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RESEARCH ARTICLE

Brood Parasitism Defense Behaviors Along an Altitudinal Gradient in the American Robin (*Turdus Migratorius*)

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Abstract: Some host species accept eggs from brood parasites over parts of their range and reject them in other areas representing an “evolutionary lag” in the development of rejection behavior or the loss of an adaptive behavior when the selection pressure of brood parasitism is removed. Hosts may deter brood parasitism through egg rejection and aggressive nest defense behavior specifically targeting female brood parasites during the egg incubation period. In areas where parasitism frequencies are spatially and temporally variable, anti-parasite behaviors may decline as costs outweigh the benefits. Along the Colorado Front Range, American robins (*Turdus migratorius*) breed from low elevations where the brood parasitic Brown-headed Cowbird (*Molothrus ater*) is abundant to near timberline (3700 m) where cowbirds are uncommon. We tested the hypothesis that egg rejection and nest defense behaviors decline with reduced probability of parasitism. We found that robins accepted 100% of immaculate (robin-like) experimental eggs at both low and high elevations, but were more likely to reject spotted (cowbird-like) experimental eggs at low elevations than high elevations. Response to egg size was more variable than to egg color. When presented with a mount of a cowbird and Song Sparrow (*Melospiza melodia*) near the nest, robins responded more aggressively to cowbird models than to sparrows (control), and nest defense behavior towards cowbirds was longer and more aggressive at the lower elevation sites where cowbirds are common. These results suggest that egg rejection and nest-site aggression are costly adaptations to cowbird parasitism, and these behaviors decline when the threat of parasitism is reduced.

Keywords: American Robin, Brood parasitism, Brown-headed Cowbird, Experimental parasitism, *Molothrus ater*, Nest defense, *Turdus migratorius*.

INTRODUCTION

The Brown-headed Cowbird (*Molothrus ater*) is an obligate brood parasite [1 - 3]. Females do not build their own nests, but lay their eggs in the nests of host species, who often raise young cowbirds to the detriment of their own young [4 - 7]. Selection should favor anti-parasite defenses that reduce the negative effects of parasitism on the host [8], such as aggression towards the parasite [9 - 11], rejection of parasitic eggs [2, 12 - 15], and nest desertion [16, 17].

The least costly anti-parasite behavior is aggressive nest defense. Aggression towards cowbirds can vary across a population, where sympatric hosts may be more aggressive towards cowbirds than allopatric species [18], but see [8]. Even at low levels of parasitism, aggression around the nest should be favored by selection when it reduces the costs of nest predation and parasitism [8, 11, 19].

“Rejecters” are potential host species that almost always (< 75%) reject the eggs of brood parasites [2, 20]. Hosts may accept cowbird eggs because cost of egg rejection, *e.g.*, a host accidentally rejecting or damaging their own eggs is greater than the cost of acceptance, *e.g.*, reduced reproductive output [21 - 24]. Smaller hosts with bill-size constraint may not be able to effectively remove a parasitic egg without puncture ejection, a process more likely to damage host

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eggs [25 - 27]. Assuming that rejection is almost always advantageous, some acceptor species have not had enough time to develop the ability to recognize a foreign egg [19] and remove it from the nest [28 - 31].

Anti-parasite responses by potential hosts can vary in sympatry and allopatry with brood parasites [18, 28, 29, 32 - 34], and in some cases defensive behaviors may decline under reduced parasitism pressure [20], but subsequent work by Lahti [35] and Cruz *et al.* [34] found high levels of rejection of nonmimetic eggs. Even when parasitism is rare or absent, anti-parasite egg rejection behavior persists in a population when rejection costs are small [29, 33, 36 - 38].

In Colorado, cowbirds have historically been associated with bison (*Bison bison*) from the Great Plains west to elevations around 3800 m and into the mountain parks of central Colorado [39]. However, when bison declined in Colorado in the 1800's the range of the cowbird presumably contracted and was limited to lower elevations, only to reexpand following the establishment of domestic livestock at higher elevations [39]. Thus, potential cowbird hosts breeding at higher elevations may be experiencing an increase in parasitism rates after a period of little or no parasitism.

