CHAPTER TWO

Do hosts of avian brood parasites discriminate parasitic vs. predatory threats? A meta-analysis

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1. Introduction

Animals experience diverse interspecific interactions, including those with "natural enemies" such as predators and parasites negatively impacting survival and reproduction (Morin, 2009; Pollock, Hoover, Uy, & Hauber, 2021).

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Encounters with predators and parasites both reduce fitness, but fitness costs differ based on the type of threat and when these threats are encountered (Raffel, Martin, & Rohr, 2008). Thus, it would be adaptive for animals to discriminate between natural enemies and choose the behavioral response that minimizes fitness losses. The ability to discriminate among threats is well-studied in predator-prey contexts, with prey species across taxa capable of discriminating between different types of predators (e.g., Burhans, 2001; Chivers & Mirza, 2001; Dorosheva & Reznikova, 2011; Ferrari, Messier, & Chivers, 2008; Fuchs, Veselý, & Nácarová, 2019; McLean, Lundie-Jenkins, & Jarman, 1996). Indeed, animals select among their own repertoire of antipredator strategies based on predator type (e.g., flying vs. aerial; Seyfarth, Cheney, & Marler, 1980; Blumstein, 1999; Rainey, Zuberbuhler, & Slater, 2004) or threat level (e.g., size or distance relative to prey; Helfman, 1989; Courter & Ritchison, 2010; Rauber & Manser, 2017), which in turn improves survival (reviewed in Griffin, 2004).

In addition to the recognition of predators that directly threaten their own survival, animals distinguish among threats specifically related to reproductive success, such as predators targeting vulnerable offspring, including eggs and dependent young. Recognizing threats to reproduction is particularly critical for birds, as nest depredation is the leading cause of reproductive failure for this lineage (Chiavacci, Benson, & Ward, 2018; Martin, 1992; Martin, 1995). Many avian species respond aggressively to nest predators to improve reproductive success odds (reviewed in Lima, 2009), recognizing that nest predators pose a high risk to nest survival but little or no risk to the adults' survival (e.g., Oteyza, Mouton, & Martin, 2021). In turn, up to 17% of bird species must also defend nests against brood parasites, which lay their eggs in the nests of "host" species that must care for the brood parasitic young (Antonson, Rubenstein, Hauber, & Botero, 2020; Davies, 2010). Behavioral responses to both types of nest threats often include aggressive mobbing behaviors to prevent nest depredation or brood parasitism from occurring (referred to as "front-loaded" defenses in the context of brood parasitism; Feeney, Troscianko, Langmore, & Spottiswoode, 2015; Feeney, Welbergen, & Langmore, 2012; Kilner & Langmore, 2011; Welbergen & Davies, 2009). However, notable differences in aggression levels toward these threats also demonstrate that avian host species discriminate between nest predators and brood parasites, such that parents adjust their behaviors to match the distinct threats specifically (Burhans, 2001; Enos, Hylund Bruno, & Hauber, 2020; Gill & Sealy, 1996; Sealy, Neudorf, Hobson, & Gill, 1998).

To explore the discrimination of unique threats posed by nest predators and brood parasites, researchers typically frame their experiments around four hypotheses about host enemy recognition. A frequently tested hypothesis about host enemy recognition poses that discrimination between nest predators and brood parasites is specific to the nest stage. Unlike nest predators, which threaten reproductive success when either eggs (referred to as "laying" and "incubation" stages) or nestlings (referred to as the "nestling" stage) are present, brood parasites mostly pose a reproductive threat if they successfully parasitize a nest while the host is actively laying or incubating eggs (Fiorini, Tuero, & Reboreda, 2009; Geltsch, Bán, Hauber, & Moskát, 2016; Wang, Zhong, He, Zhang, & Liang, 2020). Hence, hosts that discriminate between brood parasites and nest predators should primarily respond to brood parasites with aggression during laying and incubation stages (e.g., Fasanella & Fernández, 2009; Gill & Sealy, 1996; Neudorf & Sealy, 1992). In contrast, nest predators should elicit aggressive responses from hosts at all nest stages because the outcome of nest predation is often the total loss of the reproductive attempt (e.g., Fasanella & Fernández, 2009; Gill & Sealy, 1996; Ruiz, Fasanella, & Fernández, 2018). Moreover, aggression intensity toward nest predators often increases as nests progress from incubation to nestling stages, because of the high investment in advanced broods near fledging (Campobello & Sealy, 2010; Montgomerie & Weatherhead, 1988; Regelmann & Curio, 1983).

Host species' aggression intensity toward brood parasites has also been hypothesized to specifically depend on the ability to distinguish brood parasitic eggs from their own (e.g., Davies & Brooke, 1989; Manna, Moskat, & Hauber, 2017; Rothstein, 1986). Several host species physically eject parasitic eggs once recognized (Antonov, Stokke, Moksnes, & Røskaft, 2009; Rothstein, 1975; Soler, 2014). These "rejecters" also benefit from front-loaded defenses to prevent brood parasitism from occurring (i.e., aggression toward the brood parasite female to avoid host-egg removal in connection with the brood parasitic egg-laying; Croston & Hauber, 2015). However, non-rejecters, referred to as "accepters," consistently experience higher costs from being parasitized as they do not eject eggs and subsequently allocate resources toward the unrelated obligate brood parasitic young (Hauber, 2003; Kilner, Madden, & Hauber, 2004; Lichtenstein & Sealy, 1998). The difference in fitness outcomes suggests that accepters should exhibit more front-loaded aggression toward brood parasites than rejecters (Neudorf & Sealy, 1992; Rothstein, 1975; Sealy et al., 1998). In turn, both accepters and rejecters are expected to exhibit similar levels of front-loaded aggression toward nest predators because of the shared and high fitness cost of nest depredation (e.g., Enos et al., 2020).

Though it concerns host aggression rather than discrimination, a third hypothesis poses that host aggression intensity should depend on the competitive strategy utilized by brood parasitic nestlings after hatching. For example, some species of brood parasitic nestlings, including common cuckoos (*Cuculus canorus*) and striped cuckoos (*Tapera naevia*), evict or directly kill all nestmates, typically resulting in total loss of fitness for the host (Davies, 2010; Kilner & Davies, 1999; Mark & Rubenstein, 2013). In contrast, brood parasitic species that do not evict host nestmates, including the brown-headed cowbird (*Molothrus ater*) and the Great Spotted Cuckoo (*Clamator glandarius*), often lead to only partial host-fitness loss as brood parasitic nestlings compete for resources from parents, therefore reducing the survival of some, but typically not all, host nestlings (Hauber, 2003; Soler et al. 2014). As such, hosts may respond differently depending on the species and reproductive strategy of brood parasites, specifically whether they are nest-sharers or nestmate-evictors.

The final hypothesis is that geographic isolation between hosts and brood parasites influences enemy recognition and discrimination among hosts. In areas of geographic overlap or sympatry, hosts should exhibit higher aggression toward brood parasites during the laying and/or incubation stage compared to the nestling stage (as discussed above under the stage-specific enemy recognition hypotheses). In contrast, "naive" or allopatric host populations that have been geographically isolated from brood parasites may not recognize brood parasites as unique threats to reproduction (Briskie et al., 1992; Kuehn, Peer, Mccleery, & Rothstein, 2016). In this case, hosts would respond to brood parasites and nest predators with the same level of aggression and also increase aggression intensity toward both threats during the nestling stage (e.g., Lawson, Leuschner, Gill, Enos, & Hauber, 2020). Alternatively, host populations that are geographically isolated from brood parasites may not recognize brood parasites as a reproductive threat, and may instead perceive them as non-threatening heterospecific intruders.

