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

by

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ABSTRACT

Many ecologists have searched for species that contribute strongly to the structure and composition of communities of organisms. It is widely believed that the Brown-headed Cowbird, 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 have evolved egg ejection behaviour, nest in cavities, feed cowbird nestlings an unsuitable diet or are too big to parasitize, will generally escape the effects of cowbird parasitism. Thus, cowbirds may change the composition of entire songbird communities by depressing numbers of suitable host individuals. I tested this hypothesis using an existing cowbird removal program in the state of Michigan, USA. This removal program was designed to protect the endangered Kirtland's Warbler from high levels of cowbird parasitism, throughout its 19 200 km^2 breeding range. I compared songbird composition in stands of young jack pine where cowbirds had been removed for 5-11 years to Control sites 5-10 km from cowbird traps and Control sites >10 km from cowbird traps. I predicted that cowbird Removal sites would support greater songbird diversity and a greater proportion of suitable host *vs.* unsuitable host individuals relative to Control sites. Results from songbird point counts revealed that species diversity was very similar at cowbird Removal and Control sites but Removal sites contained 4.0 - 8.7 % more suitable hosts than Control sites. I conclude that cowbirds only weakly influence the composition of songbird communities in jack pine forests of Michigan. It remains to be shown that cowbirds affect songbird community composition more strongly in other areas, e.g., mid-western USA, where cowbirds are more abundant.

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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) generated considerable research into the role of predators in other systems (see Power et.al. 1996 and Hurlbert 1997 for reviews). This research expanded to include herbivores, producers and mutualists, often using experimental removal or exclusion to determine the effects of individual species on a community of organisms (Power et al. 1996, Hurlbert 1997). To my knowledge, this is the first study to search for community-wide effects generated by an obligate brood parasite.

Generalist brood parasites have the potential to change the composition of entire host communities. Their lack of host specificity allows them to strongly affect a number of host species, without the negative feedback on their own numbers generally associated with single host-parasite interactions (Mayfield 1977, May and Robinson 1985, James and McCulloch 1995). The brood-parasitic Brown-headed Cowbird (*Molothrus ater*) of North America uses over 220 songbird hosts (Friedmann et al. 1977, Lowther 1993) and has greatly expanded its range during the past two centuries. This range expansion is causing concern among ornithologists, since it has exposed previously naïve songbird populations to the threat of brood parasitism (Mayfield 1977, Rothstein 1994). It is widely believed that nest parasitism by cowbirds has contributed to declines in some songbird populations, and that cowbirds can 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 *in press*).

Songbird communities (excluding cowbirds) can be divided into two groups, depending on their value to cowbirds as hosts. S*uitable hosts* accept cowbird eggs and feed their young a largely animal-based diet. U*nsuitable hosts* include cavity nesters, species that feed their young a mainly plant-based diet, corvids, and species that reject cowbird eggs from their nests (Rothstein 1975, Rohwer and Spaw 1988). Cowbird pressure on suitable hosts may reduce their abundance, relative to the abundance of unsuitable hosts with which the cowbird does not interact strongly. Some suitable host species may even be extirpated from communities where cowbird pressure is intense. If several host species are affected, cowbird pressure may eventually change the composition of entire songbird communities.

However, 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 *in press*, Strausberger and Ashley 1997, Sedgwick and Iko *in press*), there is still little evidence that cowbird parasitism regulates songbird populations and communities (May and Robinson 1985, Pease and Grzybowski 1995, Sedgwick and Iko *in press*). Therefore, I designed a controlled experiment to measure the effects of cowbirds on songbird community structure.

The effects of long-term removal of Brown-headed Cowbirds on songbird communities: hypothesis and predictions

I used cowbird removal 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 to areas in similar habitat where cowbird densities are unmanipulated, (2) species diversity 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. 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 assemblages (James 1971, Karr and Roth 1971, Probst et al. 1992). If differences in songbird community composition are due to local habitat variables, I should find differences in vegetation structure and composition between cowbird removal sites and experimental controls, despite attempts to control for habitat variables.

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 (Martin 1988a, Martin 1988b, Wiens 1989b). This alternative hypothesis should be considered if patterns 1 & 2 above are accompanied by a lower rate of predation of suitable host nests in cowbird removal sites compared to experimental controls.

The extensive cowbird removal program designed to protect the Kirtland's Warbler (*Dendroica kirtlandii*) in Northern Michigan provided an experimental framework in which to test the hypothesis that cowbirds change songbirds communities. The Kirtland's Warbler is an endangered neotropical migrant songbird with very specific habitat preferences and a limited breeding range. They nest 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 (Mayfield 1972). Researchers suggested that high levels of nest parasitism by cowbirds contributed to this decline (Mayfield 1972, Walkinshaw 1972, Ryel 1981), thus cowbird removal from Kirtland's Warbler breeding areas began in 1972 and has continued every year since (Walkinshaw 1983, DeCapita *in press*). This cowbird removal program, represents a classic PRESS perturbation (Bender et al. 1984) whereby cowbird removal at individual sites was sustained for 5-11 years. I compared songbird communities on these 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 heavily forested, with a mosaic of managed stands of conifers and pockets of deciduous forest. Study sites were in stands of even-aged jack pine (*Pinus banksiana*), often interspersed with oak (*Quercus* spp.) and pin cherry (*Prunus pensylvanica*) and occasionally 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 members of the Heath family (*Ericaceae*). Appendix, Table 1 gives a complete list of trees, shrubs and ground cover found on study sites.

Cowbird traps were erected and maintained by the U.S. Fish and Wildlife Service across a 19 200 km^2 area where most nesting Kirtland's Warblers occur (DeCapita *in press*). Up to 67 traps (mean = 41 traps) operated between 1972 and 1997. These traps removed a total of 105 309 cowbirds (mean = 4050 cowbirds/per year) from Kirtland's Warbler breeding areas (Deloria and DeCapita 1997).

I chose ten cowbird Removal sites adjacent to active cowbird traps that had been in operation for 5-11 consecutive years (mean 7.6 years). Choice of Removal sites was limited by permits which prohibited my access to some Kirtland's Warbler breeding sites. Ten Control sites were chosen to best match the habitat characteristics of cowbird Removal sites (total number of sites in 1996 = 20). I located suitable Control areas using survey maps, followed by extensive ground truthing. All Control sites were at least 5 km from cowbird traps and from any area that had experienced cowbird removal within the past five years. 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 (total number of sites = 24).

Site area encompassed a half circle of radius one 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 needed to conform with conditions of my entry permit.

Songbird point counts

Songbird point counts were conducted to test the prediction that songbird communities in cowbird Removal areas differed in composition from Control areas at least 5 km from cowbird traps. Four one km transect lines, each 60° apart, were flagged within each site and six permanent count stations were chosen along these transects (Fig. 2). Locations of count stations were chosen randomly. However, to avoid re-counting individual songbirds, it was necessary to restrict 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 for point counts in 1997. I trained observers over a four week 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, potential observer biases in the data were balanced out by ensuring that each observer counted the same number of Removal sites as Control sites.

We performed eight minute, unlimited radius point counts between dawn and 10:00 a.m., identifying birds by song, calls or visual observation; noting species, distance from the observer, and time (minute) of first detection. Counts were conducted on most mornings weather permitting, i.e., no heavy rain or constant drizzle and winds < 25 km/hr. 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 ensured there were no biases due to differences in weather conditions during count periods. We counted all sites twice between early June and mid-July in 1996 and three times between mid May and early July in 1997.

In 1997, I extended the point count duration to ten minutes, after analysis of detection curves from 1996 indicated that the rate of detection was not leveling off in the last few minutes of the 1996 point counts (Appendix, Fig. 1).

Cowbirds 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, five minutes of playback of cowbird female chatter calls was added after each ten minute point count to improve the likelihood of detecting cowbirds (Miles and Buehler *in press*, Rothstein and Cook *in press*), following very low cowbird detection rates in 1996.

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 compared to Removal sites. We checked nests every 3-5 days in 1996 and every 3-6 days in 1997. We targeted suitable cowbird hosts for monitoring, but unsuitable host species' nests were monitored opportunistically to assess their survival rates.

Habitat measures

Several vegetation variables were measured to test the alternative hypothesis that significant 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.

I randomly selected two (1996) or six (1997) 20 x 20 m plots between 0-100 m from point count stations at each site. We counted trees, shrubs and snags within these plots, noting species and circumference of trunks at breast height. I later converted circumference measurements to diameter at breast height (dbh). Within each 20 x 20m plot, I randomly selected one (1996) or four (1997) 1 x 1 m plots within which we estimated the proportion of each ground cover type (e.g., grasses and sedge, Ericaceous shrubs, leaf litter) to the nearest five percent. We measured ground and understory (0-1 m) vegetation density at one (1996) or two (1997) of the 1 x 1 m plots using a 1 x1 m board with a painted grid composed of 100 squares. We fixed the board in a vertical position on the ground and then counted the number of 0.1 x 0.1 m squares on the board that were unobscured, < half obscured, > half obscured or completely obscured by vegetation. Observations were made from 15 m away and from each cardinal direction. I later summed these values and assigned them the following weights; 0 for unobscured, 0.25 for < half obscured, 0.5 for > half obscured or 0.75 for completely obscured. The sum of these weighted values gave an overall vegetation density score.

Statistical Analysis

I 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. Kruskall-Wallis and Mann-Whitney non-parametric tests were applied when data did not meet the assumptions of a parametric Analysis of Variance. In 1997, I 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 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 statistically independent sampling units. Therefore, I 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. I tested for differences in the mean proportion of suitable hosts in cowbird Removal and Control sites using Repeated Measures Analysis of Variance (Kuehl 1994). I repeated this procedure using the mean number (*vs* mean proportion) of suitable hosts as the dependent variable.

I 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. I then analyzed mean values using One-way Analysis of Variance (ANOVA) or Kruskall-Wallis/Mann-Whitney tests as outlined above.

I calculated Renkonen (Percent similarity) indices to quantify the percentage difference in species composition and used Brillouin indices to compare species richness and evenness in Removal and Control sites (Krebs 1989).

NEST DATA - I followed methods in Bart and Robson (1982) for calculation of maximum likelihood estimates of daily nest survival rates. Nests monitored in 1996 and 1997 were pooled to achieve greater statistical power, after testing for between year differences in estimated daily nest survival rates. I computed estimates of 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, I used all original variables in Multivariate Analyses of Variance (MANOVA) to test for differences among Removal, Controls 5-10 km and Controls >10 km from cowbird 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 to Control sites 5-10 km from cowbird traps (Repeated Measures ANOVA, $F_{1,18} = 11.76$, $p = .003$). 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 (Fig. 3; Appendix Table 2 & 3).

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 (Fig. 4; Appendix Table 4 & 5). These differences were not statistically significant (Repeated Measures ANOVA, $F_{2,21} = 2.86$, $p = .08$).

