MULTIPLE PARASITISM OF THE RED-WINGED BLACKBIRD: FURTHER EXPERIMENTAL EVIDENCE OF EVOLUTIONARY LAG IN A COMMON HOST OF THE BROWN-HEADED COWBIRD

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ABSTRACT.—We tested whether a common host of the brood parasitic Brown-headed Cowbird (*Molothrus ater*), the Red-winged Blackbird (*Agelaius phoeniceus*), accepts cowbird eggs in its nest because the blackbird does not recognize foreign eggs (evolutionary-lag hypothesis) or because the cost of rejecting eggs or deserting the nest and re-laying exceeds the benefits of egg rejection (evolutionary-equilibrium hypothesis). We reasoned that, if egg acceptance is due to the high cost of rejection, increasing the cost of acceptance should cause the blackbirds to attempt to reject cowbird eggs, or desert the nest and renest elsewhere. We increased the cost of acceptance by adding one, two or three cowbird eggs to Red-winged Blackbird nests, and by removing one host egg for every cowbird egg added. We found no rejection at any level of parasitism. Additionally, we found that Red-winged Blackbirds incubated parasitized clutches that contained none of their own eggs. We conclude that evolutionary lag is the reason for egg acceptance in Red-winged Blackbirds. *Received 23 May 1995, accepted 22 September 1995.*

THE ANALOGY of an "arms race" has frequently been used to describe the evolution of adaptations and counteradaptations in host-parasite systems (Dawkins and Krebs 1979, Davies et al. 1989), including those between obligately brood-parasitic birds, such as cuckoos and their hosts (Davies and Brooke 1988). However, some have criticized this view, claiming that either a short-term dynamic (or even a stable) equilibrium is possible (Rohwer and Spaw 1988, Lotem et al. 1992), or that evolutionary lag occurs (Rothstein 1975a, 1990). These interpretations often grade into one another, and they are not always mutually exclusive. For example, the arms-race analogy implies that there are periods of evolutionary lag before counteradaptations evolve.

The prevailing opinion about the interaction between brood-parasitic Brown-headed Cowbird (*Molothrus ater*) and many of their songbird hosts in western North America is that these hosts lag behind the Brown-headed Cowbird in producing counteradaptations to the former's parasitic habits (Rothstein 1975a, May and Robinson 1985). It has often been claimed that cowbird-egg acceptance is due to the expansion of the range of Brown-headed Cowbirds from the Great Plains to the West in the last 150 years, following the introduction of cattle herds by European settlers, and that there has been insufficient time for counteradaptations to have evolved in the hosts (e.g. Terborgh 1992). However, there is evidence that Brown-headed Cowbirds were present in the Great Basin, Intermountain Region, Arizona, and New Mexico long before then (Rothstein 1994). Indeed, Grinnell (1909) considered the morphological separation of two subspecies—*M. a. artemisiae* and *M. a. obscurus*—in the West to be evidence that Brown-headed Cowbirds had been there long enough for this differentiation to occur.

Host species purported to exhibit lag typically accept 100% of Brown-headed Cowbird eggs laid in their nests (henceforth, "acceptor species"; Rothstein 1975a), while other species reject all Brown-headed Cowbird eggs laid in their nests ("rejector species"). The virtual absence of partial rejection behavior led Rothstein (1975a) to suggest that, once rejection evolves, it should go to fixation in a short time.

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More recently, however, the evolutionary-lag argument for acceptor species has been criticized by Rohwer and Spaw (1988). They found that most acceptor species had significantly smaller bills than rejector species (see also Rothstein 1975b). Those few rejector species that had small bills (within the range of bill sizes of acceptors) were puncture ejectors, rather than grasp ejectors. In other words, species with small bills appeared to be unable to eject Brown-headed Cowbird eggs by grasping them and lifting them out of the nest, and needed to puncture them first. Brown-headed Cowbird eggs have disproportionately thick shells for their size (Blankespoor et al. 1982, Spaw and Rohwer 1987, Weatherhead 1991), possibly preventing small-billed host species from puncture-ejecting them. Rohwer and Spaw (1988) suggested that acceptor species run the risk of puncturing their own eggs when attempting to puncture Brown-headed Cowbird eggs. They further suggested that an evolutionary equilibrium has been reached between Brown-headed Cowbirds and acceptors because the cost of accepting Brown-headed Cowbird eggs is less than the cost of either attempting to eject Brown-headed Cowbird eggs or deserting the nest, building a new nest, and laying a clutch.