Support for these four hypotheses about enemy recognition by hosts largely come from visual, model-presentation experiments (sometimes coupled with acoustic playbacks), where researchers place taxidermic models or effigies of predators, brood parasites, and/or non-threatening control species at nests and then record the host's aggressive responses to model treatments (reviewed in Soler et al., 2017). However, most experiments are not designed to compare host responses across all three model treatments, or across all nesting stages, within a single study (but see

Gill & Sealy, 1996). Additionally, most studies only test one or a few host species and only one brood parasite at a time (but see for multi-host species studies: Robertson & Norman, 1976; Moksnes et al., 1991; Sealy et al., 1998). Undoubtedly, host type (accepter vs. rejecter), nest stage (laying, incubation and nestling), threat type (nestmate-evictor vs. nest-sharer, nest predator vs. adult predator) and host exposure to brood parasites (sympatry vs. allopatry) are not mutually exclusive factors influencing host enemy recognition and discrimination. It is thus critical to evaluate all factors at once to better address existing hypotheses about enemy recognition by avian hosts.

We conducted a systematic literature review of studies adopting model presentation experiments to evaluate support for the four hypotheses about host descrimation between predators and brood parasites. We then used a formal, phylogenetically-controlled meta-analysis (Koricheva, Gurevitch, & Mengersen, 2013) to quantitatively test the following predictions for each hypothesis:

1. *Host-specific Discrimination*: differential aggression in responses of hosts toward brood parasites vs. predators will be greater in species that do not eject parasite eggs (accepters) than in those that do (rejecters).
2. *Stage-specific Discrimination*: hosts will be more aggressive toward brood parasite models during the laying and incubation stages compared to the nestling stage, whereas responses to predators would either stay the same or increase with the progression of these nest stages.
3. *Threat-specific Discrimination*: the type of the brood parasite (nestmate evictor vs. nest-sharer) and predator it is compared to (nest predator vs. adult predator) influences host aggression, with nestmate-evictor parasites and adult predators receiving more aggression from hosts.
4. *Exposure-based Discrimination*: hosts will be more aggressive toward brood parasites with geographic overlap in populations (sympatry) compared to geographically isolated populations (allopatry).

With our new results, we discuss existing support for each hypothesis about threat discrimination in avian hosts of obligate brood parasitism, and address current gaps or biases in the literature to date that should be remedied in future studies.

2. Methods

We searched the published literature through Google Scholar and Web of Science using the following boolean search string: "brood parasite" predator AND aggres* bird OR egg OR model OR nestling OR brood OR playback. We only included studies that met the following five criteria:

(i) studies had to experimentally test for host responses with model, playback, and/or live stimulus presentation near a host nest or on a host territory;

(ii) experiments had to compare host responses to both an obligate brood parasite and predator model within one nest stage or across multiple nest stages;

(iii) host aggression toward models had to be numerically or categorically quantified (e.g., alarm call rate, number of strikes or swoops, closest approach, aggression score) and compared between the types of models and nesting stages tested. Studies that only examined responses that were not directly related to aggression and nest defense, such as time spent foraging, were excluded;

(iv) researchers needed to provide host aggression data for one or more known stages: laying and incubating (considered "egg" stage in our review), or nestling, and data had to be provided separately for each stage tested; and, critically,

(v) studies were required to use a control model/playback in order to generate effect sizes.

For the publications focusing on multiple host species, we assessed each species tested in the study as a separate sample. For studies that presented two types of predators (adult vs. nest), we also separated the response to each type as its own sample. We labeled hosts as accepters or rejecters based on the authors' own categorization, or on other publications if not categorized by authors (e.g., Moksnes et al., 1991; Robertson & Norman, 1976); these accepter vs. rejecter labels were based on the hosts' responses to naturally laid brood parasitic eggs. This allowed us to compare studies with hosts of cowbirds and cuckoos, despite differences in egg rejection abilities between the hosts of these different lineages of brood parasites (e.g., Luro & Hauber, 2020). For example, most common cuckoo hosts are rejecters of non-mimetic (model) eggs (Stoddard & Stevens, 2010), but this may be so simply because the coevolutionary arms-race has progressed far in many of this brood parasite's host species (Stoddard & Hauber, 2017). However, these hosts often still accept the now closely mimetic cuckoo eggs at high rates when laid naturally or inserted experimentally (e.g., Hauber et al., 2015), thus we still classified those hosts behaviorally as accepters. Last, we also labeled hosts as sympatric or allopatric with the brood parasite(s) to separate studies in sympatry from allopatric samples. Studies that used hosts labeled as "unsuitable" (very rarely parasitized when in sympatry with brood parasite or brood parasite cannot survive in the nest) for parasitism were excluded.

We then formalized our meta-analysis by extracting the effect sizes for each aggression metric from published studies (Koricheva et al., 2013). To do so, we first extracted the mean, sample size, and standard deviation from the text of each study for all aggression responses to controls, brood parasites, and predators. For those studies where these data were not provided in-text, we used the R package metaDigitise (Pick, Nakagawa, & Noble, 2019) to digitize these values from the figures within the published papers. We calculated Hedges' G effect sizes from the mean, sample size, and standard deviation of the specific treatment group (brood parasite or predator) and the mean, sample size, and standard deviation of the control group (Hedges, 1981). As it was possible for the aggression effect sizes to be positive or negative depending on context of the aggression (e.g., a higher number of strikes and a smaller latency would both signify strong aggression), we transformed effect sizes by taking their absolute value, so that we could focus our analyses on the magnitude of the effect size.

2.1 Statistical analysis

We conducted a linear mixed model with nest stage, threat type (brood parasite vs. predator), and host type (accepter vs. rejecter) as fixed effects, and avian family as a random effect (for phylogenetic correction) to analyze whether these affected the aggression effect sizes (Hedges G) between threat models and their respective controls. This was only done with data from presentations in sympatry, as there were a number of comparisons that could not be made with allopatric data because of lack of data. To analyze whether the type of brood parasite (nestmate evictor vs. non-evictor) or predator (adult predator vs. nest predator) affected the aggression effect sizes, we conducted another linear mixed model with nest stage, specific threat type (nestmate evictor brood parasite, non-evictor brood parasite, adult predator, nest predator), and host type (accepter vs. rejecter) as fixed effects, and taxonomic family as a random effect. For our geographic overlap with brood parasites comparison (sympatry vs. allopatry) we used a subset of the data with just the brood parasite model presentations to compare responses. Hosts were determined to be in sympatry if the host population overlapped with the brood parasite species presented in each study. Our search to generate the meta-analysis dataset did not return any studies on rejecter hosts in allopatry so we could not include host type as a fixed effect. This second model had geographic overlap (sympatry or allopatry) as a fixed effect, and avian family as a random effect.

We were also interested in whether the sampling method or type of aggression measured had an influence on how aggressive hosts were toward threat presentations. For the sampling method, we categorized the studies based on the number of birds tested per stimulus sample, the number of stimuli each subject was tested with, and the number of nest stages subjects were tested across. This resulted in four sampling method categories: one bird/one stimulus/one stage, one bird/multiple stimuli/one stage, one bird/multiple stimuli/multiple stages, multiple birds/multiple stimuli/one stage. We then ran a linear mixed model with sampling method as a fixed effect and avian family as a random effect. For type of aggression, we categorized behaviors measured as physical aggression (e.g., strikes, swoops, approach), vocal aggression (e.g., alarm calls), or combined/other response type (e.g., aggression scores, latency to respond). We ran a linear mixed model with aggression type as a fixed effect and avian family as a random effect. To determine if host type and threat type influences whether hosts favor vocal vs. physical behaviors in their defense, we ran a linear mixed model only with samples that included strictly physical or vocal aggressive behaviors, and included aggression type, threat type, and host type as fixed effects and avian family as a random effect.

3. Results

Our initial boolean search yielded 1270 results, but after applying the rigorous criteria required for the meta-analytic techniques, the literature review resulted in 29 publications (see Table 1 for the full list). In total, 25 host species, 7 brood parasite species, and 17 predator species were represented across the collected studies for our review. The focal brood parasitic species for most samples were from brown-headed cowbirds, followed by common cuckoos, the two best-studied obligate brood parasites (reviewed in Davies, 2010), with most studies also occurring in the temperate zones of the Northern Hemisphere (69% of samples). The most common nest predator species used were blue jays (*Cyanocitta cristata*; 5%), common grackles (*Quiscalus quiscula*; 25%), and Eurasian sparrowhawks (*Accipiter nisus*, primarily an adult predator; 6%). Nevertheless, studies in our sample were conducted on hosts and with parasites and/or predators native to six continents - North America, South America, Europe, Asia, Africa, and Australia. We also found some biases toward three host species in our data set: yellow warblers (*Setophaga petechia*, 17% of samples), Eurasian reed warblers (*Acrocephalus scirpaceus*, 14% of samples), and red-winged blackbirds

Table 1 Summary of avian studies that compared host aggressive responses to presentations of brood parasites and predators.