Numbers of suitable and unsuitable hosts

The increase in the proportion of suitable hosts detected in Removal sites compared to Control sites (1996 and 1997) was due in large part to an increase in numbers of suitable host individuals detected in Removal sites. However, the effect was also due to fewer unsuitable host individuals in Removal sites.

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 to Control sites 5-10 km from cowbird traps (Fig. 5). However, with the exception of cavity nesters (Mann-Whitney U, $z = 3.04$, $p = .002$), these trends were not statistically significant (Mann Whitney U, $z < .99$, $p > .05$). In 1997, mean numbers of unsuitable hosts were consistently lower in cowbird Removal sites compared to Control sites >10 km from cowbird traps. 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. 6). None of the differences among groups were statistically significant in 1997 (Kruskall Wallis, $\chi^2_{.05,2} < 2.65$, $p > .05$).

Removal of unsuitable hosts from the analysis by using absolute numbers (*vs*. proportions) of suitable hosts still reveals a statistically significant difference between Removal and Control sites in 1996 (Repeated Measures ANOVA, $F_{1,18} = 7.50$, $p = .01$), confirming that changes in suitable hosts numbers influenced differences in songbird community composition in Removal and Control sites. In 1997, analysis of numbers (*vs*. proportions) of suitable hosts continues to yield non-significant differences (Repeated Measures ANOVA, $F_{2,21} = 1.88$, $p = .18$) among Removal, Control sites 5-10 km and Control sites >10 km from cowbird traps.

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, Tables 2-5). 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 to Control sites. Removal sites were 80.8% similar to Control sites in 1996, and 83% similar to Control sites 5-10 km from cowbird traps and Control sites >10 km from cowbird traps in 1997. Control sites 5-10 km and Control sites >10 km from cowbird traps were 87% similar. Species evenness was also very similar across Removal sites, Control sites 5-10 km from traps and Control sites >10 km from cowbird traps in both 1996 (Fig. 7, Table 1) and 1997 (Fig. 8, Table 1). Species richness was only marginally higher in Removal sites compared to Controls in both years of the study (Table 1).

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 increased over six fold at Control sites 5-10 km from cowbird traps compared to cowbird Removal sites (Table 2; Mann Whitney U, $z = 2.17$, $p = .03$).

In 1997, the number of female and male cowbird detections during the five minute playback period differed significantly among Removal, Control sites 5-10 km and Control sites >10 km from cowbird traps (Table 2; Kruskall Wallis, females $\chi_{.05,2} = 11.01$, $p = .004$; males $\chi_{.05,2} = 18.79$, $p<0.001$). Mean number of female cowbird detections more than doubled and male numbers increased more than nine-fold from Removal sites 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 = .21,

$p > .05$; males Dunnett T3, Mean Difference = 1.37, $p = .001$). Ten times more female cowbirds and twenty times more males were counted at Control sites >10 km from cowbird traps compared to Removal areas. (Table 2; females Dunnett T3, Mean Difference = 1.21, $p = .01$; males Dunnett T3, Mean Difference = 3.29, $p = .003$). Female cowbird numbers increased four-fold and male abundance doubled from Control sites 5-10 km from traps to Controls >10 km (Table 2; females Dunnett T3, Mean Difference = 1.00, $p = .025$; males Dunnett T3, Mean Difference = 1.92, $p = .046$).

Nest parasitism and rates of daily nest survival

There were no significant differences between maximum likelihood estimates of daily nest survival in 1996 and 1997 for suitable or unsuitable hosts (see Table 3). Therefore, I 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 per day. This was slightly lower than the survival rate of 35 suitable host nests in Control sites 5-10 km (0.975/day) and 20 suitable host nests in Controls >10 km from cowbird traps (0.974/day) (Fig. 9). 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, 0.979/day, 0.982/day and 0.982/day of 15 unsuitable host nests in cowbird Removal sites, 16 nests at Control sites 5-10 km and 6 nests on Controls >10 km from cowbird traps respectively, were small and also not statistically significant ($Z = 0.22$, $p = 0.41$; Fig. 9).

No parasitized nests were located in 1996 (Table 4) nor were any cowbird fledglings detected while performing other work on the sites or during careful observation of 29 fledgling families of suitable hosts. In 1997, no parasitized nests were located on cowbird Removal sites. However, six parasitized nests (25%) containing a total of 10 cowbird eggs were located on Control sites 5-10 km from cowbird traps and five parasitized nests (25%) containing 7 cowbird eggs were located on Control sites >10 km from cowbird traps (Table 4). When samples of nests from 1996 and 1997 are pooled, observed parasitism rates increase from 0% in cowbird Removal sites, 17.1% in Control sites 5-10 km from cowbird traps to 25% in Control sites >10 km from cowbird traps (Table 4).

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. I only observed parasitism of 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 for host species other than Hermit Thrushes made it difficult to assess the frequency of host use on my study sites.

Habitat measures

Numbers and composition of tree species counted on 20 x 20 m plots did not differ significantly between cowbird Removal and Control sites in either 1996 (Fig. 10, Pillai's Trace multivariate test, $F_{1,18} = 1.59$, $p > .05$) or 1997 (Fig. 11, Roy's Largest Root multivariate test, $F_{2,21} = 2.82$, $p > .05$).

Ground cover composition measured in 1 x 1 m plots was not significantly different between Removal and Controls in 1996 (Fig. 12, Pillai's Trace multivariate test, $F_{7,12} = 0.93$, p > .05). There was however, a small but statistically significant difference in ground cover composition among 1997 Removal sites, Control sites 5-10 km from traps and Control sites >10 km from traps (Fig. 13, 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 and Controls >10 km from traps ($F_{2,21} < 2.03$, $p > .05$).

In 1996, there were no significant differences in vegetation density from 0 - 1 m between cowbird Removal and Control sites 5-10 km from traps (Fig. 14, Mann-Whitney U, ground cover $z = .79$, $p > .05$, low cover $z = .95$, $p > .05$, high cover $z = .45$ $p > .05$). There were no significant differences in vegetation density in 1997 among Removal, Control sites 5-10 km and Control sites >10 km from cowbird traps (Fig. 15, one-way ANOVA, ground cover $F_{2,23} = 1.07$, $p > .05$, low cover $F_{2,23} = 1.16$, $p > .05$, high cover $F_{2,23} = 1.13$, $p > .05$).

DISCUSSION

There is considerable concern that the brood-parasitic activities of Brown-headed cowbirds are contributing to declines in some songbird populations, and that cowbirds generate widespread changes in songbird community composition (Mayfield 1977, Brittingham and Temple 1983, Terborgh 1989, Wiens 1963, Böhning-Gaese et al. 1993). I used an existing cowbird removal program to measure the effects of cowbirds on songbird communities.

I compared the composition of songbird communities in cowbird Removal areas to Control sites 5-10 km from cowbird traps and Controls >10 km from traps to test the predictions that songbird communities in cowbird Removal areas would contain: (1) a greater proportion of suitable *vs.* unsuitable host individuals, (2) greater songbird diversity, and that (3) these effects would strengthen with increasing distance from cowbird Removal sites.

Contrary to my predictions, the proportion of suitable host individuals did not increase strongly from sites 5-10 km from traps to sites >10 km from cowbird traps and I found no support for the prediction that songbird species diversity would increase as a result of long-term (>5 years) cowbird removal. Species richness and evenness were very similar across Removal sites and all Control sites in both years of the study. While my results do support the first prediction, the magnitudes of these changes are small and support is weak in the second year of the study. The songbird communities in cowbird Removal sites supported 8.7 % more suitable host individuals compared to Control sites 5-10 km from traps in 1996. In the following year, there was a 4.0 % difference observed 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. On average cowbird Removal sites contained 6% more suitable host individuals than all Control sites in the two years of the study.

These differences are small when compared to 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 to 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 fold 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 I consider the limits to cowbird-induced changes on songbird communities in detail, I first discuss the alternative explanations for the small differences in songbird communities observed in my study.

Habitat differences

Songbird community composition is often correlated with the structure and composition of vegetation (MacArthur and MacArthur 1961, MacArthur et al. 1962, James 1971, Karr and Roth 1971, Willson 1974, Cody 1981, Probst et al. 1992), therefore I carefully matched the habitat of experimental Controls to cowbird Removal sites. However, I also measured habitat variables in detail, to test the alternative hypothesis that observed differences in songbird community structure were the result of differences in habitat.

The majority of suitable hosts in the community are ground nesters, thus, composition of ground cover is likely to be the most important component of vegetation, followed by composition and density of surrounding trees and shrubs, and number of snags. Based on detailed sampling 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. More cavity nesters were detected on Control sites relative to cowbird Removal areas in 1996, suggesting that Control sites may have had significantly more snags than Removal sites. Therefore, habitat differences might still account for some of the observed differences in songbird community composition between cowbird Removal sites and Controls 5-10 km from cowbird traps in 1996. I confidently reject this alternative hypothesis for the 1997 data, and consider that I successfully matched habitats at Control and Removal sites.

Nest predation

I 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 1988a, Martin 1988b, Wiens 1989a). If nest predators were responsible for the slightly lower proportion of suitable host individuals found on Control sites, then I expected to find a lower rate of daily nest survival in Control areas compared to cowbird Removal sites. Estimates of daily nest survival were actually slightly **higher** in Controls sites 5-10 km from traps and Controls >10 km from cowbird traps compared to cowbird Removal sites; clearly refuting 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) source-sink population dynamics of host populations and (3) an inability of cowbirds at moderate densities, to limit host populations. I now discuss each of these possibilities.

Spatial and temporal scale of cowbird removal

Paradoxically, the absence of strong shifts in songbird community composition in my 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. I was able to verify my 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 a plausible result given that cowbirds may commute up to 7 km from breeding to feeding ranges (Rothstein et al. 1984, Thompson 1994). However, in this heavily forested region of Northern Michigan, cowbirds are likely to commute shorter distances than the recorded maximum. Areas well beyond 10 km from cowbird traps may have supported even greater cowbird densities and thus lower abundances of suitable host individuals. However, habitat at this range is too different from habitat on Removal areas to test this prediction adequately.

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. Twice as many female cowbirds were detected in shorter count intervals (6 min *vs.* 10 min point counts performed in this study) in forests of Illinois (Robinson et al. *in press*). Breeding Bird Survey (BBS) data indicate that cowbirds are only about a third as abundant in Northern Michigan (10-30 cowbirds per BBS route) relative to regions of midwestern USA (30 - 100 or >100 cowbirds per BBS route) (Peterjohn et al. *in press*).

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 had been trapped for the full 26 years of the removal program. Cowbird Removal sites censused in this study had been trapped annually for 5-11 years. A marked shift in community composition 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.

