COMMUNITY-WIDE IMPACTS OF A GENERALIST BROOD PARASITE, THE BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*)

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Abstract. Many ecologists have searched for species that contribute strongly to the structure and composition of communities of organisms. It has been speculated that the Brown-headed Cowbird (*Molothrus ater*), a generalist brood parasite, is capable of changing songbird communities. Cowbird parasitism may reduce numbers of suitable hosts, i.e., songbirds that accept cowbird eggs and raise cowbird young. In contrast, songbird species that eject cowbird eggs, nest in cavities, feed their nestlings mainly seeds or fruits, or are too big to parasitize, should escape the effects of cowbird parasitism. Thus, cowbirds may change the composition of songbird communities by selectively depressing numbers of suitable host individuals and species. We tested this hypothesis using an existing cowbird removal program in the state of Michigan, USA. This program was designed to protect the endangered Kirtland's Warbler (*Dendroica kirtlandii*) from cowbird parasitism throughout its 19 200-km² breeding range. We compared songbird community composition in stands of young jack pine *(Pinus banksiana)* where cowbirds had been removed for 5–11 yr to communities in Control sites 5–10 km from cowbird traps and >10 km from cowbird traps. We predicted that cowbird Removal sites would support greater songbird richness and evenness and a greater proportion of suitable host vs. unsuitable host individuals relative to Control sites. Results from songbird point counts revealed that species richness and evenness were very similar at cowbird Removal and Control sites and that Removal sites contained only 4.0–8.7% more suitable host individuals than Control sites. Our results suggest that cowbirds do not strongly influence the composition of songbird communities in jack pine forests of Michigan. Several factors may explain a lack of community-wide response to long-term cowbird removal, including the population dynamics of songbirds on a broader scale. We conclude that there is little support for adding cowbirds to the short list of species that can regulate entire communities. Our results have implications for the increasingly widespread use of cowbird removal as a management tool.

Key words: acceptors; brood parasite; Brown-headed Cowbird; community composition; cowbird removal; demography; Dendroica kirtlandii; *Kirtland's Warbler;* Molothrus ater; *rejecters; songbirds; species diversity.*

INTRODUCTION

Community ecologists are primarily interested in determining factors that maintain or alter community structure. Early observations of the importance of some predators in regulating freshwater aquatic communities (Brooks and Dodson 1965, Hall et al. 1970, Hurlbert et al. 1972) have generated considerable research into the role of predators in other systems (see Power et al. [1996] and Hurlbert [1997] for reviews). Subsequent work found that herbivores, producers, and mutualists may also have strong effects on communities (Power et al. 1996), but such effects are uncommon in experimental studies (Hurlbert 1997). In this paper, we investigate whether a brood parasite can generate changes in community composition. To our knowledge, this is the first study to search for such regulatory ability in a brood parasite.

The Brown-headed Cowbird (*Molothrus ater*) of North America is an obligate and generalist brood parasite, with >220 known songbird hosts (Friedmann et al. 1977, Lowther 1993). Generalist brood parasites have the potential to change the composition of entire host communities. Their lack of host specificity allows them to affect a number of host species strongly, without the negative feedback on their own numbers that is generally associated with single host–parasite interactions (Mayfield 1977, May and Robinson 1985, James and McCulloch 1995). The Brown-headed Cowbird is causing concern among ornithologists because it has greatly expanded its range during the past two centuries (Mayfield 1965, Rothstein 1994), exposing previously naïve songbird populations to the threat of brood parasitism (e.g., Mayfield 1977).

Songbird communities (excluding cowbirds) can be divided into two groups, depending on their value to cowbirds as hosts. *Suitable hosts* accept cowbird eggs

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and feed their young largely on arthropods. *Unsuitable hosts* include cavity nesters, species that feed their young mainly seeds and fruits, corvids, and species that reject cowbird eggs from their nests (Rothstein 1975, Rohwer and Spaw 1988). Cowbird pressure on suitable hosts can be severe. For example, in small (<500 ha) forest fragments in Illinois, 64% of suitable host nests are parasitized with an average of two cowbird eggs (Robinson et al. 1995). Cowbird pressure on suitable hosts may reduce their abundances relative to the abundances of unsuitable hosts with which the cowbird does not interact strongly. If several host species are affected and if intense parasitism persists over many generations, cowbird pressure may eventually change the composition of entire songbird communities. In a model simulating cowbird effects on host communities, Gryzbowski and Pease (1999*a*) predict that extinction-prone hosts could be extirpated from communities where cowbird pressure is intense.

There has been widespread speculation that nest parasitism has contributed to declines in some songbird populations, and that cowbirds may change the composition of entire songbird communities (Mayfield 1977, Brittingham and Temple 1983, Terborgh 1989, Wiens 1989a, Böhning-Gaese et al. 1993, Griffith and Griffith 2000, reviewed in Smith and Rothstein 2000). These speculations have led both to claims that cowbirds indeed threaten entire songbird communities (Schram 1994), and to management prescriptions that assume that cowbirds often harm songbird populations (Grzybowski and Pease 1999*b*). Over one million dollars is spent annually on cowbird control in California alone (Rothstein and Cook 2000).

Despite ample evidence that cowbird parasitism causes reproductive losses for hosts (Walkinshaw 1983, Marvil and Cruz 1989, Donovan et al. 1995, James and McCulloch 1995, Romig and Crawford 1996, Braden et al. 1997, Sedgwick and Iko 1999, Strausberger and Ashley 1997), there is little evidence that cowbird parasitism regulates songbird populations and communities (May and Robinson 1985, Pease and Grzybowski 1995, Ortega 1998, Sedgwick and Iko 1999). Furthermore, there is evidence that local reproductive success and songbird population trends may become uncoupled due to immigration from distant source populations (Donovan et al. 1995, Robinson et al. 1995, Brawn and Robinson 1996). Thus, with the exception of cowbird removal programs designed to protect an endangered species with little hope of demographic rescue, there is no clear justification for cowbird removal programs. Therefore, an empirical test of the hypothesis that a brood parasite generates community-wide changes in songbird communities is an interesting ecological question that also has broad management implications.

The Effects of Long-Term Removal of Brown-Headed Cowbirds on Songbird Communities: Hypothesis and Predictions

We used an existing cowbird removal program and added experimental controls to test the following hypothesis regarding cowbird-induced changes to songbird communities: *Brown-headed Cowbirds change the composition of songbird communities by depressing numbers of suitable host individuals.*

Three predictions of this hypothesis are: (1) suitable host individuals will make up a larger proportion of songbird communities in areas where cowbirds have been removed on a long-term basis, compared with areas in similar habitat where cowbird densities are unmanipulated, (2) songbird species richness and evenness will be greater in cowbird removal areas, and (3) differences between cowbird removal sites and unmanipulated sites will increase with increasing distance from cowbird removal areas.