Host species	Parasite species	Predator species	Control species	Reference
American Robin (*Turdus migratorius*)	Brown-headed Cowbird (*Molothrus ater*)	Eastern Chipmunk (*Tamias striatus*)	European Starling (*Sturnus vulgaris*)	Enos et al. (2020)
American Robin (*Turdus migratorius*)	Brown-headed Cowbird (*Molothrus ater*)	Blue Jay (*Cyanocitta cristata*), Common Grackle (*Quiscalus quiscula*)	Fox Sparrow (*Passerella iliaca*)	Sealy et al. (1998)
Baltimore Oriole (*Icterus galbula*)	Brown-headed Cowbird (*Molothrus ater*)	Common Grackle (*Quiscalus quiscula*)	Fox Sparrow (*Passerella iliaca*)	Neudorf and Sealy (1992)
Barn Swallow (*Hirundo rustica*)	Common Cuckoo (*Cuculus canorus*)	Eurasian Sparrowhawk (*Accipiter nisus*)	Eurasian Collared Dove (*Streptopelia decaocto*), Oriental Turtledove (*Streptopelia orientalis*), Wood Pigeon (*Columba palumbus*)	Liang and Møller (2015)
Eurasian Blackcap (*Sylvia atricapilla*)	Common Cuckoo (*Cuculus canorus*)	Eurasian Jay (*Garrulus glandarius*)	European Turtle Dove (*Streptopelia turtur*)	Požgayová, Procházka, and Honza (2009)
Carolina Wren (*Thryothorus ludovicianus*)	Brown-headed Cowbird (*Molothrus ater*)	Blue Jay (*Cyanocitta cristata*)	Swainson's Thrush (*Catharus ustulatus*)	D'Orazio and Neudorf (2008)
Cedar Waxwing (*Bombycilla cedrorum*)	Brown-headed Cowbird (*Molothrus ater*)	Common Grackle (*Quiscalus quiscula*)	Fox Sparrow (*Passerella iliaca*)	Neudorf and Sealy (1992)

Continued

Table 1 Summary of avian studies that compared host aggressive responses to presentations of brood parasites and predators.—cont'd

Host species	Parasite species	Predator species	Control species	Reference
Clay-colored Sparrows (*Spizella pallida*)	Brown-headed Cowbird (*Molothrus ater*)	Franklin's ground squirrel (*Poliocitellus franklinii*), Common Grackle (*Quiscalus quiscula*)	Fox Sparrow (*Passerella iliaca*)	Grieef (1995)
Common Grackle (*Quiscalus quiscula*)	Brown-headed Cowbird (*Molothrus ater*)	Blue Jay (*Cyanocitta cristata*), Common Grackle (*Quiscalus quiscula*)	Fox Sparrow (*Passerella iliaca*)	Sealy et al. (1998)
Eastern Kingbird (*Tyrannus tyrannus*)	Brown-headed Cowbird (*Molothrus ater*)	Common Grackle (*Quiscalus quiscula*)	Fox Sparrow (*Passerella iliaca*)	Bazin and Sealy (1993)
Eastern Phoebe (*Sayornis phoebe*)	Brown-headed Cowbird (*Molothrus ater*)	Eastern Chipmunk (*Tamias striatus*)	European Starling (*Sturnus vulgaris*)	Enos et al. (2020)
Eurasian Reed Warbler (*Acrocephalus scirpaceus*)	Common Cuckoo (*Cuculus canorus*)	Eurasian Sparrowhawk (*Accipiter nisus*)	Eurasian Teal (*Anas crecca*) and general parrot	Welbergen and Davies (2012)
Eurasian Reed Warbler (*Acrocephalus scirpaceus*)	Common Cuckoo (*Cuculus canorus*)	Eurasian Sparrowhawk (*Accipiter nisus*)	Eurasian Collared Dove (*Streptopelia decaocto*)	Welbergen and Davies (2011)
Eurasian Reed Warbler (*Acrocephalus scirpaceus*)	Common Cuckoo (*Cuculus canorus*)	Eurasian Magpie (*Pica pica*)	Rock Pigeon (*Columba livia*)	Campobello and Sealy (2010)
Eurasian Reed Warbler (*Acrocephalus scirpaceus*)	Common Cuckoo (*Cuculus canorus*)	Eurasian Sparrowhawk (*Accipiter nisus*)	Eurasian Teal (*Anas crecca*)	Welbergen and Davies (2008)

Fan-tailed Gerygone (*Gerygone flavolateralis*)	Shining Bronze-Cuckoo (*Chrysococcyx lucidus*)	New Caledonian Crow (*Corvus moneduloides*)	Common Chaffinch (*Fringilla coelebs*)	Attisano, Hlebowicz, Gula, and Theuerkauf (2020)
Field Sparrows (*Spizella pusilla*)	Brown-headed Cowbird (*Molothrus ater*)	Blue Jay (*Cyanocitta cristata*)	Fox Sparrow (*Passerella iliaca*)	Burhans (2001)
Gray Catbird (*Dumetella carolinensis*)	Brown-headed Cowbird (*Molothrus ater*)	Common Grackle (*Quiscalus quiscula*)	Fox Sparrow (*Passerella iliaca*)	Neudorf and Sealy (1992)
Great Tit (*Parus major*)	Common Cuckoo (*Cuculus canorus*)	Eurasian Sparrowhawk (*Accipiter nisus*)	Oriential Turtle Dove (*Streptopelia orientalis*)	Yu et al. (2017)
Large-billed Gerygone (*Gerygone magnirostris*)	Shining Bronze-Cuckoo (*Chrysococcyx lucidus*)	Collared Sparrowhawk (*Accipiter cirrocephalus*), Brown Goshawk (*Accipiter fasciatus*)	Willie Wagtail (*Rhipidura leucophrys*)	Noh (2020)
Oriental Reed Warbler (*Acrocephalus orientalis*)	Common Cuckoo (*Cuculus canorus*)	Eurasian Sparrowhawk (*Accipiter nisus*)	Spotted Dove (*Spilopelia chinensis*)	Li, Zhang, Grim, Liang, and Stokke (2016)
Reed Parrotbill (*Paradoxornis heudei*)	Common Cuckoo (*Cuculus canorus*)	Eurasian Sparrowhawk (*Accipiter nisus*)	Spotted Dove (*Spilopelia chinensis*)	Li et al. (2016)
Red Wattlebird (*Anthochaera carunculate*)	Pacific Koel (*Eudynamys orientalis*)	Pied Currawong (*Strepera graculina*)	Crimson Rosella (*Platycercus elegans*)	Abernathy (2017)

Continued

Table 1 Summary of avian studies that compared host aggressive responses to presentations of brood parasites and predators.—cont'd

Host species	Parasite species	Predator species	Control species	Reference
Red-crested Cardinal (*Paroaria coronate*)	Shiny Cowbird (*Molothrus bonariensis*)	Guira Cuckoo (*Guira guira*)	Grayish Baywing (*Agelaioides badius*)	Segura and Reboreda (2012)
Red-winged Blackbird (*Agelaius phoeniceus*)	Brown-headed Cowbird (*Molothrus ater*)	Blue Jay (*Cyanocitta cristata*)	Wood Thrush (*Hylocichla mustelina*)	Lawson, Enos, Mendes, Gill, and Hauber (2020)
Red-winged Blackbird (*Agelaius phoeniceus*)	Brown-headed Cowbird (*Molothrus ater*)	Common Grackle (*Quiscalus quiscula*)	Song Sparrow (*Melospiza melodia*)	Armstrong (2002)
Red-winged Blackbird (*Agelaius phoeniceus*)	Brown-headed Cowbird (*Molothrus ater*)	Common Grackle (*Quiscalus quiscula*)	Fox Sparrow (*Passerella iliaca*)	Neudorf and Sealy (1992)
Superb Fairy Wren (*Malurus cyaneus*)	Horsfield's Bronze Cuckoo (*Chrysococcyx basalis*)	Currawong (*Strepera*), Eastern Brown Snake (*Pseudonaja textilis*), Eurasian Sparrowhawk (*Accipiter nisus*)	Honeyeater (*Meliphagidae*)	Feeney et al. (2013)
Whitehead (*Mohoua albicilla*)	Long-tailed Cuckoo (*Urodynamis taitensis*)	Morepork Owl (*Ninox novaeseelandiae*)	Song Thrush (*Turdus philomelos*)	Lawson, Leuschner, et al. (2020)
Yellow Warbler (*Setophaga petechia*)	Brown-headed Cowbird (*Molothrus ater*)	Blue Jay (*Cyanocitta cristata*)	Wood Thrush (*Hylocichla mustelina*)	Lawson, Enos, Mendes, Gill, and Hauber (2021)

