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Nest Desertion by Field Sparrows and its Possible Influence on the Evolution of Cowbird Behavior

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Abstract.—In this study, Field Sparrows (*Spizella pusilla*) deserted 46% of nests, parasitized by Brown-headed Cowbirds (*Molothrus ater*) and only 1% of unparasitized nests suggesting that desertion functions primarily as an antiparasite defense. Sparrows did not desert nests following various clutch manipulations that are often associated with parasitism, indicating that desertion was not in response to the presence of cowbird eggs. Sparrows often deserted nests following encounters with real or mounted cowbirds, suggesting that nest desertion is a response to adult cowbirds. Sparrows deserted nests only in stages most vulnerable to the effects of parasitism. That finding is consistent with the possibility that desertion is a parasite-specific response. Sparrows arrived at nests earlier in the day at our Illinois site, where parasitism was greater, than in Missouri. Our findings confirm that host vigilance can prevent successful parasitism, and we provide the first direct evidence that encounters with cowbirds may cause hosts to desert nests. Our findings may help explain why cowbirds parasitize nests extremely early in the morning and lay rapidly. We suggest that consideration be given to host response following interactions with adult brood parasites because those interactions may have implications for both the ecology and evolution of both the parasite and host.

Avian obligate brood parasites require "host-birds" to provide costly parental care for their eggs and young. As a result, hosts evolve behaviors to minimize effects of parasitism, whereas parasites evolve counter defenses (Rothstein 1975). Probably the best-studied host defense is rejection of parasitic eggs. Experiments indicate that most species either accept nearly all nonmimetic eggs (i.e. accepters), or reject them (i.e. rejecters) usually by ejection, but sometimes by burial, or nest desertion (Rothstein 1975, Sealy 1995). Many species that accept experimentally placed eggs sometimes desert naturally parasitized nests (e.g. Rothstein 1975, Hill and Sealy 1994, but see Rothstein 1976); egg-placement experiments alone fail to consider the possibility that hosts use alternative cues that indicate parasitism. Further, many species are apparently inconsistent in their response to naturally parasitized nests (Ortega 1998, Hosoi and Rothstein 2000). In those cases, desertion of naturally parasitized nests may occur in response to clutch alteration, encountering an adult parasite near the nest or nest area (e.g. Davies and Brooke 1988, Brooke et al. 1998, Hill and Sealy 1994), or both. Experiments have shown that hosts increase rejection following an encounter with an adult Common Cuckoo (*Cuculus canorus*) near the nest (e.g. Davies and Brooke 1988, Moksnes et al. 1993, Davies et al. 1996). However, for Brown-headed Cowbirds (*Molothrus ater*), experiments indicate those species that have been tested do not desert nests following an encounter with a cowbird model (Hill and Sealy 1994, Sealy 1995, Sealy et al. 1995).

The Brown-headed Cowbird is a host-generalist brood parasite that sometimes also depredates partial or entire clutches (Lowther 1993, Arcese et al. 1996). In their study of 35 host species, Hosoi and Rothstein (2000) found that those having a longer period of sympatry with Brown-headed Cowbirds (hereafter "cowbird") more often deserted parasitized nests compared to species only recently exposed to cowbirds. After ruling out factors including differences in predation, they concluded that desertion was likely an evolved response to parasitism.

Field Sparrows (*Spizella pusilla*), a common cowbird host, do not eject cowbird eggs, but they do desert 55–75% of parasitized nests (see Carey et al. 1994). Field Sparrows presumably benefit from desertion because of costs associated with cowbird parasitism (Burhans et al. 2000). Burhans et al. (2001) found a positive relationship between regional Field Sparrow nest-defense behavior and frequency of parasitism, which possibly results from an aspect of sparrow-cowbird interactions. In this study, we examine response of Field Sparrows to both naturally parasitized and experimentally manipulated nests. We test alternative hypotheses regarding the stimulus responsible for nest desertion and we test the desertion response of Field Sparrows to cowbird models during different stages of the nesting cycle. Finally, we discuss our behavioral data in context of possible fitness advantages.

