



Habitat selection for parasite-free space by hosts of parasitic cowbirds

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Choice of breeding habitat can have a major impact on fitness. Sensitivity of habitat choice to environmental cues predicting reproductive success, such as density of harmful enemy species, should be favored by natural selection. Yet, experimental tests of this idea are in short supply. Brown-headed cowbirds *Molothrus ater* commonly reduce reproductive success of a wide diversity of birds by parasitizing their nests. We used song playbacks to simulate high cowbird density and tested whether cowbird hosts avoid such areas in habitat selection. Host species that made settlement decisions during manipulations were significantly less abundant in the cowbird treatment as a group. In contrast, hosts that settled before manipulations started and non-host species did not respond to treatments. These results suggest that hosts of cowbirds can use vocal cues to assess parasitism risk among potential habitat patches and avoid high risk habitats. This can affect community structure by affecting habitat choices of species with differential vulnerability.

Breeding habitat selection is one of the most important decisions in the life of all animals because it can strongly affect reproductive success (Cody 1985, Jaenike and Holt 1991, Martin 1998). In that process, animals can be expected to take into account factors that positively (e.g. good food resources and habitat quality) and negatively (e.g. abundance of predators, parasites and competitors) affect reproductive success. Given the importance of reproductive success to fitness, natural selection can favor choice of high quality habitats that enhance reproductive success (Jaenike and Holt 1991, Martin 1998). However, habitats vary substantially in space and time with respect to abundance of resources and enemies (Robinson et al. 1995, Forsman et al. 1998, Sieving and Willson 1998), both of which can influence reproductive success and, hence, habitat quality. Consequently, organisms are faced with unknown and variable habitat quality that needs to be assessed prior to choice of breeding habitat. Given time limitations imposed by a finite breeding season, reliable cues to habitat quality should play important roles in habitat choice. Reliable cues may be particularly critical for migratory birds, which must assess and choose breeding habitats in a short period after arrival on the breeding grounds because even slight delays in the onset of breeding decrease reproductive success (Siikamäki 1998).

One potential set of reliable and current information of habitat quality might be the presence of other species occupying a habitat. Recent evidence suggests that many migratory birds use the presence or density of earlier established species as proximate cues in nest-site (Seppänen

and Forsman 2007) and habitat selection decisions (Mönkkönen et al. 1990, Forsman et al. 2002, 2008, Thomson et al. 2003, Fletcher 2007). Earlier established species presumably have more time to assess and choose, and thereby signal, high quality habitats, which makes them profitable cues for subsequent species. In contrast, densities of species that reflect risk of enemy (i.e. predators, parasites) attack might serve as important cues of low quality habitats that should be avoided. Risk of mortality commonly increases with densities or proximity of enemies and recent studies have demonstrated that birds take into account risk of nest and adult predation in habitat selection and offspring investment (Forsman et al. 2001, Eggers et al. 2006, Fontaine and Martin 2006a, 2006b, Thomson et al. 2006, Sergio et al. 2007, Mönkkönen et al. 2007). Brood parasites also can have strong effects on fitness but their effects on habitat selection at larger scales have rarely been tested. Most studies of brood parasitism in birds have focused on behavioral adaptations of hosts against parasitism after the initiation of breeding (Rothstein and Robinson 1998, Davies 2000). Breeding habitat selection relative to perceived parasite density can be an effective means of reducing risk of parasitism before investment in breeding, but this possibility is poorly studied (Soler et al. 1998).

Migratory birds that serve as hosts of the parasitic brown-headed cowbird (*Molothrus ater*, cowbird hereafter) provide a suitable study system for this question. The cowbird is a generalist brood parasite for more than 200 bird species in North America (Rothstein and Robinson

1998, Davies 2000) and cowbirds can significantly reduce reproductive success and viability of host populations (Robinson et al. 1995, Smith et al. 2002, Zanette et al. 2005). Cowbirds establish and defend territories during the settling period of migrants and search for nests to be parasitized later (Rothstein et al. 1984, Gates and Evans 1998). Given that hosts can recognize cowbirds by sight and vocalization (Gill et al. 1997), hosts could use vocal cues of cowbird abundance to influence settling decisions as a means of reducing the risk of parasitism.

