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# Regional Variation in Response of Field Sparrows to the Threat of Brown-headed Cowbird Parasitism

DIRK E. BURHANS,[1,4] BILL M. STRAUSBERGER,[2] AND MICHAEL D. CAREY[3]
[1]*North Central Research Station, USDA Forest Service, 202 ABNR, University of Missouri, Columbia, Missouri 65211-7260, USA;*
[2]*University of Illinois at Chicago, Department of Biological Sciences (M/C 066), 845 W. Taylor Street, Chicago, Illinois 60607, USA; and*
[3]*Department of Biology, University of Scranton, Scranton, Pennsylvania 18510-4625, USA*

ABSTRACT.—We conducted aggression experiments using model cowbirds on nesting Field Sparrows (*Spizella pusilla*) in heavily, moderately, and rarely parasitized populations. We also documented Field Sparrow morning nest arrival times during the laying period, because Field Sparrows appear to desert nests in response to encounters with laying female cowbirds. Field Sparrows responded most aggressively to cowbird models and arrived the earliest in Illinois, where they were most heavily parasitized. Field Sparrows responded the least to models in Pennsylvania, where they are almost never parasitized. Our results suggest that those host behaviors result from some aspect of host–cowbird interactions, but the extent to which such behaviors are genetic or learned needs further study.

Interspecific brood parasitism generally lowers host fitness and reduces host nesting success (Marvil and Cruz 1989, Payne and Payne 1998, Clotfelter and Yasukawa 1999). Brood parasitism can be a strong selective force in the evolution of host nesting behavior, resulting in adaptations to reduce the effects of parasitism (Rothstein 1990). However, occurrence of brood parasitism is not always uniform over the range of a host species. Brown-headed Cowbird (*Molothrus ater*) abundance varies regionally, and that is generally reflected in parasitism frequencies that vary in direct proportion to cowbird abundance (Hoover and Brittingham 1993). If parasitism frequencies vary regionally and parasitism selects for defensive responses by hosts (Rothstein 1990), it is reasonable to expect host responses to parasitism to vary accordingly. Behavioral responses to parasitism in hosts that either rarely or never encounter cowbirds should be weak or nonexistent, whereas hosts that frequently encounter cowbirds should show strong responses. For example, Briskie et al. (1992) found that Yellow Warblers (*Dendroica petechia*) and American Robins (*Turdus migratorius*) that were sympatric with cowbirds showed strong responses to cowbird eggs or model cowbirds, whereas the same

[4] E-mail: dburhans@fs.fed.us

hosts in populations allopatric with cowbirds did not.

Field Sparrows (*Spizella pusilla*) are relatively small-bodied hosts of the Brown-headed Cowbird that frequently desert parasitized nests. In previous studies in central Missouri, Field Sparrows showed aggressive responses to model cowbirds compared to a control (Burhans 1996, 2000a). In addition, recent studies indicate that Field Sparrows desert parasitized nests following early morning encounters with female cowbirds at the nest (Burhans 2000a, B. Strausberger and D. Burhans unpubl. data). Desertion is sometimes considered an anti-brood-parasite defense that allows hosts to renest and avoid raising a parasitized brood (Goguen and Matthews 1996, Hosoi and Rothstein 2000, but see Hill and Sealy 1994). Female cowbirds visit nests to lay in the predawn hours (Scott 1991, Neudorf and Sealy 1994) and nest desertion in Field Sparrows appears to be at least in part contingent upon hosts encountering female cowbirds at the nest (Burhans 2000a, B. Strausberger and D. Burhans unpubl. data). In another study, Field Sparrows did not desert nests where they failed to detect cowbirds if the latter species arrived earlier in the morning. They also did not desert nests where cowbird eggs were experimentally added (B. Strausberger and D. Burhans unpubl. data).

To determine whether presumed anti-brood-parasite behaviors vary according to parasitism pressure from cowbirds, we conducted aggression experiments on heavily, moderately, and rarely parasitized Field Sparrow populations in Illinois, Missouri, and Pennsylvannia.

We also observed predawn nest arrivals by Field Sparrows during the laying stage, which is considered the optimal time for cowbirds to lay eggs (Scott 1991, Neudorf and Sealy 1994). We predicted that intensity of aggressive response of Field Sparrows would be directly proportional to the frequency of cowbird parasitism and that Field Sparrow nest arrivals would occur earlier as cowbird parasitism frequency increased.