Source-sink dynamics of host populations

Many authors have suggested that cowbird pressure can drive host population declines (Mayfield 1977, Brittingham and Temple 1983, Terborgh 1989, Böhning-Gaese et al. 1993). My results do not strongly support this claim. However, 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 (Pulliam

1988). There is increasing evidence that these processes can operate in avian populations (Pulliam and Danielson 1991, 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 possible that source-sink population dynamics reduce the magnitude of cowbird-induced changes in host populations. Songbirds nesting within cowbird Removal areas may even contribute immigrants to less productive areas outside of cowbird Removal sites. Empirical data on host dispersal distances and further study on host seasonal productivity in these populations are required to test these hypotheses.

The effects of cowbird parasitism on host communities and populations

My 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 *in press* b). Mayfield (1977) suggested that some small hosts would be in danger if rate of parasitism exceeded 30% of nests. Smith (*in press*) predicts that many otherwise healthy host populations could sustain parasitism levels of 60%. This estimate is supported by modeling of cowbird-host demography (Grzybowski and Pease *in press* a). 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 *in press*).

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 *in press*, Griffith and Griffith *in press*, Hayden et al. *in press*, Whitfield *in press*). Numbers of Kirtland's Warblers stabilized after cowbird trapping began in 1972, however, numbers did not increased significantly until a large tract of breeding habitat became available in the 1990's (DeCapita *in press*). 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 *in press*). Griffith and Griffith (*in press*), Hayden et al. (*in press*) and Whitfield (*in press*) 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 trailii extimus*) populations respectively. However, only Whitfield's data are part of a controlled experiment, in which cowbird removal areas are compared to reference areas with no cowbird removal (Rothstein and Cook *in press*). Therefore there is still limited information available on the extent to which cowbirds affect host populations.

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 *in press* b). However, many key parameters required in this and other host demographic models are unknown or vary tremendously among host species (Grzybowski and Pease *in press* b). 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. (Martin 1988a, Martin 1988b, Wiens 1989b, Newton 1994, Rotenberry et al. 1995, Holmes et al. 1992, Côté and Sutherland 1997)

This study documented small differences in songbird community composition in areas where cowbirds were removed for 5 - 11 years compared to control areas with moderate cowbird densities. I believe that cowbird impacts on other songbird communities are limited, and will be roughly proportional to their relative abundance in the community. Thus large effects are only likely in landscapes where cowbirds are dominant members (>6%) of the songbird community. I recommend further tests of this hypothesis using existing cowbird removal programs combined with experimental controls, in landscapes that support greater densities of cowbirds.

CONCLUSIONS

This is the first experimental study to investigate the demographic consequences of cowbird parasitism on entire songbird communities. I used an existing cowbird removal program to test the hypothesis that cowbirds change the composition of songbird communities by reducing numbers of suitable host individuals. I compared the songbird communities of sites where cowbirds had been removed annually for 5 - 11 years to Control sites 5-10 km from cowbird traps and Control sites >10 km from cowbird traps.

Cowbird traps were very effective at removing cowbirds from the area 0 - 1 km from traps. Cowbird densities increased moderately at sites 5 - 10 km from cowbird traps and increased sharply at sites >10 km from traps. My study is the first to document landscape-scale effects of a network of cowbird traps on cowbird densities.

Songbird census data support the prediction that songbird communities in cowbird Removal areas contain a greater proportion of suitable *vs*. unsuitable host individuals relative to Control areas. However, the size of this effect is small (4.0 - 8.7%) and it was not statistically significant in the second year of the study. Contrary to predictions, I did not observe a significantly greater proportion of suitable hosts in the songbird communities of Control sites >10 km from traps compared to Controls 5-10 km from cowbird traps. I also found no support for the prediction that songbird diversity would increase in cowbird Removal areas relative to Control sites. I conclude that the influence of cowbirds on communities of hosts is generally weak, however I recommend further investigation of the effects of cowbird parasitism on songbird community structure in landscapes supporting greater densities of cowbirds.

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TABLE 1. Brillouin's index of species diversity for 1996 and 1997 Removal sites, Control sites 5-10 km from traps and Control sites >10 km from cowbird traps.

	1996		1997		
	Removals	Controls 5-10 km	Removals	Controls 5-10 km	Controls >10 km
Brouillouin'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

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Evenness	0.791	0.880	0.811	0.798	0.802

TABLE 2. Mean number of cowbirds detected in cowbird Removal sites, Control sites 5-10 km from cowbird traps and Control sites >10 km from cowbird traps.

		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 5-10 km	Mean	0	0.167	0.069	0.326	0.056	0.257
	SE	0	0.069	0.025	0.062	0.021	0.035
CONTROL SITES >10 km	Mean	-	-	0.174	0.583	0.222	0.576
	SE	-	-	0.062	0.081	0.047	0.103

TABLE 3. Tests for differences between 1996 and 1997 maximum likelihood estimates of daily nest survival in cowbird Removal sites and Control sites 5-10 km from cowbird traps. Number of nests in brackets.

		Daily nest survival rate		SE of estimate		Z	P (one-tailed test)
		1996	1997	1996	1997		
Removal sites	suitable hosts	0.953 (12)	0.959 (29)	0.019	0.010	0.255	0.397
	unsuitable hosts	0.974 (4)	0.982 (11)	0.018	0.010	0.368	0.386
Controls 5-10 km	suitable hosts	0.987 (11)	0.970 (24)	0.009	0.009	1.276	0.100
	unsuitable hosts	0.974 (6)	0.986 (10)	0.018	0.009	0.603	0.274

TABLE 4. Incidence of parasitism among suitable hosts in cowbird Removal sites, Control sites 5-10 km and Control sites >10 km from cowbird traps.

		1996	1997	'96 & '97 combined
Removal sites	# of suitable host nests parasitized	0 / 12	0 / 29	0 / 41
	% parasitized nests	0%	0%	0%
Controls 5-10 km	# of suitable host nests parasitized	0 / 11	6 / 24	6 / 35
	% parasitized nests	0%	25%	17.1%
Controls >10 km	# of suitable host nests parasitized	-	5 / 20	-
	% parasitized nests	-	25%	-

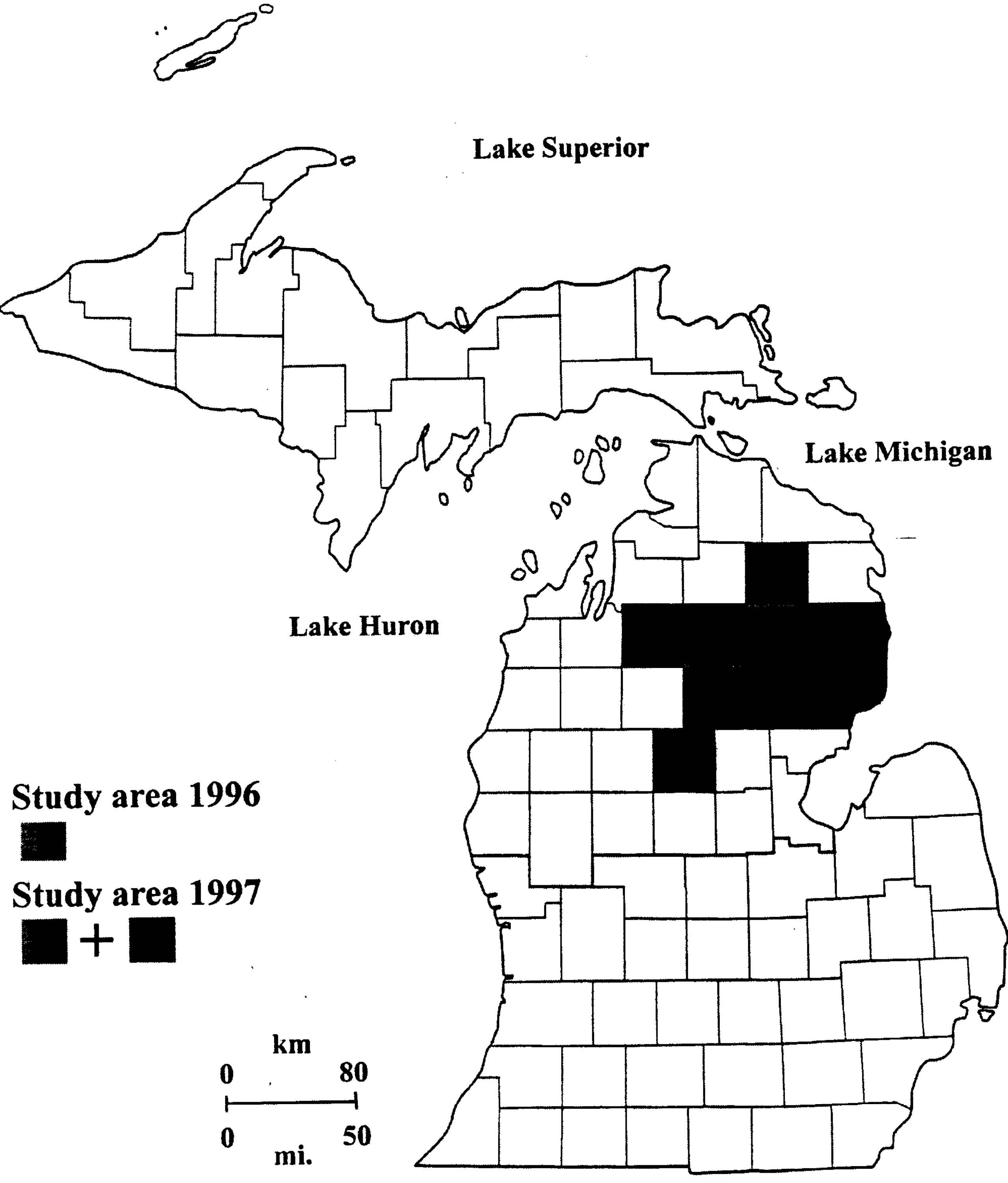


Fig. 1: Map of Michigan (modified from Brewer et al. 1991) showing location of study.

