Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs

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Why do many hosts accept costly avian brood parasitism even when parasitic eggs and nestlings differ dramatically in appearance from their own? Scientists argue that evolutionary lag or equilibrium can explain this evolutionary enigma. Few, however, consider the potential of parasitic birds to enforce acceptance by destroying eggs or nestlings of hosts that eject parasitic eggs and thereby reject parasitism. This retaliatory "mafia" behavior has been reported in one species of parasitic cuckoo but never in parasitic cowbirds. Here we present experimental evidence of mafia behavior in the brown-headed cowbird (*Molothrus ater*), a widely distributed North American brood parasite. We manipulated ejection of cowbird eggs and cowbird access to predator-proof nests in a common host to test experimentally for mafia behavior. When cowbird access was allowed, 56% of "ejector" nests were depredated compared with only 6% of "accepter" nests. No nests were destroyed when cowbird access was always denied or when access was denied after we removed cowbird eggs, indicating that cowbirds were responsible. Nonparasitized nests were depredated at an intermediate rate (20%) when cowbirds were allowed access, suggesting that cowbirds may occasionally "farm" hosts to create additional opportunities for parasitism. Cowbirds parasitized most (85%) renests of the hosts whose nests were depredated. Ejector nests produced 60% fewer host offspring than accepter nests because of the predatory behavior attributed to cowbirds. Widespread predatory behaviors in cowbirds could slow the evolution of rejection behaviors and further threaten populations of some of the >100 species of regular cowbird hosts.

brood parasitism | host–parasite evolution | *Molothrus ater* | nest predation | *Protonotaria citrea*

Hosts of avian brood parasites pay severe costs for rearing unrelated young (1–3). Cuckoo (*Cuculidae*) hosts typically eject parasitic eggs that do not mimic their own (4–6). Why then do most cowbird (*Molothrus* spp.) hosts accept parasitic eggs that differ dramatically in appearance from their own (2, 6)? At least three nonexclusive hypotheses have been suggested to resolve this paradox of nonrejection in the face of costly brood parasitism: (*i*) evolutionary lag [short time of coexistence (2, 7, 8)]; (*ii*) nonrandom association of parasitism status with individual hosts' repeated breeding attempts [i.e., limited horizontal transmission (9, 10)]; and (*iii*) evolutionary equilibrium [rejection costs and errors (11–13)] through cognitive and physiological constraints on detection and rejection (14–16).

Proponents of evolutionary equilibrium tend to focus on the limited abilities of hosts to recognize or reject parasitism. Few have explored the possibility that avian brood parasites could enforce acceptance by destroying eggs or nestlings of hosts that eject parasitic eggs (17). This "mafia-like" retaliatory behavior has been reported in one species of parasitic cuckoo (18), but there has never been an experimental test of whether parasites themselves are destroying nests of hosts that eject parasitic eggs. Mafia behavior has not been documented in parasitic cowbirds (2), but results from two studies suggest that brown-headed cowbirds (*Molothrus ater*) may occasionally depredate nonparasitized host nests, thereby creating opportunities to parasitize those hosts' renesting attempts ["farming" (19, 20)]. Here we present evidence of a mafia-like behavior in the brown-headed cowbird, the most abundant and widely distributed avian brood parasite in North America (21).

We studied the effects of cowbird parasitism on a cavity-nesting host, the prothonotary warbler (*Protonotaria citrea*), in the Cache River watershed in southern Illinois [37°18′N, 88°58′W (3, 22)]. During 1996–2002, we attempted to make some nests (n = 472) predator-proof by attaching nest-boxes to pieces of greased conduit instead of attaching them to trees (23), and we never removed brown-headed cowbird eggs from the parasitized warbler nests (n = 230). As a result, nearly all (>95%) nests in predator-proof nest-boxes were successful regardless of parasitism status (3, 23). In 2002, as part of a separate study, we removed cowbird eggs from some parasitized predator-proof nests (n = 50), and only 60% were successful, indicating that cowbirds may depredate nests in response to our rejection of their eggs (mafia-like retaliation). This finding led us to test experimentally for both mafia and farming behaviors in cowbirds. Specifically, we removed (ejected) or accepted cowbird eggs and controlled cowbird access to otherwise predator-proof nests of prothonotary warblers to determine whether cowbirds were retaliating (mafia behavior), farming, or having no predatory effect on the warbler nests in our study system.

