Behavioral Defenses Against Brood Parasitism in the American Robin (*Turdus migratorius*)

A Final Report

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ABSTRACT

In response to avian brood parasitism, hosts may develop a number of defenses to reduce the negative consequences parasitism can have on the host's reproductive success. These behaviors may include aggression towards a parasite, rejection of parasitic eggs, or nest desertion. Comparisons of populations that are exposed to parasitism and populations where parasitism is rare or absent may be useful to explain the evolution and maintenance of these behaviors. In a study of American robins (*Turdus migratorius*) living sympatrically and allopatrically with a brood parasite, the brown-headed cowbird (*Molothrus ater*), artificial parasitism and model presentation experiments were performed and the results compared between sites. Robins rejected 100% of artificial cowbird eggs at high and low elevation sites. In addition, there was no significant increase in aggression towards a cowbird model between the sympatric and allopatric sites. These results suggest that the allopatric population is experiencing sufficiently high rates of gene flow in order to maintain rejection behaviors. In addition, aggressive behaviors may not be a significant defense in these birds.

INTRODUCTION

Obligate avian brood parasites do not build their own nests, but lay their eggs in the nests of host species. Brood parasitism can have negative impacts on a host's reproductive success (Marvil and Cruz 1989; Trine et al. 1998). Selection should therefore favor host defenses against brood parasitism. Behaviors can be categorized as anti-parasite defenses if they reduce the negative effects of parasitism on the host and if they evolved in response to the pressures of brood parasitism (Sealy et al. 1998). Some defenses observed include aggression towards the parasite, rejection of parasitic eggs, or nest

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desertion. Host species are categorized as "acceptors", meaning they almost always accept parasitic eggs, or "rejectors" because they nearly always reject the eggs of brood parasites (Cruz and Wiley 1989). Some species show high levels of aggression towards parasites, whereas others show relatively little aggression (Robertson and Norman 1977). Although aggression may be beneficial in that it deters parasitism before it occurs, it can be energetically expensive and dangerous for the host (Cruz et al. 1990).

The potential for parasitism has increased recently in some areas locally. Many brood parasites thrive on forest edges, and fragmentation creates more edges that expose more individuals to parasitism (Robinson et al. 1995; Chace et al. 2000). Studies on host defenses can be useful by providing insights into the coevolution of hosts and parasites. By understanding how defenses evolve and are maintained within populations of hosts, it may be possible to predict the long-term effects of parasitism on new host populations.

Studies on egg rejection in Connecticut and Michigan have shown that American robins (*Turdus migratorius*) are tolerant of eggs that differ from their own eggs by only one character, but reject eggs differing by two or more characters (Rothstein 1982). Host aggression has also been studied in robins. Robertson and Norman (1977) studied robins in Canada and found that one population showed significantly higher levels of aggression towards parasite models than another population.

In addition, studies have been performed to examine the anti-parasitic strategies of populations in sympatry and allopatry with brood parasites (Davies and Brooke 1989; Briskie et al. 1992). Briskie et al. (1992) found that robins in southern Manitoba that were sympatric with brown-headed cowbirds (*Molothrus ater*) exhibited 100% rejection of artificially parasitized eggs. However, in northern Manitoba, where robins are found

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but cowbirds are not, they discovered a 66% rejection rate of artificially parasitized cowbird eggs. Davies and Brooke (1989) found similar results in a study on two hosts of the European cuckoo (*Cuculus canorus*).

The history of host-parasite relationships in Colorado provides an opportunity to perform a similar type of experiment along an altitudinal gradient. In Colorado, cowbirds have historically been associated with bison (*Bison bison*), probably at elevations up to around 3800 m (Chace and Cruz 1998). However, when the bison declined in Colorado in the 1800's, the range of the cowbird presumably contracted and limited them to lower elevations (Chace and Cruz 1998). With the recent establishment of domestic livestock at higher elevations in Colorado, the cowbird's range has likely re-expanded (Chace and Cruz 1998). Records of high altitude parasitism have been reported since after the time of this presumed re-expansion (Chace and Cruz 1998). Thus, robins at higher elevations in Colorado have probably experienced a period of about 100 years free of parasitism, and have only recently come back into contact with parasites in some areas.