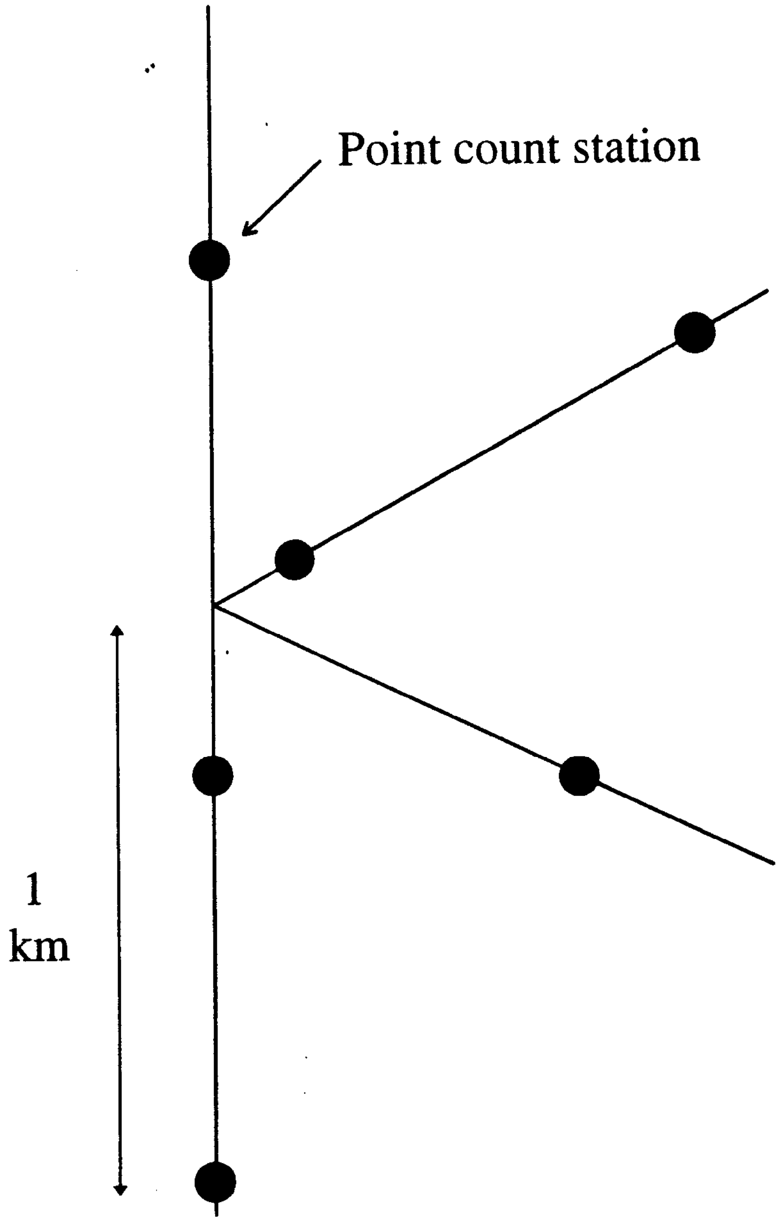


Fig. 2: Schematic of transect lines through a study area with randomly chosen point count locations.

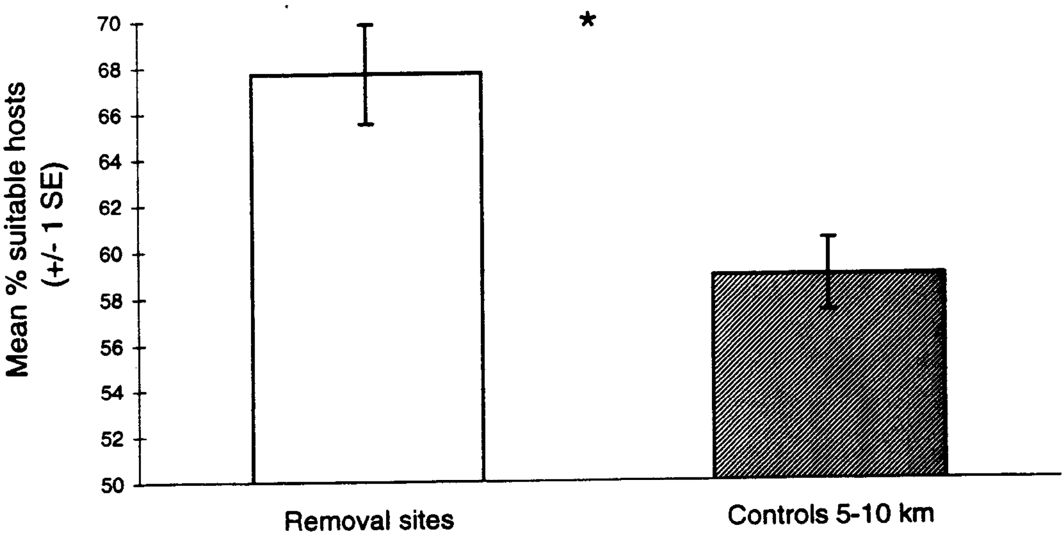


Fig. 3: Songbird community composition in 1996 at ten cowbird Removal sites and ten Control sites 5-10 km from cowbird traps

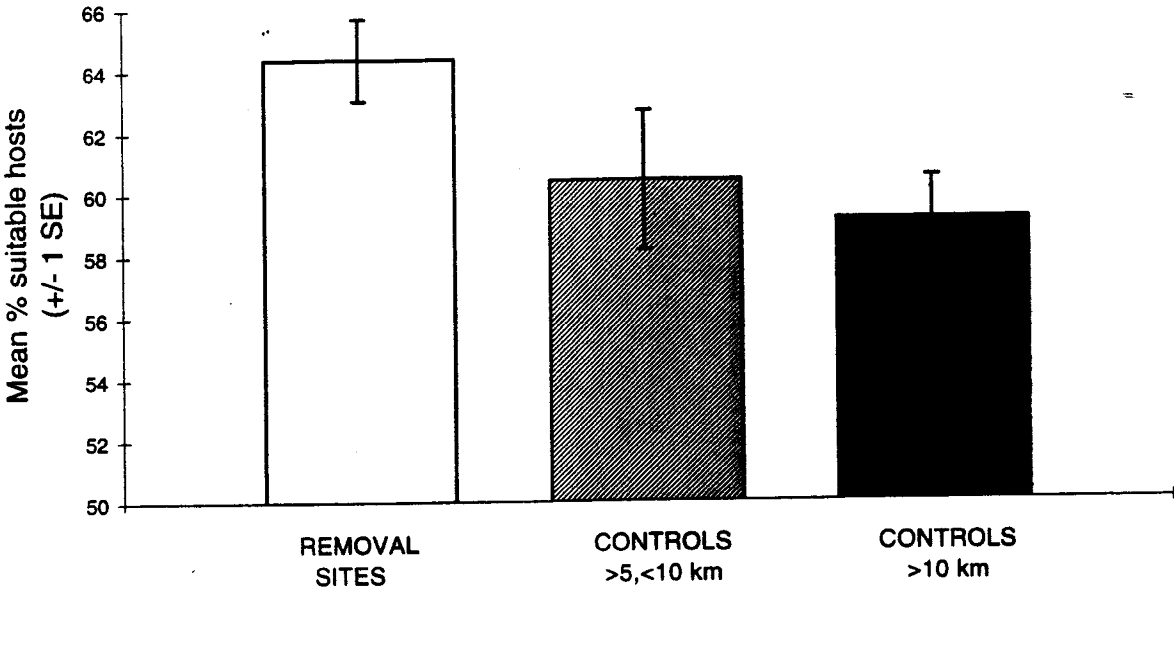


Fig. 4: Songbird community composition in 1997 at eight cowbird Removal sites, eight Control sites 5-10 km and eight Control sites >10 km from cowbird traps.

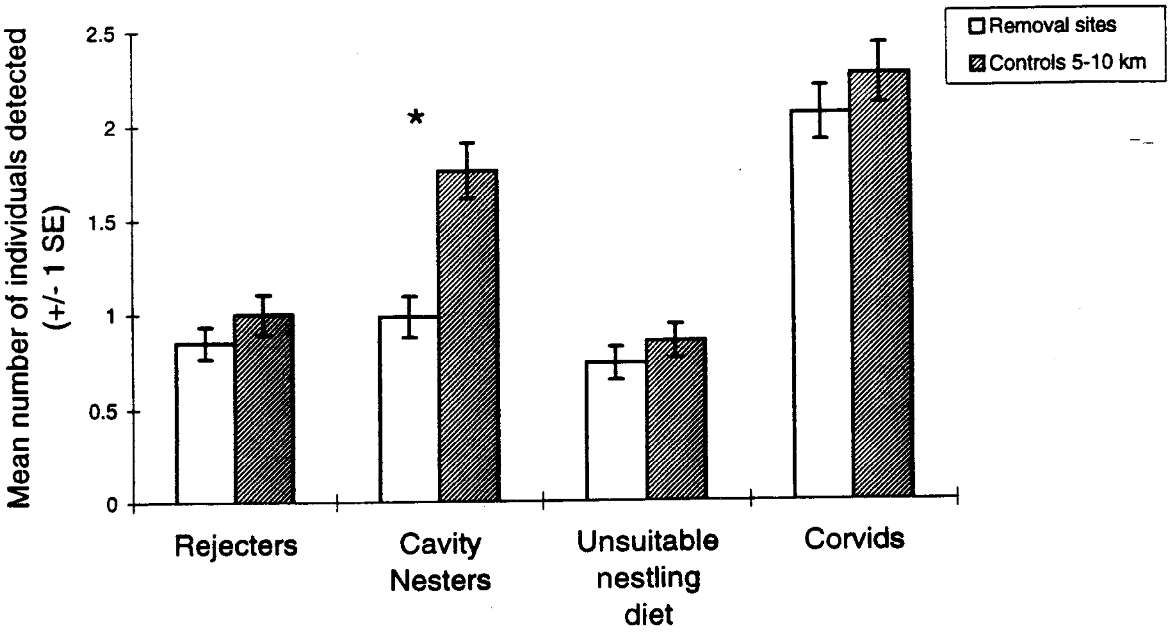


Fig. 5: Mean numbers of unsuitable hosts in 1996 detected during eight minute point counts in ten cowbird Removal sites and ten Control sites 5-10 km from cowbird traps.

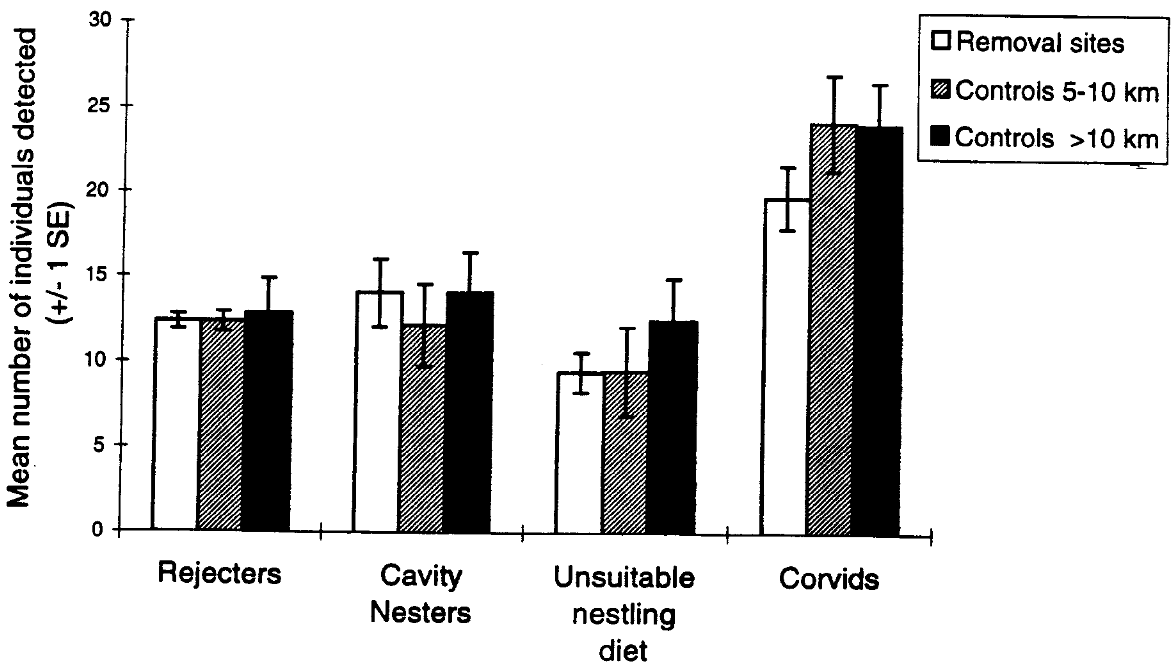


Fig. 6: Mean numbers of unsuitable hosts in 1997 detected during ten minute point counts in eight cowbird Removal sites, eight Control sites 5-10 km and eight Control sites >10 km from cowbird traps.

