Behavioral Ecology, 2026, 37, arag089
https://doi.org/10.1093/beheco/arag089
Published: 29 July 2026
Original article

Red-winged blackbirds adjust aggression with brood value and predator type, but show broadly similar responses to snake predators of differing risk

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Handling Editor: Mark Briffa

Parental investment theory predicts parents should scale investment in defending offspring with the offspring's value and the risk a predator poses to offspring versus adults. While this framework has been widely applied to nest defense against avian and mammalian predators, how it extends to snake predators—which endanger both nests and adults, and vary in their capacity to envenomate—remains unexplored. We examined how red-winged blackbirds (*Agelaius phoeniceus*) respond to nest predators, including venomous and non-venomous snakes, testing whether aggression intensity and type varies across predators and nest stage. Parental investment theory predicts that defense intensity increases with brood value, and that birds adjust the type of aggression used depending on whether predators pose higher risk to the adults, such as reducing physical aggression toward higher-risk predators. We found that blackbirds displayed stronger aggression toward predators compared to the control, and that aggression toward brood parasites declined during the nestling stage, consistent with decreasing parasitism risk, whereas responses to nest predators increased with nest age. Type of aggression was broadly consistent across predators, including 2 snake stimuli, suggesting blackbirds did not strongly alter overall defensive behavior toward snakes despite their elevated potential risk to adults. However, birds delivered fewer physical strikes to the rattlesnake than the gopher snake, indicating that particularly risky defensive behaviors may be modulated selectively. Responses to different threats were similar between sexes but reflected sex-specific differences in defense and parental care. Neighboring birds frequently joined defenses, suggesting cooperative risk management. Together, our findings suggest that blackbirds adjust overall defense intensity according to offspring value and predator context, while selectively modulating particularly costly defensive behaviors.

Keywords nest defense, parental investment theory, predator recognition, antipredator behavior, model presentation

Introduction

Recognizing and responding to dangerous stimuli are crucial for survival and reproduction. Predation is the leading cause of reproductive failure across species, shaping behavioral and morphological traits across taxa, including defense of offspring (reviewed in Caro 2005; Lima 2009; Martin and Briskie 2009; Ibáñez-Álamo et al. 2015). When defending against predators, parents must weigh risks to their offspring against risks to themselves. Parental investment theory predicts that selection should favor flexible antipredator behavior that is dependent on the type and degree of threat posed to both parent and offspring. Indeed, context-dependent parental defense has been observed across diverse taxa (eg Regelmann and Curio 1986; Montgomerie and Weatherhead 1988; Caro 2005; Fontaine and Martin 2006; Lima 2009). For example, ground squirrels harass snakes more aggressively when offspring are at greatest risk or when predators are perceived as less dangerous to the adult (Rowe and Owings 1996; Swaisgood et al. 2003). Similarly, sand goby fathers balance nest defense against egg ventilation (Lissåker and Kvarnemo 2006), and cooperative cichlids partition anti-predator defense according to whether intruders threaten eggs, young, or adults (Josi et al. 2020). Tropical skinks will defend against egg-eating snakes but abandon nests when predators pose substantial risk to the adult female (Huang and Wang 2009).

Passerine birds are particularly suited for testing questions related to parental investment and anti-predator behavior because they have altricial young that are highly vulnerable, and the risks posed to parents and offspring vary substantially with predator type and nest stage. For example, nest predators such as small mammals and corvids pose little risk to adults but high risk to offspring, whereas raptors and large predators may endanger both offspring and parents, or even parents exclusively (eg Montgomerie and Weatherhead 1988). Breeding birds also face specialized threats like brood parasites, which pose no risk to adults but impose high costs on offspring if parasitism occurs early in nesting

Received: November 14, 2025. **Revised:** June 15, 2026. **Accepted:** June 17, 2026.
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(laying/incubation) (Neudorf and Sealy 1992; Gill and Sealy 1996; Fasanella and Fernández 2009; Lawson et al. 2021a).

