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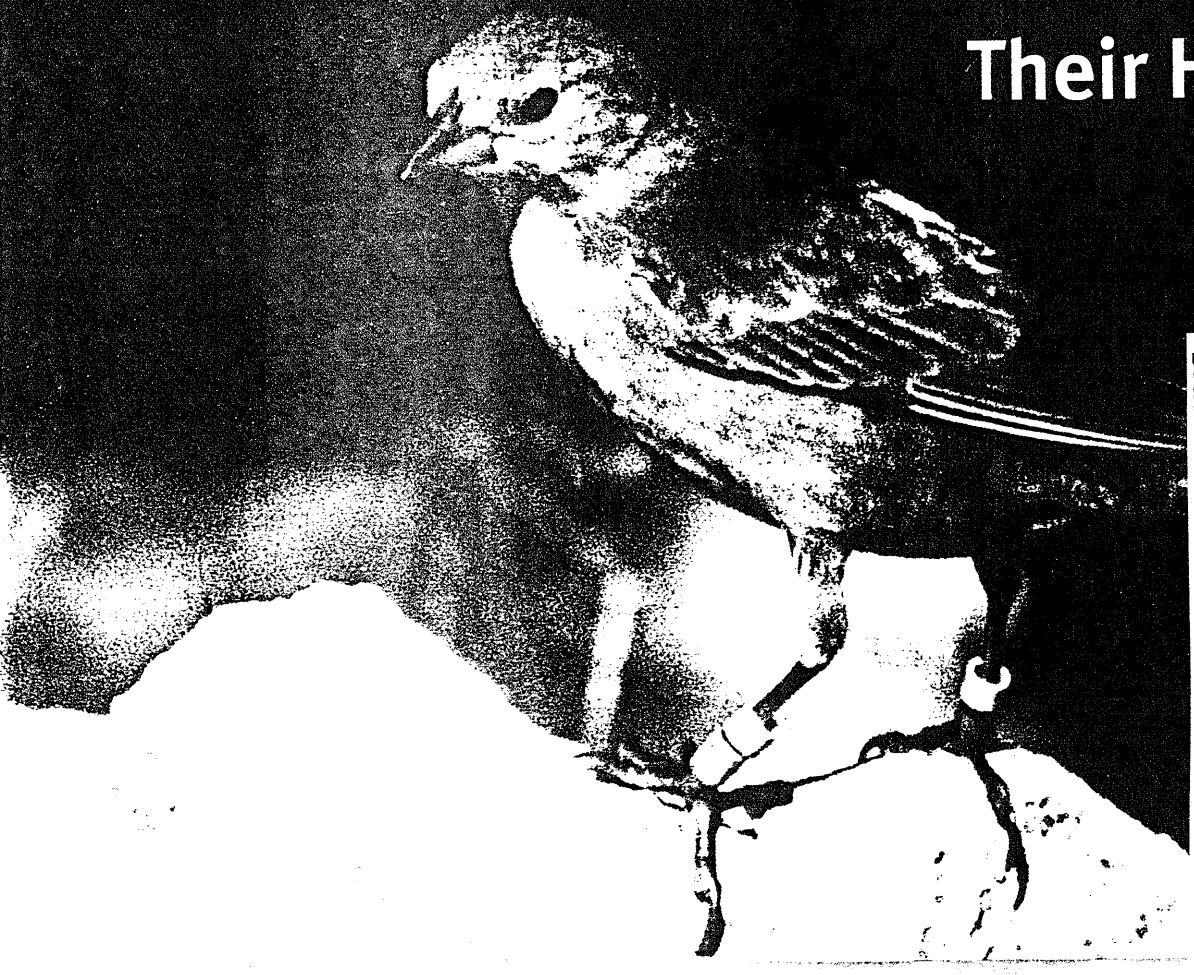
Ecology and Management of Cowbirds and Their Hosts



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Title page photograph of a flock of juvenile Brown-headed Cowbirds by Stephen I. Rothstein.

Contents

Foreword: Cowbirds and Bull-hockey
Paul R. Ehrlich vii

General Introduction: Brown-headed Cowbirds as a Model System for Studies of Behavior, Ecology, Evolution, and Conservation Biology
James N. M. Smith and Stephen I. Rothstein 1

Part I.
Population Trends of Cowbirds and Hosts and Relevant Methodology

1. Introduction
Stephen I. Rothstein and Scott K. Robinson 13
2. Temporal and Geographic Patterns in Population Trends of Brown-headed Cowbirds
Bruce G. Peterjohn, John R. Sauer, and Sandra Schwarz 21
3. Cowbird Population Changes and Their Relationship to Changes in Some Host Species
David A. Wiedenfeld 35
4. The Spread of Shiny and Brown-headed Cowbirds into the Florida Region
Alexander Cruz, John W. Prather, William Post, and James W. Wiley 47
5. Brown-headed Cowbird Population Trends at a Large Winter Roost in Southwest Louisiana, 1974–1992
Brent Ortego 58
6. An Evaluation of Point Counts and Playbacks as Techniques for Censusing Brown-headed Cowbirds
R. Kirk Miles and David A. Buehler 63
7. The Structure and Function of Cowbird Vocalizations and the Use of Playbacks to Enhance Cowbird Detectability: Relations to Potential Censusing Biases
Stephen I. Rothstein, Chris Farmer, and Jared Verner 69