Methods: Study species.—Field Sparrows are small (12–14 g) passerines that usually lay 3–4 eggs per

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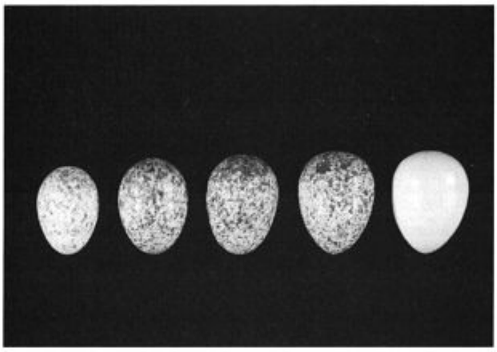

FIG. 1. Eggs typical of those mentioned in the text. From left to right: real Field Sparrow egg, real Brown-headed Cowbird egg, plaster maculated cowbird egg, wooden maculated cowbird egg, and wooden nonmaculated cowbird egg.

clutch. Field Sparrows are not known to eject cowbird eggs. Field Sparrow and cowbird eggs are often similar in appearance, but the former are ~43% smaller (Fig. 1; see Lowther 1993, Carey et al. 1994); however, some cowbird and Field Sparrow eggs approach each other in size. Both species have similar incubation periods of approximately 11–12 days.

We searched for sparrow nests at both The Morton Arboretum in northeastern Illinois from 1994–1998 as a part of another study (see Strausberger and Ashley 1997, Strausberger 1998a) and at the University of Missouri's Thomas S. Baskett Wildlife Research and Education Center in Boone County, Missouri from 1992–1995 and 1997–1998 (see Burhans 1997, 2000). Fieldwork was conducted during the cowbird's laying season (early May to early July).

We monitored nests daily for at least 2 days following treatments (see below). Nests that remained active were considered to have accepted the treatment, whereas nests without sparrow nesting activity (e.g. additional eggs laid), or cold eggs for two or more consecutive days were considered deserted. When estimating parasitism frequencies, we did not include nests deserted before host egg laying. For statistical comparisons, we used Fisher's exact and Wilcoxon rank-sum tests. We considered P-values ≤ 0.05 significant.

Egg treatments.—We tested the possibility that Field Sparrows desert nests following (1) replacement of a sparrow egg with a cowbird egg made of plaster of Paris, as described by Rothstein (1975; Fig. 1), (2) addition of eggs that differ from sparrow eggs by adding either a real, artificial maculated, or artificial nonmaculated cowbird egg (Fig. 1). We include nonmaculated eggs because recent experiments indicate that some accepters reject dissimilar nonmaculated eggs but not maculated eggs that more closely resemble their own eggs (Burhans and Freeman 1997). Artificial eggs used in egg-addition experiments were made from wooden eggs (described in Burhans 1996). All egg treatments were conducted at nonattended, unparasitized nests containing one or two host eggs.

Cowbird and human visitation treatments.—We placed a female cowbird mount (model) at 29 active nests to determine if encounters with cowbirds were a possible cause for desertion. At 30 nests, we had a visitor approach the nest without a mount to control for the human disturbance involved in setting up the mount. Models of other species were not used because we were not testing if desertion was a response unique to cowbirds. Models were supported by 12-gauge wire that protruded from their ventral side which was inserted through the rim of the nest. Models were placed on nest rims to allow sparrows to incubate or react defensively by sitting on the nest as sometimes occurs in other species (see Strausberger and Horning 1998). We did not place models in the laying position above nests because even hosts that do not recognize cowbirds could presumably desert nests because access to the nest is blocked. Additionally, we were not testing whether nest desertion is a response to cowbirds only when cowbirds are engaged in egg-laying behavior. Instead, we were interested in determining if desertion is a more general response to cowbirds when they are near nests for reasons other than egg laying. We did not place models farther away because we wanted to test the host's reaction to cowbirds at the nest, where the majority of the costs of parasitism are incurred. Models were posed in a perching posture with head and neck lowered as if looking into nests.

We conducted both model and human visitation treatments at nests in different stages. For consistency, nests were considered to be in the (1) "building stage" when under construction, (2) "early laying stage" beginning the day the first sparrow egg was laid through the following day, (3) "late laying stage" beginning two days after a nest received its first sparrow egg, and (4) "incubation stage" on the day after the final host egg was laid through the day an egg hatched. For statistical analysis, we combined the first and last two stages and called them the "building–early laying" and "late laying–incubation" stages, respectively. Treatments were conducted at unattended nests in the building stage before 0830 CST and when nests appeared cup-like. We placed models at, or before, 34 min before sunrise at nests in the early laying stage. Early morning nest placement was often necessary because, after a laying bout that usually lasts ~43 min (Burhans 2000), Field Sparrows with nests in that stage typically remain off their nest for the remainder of the day (Carey et al. 1994). One exception was a treatment where we place the model at 1005 CST (289 min after sunrise). The sparrows approached the nest 10 min later, possibly because the model was easily spotted in the mowed field where the nest was placed. For nests in the late laying stage, we conducted model treatments from 34 min before sunrise to 5 h thereafter. We were able to conduct treatments later in the day at nests in the late laying stage due to the onset of incubation; Field Sparrows typically begin incubating eggs following clutch completion, that is, the last day of the laying stages (Carey et al. 1994). Experimental tests at nests in the incubation stage were conducted throughout the day. Human-visitation treatments were conducted when sparrows were present and were included to distinguish between sparrows deserting because of manipulation and monitoring (Rothstein 1975), rather than the presence of cowbirds. Both naturally parasitized and unparasitized nests that were active were used in human visitation treatments. Only one treatment was conducted on a given sparrow territory. When the vegetation near the nest was insufficient to conceal our observations, we monitored nests from portable blinds placed 10–20 m from the nest the day before our observations.