The American Robin (*Turdus migratorius*) is a known cowbird egg rejector species [2, 15, 18, 19, 25]. The geographic distribution of cowbirds and robins in Colorado provided an opportunity to perform an experiment to test how defenses are modified in the absence of parasitism. The breeding range of robins in Colorado occurs from the riparian forests in the grasslands to timberline [40]. Cowbirds breed across a wide elevational range as well, but because of the distribution of cattle cowbirds probably do not parasitize frequently above 2400 m [39]. Here, we compare anti-brood parasite behaviors in robins, breeding sympatrically with cowbirds at lower elevations to that of a population that experiences little exposure to cowbirds at higher elevations.

METHODS

Study Area

Experiments were conducted during June and July, 2000-2002 in Boulder County, Colorado, at two distinct elevational locations of five subsites (Fig. 1). Robin nests were located in two low elevation forests, between 1760 m and 1950 m, of foothill ponderosa pine (*Pinus ponderosa*) primarily on Heil Ranch on Boulder County Open Space but also with City of Boulder Open Space, and in the three high elevation forest sites, between 2600 m and 3350 m, of montane lodgepole pine (*Pinus contorta*) and Englemann spruce (*Picea engelmannii*) forests primarily at the University of Colorado's Mountain Research Station, and also on Boulder County Open Space properties Caribou Ranch and Mud Lake. These three latter sites approach the upper elevational limit of the breeding range of the American Robin in Colorado [41]. Cowbirds were seen and heard daily at the lower elevation sites while at the high elevation sites only one male cowbird was seen at the Mountain Research Station, and male and female cowbirds were seen infrequently at Caribou Ranch and Mud Lake.

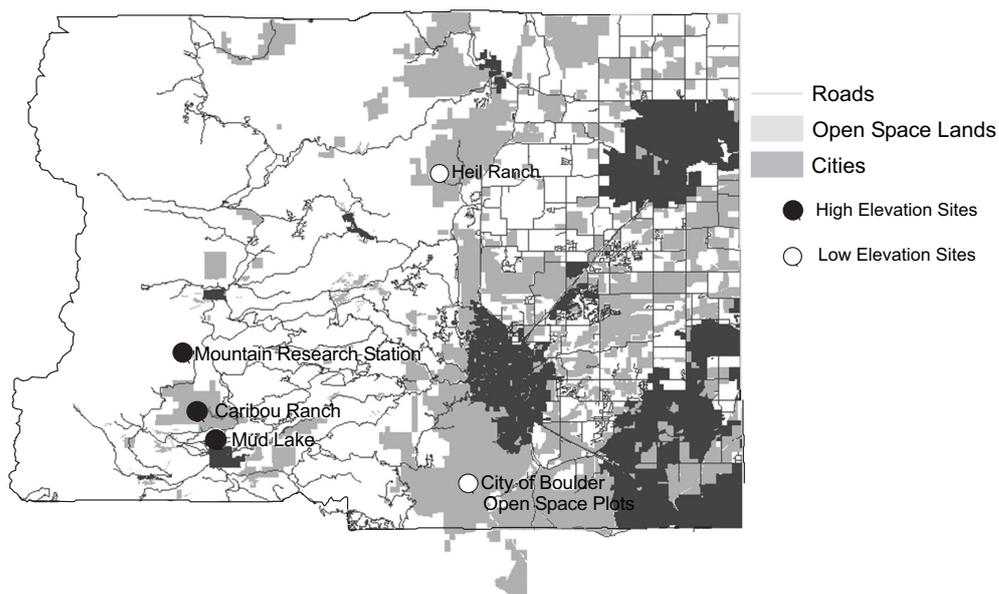


Fig. (1). Study sites in Boulder County, Colorado. Map produced using data Copyright 2001, County of Boulder, Colorado.

Experimental Parasitism

Experimental parasitism was carried out by placing artificial eggs in active robin nests. Robin and cowbird eggs differ in size, ground color, and spotting pattern. Robin eggs are larger than cowbird eggs, blue in ground color as opposed to off-white, and immaculate rather than heavily spotted. By manipulating these characteristics, we tested artificial egg types across a gradient from a robin egg to a cowbird egg (Table 1, Fig. 2). Robin-sized eggs (R), were blue immaculate (RBI), blue spotted (RBS), white immaculate (RWI) or white spotted (RWS), while cowbird-sized eggs (C): were blue immaculate (CBI), blue spotted (CBS), or white spotted (CWS). Small, immaculate, white eggs (CWI) were not tested because of their resemblance to fecal sacs, which may elicit rejection for other reasons.