Part II.
Cowbird Spacing Behavior, Host Selection, and Negative Consequences of Parasitism for Commonly Used Hosts

8. Introduction
James N. M. Smith, Spencer G. Sealy, and Terry L. Cook 83
9. Spatial Patterns of Breeding Female Brown-headed Cowbirds on an Illinois Site
Arlo Raim 87
10. Differences in Movements, Home Range, and Habitat Preferences of Female Brown-headed Cowbirds in Three Midwestern Landscapes
Frank R. Thompson III and William D. Dijak 100
11. The Effects of Host Numbers on Cowbird Parasitism of Red-winged Blackbirds
Christy A. Carello and Gregory K. Snyder 110
12. Cowbird Brood Parasitism on a Little-used Host: The Yellow-headed Blackbird
Alfred M. Dufty, Jr. 115
13. Host Selection in the Forest Interior: Cowbirds Target Ground-nesting Species
D. Caldwell Hahn and Jeff S. Hatfield 120
14. Reproductive Interactions between Brown-headed Cowbirds and Plumbeous Vireos in Colorado
Jameson F. Chace, Alexander Cruz, and Rebecca E. Marvil 128
15. Effects of Multiple Parasitism on Cowbird and Wood Thrush Nesting Success
Cheryl L. Trine 135
16. Comparing the Relative Effects of Brood Parasitism and Nest Predation on Seasonal Fecundity in Passerine Birds
Joseph A. Grzybowski and Craig M. Pease 145

18. Morning Nest Arrivals in Cowbird Hosts: Their Role in Aggression, Cowbird Recognition, and Host Response to Parasitism

DIRK E. BURHANS

Abstract

Indigo Buntings (*Passerina cyanea*) nesting in old-field habitats in central Missouri are parasitized at least four times as often as Field Sparrows. I used model cowbirds placed near nests to test if host aggression explained this difference. Although both Field Sparrows and Indigo Buntings responded to Brown-headed Cowbird models with significantly more chips than to a Fox Sparrow (*Passerella iliaca*) control, only one female Field Sparrow and one Indigo Bunting pair attacked the cowbird model.

Because the utility of aggression and cowbird recognition may depend on a host's actually encountering laying cowbirds, I also observed arrival times of hosts and cowbirds at nests near dawn during egg laying. Laying female Indigo Buntings rarely encountered laying cowbirds; the mean arrival time for Brown-headed Cowbirds at host nests was 11.4 min before sunrise ($N = 8$), and female Indigo Buntings arrived 16.7 min after sunrise ($N = 6$). Laying Field Sparrows arrived at nests before or at about the same time as cowbirds (mean arrival 17.4 min before sunrise, $N = 16$). Most parasitized Field Sparrow nests were abandoned in 1992 and 1993, suggesting that detection of female cowbirds at the nest causes Field Sparrows to desert their nests. These results suggest that aggression rarely prevents cowbirds from laying in nests of these hosts, but that recognition of brood parasites during laying elicits host nest desertion by Field Sparrows. Additionally, nest desertion by hosts may lead to underestimates of parasitism frequencies, because deserted nests are less likely to be found. Nest arrival times may limit the efficacy of host defenses against cowbirds, especially if cowbirds must commute to breeding areas from distant communal roosts.

Introduction

Many host species recognize Brown-headed Cowbirds as a threat (Robertson and Norman 1976, 1977; Smith et al. 1984; Briskie and Sealy 1989; Burgham and Picman 1989; Hobson and Sealy 1989; Neudorf and Sealy 1992). Although how aggression affects parasitism rates has not been measured, it may contribute to varying parasitism frequencies among species. For example, Briskie et al. (1990) found that Yellow Warblers (*Dendroica petechia*) were parasitized six times more frequently than Least Flycatchers (*Empidonax minimus*) nesting in the same habitat, although the Yellow Warblers were poorer hosts because they often bury cowbird eggs (Clark and Robertson 1981). The authors suggested that more aggressive nest defense by Least Flycatchers was one reason why they were infrequently parasitized.