*Study areas and methods.*—Our study sites were located at The Morton Arboretum in Dupage County, northeastern Illinois (41°50′N, 88°18′W; described in Strausberger and Ashley 1997); the University of Missouri's Thomas S. Baskett Wildlife Research and Education Center in Boone County, central Missouri (38°45′N, 92°12′W; described in Burhans 1997), and old field sites in Lackawanna County, northeastern Pennsylvania (41°33′N, 75°43′W; described in Carey 1990). Fieldwork was conducted during the cowbirds' laying season (early May to early July).

We determined parasitism status of nests by noting presence of cowbird eggs or nestlings. When calculating both parasitism and desertion frequencies, we included only active nests where Field Sparrows laid at least one egg. Parasitism frequencies of Field Sparrows were 52% ($n$ = 71; 1994–1998) and 11% ($n$ = 442; 1992–1995, 1997–1998) for Illinois and Missouri, respectively. In Pennsylvania, only 2 of 681 Field Sparrow nests were parasitized (1987–1999). Parasitism frequencies were differed among all three states ($\chi^2 = 267$, df = 2, $P < 0.0001$), as well as between Illinois and Missouri ($\chi^2 = 73.8$, df = 1, $P < 0.0001$), and between Pennsylvania and each of the other two states (Fisher's exact test, $P < 0.0001$, both cases).

Parasitism frequencies could be underestimated if deserted nests were less likely to be detected by observers (Burhans 2000a), so we compared stages during which nests were found. Nests discovered in the building stage constituted 38.0, 33.3, and 43.0% of all nests found in Illinois, Missouri, and Pennsylvania, respectively; that frequency differed among sites ($\chi^2 = 10.7$, df = 1, $P = 0.005$). However, because Pennsylvania had the highest frequency of nests found during building stage, any resultant bias would tend to underestimate parasitism frequencies in Illinois or Missouri rather than Pennsylvania. In addition, the Pennsylvania population is a small color-banded population and is closely monitored (Carey 1990) and it is unlikely that many nests were missed.

In 1999, we conducted aggression experiments using cowbird models at all three sites. Cowbird models were made from three nearly identical freeze-dried female cowbirds posed in an upright position with wings folded. We tested nesting Field Sparrows with models during the first half of the incubation period (i.e. the first 5 days; Carey et al. 1994). Although Field Sparrows are more likely to be parasitized during laying stage, they are rarely found at nests during that period except while laying eggs (Carey et al. 1994). Testing at that later period may give results that are different than those during laying (Hobson and Sealy 1989, Bazin and Sealy 1993), but the goal of those experiments was to test for regional differences between host species. We also did not test a nonthreatening control model, because our goal was only to compare Field Sparrow responses across regions. As previously mentioned, Field Sparrows tested in Missouri responded more aggressively to cowbirds than a control (Burhans 1996, 2000a).

Camouflaged blinds were set 15 to 20 m from each nest at least 30 min before presentations. We waited until birds voluntarily left the nest area before placing models. Cowbird models were placed within 0.5 m of each nest so that the model faced toward the nest cup. In order to better see responding birds in dense vegetation, models were mounted on a camouflaged telescoping brass rod so that height of the model was 1 m above the nest rim. Models were presented at each nest for 5 min.

Trials were started when at least one Field Sparrow approached within 5 m of the nest. The following responses to models were recorded on a tape recorder for each 5 min period: (1) number of "*chip*"

calls (Carey et al. 1994); (2) number of "*eee*" calls (Carey et al. 1994); (3) number of close passes at the model; and (4) number of "strikes", that is, cases where the model was contacted by the flying host. We recorded whether one or both parents responded. We also recorded location and distance of responding nest owners (below) as instantaneous samples (Altmann 1974). All instantaneous responses were number of 10 s periods during the 5 min test period. Distance of the closest individual to the model was recorded in one of three distance categories (<2 m, 2–5 m, or >5 m); other responses were combined if both parents were present. We categorized periods as "location unknown" when Field Sparrows were either behind the blind or obscured by dense vegetation. If birds took long, directed flights out of the nest area and it was clear that neither adult was present, we categorized that period as "gone from the area." Birds that landed at and remained at the nest were classified "at the nest."