While support for these predictions can provide evidence that cowbirds change the composition of songbird communities through their brood parasitic activities, there could be alternative explanations for the above patterns. Landscape-scale factors, such as proximity to agricultural areas or human populations, also influence densities of nest predators (Ambuel and Temple 1983, Wilcove 1985, Andren and Angelstam 1988). If high levels of nest predation strongly limit songbird populations, then nest predators may be more important than brood parasites in determining the structure of songbird communities. This alternative hypothesis should be considered if patterns 1 and 2 above are accompanied by a lower rate of predation of suitable host nests in cowbird removal sites compared with experimental controls.

Within a landscape context, songbird community composition may be predicted by local-scale habitat variables such as vegetation structure (height) diversity (MacArthur and MacArthur 1961, MacArthur et. al. 1962, Cody 1981, but see Willson 1974) and/or specific plant species assemblages (James 1971, Karr and Roth 1971, Probst et al. 1992). Biological factors which influence avian habitat use include availability of foraging substrate and suitable nesting sites (Mackenzie et al. 1982, Robinson and Holmes 1982, Yahner 1986, Martin 1988*a, b,* Steele 1993, Matsuoka et al. 1997). If differences in songbird community composition are due to local habitat variables, we could find differences in vegetation structure and composition between cowbird removal sites and experimental controls, despite attempts to control for habitat variables.

The extensive cowbird removal program designed to protect the Kirtland's Warbler (*Dendroica kirtlandii*) in Northern Michigan provided an experimental framework for testing the hypothesis that cowbirds change songbird communities. The Kirtland's Warbler is an endangered neotropical migrant songbird with very specific habitat preferences and a limited breeding range. It nests only in young jack pine forests (1–6 m in height) in northern Michigan (Walkinshaw 1983). Concern about Kirtland's Warblers heightened after a census in 1971 recorded only 201 singing males, a marked decline from 502 counted a decade earlier
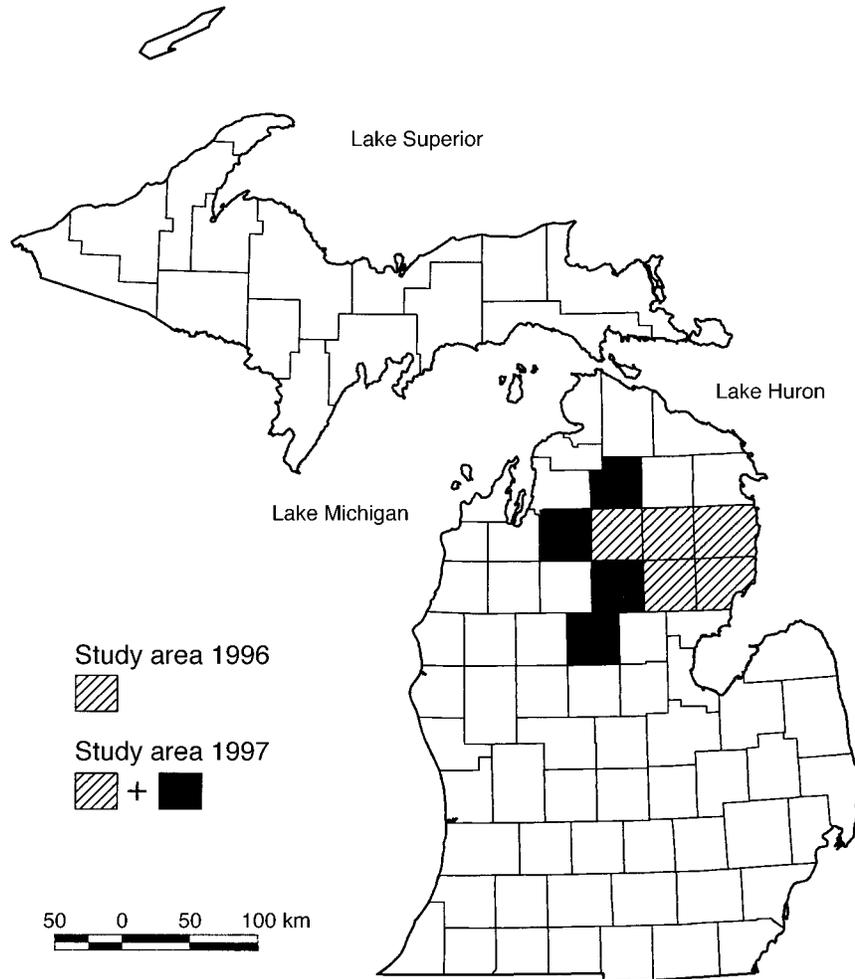
FIG. 1.   Map of Michigan (modified from Brewer et al. 1991) showing location of study.

(Mayfield 1972). Researchers suggested that limited quality and quantity of habitat, combined with high levels of nest parasitism by cowbirds, were responsible for this decline (Mayfield 1972, Walkinshaw 1972, Ryel 1981, Probst and Weinrich 1993). Cowbird removal from Kirtland's Warbler breeding areas began in 1972 and has continued every year since (Walkinshaw 1983, DeCapita 2000). This cowbird removal program represents a classic PRESS perturbation (Bender et al. 1984), wherein a manipulation to a system is maintained over a prolonged period (in contrast to a short-term, PULSE manipulation). We compared songbird communities on cowbird removal sites to experimental controls at least 5 km from cowbird removal areas.

METHODS

Study sites

Field work took place in the jack pine barrens of Northern Lower Michigan and encompassed most of the breeding grounds of the Kirtland's Warbler (Fig. 1). This landscape is moderately to heavily forested, with a mosaic of cut, regenerated, and managed stands of conifers and deciduous forest. Study sites were in 7–20-yr-old stands of even-aged jack pine (*Pinus banksiana*), often interspersed with oak (*Quercus* spp.) and pin cherry (*Prunus pensylvanica*) and occasional small stands of red pine (*Pinus resinosa*) or trembling aspen (*Populus tremuloides*). The dominant ground cover was of grasses (e.g., *Andropogon gerardii, Deschampsia flexuosa*), sedge (*Carex pensylvanica*), blueberry (*Vaccinium* spp.), and other heaths (Ericaceae). De Groot (1998) provides a complete list of trees, shrubs, and ground cover found on the study sites.