Within parental investment theory, several mechanisms can shape how parents adjust their investment in offspring defense. The offspring value hypothesis predicts that defense intensity should scale with brood value (Trivers 1974; Montgomerie and Weatherhead 1988). As offspring age and approach independence, their reproductive value increases, and parents should take greater risks to protect them (reviewed in Caro 2005; eg Redmond et al. 2009). In contrast, the offspring vulnerability hypothesis predicts the opposite pattern: that parents should invest more heavily in earlier stages when offspring are most vulnerable to predation, and less capable of escaping or surviving attacks (Trivers 1974; Montgomerie and Weatherhead 1988). Empirical studies across passerines have generally supported the offspring value hypothesis, showing that parents increase defensive risk-taking as broods mature, and adjust both the intensity and type of antipredator behavior according to brood value and risk to themselves (eg Gottfried 1979; McLean and Rhodes 1991; Winkler 1992; Ghalambor and Martin 2000; Schaef and Mumme 2012; Mahr et al. 2015; Dure Ruiz et al. 2018; Teunissen et al. 2020; Lawson et al. 2021a, 2021c; Eggleston et al. 2025).

Parents can use alternative tactics to calibrate their investment in risk versus reproduction. Vocal responses such as alarm calls warn conspecifics, may recruit mobbing allies, and are generally less costly than physical attacks, which increase the risk of injury to the adult (Knight and Temple 1988; Kleindorfer et al. 2003; Eggleston et al. 2025). Parents may also reduce provisioning rates or delay returns to the nest after predator encounters, minimizing risk exposure to themselves and their offspring (Ghalambor et al. 2013; Mutzel et al. 2013; Dure Ruiz et al. 2018). For instance, parents may take longer to return to feed nestlings after exposure to a raptor predator that threatens both nestlings and adults compared with a predator that threatens only the offspring (Schaef and Mumme 2012; Ghalambor et al. 2013). Defensive responses can also impose substantial time and energetic costs, reducing provisioning rates, delaying incubation, and increasing energetic expenditure to ward off predators. Thus, parental investment decisions during predator encounters reflect not only risk-sensitive behavior, but also the allocation of limited time and energy between current offspring care and self-maintenance.

Fine-scale discrimination among specific threats would let parents adaptively tune defensive behaviors, but may also be constrained by cognitive or sensory limits. The avian capacity for discrimination and behavioral adjustment remains an open topic of investigation. Most studies have examined parental defense investment when facing avian and mammalian nest predators, but few have explored how these trade-offs extend to other predator classes such as snakes, despite their importance as nest predators in North America (DeGregorio et al. 2014; Barends and Maritz 2022).

Snakes are often primarily a threat to eggs and nestlings but, unlike most small mammals or birds, they can also pose risk to adults, especially if they are larger, creating potential ambiguity in how parents should respond. A few studies suggest snakes are treated similarly to other nest predator classes (eg small mammals and birds that pose high risk to offspring, low risk to adults) despite the increased risk to adults, eliciting strong vocal *and* physical aggression from the defending parents (eg Kleindorfer et al. 2005; Mahr et al. 2015; Eggleston et al. 2025; Liu et al. 2025). For example, blue tits (*Cyanistes caeruleus*) consistently produced alarm calls to all predator types presented, but directed more physical aggression toward snakes and woodpeckers than toward hawks, which pose higher risk to adults (Mahr et al. 2015). House wrens (*Troglodytes aedon*) also vocalized strongly toward all predator types, but reduced physical aggression toward hawks in comparison to snakes and chipmunks (Eggleston et al. 2025). Similar patterns have been observed in mustached warblers (*Acrocephalus melanopogon*) and reed warblers (*Acrocephalus scirpaceus*) (Kleindorfer et al. 2005). These findings suggest snakes are treated as threats to offspring, but not adults. However, these experiments only compared responses to snakes versus other predators during the nestling stage, when parents are typically more willing to take risks to defend young. Snakes are phenotypically and ecologically diverse, and may merit different responses across different stages of offspring development.