Table 1. Description of artificial egg types used in experimental parasitism experiments. The abbreviation used for each egg type and the number of character differences between an American robin egg and a brown-headed cowbird egg are noted.

Egg Types (Size, Color, Spotting)	Egg Type Abbreviation	Number of Differences
Robin, Blue, Immaculate [†]	RBI	0
Robin, Blue, Spotted	RBS	1
Robin, White, Immaculate	RWI	1
Cowbird, Blue, Immaculate	CBI	1
Robin, White, Spotted	RWS	2
Cowbird, Blue, Spotted	CBS	2
Cowbird, White, Spotted [‡]	CWS	3

[†] mimetic robin egg.

[‡] mimetic cowbird egg.



Fig. (2). Photograph showing artificial eggs used for experimental parasitism of American robins nests. Egg types from left to right (size, ground color, spotting pattern): RBI, RBS, CBI, RWI, RWS, CBS, CWS.

Experimental robin egg mimics were tested to ensure that eggs were not rejected based on the artificial qualities of the eggs. Experimental eggs were constructed of self-set Sculpey™ modeling clay, which allowed puncture marks to be detected [36]. Eggs were shaped from either white or “robin’s-egg” blue clay. “Turquoise” and “mint” colored clays were mixed to create a blue that matched a robin’s egg. Spotting was created by using acrylic paints in burnt umber and medium gray in a pattern that resembled natural cowbird eggs. Eggs were then placed in a 93°C oven for 10 min to harden slightly, yet they remained soft enough so that puncture marks could be detected. Finally, the eggs were coated with a waterproof varnish that protected the paint and gave the eggs a slight sheen.

Artificial eggs were within the natural range of egg-size variation. Robin-sized eggs averaged 28.0 mm in length and 20.5 mm in width, and weighed 6.9 g (n=16). Natural robin eggs average 28.1 mm in length and 20.0 mm in width [42, 43], and weigh 6.3 g [44]. Artificial small, cowbird-sized eggs averaged 21.2 mm in length and 16.8 mm in width, and weighed 2.8 g (n=14). Natural cowbird eggs average 21.4 mm in length and 16.4 mm in width [42, 43] and weigh 2.4 g [45]

As part of a larger study, robin nests when found were experimentally parasitized with one of the seven possible egg types (Fig. 2) between June 19 and July 18, 2000 (n = 5), May 20 and July 9, 2001 (n = 9), and May 14 and July 1, 2002

(n = 16). Artificial eggs were added to 15 nests at the low elevation sites, all in Heil Ranch, and 15 nests at the high elevation sites but predominately on the Mountain Research Station property (n= 11). In total, two of each artificial egg types (RBI, RBS, RWI, RWS, CBI, CBS) and three of CWS egg type (Fig. 2) were added to robin nests at each elevation. All nests were experimentally parasitized during the final egg-laying phase (when clutch was complete) or early incubation stages of nesting. During experimental parasitism one of the artificial eggs (Fig. 2) was added per nest before 1200 h. No robin eggs were removed from the nests when the artificial eggs were added, although that is common during natural parasitism [45]. Several studies have found that rates of egg rejection do not differ when host eggs are removed during experimental parasitism and when they are not [26, 28, 33, 46 - 48]. Nests were monitored the following day for evidence of acceptance or rejection, and then on the fifth day after the experimental parasitism.

Criteria for Acceptance/Rejection

Two criteria for acceptance were used. Nests were checked approximately 24 hours after experimental parasitism, which was considered the “first-day criterion” (FDC) for rejection [19]. If the eggs remained after one day, the nests were re-checked at five days for the “full-acceptance criterion” (FAC) [19]. Eggs were considered accepted if they remained undamaged in a nest at the time of inspection [19, 20, 49]. Eggs were considered rejected if they were ejected from the nest, damaged, or if the nest was abandoned at the time of inspection.