We used chi-square and Fisher's exact tests to compare regional and between-year parasitism frequencies and the number of nest owners responding (one vs. two). To compare behavioral responses among regions, we used Kruskal-Wallis tests, which use chi-square approximations (SAS 1990). To determine which regions differed, we used a multiple comparisons test for the Kruskal-Wallis test (Siegel and Castellan 1988) on those tests having significant differences.

We obtained morning nest arrival times for female Field Sparrows from April to early July. Nest arrival times were taken at Illinois sites in 1994–1998, Missouri sites in 1993–1995, and 1997–1998; and in Pennsylvania in 1999–2000. Blinds were placed for observations 10 to 20 m from nests on the day the host laid its first egg. On the following day observers entered the blind ~30 min before scheduled sunrise. Observers stayed in blinds at least long enough to record arrival times of female Field Sparrows. We used Scott's (1991) method for relating time an event occurred to time of sunrise (SR). For example, SR − 30 min is equal to 30 min before sunrise, whereas SR + 30 min is equal to 30 min after sunrise. Local sunrise times were accurate to the nearest minute and were obtained from the U.S. Naval Observatory for Chicago, Illinois (~23 km from the Illinois site) for the Illinois site; from the National Weather Service office at Columbia, Missouri, for the Missouri site; and from Fleetville, Pennsylvania, for the Pennsylvania site. To determine if regional nest arrival times differed, we used Kruskal-Wallis tests with multiple comparisons procedures (Siegel and Castellan 1988). For that and other tests, we accepted $P \leq 0.05$ as the level of statistical significance. All tests are two-tailed and values are reported as mean ±SE.

*Results.*—Field Sparrows responded most aggressively to cowbird models in Illinois. None of the hosts at Missouri or Pennsylvania sites made strikes or close passes at the model, whereas 4 and 10 Illinois experiments involved strikes and close passes, respectively (Table 1). "*Eee*" calls only occurred at Illinois sites. Birds at Pennsylvania sites "*chipped*" the least of any of the three sites (Table 1). Field Sparrows were closest to the model in Missouri experiments. The only cases where Field Sparrows sat on the nest during experiments occurred in Pennsylvania; two females sat on the nest for most of the experiment. One Pennsylvania bird left the nest area entirely so that no hosts responded to the model after the first 2.5 min of the experiment (Table 1). Proportion of nests with both adults responding did not vary between states (Table 1).

Morning nest arrivals differed among all three sites (Illinois: SR − 23.1 ± 2.4 min ($n$ = 14); Missouri SR − 13.5 ± 1.6 min ($n$ = 36); Pennsylvania SR − 1.83 ± 6.6 min ($n$ = 18; Kruskal-Wallis test $\chi^2$ = 11.6, df = 2, $P$ = 0.003). Female Field Sparrows arrived significantly earlier in Illinois compared to both Pennsylvania and Missouri (multiple comparison for Kruskal-Wallis test), whereas there were no differences in arrival times between Missouri and Pennsylvania.

*Discussion.*—Our results suggest that the response of different Field Sparrow populations to brood parasitism is related to frequency of parasitism. Field Sparrows responded most aggressively to cowbirds where they were most parasitized. Experiments in the heavily-parasitized Illinois population had the only cases of strikes, close passes, or "*eee*" calls, the latter of which are usually associated with direct attacks on nest enemies (Carey et al. 1994). Female Field Sparrows also arrived earlier at nests in heavily parasitized Illinois sites. By contrast, the Pennsylvania population experienced almost no parasitism over 13 years of monitoring; Pennsylvania sites had the lowest number of "*chips*" (Table 1) and were the only cases where Field Sparrows resumed incubation or left the nest area entirely during experiments. Those two behaviors suggest that the hosts resumed normal nesting behavior (incubation or foraging) in the presence of the brood parasite. The latter observation is consistent with findings from Burhans (2000b) where similar behaviors were recorded in Missouri only during presentations of a control model and never in the presence of a nest enemy.