Robertson and Norman (1976) hypothesized that aggression is selected for in frequently parasitized species and that it is proportional to the frequency of parasitism on that host, especially for birds that do not regularly eject cowbird eggs (see also Neudorf and Sealy 1992). Robertson and Norman's hypothesis was supported by a direct relationship between aggression and frequencies of parasitism within taxonomic groups. Thus, although Brown-headed Cowbirds are generalist brood parasites, parasitism frequently differs among suitable hosts nesting in the same habitat (Friedmann 1929, Elliott 1977, Southern and Southern 1980, Briskie et al. 1990, Ortega and Cruz 1991), and these differences may be related to levels of aggression in the host.

However, the way in which aggression functions, its value to the host, and the period when it is most effective are not clear. Hosts acting aggressively toward cowbirds during the nest-building stage may warn cowbirds that they are vigilant nest defenders or, perhaps more likely, advertise their susceptibility to parasitism, as stated by the nesting-cue hypothesis (Robertson and Norman 1977). Host aggression can thus tip off cowbirds to the location of a host's nest, possibly resulting in higher frequencies of parasitism for that host species (Robertson and Norman 1976, 1977; Smith et al. 1984). Alternatively, no aggression may be the best response for susceptible hosts (Neudorf and Sealy 1992). McLean (1987) found that communally breeding

Whitehead (*Mohoua albicilla*) females responded to models of parasitic Long-tailed Cuckoos (*Eudynamys taitensis*) by remaining inconspicuous and hiding during the incubation period. Secretive behavior may be the best way to avoid parasitism for hosts that recognize brood parasites (McLean 1987, McLean and Rhodes 1991).

Because cowbirds usually lay during the host's laying period (Friedmann 1929), aggression after the laying period usually occurs too late to benefit hosts, even though many hosts still respond aggressively to cowbird models at this stage (Hobson and Sealy 1989, Neudorf and Sealy 1992, Bazin and Sealy 1993). If aggressive defense is to be effective, it may have to function best during the laying period, so that it repels female cowbirds that are trying to lay. Because female cowbirds lay before dawn (Scott 1991), Neudorf and Sealy (1994) recorded dawn attentiveness of 10 cowbird hosts, as well as cowbird laying times. They predicted that those species that accept cowbird eggs (acceptors) would be more vigilant than species that reject cowbird eggs (rejectors) and that rarely parasitized acceptors would be more vigilant than frequently parasitized acceptors. While they did not find the above relationships, they found that hosts that roost on nests overnight were in the best position to thwart laying cowbirds (Neudorf and Sealy 1994).

Field Sparrows and Indigo Buntings nest in the same old-field habitats in central Missouri, and their nests are often placed in the same species of plant at similar heights. Although parasitism frequencies on the two species vary depending on the study or region concerned (see Friedmann 1963 and references therein), Indigo Buntings at Missouri sites are parasitized more than four times as frequently as Field Sparrows. To determine how aggression might influence this difference, I placed model cowbirds at nests of both species and recorded host responses. I also observed nests of both species during their egg-laying periods, because this is the time during which cowbirds are most likely to lay in host nests (Friedmann 1929). If hosts do not respond to cowbird eggs and other defenses are employed, the host must be at the nest early enough to encounter laying cowbirds (Neudorf and Sealy 1994). Thus, if the aggressive defense hypothesis (Robertson and Norman 1977) applies, Indigo Buntings would either not be at their nests when cowbirds arrived to lay or would mount a less effective defense against cowbirds than Field Sparrows, based on their response to a cowbird model.

Methods

Aggression Experiments

Nests were found on old-field sites on and adjoining the Thomas S. Baskett Wildlife Research and Education Center in Boone County, Missouri (38° 45' N, 92° 12' W), from April through June in 1992 and 1993. Five old fields ranging in size from 2.8 ha to 16.3 ha were searched daily for nests. Once found, each nest was individually numbered and flagged from at least 5 m distance. Nests initiated prior to and including the day the last cowbird egg was laid were used for estimating parasitism frequencies.

Although testing aggression toward cowbirds during the host's laying period is the best way to simulate the natural phenology of cowbird egg laying, Field Sparrows and Indigo Buntings rarely visit their nests during this period except while actually laying eggs (Payne 1990, Carey et al. 1994, Burhans pers. obs.). Thus, aggression experiments were performed on nests of both species during the incubation period. Although host aggression may vary through the nesting cycle (Hobson and Sealy 1989, Bazin and Sealy 1993), I had no reason to think that there would be a period-dependent difference in host aggression between the host species. While most hosts were not color banded prior to testing, experiments were carried out during a short period (Field Sparrows, 3 May to 15 May; Indigo Buntings, 23 May to 7 June). During these periods, nesting activity overlapped temporally, so no birds were tested twice.