Here, we experimentally tested this novel hypothesis that heterospecific cues of the risk of parasitism can influence habitat choice of hosts. We used vocalization playbacks in two treatments to simulate increased densities of 1) cowbirds and 2) a neutral species as the control. We compared densities of bird species that are not commonly observed as cowbird hosts (i.e. non-hosts) with host species between the two treatments. We further divided host species into those that are resident and already present before song playbacks were initiated versus migrant host species that arrived after the initiation of experimental playbacks. If birds use cowbird vocalizations as a cue for risk of parasitism in habitat choice decisions, late arriving hosts are expected to settle at lower densities in the cowbird playback treatment than in the control playback. In contrast, resident hosts are already settled and therefore should not show differences between treatments, and non-host species should not be influenced by cowbirds and also show no difference between treatments.

Material and methods

Study area and playbacks

Experiments were conducted in western Montana, USA, in 2001 and 2002. The experimental protocol consisted of playbacks of songs and vocalizations of 1) cowbirds to simulate increased risk of parasitism, and 2) the dark-eyed junco *Junco hyemalis* as a non-threatening neutral species to serve as a control. Birds have the capability to recognize heterospecific vocalizations (Forsman and Mönkkönen 2001, Martin and Martin 2001, Fletcher 2007) making the use of playbacks feasible.

Treatment vocalizations were played using portable cassette players with 3 min loop cassettes with a maximum volume (70–80 db, both treatments) on study plots daily (ca 13 h) for about two weeks at the time of the main migrant arrival in May. Species songs and vocalizations were obtained from the Macaulay Library of Natural Sounds, Cornell Lab of Ornithology. Junco and cowbird playback tapes consisted of a mix of songs of three individuals that were recorded in western Canada and in western USA, respectively. The junco playback tape contained 2 min of continuous songs with short (10–15 s) breaks followed by one min of silence. The cowbird tape had the same structure and the two min of vocalizations consisted of a song (1 min) with chatter and whistles and a harsh rattle (1 min).

To estimate effects of treatments on community structure, birds were divided into hosts and non-hosts (Table 1).

Table 1. The observed species and the division of potential cowbird hosts into species arriving prior (resident hosts) and after (late arriving hosts) the initiation of experimental playbacks and non-hosts. Species are in the descending order of observed occurrence on the study plots. In the late arriving hosts, the first seven species occurred on four or more study plots in either of the year.

Late arriving hosts		Resident hosts		Non-hosts	
Common name	Scientific name	Common name	Scientific name	Common name	Scientific name
MacGillivray's warbler	<i>Oporornis tolmiei</i>	American robin	<i>Turdus migratorius</i>	Black-capped chickadee	<i>Poecile atricapilla</i>
Flycatchers	<i>Empidonax</i> spp.	Song sparrow	<i>Melospiza melodia</i>	Ruby-crowned kinglet	<i>Regulus calendula</i>
Warbling vireo	<i>Vireo gilvus</i>	Yellow-rumped warbler	<i>Dendroica coronata</i>	Red-breasted nuthatch	<i>Sitta canadensis</i>
Townsend's warbler	<i>Dendroica townsendii</i>	Cedar waxwing	<i>Bombycilla cedrorum</i>		
Swainson's thrush	<i>Catharus ustuatus</i>				
Yellow warbler	<i>Dendroica petechia</i>				
Orange-crowned warbler	<i>Vermivora celata</i>				
American redstart	<i>Setophaga ruticilla</i>				
Common yellowthroat	<i>Geothlypis trichas</i>				
Cassin's vireo	<i>Vireo cassinii</i>				
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>				
Western tanager	<i>Piranga ludoviciana</i>				
Willow flycatcher	<i>Empidonax traillii</i>				
Chipping sparrow	<i>Spizella passerina</i>				
Wilson's warbler	<i>Wilsonia pusilla</i>				
Western wood-pewee	<i>Contopus sordidulus</i>				
Veery	<i>Catharus fuscescens</i>				
Northern waterthrush	<i>Seiurus noveboracensis</i>				

Hosts were further divided into species settling prior to (resident hosts) and after (late arriving hosts) the initiation of playbacks. Division was based on the observations we made on the study plots in spring 2001. We considered as non-host species only cavity-nesting species (black-capped chickadee *Poecile atricapilla* and red-breasted nuthatch *Sitta canadensis*) and the ruby-crowned kinglet *Regulus calendula* (Friedmann and Kiff 1985) (Table 1) because they are never or very rarely observed to be parasitized due to their nesting habits (cavity nesters) and plausibly due to small size (ruby-crowned kinglet). Junco numbers were not included in any density estimates to avoid potential effects of playbacks on habitat choices of juncos. We conducted two separate experiments in two years to account for possible variation related to habitat or between-year effects: 'within-year' and 'within-plot between-years'.

