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Aggressive responses of Eastern Phoebes (*Sayornis phoebe*) and American Robins (*Turdus migratorius*) toward brood parasites and nest predators: A model presentation experiment

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ABSTRACT—Brood parasites reduce the reproductive success of many bird species by laying eggs in their nests. Hosts that reject parasitic eggs (“rejecters”) avoid most costs of brood parasitism altogether by physically ejecting eggs from nests or abandoning parasitized nesting attempts. Species that accept parasitic eggs once these are laid (“accepters”) may reduce or eliminate costs by aggressively responding to brood parasites at their nests to prevent parasitism from taking place. Accordingly, accepters should recognize brood parasites and nest predators as different nest threats with different levels of aggression, whereas rejecters may not. We exposed active Eastern Phoebe (*Sayornis phoebe*, an accepter host) and American Robin (*Turdus migratorius*, a rejecter host) nests to models of a female brood parasitic Brown-headed Cowbird (*Molothrus ater*), an eastern chipmunk (*Tamias striatus*, nest predator), and a European Starling (*Sturnus vulgaris*, nonthreatening control) during the incubation stage. Phoebes alarm-called equally toward the nest predator and brood parasite models, but attacked the nest predator model more than the brood parasite model. Robins, in contrast, alarm-called toward and attacked all 3 models equally. Interpreting these results is challenging due to experimental design elements, specifically small sample sizes and restricting the

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experiment to the incubation stage. Nonetheless, our experiment contributes to the paucity of comparative studies on accepter versus rejecter nest defense behavior in response to both nest parasites versus predators, and adds a new tested accepter species to the literature. *Received 21 June 2019. Accepted 29 April 2020.*

Key words: behavior, brood parasitism, cowbird, model experiment, nest threat, phoebe, robin.

Respuestas agresivas del mosquerito *Sayornis phoebe* y el zorzal *Turdus migratorius* hacia parásitos de puesta y depredadores de nidos: un experimento presentando modelos

RESUMEN (Spanish)—Los parásitos de puesta reducen el éxito reproductivo de muchas especies de aves cuando ponen huevos en sus nidos. Los hospederos que rechazan huevos de parásitos (“rechazadores”) evitan la mayoría de los costos totales del parasitismo de puesta, físicamente rechazando huevos de sus nidos o abandonando los intentos de anidación que han sido parasitados. Las especies que aceptan huevos parasitados una vez que han sido puestos en sus nidos (“aceptadores”) reducen o eliminan dichos costos por medio de respuestas agresivas a los parásitos de puesta que llegan a sus nidos para evitar que el parasitismo ocurra. De acuerdo con esto, los aceptadores deberían de reconocer a los parásitos de puesta y depredadores de nidos como diferentes amenazas con diferentes niveles de agresión, mientras que los rechazadores podrían no responder así. Presentamos modelos de una hembra del tordo *Molothrus ater* (un parásito de puesta), un chichimoco *Tamias striatus* (depredador de nidos) y un estornino *Sturnus vulgaris* (como control no-amenazante) a nidos de activos del mosquerito *Sayornis phoebe* y el zorzal *Turdus migratorius* durante la etapa de incubación. Los mosqueritos emitieron llamados de alarma hacia el depredador de nido y el parásito de puesta de igual manera, aunque atacaron el modelo del depredador de nido más que al modelo del parásito de puesta. En contraste, los zorzales emitieron llamados de alarma y ataques hacia los tres modelos de igual manera. La interpretación de estos resultados es un reto dados elementos del diseño experimental, en particular nuestros pequeños tamaños de muestra, y la restricción de nuestro experimento a la etapa de incubación. Sin embargo, nuestro experimento hace un aporte a la escasez de estudios comparativos del comportamiento de defensa de aceptadores versus rechazadores en respuesta a parásitos de nido y depredadores, además de agregar una nueva especie de aceptador a la literatura.

Palabras clave: amenaza al nido, comportamiento, experimento con modelos, mosquerito, parasitismo de puesta, tordo, zorzal.