The objectives of this study are to compare anti-brood parasite behaviors in a population of a known rejector species, the American robin, living sympatrically with a brood parasite, the brown-headed cowbird, to that of robin populations that have not been exposed to parasitism for at least 100 years. I am testing the following hypotheses:

Hypothesis 1. American robins living sympatrically with brown-headed cowbirds will be less tolerant of artificial parasitic eggs than robins in areas that cowbirds do not inhabit.

Hypothesis 2. Within each population, American robins will accept artificial eggs that mimic their own eggs, and reject eggs that mimic cowbird eggs. In addition, as the

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degree of difference between host and parasite egg increases, rates of rejection will increase.

Hypothesis 3. American robins living sympatrically with brown-headed cowbirds will show higher levels of aggression towards a parasite model than robins in areas cowbirds do not inhabit.

Hypothesis 4. Within the sympatric population, American robins will show higher levels of aggression towards a parasite model than towards a control species model. Within the allopatric population, American robins will show no difference in levels of aggression towards a parasite than towards a control species.

METHODS

Study Species and Sites

I tested anti-parasite defenses of the American robin, a species known to reject the eggs of the brown-headed cowbird (Rothstein 1982; Briskie et al. 1992). Experiments were carried out at three study sites. Two sites were at a low elevation, between 1760 m and 1950 m, on City of Boulder Open Space and Boulder County Open Space. These sites are predominantly ponderosa pine (*Pinus ponderosa*) forests that experience a range of recreational trail use. The other site was at a higher elevation, between 2800 m and 3350 m, at the University of Colorado Mountain Research Station. This site approaches the upper elevational limit of the robin's breeding range.

Experimental Procedures

Two kinds of experiments were performed. The first consisted of artificial parasitism of American robin nests. The second experiment looked at the aggressive

responses of American robins towards a brown-headed cowbird model and a control model.

Artificial Parasitism Experiments

Model Eggs

Experimental parasitism of American robin nests was carried out by placing artificial eggs in the nests. Eggs were either robin sized, "robin blue" in ground color and immaculate to mimic real robin eggs, or cowbird sized, "cowbird white" in ground color and spotted to simulate real cowbird eggs. Artificial robin eggs averaged 28.2 mm x 19.9 mm in size, as compared to an average of 28.1 mm x 20.0 mm for real robin eggs (Harrison 1975). Artificial cowbird eggs averaged 20.5 mm x 16.3 mm in size, as compared to 21.45 mm x 16.42 mm for real cowbird eggs (Harrison 1975). Artificial eggs were constructed of self-set modeling clay, which allowed puncture marks to be detected (Lotem et al. 1995).

All nests were parasitized during the egg-laying stage. One egg was added per nest, and all tests were carried out before 1200. These conditions were intended to mimic the most common occurrences of natural cowbird parasitism (Rothstein 1982).

Criteria for Acceptance/Rejection

Eggs were considered "accepted" if they remain undamaged in a nest for 5 consecutive days (Rothstein 1982; Ortega and Cruz 1988; Cruz and Wiley 1989). Eggs were considered "rejected" if they were ejected or damaged before 5 days, or if the nest was abandoned before 5 days. No nests were predated while eggs remained in the nest, so this did not factor into the results.

Analysis of Parasitism Experiments

I compared rates of rejection between populations using t-tests, with a p-value set at 0.05 for significance. I also compared rates of rejection between cowbird and robin eggs using t-tests.

Response of Hosts to Parasite Model

A female cowbird model was used to assess the aggressive responses of robins to a potential brood parasite. In addition, the song sparrow (*Melospiza melodia*) was used as a control model. This species is similar in shape and size to a cowbird, and it is not novel to either population of robins. The protocol for model presentations followed those outlined in Sealy et al. (1998) and Prather et al. (1999). Observations were made for 5-minute periods. Behaviors recorded included: no visual or audio response to model; distant (outside 5 m) silent observation; close (within 5 m) silent observation; distant alarm calling; close alarm calling; sitting in nest; hovering by the model; physically attacking the model (Robertson and Norman 1977). All experiments were carried out on naive birds at unparasitized nests during incubation.

Analysis of Model Presentation Experiments

The amount of time each focal individual spent performing each of the eight behaviors was totaled for each model presentation. Each of the behaviors was assigned a score as a measure of aggressiveness of that behavior: no response = 1, distant silent observation = 2, close silent observation = 3, distant alarm calling = 4, close alarm calling = 5, hovering by model = 6, sitting in nest = 7, physically attacking model = 8. The total amount of time each individual spent performing a behavior was multiplied by the score for that behavior. These scores were added, yielding a total score of aggressiveness for each individual during each trial. Therefore, a minimum score of 300 and a maximum

score of 2400 were possible. These scores were compared between model species, focal

individual sex, and site using t-tests, with a p-value set at 0.05 for significance.