Analysis of Parasitism Experiments

Rates of egg rejection within and between populations were compared using Fisher’s exact probability tests. For these comparisons, eggs were grouped by size (cowbird vs. robin sized) and coloration (immaculate or spotted).

Nest Defense

Response of Hosts to Parasite Model

A taxidermic mount of a female cowbird was used to assess the aggressive responses of robins to a potential brood parasite. In addition, a Song Sparrow (*Melospiza melodia*) model was used as a control. The Song Sparrow is similar in shape and size to a cowbird, it is a common breeder in all robin study sites, and poses no threat of predation or parasitism. The mounts were attached to the end of a telescopic pole, which allowed them to be positioned next to nests.

The protocol for model presentations followed those outlined by Sealy *et al.* [8] and Prather *et al.* [10]. Observations were made for 5-minute periods. Behaviors recorded included: no detectable response to the model; distant (greater than 5 m from the model) silent observation; close (less than 5 m from the model) silent observation; vocalization; alarm calling; sitting in the nest; physically attacking the model [9]. High-pitched calls or screams directed towards the model were considered alarm calls [8]. Other calls or chips were considered vocalizations. The duration of each behavior was recorded in seconds.

Hosts sitting (“cupping”) in their nests in response to a parasite has been described as an anti-parasitic defensive behavior [8, 18, 50, 51]. Instances of “nest-protection behavior” was scored as “sitting in nest” because the intent could not be determined.

Models were presented at 14 nests at the low elevation sites (Heil Ranch n =13, Boulder Open Space = 1) and 11 nests at the high elevation site (Mountain Research Station n = 10, Caribou Ranch n = 1), between June 20 and July 19, 2000 (n = 13), May 20 and July 9, 2001 (n = 7), and June 18 and July 2, 2002 (n = 5). All observations were carried out once per nest at unparasitized nests during incubation. Both models were each presented once to each nest in random order, sequentially with at least 20 minutes between observations on the same day. Models were presented during the incubation phase of the robin nesting cycle. Because some nests were located after incubation had begun, it was not possible to control for the time since initiation of incubation. However, Knight and Temple [52] reported that aggressive behaviors of robins did not change significantly over the course of the incubation stage of nesting. The models were placed approximately one m from the nest level with the nest edge. Models were set in position while the focal pair was away from the nest to decrease the effects of aggression towards the observer. At least 20 minutes was allowed between presentations to minimize the effects of carry over aggression and habituation to the models [10, 53]. Presentations were video taped and later reviewed.

Analysis of Model Presentation Experiments

Because the behavior of male and female robins was noticeably different during the incubation stage of nesting,

only the behaviors of females were analyzed. Females were more likely to be present during the model presentation, and in many cases the male was not seen during the entire observation.

Behaviors were grouped into three categories: non-aggressive, mildly aggressive, or strongly aggressive [10]. No response and distant silent observation were categorized as non-aggressive; close silent observation, vocalization were classified as mildly aggressive; and alarm calling and physically attacking the model were classified as strongly aggressive. Because behavioral data were not normally distributed, nonparametric tests of variance were performed using JMP11.0 (SAS Institute) to determine if there were significant within and between site differences in time females spent responding non-aggressively, mildly aggressively, and strongly aggressively towards the parasite and control models. One-way Wilcoxon two-sample tests with Bonferoni corrections were used to statistically compare differences in robin responses to sparrow and cowbird models as well as differences to cowbird models between low and high elevation sites.

RESULTS

Experimental Parasitism

There were no cases of nest desertion in response to artificial parasitism. No eggs that remained in the nest, either at one day or five days, appeared to have been damaged. No experimentally parasitized nests were preyed upon while artificial eggs were in the nest.

Differences Between Populations in Rejection Rates

Cowbird-sized eggs were more likely to be rejected at both elevations than robin-sized eggs; however there were no significant differences in rejection rates based on egg size (Table 1). Cowbird-sized eggs were equally likely to be rejected after five days at high and low elevation sites (one-tailed Fisher’s Exact test, $P < 0.05$; Table 2).