Obligate avian brood parasitism, wherein one bird species lays its eggs in the nest of another, is by definition costly to the host’s reproductive success (Davies 2000). Brood parasites often remove a host egg while laying their own (Peer 2006, Hoover and Robinson 2007), and competition between host and parasitic nestlings can reduce survival of the host’s own nestlings (Hauber 2003, Hoover and Reetz 2006). Hosts are therefore under strong selection pressure favoring species that can avoid being parasitized (Feeney et al. 2012).

Accordingly, many hosts have diverse behavioral adaptations to avoid brood parasitism. Hosts that physically eject parasitic eggs from the nest >75% of the time, called egg “rejecter” species (Rothstein 1975, Moksnes et al. 1990, Stokke et al. 1999, Røskaft et al. 2002), represent the most common adaptation against brood parasitism (Davies 2000). Other hosts, called “accepter” species, do not reject parasitic eggs, but may preemptively reduce brood parasitism risk with evident aggression toward adult brood parasites approaching the nest (Rothstein 1975, Krüger 2007). Such front-loaded aggressive behavior is considered an adaptation against brood parasitism by preventing it from occurring in the first place, and is well documented in many accepter species (Moksnes et al. 1990, Røskaft et al. 2002, Campobello and Sealy 2010, Feeney et al. 2012).

The Brown-headed Cowbird (*Molothrus ater*, hereafter cowbird) is a common and widespread obligate brood parasite in North America that parasitizes many different passerines (Lowther 1993). Host–parasite interactions involving cowbirds are well researched, with many studies identifying their hosts as either accepters or rejecters (Rothstein 1975, Peer and Sealy 2004). Theoretically, accepters of cowbird eggs are expected to respond differently toward cowbirds and other types of nest threats (such as nest predators) and alter their aggression levels to match (Feeney et al. 2012). Indeed, foundational experimental studies revealed that accepter species behave more aggressively toward cowbird models than to nest predator models early in the nesting cycle when nests are more vulnerable to brood parasitism, but rejecter species did not (Neudorf and Sealy 1992, Sealy et al. 1998). Only 6 host species have been examined in published studies to date, and few studies since have used the experimental design of presenting nests with both predator and brood parasite models as in Neudorf and Sealy (1992) and Sealy et al. (1998). Thus, in order to effectively determine whether accepter and rejecter hosts differ in their aggression toward cowbirds, more research is needed with this experimental approach, especially on host species yet to be tested.

Here we used a model stimulus presentation experiment, similar to that used by Neudorf and Sealy (1992) and Sealy et al. (1998), to test whether 2 common cowbird hosts, the American Robin (*Turdus migratorius*, hereafter robin), a cowbird egg rejecter (Rothstein 1975, Luro et al. 2018), and the Eastern Phoebe (*Sayornis phoebe*, hereafter phoebe), a cowbird egg accepter (Rothstein 1975, Aidala et al. 2019), differ in their aggressive responses to cowbirds, nest predators, and a nonthreatening control species. This host dyad is relevant to compare because both species lay immaculate eggs that contrast sharply with cowbird eggs (Dainson et al. 2017, Aidala et al. 2019). Unlike robins, however, phoebes do not grasp and eject cowbird eggs (Hauber et al. 2004), despite being physically predicted to be capable of doing so (Rasmussen et al. 2010). Moreover, phoebes were not included in Neudorf and Sealy (1992) or Sealy et al. (1998), making this a novel species in the study of avian host–parasite interactions.

We hypothesized that phoebes and robins should exhibit different levels of aggression near active nests toward cowbirds and other nest threats because of differences in host status (accepter and rejecter status, respectively). Based on similar model experiments of cowbird host species (described above), we predicted that if phoebes and robins both can distinguish between overall nest threats (brood parasites and nest predators) and nonthreatening species (control), then both species should be similarly more aggressive toward cowbird and nest predator models compared to a control model. Phoebes, however, should also exhibit different aggression levels toward cowbirds compared to nest predators, whereas robins may not.

Methods

This study took place in June 2012 within 50 km of Ithaca, New York, USA. Nests of both study species were located in rural and suburban residential neighborhoods, small farms, and public parks (following Wagner et al. [2013]). Regionally, both robins and phoebes breed from late April to late July, with peak nesting late May (Weeks 2011, Vanderhoff et al. 2016). We located robin and phoebe nests by searching for nests daily, focusing search efforts on accessible properties and public parks where known breeding pairs were located. We monitored nests every 2–3 d to determine whether nests were still attended and active.