Yellow Warbler (*Setophaga petechia*)	Brown-headed Cowbird (*Molothrus ater*)	Loggerhead Shrike (*Lanius ludovicianus*), Sharp-shinned Hawk (*Accipiter striatus*)	California Towhee (*Melozone crissalis*), European Starling (*Sturnus vulgaris*), Hermit Thrush (*Catharus guttatus*), Red-winged Blackbird (*Agelaius phoeniceus*), Western Meadowlark (*Sturnella neglecta*)	Kuehn et al. (2016)
Yellow Warbler (*Setophaga petechia*)	Brown-headed Cowbird (*Molothrus ater*)	Brown-headed Cowbird (presented eating egg) (*Molothrus ater*)	Fox Sparrow (*Passerella iliaca*)	Campobello and Sealy (2011a)
Yellow Warbler (*Setophaga petechia*)	Brown-headed Cowbird (*Molothrus ater*)	Common Grackle (*Quiscalus quiscula*)	Fox Sparrow (*Passerella iliaca*)	Gill and Sealy (1996)
Yellow Warbler (*Setophaga petechia*)	Brown-headed Cowbird (*Molothrus ater*)	Gray Jay (*Perisoreus canadensis*)	Fox Sparrow (*Passerella iliaca*)	Gill and Sealy (2004)
Yellow Warbler (*Setophaga petechia*)	Brown-headed Cowbird (*Molothrus ater*)	American Crow (*Corvus brachyrhynchos*)	House Sparrow (*Passer domesticus*)	Burgham and Picman (1989)
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	Brown-headed Cowbird (*Molothrus ater*)	Blue Jay (*Cyanocitta cristata*), Common Grackle (*Quiscalus quiscula*)	Fox Sparrow (*Passerella iliaca*)	Sealy et al. (1998)

(*Agelaius phoeniceus*, 17% of samples). This was often the result of the same researcher(s) conducting a series of studies on a specific host-parasite interaction.

Most studies used taxidermic models as the stimulus to evoke behaviors from hosts (92%), and the remaining studies used live stimuli (4%) or vocal playbacks (4%) exclusively (see Fig. 1 for examples of setups). Due to the sizable differences in studies with these three modalities, we were unable to statistically examine the effects of stimulus sensory modality (acoustic playback vs. visual model) on host aggression toward treatments.

3.1 Host-specific and stage-specific recognition/discrimination

We found host type had a significant effect on effect size (host type term: $F_{1,391}=4.49$, $P=0.035$), in that accepters were more aggressive toward threat models than rejecters (Fig. 2). Nest stage (stage term: $F_{1,391}=1.96$, $P=0.162$) and threat type (threat type term: $F_{1,391}=0.58$, $P=0.443$) as single terms were not significant. However, there was a significant interaction between nest stage and threat type (stage x threat type term: $F_{1,391}=11.26$, $P<0.001$), and between host type and threat type (host type x threat type term: $F_{1,391}=4.69$, $P=0.030$). There was not a significant interaction between stage and host type (stage x host type term: $F_{1,391}=0.09$, $P=0.761$), or between all three variables (host type x stage x threat type term: $F_{1,391}=0.60$, $P=0.438$). Based on post hoc pairwise comparisons, accepters were similarly aggressive to brood parasite and predator models during egg stage ($t=0.76$, $P=0.443$) but became significantly more aggressive toward predators compared to brood parasites during nestling stage ($t=3.38$, $P<0.001$), and aggressive responses overall were stronger than during egg stage ($t=3.22$, $P=0.001$). Accepters were specifically more aggressive than rejecters toward parasites during egg stage ($t=2.12$, $P=0.035$). Conversely, rejecters were more aggressive toward predators compared to brood parasites across egg ($t=2.05$, $P=0.040$) and nestling stages ($t=3.47$, $P<0.001$). Unlike accepters, rejecters did not significantly increase aggression toward predators over the nesting cycle ($t=-1.42$, $P=0.155$). All other post hoc comparisons across nest stage or threat type were non-significant (see Supplementary Table 1 in the online version at https://doi.org/10.1016/bs.asb.2021.03.002).

3.2 Threat-specific recognition/discrimination

When we defined threat types more specifically (nestmate evictor vs. nest-sharer brood parasite, or adult predator vs. nest predator), we found that

