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RESEARCH

Heterospecifics removing eggs: brood parasites or predators of nest content?

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Abstract Many bird species adjust their nest defense behavior according to the type and magnitude of perceived threats. Hosts of brood parasites – species that rely on another species effort to raise its offspring – are particularly suitable for studying such discrimination because they must defend their nests against both parasites and predators. Previous studies have typically compared host responses to brood parasites, which pose no direct threat to host adults, with responses to predators threaten, which threaten both eggs and adults. We tested whether yellow warblers (*Setophaga petechia*) discriminate between two heterospecific intruders that provide a similar functional cue – namely, the removal of an egg from the nest – by comparing their responses to the brood parasitic brown-headed cowbird (*Molothrus ater*) and predatory gray catbird (*Dumetella carolinensis*), which targets only nest contents and does not threaten adult birds. We predicted that cowbird and catbird both would elicit similar responses, and tested it through comparisons between the main behavioral responses in warbler defense repertoire. Our results confirmed a parasite-specific response to cowbirds, including *seet* calls and nest-protection behavior that differed from those elicited by catbirds. Given that cowbirds and catbirds provide similar informational cues at the nest (i.e., egg removal), it remains unclear how hosts differentially associate these two types of threats. We suggest that including nest predators that are innocuous to host adults as comparative species may help reveal the associative mechanisms underlying such refined discriminatory abilities.

Significance statement Birds must defend their nests against multiple threats, but the optimal defense strategy depends on the type of intruder. Brood parasites, such as the brown-headed cowbird, harm host fitness primarily indirectly: they remove a host egg and, during subsequent visits, lay their own, with the resulting chick eventually monopolizing parental care and substantially reducing host offspring survival. Yellow warblers, an important cowbird host species, may prevent these costs by adopting a nest-defense strategy that may position them close to the parasites without exposing themselves to risk, as cowbirds pose no direct threat to adults. Nest predators, by contrast, may also prey on adults, making close mobbing potentially risky. However, predators that target only eggs or nestlings pose no danger to adults, and in principle, close mobbing may be similarly advantageous. Remarkably, yellow warblers respond differently to cowbirds and to nest-only predators, despite the similar functional cue of egg removal. How hosts form the cognitive association underlying such refined, threat-specific defense remains unknown, revealing a critical gap in our understanding of avian-decision making and threat discrimination.

Keywords Antipredator behavior · Antiparasite behavior · Brood parasitism · Nest defense · Discriminatory ability

Introduction

Many bird species adjust their responses according to the type of threat and the level of perceived danger (Walters 1990; Kleindorfer et al. 2005; Campobello and Sealy 2010; Colombelli-Negrel et al. 2010; Tvardíková and Fuchs 2011; Trnka and Grim 2014; Maziarz et al. 2018). Within the context of parental investment, the 'threat-sensitive predator avoidance' hypothesis predicts that natural selection favors prey that accurately recognize enemies and respond appropriately to the magnitude of perceived risk (Helfman 1989;

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Edelaar and Wright 2006; Mathot et al. 2009; Strnad et al. 2012; Schneider and Griesser 2013). Moreover, nest defense should be considered in light of the trade-off between current and future reproduction (Campobello and Sealy 2010), as individuals maximize fitness by balancing investment in offspring survival against their own risk of predation (Montgomerie and Weatherhead 1988; Dale et al. 1996; Teunissen et al. 2020).

Hosts of brood parasites provide an ideal system for studying discriminatory abilities, as they must defend their nests against multiple threats, including nest predators and avian brood parasites (Królikowska et al. 2016; Dure Ruiz et al. 2018; Lawson et al. 2021a; Sovrano et al. 2024), and respond to each according to the threat they pose. Hosts may encounter both brood parasites and nest predators at the nest while these intruders remove an egg. Although the functional cue associated with these events may appear similar – namely, a heterospecific removing an egg -, some host species, such as the yellow warbler, discriminate between these threats and adjust their defensive behavior accordingly (Hobson and Sealy 1989; Neudorf and Sealy 1992; Gill and Sealy 1996, 2003, 2004; Gill and Bierema 2013; Lawson et al. 2021a).

The yellow warbler (*Setophaga petechia*) has long been known to respond differently to brood parasites and nest predators. In the presence of the brood parasitic brown-headed cowbird (*Molothrus ater*), yellow warblers utter a specific alarm vocalization, the *seet* call, and adopt nest-protection behavior by sitting tightly on the nest (Hobson and Sealy 1989; Gill and Sealy 1996, 2003, 2004). By contrast, when confronted with nest predators, such as the common grackle (*Quiscalus quiscula*), they emit more general alarm calls and engage in a more generalized defense, including distraction displays (Gill and Sealy 1996, 2003; Sealy et al. 1998). These different responses, however, may reflect differences in the level of risk posed by the intruders. While cowbirds do not represent a direct threat to adult hosts, common grackles and the other predators used in previous studies (e.g., blue jay, *Cyanocitta cristata*, Lawson et al. 2021b; loggerhead shrike, *Lanius ludovicianus*, Kuehn et al. 2016), may also prey upon adults (Johnson and Johnson 1976; Dubowy 1985; Davidson 1994; Barnard 1996; Peer and Bollinger 2020; Clark 2024). Consequently, close mobbing of such predators, similar to that performed towards cowbirds, may increase the risk to the host's survival and ultimately compromise future reproductive success.