Cowbird traps were erected and maintained by the U.S. Fish and Wildlife Service across the 19 200-km² area where most nesting Kirtland's Warblers occur (DeCapita 2000, Fig. 2). Up to 67 traps (mean = 41 traps) operated between 1972 and 1997. These traps have removed >105 000 cowbirds (mean = 4050 cowbirds/yr) from Kirtland's Warbler breeding areas (Deloria and DeCapita 1997).
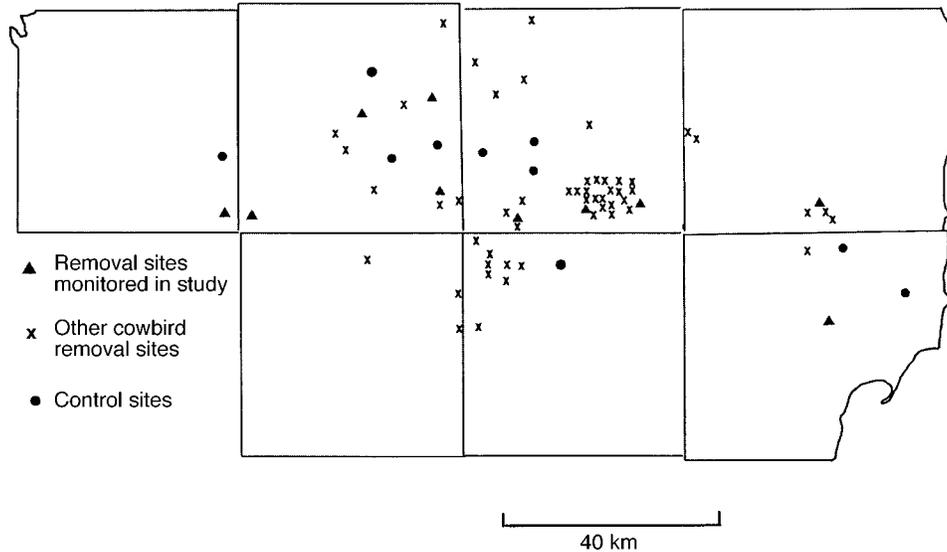
FIG. 2. Schematic diagram of the 1996 distribution of Removal sites, other active cowbird traps, and Control sites >5 km from cowbird traps.

We chose ten cowbird Removal sites adjacent to currently active cowbird traps that had been in operation for 5–11 consecutive years (mean 7.6 yr) preceding the study. Choice of Removal sites was limited by permits, which prohibited our access to most Kirtland's Warbler breeding sites; therefore, we used all removal sites that were available to us that met the above criteria. We located suitable Control sites by following several steps: we first identified areas that were ≥5 km from cowbird traps or any area that had experienced cowbird removal within the past 5 yr; we then examined survey maps (provided by the U.S. Forest Service and the Michigan Department of Natural Resources) to identify those areas that contained jack pine habitat of age class similar to that of removal sites; finally, we visited potential sites to ground truth the survey maps. We used only sites that matched the general habitat characteristics (e.g., stand height, ground cover) of the removal sites. Due to these restrictions, there were few eligible Control sites available; however, we continued to search for suitable Control sites until we had a balanced study design. Ten Removal sites and ten Control sites were used in the first year of the study (a total of 20 sites in 1996, Fig. 2). In 1997, eight cowbird Removal sites and eight Control sites 5–10 km from cowbird traps were used. In addition, the scale of the project was expanded to include eight Control sites >10 km from cowbird traps; thus in 1997 there were a total of 24 experimental sites. As a result of changes in the configuration of active cowbird traps, only half of the Removal and Control sites used in 1996 could be used again in 1997.

Site area encompassed a half circle of radius 1 km (total area = 1.57 km^2), adjacent to the cowbird trap in the case of cowbird Removal sites. A half circle was used to enable sites to be monitored without entering Kirtland's Warbler territories. As a result of the restricted access to areas that were used heavily by Kirtland's Warblers, this species was a minor component (<0.02%) of the songbird community in areas that we censused.

Songbird point counts

Field work was performed by De Groot and one assistant in the first year of the study and by De Groot and three assistants (two full-time and one half-time) in 1997. We conducted songbird point counts to test the prediction that songbird communities in cowbird Removal areas differed in composition from those in Control areas ≥5 km from cowbird traps. Four 1-km transect lines, each 60° apart, were flagged within each site. To comply with our entry permit, transect lines were oriented to avoid Kirtland's Warbler territories. Transect lines on control sites were chosen to mimic conditions on removal sites (e.g., same proportion of lines on forestry roads vs. dense habitat). Six permanent count stations were randomly chosen along these transect lines (Fig. 3). However, to avoid recounting individual songbirds, we restricted randomization so that successive count stations were not closer than 400 m.

The same two observers performed avian point counts in both 1996 and 1997. Two additional observers were trained to conduct point counts in 1997. We trained observers over a 4-wk period each year, during which all personnel performed simultaneous point counts at each sampling point. Results and observations were compared and discussed among observers before leaving count stations. After the training period, any observer biases in the data were balanced by having
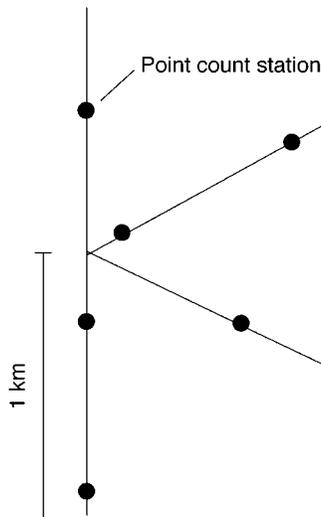
FIG. 3. Schematic diagram of transect lines through a study area with one possible distribution of randomly chosen point count locations.

each observer count the same number of Removal sites as Control sites.

We performed 8-min, unlimited-radius point counts between dawn and 1000 in the morning, identifying birds by song, calls, or visual observation; noting species, approximate distance from the observer, and time (to the nearest minute) of first detection. Counts were conducted on most mornings weather permitting, i.e., no heavy rain, constant drizzle, or strong winds. Each morning we simultaneously sampled a Removal and a Control site in 1996 and a Removal, a Control site 5–10 km, and a Control site >10 km from traps in 1997. This procedure prevented biases owing to differing weather conditions during count periods. We counted songbirds at all sites twice between early June and mid-July in 1996 and three times between mid-May and early July in 1997. Successive counts were performed at the same point count stations. In 1997, we extended the point count duration to 10 min, after analysis of detection curves from 1996 indicated that this was appropriate.

Cowbird counts

Cowbirds were censused to test the assumption that cowbird densities were greater in Controls than at cowbird Removal sites. We censused cowbirds during point counts, noting the sex of individuals. In 1997, we added 5 min of playback of cowbird female chatter calls after each point count to improve the likelihood of detecting cowbirds, following very low cowbird detection rates in 1996 (Miles and Buehler 2000, Rothstein and Cook 2000).