Camouflaged blinds were set 10 to 20 m from each nest at least half an hour before presentations. An upright freeze-dried female cowbird model was placed within 0.5 m of each nest so that it faced into the nest cup. Because nests were often hard to see from the blind, models were mounted on a camouflaged telescoping brass rod so that height of the model was kept at 1 m above each nest rim. To determine if host response was directed to cowbirds or any bird at the nest, a Fox Sparrow (*Passerella iliaca*) model was presented at each nest as a control. Fox Sparrows are about the same size as cowbirds, but are not known to prey on nests of these hosts (Hobson and Sealy 1989, Bazin and Sealy 1993). Both models were presented at each nest for 5 min. Order of presentation was random, and the second model was not presented until 15 min after the returning hosts had stopped chipping in response to the first model. Only females incubate in both species (Carey et al. 1994, Payne 1990), and they were sometimes flushed off nests during model placement, but all birds directed their attention to models during experiments and not to the blind. In all cases hosts stopped chipping soon after the first model was removed, and in almost every instance females returned to sit on the nest; a few left the immediate nest area to feed nearby.

The following responses to models were spoken into a tape recorder for each 5-min period: (1) number of chip calls (Payne 1990, Carey et al. 1994), (2) number of "eeee" calls (Payne 1990, Carey et al. 1994), (3) number of swoops or close passes at the model, and (4) number of hits (i.e., the model was contacted by the flying host). Because the effectiveness of aggression in deterring parasitism may be related to whether both parents respond to the cowbird, the actions and vocalizations of both parents were recorded. I

could not always record movement data for individual Field Sparrows, as most were not color banded. Indigo Buntings are sexually dimorphic, so I could distinguish responses by male and female parents.

Data were analyzed with nonparametric statistical tests (Siegel and Castellan 1988). Within-species comparisons between responses to Fox Sparrow and Brown-headed Cowbird models were analyzed with Wilcoxon signed-rank tests. Wilcoxon rank sum tests were used to test for species differences in response to Brown-headed Cowbird models; the number of parents responding (one or both) was tested with Fisher's exact test. I also compared chipping responses between parasitized and unparasitized Indigo Buntings with Wilcoxon rank sum tests. None of the Field Sparrow nests tested were parasitized.

Morning Nest Arrivals

Blinds were placed for observations 10 to 20 m from nests on the afternoon of the day the host laid its first egg, at which time the nest contents were examined for presence of cowbird eggs. On the following day, observers entered the blind at least 30 min before scheduled sunrise (SR - 30 min). Because of the possibility of disturbing roosting females, nests were not inspected at this time. As other studies have found that cowbirds lay before dawn (Scott 1991, Neudorf and Sealy 1994), I assume that cowbird eggs found after the observation period were laid by cowbirds that we observed and were not present prior to the observation period.

Observers spent at least one hour in the blind, recording any arrival times of hosts and female cowbirds. Upon arriving, female hosts and cowbirds sometimes perched on vegetation near the nest before flying directly to it. Where possible, arrival time was based on the time that birds were seen to fly directly to the nest, rather than arrival at the nest area. In most instances, cowbirds flew to vegetation several meters from the nest and perched for several minutes before flying to nests. If nests were obscured by vegetation, the time at which the female cowbird was seen landing on the nest plant was recorded as the arrival time.

After the observation period, nests were inspected for the presence of host and cowbird eggs. Local sunrise times were obtained from the National Weather Service office at Columbia, Missouri, and are accurate to the nearest minute; host and cowbird arrival times were also rounded to the nearest minute. As with aggression experiments, each host was tested only once, based on either color-banding information or overlap of nest phenology. Cowbirds were not color marked, so it is not known if all cowbird eggs were laid by different individuals.

Times of arrival of hosts and cowbirds in relation to sunrise were analyzed using a Kruskal-Wallis test, and differences between each species were compared using multiple comparisons analysis (Neter et al. 1990).

Results

Parasitism Frequencies

Backdating from hatching date using 11 days as the estimated incubation period for cowbirds (Lowther 1993, Burhans pers. obs.) revealed that in 1992 the last nest was parasitized by a cowbird on July 7. The sample of all nests for 1992 includes nests of Field Sparrows and Indigo Buntings that were initiated prior to this date. The last cowbird egg found in 1993 was laid on the morning of July 11, so the sample of all nests includes nests initiated prior to this date for 1993. Samples for the "all nests" category from both years include nests of Field Sparrow pairs whose nests were found soon after abandonment.

Based on nests found during building as the most conservative measure of parasitism frequency (see Discussion), Indigo Buntings were parasitized 4.4 times more frequently than Field Sparrows for the two years combined ($X^2 = 29.0$, df = 1, $P < .001$; Table 18.1).