PRELIMINARY RESULTS

Artificial Parasitism Experiments

Figure 1 summarizes the response of all nests tested at each site. American robins

rejected all artificial cowbird eggs at both the high and low sites (n_{low} = 2, n_{high} = 1). All

cowbird eggs were rejected by means of ejection from the nest within 24 hours of

experimental parasitism. Robins accepted all mimetic robin eggs at both sites (n_{low} = 1,

n_{high} = 1). All artificial robin eggs remained undamaged in the nest for 5 consecutive

days, at which point they were removed.

Model Presentation Experiments

A female brown-headed cowbird model and a female song sparrow model were

presented at seven nests (n_{low} = 5, n_{high} = 2). Figure 2 shows aggressiveness score for

cowbird and control presentations at all nests tested. Robins at low elevation sites

yielded an average aggression score of 1563.6 for the cowbird and 1376.2 for the song

sparrow. At the high elevation site, robins scored 1707 on average while exposed to the

cowbird and 2048.75 while exposed to the song sparrow. Robins were not significantly

more aggressive towards cowbirds than towards the control at either site ($p > 0.05$). There

was no significant difference in aggressiveness at high and low sites for either the

cowbird or the control models ($p > 0.05$). Females were on average more aggressive

towards the models than males, scoring 947 (cowbird) and 787.6 (sparrow) on average at

the low sites and 858 (cowbird) and 1108.25 (sparrow) on average at the high elevation

site, compared to males' average score of 616.6 (cowbird) and 588.6 (sparrow) at the low

sites and 849 (cowbird) and 940.5 (sparrow) at the high site. However, these trends were also not significant (p>0.05).

DISCUSSION

The results of the experimental parasitism experiments suggest that there is no difference in rejection rates of parasitic eggs between sites where parasitism is present and sites where parasitism is absent or rare. This might be explained in a few ways.

First, because robin and cowbird eggs are considerably different in size, ground color and maculation, robins should be expected to be more tolerant of cowbird eggs due to the costs involved in incorrectly rejecting one's own eggs.

Second, there may be sufficiently high rates of gene flow between the populations of robins, which would result in the maintenance of "rejector genes" in the high elevation population. Briskie et al. (1992) hypothesized that egg rejection in an unparasitized population of robins in Canada may have been due to gene flow between that population and populations farther to the south where parasites are found. Briskie et al. (1992) used study sites that were separated by around 500 km, whereas the sites in this study are no more than 50 km apart. Because the sites are in such close proximity to one another, gene flow between populations would probably become more likely.

Third, although most researchers feel that egg discrimination behavior probably evolved as a specific response to brood parasitism, some researchers have proposed that rejection is a generalized response to removing foreign objects from the nest. Marchetti (2000) showed that in yellow-browed leaf warblers (*Phylloscopus humei*), egg discrimination behavior was based not on the host's recognition of its own eggs, but

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rather a comparison of all eggs in the nest and removal of eggs that deviate from the majority of the other eggs.

Another explanation is that brood parasitism is more common at the high elevation site than originally thought. Although it is known that brown-headed cowbirds parasitize hosts in other areas at 3000 m and above (Chace and Cruz 1998), cowbirds at the high elevation site are extremely rare, compared to quite common at the low elevation sites (pers. obs.). In any case, it is difficult to determine trends in egg rejection because of the extremely low sample size. Briskie et al. (1992) found rejection rates of 66% in unparasitized populations of robins, which suggests that some rejection would be expected at the high elevation site as seen here.

In addition, these results suggest that the artificial eggs used in these experiments are suitable to be used to assess response to egg size, shape and color, as all artificial robin eggs were accepted. Therefore, the hosts were not responding to qualities of the egg related to composition or construction; that is, they were not rejecting the eggs simply because they were artificial.

