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REJECTION OF FOREIGN EGGS BY YELLOW-HEADED BLACKBIRDS[1]

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Egg rejection behavior is more likely to develop in avian populations that experience high levels of heterospecific brood parasitism than in populations where parasitism exerts little selection pressure to recognize and respond to foreign eggs (Davies and Brooke 1989, Brown et al. 1990, Soler and Møller 1990 [but see Zuñiga and Redondo 1992], Briskie et al. 1992). Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) are not preferred hosts of the brood-parasitic Brown-headed Cowbird (*Molothrus ater*; hereafter cowbird) and rarely are parasitized (Willson 1966, Ortega and Cruz 1988, Neudorf and Sealy 1994 [Table 1], L. Beletsky and G. Orians, pers. comm.; but see Lincoln 1920).

Consequently, low rates of heterospecific brood parasitism exert little selection pressure on Yellow-headed Blackbirds to recognize parasitic eggs, and individuals from populations with low parasitism rates do not reject nonmimetic eggs placed in their nests (Ortega and Cruz 1988). However, if a population of Yellow-headed Blackbirds were to experience significant amounts of brood parasitism, then one might expect to see evidence of egg rejection.

I investigated this hypothesis in a population of this species that is heavily parasitized (1991: 7/33 nests [21.2%]; 1992: 5/29 nests [17.2%]) by cowbirds (Dufty, in prep.). I noted responses to the presence of foreign eggs by replacing single eggs in Yellow-headed Blackbird nests with an egg of the Red-winged Blackbird (*Agelaius phoeniceus*).

STUDY AREA AND METHODS

I performed this investigation in 1992 in two neighboring abandoned lumber-holding ponds. These ponds, which total approximately 2 ha in size, are located along the Boise River about 8 km east of Boise, Idaho. Breeding habitat for Yellow-headed Blackbirds consisted primarily of cattails (*Typha* spp.) and sedges (*Scirpus* spp.). All nests occurred within the confines of the ponds. Most Red-winged Blackbird nests were located in a narrow (< 8 m wide) canal that ran adjacent to the ponds, although a few were interspersed among the Yellow-headed Blackbird nests.

One Yellow-headed Blackbird egg was collected from each of 19 nests during egg laying as part of another study. These immediately were replaced with a Red-winged Blackbird egg, and the nests were monitored subsequently. The initial purpose of adding *Agelaius* eggs was simply to prevent nest abandonment as a consequence of my egg collection activities. However, when it became apparent that Red-winged Blackbird eggs were disappearing from some of the nests, the data were used to determine whether Yellow-headed Blackbirds accept or reject foreign eggs. I checked nests every 1–2 days (usually daily). Eggs that remained for seven days were considered to have been accepted.

The reaction of Yellow-headed Blackbirds to cowbird brood parasitism could not be assessed because I removed all cowbird eggs immediately upon their appearance, for use in another study.

RESULTS

Four of the 19 artificially-parasitized Yellow-headed Blackbird nests were naturally-parasitized by cowbirds before rejection behavior could be assessed. These nests are not considered in the analysis. Red-winged Blackbird eggs disappeared from 5/15 (33.3%) of the remaining *Xanthocephalus* nests within seven days. No Yellow-headed Blackbird eggs ($n = 41$) were removed from these 15 nests during that same time span. This difference is significant ($P = 0.021$, Fisher Exact test) and suggests that Yellow-headed Blackbirds selectively removed the foreign eggs. Two Red-winged Blackbird eggs disappeared from Yellow-headed Blackbird nests within 24 hr (= day 1), and the other three disappeared on days 3, 5, and 7, respectively.

The four Yellow-headed Blackbird nests that experienced natural brood parasitism by cowbirds are also of interest. In each nest I had replaced first-laid *Xanthocephalus* eggs (= day 1 of laying) with *Agelaius* eggs. Red-winged Blackbird eggs disappeared from three of these nests, indicating that the 33% rejection rate of foreign eggs may be a minimal value; it could be as high as 42% if these latter nests were included. In addition, single Yellow-headed Blackbird eggs disappeared from two of these four naturally-parasitized clutches, which represented the only cases where single eggs disappeared. In one nest, a cowbird egg appeared on day 5, which was the same day that the Red-winged Blackbird egg and one Yellow-headed Blackbird egg disappeared. In the second nest the Red-winged Blackbird egg and one Yellow-headed Blackbird egg disappeared on day 4, and a cowbird egg appeared two days later. In the third, a cowbird egg was deposited on day 3, the Red-winged Blackbird egg disappeared on day 4 or 5, and the entire clutch disappeared on day 6 or 7. In the remaining nest, a cowbird egg was laid on day 3 or 4, and the *Agelaius* egg remained for eight days, whereupon I removed it.

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Finally, one additional clutch of three Yellow-headed Blackbird eggs was parasitized 4–5 days into incubation in conjunction with the disappearance of one egg. I replaced the cowbird egg with a Red-winged Blackbird egg, which was accepted.

DISCUSSION

Yellow-headed Blackbirds in this population removed foreign eggs from their nests. This is a common response to brood parasitism by rejecter species (e.g., Rothstein 1975a, 1976, 1977). However, the selection pressure for egg rejection in this population could arise from one (or more) of three sources.