Results

We assigned a total of 182 nests to one of five categories (Table 1) depending on parasitism status (yes or no), ejection status (cowbird eggs removed by observers or accepted), and cowbird access (always allowed, denied after incubation commenced, or never allowed). We then monitored the fates of all nesting attempts and compared actual rates of nest predation with those predicted given different effects of cowbirds (Table 1). Nest-predation events (n = 44) all occurred during the incubation period and involved the damage or destruction of most or all warbler eggs (n = 12), disappearance of most or all warbler eggs (n = 21), or both (n = 11).

When cowbird access was allowed, 56% of "ejector" nests (category 1) were depredated compared with only 6% of "accepter" nests (category 3) (Fig. 1A). Nests that were not parasitized but still accessible to cowbirds (category 2) were depredated at an intermediate rate (20%) (Fig. 1A). No nests were depredated when cowbird access to ejector nests was denied after incubation commenced (category 4) or when cowbird access was never allowed (category 5), suggesting that cowbirds were responsible for nest-predation events. These differences in rates of nest predation provide evidence that cowbirds employ both mafia and farming behaviors in this system.

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**Table 1. Nest categories and predicted rates of nest predation given different possible effects of cowbirds*

	Nest category				
Cowbird effect	1 (cowbird egg ejected, cowbird access always allowed)	2 (nonparasitized nest, cowbird access always allowed)	3 (cowbird egg accepted, cowbird access always allowed)	4 (cowbird egg ejected, cowbird access denied thereafter)	5 (cowbird access never allowed)
None	Low	Low	Low	Low	Low
Farming	Moderate	Moderate	Low	Low	Low
Mafia behavior	Moderate	Low	Low	Low	Low
Farming plus mafia behavior	High	Moderate	Low	Low	Low

*A detailed description of each category is given in *Materials and Methods*.

Relatively high rates of parasitism would be predicted for the renesting attempts (renests) of those female warblers who lost their nest to suspected cowbird predation. We were able to document the parasitism status (yes or no) of renests of 20 such female warblers for comparison with other nesting attempts ($n = 81$) that occurred within the study area during the same period. Renests linked to cowbird predation were parasitized more frequently (85%) than the other nesting attempts (36%; $\chi^2_1 = 15.65$; $P < 0.001$).

The penalty to the warblers for ejecting parasitic eggs was the destruction of clutches, presumably by cowbirds. Mafia behavior in brood parasites can hold hosts in an evolutionary state of acceptance only if hosts that accept parasitic eggs have higher reproductive output relative to hosts that reject parasitism and suffer the penalty (17). In our experiment, accepters paid some costs (3) associated with being parasitized (category 3 versus category 5) (Fig. 1*B*), but the predatory tactics of cowbirds significantly reduced the mean number of warbler offspring

Fig. 1. Effect of cowbirds on rates of nest predation and reproductive output in nests of prothonotary warblers. (*A*) Rates of nest predation were significantly different among the five categories of nests ($\chi^2_4 = 42.22$; $P < 0.001$). Bars shown with the same letter above them were not statistically different ($P > 0.05$) from each other based on pairwise comparisons using χ^2 tests. (*B*) Mean + SE numbers of warbler offspring produced per nest were significantly different among the five categories of nests (Kruskal–Wallis test; $H_4 = 40.22$; $P < 0.001$). Bars shown with the same letter above them were not statistically different ($P > 0.05$) from each other based on pairwise comparisons using Mann–Whitney *U* tests. Sample sizes for nest categories are 46, 72, 32, 16, and 16 for categories 1–5, respectively. See Table 1 and *Materials and Methods* for a description of each category.

produced per nest in ejectors (category 1) compared with accepters (category 3) (Fig. 1*B*).