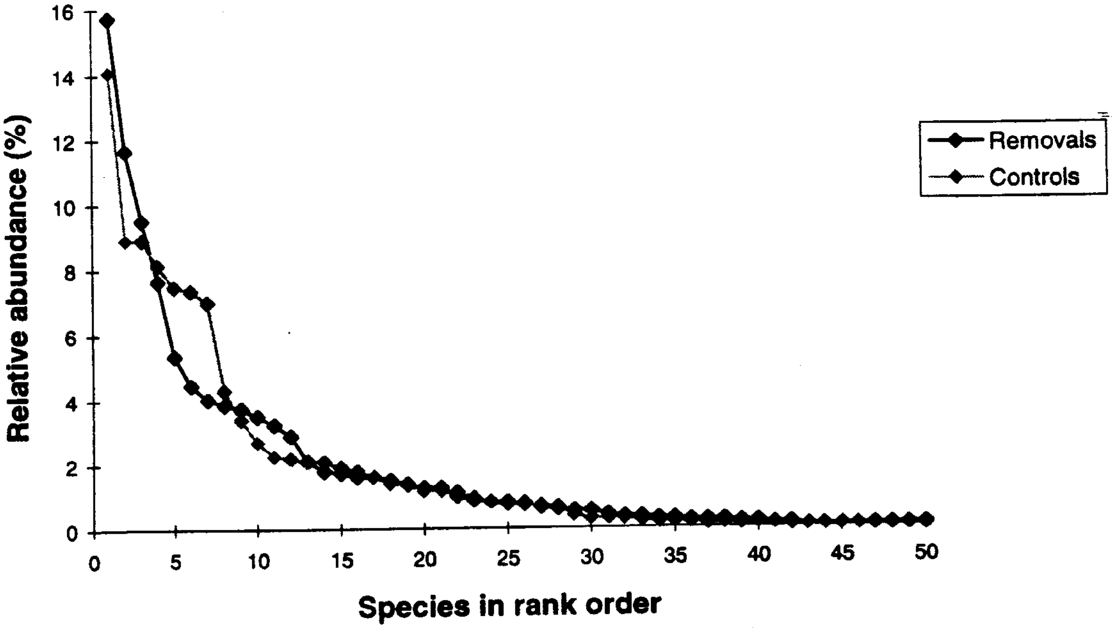


Fig. 7: Plot of species heterogeneity (richness and evenness) in 1996 at ten Removal sites and ten Control sites 5-10 km from cowbird traps.

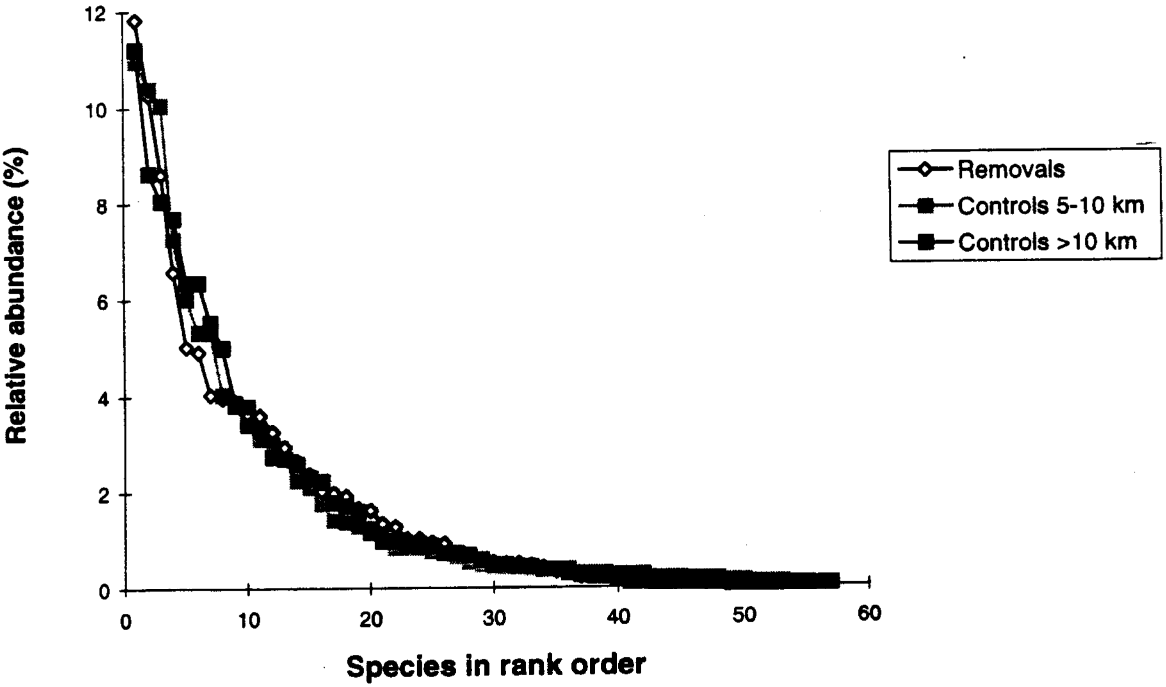


Fig. 8: Plot of species heterogeneity (richness and evenness) in 1997 at eight Removal sites, eight Control sites 5-10 km and eight Control sites >10 km from cowbird traps.

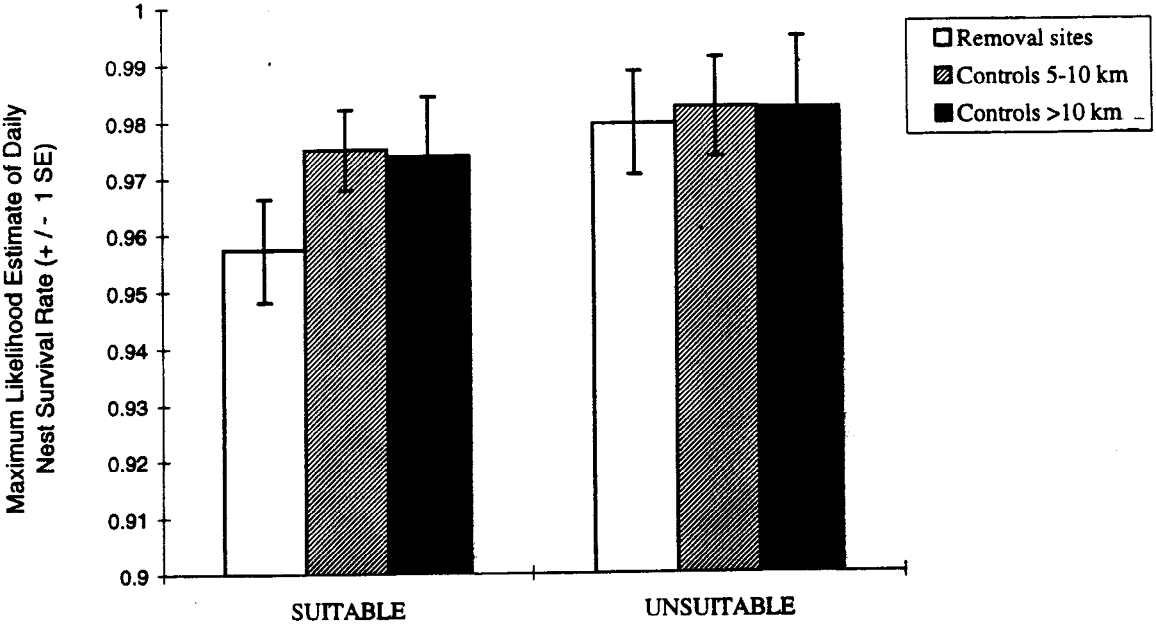


Fig. 9: Maximum likelihood estimates of daily nest survival for pooled 1996 and 1997 nests of suitable and unsuitable hosts.