We left models in place for 1 min following approach of a sparrow to within 0.5 m of the nest. Unlike other treatments, at nests in the building stage that were tested with mounts, we placed a small, stiff piece of vegetation from rim to rim following the return of a sparrow. When that vegetation remained in place on subsequent daily checks that lasted for 6 or more days, we assumed building had ceased. We assumed that small piece of grass would not induce desertion because it was not unlike the vegetation used in the nest and because it seems likely that vegetative debris would frequently fall into open-cup nests during the course of nesting. Following human visitation, model treatment, and natural acts of parasitism, we continuously monitored nests for a minimum of 40 min and then again within 6 h.

We distinguished observations where live female cowbirds approached nests from those where a model was presented. On the occasion that sparrows approached a live cowbird at a nest where a model was also present, the observation was considered a live cowbird treatment only.

There has been much speculation and study regarding function of early morning nest arrival and rapid egg laying by cowbirds (see Scott 1991, and Sealy et al. 1995). One possibility is that morning nest arrival results in desertion by hosts, which selects for earlier arrivals by cowbirds. At nests not treated with models, we recorded nest arrival time for each species. We initiated observations at nests in the laying stage without model placement ~30 min before sunrise. For nests observed on consecutive mornings, only the sparrow's arrival time on the first morning was included. We also recorded duration of cowbird laying bouts, which we defined as time during which a cowbird lands on the nest, deposits an egg, and departs (see Sealy et al. 1995). We excluded laying bouts when we could not clearly see arrival and departure of cowbirds.

Results.—A total of 71 sparrow nests were found in the laying or postlaying stages in Illinois. Of those, 37 (52%) were naturally parasitized by cowbirds. In Illinois, 14 (48%) of 29 nondepredated pairs were more likely to desert cowbird-parasitized than unparasitized nests (48% of 29 vs. 0% of 21; Fisher exact test, $P < 0.001$). A total of 442 nests were found in Missouri; of those, 49 (11%) were parasitized. Parasitism frequencies were higher in Illinois (Fisher exact test, $P < 0.001$) where the density of cowbirds was greater. Sparrows in Missouri deserted 21 (45%) of 47 parasitized nests, whereas sparrows deserted only 3 of the >300 unparasitized nests; the difference is significant (Fisher's exact test, $P < 0.001$). Desertion frequencies for unparasitized nests in Illinois (0%) and Missouri (1%) were similar (Fisher's exact test $P = 1.0$). Desertion frequencies of parasitized nests were similar in Illinois (48%) and Missouri (45%; Fisher's exact test, $P = 0.82$), yielding a combined frequency of 46% ($n = 76$).

Egg treatments.—No nest was deserted following the replacement of a sparrow egg with an artificial maculated cowbird egg ($n = 4$) or after the addition of a real ($n = 12$), artificial maculated ($n = 13$), or artificial nonmaculated ($n = 4$) cowbird egg.

Cowbird and human visitation treatments.—All nests treated with cowbird models in the building and early laying stages (i.e. building–early laying stage) were deserted, whereas three of seven (43%) and none of eight were deserted in the late laying and incubation stages (i.e. late laying–incubation stage), respectively; the differences in the four desertion frequencies among nest stages were significant (Table 1). We observed live female cowbirds at sparrow nests on 12 occasions; 11 of these were laying bouts. The one observation that was not a laying bout occurred during midmorning and was at a nest in the incubation stage (see Strausberger 1998b); the nest was not subsequently deserted. The mean ± SE duration of eight cowbird laying bouts where we observed the entire bout-sequence was 22.8 ± 5.1 sec (range = 8.0–55.0 s). Cowbirds encountered sparrows at 6 of the 11 parasitism events. Of those six encounters, four and one nest were in the early and late laying stage, respectively, and all were deserted (Table 1); one nest was depredated. Five other observations involved no interaction during parasitism. Of those five, three involved cowbirds arriving before sparrows and one after sparrows. One observation involved a cowbird laying in a nest that was already deserted. At the two nests where we observed parasitism and where models were absent, the sparrows accepted the cowbird eggs. Although no nest tested during the incubation period was deserted, naturally parasitized nests were sometimes deserted on the first or second day of incubation, indicating that nests in the incubation stage may sometimes be deserted. No desertion occurred following human visitation treatments (Table 1). We did not observe spar-