First, rejection of Red-winged Blackbird eggs could reflect naturally-occurring parasitism by redwings. This is unlikely because, other than the Red-winged Blackbird eggs I placed in Yellow-headed Blackbird nests, no such instances of brood parasitism have been observed by me or, to my knowledge, by anyone else. Similarly, Rothstein (1993) unsuccessfully attempted to induce intraspecific brood parasitism in Red-winged Blackbirds.

Second, the results may represent a response to intraspecific brood parasitism. However, I found no *Xanthocephalus* nests in which two eggs were laid on the same day, the most obvious indicator of brood parasitism. Further, Lyon et al. (1992), in a study designed to examine intraspecific brood parasitism in this species, found no evidence of its occurrence. Thus, intraspecific selection pressures for the development of egg rejection are unlikely to be strong.

Finally, egg rejection may have developed due to brood parasitism by cowbirds. The cowbird parasitism rate of Yellow-headed Blackbirds in this study is much higher than those reported for other populations (see references above), which would provide the selection pressure for the development of egg rejection. Differences in rejection behavior among populations of a species appear to be related to the intensity of brood parasitism experienced by hosts (Brown et al. 1990, Soler and Møller 1990, Rothstein 1990, Briskie et al. 1992). Further, genetic changes associated with the development of rejection behavior in response to brood parasitism may occur within 20 to 100 years (Rothstein 1975b). Such changes would be driven by differences in reproductive success between parasitized and unparasitized Yellow-headed Blackbird nests. Unfortunately, my collection of all cowbird eggs precludes such an analysis at this time.

The critical assumption in this interpretation is that rejection of Red-winged Blackbird eggs indicates similar rejection of cowbird eggs. This appears to be the most parsimonious interpretation of the data, for while cowbird eggs are more similar to Yellow-headed Blackbird eggs in maculation and color markings than are *Agelaius* eggs, cowbird eggs are readily distinguishable (at least by humans) from *Xanthocephalus* eggs. Thus, it seems unlikely that Yellow-headed Blackbirds recognized Red-winged Blackbird eggs as foreign, but would not also recognize cowbird eggs as foreign. Obviously, this interpretation should be verified by determining the fate of cowbird eggs in Yellow-headed Blackbird nests.

Additionally, cowbird eggs are smaller than Red-winged Blackbird eggs (Spaw and Rohwer 1987), which would make them easier to remove by grasp ejection, the principal means of egg removal by hosts (Rohwer and Spaw 1988). Yellow-headed Blackbirds may well be able to remove cowbird eggs by grasp ejection because Red-winged Blackbirds, which are smaller, can grasp-eject objects the size of cowbird eggs (Ortega and Cruz 1988, Ortega et al. 1993). On the other hand, Yellow-headed Blackbird bill characteristics (Dufty, unpubl.) put them within the range of known puncture ejectors (Rohwer and Spaw 1988). In addition, cowbird eggs have thicker eggshells than *Agelaius* eggs (Spaw and Rohwer 1987), which renders the former more difficult to puncture than the latter (Picman 1989).

Finally, experience with cowbirds can alter host behavior within an individual's lifetime (Smith et al. 1984). Although the length of time that this population of Yellow-headed Blackbirds has experienced brood parasitism is unknown, its occurrence may be related to land usage patterns in the immediate vicinity. Extensive urbanization and livestock grazing probably has reduced the availability of preferred cowbird hosts while providing superior cowbird foraging habitat (Dufty, unpubl. data). Thus, a reduced pool of host species may be responsible for the cowbirds' utilization of secondary hosts, such as Yellow-headed Blackbirds.

These egg rejection data contrast with those of Ortega and Cruz (1988), where an extensive investigation of artificial brood parasitism uncovered no evidence of rejection of foreign eggs by Yellow-headed Blackbirds (although this species did reject 4/32 small models of cowbird eggs). However, the population studied by these authors did not experience natural brood parasitism, so selection for egg rejection probably was slight.

Ortega and Cruz (1988) suggested that Yellow-headed Blackbirds would be unlikely to become rejecters even if parasitized, because fledging success in their artificially-parasitized nests was similar to that found in nonparasitized nests. Thus, raising cowbirds would not provide the necessary selection pressure for ejection behavior to evolve (Røskaft et al. 1990). That is, ejection of cowbird eggs would not recover the cost to the host of eggs that the cowbird removed or damaged during laying. Indeed, removal of a parasitic egg could further reduce Yellow-headed Blackbird breeding success through damage to host eggs during the ejection process (Rothstein 1976, Rohwer et al. 1989). On the other hand, if the continued presence of thick-shelled cowbird eggs were to damage host eggs during incubation (Blankespoor et al. 1982, Weatherhead 1991), or if rearing nestling cowbirds reduced the survival and, hence, the lifetime reproductive success of the adult hosts, then ejection behavior could be favored.

The only occurrences of single Yellow-headed Blackbird eggs disappearing from clutches were in nests that received both artificial and natural brood parasitism. It is tempting to speculate that the Red-winged Blackbird eggs, which were added first, were removed by Yellow-headed Blackbirds, and that the Yellow-headed Blackbird eggs were taken by cowbirds. However, I cannot rule out the possibility that both eggs were taken by cowbirds, or that both eggs were removed by Yellow-headed Blackbirds, possibly as a result of damage to a host egg during removal of the foreign egg (Rothstein 1976, Rohwer et al. 1989).

In summary, this study presents the first evidence for egg rejection by Yellow-headed Blackbirds. Although this species is little-used as a host by Brown-headed Cowbirds, I suggest that under conditions where they are exploited yellowheads can develop rejection behavior.

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