Nest monitoring

Samples of nests (33 nests in 1996 and 98 nests in 1997) were monitored within Removal and Control

sites to test for differences in rates of nest survival and to test the assumption that frequency and intensity of cowbird parasitism was higher in Control sites than in Removal sites. We checked nests every 3–5 d in 1996 and every 3–6 d in 1997, making certain to check nests just before we expected chicks to fledge and making a final check after the chicks had fledged. Nests that contained ≥1 live chick until 1–2 days before fledging and that showed no visible signs of nest predation (e.g., torn nest lining) after fledging, were scored as successful. While this procedure may have slightly underestimated true rates of nest failure, our goal was to compare relative nest failure rates in cowbird removal and experimental control areas. We targeted suitable cowbird hosts for monitoring, but also monitored unsuitable host species' nests opportunistically (~26% of all nests) to assess their survival rates.

Habitat measures

Several vegetation variables were measured to test the alternative hypothesis that habitat differences between cowbird Removal and Control sites caused differences in songbird communities. We sampled two count stations per site in 1996 and all six count stations in 1997.

We randomly selected two (1996) or six (1997) 20 × 20 m plots that were 0–100 m from point count stations at each site. We counted trees, shrubs, and snags within these plots to estimate density of trees within a plot, volume of shrubs (by counting number of stems) and composition of species. We noted circumference of trunks at breast height and later converted circumference measurements to diameter at breast height (dbh) to provide a measure of the maturity of forests, since songbird species composition may depend on stand age. Within each 20 × 20 m plot, we randomly selected one (1996) or four (1997) 1 × 1 m plots within which we estimated the proportion of each ground cover type (e.g., grasses and sedge, Ericaceae, leaf litter) to the nearest 5%. We measured a combination of ground and understory (0–1 m) vegetation density at one (1996) or two (1997) of the 1 × 1 m plots using a 1 × 1 m board with a painted grid of 100 squares. We fixed the board vertically on the ground and counted the number of 0.1 × 0.1 m squares on the board that were unobscured, <1/2 obscured, >1/2 obscured, or completely obscured by vegetation. Observations were made from 15 m away and from each cardinal direction. We later summed these values and assigned them the following weightings: 0 for unobscured, 0.25 for <1/2 obscured, 0.5 for >1/2 half obscured, or 0.75 for completely obscured. The sum of these weighted values gave an overall vegetation density score.

Statistical analysis

We used one-way analysis of variance (ANOVA) to analyze differences in mean values among Removal

sites, Control sites 5–10 km from cowbird traps, and Control sites >10 km from traps. Kruskal-Wallis and Mann-Whitney nonparametric tests were applied when data did not meet the assumptions of a parametric analysis of variance. In 1997, we used post hoc multiple comparison tests (Bonferroni and Dunnet's T3) to determine the location of significant differences among the three groups tested (Removal sites, Controls 5–10 km from traps, and Controls >10 km from traps). A significance level of 5% was used. Some additional statistical tests were used as required (see below).

Description of songbird community.—The six count stations within each site were not considered to be statistically independent sampling units. Therefore, we used mean values for each site for further analysis (Hurlbert 1984). Songbird individuals, excluding cowbirds, were placed into categories of suitable and unsuitable hosts as outlined above. We tested for differences in the mean proportion of suitable hosts in cowbird Removal and Control sites using repeated-measures analysis of variance (Kuehl 1994). We repeated this procedure using the mean number (vs. mean proportion) of suitable hosts as the dependent variable.

We investigated differences in relative abundance of unsuitable hosts in Removal and Control areas by dividing unsuitable hosts into the following categories: (a) rejecters, (b) cavity nesters, (c) corvids, and (d) species that feed nestling cowbirds an unsuitable diet for growth and survival. We then analyzed mean values using one-way Analysis of variance (ANOVA) or Kruskal-Wallis/Mann-Whitney tests as outlined above.

We calculated Renkonen indices to provide descriptive coefficients of differences among communities (Krebs 1989). We also used Brillouin indices to compare species richness and evenness in Removal and Control sites (Krebs 1989).

Nest data.—We calculated maximum likelihood estimates of daily nest survival rates (Bart and Robson 1982). Maximum likelihood estimates use an iterative process to find the most probable values, based on the data provided. This method corrects for biases in Mayfield estimates when nests are visited at irregular intervals (Bart and Robson 1982). Due to small sample sizes, nests monitored in 1996 and 1997 were pooled to achieve greater statistical power, after testing for significant between-year differences in daily nest survival rates and failing to find any. We estimated daily nest survival rates for suitable hosts and unsuitable hosts separately, for Removal sites, Control sites 5–10 km from traps, and Control sites >10 km from cowbird traps.

Vegetation.—Principal components analyses (PCA) were applied to attempt to reduce the number of variables in the tree and ground cover data sets. However, the new PCA factors did not sufficiently explain the variation in the data according to the broken-stick model (Legendre and Legendre 1983, Jackson 1993). Thus, we used all original variables in Multivariate Analyses

of Variance (MANOVA) to test for differences among Removal, Controls 5–10 km from cowbird traps, and Controls >10 km from traps.

RESULTS

Songbird community composition

Proportion of suitable host individuals.—In 1996, there was a significantly greater proportion of suitable host individuals in the songbird communities of cowbird Removal sites compared with Control sites 5–10 km from cowbird traps (repeated-measures ANOVA, $F_{1,18} = 11.76$, $P = 0.003$). On average 67.4% of songbirds detected at cowbird Removal sites were suitable cowbird hosts, whereas only 58.7% of the songbird community was composed of suitable host individuals on Control sites 5–10 km from cowbird traps.

In 1997, suitable hosts comprised 64.4% of the songbird individuals detected on cowbird Removal sites, 60.4% on Control sites 5–10 km, and 59.1% on Control sites >10 km from cowbird traps. These differences were not statistically significant (repeated-measures ANOVA, $F_{2,21} = 2.86$, $P = 0.08$).

Numbers of suitable and unsuitable hosts.—We examined the proportion of suitable hosts within the songbird community because we expected an increase in numbers of suitable hosts relative to unsuitable hosts, not expecting the latter to be strongly affected by cowbird activity. Thus, the use of proportions helps to distinguish effects of cowbirds from other factors such as habitat quality, which may cause both suitable and unsuitable host numbers to be higher in some sites relative to others. However, the increase in the proportion of suitable hosts from 0.587 to 0.674 in Control sites compared with Removal sites in 1996 and from 0.591 to 0.644 in 1997 was the combined effect of both greater numbers of suitable host individuals and fewer unsuitable host individuals in Removal sites (Appendix A, Fig. 4).

In 1996, there were fewer unsuitable host individuals of all types, i.e., rejecters, cavity nesters, corvids, and songbirds that feed cowbird young an unsuitable diet, at cowbird Removal sites compared with Control sites 5–10 km from cowbird traps (Fig. 4). However, with the exception of cavity nesters (Mann-Whitney U, $z = 3.04$, $P = 0.002$), these trends were not statistically significant (Mann Whitney U, $z < .99$, $P > 0.05$). In 1997, mean numbers of unsuitable hosts were consistently lower in cowbird Removal sites compared with Control sites >10 km from cowbird traps (Fig. 4). However, there were no clear trends between mean numbers of unsuitable host individuals in Control sites 5–10 km from traps and cowbird Removal sites (Fig. 4). None of the differences among groups were statistically significant in 1997 (Kruskal-Wallis, $\chi^2_{0.05,2} < 2.65$, $P > 0.05$).