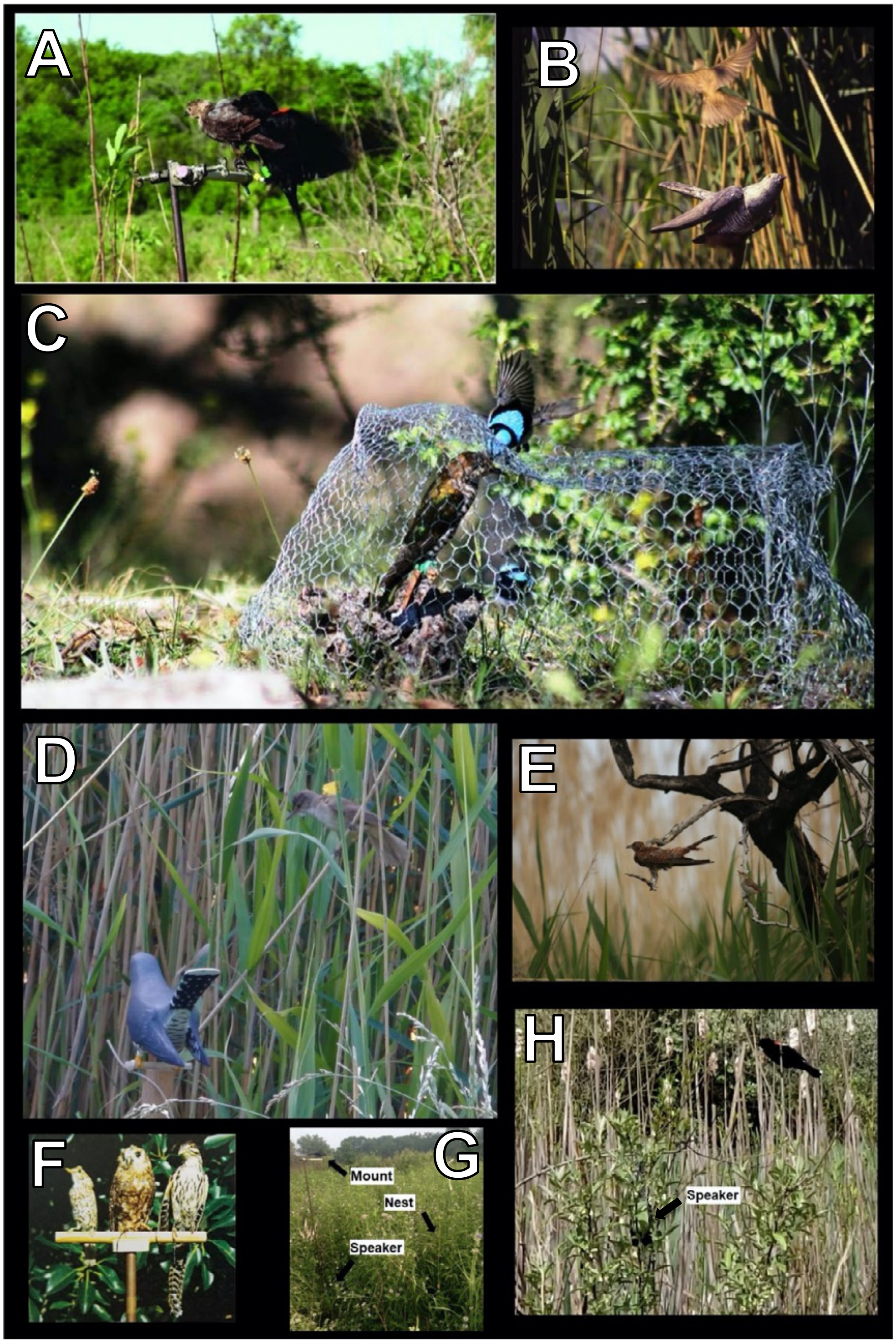

Fig. 1 Photos of sample setups in model/playback brood parasite presentation studies. (A) A red-winged blackbird attacking a female brown-headed cowbird dummy (photo credit: K. Yasukawa), (B) a great reed attacking a female common cuckoo dummy (O. Mikulica), (C) a superb fairy wren attacking a stuffed shining-bronze cuckoo dummy (W. Feeney), (D) a great reed warbler approaching a 3D printed, painted plastic common cuckoo model, (E) a sedge warbler alarm calling at a stuffed common cuckoo dummy, (F) from left to right, a song thrush (control), morepork owl (predator), and long-tailed cuckoo (brood parasite) to be presented at whitehead nests (N. Leuschner and B. Gill), (G) female brown-headed cowbird presented and its chatter called played back near an active red-winged blackbird nest (J. Lindsey), (H) a red-winged blackbird alarm calling at a speaker playing female brown-headed cowbird chatter (S. Lawson).

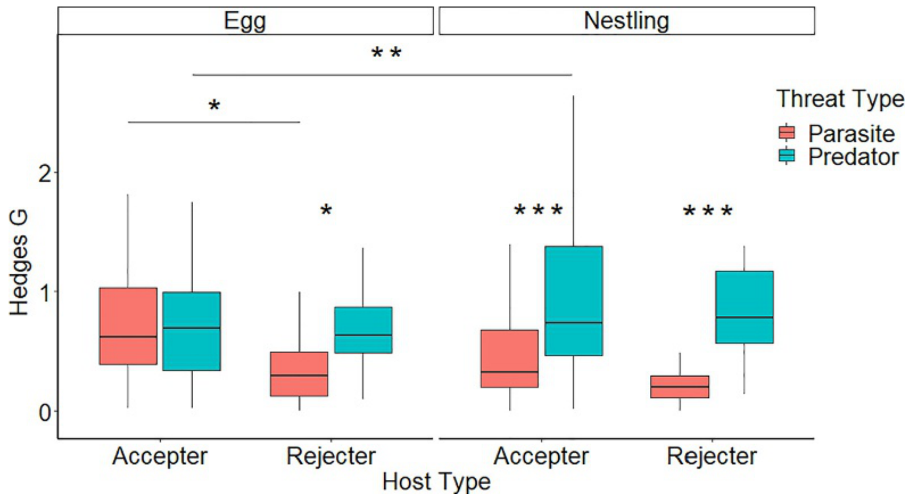

Fig. 2 Pooled effect sizes (Hedges G) of aggression by hosts between threat types and their respective controls across studies. Effect sizes are also separated by host type and nesting stage. Box plots illustrate median values (bar), interquartile range (box), and minimum and maximum effect sizes (lines). Significant post hoc differences between groups are represented with asterisks (*** $P<0.001$,** $P<0.01$, * $P<0.05$).

nest stage as a single term was significant (stage term: $F_{1,391}=14.87$, $P<0.001$), in that hosts (types: accepters and rejecters) were more aggressive to threat presentations during nestling stage compared to egg stage (Fig. 3). Host type (host type term: $F_{1,391}=1.40$, $P=0.236$) and threat type (threat type term: $F_{1,391}=0.60$, $P=0.614$) as single terms were not significant in the specific threat type model. However, similar to the general threat type model (i.e., brood parasite vs. predator), there was a significant interaction between nest stage and threat type (stage x threat type term: $F_{1,391}=7.55$, $P<0.001$), and between host type and threat type (host type x threat type term: $F_{1,391}=4.51$, $P<0.01$). There was not a significant interaction between stage and host type (stage x host type term: $F_{1,391}=1.44$, $P=0.229$), or between all three variables (host type x stage x threat type term: $F_{1,391}=0.95$, $P=0.329$).

Based on post hoc pairwise comparisons across nest stages, accepters were more aggressive toward adult ($t=3.85$, $P<0.001$) and nest predators ($t=1.98$, $P=0.048$) during the nestling stage compared to the egg stage. Accepters were more aggressive toward non-evictor brood parasites when their nests had eggs compared to nestlings ($t=2.04$, $P=0.041$). For evictor brood parasites, accepter aggression did not change across nest stages ($t=-0.01$, $P=0.959$). During nestling stage, accepters were more aggressive to adult predators compared to nest predators ($t=3.03$, $P=0.013$), evictor brood parasites ($t=3.49$, $P<0.01$), and non-evictor brood parasites

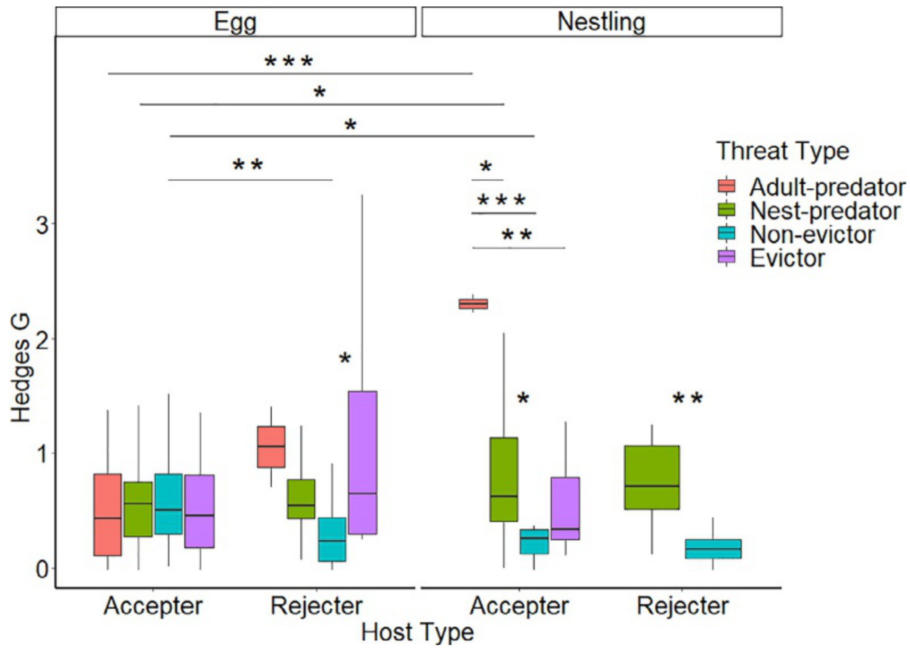

Fig. 3 Pooled effect sizes (Hedges G) of aggression by hosts between specific threat types and their respective controls across studies. Effect sizes are also separated by host type and nesting stage. Box plots illustrate median values (bar), interquartile range (box), and minimum and maximum effect sizes (lines). Significant post hoc differences between groups are represented with asterisks (*** $P<0.001$, ** $P<0.01$, * $P<0.05$).

($t=4.09$, $P<0.001$). Accepters were equally aggressive toward all threat types during egg stage, but during the nestling stage accepters were more aggressive to adult predators compared to nest predators ($t=3.03$, $P=0.013$), evictor brood parasites ($t=3.49$, $P<0.01$), and non-evictors ($t=4.09$, $P<0.001$). Accepters were also more aggressive to nest predators than non-evictors when they had nestlings ($t=2.88$, $P=0.021$).