Table 2. Summary of results of artificial parasitism experiments. First Day Criterion (FDC) represents egg rejection status after one day; and Full Rejection Criterion (FAC) represents egg rejection status after 5 days.

Egg Parameter	LOW			HIGH		
	<i>n</i>	FDC	FRC	<i>n</i>	FDC	FRC
<i>Size</i>						
Cowbird Size	7	5	5	7	2	2
Robin Size	8	1	2	8	0	0
<i>Coloration</i>						
Spotted	9	6	7	9	2	2
Immaculate	6	0	0	9	0	0

All immaculate, mimetic robin, eggs, were accepted for five days at both the high and low elevation sites (Table 2). Spotted eggs were rejected more often than immaculate eggs at low elevation sites (one-tailed Fisher’s Exact Test, $P < 0.05$), while there was no significant difference in rejection rates at high elevation sites (Table 2). Rejection rates of spotted eggs was higher at low elevation sites than high elevation sites (one-tailed Fisher’s Exact Test, $P < 0.05$; Table 2).

Conspecific Brood Parasitism

No evidence was found of conspecific brood parasitism at either the high or low elevation sites. Of 52 nests monitored and/or experimented, no instances of gaps in the egg laying cycle, multiple eggs appearing on one day, or abnormally high clutch sizes were observed.

Nest Defense

Within Sites Comparisons

At the low elevation sites, female robins ($n = 14$) spent nearly significantly (adjusted alpha = 0.008) more time responding non-aggressively to the sparrow model than towards the cowbird model ($Z = 3.8385$, $df = 1$, $P = 0.05$). However, there was no significant difference between mildly aggressive or strongly aggressive behaviors directed towards the cowbird or sparrow models (Tables 3 and 4).

Table 3. Response times (s) (mean ± S.E.) of female American Robins to Brown-headed Cowbird and Song Sparrow models at low and high elevation sites (n_{low}=14 nests; n_{high}=11 nests) for each behavioral category. P values * P < 0.05, * P < 0.01, * P < 0.001.

Behavior [†]	Low			High			
	Cowbird	Sparrow	P ^a	Cowbird	Sparrow	P ^b	P ^c
Non-Aggressive	61.4 ± 26.5	152.4 ± 36.3	*	185.3 ± 35.9	121.1 ± 35.7	NS	*
Mildly Aggressive	135.6 ± 29.7	71.9 ± 23.7	NS	96.7 ± 30.9	99.4 ± 27.0	NS	NS
Strongly Aggressive	93.5 ± 29.9	60.5 ± 30.6	NS	16.4 ± 7.4	51.3 ± 24.5	NS	*

[†]Time spent performing behavior during 5-minute trials

^aComparisons between models within low elevation sites.

^bComparisons between models within high elevation sites.

^cResults of multiple comparisons among cowbird model presentations between sites.

Table 4. Responses (seconds) (mean ± S.E.) of female American robins to brown-headed cowbird and song sparrow models at low and high elevation sites (n_{low}=14 nests; n_{high}=11 nests) for each behavior.

Behavior [†]	Low		High	
	Cowbird	Sparrow	Cowbird	Sparrow
No Reaction	20.0 ± 14.4	88.1 ± 33.3	128.8 ± 42.0	60.4 ± 29.3
Distant Silent Observation	41.4 ± 25.0	64.3 ± 29.4	56.4 ± 27.5	60.7 ± 27.5
Close Silent Observation	107.1 ± 31.7	52.9 ± 23.4	83.9 ± 30.6	91.3 ± 26.5
Distant Alarm Call	28.6 ± 14.4	19.1 ± 13.2	11.9 ± 6.3	4.9 ± 3.2
Close Alarm Call	85.3 ± 30.3	60.5 ± 30.7	16.5 ± 7.4	51.3 ± 24.5
Attacking Model	8.2 ± 8.1	0 ± 0	0 ± 0	0 ± 0

[†]Time (seconds) spent performing behavior during 5-minute trials

At the high elevation sites, female robins (n = 11) spent statistically equal time in all three aggressive behavioral categories towards sparrow and cowbird models. There was no significant difference between female robins' behaviors directed towards either the cowbird or sparrow models (Tables 3 and 4).