Aggression Experiments

Experiments were performed on 14 Field Sparrow nests and 13 Indigo Bunting nests during the incubation period. Chipping frequencies for both hosts (Table 18.2) toward the cowbird model were significantly higher than toward the Fox Sparrow (Wilcoxon signed rank test: Field Sparrows, $Z = -3.23$, $P = .001$; Indigo Buntings, $Z = -2.90$, $P = .004$). Only 1 of 14 Field Sparrow responses involved an attack resulting in "eeee" calls, swoops, or hits on the cowbird model; this attack was by a female that had been incubating. No Field Sparrows attacked the Fox Sparrow model. Only 1 of 13 Indigo Bunting tests elicited an attack on the cowbird model (Table 18.2); in this case both the male and female re-

Table 18.1. Frequency (%) of Parasitized Nests by Stage (Parasitized/Total Nests Found in Stage)

Year	Stage Found	Field Sparrow	Indigo Bunting
1992	Building	28 (5/18)	83 (5/6)
	Before last egg	22 (5/23)	67 (6/9)
	All nests	11 (7/62)	65 (24/37)
1993	Building	13 (3/24)	92 (11/13)
	Before last egg	12 (5/42)	80 (20/25)
	All nests	15 (13/86)	54 (36/67)

Note: Includes only nests found during seasonal period of cowbird activity. "All nests" includes five Field Sparrow nests of known active pairs whose nests were found after abandonment.

sponded with "eeee" calls, swoops, and hits. No Indigo Buntings attacked the Fox Sparrow control.

Field Sparrow and Indigo Bunting responses to cowbird models did not differ statistically. In 11 of 14 Field Sparrow nests both parents responded to the cowbird model, compared to 9 of 13 bunting nests with both parents responding (Fisher's exact test, $P = .29$). Field Sparrows and Indigo Buntings responded to the cowbird model with an equivalent number of chips per 5-min period (Table 18.2; Wilcoxon rank sum test, $Z = -0.58$, $P = .56$). As stated above, only 1 of 14 Field Sparrow nests involved attacks on the model, compared to 1 of 13 Indigo Bunting nests (Fisher's exact test, $P = .52$). Parasitized and unparasitized Indigo Buntings did not differ in their chipping response to the cowbird model, although sample sizes were small (parasitized Indigo Buntings 244.20 ± 68.45 chips/5 min, $N = 5$; unparasitized buntings 273.38 ± 51.36 chips/5 min, $N = 8$; $Z = -0.29$, $P = .77$).

Morning Nest Arrivals

Field Sparrows arrived at nests to lay their second eggs on average 17.4 ± 2.3 (SE) min before sunrise ($N = 16$). The earliest arrival during the observation period was 25 min before sunrise (18 May, 0529 CDT), and the latest was 10 min after sunrise (15 May, 0606 CDT). Seven birds flew directly to nests, and 8 of 16 landed on vegetation near nests before flying to them. The latter birds perched an average of 35.25 ± 7.4 sec before landing at nests ($N = 8$, range 12–62 sec). A Field Sparrow that was on the nest before the observation may have roosted there overnight and was removed from the sample, as was a Field Sparrow that arrived to lay after the observation period was over. Field Sparrow laying bouts, defined as the interval from the time a female lands on the nest, deposits an egg, and departs (Sealy et al. 1995), averaged 42.1 ± 3.2 min ($N = 14$, range 20–60 min). The latter sample does not include one bird that was still on the nest at the end of the observation period and one that was chased off by a cowbird (see below).

Of 10 Indigo Bunting nests observed, 4 were abandoned, apparently before the observation took place; 6 other females arrived during the observation period. Average arrival time for Indigo Buntings was 16.7 ± 5.2 min after sunrise ($N = 6$, range SR - 1 min to SR + 30 min). Two birds flew directly to their nests, whereas 4 of 6 perched in the nest vicinity for an average of 223.50 ± 87.7 sec before flying to the nest ($N = 4$, range 15–431 sec). Abandonment of the other bunting nests may have been due to our setting blinds near them early in the nesting period, as Indigo Buntings rarely abandon nests due to cowbird parasitism unless the nest is parasitized before the first egg is laid (Payne 1990, Burhans pers. obs.). As far as I know, our blinds did not affect arrival times of buntings that did not desert nests, with the possible exception of a bird that appeared to chip at the blind. This female remained in the nest area for 431 sec before flying to the nest. As Indigo Buntings arrived comparatively late, we did not always record the lengths of laying bouts; most birds were still on the nest by the end of the observation period.

Table 18.2. Summary of mean (± SE) aggressive responses of Field Sparrows (N = 14 nests) and Indigo Buntings (N = 13 nests) to Brown-headed Cowbird and Fox Sparrow Models over 5-min Periods

Response	Model	Field Sparrow	Indigo Bunting
Nests with both parents responding	Cowbird	11/14 nests	9/13 nests
	Fox Sparrow	10/13 nests	4/13 nests
Chips	Cowbird	220.4 ± 32.7	262.2 ± 39.6
	Fox Sparrow	56.0 ± 15.0	151.0 ± 20.4
Eeee call	Cowbird	2.2 ± 2.2	0.5 ± 0.5
	Fox Sparrow	0	0
Swoops	Cowbird	0.6 ± 0.6	0.9 ± 0.9
	Fox Sparrow	0	0
Hits	Cowbird	0.3 ± 0.3	0.7 ± 0.7
	Fox Sparrow	0	0

One female bunting observed leaving the nest had been on the nest for 33 min; other female buntings had been on nests for an average of 23.40 ± 5.8 min (N = 5, range 3–38 min) when observers left the blinds.