TABLE 1. Percentage of total number of Field Sparrow nests (n)[a] that were deserted following a given treatment at nests at different stages.

	% deserted (n)						
	Stage			Stage			
Treatment[b]	Building	Early-laying	**Total**	Late-laying	Incubation	**Total**	P[c]
Model cowbird	100(7)	100(7)	**100(14)**	43(7)	0(8)	**20(15)**	<0.001
Live cowbird	0	100(4)	**100(4)**	100(1)	0(1)	**50(2)**	—
Human visitation	0(4)	0(5)	**0(9)**	0(11)	0(10)	**0(21)**	1

[a] Total number (n) of nests tested.

[b] Only those visits that involved an interaction with Field Sparrows are included.

[c] Results of Fisher exact tests comparing the percentage of total nests (n) deserted in the building–early laying and late laying–incubation stage.

rows at nests in the early laying stage during our predawn nest checks (n = 46) and eggs present were cold, indicating that they did not incubate eggs overnight.

Sparrows arrived at nests to lay earlier in Illinois (Table 2), where the probability of parasitism was greatest. At both sites, the mean arrival times for laying sparrows closely matched those of cowbirds (Table 2). Sparrows that deserted nests following encounters with either live or model cowbirds were never observed returning to nests, suggesting that the desertion response was immediate. In all trials (n = 7) during the building stage, the vegetation placed across nests remained in place, indicating that nest-building never resumed. No birds that resumed activity following model presentation later deserted.

Discussion.—This study provides evidence suggesting that Field Sparrows desert nests after encountering a brood parasite model, even when there is no detectable change in their clutch. Our findings may help account for differences in species' typical reaction toward naturally parasitized nests and artificially deposited parasitic eggs. Further, because the majority of nests are usually found in late stages (Mayfield 1975), our findings suggest that actual parasitism frequencies may be underestimated for species like Field Sparrows that desert nests parasitized in early stages (Burhans 2000).

Ecological and evolutionary implications for cowbirds.—Sparrows with nests in the building to early laying stage that encountered cowbirds always deserted nests, indicating cowbirds should avoid detection. Our findings of nest desertion in response to cowbird encounters at or on nests support Gill et al.'s (1997) conclusion that nest defense is unlikely to be used by cowbirds for finding potential host nests.

The observation that sparrows desert nests when they encounter a live or model cowbird suggests selection for rapid nest visits by cowbirds. In this and other studies (see Sealy et al. 1995, Burhans 2000), cowbirds usually spent <60 s on nests when ovipositing. At one nest, a cowbird arrived, laid, and departed within 2 min before the arrival of a sparrow (B. Strausberger unpubl. data). Whereas Sealy et al. (1995) indicated that rapid laying reduces risk of attack by hosts on cowbirds, our study suggests that it may also reduce the risk of a cowbird's egg being rejected.

Our results are consistent with the possibility that cowbirds' extremely early morning egg-laying behavior helps ensure that Field Sparrows accept cowbird eggs. Cowbirds in this study and others generally parasitized nests well before sunrise, when many potential hosts are likely to be away (Scott 1991, but see Neudorf and Sealy 1994). In our study, Field Sparrows with nests in the early laying stage never roosted on their nest overnight. Instead, they first arrived at nests before sunrise and sometimes later in the day. Further, Field Sparrows typically remained on nests for the remainder of the day following clutch completion (B. Strausberger and D. Burhans unpubl. data; see also Carey et al 1994). As a result, cowbirds that parasitize nests after Field Sparrows arrive may risk detection and egg rejection.