Discussion

Implicating Cowbirds. We removed cowbird eggs from nests of a cowbird host that presently accepts brood parasitism (22), and by doing so, we were able to test experimentally for and demonstrate a significant increase in nest predation in response to the ejection of parasitic eggs. These nest-predation events during the incubation period fit well with how cowbirds typically damage or remove host eggs from nests (2, 6, 24). Can any other organism be responsible for the variation in rates of nest predation that we observed? House wrens (*Troglodytes aedon*), a species known to destroy nests of rival cavity-nesting species (25), do not occur in our study system. Carolina wrens (*Thryothorus ludovicianus*) occasionally use our nest-boxes (including those with openings that exclude cowbirds), but in 13 years of research, we have no evidence that they depredate or take over warbler nests.

Some cowbird hosts may desert nests in response to egg loss [a reduction in clutch size (26)]. One could argue that in our study, the prothonotary warblers themselves removed or damaged their own eggs and deserted nests in response to our removal of cowbird eggs, giving the appearance that the nest had been depredated by a cowbird. However, this argument does not hold for two reasons. First, clutch size at the onset of incubation was not different between categories 1 and 4 (mean ± 1 SE = 4.04 ± 0.18 and 4.12 ± 0.18 eggs, respectively; $t_{60} = 0.257$; $P = 0.78$). We removed cowbird eggs from nests in both categories, yet nests were depredated only when we continued to allow cowbird access (category 1) (Fig. 1*A*). Second, clutch size was not different between nests that were depredated in category 1 and those that were not (4.04 ± 0.26 and 4.05 ± 0.29 eggs, respectively; $t_{44} = 0.032$; $P = 0.97$).

One additional piece of evidence implicating cowbirds is that naturally nonparasitized warbler nests ($n = 17$), initiated late in the breeding season after cowbirds had stopped laying eggs in warbler nests, were never depredated even though cowbird access to nests was allowed. Rates of nest predation for the nests where we removed cowbird eggs and continued allowing cowbird access (category 1) were consistently high (54–66%) across 4 years of experimental manipulation. There is no logical alternative to retaliation by cowbirds that can explain why nests where cowbird eggs were accepted (category 3) remained safe, whereas the majority of nests where we removed cowbird eggs (category 1) were depredated.

Brown-headed cowbirds make their living by finding host nests and monitoring them to synchronize their egg laying with that of the host (2, 6, 21). Cowbirds are adept egg predators, and they often remove a host egg before laying one of their own in a nest (2, 6, 24). A number of studies report personal observations (27) or video documentation (28–31) of nest predation by female cowbirds of host eggs and nestlings (rarely) in a variety of host species. Although these observations do not show cowbirds
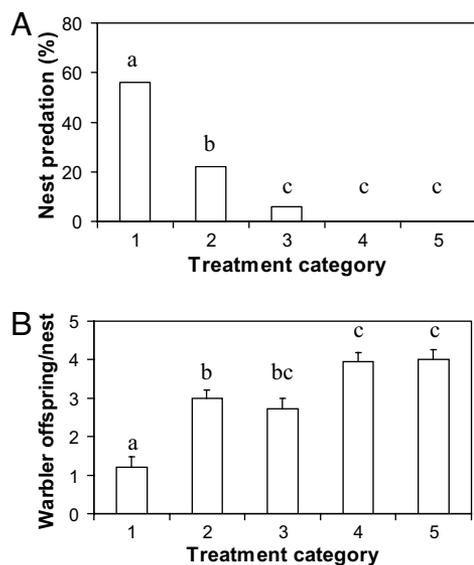
depredating a substantial number of nests, they do show that cowbirds occasionally destroy entire clutches or broods of hosts.