An additional question concerns how hosts recognize cowbirds as brood parasites. Unlike cuckoos, which typically remove a host egg and lay their own during the same visit to the nest (Davies and Brooke 1988), cowbirds remove a host egg and return to the nest to lay their own one or more days later (Sealy 1992). As a result, cowbird hosts, unlike cuckoo hosts, are prevented from learning to associate the egg-removing parasite with the presence of a foreign egg in their clutch. Associative learning, however, is the mechanism that allows yellow warblers to refine their nest defense (Campobello and Sealy 2011b). Contrary to other cuckoo hosts that rely on social learning (Campobello and Sealy 2011a), yellow warblers learn from personal experience (Campobello et al. 2017), which requires cognitive abilities able to create an association between one species and the danger it poses (Menzel 2013). Specifically, associative learning enables individuals to form connections between stimuli and outcomes, thereby improving the efficiency of defense responses (Shettleworth 1998). Because hosts often rely on incomplete information when assessing nest threats, similar cues may elicit similar defensive responses. Thus, the presence of a heterospecific intruder at the nest associated with egg removal may provide hosts with a shared, yet incomplete, functional cue on which such associations are built.

In this study, we tested whether hosts discriminate between two species that provide a similar functional cue—the removal of an egg from a heterospecific that does not endanger adults. We elicited yellow warbler responses toward a cowbird and a gray catbird (*Dumetella carolinensis*, hereafter catbird), a nest predator that primarily removes passerine eggs and only rarely preys on nestlings (Sealy 1994; River and Sandercock 2004), with no evidence of predation on adult warblers. Specifically, we asked whether these two intruders, cowbirds and catbirds, elicit similar defensive responses or whether hosts recognize them as distinct threats and respond with species-specific defensive behaviors consistent with antiparasite and antipredator defenses, respectively. We hypothesize that if warblers perceive cowbirds as predators of nest contents only, their reactions should resemble those elicited by catbirds. Accordingly, we predict similar frequencies of *seet* calls and nest-protection responses toward both species. Conversely, if these behaviors represent antiparasite defenses, we expected them to be expressed more frequently in response to cowbirds than to catbirds.

Methods

Study site and species

We conducted this study during spring/summer 2003 at Delta Marsh (Portage la Prairie, Manitoba, Canada). Yellow warblers return to the site in mid-to-late May, where they nest in wet, deciduous thickets and building their cup-shaped nest low in the canopy (MacKenzie 1982) into which they lay clutches 4–5 eggs. They are a common host of the cowbird, with roughly 18% of nests being parasitized (Goossen and Sealy 1982; Sealy 1995; Campobello et al. 2017). All warbler nests were unparasitized (i.e., we follow them since the building stage) and checked every 1–3 days through clutch completion.

Model presentations

We exposed 41 warbler nests to simulated visits from taxidermic mounts of three different species: cowbird (CB) as a brood parasite, gray catbird (GC) as a nest predator, and fox sparrow (FS) (*Passerella iliaca*, hereafter sparrow), as a nonthreatening species. The gray catbird is an abundant species at the study site. Underwood and Sealy (2006) reported 107 nests in 2000 (approximately 12 nests/ha), making this population one of the densest nesting catbird populations compared with other suitable sites (Smith et al. 2020). Unlike other nest predators, catbirds reportedly remove only partial nest contents, including cases in which a single egg is taken (Hauber 1998; Rivers and Sandercock 2004). Unparasitized nests found during the laying and incubation stages were tested because these are the periods when warblers manifest specific nest defense against cowbirds (Hobson and Sealy 1989; Gill and Sealy 1996). The responses recorded during presentations of cowbirds and sparrows were also used as a control group in a broader investigation, where we tested whether warblers learn individually or socially (Campobello and Sealy 2011a). On the same day, each nest was exposed to the three models with the order of presentation chosen randomly, with at least a 20-min break between presentations. To minimize habituation due to repeated exposures of the stimuli (Knight and Temple 1986a, b), we restricted each trial to 2 min. Mounts were taxidermic specimens of cowbird females clipped to vegetation in a perched position within 0.5 m of the nest. We used two taxidermic mounts per species, each chosen randomly for each presentation. We compared female warblers' motor and vocal responses across treatments. Specifically, we recorded six behavioral variables (Hobson and Sealy 1989; Gill and Sealy 1996, 2003, 2004) as the number of events for *chip* (CHIP) and *seet* (SEET) calls, perch changes (CHANGE, change of position on surrounding vegetation) and strikes (STRIKE, sudden attacks on the dummy), and as the number of 10-s intervals in which individuals performed distraction displays (DISTR, distraction behavior in front of the dummy) and nest-protection (NP, host sitting on the nest) behaviors. *Chip* and *seet* calls represent the generic and functionally referential alarm calls, respectively, the first being elicited by a variety of intruders at the nest, whereas the second is widely recognized as cowbird-specific (Hobson and Sealy 1989; Neudorf and Sealy 1992; Gill and Sealy 1996, 2003, 2004; Gill and Bierema 2013; Lawson et al. 2021a). Observed warbler behaviors were spoken into an audio recorder from a blind 2–5 m from the nest. It was not possible to record data blind because our study involved focal animals in the field. Trials were conducted between 0500 and 1930 h Central Standard Time.