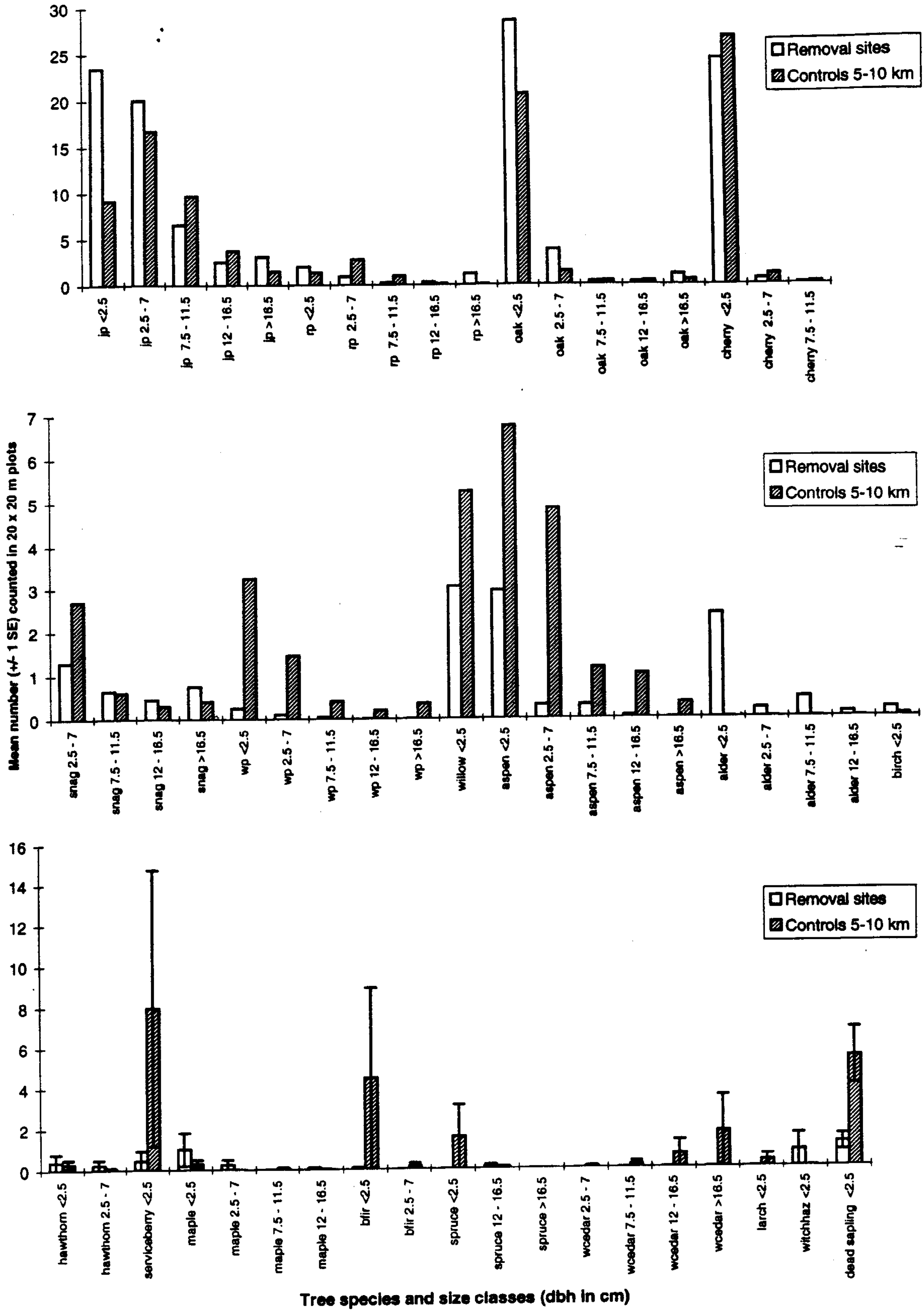
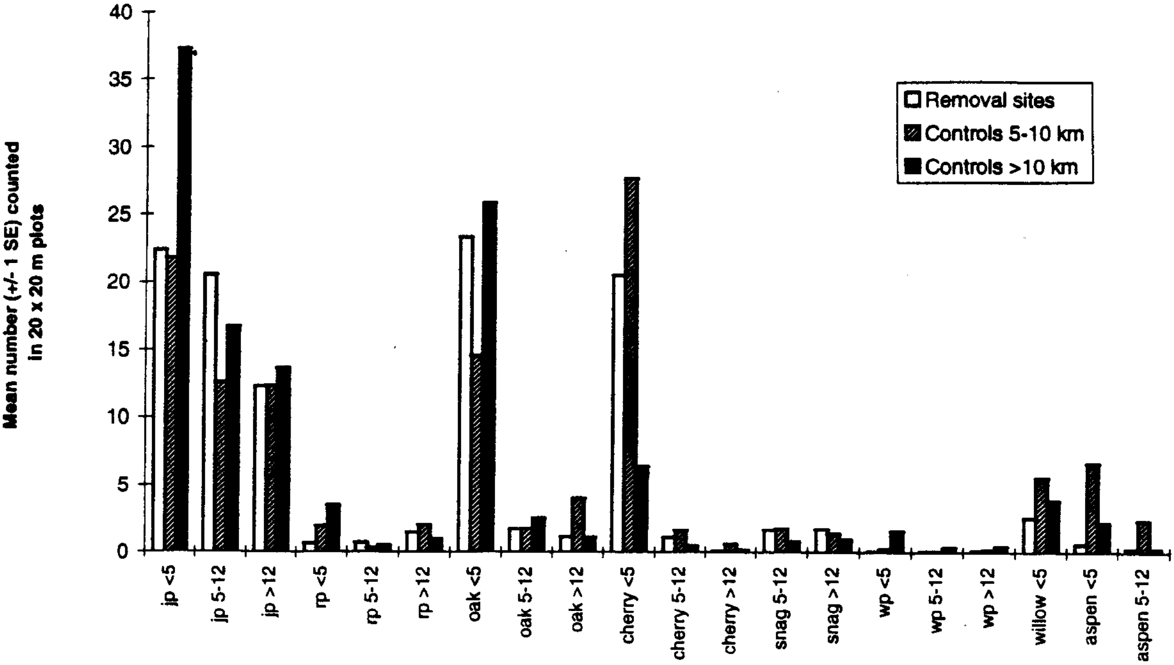


Fig. 10: Mean numbers of trees counted in 20 x 20 m plots (2 plots/site) in ten Removal sites and ten Control sites 5-10 km from cowbird traps in 1996. See Appendix Table 1 for species names.



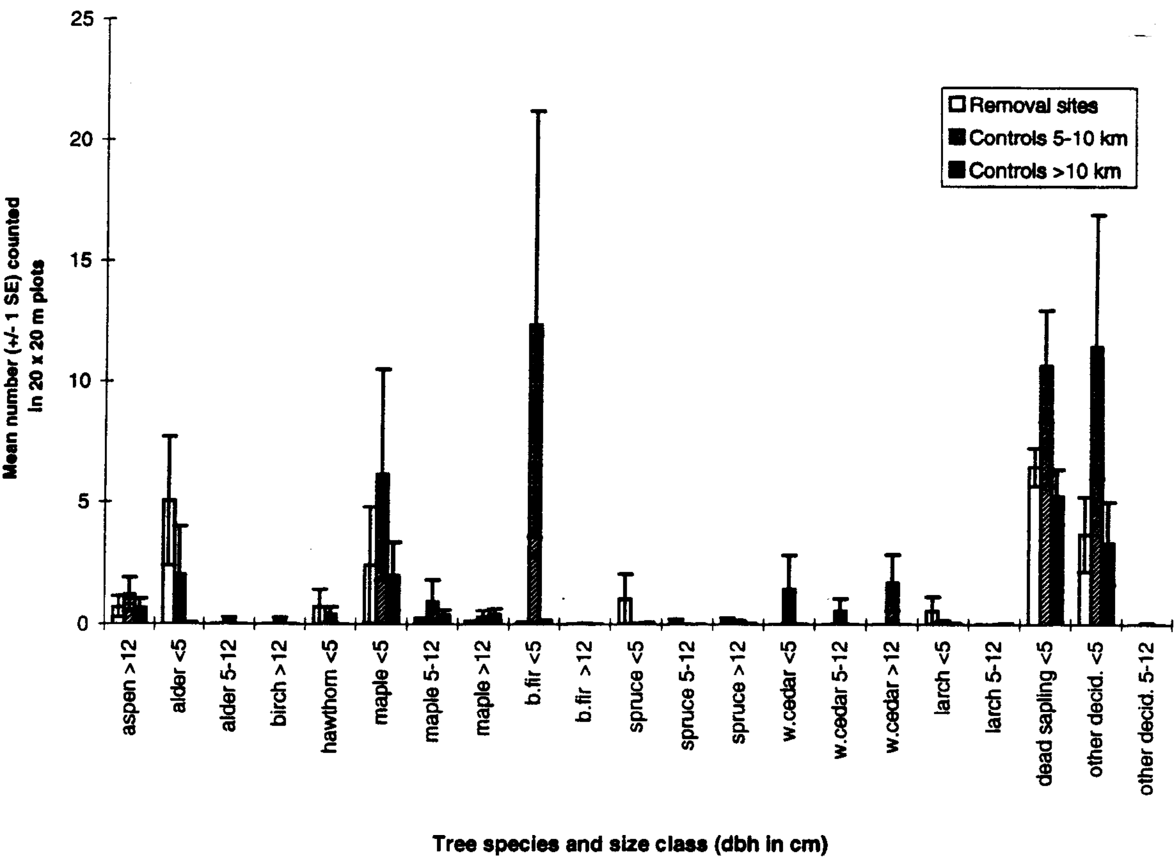


Fig. 11: Mean numbers of trees counted in 20 x 20 m plots (6 plots/site) in eight Removal sites, eight Control sites 5-10 km and eight Control sites >10 km from cowbird traps in 1997. See Appendix Table 1 for species names.

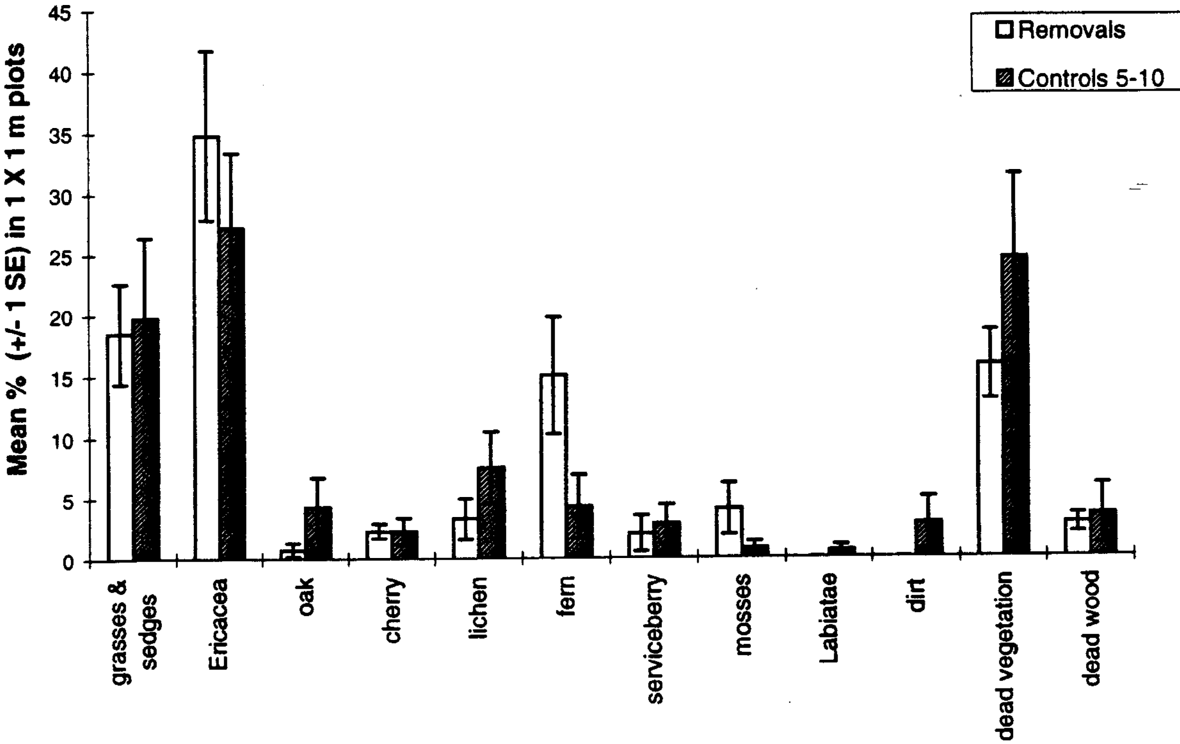


Fig. 12: Mean percentage of each ground cover type in 1 x 1 m plots (2 plots/site) in ten Removal sites and ten Control sites 5-10 km from cowbird traps. See Appendix Table 1 for species names.