Our results show that cowbirds often retaliated against the removal of their eggs by depredating the warbler nests from which cowbird eggs were ejected experimentally. To a lesser extent, additional opportunities for parasitism were created when some nonparasitized nests were also depredated. By manipulating cowbirds' access to host nest-boxes that were otherwise predator-proof, our results provide strong evidence for mafia-like retaliatory behavior in these brood parasitic cowbirds. The presence of mafia and farming behaviors in cowbirds suggests that the parasitic and predatory behaviors of this species are even more sophisticated than previously thought. How common or widespread these behaviors are is still unknown.

Evidence from Other Systems. If cowbirds more than occasionally depredate host nests, then one would predict a positive correlation between rates of nest predation and rates of cowbird parasitism in numerous study systems. However, this correlation is often not found (32), or, when rates are correlated, scientists suggest that it is the result of coincidental preferences by other nest predators and cowbirds for particular habitat features (33, 34). Cowbird control programs, where cowbird numbers are reduced in an effort to increase nesting success for particular hosts, provide opportunities to test the prediction that rates of nest predation decrease when cowbird numbers decrease. Results from these studies show no clear pattern, and many report no change in rates of nest predation (35, 36), whereas others do report lower rates of nest predation (37) when cowbird numbers are reduced.

Farming by cowbirds has been put forward as a possible explanation only when nonparasitized nests are depredated more frequently than parasitized nests within a particular study system (19, 20, 38). Numerous other studies have found no evidence of farming in various cowbird hosts (32, 39, 40). However, a lack of association between parasitism status and rates of nest predation (3) does not necessarily indicate a lack of nest predation by cowbirds. Cowbird farming behavior could elevate rates of nest predation for unparasitized nests (19), whereas other nest predators could be attracted to parasitized nests [e.g., certain nest sites prone to discovery by cowbird and predator, loud begging of cowbird nestlings, increased provisioning of nestlings by host adults (32, 39)], resulting in rates of nest predation that appear to be unrelated to parasitism status.

Predatory behaviors in cowbirds may be difficult to uncover in conventional studies of the nesting success of cowbird hosts. Even within our own study system, we did not observe an association between parasitism status and nest predation before manipulating nests to reduce the effects of other nest predators (3) and removing cowbird eggs from some nests and not others. Until now there has never been an experimental test for farming and mafia behaviors in cowbirds whereby the effects of other nest predators were eliminated and cowbird access to nests was controlled. Our results provide clear evidence that these predatory behaviors exist.

Farming. The results we present here strongly support two other studies that found compelling, albeit indirect evidence that cowbirds may farm two additional hosts (19, 20). These two study systems consisted of relatively simple bird communities [(*i*) an island population of song sparrows, *Melospiza melodia* (19) and (*ii*) red-winged blackbirds, *Agelaius phoeniceus*, nesting in grass and sedge meadows (20)] where the availability of relatively few alternative hosts may have permitted closer monitoring by cowbirds and increased the importance of farming behavior. In simple systems, farming behavior may force nesting asynchrony on a host population that is essential for a cowbird that can only

lay one egg per day. Prothonotary warblers, on the other hand, nest in diverse bird communities with many alternative hosts (41) where we would predict cowbirds to focus less on one particular host.

Prothonotary warblers are excellent hosts (3) and differ from nearly all other cowbird hosts in being secondary cavity nesters (42). Secondary cavity nests, especially the nest-boxes used in this study, may be much more predictable nest sites than the ephemeral, often-hidden open-cup-shaped nests of other hosts. As such, they could be much easier for cowbirds to locate and monitor. Therefore, prothonotary warblers may be more vulnerable than most hosts to farming by cowbirds. Nevertheless, the fact that farming has now been reported in multiple study systems suggests that many hosts may be susceptible to this behavior.