Removal of unsuitable hosts from the analysis by using absolute numbers (vs. proportions) of suitable
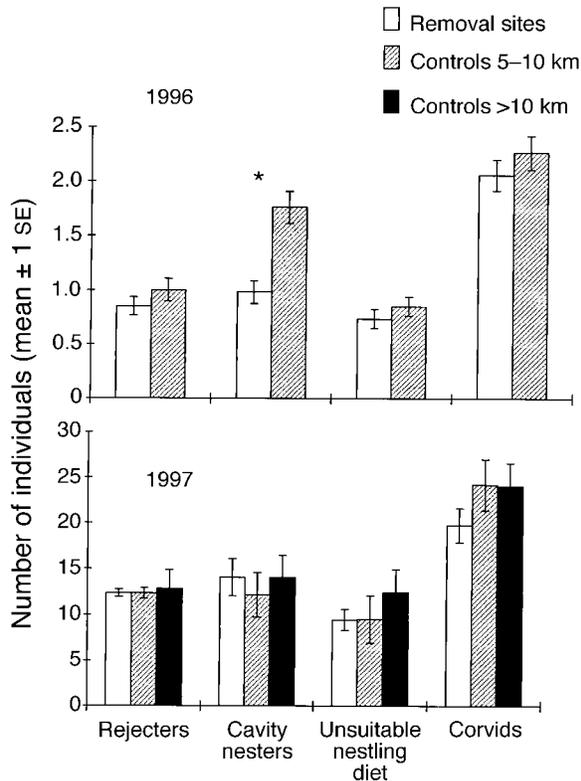
FIG. 4. Numbers of unsuitable hosts detected in cowbird Removal sites, Control sites 5–10 km from cowbird traps, and Controls >10 km from traps.

hosts still reveals a statistically significant difference between Removal and Control sites in 1996 (repeated-measures ANOVA, $F_{1,18} = 7.50$, $P = 0.01$), confirming that changes in suitable host numbers influenced differences in songbird community composition in Removal and Control sites. In 1997, analysis of numbers (vs. proportions) of suitable hosts continued to yield nonsignificant differences (repeated-measures ANOVA, $F_{2,21} = 1.88$, $P = 0.18$) among Removal sites, Control sites 5–10 km from cowbird traps, and Control sites >10 km from cowbird traps.

Robustness of the general results.—When communities are being compared, it is useful to ask how much particular species contribute to overall differences or similarities. In our case, common species that use habitats selectively, or are unusual in their parasitism status, might have hidden larger differences among Removal and Control sites. We therefore removed three species from our analysis: the deciduous-dependent Red-eyed Vireo (*Vireo olivaceus*) and Indigo Bunting (*Passerina cyanea*), and the Red-winged Blackbird (*Agelaius phoeniceus*), which is generally associated with small wetland areas within or adjacent to jack pine stands. When these three species were removed, we still found a greater proportion of suitable hosts at Removal sites in 1996 (repeated-measures ANOVA, $F_{1,18} = 12.46$, $P = 0.002$). When absolute numbers, rather

than proportions of suitable hosts are compared, the level of significance drops from $P = 0.01$ to $P = 0.04$ (repeated-measures ANOVA, $F_{1,18} = 4.78$, $P = 0.04$). In 1997, removal of the three species still did not reveal a significant difference in proportions of suitable and unsuitable hosts between Control and Removal sites (repeated-measures ANOVA, $F_{2,21} = 2.34$, $P = 0.12$, vs. $P = 0.08$ for the original analysis). The results for absolute numbers in 1997 (repeated-measures ANOVA, $F_{2,21} = 1.39$, $P = 0.27$) are also consistent with the original analysis ($P = 0.18$).

When four ''poor'' hosts (see *Discussion: Categorization of suitable and unsuitable hosts*), Chipping Sparrows (*Spizella passerina*), Clay-colored Sparrows (*Spizella pallida*), and Field Sparrows (*Spizella pusilla*), and the Common Grackle (*Quiscalus quiscula*), were moved from the suitable to the unsuitable host category the difference in the proportion of suitable host individuals in Removal vs. Control sites is no longer statistically significant in 1996 (repeated-measures ANOVA, $F_{1,18} = 4.16$, $P = 0.06$ vs. $P = 0.003$ for the original analysis). The level of significance does not change as greatly when absolute numbers of suitable hosts are analyzed (repeated-measures ANOVA, $F_{1,18} = 5.69$, $P = 0.03$ vs. $P = 0.01$ for the original analysis). In 1997, reanalysis of the proportion of suitable hosts (repeated-measures ANOVA, $F_{2,21} = 2.20$, $P = 0.14$ vs. $P = 0.08$ for the original analysis) and absolute numbers of suitable hosts (repeated-measures ANOVA, $F_{2,21} = 1.85$, $P = 0.18$ vs. $P = 0.18$ for the original analysis) in Removal and Control sites does little to change the original results.

Community similarity and species diversity.—The shift to a greater proportion of suitable cowbird hosts in the songbird communities of cowbird Removal sites was a result of small responses of many host populations rather than a qualitative change in species composition. There were no species absent on Control sites that were abundant on Removal areas and vice versa (Appendix A). Rather, the shift in proportions of suitable hosts was a result of small positive shifts in the abundance of host individuals in cowbird Removal sites, compared with Control sites. Removal sites were 80.8% similar to Control sites in 1996, and 83% similar to the two types of Control sites in 1997. Control sites 5–10 km from cowbird traps were 87% similar to sites >10 km from traps. Species richness and evenness were also very similar in Removal sites compared with Controls in both years of the study (Table 1). Species richness was higher in Removal sites but only marginally (Table 1).

Habitat measures

Density of trees, shrubs, and snags on 20 × 20 m plots, and species composition, size classes (dbh), and volume (number of stems) of shrubs did not differ significantly between cowbird Removal and Control sites in either 1996 (Pillai's trace multivariate test, $F_{1,18} = $

TABLE 1. Effects of Brown-headed Cowbird (*Molothrus ater*) removal on the songbird community in Michigan jack-pine stands.

Index	1996		1997		
	Removals	Controls 5–10 km	Removals	Controls 5–10 km	Controls >10 km
Brillouin's diversity, *H* (bits/individual)	4.377	4.334	4.623	4.583	4.576
Evenness	0.791	0.880	0.811	0.798	0.802

Notes: Values are Brillouin's index of songbird species diversity and evenness for 1996 and 1997 Removal sites, Control sites 5–10 km from cowbird traps, and Control sites >10 km from traps.