Between Sites Comparisons

Female robins spent significantly more time responding non-aggressively to the cowbird model at the high elevation sites than at the low elevation sites (Tables 3 and 4). There was a nearly significant difference (adjusted alpha = 0.02) in time female robins spent performing strongly aggressive behaviors towards the cowbird model at the high and low elevation sites (Z= 4.0721, df = 1, P = 0.044; Table 3).

DISCUSSION

Egg Rejection

The results of experimental parasitism suggest that differences exist between the high and low elevation sites in regards to egg recognition and rejection. While mimetic robin eggs and eggs that deviated from robin eggs by only one character were accepted at both the high and low elevation sites, cowbird eggs were rejected less frequently at the high elevation sites than at the low elevation sites.

Similar to Rothstein's [19] findings that that size is relatively more important than color or spotting pattern in eliciting an early rejection response, our study found that robins were likely to reject smaller eggs at the low elevation sites (Table 2). Smaller eggs may be rejected more quickly because the size difference can be detected by the host through tactile perception [19]. We also detected a possible "threshold effect" for egg rejection in robins at the low elevation sites, similar to the results of Rothstein [19], where only eggs that differed by two or more parameters were rejected. "Runt eggs" (substantially smaller) have been reported to occur frequently in robins, and white or spotted eggs are reported to occur rarely [44]. However, the probability of two of these abnormalities occurring simultaneously in any egg is very low, and so a threshold of two differences for rejection minimizes rejection errors.

The results of the parasitism experiments suggest that while some differences exist in rejection rates of cowbird eggs between sites where cowbirds are present and sites where cowbirds are absent or rare, the majority of cowbird eggs were rejected at both sites. This might be explained in a few ways.

First, robins may have retained egg recognition abilities over the period of time in which cowbirds have been absent. If this were the case, it would support the evolutionary lag hypothesis for acceptance *versus* rejection that suggests that once egg rejection appears in a population, it will remain unchanged. Retention of egg rejection would indicate that the costs of egg rejection behavior are sufficiently small such that the behavior can be retained at essentially no cost to the host [33, 38].

A second explanation is that brood parasitism is more common at the high elevation site than originally thought. This explanation seems unlikely, even though it is known that cowbirds parasitize hosts in other areas at 3000 m and above [39]. Although the nests of other host species were not monitored to estimate overall rates of cowbird parasitism at the high elevation sites, cowbird sightings at the high elevation sites were infrequent, as compared to sightings being common at the low elevation sites (pers. obs.). It is therefore unlikely that parasitism occurred commonly in the absence of observed adult parasites.

Third, there may be sufficiently high rates of gene flow between the populations of robins, which would result in the maintenance of “rejecter genes” in the high elevation population. Briskie *et al.* [18] hypothesized that egg rejection in an unparasitized population of robins in Canada may have been due to gene flow between that population and others farther to the south where brood parasites are found. The study sites of Briskie *et al.* [18] were separated by around 500 km, whereas the sites in this study are no more than 25 km apart along an altitudinal gradient. Because the sites are in such close proximity to one another, gene flow between populations is likely.

Even though gene flow may occur between populations, differences may still exist. A parasitized populations reed warblers (*Acrocephalus scirpaceus*) in England often reject parasitic Common Cuckoo (*Cuculus canorus*) eggs, while other unparasitized populations accept parasitic eggs [54]. The unparasitized populations in England were separated from parasitized populations by no more than 80 km [54]. It seems likely that egg rejection is a plastic trait in these populations. Because parasitism by cuckoos is variable across these habitats, it benefits individuals to express rejection facultatively based on perceived costs of rejection [34, 54, 55].