The farming and mafia behaviors create opportunities for cowbirds to parasitize renesting attempts of hosts while simultaneously reducing host reproductive output via nest predation and subsequent parasitism of renests (19). Farming and mafia behaviors are adaptive for the individual cowbirds using these behaviors only if they parasitize the renesting attempts caused by their predatory behaviors. Renesting attempts of female warblers whose nests were lost to suspected cowbird nest predation were parasitized at a very high rate (85%), suggesting that cowbirds do benefit from their own predatory behaviors.

Mafia Retaliation. Unlike farming, mafia behavior in a brood parasite can slow the evolution of ejection behavior in hosts (17, 18). Retaliation may also mediate a change in rejection behavior of individual hosts, resulting in those individuals being more likely to accept subsequent parasitism (43). The depredation of ejectors' nests also directly reduces or eliminates the production of ejector progeny. This reduction in the reproductive output of hosts dilutes or greatly reduces the value of ejection to hosts, thereby diminishing selection for the evolution of ejection behavior. Ejection behavior in hosts would be particularly slow to evolve if mafia-like behavior in parasites occurred in systems where individual host females were likely to be parasitized repeatedly within [high parasitism rates for renests after the failure of a parasitized first attempt (10)] or across breeding seasons (9, 10).

Central to the persistence of mafia-like behavior in brood parasites and acceptance in hosts is the fact that hosts produce significantly more offspring by accepting parasitism rather than ejecting parasitic eggs (17). As a result of our removal of cowbird eggs and the subsequent depredation of host nests, the warblers in our experiment produced significantly more offspring by "complying" with the mafia-like parasite (category 3 versus category 1) (Fig. 1*B*). This relationship provides positive feedback between a retaliating parasite and a compliant host, further enhancing selective pressure favoring continued acceptance in the host and predatory behavior in the parasite (18). Mafia behavior would be unlikely to affect evolution of ejection behavior in a handful of cowbird hosts that usually lose all or nearly all of their own offspring when parasitized, because these hosts gain nothing by accepting parasitism (6). This situation applies to some of the smallest cowbird hosts or those with relatively long incubation periods (44, 45).

For the purpose of our experiment, we manipulated just one nesting attempt of each individual pair of warblers and could therefore only compare reproductive output per nest in each category rather than season-long productivity per pair. If the warblers in category 1 (ejectors) that lost clutches had escaped cowbird parasitism when they renested, then their season-long productivity may have been more similar to the accepters (category 3). However, this result seems unlikely given that most renesting attempts of ejectors were parasitized. It will be necessary to measure additional potential costs, such as the effect

of parasitism on the mass and quality of fledglings (3, 46), survival of adults (46), and lifetime reproductive output, to determine the strength of selection favoring acceptance given different levels of mafia nest predation.

Arguably, loss of habitat along with increases in nest predation (by generalist nest predators) and cowbird parasitism linked to breeding habitat fragmentation pose the greatest threats to populations of birds that serve as cowbird hosts (47–49). However, farming and mafia behaviors in cowbirds could exacerbate these threats and further jeopardize populations of some cowbird hosts. In addition, if mafia behavior is widespread or becoming more prevalent in cowbirds, it could factor prominently in delaying the evolution of ejection behaviors in some of the >100 species that currently accept cowbird parasitism.

Materials and Methods

Study System. Prothonotary warbler nests were experimentally manipulated during 2003–2006 within a 150-ha complex of connected forested wetlands within the Cache River watershed in southern Illinois (37°18′N, 88°58′W). Detailed descriptions of these forested wetlands are provided in refs. 23 and 50. The prothonotary warbler is a migratory songbird that winters in the Neotropics and breeds in the central and eastern United States (42). This species is territorial and socially monogamous, nests in secondary cavities, associates closely with standing water in bottomland and swamp forests, readily uses nest-boxes, and is a host of the parasitic brown-headed cowbird (3, 22, 41, 50). In our system, rates of cowbird parasitism are similar between nests in nest-boxes and natural cavities with the same entrance hole size (3). Adult warblers weigh 14–16 g (42), whereas female cowbirds weigh 35–42 g (21). Prothonotary warblers accept cowbird eggs and nestlings (3), and previous observational and experimental work on warblers in our study system showed an apparent lack of adaptive responses by the warblers to costly cowbird parasitism (3, 22). Our study site contained 45–54 pairs of individually color-banded warblers during each of the four breeding seasons.