Statistical analysis

We analyzed host responses with six separate Generalized Linear Mixed Models (GLMMs), one for each behavior, where the six behaviors were treated as response variables – the model species (SPECIES with three levels, CB, GC, FS) as a fixed factor, and the nest ID as a random effect. Because trials were conducted within a restricted portion of the breeding season and at comparable nesting stages, variation in laying date and nest age among nests was limited; therefore, these variables were not included in the analyses. All six variables showed high variance-to-mean ratios, which indicates overdispersion; hence, we treated them with Negative Binomial I (CHIP), Negative Binomial II (STRIKE, DISTR) and Tweedie (SEET, CHANGE, NP) regressions, which showed the best fits. Models were evaluated using Akaike Information Criterion (AIC) and simulated residual diagnostics implemented in the R package DHARMa, where we tested deviations from expected residual distributions, dispersion and zero-inflation. We also ran post hoc tests to assess all between-group comparisons as well as within-group and within-trial comparisons, using a Tukey p-value adjustment for family-wise error rate (FWER). All analyses were conducted in the statistical program R 4.1.1 (R Core Team 2021), using the glmmTMB (Brooks et al. 2017), DHARMa (Hartig 2020) and emmeans (Lenth 2021) packages.

Results

Yellow warblers responded to each model presented at every nest tested. Warblers uttered significantly more *seet* calls in response to cowbirds (mean ± SE, 28.9 ± 7.31) than to both catbirds (7.67 ± 2.43) and sparrows (6.80 ± 4.96, Fig. 1; Tables 1 and 2). A similar pattern was observed for nest protection behavior: this was performed significantly more often toward cowbirds (5.95 ± 1.16) than toward sparrow (1.60 ± 0.83), but did not differ significantly between cowbirds and catbirds or between catbirds and sparrows (2.10 ± 0.90) (Fig. 1; Tables 1 and 2). *Chip* calls were elicited at similar rates by all three model species (Tables 1 and 2). Warblers performed more perch changes in response to the catbird model (8.57 ± 1.60), although this difference was significant only when compared with cowbirds (3.90 ± 0.96, Fig. 2; Tables 1 and 2). Strikes were significantly higher in response to both cowbirds (1.50 ± 0.66)

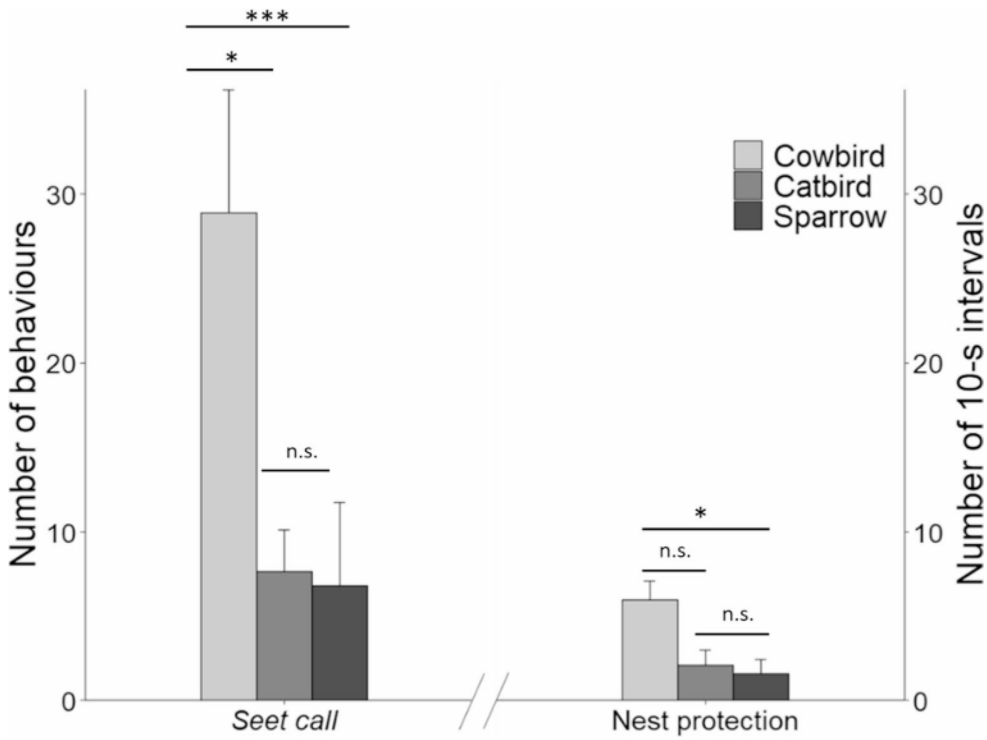

Fig. 1 Antiparasite responses (mean + SE) of yellow warblers during the presentation of brown-headed cowbird (n=20), gray catbird (n=21) and fox sparrow (n=20) models. Post hoc statistical differences are indicated by * $P \leq 0.05$, *** $P \leq 0.001$, n.s. $P > 0.05$