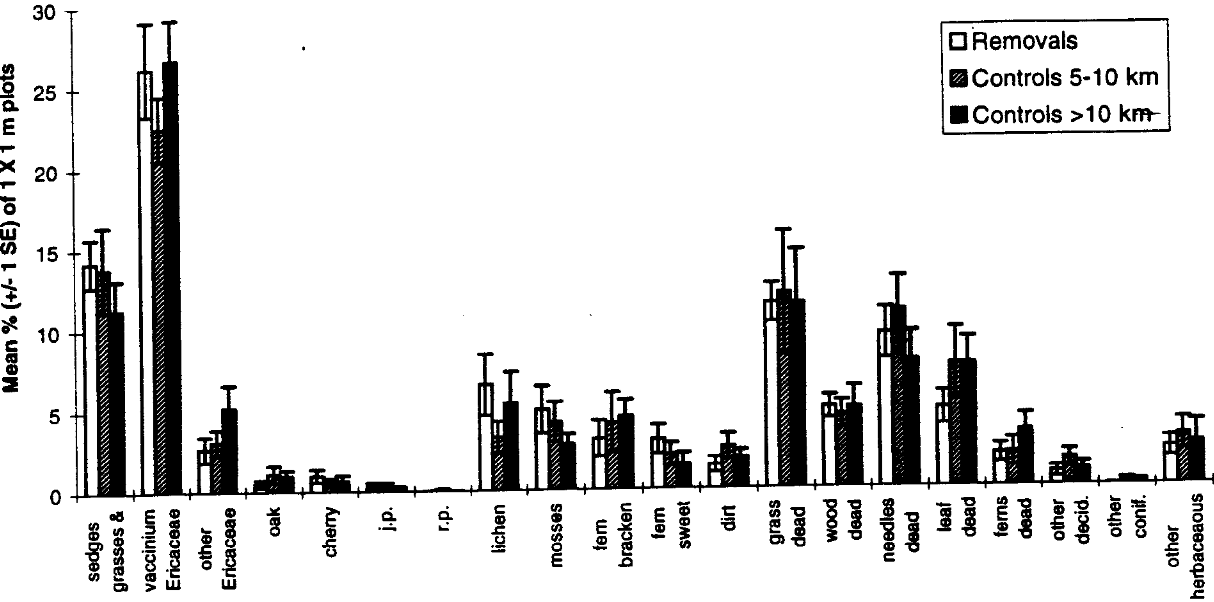


Fig. 13: Mean percentage of each ground cover type in 1 x 1 m plots (24 plots/site) in eight Removal sites, eight Controls 5-10 km and eight Controls >10 km from cowbird traps in 1997. See Appendix Table 1 for species names.

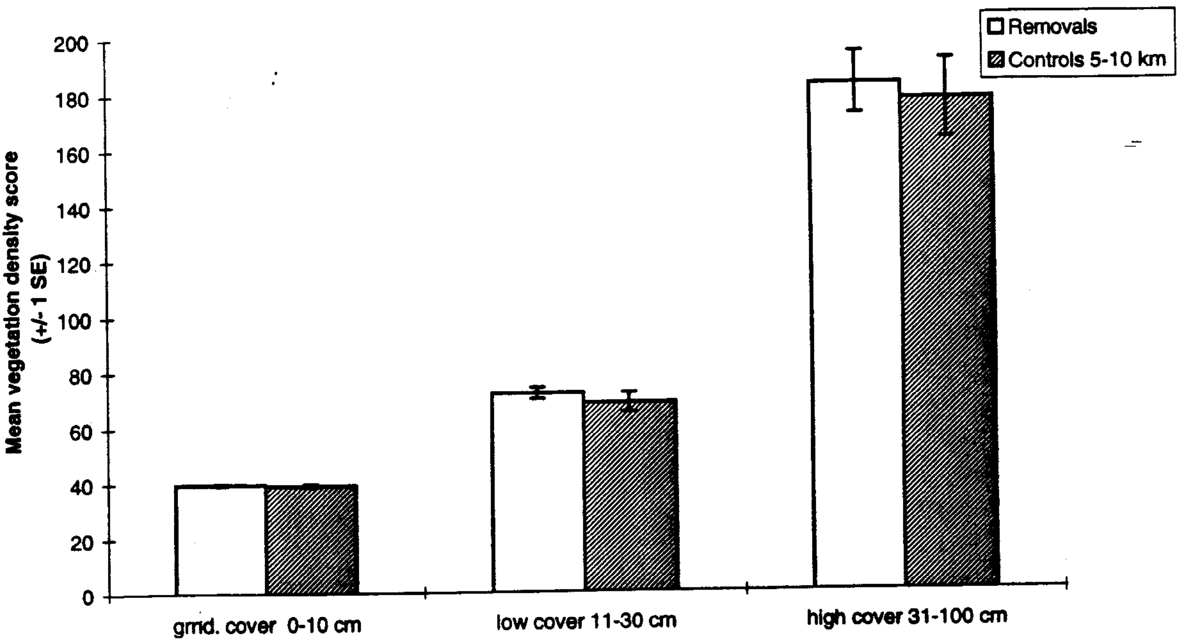


Fig. 14: Mean density of vegetation measured at two plots per site at ten Removal sites and ten Control sites 5-10 km from cowbird traps in 1996.

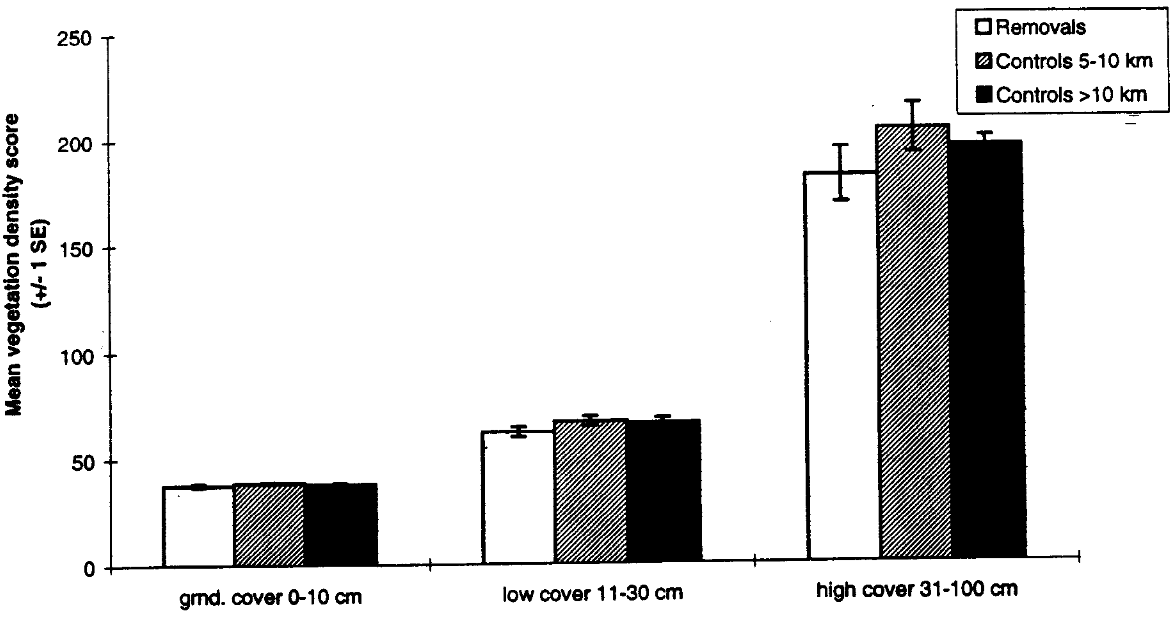


Fig. 15: Mean density of vegetation measured at twelve plots per site at eight Removal sites, eight Control sites 5-10 km and eight Control sites >10 km from cowbird traps in 1997.

APPENDIX

TABLE 1. Trees, shrubs and ground vegetation found in study plots.

TREES AND SHRUBS	GROUND COVER
Jack pine (*Pinus banksiana*)	Blueberry (*Vaccinium angustifolium*)
Red pine (*Pinus resinosa*)	Common bearberry (*Arctostaphylos uva-ursi*)
Eastern white Pine (*Pinus strobus*)	Wintergreen (*Gaultheria procumbens*)
Northern pin oak (*Quercus ellipsoidalis*).	Hairgrass (*Deschampsia flexuosa*)
Pin cherry (*Prunus pensylvanica*)	Big bluestem grass (*Andropogon gerardii*)
Trembling aspen (*Populus tremuloides*)	Sedge (*Carex pensylvanica*)
Large-toothed aspen (*Populus grandidentata*)	Sweet Fern (*Comptonia peregrina*)
Willow (*Salix* spp.)	Bracken Fern (*Gaultheria procumbens*)
White spruce (*Picea glauca*)	Reindeer Moss (*Cladonia mitis*)
Balsam fir (*Abies balsamea*)	
Northern white cedar (*Thuja occidentalis*)	
Larch (*Larix laricina*)	
Red maple (*Acer rubrum*)	
Black alder (*Alnus glutinosa*)	
White birch (*Betula papyrifera*)	
Hawthorn (*Crataegus* spp.)	
Serviceberry (*Amelanchier arborea*)	
Witch Hazel (*Hamamelis virginiana*)	

TABLE 2. Mean number of suitable host individuals detected at ten Removal and ten Control sites 5-10 km from cowbird traps in 1996.

		Removal	Control 5-10 km
Suitable	Kirtland's Warbler (*Dendroica kirtlandii*)	4.5	0
(33 spp.)	Yellow-Rumped Warbler (*Dendroica coronata*)	29	16
	Nashville Warbler (*Vermivora ruficapilla*)	97	74.5
	Pine Warbler (*Dendroica pinus*)	0.5	1
	Ovenbird (*Seiurus aurocapillus*)	44.5	61.5
	American Redstart (*Setophaga ruticilla*)	0.5	1
	Common Yellowthroat (*Geothlypis trichas*)	5	1
	Black-and-white Warbler (*Mniotilta varia*)	0.5	0.5
	Black-throated Green Warbler (*Dendroica virens*)	0.5	0.5
	Red-eyed Vireo (*Vireo olivaceus*)	7	18.5
	Eastern Wood-pewee (*Contopus virens*)	11.5	22.5
	Eastern Phoebe (*Sayornis phoebe*)	1	0
	Olive-sided Flycatcher (*Contopus borealis*)	0.5	0.5
	Least Flycatcher (*Empidonax minimus*)	0	2.5
	Chipping Sparrow (*Spizella passerina*)	63.5	62.5
	Vesper Sparrow (*Pooecetes gramineus*)	27	17.5
	Lincoln Sparrow (*Melospiza lincolnii*)	14.5	11.5
	Clay-coloured Sparrow (*Spizella pallida*)	2.5	1
	White-throated Sparrow (*Zonotrichia albicollis*)	10.5	8
	Song Sparrow (*Melospiza melodia*)	5.5	0
	Field Sparrow (*Spizella pusilla*)	31	17.5
	Swamp Sparrow (*Melospiza georgiana*)	2.5	0.5
	Savannah Sparrow (*Passerculus sandwichensis*)	0.5	0
	Dark-eyed Junco (*Junco hyemalis*)	17.5	13.5
	Eastern Towhee (*Pipilo erythrophthalmus*)	13.5	6
	Indigo Bunting (*Passerina cyanea*)	7.5	7
	Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	6.5	10
	Hermit Thrush (*Catharus guttatus*)	131	118
	Veery (*Catharus fuscescens*)	0	2.5
	Red-winged Blackbird (*Agelaius phoeniceus*)	13.5	1
	Common Grackle (*Quiscalus quiscula*)	2	0
	Scarlet Tanager (*Piranga olivacea*)	2	6
	TOTAL	**553**	**482.5**

TABLE 3. Mean number of unsuitable host individuals detected at ten Removal and ten Control sites 5-10 km from cowbird traps in 1996.