To test whether robins and phoebes differ in their aggression levels during the incubation stage, we presented taxidermy models of a female cowbird (brood parasite), an eastern chipmunk (*Tamias striatus*, nest predator; Weeks 2011, Vanderhoff et al. 2016), and a European Starling (*Sturnus vulgaris*, control, hereafter starling). We explicitly acknowledge we used one model per treatment as this was all we could procure. We selected the starling as a control because in our study area the species is common and nonthreatening to robin and phoebe nests.

Model presentations occurred in June between 0800 and 1900 h. Nests were randomly assigned 1 of the 3 model treatments, and when possible presented with the remaining 2 treatments in a randomized order, spaced 4–24 h apart (time constraints precluded us from retesting nests in standardized time intervals, as recommended by Sealy et al. [1998]). In many cases it was not possible to test nests with all 3 treatments. Specifically, some nests were not retested with the chipmunk model because it was not available until later in the season (robins, $n = 2$; phoebes, $n = 5$). Likewise, we could not retest one robin nest with the cowbird model presentation due to logistical reasons. We recognize the small and uneven sample sizes are considerable shortcomings in our experimental design, as is only testing nests during the incubation phase. We return to these limitations in the Discussion.

Model presentations were performed conditional on one or both parents (i.e., nearby unmarked adults) seen on or visible to us when standing at the nest. Models were placed within 1 m of the focal nest, positioned facing the nest, and a camera (Flip UltraHD model U260W, Cisco Systems, San Jose, California, USA) was placed ~5 m from the nest to record behavioral responses for data collection. We collected data from recordings exclusively. We made efforts to not flush parents off nests while placing equipment, but started data collection at the 1 min timestamp on recordings or as soon as the first parent was observed in the vicinity of the nest, whichever occurred later, to avoid confounds of our disturbance.

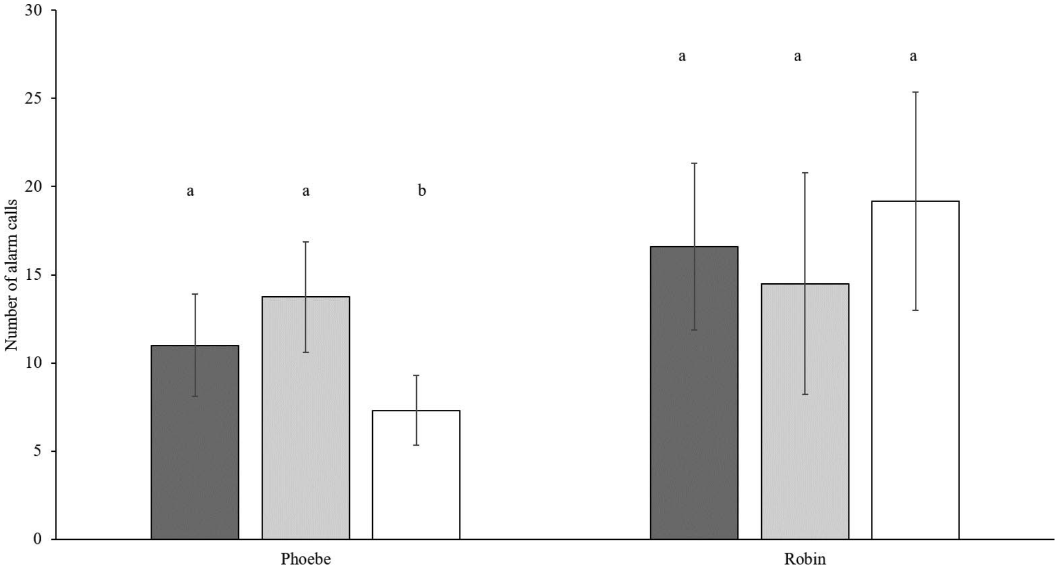

Figure 1. Mean number of alarm calls by Eastern Phoebes (Phoebe) and American Robins (Robin) toward models of a Brown-headed Cowbird (dark gray bars), eastern chipmunk (light gray bars), and European Starling (white bars) during model presentations for 5 min at nests in Ithaca, New York, in 2012. Bars represent standard error; different letters denote significantly post hoc different means of responses to treatments within each species' statistical model, not between the species' statistical models.