Table 1 GLMMs statistics showing the effect of different model species on the defense response of yellow warblers

	z	Estimate	CI	P
Chip calls				
Intercept (Ref: CB baseline)	1.07	0.64	[-0.52; 1.80]	0.283
GC (vs. Ref)	1.36	0.45	[-0.77; 1.67]	0.471
FS (vs. Ref)	0.72	0.67	[-0.30; 1.65]	0.175
Seet calls				
Intercept	9.11	3.02	[2.37; 3.66]	**<0.001**
GC	-2.60	-1.25	[-2.19; -0.31]	**0.009**
FS	-3.66	-1.59	[-2.44; -0.74]	**<0.001**
Perch change				
Intercept	5.02	1.28	[0.78; 1.78]	**<0.001**
GC	2.61	0.79	[0.20; 1.38]	**0.009**
FS	2.14	0.60	[0.05; 1.15]	**0.032**
Strike				
Intercept	0.59	0.41	[-0.94; 1.75]	0.554
GC	0.89	0.84	[-1.02; 2.70]	0.375
FS	-1.87	-2.01	[--4.12; 0.09]	**0.060**
Distraction display				
Intercept	0.20	0.10	[-0.84; 1.03]	0.841
GC	0.45	0.29	[-0.99; 1.58]	0.653
FS	-2.61	-3.09	[-5.41; -0.77]	**0.009**
Nest protection				
Intercept	4.30	1.71	[0.93; 2.49]	**<0.001**
GC	-2.13	-1.08	[-2.06; -0.09]	**0.033**
FS	-2.55	-1.37	[-2.42; -0.32]	**0.011**

A total of 41 yellow warbler nests was presented with cowbird (CB), catbird (GC) and sparrow (FS) models. Statistically significant p-values are highlighted in bold

and catbirds (3.48 ± 1.84) than to sparrows (0.20 ± 0.14, Fig. 2; Tables 1 and 2). Distraction displays were performed significantly less frequently in response to sparrows (0.05 ± 0.05) than to cowbirds (1.10 ± 0.48) and catbirds (1.48 ± 0.56), with no significant difference between the latter two species (Fig. 2; Tables 1 and 2). Pairwise comparisons not reported above were not statistically significant.

Discussion

Our results did not support the hypothesis that yellow warblers perceive the cowbird as a predator of nest contents only, as suggested for the gray catbird. Instead, warblers defended their nest against cowbirds with species-specific responses. In particular, *seet* calls were produced more frequently in response to cowbirds than to catbirds, supporting previous studies that have described this response as a specific antiparasite behavior (Burgham and Picman 1989; Hobson and Sealy 1989; Gill and Sealy 1996, 2003, 2004).

Nest protection behavior was also elicited more frequently by cowbirds than by catbirds, although this difference only approached statistical significance. Catbirds share the same breeding habitat at Delta Marsh (MacKenzie 1982; MacKenzie et al. 1982) and have been reported to prey on eggs and nestlings of several passerine species (Sealy 1994; Rivers and Sandercock 2004). Although annual parasitism of warblers at this site occurs in approximately 18% of nests (Campobello et

Table 2 Results of post hoc tests showing for each behavior pairwise comparisons between responses of warblers when confronted with cowbird (CB), catbird (GC) and sparrow (FS) models

Response	Cowbird^{CB}	Catbird^{GC}	Sparrow^{FS}	CB vs. GC		CB vs. FS		GC vs. FS	
	Mean ± SE	Mean ± SE	Mean ± SE	z	*P*	z	*P*	z	*P*
Chip call	3.35 ± 1.88	5.10 ± 2.18	7.55 ± 3.55	-0.72	0.750	-1.36	0.365	0.39	0.922
Seet call	28.9 ± 7.31	7.67 ± 2.43	6.80 ± 4.96	2.60	**0.026**	3.66	**< 0.001**	-0.58	0.829
Perch change	3.90 ± 0.96	8.57 ± 1.60	7.10 ± 1.39	-2.61	**0.025**	-2.14	0.081	-0.68	0.776
Strike	1.50 ± 0.66	3.48 ± 1.84	0.20 ± 0.14	-0.89	0.649	1.87	0.146	-2.70	**0.019**
Distraction display	1.10 ± 0.48	1.48 ± 0.56	0.05 ± 0.05	-0.45	0.895	2.61	**0.025**	-3.39	**0.011**
Nest protection	5.95 ± 1.16	2.10 ± 0.90	1.60 ± 0.83	2.13	0.084	2.55	**0.029**	-0.49	0.877