Ecological and evolutionary implications for Field Sparrows.—Timing of Field Sparrow responses to parasitism are similar to those of Yellow Warblers (*Dendroica petechia*). Yellow Warblers reject nearly all cowbird eggs laid before their own, many of the eggs laid during the first half of the nest's laying stage, and almost no eggs later (e.g. Clark and Robertson 1981, Sealy 1995). In our study, Field Sparrows that encountered a cowbird throughout the first half of their laying stage deserted, whereas those in later stages usually did not desert. Although imperfect, the apparent dichotomy of rejection behavior and its correspondence with nesting stage may result from the high cost of rejection and from lower costs of parasitism in later stages (e.g. Clark and Robertson 1981, Sealy 1995).

Experiments indicating that hosts react most intensely to brood parasites when their nests are in stages vulnerable to parasitism suggest that hosts likely recognize the specific threat posed by brood parasites (e.g. Neudorf and Sealy 1992). The strong correlation between desertion and a nest's vulnerability to parasitism raises the possibility that Field

TABLE 2. Nest arrival times of laying Brown-headed Cowbirds and Field Sparrows are closely correlated at each study site.

Species	Illinois: Mean arrival time (n)[a]	Illinois: Range	Missouri: Mean arrival time (n)[a]	Missouri: Range	Z^b	P
Cowbird	SR − 22.0 ± 1.5[c] (3)	SR − 25 to SR − 20	SR − 14.7 ± 2.17 (6)	SR − 22 to SR − 9	−0.75	0.45
Sparrow	SR − 23.1 ± 2.44 (14)	SR − 33 to SR − 1	SR − 13.5 ± 1.59 (36)	SR − 28 to SR + 22	−3.1	0.002

[a] Values represent arrival times in relation to sunrise (SR) ± SE, followed by n in parentheses. For example, SR–30 is equal to 30 min before sunrise (see Scott 1991). Local sunrise times are accurate to the nearest minute and were obtained for Chicago (~23 km from the IL site) and Missouri from the US Naval observatory and from the National Weather Service office at Columbia MO, respectively.

[b] Wilcoxon rank-sum test value.

[c] One unusually late arrival time (SR + 21 min) was excluded because it strongly affected both the mean arrival time and SE value.

Sparrows recognize cowbirds as brood parasites. Unparasitized nests in ours and Walkinshaw's (1978) study were rarely desert suggesting that if other forms of disturbance occur, they do not result in nest desertion. Field Sparrows did not desert nests in the human-visitation treatment, indicating that they do not desert in response to all intruders at the nest. It is also unlikely that desertion is a response to intraspecific brood parasitism. We found no evidence of intraspecific brood parasitism, which rarely occurs in Field Sparrows (Carey et al. 1994). However, we have not placed models of other predators at nests to determine whether desertion is restricted to the threat of cowbird parasitism or also occurs in response to cues indicating predation threat.

It may not seem optimal for Field Sparrows to desert nests following a visit from a cowbird when no parasitic eggs have been laid. However, if nests where sparrows encounter cowbirds have a high probability of parasitism, then sparrows that desert immediately will renest sooner and possibly escape parasitism to a greater degree than individuals relying on the presence of a cowbird's egg to elicit desertion (see also Goguen and Matthews 1996). In our study, sparrows deserted nests that were in the building stage, suggesting that their response is timed to minimize future losses. Also, they sometimes began renesting the same day, indicating rapid renesting is a possible benefit.

It is unclear why Field Sparrows do not recognize cowbird eggs. It seems unlikely that insufficient time has passed for egg recognition to develop because Field Sparrows have been historically sympatric with cowbirds (Lowther 1993, Carey et al. 1994), with records of parasitism dating back over a century (Poling 1989). One possibility is that sparrows may benefit by using the stimulus of an adult cowbird, rather than presence of cowbird eggs, to trigger desertion because the former eliminates costs associated with egg-recognition errors (Davies and Brooke 1989, Marchetti 1992). Although Field Sparrow eggs are usually smaller, they resemble cowbird eggs (Fig. 1), increasing the likelihood of mistaken acceptance or rejection.

Cowbird brood parasitism and nest desertion may select earlier nest arrivals by laying Field Sparrows Consistent with this hypothesis, heavily parasitized Field Sparrows in the Illinois population arrived at their nests significantly earlier than those in Missouri, where parasitism occurred significantly less frequently. Further, the mean nest-arrival time for cowbirds and sparrows in a given state were strikingly similar to one another, suggesting that they are correlated. In Illinois, sparrows and cowbirds arrived at nests at 23.1 and 22.0 min before sunrise, respectively. In Missouri, sparrows and cowbirds arrived at nests at 13.5 and 14.7 min before sunrise, respectively.

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

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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

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