Red-winged blackbirds (*Agelaius phoeniceus*) are aggressive nest defenders with a broad geographic range across North America, on which many prior studies of predator recognition and nest defense have been tested (Beletsky et al. 1986; Knight and Temple 1988; Yasukawa 1989; Neudorf and Sealy 1992; Yasukawa and Searcy 1995; Henger and Hauber 2014; Lawson et al. 2020, 2021b). Blackbirds have been shown to adjust vocal and physical aggression according to predator type and nest stage, consistent with parental investment theory (Knight and Temple 1988; Neudorf and Sealy 1992; Henger and Hauber 2014; Shew et al. 2016; Lawson et al. 2020, 2021b). Red-winged blackbirds also experience significant nest predation from snakes (DeGregorio et al. 2014; Barends and Maritz 2022). Biermann and Robertson (1981) found that female red-winged blackbirds responded more intensely to a green-and-black snake model when they had nestlings compared to eggs, but these responses were not compared against other predator types or controls, nor was the model visually representative of a sympatric species of snake. As such, how blackbirds recognize and weigh the risks of ecologically relevant snakes across nesting stages remains unknown.

We presented models of mammalian, corvid, and ophidian nest predators, along with brood parasites and controls, at nests of breeding red-winged blackbirds across nest stages, and measured behavioral responses of adults. Incorporating snakes that differ in their potential danger to defending adults, alongside well-studied nest predators such as corvids, small mammals, and brood parasites that primarily threaten offspring, allowed us test how finely blackbirds modify their investment in offspring defense according to predator type.

We tested the predictions that blackbirds would (i) increase nest-defense intensity across the nesting cycle toward all nest predators as brood value increased (except for the brood parasite, for which the opposite pattern is predicted), (ii) employ vocal aggression toward the snake stimuli earlier in nesting, and shift to physically risky behaviors (eg swoops and strikes) later in nesting, reflecting greater willingness to incur personal risk for valuable offspring, and (iii) exhibit greater caution toward the venomous rattlesnake than the nonvenomous gopher snake if blackbirds respond to viperid venom-associated cues, consistent with risk assessment balancing self-preservation against offspring defense.

Materials and methods

Sites and nest monitoring

The study took place in 2025 across 12 sites that varied in size and habitat structure around Corvallis, Oregon, USA. Red-winged blackbird nesting occurred in marsh and wetland habitats at these sites,

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consisting of stands of reeds (*Phragmites* spp.), cattails (*Typha* spp.), and various mesic grasses and sedges, often located along or within bodies of water. Red-winged blackbirds nested from early April through late June, with peak breeding activity occurring in mid-to-late May. We systematically searched each site 1 to 2 times per week to locate active nests, and monitored their contents until fledging or failure, tracking age of nest and nestlings (if applicable) during trials. If reason for failure could be determined it was recorded. The number of nests sampled per site varied, ranging from 1 to 9.

In our sites in Oregon, non-venomous Pacific gopher snakes (*Pituophis catenifer catenifer*) are a major nest predator (Morrison and Bolger 2002; Rodríguez-Robles 2002; Patten and Bolger 2003). Gopher snakes are thought to mimic venomous western rattlesnakes (*Crotalus oreganus*), as these species differ little in pattern and coloration, with head shape, body thickness, and the presence of a rattle serving as the main distinguishing cues. Western rattlesnakes were historically present in the region but were largely extirpated west of the Cascades in the 19th century, though pockets of populations remain. As a result, local blackbird populations are unlikely to have direct experience with rattlesnakes during breeding season (though they likely encounter similar viperids during migration and overwintering). Any ability to discriminate between the 2 species could reflect either innate recognition or generalization of viperid traits. This resemblance to gopher snakes presented a compelling opportunity to explore whether blackbirds are sensitive to viperid-associated features that would indicate high risk to adults, even when ecological experience is limited.