Statistically significant comparisons are highlighted in bold

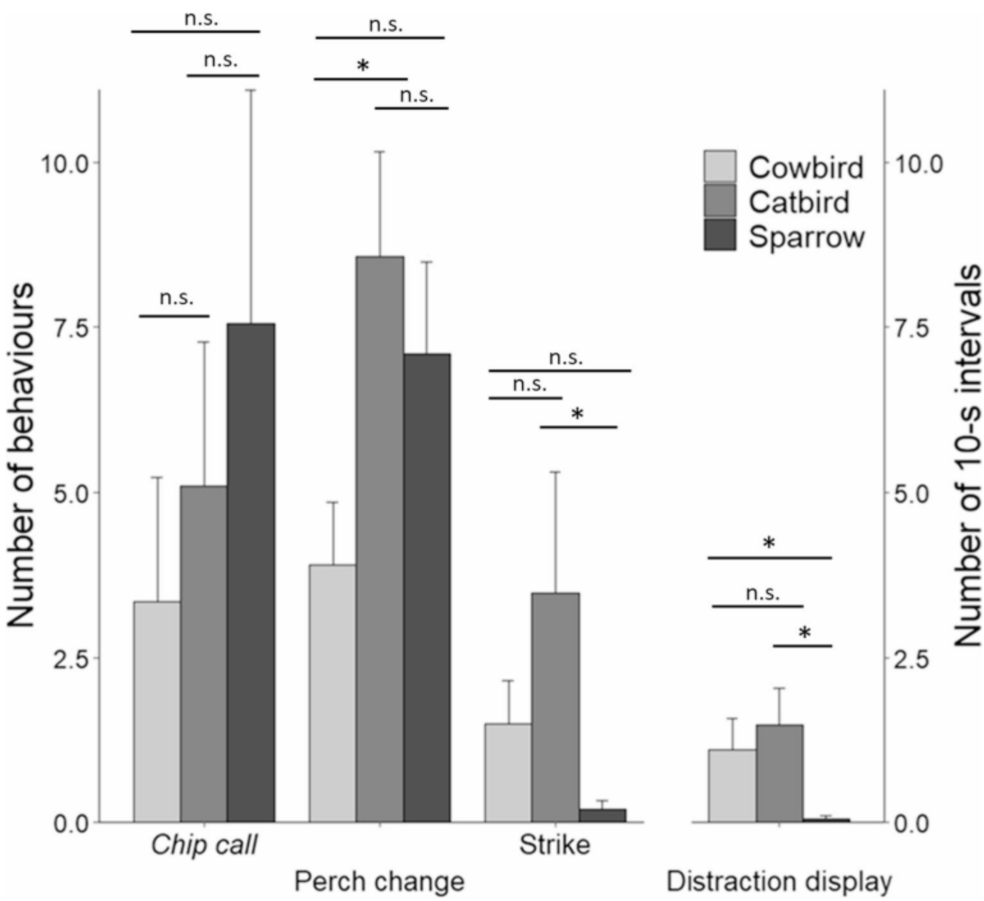

Fig. 2 Generic threat and anti-predator responses (mean + SE) of warblers during presentation of cowbird (n = 20), catbird (n = 21) and sparrow (n = 20) models. Post hoc statistical differences are indicated by * $P \leq 0.05$, n.s. $P > 0.05$

al. 2017), the exact predation pressure exerted by catbirds on yellow warblers at Delta Marsh remains unknown. Nevertheless, catbird abundance at the study site has been estimated at 12 nests/ha in 2000 (Underwood and Sealy 2006) and reported as generally high in studies (MacKenzie et al. 1982; Lorenzana and Sealy 2001), suggesting a high likelihood of frequent encounters between catbirds and warblers.

Warblers responded to the catbird model not only differently from cowbirds but also from nonthreatening sparrows. Although the number of *chip* calls and perch changes did not differ significantly among treatments, warblers performed more strikes and distraction displays when confronted with the catbird. This pattern is consistent with previous studies, showing that *chip* calls and perch changes are commonly elicited by both predators and nonthreatening intruders, whereas strikes and distraction displays, represent more direct attempts to deter nest predators (Hobson et al. 1988; Hobson and Sealy 1989; Gill and Sealy 1996, 2003; Sealy et al. 1998).

Our results suggest that cowbirds and catbirds are perceived as threats, but they elicited different responses, indicating that the reproductive costs associated with each threats type differ (Montgomerie and Weatherhead 1988; Pease and Grzybowski 1995). Although nest abandonment is a common response to both predation and parasitism (Sealy 1995; Guigueno and Sealy 2010), this decision depends on the perceived value of the remaining clutch. Nest predation typically results in partial or total clutch loss. In contrast, in cases of parasitism, warblers cannot correctly assess clutch value solely on the number or volume of eggs remaining in the nest (Rothstein 1982, 1986; Sealy 1992), as this does not account for the presence of a foreign egg, which they do not discriminate from their own (Lorenzana and Sealy 1998). However, raising a parasitized clutch entails substantial costs, combining reduced current reproductive success (Clark and Robertson 1981) with decreased future reproductive potential due to the time invested in parental care rather than renesting (Perrins 1970; Verhulst et al. 1995; Mermoz and Reboreda 1998). Therefore, the ability to recognize adult cowbirds as a distinct threat and to deploy an appropriate frontline defense early in the nesting cycle would likely reduce the risk of incurring these costs (Lawson et al. 2021a).

As yellow warblers responded to cowbirds as a unique threat to their nest, they must have learned to associate cowbirds with a specific cue distinct from predation risk directed at themselves or their offspring. The specific suite of responses directed toward cowbirds suggest that warblers associate cowbird egg removal with a negative reproductive outcome. This outcome occurs days after parasitism, when the cowbird chick hatches and host reproductive success is reduced or fails entirely due to parental care being monopolized by the parasitic chick (Lorenzana and Sealy 1999). Regardless of the underlying mechanism, warblers appear to possess a front-line defense, similar to that described in cuckoo hosts (Feeney et al. 2012), enabling them to discriminate brood parasites from nest predators (Clark and Robertson 1981; Burgham and Picman 1989). The mechanisms underlying the formation of such associations remain, however, unclear.

Studies of animal associative learning indicate that the probability of forming a link between a conditioned and an unconditioned stimulus declines as the temporal gap between them increases (Kalat and Rozin 1973; Campobello and Hare 2007), with most associations forming when events occur about within a short time window, even within one minute apart (Boakes and Costa 2014). In cuckoo systems, hosts may associate the species removing their egg with the simultaneous appearance of a foreign egg (Davies and Brooke 1989). In contrast, in cowbird systems, egg removal and egg laying occur at different days (Sealy 1992), making it less likely that hosts may associate these two events. When cues are temporally separated, different heterospecific intruders - such as nest predators that only remove eggs or brood parasites – may provide a similar functional information, potentially leading to similar responses. Instead, our results show that yellow warblers respond differently to these intruders, consistent with previous studies involving predators that also threaten host adults. Thus, although the initial association may be triggered by egg removal, selection for a cowbird-specific defense strategy may have been reinforced by the ultimate fitness consequences of parasitism. This may occur even if hosts cannot directly associate egg addition with reproductive failure, similar to cuckoo hosts that recognize odd egg but do not discriminate odd chicks from their own (Davies and Brooke 1989). This topic remains understudied and future research on yellow warblers and other cowbird hosts should clarify the extent to which associative learning play a role in shaping their nest defense strategies.