		Removal	Control 5-10 km
Unsuitable	Great Crested Flycatcher (*Myiarchus crinitus*)	6.5	12
(18 spp.)	Eastern Kingbird (*Tyrannus tyrannus*)	3	2
	Brown Thrasher (*Toxostoma rufum*)	24	10
	American Robin (*Turdus migratorius*)	15	28.5
	American Goldfinch (*Carduelis tristis*)	10.5	15
	Mourning Dove (*Zenaida macroura*)	33.5	36
	Cedar Waxwing (*Bombycilla cedrorum*)	8.5	19
	White-breasted Nuthatch (*Sitta carolinensis*)	3	5.5
	Red-breasted Nuthatch (*Sitta canadensis*)	4.5	7
	Winter Wren (*Troglodytes troglodytes*)	0.5	1.5
	Eastern Bluebird (*Sialia sialis*)	2	3.5
	Black-capped Chickadee (*Parus atricapillus*)	37	74.5
	Brown Creeper (*Certhia americana*)	3.5	0
	Blue Jay (*Cyanocitta cristata*)	79	68
	Tree Swallow (*Tachycineta bicolor*)	1.5	1.5
	Common Raven (*Corvus corax*)	12.5	9.5
	American Crow (*Corvus brachyrhyncos*)	32	58.5
	Baltimore Oriole (*Icterus galbula*)	1	0.5
	TOTAL	**279.5**	**356.5**

TABLE 4. Mean number of suitable host individuals detected at eight Removal sites, eight Control sites 5-10 km and eight Control sites >10 km from cowbird traps in 1997.

		Removal	Control 5-10 km	Control >10 km
Suitable (41 spp.)	Kirtland's Warbler (*Dendroica kirtlandii*)	12.7	1.7	2.0
	Yellow-Rumped Warbler (*Dendroica coronata*)	37.3	34.3	31.3
	Nashville Warbler (*Vermivora ruficapilla*)	97.0	88.7	74.0
	Pine Warbler (*Dendroica pinus*)	1.7	1.0	4.3
	Ovenbird (*Seiurus aurocapillus*)	46.3	63.0	70.7
	American Redstart (*Setophaga ruticilla*)	0.7	1.7	0.0
	Common Yellowthroat (*Geothlypis trichas*)	15.3	4.7	14.7
	Black-and-white Warbler (*Mniotilta varia*)	2.0	2.3	2.0
	Black-throated Green Warbler (*Dendroica virens*)	1.7	0.3	0.0
	Chestnut-sided Warbler (*Dendroica pensylvanica*)	0.3	1.3	0.7
	Black-throated Blue Warbler (*Dendroica caerulescens*)	0.3	0.0	0.0
	Canada Warbler (*Wilsonia canadensis*)	0.0	1.7	0.0
	Northern Waterthrush (*Seiurus noveboracensis*)	0.0	3.3	0.0
	Mourning Warbler (*Oporornis philadelphia*)	0.0	0.3	0.0
	Red-eyed Vireo (*Vireo olivaceus*)	2.0	7.3	8.0
	Solitary Vireo (*Vireo solitarius*)	0.3	1.3	0.3
	Eastern Wood-pewee (*Contopus virens*)	6.7	6.3	15.7
	Eastern Phoebe (*Sayornis phoebe*)	1.7	0.7	0.7
	Olive-sided Flycatcher (*Contopus borealis*)	2.0	0.0	0.0
	Least Flycatcher (*Empidonax minimus*)	0.3	2.3	0.7
	Alder Flycatcher (*Empidonax alnorum*)	0.0	1.7	0.3
	Chipping Sparrow (*Spizella passerina*)	62.0	46.7	58.3
	Vesper Sparrow (*Pooecetes gramineus*)	25.0	27.3	24.7
	Lincoln Sparrow (*Melospiza lincolnii*)	34.0	12.3	9.0
	Clay-coloured Sparrow (*Spizella pallida*)	1.3	3.7	1.7
	White-throated Sparrow (*Zonotrichia albicollis*)	19.0	12.0	4.3
	Song Sparrow (*Melospiza melodia*)	4.7	4.0	6.3
	Field Sparrow (*Spizella pusilla*)	36.7	26.3	35.0
	Swamp Sparrow (*Melospiza georgiana*)	5.3	0.7	0.7
	Dark-eyed Junco (*Junco hyemalis*)	18.0	6.7	10.7
	Eastern Towhee (*Pipilo erythrophthalmus*)	9.0	11.3	16.3
	Indigo Bunting (*Passerina cyanea*)	2.7	5.7	5.3
	Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	5.3	18.3	4.0
	Northern Cardinal (*Cardinalis cardinalis*)	0.0	0.0	0.3
	Hermit Thrush (*Catharus guttatus*)	111.7	96.3	103.0
	Veery (*Catharus fuscescens*)	0.3	2.7	1.0
	Wood Thrush (*Hylocichla mustelina*)	0.0	0.0	0.3
	Red-winged Blackbird (*Agelaius phoeniceus*)	34.3	10.0	9.0
	Brewer's Blackbird (*Euphagus cyanocephalus*)	0.3	0.0	0.7
	Common Grackle (*Quiscalus quiscula*)	3.0	11.0	8.3
	Scarlet Tanager (*Piranga olivacea*)	1.3	3.3	8.3
	TOTAL	**603**	**522.3**	**532.7**

TABLE 5. Mean number of unsuitable host individuals detected at eight Removal sites, eight Control sites 5-10 km and eight Control sites >10 km from cowbird traps in 1997.

		Removal	Control 5-10 km	Control >10 km
Unsuitable (20 spp.)	Great Crested Flycatcher (*Myiarchus crinitus*)	8.7	7.3	21.0
	Eastern Kingbird (*Tyrannus tyrannus*)	5.0	2.3	1.0
	Gray Catbird (*Dumetella carolinensis*)	0.0	0.3	0.0
	Brown Thrasher (*Toxostoma rufum*)	30.7	19.7	20.3
	American Robin (*Turdus migratorius*)	22.3	35.3	30.3
	American Goldfinch (*Carduelis tristis*)	18.7	23.7	23.7
	Pine Siskin (*Carduelis pinus*)	0.0	0.0	0.3
	Mourning Dove (*Zenaida macroura*)	38.0	33.3	50.7
	Cedar Waxwing (*Bombycilla cedrorum*)	15.7	15.3	25.0
	White-breasted Nuthatch (*Sitta carolinensis*)	1.0	2.3	2.3
	Red-breasted Nuthatch (*Sitta canadensis*)	12.0	3.7	4.0
	Winter Wren (*Troglodytes troglodytes*)	0.0	2.7	0.3
	Eastern Bluebird (*Sialia sialis*)	4.7	0.7	3.3
	Black-capped Chickadee (*Parus atricapillus*)	47.3	52.7	46.0
	Brown Creeper (*Certhia americana*)	1.0	0.3	0.7
	Blue Jay (*Cyanocitta cristata*)	81.3	91.3	79.3
	Tree Swallow (*Tachycineta bicolor*)	9.7	3.3	6.7
	Common Raven (*Corvus corax*)	9.7	7.3	6.7
	American Crow (*Corvus brachyrhyncos*)	27.7	46.7	58.3
	Baltimore Oriole (*Icterus galbula*)	0.3	1.0	0.3
	TOTAL	**342**	**356.3**	**386.3**

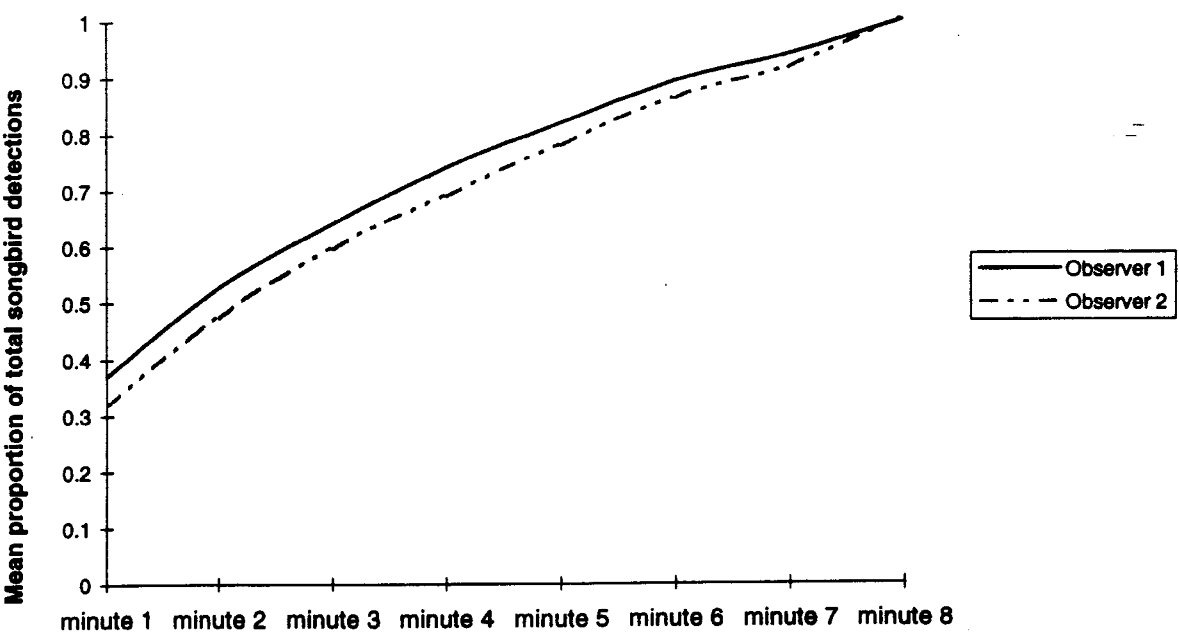


Fig. 1: Mean detection curves for point count observers, representing cumulative proportion of total songbird detections over time.