Our results are similar to those of Briskie et al. (1992) who found strong regional differences in host defensive behaviors depending upon sympatry. Robertson and Norman's (1977) regional comparison similarly found increased aggressive responses for several hosts where they had longer sympatry with cowbirds. Within a region, Hobson and Villard (1998) found increased aggression toward cowbird models by American Redstarts (*Setophaga ruticilla*) nesting in fragmented compared to forested landscapes, even though extensive forest was within 20 km of the fragmented sites. They believed that red-

TABLE 1. Mean (±standard error) response of Field Sparrows to Brown-headed Cowbird models and results of Kruskal-Wallis tests for differences among regions. Categories of distance (last six rows) were sampled as number of 10 s periods (out of 30) bird was performing these behaviors. Other variables were sampled as actual number of occurrences within trial.

| Response variable[a] | Illinois (52%)[b] | Missouri (11%) | Pennsylvania (<1%) | $X^2$ |
|---|---|---|---|---|
| Number of nests with both adults present during experiment (total number of nests tested) | 11(12) | 16(17) | 10(15) | 5.2 |
| Chips | 430.7 ± 42.1A | 411.3 ± 47.9A | 139.4 ± 26.4B | 20.3**** |
| Eee call | 0.3 ± 0.2 | 0 | 0 | 5.5 |
| Close passes | 7.7 ± 2.0B | 0A | 0A | 33.0**** |
| Strikes | 2.0 ± 1.2A | 0A | 0A | 11.4** |
| Distance | | | | |
| <2 m | 14.4 ± 3.4AB | 20.1 ± 2.9A | 6.1 ± 2.7B | 10.0** |
| 2–5 m | 12.1 ± 3.1A | 6.6 ± 2.4A | 13.7 ± 3.1A | 5.8* |
| >5 m | 1.6 ± 0.8A | 0A | 4.9 ± 2.6A | 6.9* |
| Distance unknown | 2.3 ±0.5A | 3.4 ± 1.7AB | 0B | 13.5*** |
| Gone from the area | 0 | 0 | 1.7 ± 1.7 | 1.9 |
| At the nest | 0 | 0 | 3.7 ± 2.5 | 4 |

[a] Number of adults present tested with Pearson chi-square test; results from other tests are chi-square approximations from Kruskal-Wallis tests (df = 2, all tests), ****$P \leq 0.0001$, ***$P \leq 0.001$, **$P \leq 0.01$, *$P \leq 0.05$. Means sharing the same letter are not different.

[b] (Percent) indicates parasitism frequency for the study site.

starts were more familiar with cowbirds in fragmented landscapes where cowbirds were more common compared to contiguous forests. Their results suggested that either dispersal distances by redstarts were small or that there is a learned component to recognition of brood parasites. Brooke et al. (1998) found a decline in defenses by Reed Warblers (*Acrocephalus scirpaceus*) to Common Cuckoos (*Cuculus canoris*) both within and between-season. They believed that phenotypic flexibility in host response best explained their findings, because the changes occurred too rapidly to reflect genetic change; an unparasitized population only 11 km away did not show any defenses.

Early nest arrival appears to be advantageous in allowing Field Sparrows to detect female cowbirds and enabling subsequent nest desertion (Burhans 2000a, D. Burhans and B. Strausberger unpubl. data). Because early arrival helps ensure detection of cowbirds at the nest, female Field Sparrows may have arrived earlier in Illinois because cowbirds were more common. However, although we found that Field Sparrows arrived earlier in Illinois, they deserted parasitized nests at similar frequencies at Illinois and Missouri sites (48 vs. 45%, respectively; B. Strausberger and D. Burhans unpubl. data). If early morning nest arrival times correspond to parasitism frequencies, late arrivals where parasitism is relaxed would suggest the possibility that there may be a cost to arriving early. Arriving later to lay in the morning could allow females to forage earlier and replenish themselves after fasting overnight. If early arrivals are part of a defense and entail a cost, we expected that morning nest arrivals would be latest for the rarely parasitized Pennsylvania population. Mean nest-arrival times were later in Pennsylvania compared to Illinois, but not in Pennsylvania compared to Missouri.

In summary, our study indicates that behavioral responses to brood parasites varied regionally, not only in frequency of occurrence of behaviors, but in presence or absence of some behaviors. Both intensity of defense and nest-arrival behaviors were positively correlated at least in part with regional parasitism frequencies. That is consistent with the hypothesis that prevalence of certain host behaviors varies with population and that those behaviors result from some aspect of host–cowbird interactions. However, the extent to which variation in host responses is genetic or learned requires information on the nature of dispersal, which is notoriously difficult to acquire for many passerines (Greenwood and Harvey 1982). Further study is needed to determine both whether aggressive responses are genetic and the extent to which morning nest-arrival times during laying correspond to the threat of parasitism.

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