Design of the 'within-plot between-years' experiment

This experiment was carried out in the Bitterroot Valley, western Montana (USA), in 2001 and 2002 and was designed to control for habitat effects by first estimating baseline densities of birds in the first year (reference year) and applying manipulations in the second year (manipulation year) on the same plots. Six study plots were located along three creeks in the foothills of the Bitterroot Mountains. Each creek contained two rectangular shaped study plots (4.5–5.0 ha) and the distances between plots varied between 400 m and 600 m. Such distances between sampling units are commonly regarded adequate (Hutto et al. 1986, Fletcher 2007). Plots were placed with the creek in the middle of the plot and depending on the shape of the creek extended 50–100 m beyond the creek on both sides. We aimed to keep the area of the riparian part comparable across plots. The vegetation in the riparian portion of plots was dominated by deciduous trees and shrubs, including black cottonwood *Populus balsamifera*, trembling aspen *P. tremuloides* and black hawthorn *Crataegus douglasii*. At the outer edges of plots, vegetation was dominated by ponderosa pine *Pinus ponderosa*, engelmann spruce *Picea engelmannii* and douglas-fir *Pseudotsuga menziesii*. For a more detailed description of the study area see Tewksbury et al. (1998).

The experiment consisted of a reference year and a manipulation year. Year 2001 was a reference year and breeding densities of all birds were surveyed using the standard territory mapping method (Robbins 1970). Each plot was censused three times after the settlement of all migrant birds, between 31 May and 21 June, in both years. Censuses were carried out in fair weather by the same person (JTF) between 06:00 and 11:00 h and every census occasion took place at different times of the morning to control for the effect of birds' singing activity on abundance estimates. All observations (singing males, warning males/females, observed silent birds) were placed onto schematic maps and were later interpreted by the same person (JTF) to estimate densities. A 50 × 50 m grid system was flagged on plots to aid censusing and transferring observations to census maps. Observations were located on maps relative to the nearest flagged grid corner with the accuracy of ca ± 15 m. Observations were interpreted as a breeding pair if an

individual of the same species was observed within 50 m during at least two visits or a pair was observed once.

Manipulations took place in 2002. Study plots along each creek formed a block to which the treatments were randomly assigned. Playbacks were started 15 May when the first tropical migrants were observed on study plots. Due to the relatively high altitudinal location of the study area (ca 1300 m a.s.l.), only true residents and early arriving short-distance migratory species (resident hosts) were present at that time. The density of recorders in the cowbird and junco treatments was set based on observed number of these species on these plots in the reference year. The number of observed female cowbirds and junco pairs were relatively constant across plots (2–3 and 1–2, respectively) and thus six cassette players were used in each cowbird treatment plot and four in control plots. We kept the distance of recorders on the plot even to enable as broad coverage of playbacks as possible. The range of both playbacks usually was audible about 30–40 m from the loudspeaker. Locations of recorders were changed every second day. Playbacks ceased after 30 May when tropical migrant flycatcher species were present in great numbers and no obvious immigration was observed. Breeding bird surveys on the plots were then started.

Design of the 'within-year' experiment

This experiment was carried out in spring 2001 near Missoula, Montana, as a pilot test of the feasibility and effects of cowbird playbacks on migratory birds. Because this experiment was conducted in one year, it can control for potential effects of between-year variation in bird densities that may mask the effects of treatments in the 'within-plot between years' experiment. Study plots (2 ha) were assigned along two creeks in a forested mountain area and the distances between plots within a creek system were 400 m and 200 m. Such distances between sampling units are commonly regarded adequate (Hutto et al. 1986, Fletcher 2007). Both creeks contained two plots and treatments were randomly assigned within each creek. We used five cassette players (above) on each plot and treatment between 13 and 28 May from dawn for about 13 h. The abundance of birds on plots was estimated by a single visit mapping method (above) in which plots were carefully surveyed by walking along parallel lines 25 m apart.