Female cowbirds laid during eight nest observations; seven times at Indigo Bunting nests and once at a Field Sparrow nest. The average nest arrival time of female cowbirds was 11.4 ± 1.8 min before sunrise (N = 8, range SR - 20 min to SR - 5 min). Two abandoned Indigo Bunting nests were parasitized, and one active Indigo Bunting nest was parasitized twice in one morning before the female bunting arrived. Buntings that were parasitized never encountered cowbirds. Mean difference between departure time of cowbirds and arrival time of female buntings at the same nest was 34 ± 5.1 min (N = 5, range 20–48 min). Seven of eight female cowbirds perched in trees or shrubs near nests for some time before flying to them. The average time cowbirds spent perching near nests within view of the blinds was 190.50 ± 57.6 sec (N = 6, range 48–426 sec), not including one cowbird that encountered a Field Sparrow at its nest (see below). Two cowbirds flew to the host plant or near to it after perching nearby, but then moved through the immediate vegetation for some time until they apparently located nests. We could not tell exactly when the latter birds landed on host nests. Thus a conservative estimate for the average cowbird laying bout is 97.5 ± 32.6 sec (N = 8, range 16–275 sec).

Differences in nest arrivals of Field Sparrows, Brown-headed Cowbirds and Indigo Buntings were significant (Kruskal-Wallis test, $X^2 = 16.86$, df = 2, $P = .000$). Field Sparrows tended to arrive at nests earlier than cowbirds ($.15 < P < .20$, multiple comparison procedure for Kruskal-Wallis test), and Indigo Buntings tended to arrive at nests later than cowbirds ($.10 < P < .15$).

The Field Sparrow whose nest was parasitized during the observation (D. Martasian pers. obs.) arrived to lay 21 min before sunrise (arrival time 05:22:12 CDT). At 05:28:30, a female cowbird arrived about 10 m from her nest and was approached by a chipping Field Sparrow, presumably the mate of the laying female. The cowbird was briefly out of sight, then flew to the ground within 1 m of the nest while the male Field Sparrow continued to chip. At 05:34:55, the female cowbird chased the female Field Sparrow off the nest and flew after her for 10 m. The female Field Sparrow was on the nest for 12 min and 7 sec before being chased off. The female cowbird landed on the nest at 05:35:50 and flew off the nest 16 sec later. The Field Sparrows flew about the nest vicinity for the next 2 min but then left the nest area and were not seen again during the observation. The nest contained one cowbird egg and one Field Sparrow egg after the observation, so the Field Sparrow apparently did not get a chance to lay her second egg in the nest. The nest was abandoned, and no Field Sparrows were seen at or near it during the next several days.

Discussion

Both Field Sparrows and Indigo Buntings clearly recognized cowbirds as threats, because of differences in chipping frequencies toward the cowbird and Fox Sparrow models (Table 18.2). If these hosts respond to live cowbirds as they do to models, neither host response could be expected to deter laying cowbirds. Actual attacks by both host species were rare. Other studies using cowbird models have documented low aggression levels for some cowbird hosts (Robertson and Norman 1976, Smith et al. 1984, Hobson and Sealy 1989, Neudorf and Sealy 1992). Other hosts, however, may attack cowbird models vigorously (Robertson and Norman 1976, Folkers and Lowther 1985, Briskie and Sealy 1989, Neudorf and Sealy 1992, Bazin and Sealy 1993).

Observations on nests of larger hosts such as Gray Catbirds (*Dumetella carolinensis*) and American Robins (*Turdus migratorius*) indicate that these species use aggression to repel live cowbirds from nests (Friedmann 1929, Scott 1977). In one case, a robin injured the cowbird (Leathers 1956). Smaller hosts may have more difficulty; Clay-colored Sparrows (*Spizella pallida*) drove away a cowbird, but the cowbird immediately returned to parasitize the nest successfully (Neudorf and Sealy 1994; see also Hill and Sealy 1994). During three observations at Yellow Warbler nests, host females that were on the nests attacked cowbirds when the cowbird arrived. Parasitism occurred at two nests, followed by acceptance of cowbird eggs by the hosts. One attempt may have been thwarted (Sealy et al., Chapter 19, this volume). S. I. Rothstein and A. O'Loghlen (unpubl. data) found that cowbirds attracted by playbacks to sites defended by Western Wood-Pewees (*Contopus sordidulus*) did not retreat despite repeated attacks. When attracted to areas defended by larger species such as American Robins, Red-winged Blackbirds, or Brewer's Blackbirds (*Euphagus cyanocephalus*), cowbirds always retreated. Thus, larger hosts can mount more effective nest defenses than smaller hosts.

