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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