Brown-headed cowbird females are known to occupy and defend breeding areas within a particular habitat, and these areas may overlap little or greatly with other females (51–54). The average size of a cowbird's breeding area is often <10 ha (52, 54–56), and cowbirds often are philopatric to breeding areas both within and between breeding seasons (52, 54). Familiarity with and time spent in a defined breeding area likely enhances a female cowbird's ability to find, monitor, and successfully parasitize host nests throughout the breeding season. Individual female cowbirds can lay no more than one egg on a given day (21). In each of the 4 years of this study, we have documented that six to eight cowbird eggs were deposited among different warbler nests alone on the same morning. This number of eggs indicates that there were at least six to eight different female cowbirds on the study site, and possibly >15 given the size of our study site (150 ha) and the average size of cowbird breeding areas mentioned above.

Monitoring Nesting Attempts. We attached nest-boxes made from modified 1.9-liter cardboard juice cartons to trees in a grid formation (35-m interbox spacing) covering all suitable breeding habitat. Each nest-box was placed 1.7 m above ground level and had an entrance hole that was initially 44 mm in diameter, which allowed both warblers and female cowbirds to enter (3). Entrance holes 32 mm in diameter were small enough to deny entry to cowbirds but not warblers (3). Nest-boxes that contained new complete but empty nests (before the first egg had been laid) were removed from trees and reattached to two pieces of 1.50-cm-diameter greased conduit placed in the ground and standing 1 m away from the original nest tree. Nearly all (>95%) nest-boxes placed on conduit were safe from nest predation in

years before our experiment (23). We monitored nest-boxes every third day throughout the breeding season. On each visit, we recorded the number of warbler and cowbird eggs or nestlings that were present. We knew the fate of every nesting attempt on the study area and the number of fledglings produced per attempt (50). We captured every male and female warbler, color-marked each with a unique combination of leg bands, and knew the identities of males and females associated with every nesting attempt (23, 50).

Experimental Manipulations. All nests were on greased poles and therefore safe from the nest predators typically responsible for nesting failures (23, 50). Each nesting attempt in our analysis came from a different pair of warblers. In other words, individual pairs of warblers were never resampled either within a given year or across years. We visited every nest a similar number of times and reached into each nest with our hands one time at the commencement of incubation regardless of whether we removed cowbird eggs. Each nest in categories 1–4 had a 44-mm-diameter entrance hole throughout the egg-laying period that allowed cowbird entry. All nests in categories 1, 3, and 4 were parasitized naturally by cowbirds during the egg-laying period, and the average number of cowbird eggs per nest (2.06, 1.72, and 1.88 eggs, respectively) was not different among categories ($P > 0.13$ for all pairwise Mann–Whitney U tests). Additional details of each category are as follows: For category 1, we removed cowbird eggs on the day incubation commenced, and the entrance-hole diameter remained 44 mm. For category 2, these nests were not parasitized by cowbirds, and the entrance-hole diameter remained 44 mm. For category 3, we did not remove cowbird eggs, and the entrance-hole diameter remained 44 mm. For category 4, we removed cowbird eggs and reduced the entrance-hole diameter to 32 mm on the day incubation commenced, thereby preventing further cowbird (but not warbler) entry. For category 5, we reduced the entrance-hole diameter to 32 mm before the appearance of the first warbler egg in the nest, thereby preventing cowbird entry. We reduced the size of entrance holes by inserting a piece of cardboard (painted the color of the nest-box) that had a 32-mm hole cut out of it between the outer and inner layers of the front side of the box and centering the smaller hole within the larger.