Differences in aggression between Indigo Buntings and Field Sparrows do not seem to account for differences in parasitism frequency, because their chipping rates and frequency of attacks were so similar. Field Sparrows at these sites probably encounter laying cowbirds most of the time. If aggression directed toward models is similar to that directed toward live cowbirds, they are probably not able to repel laying cowbirds. Additional nest observations of cowbird interactions with these hosts, collected since the present study, support this interpretation (Burhans unpubl. data). Indigo Buntings probably rarely encounter laying cowbirds at their nests, and the rarity of attacks in my experiments suggests that they would do little to deter them if they did. Neither host at the Field Sparrow nest that was visited by a laying cowbird attempted to drive her away, although the male did approach her when she initially flew to the nest area.

Field Sparrows have been observed chasing female cowbirds during nest building (Crooks 1948, D. Dearborn pers. obs.). This is thought to be the time when cowbirds cue on host nests (Friedmann 1929, Hann 1941, Norman and Robertson 1975). Aggression in this situation can be counterproductive, because cowbirds may use such behavior to locate host nests, as predicted by the nesting-cue hypothesis (Robertson and Norman 1977, S. A. Gill et al. unpubl. data). Walkinshaw (1968) noted that Field Sparrows dropped nest material and began to feed in the presence of cowbirds. Although we never observed such behavior during many observations of Field Sparrow nest building (Carey et al. 1994), inconspicuous behavior during nest building should be advantageous to hosts, if it reduces the likelihood of detection by cowbirds.

Neudorf and Sealy (1994) defined a critical period of 30 min around sunrise during which parasitism was most likely to occur, based on acts of cowbird parasitism observed in Manitoba. They found no relationship between presence of hosts near their nests and frequency of parasitism for the ten acceptor species they observed, nor did acceptors spend more time guarding their nests during this period than rejectors. However, females that roosted overnight on nests were more likely to be on their nests during the critical period for cowbird parasitism, and females that did not roost overnight were not likely to be near the nest area at all (Neudorf and Sealy 1994). Field Sparrows rarely roost overnight on nests and may be unusual in arriving to lay before cowbirds. In observations at nests of Clay-colored Sparrows, congeners of Field Sparrows, five out of seven different females arrived at the nest during the critical period for parasitism. This includes a female that roosted overnight, was accidentally flushed from the nest, and returned to encounter a cowbird (S. G. Sealy pers. comm.).

Although cowbirds perched briefly in trees, shrubs, or fence lines before flying to nests, their manner of flight from the perch suggests that cowbirds had located nests in advance, as also suggested by Neudorf and Sealy (1994). Perching nearby in shrubs may allow female cowbirds to see if the host is on the nest, giving the cowbird the option of parasitizing the nest later if the host is present. This provides another possible explanation for differences in parasitism between Field Sparrows and Indigo Buntings. Female cowbirds may observe Field Sparrows flying toward or sitting on nests and decide not to parasitize these nests at the risk of eliciting desertion by the host (J. N. M. Smith pers. comm.). Placing Indigo Bunting models on nests before female buntings arrive and comparing parasitism frequencies on these nests versus unmanipulated nests could test this hypothesis.

As in Neudorf and Sealy's (1994) observations, cowbirds did not vocalize during flight near nests. Although mean time for cowbird laying bouts in my study was greater than in Neudorf and Sealy's study (63 ± 12.3 sec vs. 97.5 ± 32.6 sec in this study), our difficulty in detecting exactly when cowbirds landed on some nests may account for this difference. Even the two female cowbirds that moved about the nest plant before laying flew directly to the nest plant or its immediate vicinity. Silent, direct flight and rapid laying all suggest that cowbirds try to remain undetected when they parasitize nests, either because hosts sometimes thwart parasitism attempts (Neudorf and Sealy 1994, Sealy et al. 1995) or to avoid nest abandonment by hosts (see below).

The time of nest arrival around sunrise has other consequences besides aggression for host responses to parasitism. Field Sparrows regularly abandon parasitized nests, at least throughout the midwestern portions of their range. At Missouri sites, Field Sparrows deserted 6 of 8 (75%) parasitized nests found during nest building in 1992–1993 and deserted 15 out of all 20 (75%) parasitized nests found. Similar desertion frequencies have been found in Michigan and Illinois (Walkinshaw 1968, Best 1978).