Statistical analyses

In the 'within-plot between-years' experiment, we measured the response of birds to treatments as a change in pair numbers within each plot between the reference and the treatment year. In the within-year experiment, actual abundances per treatments were used as the response variable. Because we predicted that late arriving hosts would avoid cowbird treatment, we used one-tailed testing. At the species level we analyzed the response of those species that occurred on at least four study plots in either year (Table 1). Lower incidence (≤ 3 plots) decreases power of the test to detect effects of manipulation. The occurrence of other species was too uneven to allow testing. The abundance of single species may vary greatly among plots,

which may violate distribution requirements of variables of parametric statistical tests. We therefore examined species response to treatments by resampling techniques. Also the effect of treatments on the abundance of cowbirds on plots was examined by this method. Resampling analyses are efficient and free of distribution requirements of variables (Manly 1997). Resampling analyses were done using Resampling stats add-in for Excel (Resampling Stats 2004).

In the within-plot experiment, for each species included in the analysis, we calculated the change in pair numbers within each plot between the treatment and the reference year (treatment – reference year). Difference was then summed across all plots for both treatments. If cowbirds have a negative effect on settling decisions, decreases in density between years should be stronger in the cowbird treatment than in the control treatment. To test how likely it is to observe this or more extreme effect sizes, the observed changes in density were shuffled between plots and the sum of changes was calculated for both treatments in these randomized data. This was then repeated 1000 times. The number of resampled cases in which the difference between treatments was equal or higher than in the observed data constitutes a one-tailed probability that the observed effect is due to chance alone.

In the within-year experiment, for each species included in the analysis, we first calculated the observed average abundances in each treatment and the difference between treatments (cowbird–junco). If cowbirds have an inhibitory effect on habitat choices, host abundance should be lower in the cowbird treatment compared with the junco (control) treatment. To test how extreme the observed difference is, we created a randomized data for each species by shuffling observed abundances between study plots and calculating their average difference. This was repeated 1000 times and the number of resampled cases in which the difference between treatments was equal or more negative than the observed result indicates a one-tailed probability that the observed effect is due to chance alone.

Effects of treatments at the community level (abundance of late arriving hosts versus abundance of resident and non-hosts) were examined by t-tests because pooled abundances better fulfilled the distribution requirements of parametric tests. Density differences and densities of species groups between treatments were compared in the within-plot and within-year experiments, respectively. Because both independent experiments tested the same hypothesis, we combined their significance values using the method suggested by Sokal and Rohlf (1995, pp. 794). Analyses were conducted by SPSS 11.5.

Results

In the within-year experiment, only one cowbird was observed during bird surveys in the cowbird treatment plot. In the within-plot experiment, cowbirds were observed on all plots (mean: 2.5, range: 1–5 males and females) during the reference and the treatment years. There was no difference in the abundance of cowbirds among treatments between the reference and the treatment year (randomization test: difference = 0.0, $p = 0.683$). Hence, playbacks did not affect cowbird abundance on study plots and any

differences in the abundance of birds between treatments are most likely due to experimental playbacks only.

At the species level, treatment effects were weak. Abundance and occurrence of most species were low and for most species treatment effects were not detected (randomization test: $p > 0.2$). However, the MacGillivray's warbler *Oporornis tolmiei* was relatively abundant and present in all plots in both years and showed avoidance of cowbird treatment in the within-year experiment (randomization test: difference = 1.0 pair, $p = 0.162$) and in the within-plot between years experiment (density change was more negative in the cowbird (–3.0 pairs) than in the control treatment (+5.0 pairs; randomization test: $p = 0.046$). The combined probability of these experiments suggest that MacGillivray's warblers avoid high perceived density of cowbirds in habitat choices (test combining significance values: test value = 9.798, DF = 4, 1-way $p = 0.044$).

Treatment effects were more obvious among groups of species based on parasitism risk. As expected, neither the density of non-hosts (of which most were cavity-nesting resident birds) (test combining significance values: test value = 6.456, DF = 4, 1-way $p = 0.168$) nor resident hosts (test combining significance values: test value = 6.465, DF = 4, 1-way $p = 0.167$) differed between treatments (Fig. 1A–B). In contrast, host species that settled during playback treatments as a group showed a clearer response to the treatments. In the within-year experiment, the pooled density of later arriving hosts was suggestively lower in the cowbird than in the control treatment (t-test: $t_2 = 2.50$, $p = 0.065$) (Fig. 1A). In the within-plot between year experiment, when treatments were applied in the second year, abundance of later arriving hosts declined more strongly on the cowbird treatments (on average –2.83 pairs) than on the control treatments (on average +4.67 pairs) (t-test: $t_4 = 2.13$, $p = 0.05$) (Fig. 1B). The decline in the abundance of late arriving hosts in the cowbird treatment was consistent across all three treatment plots (–0.5, –3.0 and –5.0 pairs), whereas the increase in abundance in the control treatment was mostly due to one of the control plots (+11.0, +3.0 and 0 pairs). The combined probability of the experiments suggest that cowbird treatment had an inhibitory effect on settling decisions of later arriving hosts (test combining significance values: test value = 11.46, DF = 4, 1-way $p = 0.022$).