From video recordings, we collected and combined behavioral data from one or both unmarked presumed parents for 5 min. During this time, we recorded 2 aggressive behaviors toward the models: the total number of physical contact attacks from either parent (hereafter "attacks") delivered to the model, and the total number of alarm calls from either parent (hereafter "alarm calls"). We chose to combine data from parents because in many cases it was difficult to discern individual behaviors on the recordings. Both robins and phoebes give various alarm calls while mobbing nest threats (McLean et al. 1986, Gottfried et al. 1985, Weeks 2011). Thus, for each species we chose to pool all alarm calls into a single tally because we did not know if the alarm calls have any contextual or referential meaning (Vanderhoff and Eason 2009, Weeks 2011).

Using software in SAS 9.4 (SAS Institute Inc., Cary, North Carolina, USA), we evaluated whether aggressive behaviors changed depending on the nest threat present. For each species we built 2 separate models, one per response variable (alarm calls and attacks; 4 models total). Response variables were not correlated for either species (Pearson's $r < 0.20$, $P > 0.05$). For robins we used nonparametric Kruskal-Wallis tests, with treatment as the independent variable (Gotelli 2013). For phoebe data we used generalized linear models as data were not normally distributed, fitted with a Poisson distribution and a log link function (Gotelli 2013). As fixed effects we included model treatment, order of model presentation, time of day, and nest ID to control for any influence individual pairs had on responses. In both analyses we removed nonsignificant effects from the full model, then reanalyzed reduced models (Quinn and Keough 2002). For phoebe data, we conducted Student's *t*-tests for post hoc analyses; in all tests, $\alpha \leq 0.05$.

Results

In total, we studied 6 robin nests (treatment sample sizes: $n = 5$ cowbird, $n = 4$ chipmunk, $n = 6$ starling) and 13 phoebe nests (treatment sample sizes: $n = 13$ cowbird, $n = 8$ chipmunk, $n = 13$ starling). For robins, alarm calling behavior did not significantly differ across model treatments ($\chi^2 = 0.69$, $P = 0.71$, df $= 2$; Fig. 1) nor did attack behavior ($\chi^2 = 2.78$, $P = 0.25$, df $= 2$; Fig. 2).