In conclusion, we provide evidence that yellow warblers discriminate between brood parasites and predators of nest contents, responding specifically to cowbirds, particularly through *seet* calls. Although this suggests that hosts form an association between cowbirds and a unique threat, the mechanisms underlying this association remain unresolved, especially given the temporal separation between egg removal and fitness costs of parasitism. Further studies are needed to investigate how hosts distinguish among heterospecifics intruders encountered at the nest during egg removal events.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-026-03755-z.

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Author contributions DC conceived and designed the study. DC collected the data. NR analyzed the data with assistance from DC. NR and DC wrote the manuscript with contributions from SGS. SGS and DC supervised the research. All authors contributed to the manuscript and approved the submitted version. We are grateful to four anonymous referees for providing valuable comments and suggestions.

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Data availability All raw data supporting the results of this study are provided as a CSV file in the Supplementary Material and are available to reviewers and readers without restriction.

Declarations

Ethics approval Field work at Delta Marsh was conducted under Canadian Wildlife Service Permit (CWS03 - M013) with animal ethics approval from the University of Manitoba's Committee on Animal Care (protocol no. F02-008/1, F04-044 ⁄ 45). The use of animals adheres to the guidelines set forth by the Animal Behavior Society.

Competing interests The authors declare no competing interests.

References

Barnard WH (1996) Juvenile Gray Jay preys upon Magnolia Warbler. J Field Ornithol 67:252–253

Boakes RA, Costa DSJ (2014) Temporal contiguity in associative learning: interference and decay from an historical perspective. J Exp Psychol Anim Learn Cogn 40:381–400. https://doi.org/10.1037/xan0000040

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Burgham MCJ, Picman J (1989) Effect of brown-headed cowbirds on the evolution of yellow warbler anti-parasite strategies. Anim Behav 38:298–308. https://doi.org/10.1016/s0003-3472(89)80091-0

Campobello D, Hare JF (2007) Information transfer determined by association of neighbours in European bee-eater (*Merops apiaster*) colonies. Ethol Ecol Evol 19:237–243. https://doi.org/10.1080/08927014.2007.9522565

Campobello D, Sealy SG (2010) Enemy recognition of reed warblers (*Acrocephalus scirpaceus*): threats and reproductive value act independently in nest defence modulation. Ethology 116:498–508. https://doi.org/10.1111/j.1439-0310.2010.01764.x

Campobello D, Sealy SG (2011a) Use of social over personal information enhances nest defense against avian brood parasitism. Behav Ecol 22:422–428. https://doi.org/10.1093/beheco/arq225

Campobello D, Sealy SG (2011b) Nest defence against avian brood parasites is promoted by egg-removal events in a cowbird-host system. Anim Behav 82:885–891. https://doi.org/10.1016/j.anbehav.2011.07.028

Campobello D, Sealy SG, Welbergen JA (2017) Anti-brood parasite defences: the role of individual and social learning. In: Soler M (ed) Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution. Springer, Cham, pp 421–436. https://doi.org/10.1007/978-3-319-73138-4_23

Clark H (2024) Loggerhead Shrike (Lanius ludovicianus) predation of a Horned Lark (Eremophila alpestris). West Wildl 11:9–10

Clark KL, Robertson RJ (1981) Cowbird parasitism and evolution of antiparasite strategies in the yellow warbler. Wilson Bull 93:249–258. https://www.jstor.org/stable/4161464

Colombelli-Negrel D, Robertson J, Sulloway FJ, Kleindorfer S (2010) Extended parental care of fledglings: parent birds adjust anti-predator response according to predator type and distance. Behaviour 147:853–870. https://doi.org/10.1163/000579510X495771

Dale S, Gustavsen R, Slagsvold T (1996) Risk taking during parental care: A test of three hypotheses applied to the pied flycatcher. Behav Ecol Sociobiol 39:31–42. https://doi.org/10.1007/s002650050264

Davidson AH (1994) Common grackle predation on adult passerines. Wilson Bull 106:174–175

Davies NB, Brooke MD (1989) An experimental-study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts.1. Host egg discrimination. J Anim Ecol 58:207–224. https://doi.org/10.2307/4995

Davies NB, Brooke MDL (1988) Cuckoos versus reed warblers: adaptations and counteradaptations. Anim Behav 36:262–284.https://doi.org/10.1016/S0003-3472(88)80269-0

Dubowy PJ (1985) Aerial capture of fledgling mourning dove by blue jay. Prairie Nat 17:40

Dure Ruiz NM, Fasanella M, Fernandez GJ (2018) Breeding southern house wrens exhibit a threat-sensitive response when exposed to different predator models. J Ethol 36:43–53. https://doi.org/10.1007/s10164-017-0528-6