Nests within the same category were separated spatially by at least three warbler territories (250 m) within a given year and therefore distributed across the entire study area. We sampled/manipulated nesting attempts that were initiated (onset of incubation) during the period from the beginning of the warblers' breeding season (last week of April) through the third week of June. We included nests initiated up to this end date because if they were depredated during the incubation period, cowbirds could still potentially parasitize renesting attempts given the time needed by warblers to initiate renests (build a new nest and lay eggs) and given when the cowbird breeding season ends (3, 10). To reduce any temporal bias, parasitized nests were assigned to categories 1, 3, and 4 in the following way. In order of initiation date, the first six suitable parasitized nests of a season were assigned to categories 3, 1, 4, 1, 3, and 1, respectively, as were the next six parasitized nests, and so on. This sequence was occasionally modified in cases in which nests of the same category were going to be too close together. We assigned fewer nests to categories 4 and 5 because results from previous experiments in our study system showed that nests with a 32-mm opening would not be parasitized (22) and that nest-boxes with this opening size placed on greased poles would almost never be depredated (22, 23). One nesting

attempt was assigned to category 5 approximately every 15 days within each breeding season, again, to reduce any temporal bias.

We were able to document the parasitism status of renests associated with nest-predation events for 20 different pairs of warblers (confined to those that renested in nest-boxes that had openings allowing cowbird entry and that were on greased poles). We then compared the frequency of cowbird parasitism in these nests with suitable nests ($n = 81$) initiated during the same time period that were not renests associated with nest predation. Re-search was approved by the Institutional Animal Care and Use Committee at the University of Illinois at Urbana–Champaign.