Model stimuli

For our experiment we presented 6 different model stimuli at active blackbird nests: (i) California Scrub Jay (*Aphelocoma californica*, sympatric nest predator, minor risk to adults; hereafter: scrub jay), (ii) California Ground Squirrel (*Otospermophilus beecheyi*, sympatric nest predator, minor risk to adults; hereafter: ground squirrel), (iii) Pacific gopher snake (sympatric nest predator, intermediate risk to adults; hereafter: gopher snake), (iv) western rattlesnake (historically sympatric, now largely allopatric nest predator, high risk to adults; hereafter: rattlesnake), (v) brown-headed cowbird (*Molothrus ater*, sympatric brood parasite, no risk to adults; hereafter: cowbird), and (vi) song sparrow (*Melospiza melodia*, innocuous heterospecific control, ie sympatric with red-winged blackbirds) (Table 1). Risk classifications were based on the likelihood that predators could injure defending adult blackbirds during nest defense encounters. Both snake species are capable of injuring adult birds, but the rattlesnake was considered relatively more dangerous due to the added risk of envenomation. Because both snakes are similar in size, this distinction was based primarily on morphological differences rather than direct evidence of differential predation on adult blackbirds. Mammalian and avian nest predators, as well as brood parasites, were classified as low- or no-risk stimuli because they pose comparatively little direct threat to defending adults.

Table 1 Nest predator models presented at red-winged blackbird nests with their corresponding risk to offspring and adults.

Treatment	Risk to offspring	Risk to parents
Scrub jay	High	Low
Ground squirrel	High	Low
Gopher snake	High	Medium
Rattlesnake	High	High
Cowbird	High	None
Song sparrow	None	None

We aimed for stimuli to be as realistic as possible (Fig. 1). The rattlesnake and gopher snake models were rubber replicas (~36 in length, *Amazon.com*) representing large adult sizes of each species, capable of raiding nests and injuring/killing adult birds. While similar in size, the rattlesnake model differed from the gopher snake in a few key traits: a thicker body, triangular head, and the presence of a rattle, all features that differentiate rattlesnakes from gopher snakes. We used acrylic paint (*Liquitex*) to match the reflectance spectra of frozen specimens (which accurately preserves reptile colors) of each species, which were nearly identical. We used the same pattern on each specimen, representative of wild individuals, and adjusted for differences in shape.

The bird models were wool-felted replicas handmade to match the size and plumage coloration of each species (obtained via Etsy seller *BirdlandGifts*). For the brown-headed cowbird we specifically used a female model, as hosts primarily recognize and respond aggressively to cues of the female, which poses a direct threat of brood parasitism, as opposed to the male (eg Gill et al. 1997). The ground squirrel model was a realistic plush (obtained from *Hansa Toys*) that we custom-painted to match the pelage coloration of that species.

Trial design and procedure

Trials were conducted between 06:00 and 12:00, when avian activity is typically highest. Each model stimulus was mounted on a black metal stand and secured in place with Velcro. The stand height was adjusted to align with the nest height for each trial. For nests over water, a weighted base was used to ensure stability.

Birds were unbanded, so to maintain independence among observations we only tested nests ≥30 m apart, as this distance exceeds the average male territory diameter for this species in marsh habitats (Yasukawa and Searcy 1995). Red-winged blackbirds are polygynous, and males often maintain multiple nests with different females on their territory. To identify the focal female for each trial, we observed the nest from a distance before and during trials; the female that either incubated eggs (incubation stage) or fed chicks (nestling stage) was designated as the focal female. If multiple males responded to stimuli, we designated the male seen interacting most with the focal female and/or focal nest (eg feeding mate/chicks, mate-guarding, cooperatively defending nest) as the focal male.