Nest desertion has been widely reported among cowbird hosts, particularly in small birds (Friedmann 1963, Clark and Robertson 1981, Graham 1988, Sedgwick and Knopf 1988), which presumably have difficulty in grasp-ejecting cowbird eggs. Puncture ejection, however, has recently been documented in a small (15 g) host (Sealy 1996). However, with few exceptions (Rothstein 1976, Burgham and Picman 1989), nest desertion is not induced in small hosts by experimental addition of real or artificial cowbird eggs (Rothstein 1975, Hill and Sealy 1994, Sealy 1995), while grasp-ejection is easily documented experimentally in grasp-ejecting hosts (Rothstein 1975).

Further experiments with Field Sparrows have indicated that they do not desert simply in response to addition of artificial or real cowbird eggs (Burhans unpubl. data). It may be that detection of laying parasites at the nest is the cue required by Field Sparrows to induce nest desertion. Additional observations of Field Sparrow–cowbird interactions at the nest also support this possibility (Burhans unpubl. data).

Methodological and Conservation Implications

Nest desertion may serve as an index of the vulnerability of host species to parasitism. Many studies present parasitism frequencies that include nests found during all stages of the nesting cycle. However, if hosts are prone to deserting parasitized nests, such a sample likely underestimates the true parasitism frequency, because deserted nests that lack host activity are usually hard for field workers to find. In my study, this held true for Field Sparrow nests (Table 18.1). Of nests found during nest building, 19.0% (8/42) were later parasitized. The number decreases to 15.4% (10/65) for all nests found prior to incubation and decreases further to 13.5% (20/148) for the total sample of nests, even including 5 parasitized nests in the last group that were abandoned before they were found. Such a trend may prevail for reasons other than nest abandonment, including egg rejection, partial

clutch loss due to predation, or brood reduction (Briskie et al. 1990, Hill and Sealy 1994, Pease and Grzybowski 1995). While a tendency for parasitism frequencies to decline over the sampling period was also observed for Indigo Buntings, which do not usually abandon parasitized nests (Table 18.1), nest-deserting species are likely to exaggerate the trend (Sedgwick and Knopf 1988). For these reasons, researchers may prefer to use the cohort parasitism fraction, or percentage of a cohort of nests started, to measure parasitism frequencies more conservatively (Pease and Grzybowski 1995; Grzybowski and Pease, Chapter 16, this volume).

In addition, vulnerability to parasitism may be affected by the interaction of nest arrival time with either nest defenses or nest desertion behavior. Defense of the nest is probably most useful if hosts are at or near the nest when cowbirds arrive to lay (Neudorf and Sealy 1994). Similarly, if nest desertion is a viable defense and detection of the cowbird stimulates nest desertion, species that arrive later to lay may be more vulnerable to parasitism. Although data are sparse, there may be considerable regional variability in cowbird nest arrival times. Scott's (1991) review documented 20 direct observations of cowbird laying, with mean time of laying at 11.00 ± 4.05 min before sunrise, not including one record of a cowbird that arrived 3 hr after sunrise; Scott's nest arrival times agree closely with those of this study (11.4 ± 1.8 min). However, mean arrival time for cowbirds at Delta Marsh, Manitoba, was 35.6 ± 2.4 min before sunrise (range 44–25 min before sunrise, $N = 7$, Neudorf and Sealy 1994). Earlier arrival times could be partly due to earlier onset of civil twilight in relation to sunrise in northern latitudes. Onset of civil twilight in June occurs between 43 and 45 min before sunrise in Manitoba, compared to 31 and 32 min in Missouri (United States Naval Observatory 1946). However, this difference does not account for all of the disparity in cowbird arrival times between Manitoba and Missouri. Earlier arrival times may also be the result of cowbirds roosting closer to host nest sites at Delta Marsh and not having to spend as much time traveling to nests (S. G. Sealy pers. comm.).

Recent radiotelemetry studies of cowbirds in the Midwest indicate that most cowbirds do not roost where they breed, but either have distinct roosting areas or roost near feeding areas (Thompson 1994; Thompson and Dijak, Chapter 10, this volume). At one site, a communal roost of more than 200 Brown-headed Cowbirds was discovered. Hosts near such large roosts may be parasitized earlier in the day and may arrive to lay their own eggs after cowbirds have already visited the nest. For hosts that do not regularly roost overnight on the nest during laying, proximity of the nest to cowbird roosts may thus be crucial in limiting the effectiveness of their defenses, regardless of whether the defense is aggression, protection behavior, or desertion.

Further study of the relationship between cowbird roost distance and cowbird arrival times at nests may help to understand host defenses. If nest defense and nest desertion by hosts do sometimes deter cowbirds, managers may want to consider cowbird and host arrival times, as well as proximity of cowbird roosts, when assessing vulnerability of local host populations to parasitism. Local host populations that are close to cowbird roosts may benefit from roost disruption and cowbird control to a greater degree than populations far from roosts, because hosts nesting farther from cowbird roosts may have a better chance of detecting cowbirds at dawn and using their own defenses.

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