1. Payne RB (1977) *Annu Rev Ecol Syst* 8:1–28.
2. Rothstein SI, Robinson SK, eds (1988) *Parasitic Birds and Their Hosts: Studies in Coevolution* (Oxford Univ Press, New York).
3. Hoover JP (2003) *Anim Behav* 65:923–934.
4. Brooke MdeL, Davies NB (1988) *Nature* 335:630–632.
5. Lotem A, Rothstein SI (1995) *Trends Ecol Evol* 10:436–437.
6. Davies NB (2000) *Cuckoos, Cowbirds and Other Cheats* (Academic, London).
7. Davies NB (1999) *Ostrich* 70:71–79.
8. Hosoi SA, Rothstein SI (2000) *Anim Behav* 59:823–840.
9. Hauber ME, Yeh PJ, Roberts JOL (2004) *Proc R Soc London Ser B* 271:S317–S320.
10. Hoover JP, Yasukawa K, Hauber ME (2006) *Anim Behav* 72:881–890.
11. Lotem A, Nakamura H, Zahavi A (1992) *Behav Ecol* 3:128–132.
12. Davies NB, Brooke MdeL, Kacelnik A (1996) *Proc R Soc London Ser B* 263:925–931.
13. Rodríguez-Gironés MA, Lotem A (1999) *Am Nat* 153:633–648.
14. Rohwer S, Spaw DD (1988) *Evol Ecol* 2:27–36.
15. Lotem A (1993) *Nature* 362:743–745.
16. Lawes MJ, Marthews TR (2003) *Behav Ecol* 14:757–770.
17. Zahavi A (1979) *Am Nat* 113:157–159.
18. Soler M, Soler JJ, Martinez JG, Møller AP (1995) *Evolution (Lawrence, Kans.)* 49:770–775.
19. Arcese P, Smith JNM, Hatch M (1996) *Proc Natl Acad Sci USA* 93:4608–4611.
20. Clotfelter ED, Yasukawa K (1999) *Condor* 101:105–114.
21. Lowther PE (1993) in *The Birds of North America*, eds Poole A, Gill F (The Birds of North America, Philadelphia), Vol 47, pp 1–24.
22. Hoover JP (2003) *Anim Behav* 65:935–944.
23. Hoover JP (2003) *Ecology* 84:416–430.
24. Sealy SG (1992) *Condor* 94:40–54.
25. Johnson LS (1998) in *The Birds of North America*, eds Poole A, Gill F (The Birds of North America, Philadelphia), Vol 380, pp 1–32.
26. Kosciuch KL, Parker TH, Sandercock BK (2006) *Behav Ecol* 17:917–924.
27. Scott DM, Weatherhead PJ, Ankney CD (1992) *Condor* 94:579–584.
28. Granfors DA, Pietz PJ, Joyal LA (2001) *Auk* 118:765–769.
29. Stake MM, Cimprich DA (2003) *Condor* 105:348–357.
30. Small SL (2005) *J Field Ornithol* 76:252–258.
31. Elliott PF (1999) *J Field Ornithol* 70:55–57.
32. McLaren CM, Sealy SG (2000) *Auk* 117:1056–1060.
33. Donovan TM, Jones PW, Annand EM, Thompson FR, III (1997) *Ecology* 78:2064–2075.
34. Tewksbury JJ, Hejl SJ, Martin TM (1998) *Ecology* 79:2890–2903.
35. Whitfield MJ (2000) in *Ecology and Management of Cowbirds and Their Hosts*, eds Smith JNM, Cook TL, Rothstein SI, Robinson SK, Sealy SG (Univ of Texas Press, Austin, TX), pp 371–377.
36. Stutchbury BJM (1997) *Wilson Bull* 109:74–81.
37. Hayden TJ, Tazik DJ, Melton RH, Cornelius JD (2000) in *Ecology and Management of Cowbirds and Their Hosts*, eds Smith JNM, Cook TL, Rothstein SI, Robinson SK, Sealy SG (Univ of Texas Press, Austin, TX), pp 357–370.
38. Hauber ME (2000) *J Field Ornithol* 71:389–398.
39. Payne RB, Payne LL (1998) *Behav Ecol* 9:64–73.
40. Rogers CM, Taitt MJ, Smith JNM, Jongejan G (1997) *Condor* 99:622–633.
41. Robinson SK, Hoover JP, Herkert JR (2000) in *Ecology and Management of Cowbirds and Their Hosts*, eds Smith JNM, Cook TL, Rothstein SI, Robinson SK, Sealy SG (Univ of Texas Press, Austin, TX), pp 280–297.
42. Petit LJ (1999) in *The Birds of North America*, eds Poole A, Gill F (The Birds of North America, Philadelphia), Vol 408, pp 1–24.
43. Soler JJ, Sorci G, Soler M, Møller AP (1999) *Behav Ecol* 10:275–280.
44. Rothstein SI (1982) *Am Zool* 22:547–560.
45. Rothstein SI (1986) *Anim Behav* 34:1109–1119.
46. Hoover JP, Reetz MJ (2006) *Oecologia* 149:165–173.
47. Donovan TM, Thompson FR, III, Faaborg J, Probst JR (1995) *Conserv Biol* 9:1380–1395.
48. Robinson SK, Thompson FR, III, Donovan TM, Whitehead DR, Faaborg J (1995) *Science* 267:1987–1990.
49. Faaborg J, Brittingham MC, Donovan T, Blake J (1995) in *Ecology and Management of Neotropical Migratory Birds*, eds Martin TE, Finch DM (Oxford Univ Press, New York), pp 357–380.
50. Hoover JP (2006) *Biol Conserv* 127:37–45.
51. Dufty AM, Jr (1982) *Anim Behav* 30:1043–1052.
52. Darley JA (1983) *Can J Zool* 61:65–69.
53. Rothstein SI, Yokel DA, Fleischer RC (1986) *Curr Ornithol* 3:127–185.
54. Raim A (2000) in *Ecology and Management of Cowbirds and Their Hosts*, eds Smith JNM, Cook TL, Rothstein SI, Robinson SK, Sealy SG (Univ of Texas Press, Austin, TX), pp 87–99.
55. Teather KL, Robertson RJ (1985) *Can J Zool* 63:218–222.
56. Gates JE, Evans DR (1998) *Ecol Appl* 8:27–40.

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