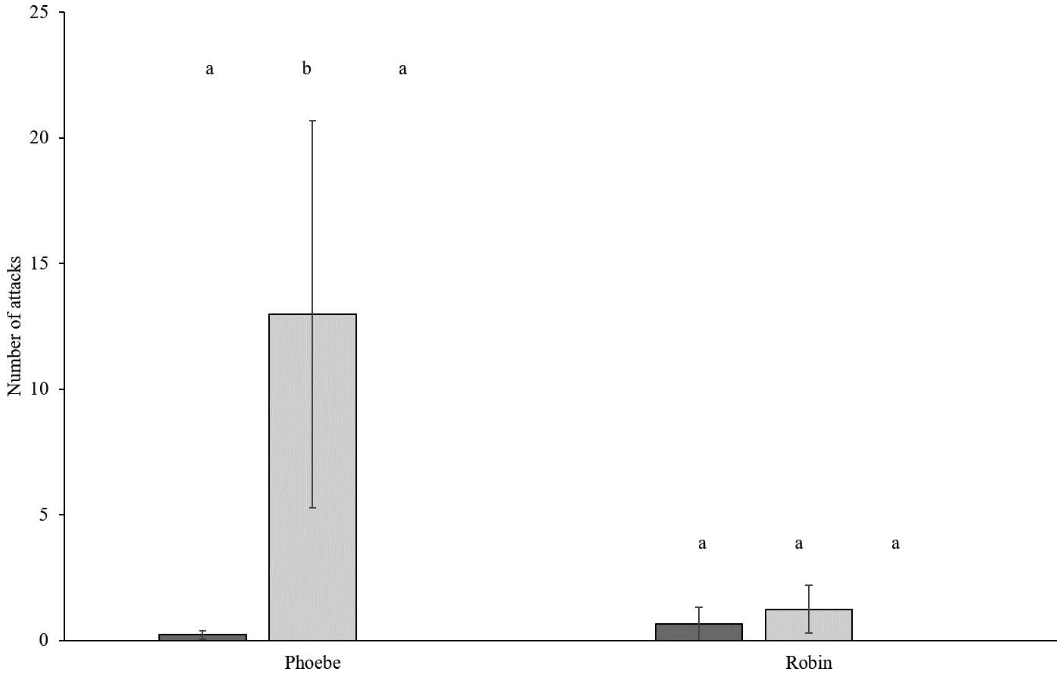

Figure 2. Mean number of attacks by Eastern Phoebes (Phoebe) and American Robins (Robin) toward models of a Brown-headed Cowbird (dark gray bars), eastern chipmunk (light gray bars), and European Starling (white bars) during model presentations for 5 min at nests in Ithaca, New York, in 2012. Bars represent standard error; different letters denote significantly post hoc different means of responses to treatments within each species' statistical model, not between the species' statistical models.

For phoebes, there was no significant effect of model presentation order, time of day, or nest ID on alarm calling or attacks (all terms in both full models: $F_{1\text{–}12,15\text{–}16} < 1.00$, $P > 0.05$). Phoebes alarm called significantly more toward chipmunk and cowbird models compared to starling models, but alarm calling did not differ between chipmunk and cowbird models (reduced model, treatment term only: $F_{2,31} = 10.39$, $P = 0.004$; Fig. 1, Table 1a for post hoc comparisons). Phoebes attacked chipmunk models significantly more than cowbird and starling models (reduced model, treatment term only: $F_{2,30} = 23.6$, $P < 0.0001$; Fig. 2, Table 1b for post hoc comparisons).

Table 1. Results from post hoc analyses comparing least-square mean estimates for (a) number of alarm calls and (b) number of attacks by Eastern Phoebes toward eastern chipmunk (chipmunk), Brown-headed Cowbird (cowbird), and European Starling (starling) experimental models. Estimates are based on generalized linear model results regressing mean number of the response variable (alarm calls or attacks) on model exposure treatment. Experiment was conducted on nests in Ithaca, New York, in 2012.

	Estimate	SE	*t*	*P*
(a) Alarm call statistical model				
chipmunk vs. starling	0.63	0.14	4.51	<0.0001
cowbird vs. starling	0.41	0.13	3.09	0.004
chipmunk vs. cowbird	0.22	0.13	1.76	0.09
(b) Attack statistical model				
chipmunk vs. starling	2.56	0.10	24.47	<0.0001
cowbird vs. starling	−14.69	430.13	0.03	0.97
chipmunk vs. cowbird	−1.47	0.58	6.87	0.01

Discussion

Here we did not find evidence that (an accepter species) were any more aggressive toward model presentations of a cowbird than were robins (a rejecter species). Phoebes did, however, distinguish between threatening and nonthreatening models at their nests: phoebes alarm called more toward the chipmunk and cowbird models compared to the starling model (Fig. 1), and the chipmunk model elicited the most attacks compared to the starling and cowbird models (Fig. 2). In contrast, with our small sample sizes, robins showed no statistical evidence of discrimination and were similarly aggressive toward all models presented at their nests.

Accepter species of cowbird eggs typically pay higher reproductive costs to brood parasitism than rejecter species (Hauber 2003, Peer and Sealy 2004, Feeney et al. 2012). Accepter species should therefore be more aggressive toward brood parasites to prevent parasitism from taking place at all (Rothstein 1975, Neudorf and Sealy 1992). We recognize that it is crucial to consider when during the nesting cycle (laying, incubation, or nestling stages) models are presented to assess unique nest threat recognition, which we did not do. Many model experiments demonstrate that host species behave most aggressively toward brood parasites during the laying or incubation stage, which is the stage most vulnerable to brood parasitism (Neudorf and Sealy 1992, Gill and Sealy 1996, Fasanella and Fernandez 2009, Trnka and Prokop 2012). In contrast, aggression toward nest predators typically increases during the nestling stage (Gill and Sealy 1996, Fasanella and Fernandez 2009, Duré Ruiz et al. 2018). Our experimental analyses of data were restricted to the incubation stage, which should control for any effect nest stage had on host aggression toward nest threats. We also recognize our sample sizes were small, which may limit interpretation of results, especially for robins. Nonetheless, our results merit discussion of behavioral responses to different nest threats within a nest stage for each species, if not between.