Edelaar P, Wright J (2006) Potential prey make excellent ornithologists: adaptive, flexible responses towards avian predation threat by arabian babblers *Turdoides squamiceps* living at a migratory hotspot. Ibis 148:664–671. https://doi.org/10.1111/j.1474-919X.2006.00567.x

Feeney WE, Welbergen JA, Langmore NE (2012) The frontline of avian brood parasite-host coevolution. Anim Behav 84:3–12. https://doi.org/10.1016/j.anbehav.2012.04.011

Gill SA, Bierema AMK (2013) On the meaning of alarm calls: a review of functional reference in avian alarm calling. Ethology 119:449–461

Gill SA, Sealy SG (1996) Nest defence by yellow warblers: Recognition of a brood parasite and an avian nest predator. Behaviour 133:263–282. https://doi.org/10.1163/156853996X00143

Gill SA, Sealy SG (2003) Tests of two functions of alarm calls given by yellow warblers during nest defence. Can J Zool 81:1685–1690. https://doi.org/10.1139/Z03-162

Gill SA, Sealy SG (2004) Functional reference in an alarm signal given during nest defence: seet calls of yellow warblers denote brood-parasitic brown-headed cowbirds. Behav Ecol Sociobiol 56:71–80. https://doi.org/10.1007/s00265-003-0736-7

Goossen JP, Sealy SG (1982) Production of young in a dense nesting population of yellow warblers, *Dendroica petechia*, in Manitoba. Can Field Nat 96:189–199. https://doi.org/10.5962/p.354812

Guigueno MF, Sealy SG (2010) Clutch abandonment by parasitized yellow warblers: egg burial or nest desertion? Condor 112:399–406. https://doi.org/10.1525/cond.2010.090135

Hartig F (2020) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.3.3.0. https://search.r-project.org/CRAN/refmans/DHARMa/html/00Index.html?utm_source=chatgpt.com

Hauber ME (1998) Single-egg removal from an artiicial nest by the Gray Catbird. Wilson Bull 426–429

Helfman GS (1989) Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. Behav Ecol Sociobiol 24:47–58. https://doi.org/10.1007/bf00300117

Hobson KA, Bouchart ML, Sealy SG (1988) Responses of naive yellow warblers to a novel nest predator. Anim Behav 36:1823–1830

Hobson KA, Sealy SG (1989) Responses of yellow warblers to the threat of cowbird parasitism. Anim Behav 38:510–519

Johnson KW, Johnson JE (1976) An incident of blue jay predation on a yellow-rumped warbler. Wilson Bull 88:467

Kalat JW, Rozin P (1973) Learned safety as a mechanism in long-delay taste-aversion learning in rats. J Comp Physiol Psychol 83:198–207. https://doi.org/10.1037/h0034424

Kleindorfer S, Fessl B, Hoi H (2005) Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. Anim Behav 69:307–313. https://doi.org/10.1016/j.anbehav.2004.06.003

Królikowska N, Szymkowiak J, Laidlaw RA, Kuczyński L (2016) Threat-sensitive anti-predator defence in precocial wader, the northern lapwing Vanellus vanellus. Acta Ethol 19:163–171. https://doi.org/10.1007/s10211-016-0236-1

Kuehn MJ, Peer BD, McCleery RA, Rothstein SI (2016) Yellow warbler defenses are retained in the absence of brood parasitism but enhanced by experience with cowbirds. Behav Ecol 27:279–286. https://doi.org/10.1093/beheco/arv145

Lawson SL, Enos JK, Antonson ND, Gill SA, Hauber ME (2021a) Do hosts of avian brood parasites discriminate parasitic vs. predatory threats? A meta-analysis. Adv Stud Behav 53:63–95. https://doi.org/10.1016/bs.asb.2021.03.002

Lawson SL, Enos JK, Mendes NC (2021b) Pairing status moderates both the production of and responses to anti-parasitic referential alarm calls in male yellow warblers. Ethology 127:385–394. https://doi.org/10.1111/eth.13139

Lenth RV (2021) emmeans: Estimated marginal means, aka least-squares means, version 1.6.3. https://www.rdocumentation.org/packages/emmeans/versions/1.6.3?utm_source=chatgpt.com

Lorenzana JC, Sealy SG (1998) Adult brood parasites feeding nestlings and fledglings of their own species: A review. J Field Ornithol 69:364–375. http://www.jstor.org/stable/4514331

Lorenzana JC, Sealy SG (1999) A meta-analysis of the impact of parasitism by the brown-headed cowbird on its hosts. Stud Avian Biol 18:34

Lorenzana JC, Sealy SG (2001) Fitness costs and benefits of cowbird egg ejection by gray catbirds. Behav Ecol 12:325–329

MacKenzie DI (1982) The dune-ridge forest, Delta Marsh, Manitoba: overstory vegetation and soil patterns. Can Field Nat 96:61–68

MacKenzie DI, Sealy SG, Sutherland GD (1982) Nest-site characteristics of the avian community in the dune-ridge forest, Delta Marsh, Manitoba: a multivariate analysis. Can J Zool 60:2212–2223

Mathot KJ, van den Hout PJ, Piersma T (2009) Differential responses of red knots, *Calidris canutus*, to perching and flying sparrowhawk, *Accipiter nisus*, models. Anim Behav 77:1179–1185. https://doi.org/10.1016/j.anbehav.2009.01.024