1.59, $P > 0.05$) or 1997 (Roy's largest root multivariate test, $F_{2,21} = 2.82$, $P > 0.05$).

Ground cover composition measured in 1×1 m plots was not significantly different between Removal and Controls in 1996 (Pillai's trace multivariate test, $F_{7,12} = 0.93$, $P > 0.05$). There was a small but statistically significant heterogeneity in ground cover composition among 1997 Removal sites, Control sites 5–10 km from traps, and Control sites >10 km from traps (Roy's largest root multivariate test, $F_{3,20} = 11.00$, $P = 0.03$). However, one-way analysis of variance on each of the 20 variables revealed that no single ground cover variable differed significantly among Removal, Controls 5–10 km from traps, and Controls >10 km from traps ($F_{2,21} = 2.03$, $P > 0.05$).

In 1996, there were no significant differences in density of 0–1 m height vegetation between cowbird Removal sites and Control sites 5–10 km from traps (Mann-Whitney *U*, ground cover $z = 0.79$, $P > 0.05$, low cover $z = 0.95$, $P > 0.05$, high cover $z = 0.45$, $P > 0.05$). There were also no significant differences in vegetation density in 1997 among Removal sites, Control sites 5–10 km from traps, and Control sites >10 km from cowbird traps (one-way ANOVA, ground cover $F_{2,23} = 1.07$, $P > 0.05$, low cover $F_{2,23} = 1.16$, $P > 0.05$, high cover $F_{2,23} = 1.13$, $P > 0.05$).

Cowbird numbers as a function of distance from traps

Cowbird traps 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 detected during point counts on Removal or Control sites (Table 2). Male cowbird numbers were >6× greater at Control sites 5–10 km from cowbird traps compared with cowbird Removal sites (Table 2; Mann Whitney *U, z =* 2.17, $P = 0.03$).

In 1997, the number of female and male cowbird detections during the 5-min playback period differed significantly among Removal sites, Control sites 5–10 km from cowbird traps, and Control sites >10 km from traps (Table 2; Kruskal-Wallis, females $\chi_{05,2} = 11.01$, $P = 0.004$; males $\chi_{05,2} = 18.79$, $P < 0.001$). Mean number of female cowbird detections was twice as great and male numbers were >9× greater from Removal sites relative to Controls 5–10 km from traps. However multiple comparison tests reveal that these differences are statistically significant for male abundance only (Table 2; females Dunnett T3, mean difference = 0.21, $P > 0.05$; males Dunnett T3, mean difference = 1.37, $P = 0.001$). Ten times more female cowbirds and twenty times more males were counted during the playback period at Control sites >10 km from cowbird traps compared with Removal areas. (Table 2; females Dunnett T3, mean difference = 1.21, $P = 0.01$; males Dunnett T3, mean difference = 3.29, $P = 0.003$). Female cowbird numbers were four times as large and male abundance twice as great at Control sites 5–10 km from traps compared to Controls >10 km away (Table 2; females Dunnett T3, mean difference = 1.00, $P = 0.025$; males Dunnett T3, mean difference = 1.92, $P = 0.046$).

Nest parasitism and rates of daily nest survival

There were no significant differences between maximum likelihood estimates of daily nest survival in

TABLE 2. Number of cowbirds detected per count station in cowbird Removal sites, Control sites 5–10 km from cowbird traps, and Control sites >10 km from cowbird traps.

Study sites	1996		1997			
	8-min point counts		10-min point counts		5-min playback	
	Females	Males	Females	Males	Females	Males
Removal sites	0 (0)	0.025 (0.018)	0 (0)	0.063 (0.034)	0.021 (0.015)	0.028 (0.015)
Control sites 5–10 km	0 (0)	0.167 (0.069)	0.069 (0.025)	0.326 (0.062)	0.056 (0.021)	0.257 (0.035)
Control sites >10 km	…	…	0.174 (0.062)	0.583 (0.081)	0.222 (0.047)	0.576 (0.103)

Note: Number of cowbirds are means, with 1 SE in parentheses.

1996 and 1997 for suitable or unsuitable hosts ($Z <$ 1.28, $P < 0.10$ [test method described in Bart and Robson 1982]). Therefore, we pooled data from 1996 and 1997 nests for analyses of nest survival rates from cowbird Removal and Control sites 5–10 km from cowbird traps.

The 41 nests of suitable hosts in cowbird Removal sites survived at a rate of 0.957 d^{-1}. This was slightly lower than the survival rate of 35 suitable host nests in Control sites 5–10 km away (0.975 d^{-1}) and 20 suitable host nests in Controls >10 km from cowbird traps (0.974 d^{-1}) (see Appendix B for details on the sample of nests monitored). However, this result was not statistically significant ($Z = 1.53$, $P = 0.063$; $Z = 1.19$, $P = 0.117$). Differences in daily nest survival estimates of 15 unsuitable host nests in cowbird Removal sites (0.979 d^{-1}), 16 nests at Control sites 5–10 km away from cowbird traps (0.982 d^{-1}), and 6 nests on Controls >10 km from traps (0.982 d^{-1}), respectively, were small and also not statistically significant ($Z = 0.22$, $P = 0.41$).

No parasitized nests were located on Control or Removal sites in 1996 (Appendix B), nor were any cowbird fledglings detected during careful observation of 29 fledgling families of suitable hosts. In 1997, no parasitized nests were located on cowbird Removal sites (Appendix B). However, six parasitized nests (25% of suitable host nests) containing a total of 10 cowbird eggs were located on Control sites 5–10 km from cowbird traps and five parasitized nests (25% of suitable host nests) containing 7 cowbird eggs were located on Control sites >10 km from cowbird traps (Appendix B).

The primary host at all Control sites was the Hermit Thrush (*Catharus guttatus*). Five of eight (62.5%) thrush nests were parasitized on Controls 5–10 km from traps and four of six (66.6%) were parasitized on Controls >10 km from cowbird traps. These nine nests contained an average of 1.9 cowbird eggs each. We observed parasitism of only two other host species. One Ovenbird (*Seiurus aurocapillus*) nest and one Song Sparrow (*Melospiza melodia*) nest were found containing a single cowbird egg. However, low sample sizes of nests made it difficult to assess the frequency of host use on our study sites.

DISCUSSION

Contrary to our prediction, the proportion of suitable host individuals did not decrease strongly from cowbird removal sites to sites 5–10 km and >10 km from cowbird traps. The songbird communities in cowbird Removal sites supported 8.7% more suitable host individuals compared with Control sites 5–10 km from traps in 1996. In the following year, there was a 4.0% difference between cowbird Removal sites and Controls 5–10 km from traps and a 5.3% difference between Removal sites and Controls >10 km from cowbird traps. This result was statistically significant in 1996 only. We found no support for the prediction that songbird species richness and evenness would increase as a result of long-term (>5 yr) cowbird removal.