Although robins seem to have retained the ability to recognize foreign eggs, in that the high elevation robins rejected two of three cowbird eggs, their rejection response appears to have been relaxed. Relaxation of rejection behaviors in the absence of the selective pressures of parasitism suggests that there is some cost to egg rejection. These costs must be sufficient enough [56] to favor a reduced rate of egg rejection or increased tolerance of foreign eggs. If egg rejection is lost or relaxed in the absence of parasitism, then the equilibrium hypothesis for the evolution of egg rejection behavior is supported. The opposing hypothesis, evolutionary lag, suggests that once egg rejection appears in a population, it will remain unchanged because the costs of rejection are insignificant [33]. If egg recognition errors occur at nests of unparasitized populations, acceptance would be favored because these costs would outweigh the nonexistent benefits of rejection. While some studies have found that rejection errors in unparasitized populations can be costly enough to favor acceptance [23, 37, 57], other studies suggest that these costs are negligible [33]. Ejection costs for American robins have been estimated from 0.03 to 0.08 host eggs lost per ejection [25, 58], an average cost of ejection for grass-ejectors (0.06 host eggs lost per ejection) [58].

Relaxation of egg discrimination in the absence of parasitism suggests that rejection costs may not be negligible for unparasitized populations and sufficient to cause an increased tolerance towards foreign eggs in areas where parasites are absent. Similar to robins in this study, gray catbirds (*Dumetella carolinensis*) in Bermuda, where no brown-headed cowbirds are present, have demonstrated some degree of increased tolerance in the absence of parasitism [33, 38].

Egg rejection may function as a plastic behavior in robins. Robins at the high elevation sites rejected the majority of cowbird eggs, suggesting that the majority of robins can recognize parasitic eggs. The evolution of egg rejection behavior may involve the ability to recognize one’s own eggs, as well as the decision to reject odd eggs [29]. In the absence of parasitism, hosts need not lose their ability to reject eggs altogether. Instead, they may relax their discrimination against foreign eggs [33, 34], as was found in this study. Phenotypic plasticity of egg rejection behavior suggests that parasitized and unparasitized populations are equally able to recognize parasitic eggs, but that differences exist in decisions to reject those eggs [34, 54]. If cowbirds are rare or absent, as at the high elevation site, then selection would favor minimizing the costs of rejection and increasing the tolerance of foreign eggs.

Although rejection may be acting in a plastic manner, we cannot rule out the possibility that robins may have retained egg recognition abilities as a result of robin populations that were exposed to parasitism historically [38]. As Kuehn *et al.* [38] noted, in allopatric robins (no cowbirds) in Alaska and sympatric populations in Connecticut and Michigan the “nearly identical responses of sympatric and naïve populations indicates that a high level of exposure to

cowbirds is not required for the full expression of rejection behaviour, which suggests that phenotypic plasticity may not explain the reduced responsiveness of allopatric populations.” Similarly, in our study the non-mimetic eggs were rejected at both the high and low elevations sites, but in a more relaxed fashion at the high elevation sites.

Nest Aggression

The results of the model presentation experiments showed that robins at the lower elevation sites alarm called more often when presented with a cowbird model than with a sparrow model, whereas this difference was not found at the high elevation site. Female robins at high elevation sites spent less time responding aggressively to the cowbird model than robins at the low elevation sites while no differences were found between sites in responses to the sparrow model. These results suggest a relaxation of nest defense behaviors of robins at the high elevation sites where cowbirds are infrequent.

It is difficult to determine from these data if the aggressive nest defense behaviors of robins are specific to the threat of brood parasitism or are a generalized response to intruders near the nest. Robins at the high elevation sites were less aggressive towards the cowbird model, yet avian nest predators, *e.g.*, Steller’s Jay (*Cyanocitta stelleri*), are common at this site. These robins are therefore encountering predators at their nests and would have no reason to have a relaxed generalized response towards any intruder.

CONCLUSION

Studying host defenses against brood parasitism can be useful for understanding the evolution and maintenance of anti-parasitic behaviors. Nest defense may function as a plastic behavior in hosts, that is heightened in regions where the selection pressure is greater and relaxed when the brood parasites are less common. There is a generalized aggressive response to intruders at the nest that would benefit the host because the potential threats of different nest predators are common and suite of potential nest predators varied. The costs of nest defense are minimal compared to the potential costs of recognizing and rejecting a host egg rather than a cowbird egg. While nest defense may be a more general response, egg rejection is very specific to a single species interaction. We found relaxed egg recognition and egg rejection of foreign eggs by robins in high elevations areas with lower cowbird populations, but no difference in the low-cost generalized aggressive response to any intruder at the nest.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interest.

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