In the within plot between year experiment, densities of bird groups were similar among treatments in the reference year (2001). The densities (pairs/4 ha \pm SEM) of later arriving hosts in the forthcoming cowbird and control treatments were $13.34 \pm 2.54/13.48 \pm 2.06$ and resident hosts were $2.03 \pm 0.80/2.07 \pm 0.30$. The density of non-hosts was somewhat more variable ($1.14 \pm 0.27/2.07 \pm 0.60$) but the difference was not statistically different (t-test: $t_4 = 1.43$, $p = 0.225$). Hence, plot effects were minimal, which further emphasize the effect of cowbird playback on host density.

Discussion

Most research on cowbirds, and brood parasites in general, has focused on habitat selection of parasites, effects of

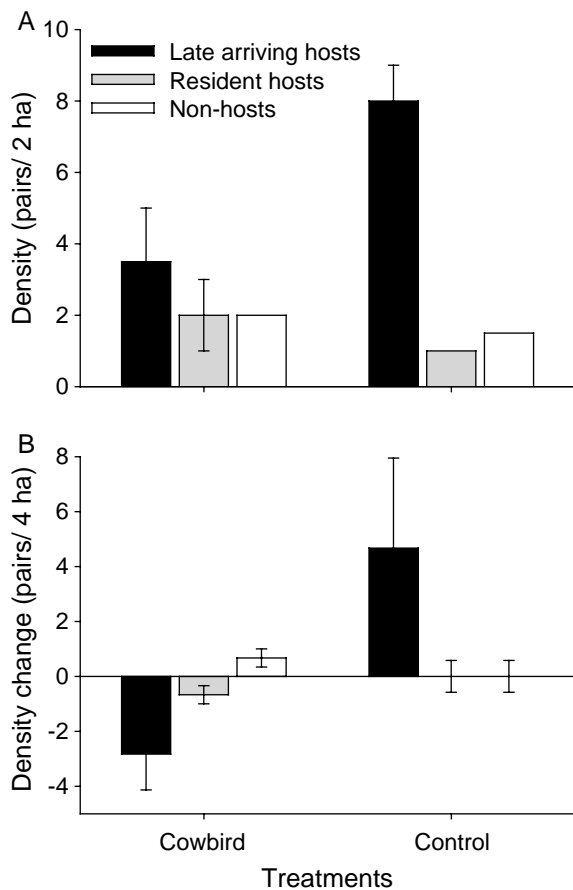


Figure 1. Density responses of different bird groups based on their risk of parasitism to experimental treatments in two separate experiments. (A) within-year experiment. Average densities of late arriving hosts, resident hosts and non-hosts in cowbird and control treatments within the same year (± 1 SEM); (B) within-plot experiment. Average change in density within plots for late arriving hosts, resident hosts and non-hosts between reference and manipulation years (manipulation–reference) among the treatments (± 1 SEM).

parasitism on demography and viability of host populations, and coevolutionary arms-race between parasites and hosts (Rothstein and Robinson 1998, Morrison et al. 1999, Davies 2000). This study contributes new information to the understanding of interactions between cowbirds and its hosts in two major ways. First, the results suggest that potential cowbird hosts can use vocal cues to perceive the density of cowbirds and local parasitism risk in their habitat choice decisions. The importance of parasitism risk to habitat choice was emphasized by the differential responses of the bird groups: hosts that made habitat choice decisions after the initiation of playbacks avoided the cowbird treatments, while densities of hosts that settled prior to playbacks, and densities of non-hosts did not differ between treatments. Second, most studies of behavioral adaptations against parasitism occur after the initiation of egg-laying, such as aggression towards cowbirds, defense of nests, and rejection of cowbird eggs (Rothstein 1990, Rothstein and Robinson 1998). This study is the first to show that hosts can respond to cowbirds prior to initiation of nesting activities and are able to assess cowbird density at larger

spatial scales using vocal cues in their habitat choices. Soler et al. (1998) similarly suggested that such a mechanism might explain the population dynamics of the magpie *Pica pica* and its brood parasite, the great spotted cuckoo *Clamator glandarius*, but did not experimentally test this possibility.