For rejecters, the data only allowed us to compare nest predators ($t=-1.44$, $P=0.149$) and nest-sharer (non-evictor) brood parasites ($t=0.23$, $P=0.817$) between nest stages, though there were no significant differences for either. Post hoc comparisons across threat types found that during the egg stage, rejecters were significantly more aggressive toward evictor brood parasites than non-evictors ($t=2.72$, $P=0.034$). During the nestling stage, rejecters were more aggressive toward nest predators than non-evictor brood parasites ($t=3.47$, $P<0.01$). Comparisons between host types found that accepters were more aggressive than rejecters toward specifically non-evictor parasites during egg stage ($t=3.19$, $P=0.001$). All other post hoc comparisons across nest stage, threat type, and host type were non-significant (see Supplementary Table 2 in the online version at https://doi.org/10.1016/bs.asb.2021.03.002).

3.3 Recognition/discrimination by geographic overlap

Our model found a significant difference in host aggression based on sympatry (geographic overlap) or allopatry (geographic isolation) between host and brood parasite populations (geography term: $F_{1,201}=5.40$, $P=0.021$; Fig. 4). Specifically, hosts were more aggressive toward brood parasites in allopatry compared to sympatry with brood parasites.

3.4 Sampling methodology and host aggression metrics

Type of sampling method used (single or multiple birds tested, single or multiple stimuli used or nest stages tested) did not significantly influence effect sizes ($F_{1,417}=0.77$, $P=0.567$). However, effect sizes were significantly different based on the type of behavioral aggression measured (aggression term: $F_{1,417}=12.83$, $P<0.001$; Fig. 5). We found that behaviors that included both vocal and physical components had higher effect sizes than vocal ($t=3.95$, $P<0.001$) or physical ($t=5.09$, $P<0.001$) behaviors alone. We also examined whether host type and threat type influenced whether hosts use vocal or physical behaviors more frequently in their defense. We did not find any significant interactions between aggression type and threat type

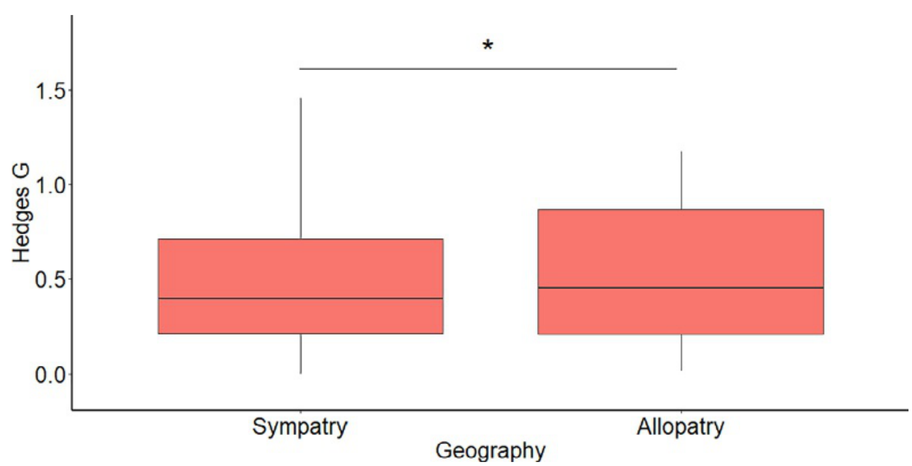

Fig. 4 Pooled effect sizes (Hedges G) of aggression by accepter hosts between parasite models and their respective controls across studies. Effect sizes are also separated by nesting stage. Box plots illustrate median values (bar), interquartile range (box), and minimum and maximum effect sizes (lines). Significant post hoc differences between groups are represented with asterisks (* $P<0.05$).

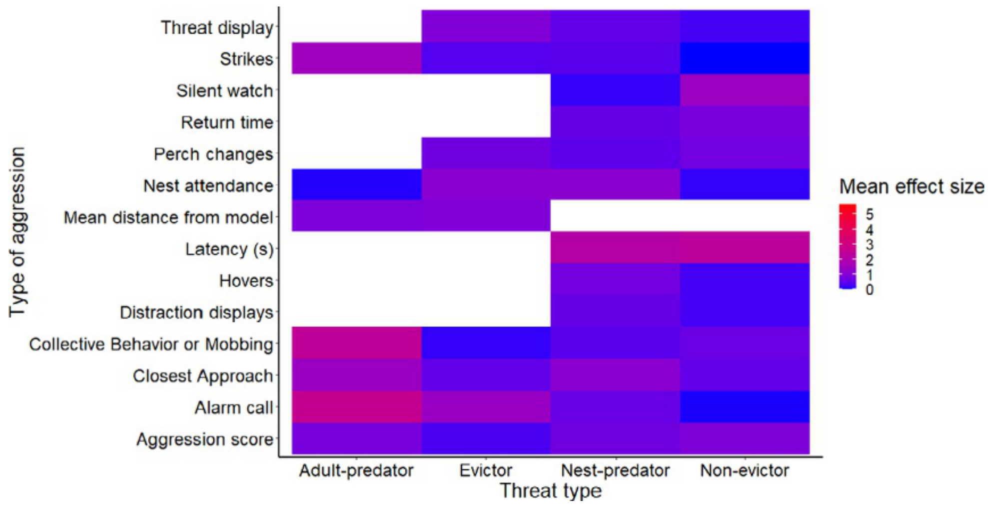

Fig. 5 A heat map describing patterns of the mean effect sizes for each threat type based on the type of aggression measured. Lighter colors (red) show an effect size with a greater magnitude. The areas with an absence of color on the plot represent gaps in the collected literature where no studies currently exist.

(aggression x threat type term: $F_{1,417}=1.88$, $P=0.170$) or between aggression type and host type (aggression x host type term: $F_{1,417}=2.35$, $P=0.125$).

4. Discussion

4.1 Host-specific and stage-specific recognition/discrimination

Overall we found that both host types and nest stage influence the effect sizes of aggression by parental birds in response to brood parasitic or predatory intruders at the nest (Fig. 6). Accepters were more aggressive than rejecters to threats, likely because of the differences in their responses to brood parasites. Accepters were equally aggressive to brood parasite and predator presentations when they had eggs, but compared to brood parasites, accepters became significantly more aggressive toward predators during the nestling stage. Conversely, rejecters were consistently more aggressive toward predators compared to brood parasites across nest stages.

Taken together, our results found patterns consistent with our predictions, in that accepters respond aggressively toward brood parasites predominantly during laying and incubation stages when brood parasitism poses the highest risk. In contrast, rejecters, which rely on egg discrimination rather than front-loaded defenses, do not respond as aggressively to brood parasites

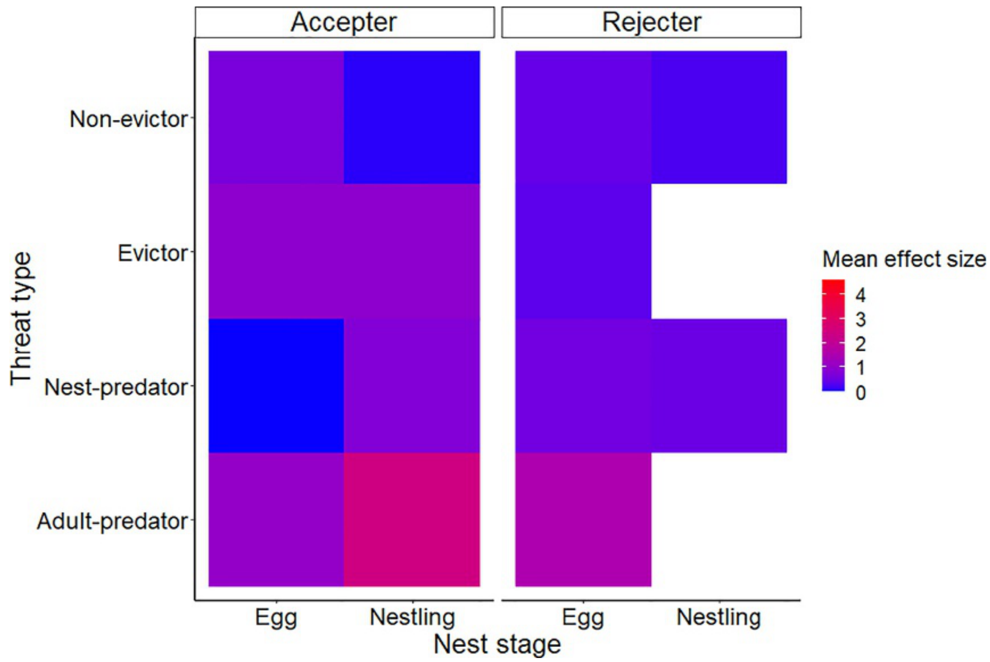

Fig. 6 A heat map describing patterns of the mean effect sizes for three focal comparisons: threat type (brood parasite vs. predator), host type (accepter vs. rejecter), and nesting stage (egg vs. nestling). Lighter colors (red) show an effect size with a greater magnitude. The areas with an absence of color on the plot represent gaps in the collected literature where no studies currently exist.