We tested the conflicting evolutionary-lag and equilibrium hypotheses using a common host of the Brown-headed Cowbird, the Red-winged Blackbird (*Agelaius phoeniceus*), an acceptor species (Rothstein 1975a). There is no overlap in the color of Brown-headed Cowbird and Red-winged Blackbird eggs; the former have heavy brown speckles with a white ground color, while the latter are blue with occasional brown flecks and squiggles. Thus, acceptance of Brown-headed Cowbird eggs by Red-winged Blackbirds is unlikely a simple effect of inability to recognize similar eggs. This host suffers about 11% parasitism in our study area, the Okanagan Valley, southern British Columbia ($n = 258$ nests; Cannings et al. 1987). This is similar to the 8.9% recorded 100 km further south by Orians et al. (1989, $n = 2,039$ nests). The Brown-headed Cowbird has been considered common in this valley for at least 100 years (Parham 1937, Cannings et al. 1987), a time considered sufficient for a gene coding for an appropriate counteradaptation (e.g. recognition of foreign eggs in the nest) to reach fixation once such a mutation has arisen (Rothstein 1975a). Brown-headed Cowbirds in the Okanagan Valley are morphologically distinct from both subspecies recorded from the West and do not represent a hybrid of these subspecies (Ward and Smith unpubl. manuscript), further suggesting that they have been there for a long time.

Three factors suggest that Red-winged Blackbirds have both had sufficient time to evolve suitable counteradaptations to brood parasitism and that an evolutionary equilibrium between host and parasite is possible:

(1) The range of Red-winged Blackbirds is contiguous with that of the Brown-headed Cowbird over all of North America, even in the Brown-headed Cowbird's ancestral range on the Great Plains (Rothstein 1975a).

(2) They have bills as long as those of many grasp ejectors (Rothstein 1975b, Rohwer and Spaw 1988). Rohwer and Spaw (1988) have claimed that Red-winged Blackbird bills are much narrower than those of most rejector species. They suggest that this narrowness reduces grasp ability (using an index defined as length × [commisural breadth]²), so that they are unable to grasp-eject Brown-headed Cowbird eggs. However, Ortega and Cruz (1988) and Ortega et al. (1993) have recently shown in a series of experiments that Red-winged Blackbirds reject inanimate objects (dowel sticks) of the same size, color and hardness as Brown-headed Cowbird eggs.

(3) Brown-headed Cowbird young are smaller than Red-winged Blackbird young and, therefore, less costly to raise (Ortega and Cruz 1991). Also, in spite of the loss of at least one egg each time they are parasitized (Roskaft et al. 1990), parasitized and unparasitized Red-winged Blackbirds in Colorado may have similar reproductive success because of considerable inherent or environmentally-induced variance in nesting success (Ortega and Cruz 1991). Thus, the cost of acceptance behavior may be relatively small.

We surmised that if acceptance of Brown-headed Cowbird eggs is at equilibrium in Red-winged Blackbirds, an experimental increase in the cost of acceptance should increase the probability of either attempted ejection or nest desertion and renesting (Rothstein 1982, 1986 used a similar argument in studies in eastern North America). To increase the cost of acceptance, we multiply parasitized Red-winged Blackbird nests with two or three dummy Brown-headed Cowbird eggs. Because Brown-headed Cowbirds typically remove one blackbird egg for every

TABLE 1. Responses of Red-winged Blackbirds to experimental multiple parasitism.

No. eggs added	No. clutches	No. rejected
1	11	1
2	9	0
3	10	0
Control	10	0

egg laid (Roskaft et al. 1990), we did this too, further increasing the cost of acceptance. Multiple parasitism is relatively common in natural populations of Red-winged Blackbirds; Orians et al. (1989) recorded 21.2% multiple parasitism in 198 parasitized Red-winged Blackbird nests in central Washington state, whereas Linz and Bolin (1982) recorded 39.4% multiple parasitism in 109 nests in North Dakota. Friedmann (1963) reported that about one-third of all parasitized species' nests get more than two eggs. Hence, multiple parasitism is not a novelty that may never have been selected for.

