat from year to year, being lower for an unknown reason in 1995 (Fig. 2). Nest failure rates at the control sites were higher in 1996, and significantly higher in 1997, compared to failure rates at the removal site. Parasitism levels also varied among years, being high in 1995 and significantly lower after cowbird removal was initiated in 1996. Parasitism rates at control sites remained high in 1996 and 1997.

The two principal nest finders had 20 and 7 years experience in locating Song Sparrow nests and attempted to find and monitor all nests of

10 to 45 breeding pairs at each site. It is therefore unlikely that differences in nest failure and parasitism rates among years were due to differential sampling of well-concealed and poorly-concealed nests across years.

Cowbird abundance and local nest failure rates in Song Sparrows were also correlated on Mandarte Island, British Columbia, where cowbird abundance is moderate to low (Smith and Arcese 1994, Arcese et al. 1996). These data suggest that cowbird parasitism and predation may influence the metapopulation dynamics of Song Sparrows in coastal British Columbia (Arcese et al. 1992, Smith et al. 1996, Arcese et al. 1996, Rogers et al. 1997).

Song Sparrows in coastal British Columbia reproduce poorly at sites with high cowbird abundance (Smith et al. 1996, Rogers et al. 1997). These sites, however, are probably not representative of regions where cowbird abundance is declining (Peterjohn et al. in press, Wiedenfeld in press), and where most Song Sparrows and other host species may live in healthy metapopulations. Neither Whitfield (in press) nor Stutchbury (1997) found strong effects of cowbird removal on nest failure rates of Southwestern Willow Flycatchers (*Empidonax traillii extimus*) and Hooded Warblers (*Wilsonia citrina*), respectively.

COWBIRD REMOVALS AS ECOLOGICAL EXPERIMENTS—RECOMMENDATIONS

The removal studies discussed here suggest that cowbirds may have strong effects on host populations and communities. However, this conclusion is tentative and our results should not be used to justify cowbird removal programs in general. We advocate further investigation and present recommendations for ways managers and researchers can learn from cowbird control programs.

Researchers and managers should obtain pre-trapping baseline data on cowbird and host abundance and host reproductive success and, after the onset of trapping, they should monitor changes in host demographics and cowbird abundance across time and space (i.e., compare songbird populations and communities in cowbird removal areas to reference populations in similar habitat). It is important to note that temporal comparisons alone are not sufficient (see above), as year to year variation in host breeding success can mimic the effects of cowbird removal.

Managers who follow these guidelines will learn whether cowbird removal will be useful, before the initiation of a costly removal program. Pre- and post-trapping demographic data on host numbers and nesting success will allow managers to evaluate the effectiveness of the removal program in achieving its goals, and whether cowbird removal is still necessary.

When it is not feasible to design an experimental cowbird removal program from the outset, the next best approach for researchers is to use an existing cowbird removal program, and to add a monitoring program at both removal sites and non-removal sites, as illustrated in our northern Michigan study. Following these guidelines for data collection will allow powerful tests of the effects of cowbirds on host population and community dynamics. Finally, information from cowbird removal programs may illuminate other aspects of cowbird biology. For example, behavioral tests of the responses of hosts to cowbirds (e.g., Neudorf and Sealy 1992) in removal and control areas might reveal how quickly hosts alter anti-parasite behaviors. Removal programs represent an almost untapped resource for improving our understanding of the ecological impacts of parasitic cowbirds.

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