The magnitude of differences between cowbird removal and control sites are also small when compared with the community-wide effects generated in some well-known removal studies. Removal of a sea star predator resulted in clearly visible dominance of mussels in rocky intertidal communities, compared with the diverse assemblages of species in experimental controls (Paine 1974). Experimental removal of a predaceous fire ant from corn and squash plants resulted in 0.17–49× increases in abundance of 35 arthropod species, relative to controls (Risch and Carroll 1982). However, these two examples come from relatively simple systems. The regulation of avian community composition may be so complex that removal of a single factor only results in small observable effects. Before we consider the limits to cowbird-induced changes on songbird communities in detail, we first discuss alternative explanations for the small differences in songbird communities observed in our study.

Categorization of suitable and unsuitable hosts

Placing songbird species into suitable and unsuitable host categories is not completely straightforward. Some hosts that can rear cowbirds (such as Chipping, Clay-colored, and Field Sparrows) often abandon parasitized nests (Friedmann et al. 1977). The large Common Grackle is rarely used as a host and when it is parasitized experimentally, few cowbird young are reared from parasitized nests (Peer and Bollinger 1997). When these four species are moved to the unsuitable category, the proportion of suitable hosts is no longer significantly greater at Removal sites in 1996. This result further weakens the suggestion that cowbirds influence the composition of this songbird community.

Habitat differences

The vegetation variables that are most relevant to birds are likely to be those that quantify the availability of essential resources (Karr 1980, James and Rathbun 1981, Mills et al. 1991). Several studies have noted the importance of foliage volume and/or structure for providing foraging substrate (e.g., Robinson and Holmes 1982, Yahner 1986). Recently, ecologists have investigated other factors that affect avian habitat use. Nest failure due to predation is so prevalent that it could act as a strong evolutionary force affecting habitat choice in birds (Martin 1988*a*). There is increasing evidence that the availability of suitable nesting sites may be at least as important in influencing avian habitat use as the availability of foraging substrates (Martin 1988*a, b,* Steele 1993, Matsuoka et al. 1997). Martin (1988*b*) predicted that higher vegetation density provides greater security from nest predators since predators are forced to search a greater number of potential nest sites.

This potential-prey-site hypothesis is supported by a study of nest success in Hermit Thrushes and Mac-Gillivray's Warblers (Martin and Roper 1988, Martin 1993).

We spent considerable time locating experimental Controls that, to our eye, best matched the stand age and vegetation structure of cowbird Removal sites. However, we also measured habitat variables in detail, to test the alternative hypothesis that observed differences in songbird community structure were the result of important differences in habitat such as the availability of nesting sites (most species nest on the ground in this habitat) and foraging substrate.

Based on the vegetation variables we measured within each study plot, structure and composition of vegetation were not discernibly different in Removal and Control sites. However, the intensity of vegetation sampling on the 1996 study sites was much lower than in 1997. Further analysis of the songbird data suggests that habitat differences may account for some of the observed differences in songbird community composition in Removal sites and Control sites in 1996. Although differences were still statistically significant, the level of significance was reduced when two deciduous- and one wetland-associated species were removed from the analysis. In addition, more cavity-nesting songbirds were detected in Control sites than in cowbird Removal areas in 1996. These analyses suggest that Control sites had more snags and a lower deciduous and wetland component than Removal sites. A higher number of snags could also attract cowbirds and some avian predators.

To address the possible problem of insufficient sampling in 1996, we applied a more intensive sampling scheme in 1997. We still did not detect differences in the habitat variables measured. However, it remains possible that there were important vegetation variables that we did not measure that might have differed between Removal and Control sites.

Nest predation

We checked for differences in rates of nest survival in Removal and Control sites to test the alternative hypothesis that nest predation rather than nest parasitism was driving songbird community composition (Martin 1988*a, b,* Wiens 1989*b*). If nest predators rather than brood parasites were responsible for the slightly lower proportion of suitable host individuals found on Control sites, then we expected to find a lower rate of daily nest survival in Control areas compared with cowbird Removal sites. Estimates of daily nest survival were actually slightly *higher* in Control sites 5–10 km from cowbird traps and Controls >10 km from cowbird traps, compared with cowbird Removal sites; these observations clearly refute this alternative hypothesis.

Can cowbirds exert strong demographic effects on host communities?

The absence of strong shifts in songbird community composition may be due to one or more of the following reasons: (1) the large spatial scale of effective cowbird removal and an insufficient time scale over which to detect host demographic changes, (2) dispersal dynamics of host populations, and (3) an inability of cowbirds at moderate densities, to limit host populations. We now discuss each of these possibilities.

Spatial and temporal scale of cowbird removal.— Paradoxically, the absence of strong shifts in songbird community composition in our data may be mainly due to a strong treatment effect. Cowbird removal was so effective that it reduced cowbird densities to near zero on Removal sites as well as on Control sites 5–10 km from cowbird traps. We were able to verify our assumption that cowbirds were present in very low densities in cowbird Removal areas and in higher densities on experimental Controls. However, there was a strong gradient effect, whereby cowbirds were almost eliminated from the area directly adjacent to the cowbird trap, densities increased slightly at sites 5–10 km from traps, and increased strongly at sites >10 km from cowbird traps. These data suggest that the network of cowbird traps in northern Lower Michigan affects within-year cowbird densities at least 5 km from cowbird removal areas. This is the first study to document such landscape-scale effects but it is not a surprising result given that cowbirds may commute >9 km from breeding to feeding ranges (Rothstein et al. 1984, Thompson 1994, Gates and Evans 1998). It is possible that areas well beyond 10 km from cowbird traps supported even greater cowbird densities. However, habitat at this range was too different to test the prediction that these areas contained lower abundances of suitable host individuals.

Despite a marked increase in female cowbird numbers at sites >10 km from cowbird traps, cowbird densities on these sites are still low relative to some regions in North America. Three times as many female cowbirds were detected in shorter count intervals (6 min vs. the 10-min counts performed in this study in 1997) in host-rich forests of Illinois (Robinson et al. 2000). Breeding Bird Survey (BBS) data also indicate that cowbirds are only about a third as abundant in Northern Michigan (10–30 cowbirds per BBS route) relative to Illinois (30–100 or >100 cowbirds per BBS route) (Peterjohn et al. 2000). Differences in cowbird abundance between these two regions of the USA may increase in future because cowbirds are declining in Northern Michigan and increasing in Illinois (Peterjohn et al. 2000). Furthermore, BBS records may overestimate the number of cowbirds using jack pine forest in Michigan because most BBS routes through this area are in deciduous habitat (observations from unpublished BBS route maps [available from Cornell Laboratory of Ornithology, Ithaca, New York, USA]).