MATERIALS AND METHODS

Dummy eggs were made of self-set modeling clay (L. A. Reeves Ltd., Downsview, Ontario) to resemble a Brown-headed Cowbird egg. Their reliability as mimics of real eggs was tested on five pairs each of American Robins (*Turdus migratorius*) and Gray Catbirds (*Dumetella carolinensis*), and two pairs of Eastern Kingbirds (*Tyrannus tyrannus*), all rejector species (Rothstein 1975a). All pairs of these three species ejected the dummy eggs.

We used three experimental treatments (one, two or three dummy eggs added and the same number of host eggs removed). Eggs in control nests were handled in a similar manner to experimental nests. Different dummy eggs were used in each replicate to avoid pseudoreplication. Red-winged Blackbird nests were selected at random from three different marshes in the southern Okanagan Valley. Nests were checked two and seven days after the experiment was initiated.

RESULTS

Initially, 55 nests were included in this experiment, but due to predation of some nests in certain treatments, these were excluded from the analysis. All but one pair accepted the dummy Brown-headed Cowbird eggs (Table 1). In the single nest where rejection occurred, one of the birds' own eggs was also ejected. It is not known whether this ejection was conducted by the parents or by a predator.

A further experiment that has been suggested to test the evolutionary-equilibrium hypothesis is to force desertion in parasitized nests and to measure reproductive success in the new nests (Rothstein 1982, Rohwer and Spaw 1988). Under the equilibrium view, renesting possibilities are limited and/or new nests should have lower reproductive success than parasitized nests; hence, acceptance is less costly than desertion. There were only three cases of natural parasitism in Red-winged Blackbird nests in our study area during the experimental period (*n* = 113 nests), so we were unable to test this supposition. However, as a result of our randomized treatment application, we were able to test further the equilibrium hypothesis. Some Red-winged Blackbird nests that were randomly assigned to two or three cowbird-egg supplementation had only as many or fewer of their own eggs in the nest (three nests with two cowbird eggs per nest and four nests with three cowbird eggs per nest). When we removed one host egg for each dummy egg added, these nests had no remaining eggs of their own. It would always be adaptive for these birds to desert and renest. However, none of these birds deserted, even after seven days of incubating dummy eggs only.

DISCUSSION

Our results are consistent with the hypothesis of evolutionary lag. This contrasts with the conclusions of Roskaft et al. (1990). They found that the loss of an egg removed by Brown-headed Cowbirds prior to egg laying is one of the main costs of parasitism for Red-winged Blackbirds. Red-winged Blackbirds cannot recover this loss by rejecting Brown-headed Cowbird eggs. Although their study shows there to be significant residual costs to parasitism that could be avoided by cowbird-egg rejection, Roskaft et al. (1990) considered that rejection behavior has not evolved because a female Red-winged Blackbird risks damaging her own eggs while attempting to eject the Brown-headed Cowbird egg. They base this risk on the demonstration of damage of eggs by Northern Orioles (*Icterus galbula bullocki*) attempting to eject Brown-headed Cowbird eggs in artificially parasitized nests (Rothstein 1977, Rohwer et al. 1989). However,

this comparison is not apposite. Northern Orioles have deep, baglike nests, while Red-winged Blackbirds have open cup-shaped nests; hence, it is considerably more difficult to remove an egg from an oriole nest than from a blackbird nest.

Avoidance of mistaken ejection of a host's own eggs because of overlap in egg coloration is a possible cause of acceptance behavior in two common hosts of the Brown-headed Cowbird in our study area, the Yellow Warbler (*Dendroica petechia*) and the Song Sparrow (*Melospiza melodia*), both of which are acceptor species (Rothstein 1982, pers. obs.). Roskaft et al. (1990) considered mistaken rejection unlikely in Red-winged Blackbirds because of the great difference in appearance between Brown-headed Cowbird and Red-winged Blackbird eggs.