during either nest stage. Furthermore, parents are expected to invest more energy into defending their young from predatory threats with increased investment in offspring, as well as parental assurance in the survival of the offspring (Montgomerie & Weatherhead, 1988; Regelmann & Curio, 1983). The patterns we found support this, as host aggression toward predators either remained high across nest stages, as was the case for rejecters, or increased with nest age as we observed for accepters.

4.2 Theat-specific recognition/discrimination

4.2.1 Brood parasite type

Brood parasites were classified as evictor parasites, which eject or kill nestmates, or non-evictor parasites, which share the nest, and may even benefit from host nestlings in it (Hauber, 2003; Kilner et al. 2004; Winnicki et al., 2021). For accepters, we found, against our prediction, that aggression levels toward evictor and non-evictor brood parasites were the same, regardless of nest stage. Though non-evictor nestlings are considered less costly to fitness than evictor nestlings (Kilner, 2005), encounters with adult non-evictors may be costly, which model presentation experiments simulate. For example, non-evicting adult brown-headed cowbirds can cause total nest failure by depredating non-parasitized nests to regulate the timing of their parasitism opportunities (referred to as "farming;" Arcese, Smith, & Hatch, 1996; Clotfelter & Yasukawa, 1999). In this case, hosts may instead recognize non-evicting brood parasites as nest predators, with continued high aggression toward brood parasites during the nestling stage. For accepter species, discriminating between reproductive threats may thus depend on personal experience with the brood parasite more so than the brood parasite's reproductive strategy (nestmate evicting vs. non-evicting). Yellow warblers, for example, are more aggressive toward brown-headed cowbirds when they experience the brood parasite as an egg predator (Campobello & Sealy, 2011a). Additional studies on other accepter hosts and brood parasite types (e.g., Campobello & Sealy, 2011b) are necessary to further explore the effect of personal experience on enemy recognition.

Rejecters responded with consistently low levels of aggression toward non-evictors across nest stages, as predicted. However, rejecters exhibited more aggression overall toward evictors than non-evictors, despite little risk of parasitism from either. This result may be an artifact of the small sample size in our dataset representing rejecter host species with an evictor brood parasite ($n=4$ samples). Additionally, only three rejecter hosts - great tits (*Parus major*), reed parrotbills (*Paradoxornis heudei*), and Eurasian blackcaps (*Sylvia atricapilla*) - are represented in these samples, two of which are parasitized at lower rates (great tits and reed parrotbills; Li et al., 2016; Liang et al., 2016). Moreover, great tits and Eurasian blackcaps are considered generally aggressive across ecological contexts (great tits: Lang & Leimer, 2001; Samplonius, 2018; Eurasian blackcaps: Darolová, Krištofík, Knauer, & Hoi, 2020; Morganti, Assandri, Ignacio, et al., 2017). As such, aggression responses we observed among rejecters may be related to species-specific baseline aggression levels, and not related to brood parasite type per se.

4.2.2 Predator type

We classified predators as either nest predators, which are strictly threats to reproductive success, or adult predators, which hosts recognize as direct threats to their own survival (e.g., genus *Accipiter* hawks and "small" owls; Congdon, Hahn, Campbell, et al., 2020; Sieving, Hetrick, & Avery, 2010). There were no significant differences in aggression toward predator types (compared to each other and to parasite types) during the egg stage. In contrast, during the nestling stage hosts were more aggressive toward adult predators compared to other threats (nest predators, evictor brood parasites, non-evictor brood parasites). Notably, adult predation risk literature suggests that birds often invest in their own survival over reproductive effort when perceived adult predation risk is high (made apparent by models or playbacks of adult predators at nests; LaManna & Martin, 2016; Oteyza et al., 2021; Zanette, White, Allen, & Clinchy, 2011). However, short-lived species are more likely than long-lived species to defend nests against adult predators, because of the high premium placed on annual reproductive output in short-lived species (e.g., Oteyza et al., 2021). All host species included in this specific analysis are considered short-lived or "fast" life-history species ($n=9$ species, see Table 1). Our results could thus reflect tradeoffs that occur between survival and reproduction as nests approach fledging, with parents highly invested in reproductive success willing to defend nests against adult predators despite potential risks to survival.

During the nestling stage, hosts responded significantly more aggressively toward nest predators than non-evictor brood parasites, but not toward evictors. Responses toward non-evictor brood parasites during the nestling stage support our prediction, but responses toward evictor brood parasites do not. Why respond with equal aggression levels toward nest predators and any type of brood parasite, if the latter is only a threat while hosts are laying and incubating? Curiously, most studies evaluating host responses to evictor parasites used common cuckoo models, a species that superficially resembles an adult predator, the Eurasian sparrowhawk *Accipiter nisus* (Ma, Yang, & Liang, 2018 and references therein). It is possible that in these cases, hosts instead perceived brood parasite models as adult predators and responded aggressively due to high reproductive investment during the nestling stage (despite potential survival risks, discussed above). Some Cuculidae species can also be nest predators themselves, and as such they may still pose a risk to reproductive investment even during the nestling stage (Gill, Zhu, & Patel, 2018; Zahavi, 1979).

4.3 Recognition/discrimination by geographic overlap

We found that hosts in geographic isolation from brood parasites (i.e., allopatric) were significantly more aggressive toward the brood parasite presentations compared to sympatric populations. Our result, however, only provide limited support for the hypothesis that allopatric host populations no longer recognize brood parasites as a unique threat (or nest threat at all; sensu Briskie et al., 1992; Kuehn et al., 2016). Our small sample size of allopatric studies for this analysis ($n = 6$) precluded us from addressing two important issues. First, we could not consider the effect of nest stage on allopatric host aggression levels, which as demonstrated in this review is crucial to address host discrimination between brood parasites and nest predators. Indeed, only one study was conducted in allopatry during the nestling stage (Lawson, Leuschner, et al., 2020). Second, we could not compare allopatric host aggression between accepter and rejecter hosts, as there were no studies conducted on rejecter host populations that were allopatric from brood parasites. Future experiments evaluating loss of enemy recognition in host species should aim to include more host species and conduct exposure experiments throughout the nesting cycle.