Model presentation data from these experiments implies similar conclusions as the artificial parasitism experiments, which is to say that there was no difference in defensive behaviors between the low elevation and high elevation sites. The data also suggest that aggressiveness toward parasites is not a significant defense for American robins due to the fact that no significant difference was observed between the parasite and control presentations. In fact, a recent study suggested that host aggression may not be an effective method against parasitism (Olendorf and Robinson 2000), and others have noted that American robins seem to be less aggressive towards cowbirds in general as

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compared to other species (Robertson and Norman 1977; Briskie et al. 1992). In addition, some studies have found that aggressiveness towards cowbirds may be higher earlier in the breeding season when parasitism is occurring more frequently (Briskie and Sealy 1989; Hobson and Sealy 1989). This may explain these results because this study was conducted later in the breeding season. The difference in aggressiveness between male and female robins, although not significant, was apparent during the observation periods. This difference is most likely due to the fact that females are more likely to be present at the nest than males during the incubation stage (pers. obs.). This may present difficulty when analyzing the data. Although females may spend more time at the nest, and therefore generate a higher score of aggressiveness, true aggressiveness of the males may be underrepresented because males arrive at the nest after the observation has begun.

FUTURE WORK

More trials of artificial parasitism and model presentation experiments need to be conducted in order to gain a more accurate picture of anti-parasite defenses of these birds. This project will be continued in the upcoming field season with some additions to and modification of the methodology.

Artificial Parasitism Experiments

Experimental parasitism of American robin nests will be performed in the upcoming field season, as described in the methods section above. In addition to cowbird and robin eggs, other combinations of egg color, spotting pattern, and size will be used in order to assess the relative importance of these characteristics in eliciting a rejection response. Three sizes will be tested to simulate robin and cowbird sized eggs, as well as an intermediate size. Eggs will be "robin blue" or "cowbird white" in ground color, and

immaculate or spotted to simulate the maculation of real cowbird eggs. 12 possible combinations of model eggs are therefore possible (Table 1).

Increasing the sample size will provide an opportunity for more accurate rates of rejection to be established. Coordination of work between sites based on timing of breeding is important. Robins at lower elevations were observed building nests by the beginning of May, and frequently renest. However, at the higher elevation site, robins were not seen nesting until mid-June and probably had only one clutch. Spending sufficient time early in the season at the lower elevation sites and moving to the higher elevation site in the middle of the season should maximize the sample size.

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Site	Egg model used	First Day Criteria	Full Acceptance Criteria
Heil Ranch (low elevation)	CWS (cowbird size, cowbird white, spotted)	Reject	n/a
Heil Ranch (low elevation)	CWS	Reject	n/a
Heil Ranch (low elevation)	RBI (robin size, robin blue, immaculate)	Accept	Accept
Mt. Research Station (high elevation)	CWS	Reject	n/a
Mt. Research Station (high elevation)	RBI	Accept	Accept

Figure 1. Summary of artificial parasitism experiments at low elevation and high elevation sites.

Site	Models presented	Total aggressiveness - BHCO, female + male (female, male)	Total aggressiveness - SOSP, female + male (female, male)
Heil (low elevation)	BHCO, SOSP	1345 (404, 941)	834 (534, 300)
Heil (low elevation)	SOSP, BHCO	1887 (1204, 683)	1276 (440, 836)
Heil (low elevation)	BHCO, SOSP	942 (642, 300)	600 (300, 300)
Heil (low elevation)	BHCO, SOSP	2339 (1480, 859)	2403 (1196, 1207)
D-3 (low elevation)	SOSP, BHCO	1305 (1005, 300)	1768 (1468, 300)
Mt. Research Station (high elevation)	SOSP, BHCO	1489 (736, 753)	1498 (1198, 300)
Mt. Research Station (high elevation)	SOSP, BHCO	1925 (980, 945)	1891 (843, 1048)

Figure 2. Summary of aggressiveness towards parasite and control models at low elevation and high elevation sites (BHCO = brown-headed cowbird (*Molothrus ater*), SOSP = song sparrow (*Melospiza melodia*))

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Model Egg (size, ground color, maculation)	Number of Differences
Robin size, blue, immaculate (robin egg)	0 – (control)
Robin size, blue, spotted	1
Robin size, white, spotted	2
Robin size, white, immaculate	1
Intermediate size, blue, immaculate	1
Intermediate size, blue, spotted	2
Intermediate size, white, spotted	3
Intermediate size, white, immaculate	2
Cowbird size, blue, immaculate	1
Cowbird size, blue, spotted	2
Cowbird size, white, spotted (cowbird egg)	3
Cowbird size, white, immaculate	2

Table 1. Description of model eggs and the number of differences from an American robin egg.