To date only 2 studies have simultaneously experimented with an accepter and rejecter species to compare aggressive behaviors between these 2 types of cowbird hosts (Neudorf and Sealy 1992, Sealy et al. 1998). Our study adds to the paucity of data in this field of research, and importantly, also adds novel species data. To our knowledge, this is the first experiment evaluating whether Eastern Phoebes respond with different aggression levels toward parasitic cowbirds versus nest predators. The phoebes' elevated aggression we observed here toward the cowbird model compared to the control model is similar to that reported in earlier studies on this species (Robertson and Norman 1976, 1977). We can now also add that Eastern Phoebes are more aggressive toward nest predators than brood parasites during the incubation stage, leastwise in terms of attacking behavior.

The differences in the phoebes' attack intensity we observed could reflect the type of hazard at hand. When a nest predator finds a nest, which is the scenario our experiment effectively simulated, complete reproductive failure typically occurs (Martin 1993, Latif et al. 2012). In this scenario, nest predators would be a higher threat than cowbirds, as phoebes still have a chance at fledging at least one young if parasitized (Hauber 2003), but none if depredated (Martin 1993). We suggest this interpretation with caution, however, as we did not collect nuanced alarm calling data to truly test for unique responses to cowbirds. For example, it is possible phoebes give different alarm calls toward cowbirds and nest predators (e.g., as do Yellow Warblers [*Setophaga petechia*]; Gill and Sealy 1996, 2004; Kuehn et al. 2016). In this case, heightened aggression toward cowbirds would manifest itself as prevalence of unique, cowbird-specific alarm calls, not as a positive correlation between number of alarm calls and threat level (sensu Welbergen and Davies 2008, Hetrick and Sieving 2011). Determining if Eastern Phoebes give unique alarm calls toward Brown-headed Cowbirds would be a fruitful direction for future model presentation experiments.

We expected robins to exhibit the greater aggression toward the nest predator model than the cowbird model due to their rejecter status with little recoverable cost to receiving parasitic eggs (Rothstein 1975, Croston and Hauber 2015). We found robins alarm called at any nest intruder regardless of the threat level (threatening or nonthreatening control model) or threat type (cowbird or nest predator model; Fig. 1). Robins also rarely attacked any nest intruder (Fig. 2). Our results are notably different from what Sealy et al. (1998) found. Our experimental design differed from Sealy et al. (1998), which used an avian (aerial) predator and not a mammalian (terrestrial) nest predator, which elicit different vocalizations and nest defense behaviors in robins (Gottfried et al. 1985, Vanderhoff and Eason 2009). We again did not parse robin alarm calls into their different types (e.g., "chucks" vs. "chirps"; Gottfried et al. 1985, Vanderhoff et al. 2016), and as such we may have lost the resolution needed to detect changes in alarm calling behavior for this species. Robins are generally variable in their responses to model exposures at nests: McLean et al. (1986) observed equal responses to a nest predator and control in their study, whereas Carmody et al. (2016) found higher aggression toward cowbird models compared to controls, and both of these differ from our results as well as from Sealy et al. (1998).

Our understanding of how accepter and rejecter hosts compare in their defenses against brood parasites is based on studies of just a handful of simultaneous experimental tests on select species. Here we compared just one accepter and one rejecter host species, but more research is needed to better our understanding of host-parasite interactions. Future model exposure experiments could test several accepter and rejecter host aggression toward nest threats, which would allow for phylogenetic control during accepter and rejecter host comparisons. Furthermore, designing studies that consider other potential mitigating factors, such as breeding experience and investment into young, will also better our understanding of the interplay between hosts' antiparasitic egg response status (accepter or rejecter) and their nest defense behaviors.

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