5. Research needs and future directions

To date, most studies have addressed enemy recognition by accepter hosts in sympatry with their non-evicting brood parasites (Fig. 7). Compared to hosts of non-evictors, fewer studies address enemy recognition

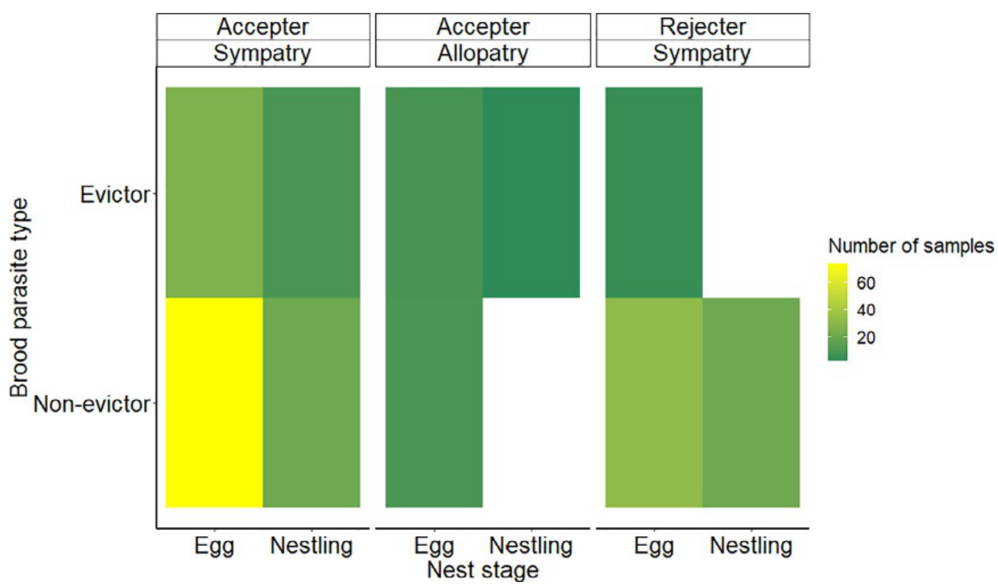

Fig. 7 A heat map describing bias of samples in our meta-analysis dataset on enemy recognition (brood parasite vs. predator) based on four focal comparisons: brood parasite type (evictor vs. non-evictor), host type (accepter vs. rejecter), nesting stage (egg vs. nestling), and geographical overlap (sympatry vs. allopatry). Lighter colors (yellow) show an effect size with a greater magnitude. The areas with an absence of color on the plot represent gaps in the collected literature where no studies currently exist. Our meta-analysis did not contain any studies with rejecter hosts tested in allopatry so this column was omitted.

by hosts of evictor brood parasites. Enemy recognition by rejecter hosts of evictor parasites has received the least attention, with studies solely testing aggressive responses during the egg stage in sympatric populations. Our literature review also revealed two knowledge gaps in the literature on host enemy recognition and nest threat discrimination. Currently, too few studies address whether (1) rejecter hosts of evictor parasites discriminate between nest threats during the nestling stage, specifically when populations are sympatric and (2) accepter hosts of non-evictor brood parasites still discriminate between nest threats during the nestling stage when a host population is allopatric from the brood parasite.

Although a relatively rare reproductive strategy, brood parasitism occurs in diverse orders of birds and involves diverse orders of host species. Our analyses only included hosts of brood parasites from Passeriformes (i.e., passerine birds), whereas brood parasites primarily were cuckoos (Cuculiformes: Cuculidae) and cowbirds (Icteridae). All passerine hosts in our review have similar life-history traits: most are open-cup nesting species (but see Liang et al., 2016 for a cavity-nester) and all have altricial young that require intensive parental care. However, our literature review does not include parasitic finches (Viduidae; i.e., Feeney et al., 2015) or brood parasitic species from other taxonomic groups with different life-history traits, such as honeyguides (Piciformes: Indicatoridae) and the only brood parasitic waterfowl species (Anseriformes, black-headed duck, *Heteronetta atricapilla*; Lyon & Eadie, 2013). Honeyguides, for example, are nestmate-killing parasites and primarily parasitize cavity-nesting hosts, which generally experience low predation risk compared to open-cup nesters (Spottiswoode, 2013). Honeyguide hosts, which are primarily woodpeckers and allies (Piciformes) and bee-eaters and allies (Coraciiformes), may thus perceive brood parasitism and nest predation risk differently than their open cup-nesting counters with non-evicting brood parasites. The black-headed duck is unique in that offspring are precocial and take care of themselves soon after hatch day (Cabrera, Montalti, & Segura, 2017), relieving host parents of any cost to brood parasitism. Several waterfowl species recognize both facultative brood parasites and predators as nest threats (Sorenson, 1997), but it is unknown if hosts treat the black-headed duck as a nest threat or a non-threatening heterospecific intruder. Testing hosts from these taxa with diverse life-history traits will greatly advance our understanding of enemy recognition and associated nest defense by avian hosts.

We also found a clear bias of host focal species, with the yellow warbler, red-winged blackbird, and Eurasian reed warbler being the most commonly tested hosts. These species have specialized nest defense behaviors that are not necessarily broadly applicable to other host species, therefore limiting our ability to generalize our findings across the avian taxa. Yellow warblers, for example, use referential alarm calls to specifically inform their mates of brown-headed cowbirds at the nest, which elicits a cowbird-specific defense of "sitting tightly" on the nest (Gill & Sealy, 1996; Gill & Sealy, 2004; Lawson, Enos, Mendes, Gill, & Hauber, 2021). Red-winged blackbirds and Eurasian reed warblers use social information from neighbors to assess brood parasitism risk and adjust their aggression levels accordingly (Campobello & Sealy, 2011b; Lawson, Enos, et al., 2020), but it is unknown how widespread social information use is for nest defense purposes in other host lineages (but see: Feeney & Langmore, 2013). Future studies should experiment with other common hosts to determine if our findings are broadly indicative of host discrimination, or strictly indicative of those with unique, adaptive behaviors to combat brood parasitism with (such as referential alarm calling and social information use).

Almost all studies that met our inclusion criteria used taxidermic and/or artificial models as a visual stimulus in their presentations at nests. Vocal playbacks are also used as a brood parasite or predator stimulus in the literature (e.g., Lawson, Enos, et al., 2020; Lawson, Enos, et al., 2021) yet only two such studies using vocal playbacks as the sole stimulus fit the criteria described above. In turn, we did not find any significant differences between physical and vocal aggression depending on host types or type of threat presented. Still, the sensory modality of the stimulus presented, whether visual, acoustic, or even olfactory (Soler et al., 2014), could affect the type of behaviors and/or magnitude of responses that hosts include in their nest defense repertoires (Duckworth, 1991; Grieef, 1995). Thus, we suggest future studies that compare aggressive responses of hosts to brood parasites and predators expand to using acoustic playbacks and other sensory forms of stimuli to simulate nest threats to hosts.

Another noteworthy observation is that there is considerable bias in which brood parasite type is paired with which predator type in the literature collected. Specifically, the majority of studies in our collection paired non-evictor brood parasites with nest predators (54%), or evictor brood parasites with adult predators (29%). Our findings show that certain pairings are associated with higher effect sizes between treatments, suggesting that researchers may draw different conclusions from their study depending on which pairing they had decided on for experimentation. With the potential for hosts to respond differently depending on the brood parasite and the predator models used, future studies should utilize multiple brood parasite-predator dyads to diversify the models used to evoke aggression responses. Additionally, future studies should diversify the aggressive behaviors by hosts that are measured. Our results suggest that measures that incorporate both physical and vocal responses by hosts are associated with larger effect sizes and may be better at teasing apart differences in response between threat models and controls. However, we caution about the use of combined aggression scores in particular, as these scores can be subject to biases which may exaggerate differences between groups.

We found that there was also a bias in sampling methodology across studies in our dataset, where most presented multiple stimuli to the same subject (individual, nest, or territory), and often across multiple nest stages, leading to possible habituation or sensitization by focal hosts. However, we found that sampling method type did not bias effect size data, suggesting that robust responses to models by host populations can be consistently measured across contexts without confounds due to the sampling paradigm. Still, it should be noted that studies included herein effectively randomized models to reduce bias and avoided pseudoreplication of results both on an individual and temporal basis. We suggest that future presentation experiments with brood parasite vs. predator models continue to make these efforts to minimize pseudoreplication (e.g., Kroodsma, Byers, Goodale, Johnson, & Liu, 2001).

6. Conclusions

1. Enemy recognition by avian host species depends on the magnitude of the threat to reproductive success, which is shaped by specific traits of the host (accepter vs. rejecter), the brood parasite (nestmate-evictor vs. nest-sharer), the predator (adult vs. nest predator), and how predictably hosts are exposed to brood parasitic threats (sympatry vs. allopatry).
2. Host discrimination between reproductive threats is likely an adaptive behavior, and may be widespread among all avian lineages experiencing different types of nest threats, including brood parasitism, nest predation, or other (such as highly aggressive conspecific or heterospecific competitors).
3. Future studies addressing the knowledge gaps identified here, or overlaying additional factors that influence discrimination capabilities (such as personal vs. social information use or life-history traits) will greatly improve our understanding of avian enemy recognition and its payoffs to reproductive success.

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