The magnitude of changes in host demography is also likely to be a function of the duration of cowbird removal. Due to the shifting nature of suitable Kirtland's Warbler breeding habitat, no cowbird Removal

areas were trapped for the full 26 yr of the removal program. Cowbird removal sites censused in this study had been trapped annually for 5–11 years. If a marked shift in community composition due to cowbirds is possible, it would be more likely in areas that support higher cowbird densities, and where cowbird removal is continuous at the same location over a longer period.

Dispersal dynamics of host population.—Dispersal of individuals can act to limit the impact of cowbird-induced population changes. Immigration from productive ''source'' populations may compensate for reduced recruitment in ''sink'' populations (Brown and Kodric-Brown 1977, Brown 1984, Pulliam 1988). There is increasing evidence that these processes can operate in avian populations (Pulliam and Danielson 1991, Probst and Weinrich 1993, Brawn and Robinson 1996). Many host species present in the jack pine ecosystem are habitat generalists with an extensive range across North America. The Kirtland's Warbler is a notable exception, in that it has very specific habitat requirements and a limited breeding range. It is therefore likely that source–sink population dynamics reduce the magnitude of cowbird-induced changes in these host populations.

Source–sink dynamics may even have operated within our study area. Songbirds nesting in cowbird Removal areas could contribute immigrants to less productive areas outside of cowbird Removal sites. The large spatial scale across which Removal and Control sites were distributed (Figs. 1 and 2) lends credibility to this argument. In addition, capture–recapture data from a banding study has revealed that Kirtland's Warblers can travel up to 160 km within a single breeding season (J. Probst, *personal communication*). Empirical data on host dispersal distances in other songbird species and further study on host seasonal productivity are required to test these hypotheses.

The effects of cowbird parasitism on host communities and populations.—Our data on songbird community composition and community-wide parasitism rates suggest that moderate cowbird pressure is not sufficient to generate strong demographic effects in host communities in the jack pine forests of Northern Michigan. This statement begs the question: what levels of parasitism are required to generate detectable changes in songbird communities?

It is clear that the cost of parasitism varies from host to host within a community (Friedmann 1963, Rothstein 1975). A critical level of parasitism logically exists (and may vary geographically) for each host species, above which host population declines will ensue without steady immigration from source populations. Maximum sustainable levels of parasitism for individual host species are unknown, although there have been efforts to model the consequences of nest parasitism on host demography (May and Robinson 1985, Pease and Grzybowski 1995, Grzybowski and Pease 1999*a*). Mayfield (1977) suggested that some small hosts would

be in danger if the rate of parasitism exceeded 30% of nests. Smith (1999) predicted that many otherwise healthy host populations could sustain parasitism levels of 60%. This estimate is consistent with modeling of cowbird–host demography (Grzybowski and Pease 2000: Table 16.3). However, no empirical data exist to determine whether these estimates are reasonable, or how these estimates should vary depending on host size, number of broods per breeding season, and incubation period (Mayfield 1977, Smith 1999).

Many managers and researchers report significantly lower rates of nest parasitism on nests of individual host species following the onset of cowbird removal (Stutchbury 1997, DeCapita 2000, Griffith and Griffith 2000, Hayden et al. 2000, Whitfield 2000). Numbers of Kirtland's Warblers stabilized after cowbird trapping began in 1972, however, numbers did not increase significantly until a large tract of breeding habitat became available in the 1990's (Probst and Weinrich 1993, DeCapita 2000). Unfortunately, it is impossible to determine whether cowbird trapping arrested the decline of Kirtland's Warbler or whether this was due to other causes on the breeding and/or wintering range (Probst 1986, James and McCulloch 1995, Haney et al. 1998, Rothstein and Cook 2000). Griffith and Griffith (2000), Hayden et al. (2000), and Whitfield (2000) all report that cowbird trapping resulted in growth of Least Bell's Vireo (*Vireo bellii pusillus*), Black-capped Vireo (*Vireo atricapillus*), and Southwestern Willow Flycatcher (*Empidonax traillii extimus*) populations, respectively. However, only Whitfield's data are part of a controlled experiment in which cowbird removal areas are compared with reference areas with no cowbird removal (Rothstein and Cook 2000). Therefore there is still only limited information available on the extent to which cowbirds affect host populations.

It is also clear that many factors other than parasitism by cowbirds can influence songbird population dynamics and thus shape songbird communities. Songbird recruitment depends not only on nesting success but also on survival until the next breeding season. Food availability, weather, predation, and habitat deterioration can all influence survival throughout the year and contribute to the inherent variability in songbird populations (Martin 1988*a, b,* Wiens 1989*b,* Newton 1994, Rotenberry et al. 1995, Holmes et al. 1992, Côté and Sutherland 1997).

A recent simulation model of the effects of cowbird parasitism on songbird communities provides a theoretical framework with which to understand cowbird–host interactions and suggests that community-wide effects are possible (Grzybowski and Pease 1999*a*). However, many key parameters required in this and other host demographic models are unknown or vary tremendously among host species (Grzybowski and Pease 1999*a*). Our study is the first to directly test predictions from the Grzybowski and Pease model. However, other evidence from fragmented forests in

Illinois suggests that even very intense cowbird parasitism does not affect local host species richness (Robinson et al. 2000).

CONCLUSIONS

We did not find significant differences in songbird community composition in areas where cowbirds had been removed for 5–11 yr compared to control areas with moderate cowbird densities. It remains possible that cowbirds cause larger changes in songbird community composition in isolated areas where the effects of cowbirds are not ameliorated by immigration from distant source populations (Robinson et al. 2000). Further tests of this hypothesis could be conducted in western riparian forests where there are several threatened or endangered songbird races, as well as frequent cowbird parasitism.

If Brown-headed Cowbirds influence songbird community composition only to a moderate degree when they are dominant members of the songbird community, they are not remarkable in their ability to influence community composition. Our results provide little support for adding cowbirds to the short list of species (Hurlbert 1997) that regulate community structure disproportionately in relation to their abundance. Thus, while cowbird removal has benefited some endangered species (e.g., Griffiths and Griffiths 2000), there is little reason to believe that it will improve the general health of songbird communities.

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APPENDIX A

A table listing the number and species of passerine individuals detected per site at cowbird (*Molothrus ater*) Removal and Control sites near habitat of the Kirtland's Warbler in northeastern Lower Michigan, USA, is available in ESA's Electronic Data Archive: *Ecological Archives* E082-010-A1.

APPENDIX B

A table listing the nests monitored and their fates in a study of the effects of cowbird (*Molothrus ater*) removal in northeastern Lower Michigan, USA, is available in ESA's Electronic Data Archive: *Ecological Archives* E082-010-A2.