The number of cassette players in treatments and the use of the vocalization of dark-eyed juncos in the control treatment raise issues worth considering. In the within plot between year experiment, the number of cassette players differed between the cowbird and the control treatment (six and four, respectively) because we attempted to simulate natural levels of manipulation based on the number of observed cowbirds and juncos in the reference year. It is possible that the mere presence or vocal disturbance of cassette players may have either attracted or repelled birds. However, the possibility of attraction can be rejected because the higher number of cassette players in the cowbird treatment was not associated with higher bird abundances. Moreover, the difference of two cassette players on 5-ha plots seems unlikely to have produced the observed effects. The vocalization of the juncos could have affected bird abundances in the control treatment if it attracts other birds. Given the recent reports on heterospecific attraction in habitat choice decisions (Forsman et al. 2002, Fletcher 2007), this is a conceivable possibility, but it is true of any species we might have chosen. There are no studies showing that juncos attract other birds, and we chose juncos because they are common throughout the study region. However, although we cannot exclude the possibility of attraction, our results indirectly suggest that it does not occur or at least its effects are minimal compared with the effects of cowbird treatment. In the within-plot between year experiment, increases in the abundance of late arriving hosts in the control treatment was due to one plot in which abundance increased by 11 pairs in the manipulation year while in the other control plots abundance remained rather stable (+3 and ± 0 pairs). This result demonstrates no consistent response to juncos across plots. Hence, our results most likely only reflect the response of birds to the experimentally increased perceived presence of cowbirds.

Cowbird parasitism has been theorized to potentially influence community structure via demographic mechanisms (Grzybowski and Pease 1999), but little evidence has been found (De Groot and Smith 2001). Our results suggest that parasitism can alter bird community structure, but through a different mechanism than demography; species or individuals capable of perceiving cowbirds in habitat selection declined more than resident hosts or non-hosts. Indeed, in the within-plot experiment, late arriving hosts on average increased (or remained stable on most plots) on control plots in the second year and this was completely reversed in habitats with greater perceived risk of parasitism; the abundance of hosts decreased roughly by 20% compared with the reference year. The effect size of this magnitude can be considered significant and is comparable to marked annual density variation of some tropical migrants in North America (Holmes and Sherry 2001). Such community consequences mediated through effects of parasitism risk on habitat selection have gone unrecognized, but suggest an important new avenue of investigation into avian community ecology.

Our design to randomize treatments within a block (creek system) and examine the hypothesis with two separate experiments, conducted among plots within a year and within plots between two years, control both habitat structure and between year variation in bird densities. The results of both experiments consistently suggested that potential hosts settling after the initiation of playbacks avoided cowbird treatment, while hosts settling before playbacks and non-hosts did not respond to treatments. Further, in the within-plot experiment, the densities of all bird groups did not differ in the reference year among would-be treatments suggesting minimal plot effects. Hence, the most likely explanation is that late arriving hosts perceived the cowbird playback as information on parasitism risk and avoided such sites.

In this study, potential hosts responded to the cowbird treatment as a group but at the species level only one species, MacGillivray's warbler, showed significant avoidance of cowbirds. This may be due to multiple tests performed, but may also reflect density-dependent processes. Parasitism risk has been shown to correlate positively with population density (Barber and Martin 1997, Tewksbury et al. 1998) and MacGillivray's warbler was the most abundant species on study plots (2.83 pairs plot⁻¹ on average). If cowbirds create a search image for nests of the most abundant species (Martin 1993), it may elicit avoidance of high risk areas among species at greatest risk. Alternatively, weak effects at the individual species level may reflect power issues: the relatively low abundances of most individual species on our plots (0–2 pairs) likely require much larger sample sizes (larger and/or more plots) to detect effects.

Thus, these results further emphasize that the presence and abundance of different species in the environment can be used to assess various elements of habitat quality in habitat choice decisions, similar to use of heterospecific information for other cues (reviewed by Seppänen et al. 2007). Given the unpredictability of habitat quality, information provided by other species can act as an effective road map for habitat selection. This mechanism also can be applied in conservation purposes by manipulating presumed external cue and either attract animals to good quality habitats and repel them from poor habitats.

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