Maziarz M, Piggott C, Burgess M (2018) Predator recognition and differential behavioural responses of adult wood warblers *Phylloscopus sibilatrix*. Acta Ethol 21:13–20. https://doi.org/10.1007/s10211-017-0275-2

Menzel R (2013) Learning, memory, and cognition: animal perspectives. In: Galizia C, Lledo PM (eds) Neurosciences – from molecule to behavior: a university textbook. Springer, Berlin, pp 447–470. https://doi.org/10.1007/978-3-642-10769-6_28

Mermoz ME, Reboreda JC (1998) Nesting success in brown-and-yellow Marshbirds: Effects of timing, nest site, and brood parasitism. Auk 115:871–878. https://doi.org/10.2307/4089506

Montgomerie RD, Weatherhead PJ (1988) Risks and rewards of nest defence by parent birds. Q Rev Biol 63:167–187. http://www.jstor.org/stable/2830999

Neudorf DL, Sealy SG (1992) Reactions of four passerine species to threats of predation and cowbird parasitism: enemy recognition or generalized responses? Behaviour 123:84–105

Pease CM, Grzybowski JA (1995) Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. Auk 112:343–363

Peer BD, Bollinger EK (2020) Common Grackle (*Quiscalus quiscula*), version 1.0. In: Poole AF, Gill FB (eds) Birds of the world. Cornell Lab of Ornithology, Ithaca, NY. https://doi.org/10.2173/bow.comgra.01

Perrins CM (1970) The timing of birds' breeding seasons. Ibis 112:242–255. https://doi.org/10.1111/j.1474-919X.1970.tb00096.x

R Core Team (2021) R: A language and environment for statistical computing, version 4.1.1. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rivers JW, Sandercock BK (2004) Predation by gray catbird on brown thrasher eggs. Southwest Nat 49:101–103. https://doi.org/10.1894/0038-4909(2004)049<0101:PBGCOB>2.0.CO;2

Rothstein SI (1982) Successes and failures in avian egg recognition with comments on the utility of optimality reasoning. Am Zool 22:547–560. https://doi.org/10.1093/icb/22.3.547

Rothstein SI (1986) A test of optimality: egg recognition in the Eastern Phoebe. Anim Behav 34:1109–1119. https://doi.org/10.1016/S0003-3472(86)80170-1

Schneider NA, Griesser M (2013) Incubating females use dynamic risk assessment to evaluate the risk posed by different predators. Behav Ecol 24:47–52. https://doi.org/10.1093/beheco/ars134

Sealy SG (1992) Removal of yellow warbler eggs in association with cowbird parasitism. Condor 94:40–54. https://doi.org/10.2307/1368794

Sealy SG (1994) Observed acts of egg destruction, egg removal, and predation on nests of passerine birds at Delta Marsh, Manitoba. Can Field-Nat 108:41–51

Sealy SG (1995) Burial of cowbird eggs by parasitized yellow warblers: an empirical and experimental-study. Anim Behav 49:877–889. https://doi.org/10.1006/anbe.1995.0120

Sealy SG, Neudorf DL, Hobson KA, Gill SA (1998) Nest defence by potential hosts of the brown-headed cowbird: methodological approaches, benefits of defence, and coevolution. In: Rothstein SI, Robinson SK (eds) Parasitic birds and their hosts. Oxford University Press, New York, pp 194–211

Shettleworth SJ (1998) Cognition, Evolution, and Behavior. Oxford University Press, New York

Smith RJ, Hatch MI, Cimprich DA, Moore FR (2020) Gray catbird *(Dumetella carolinensis)*, version 1.0. In: Poole AF (ed) Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.grycat.01

Sovrano LV, Lorenzón RE, León EJ, Beltzer AH, Giraudo AR (2024) Sex-dependent recognition and behavior against nest predators and brood parasites by chestnut-capped blackbird *Chrysomus ruficapillus*. Behav Ecol Sociobiol 78:84. https://doi.org/10.1007/s00265-024-03498-9

Strnad M, Nemec M, Vesely P, Fuchs R (2012) Red-backed shrikes (*Lanius collurio*) adjust the mobbing intensity, but not mobbing frequency, by assessing the potential threat to themselves from different predators. Ornis Fenn 89:206–215. https://doi.org/10.51812/of.133807

Teunissen N, Kingma SA, Peters A (2020) Nest defence and offspring provisioning in a cooperative bird: individual subordinates vary in total contribution, but no division of tasks among breeders and subordinates. Behav Ecol Sociobiol 74:94. https://doi.org/10.1007/s00265-020-02877-2

Trnka A, Grim T (2014) Dynamic risk assessment: does a nearby breeding nest predator affect nest defence of its potential victim? J Ethol 32:103–110. https://doi.org/10.1007/s10164-014-0400-x

Tvardíková K, Fuchs R (2011) Do birds behave according to dynamic risk assessment theory? A feeder experiment. Behav Ecol Sociobiol 65:727–733. https://doi.org/10.1007/s00265-010-1075-0

Underwood TJ, Sealy SG (2006) Influence of shape on egg discrimination in American robins and gray catbirds. Ethology 112:164–173

Verhulst s, van Balen JH, Tinbergen JM (1995) Seasonal decline in reproductive success of the great tit - Variation in time or quality. Ecology 76:2392–2403. https://doi.org/10.2307/2265815

Walters JR (1990) Antipredatory behavior of lapwings - field evidence of discriminative abilities. Wilson Bull 102:49–70. http://www.jstor.org/stable/4162824