Experiments demonstrating evolutionary lag are necessarily based on negative results. Therefore, it is possible that the results may be construed as being pertinent only to the site where the experiment was conducted. However, there are a number of lines of evidence suggesting that our results are general for the Red-winged Blackbird: (1) Rothstein (1982) found that Red-winged Blackbirds in Connecticut with all of their eggs replaced with Brown-headed Cowbird eggs ($n = 7$ nests) continued to incubate them, as did those with all but one egg replaced by Brown-headed Cowbird eggs ($n = 5$ nests). (2) Ortega and Cruz (1991) found that Red-winged Blackbirds in Colorado artificially parasitized with one ($n = 20$ nests), two ($n = 14$ nests) and three ($n = 15$ nests) Brown-headed Cowbird eggs (host eggs not removed) accepted all Brown-headed Cowbird eggs. (3) Linz and Bolin (1982) found 26 parasitized Red-winged Blackbird nests in North Dakota with no host eggs (42% of 258 nests were parasitized). (4) Facemire (1980) recorded 53% Brown-headed Cowbird parasitism of 17 Red-winged Blackbird nests in Kansas and found that "some" of the parasitized nests contained no host eggs.

The low incidence of natural parasitism during our study is another possible reason why rejection behavior was not observed. We do not believe this to be the case because the long-term level of Brown-headed Cowbird parasitism of Red-winged Blackbirds in the Okanagan Valley is fairly high (11%), and it is well known that the levels of Brown-headed Cowbird parasitism fluctuate greatly from year to year (e.g. annual Brown-headed Cowbird parasitism over

16 years in Song Sparrows on Mandarte Island, British Columbia ranged from 0 to 46%, with a mean of 21.3%; Smith and Arcese 1995). Although no data on temporal variation in parasitism of Red-winged Blackbirds are available, parasitism level in this host species is known to vary considerably over a very small spatial scale (e.g. 0.0 and 52.3% between two marshes about 15 km apart in Kansas; Facemire 1980), which suggests that selection pressures are unlikely to be consistent over time and space. Nonetheless, this temporal and spatial variability in the level of parasitism has not prevented the evolution of rejection behavior in a large number of species (Rothstein 1975a). Indeed, interpopulation variation in rejection behavior has been recorded in American Robins between populations that are allopatric (acceptor) and sympatric (rejector) with Brown-headed Cowbirds (Briskie et al. 1992). We conclude that evolutionary lag is the only appropriate explanation for egg acceptance in the Red-winged Blackbird.

Evolutionary lag may be common, especially in many small songbirds parasitized by Brown-headed Cowbirds (Rothstein 1982, Rothstein and Robinson 1994). For example, Warbling Vireos (*Vireo gilvus*) studied by us in the Okanagan Valley are heavily parasitized by Brown-headed Cowbirds (50–79% of nests parasitized, $n = 87$ nests) and have no surviving young when parasitized. Both Rothstein et al. (1984) in the Sierra Nevada and Cannings et al. (1987) for the Okanagan Valley (prior to 1978) record no surviving young in parasitized Warbling Vireo nests. Under these circumstances, the hosts should always desert the parasitized clutch and renest. None has been recorded doing so (Ward and Smith unpubl. manuscript). Similarly, Rothstein (1982, 1986) recorded Chipping Sparrows (*Spizella passerina*) and Eastern Phoebes (*Sayornis phoebe*) accepting clutches that contained none of their own eggs. Additionally, Hill and Sealy (1994) have shown that Clay-colored Sparrows (*Spizella pallida*) do not respond to cowbird models near the nest, addition of broken eggs to the nest, and changes in clutch composition (combinations of cowbird and sparrow eggs). Nonetheless, they frequently deserted their nests when parasitized (59.1% of occasions), a strategy that has been considered to be best in the face of parasitism when rejection is not possible (Rohwer and Spaw 1988). However, this behavior was found to be

a response to any egg removal rather than parasitism per se. Thus, even in instances where birds may appear to be following a strategy predicted by equilibrium theory, it is necessary to perform experiments to determine whether apparent responses are because of or in spite of the parasite.

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