Focal pairs received 3 of the 6 treatments in a psueudorandomized block design to prevent order effects. Trials conducted on the same day were separated by a minimum of 1 h, with a maximum of 24 h between trials at the same nest. Nests received 1 to 3 trials per day. All trials occurred during either the incubation or nestling stage; no nests were retested across stages or transitioned across stages between trials.

Stimuli were concealed beneath a burlap sheet before the start of each trial. An observer would approach the nest with the covered model and stand, place the stand 2 m from the focal nest, and uncover it before retreating to join a second observer positioned at least 15 m away, after which the trial would start. Trials lasted 5 min, during which all behaviors of the focal male and female within a 30 m radius of the stimulus were recorded. If neither bird was present within 30 m at the start, we waited until 1 parent entered the radius before starting

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Figure 1 Models of nest predators representing varying risk to adults, presented at red-winged blackbird nests during incubation and nestling stage. From left to right (top row): gopher snake, western rattlesnake, California ground squirrel. From left to right (bottom row): California scrub jay, brown-headed cowbird, and song sparrow.

the trial. In 2 instances the stand was placed 5 m from the nest instead of 2 m due to difficult terrain; however, blackbirds still responded similarly to the stimuli in these trials.

During trials we recorded: latency (s) to respond (time until first alarm call, aggressive posture, swoop, or strike at the model), total number of alarm calls produced, number of swoops at the model, number of physical strikes (including full-body strikes, attacks with feet, and pecks), and closest approach to the model (m). We also recorded other variables of interest including whether the female returned to the nest during the trial, total number of blackbirds responding, nest age (with start of incubation being day 0), date (used to determine day in the season), and time of day. If nests were found during or after incubation, we designated hatch day as day 12, since that is the average length of incubation in this species.

Analysis

We used a principal component analysis (PCA) to reduce the dimensionality of our behavioral metrics and capture correlated variation across alarm calls, swoops, strikes, and latency to respond. To ensure that all behaviors aligned in the same direction of increasing aggression, before conducting the PCA we transformed latency by subtracting the observed value from the total trial duration (300 s), such that higher values reflected faster responses and increased aggression.

We extracted PC1 and PC2 from the PCA, and used these components as response variables in 2 Gaussian GLMMs. Each model included stimulus treatment, nest stage (incubation vs. nestling), sex of the bird, nest age, day in season, and trial order as fixed effects, along with nest ID as a random intercept. A stimulus × nest stage interaction was included to test whether birds altered their responses to different predator types based on the vulnerability of their offspring. Interaction terms were dropped when non-significant.

Closest approach was excluded from the PCA because it reduced the variance explained by PC1 and PC2, and weakened the interpretability of the components when included; it was instead analyzed separately as a complementary measure of threat response, using a Gamma GLMM with log link, with the same fixed and random effects as the PCA models. We added a small constant to approach values (0.001) to allow use of the Gamma distribution, which does not permit zeros (from birds making contact with the stimulus).

Other response variables were analyzed using different GLMMs: (i) In addition to the PCA, strike data for the 2 snake stimuli was also analyzed separately using a generalized linear mixed model with a negative binomial distribution including NestID as a random effect. Physical strikes represent the highest-risk form of nest defense toward snake predators, and may therefore reveal variation in risk-sensitive behavior that is not fully captured by aggregate aggression metrics. (ii) Female return to the nest (yes/no) was analyzed using a binomial GLMM, with stimulus treatment and nest stage as fixed effects, and nest ID as a random effect. To prevent overfitting given the binary nature of the data, no additional covariates were included. (iii) Total number of blackbirds responding was analyzed using a Poisson GLMM with a log link. Stimulus treatment and nest stage were included as fixed effects, while nest ID, trial order, and site were random effects to account for differences in bird density across locations. We used post hoc Tukey tests to assess pairwise comparisons within predictors that were significant in the model. All statistical tests were conducted in the statistical program R 4.5.1 [packages glmmTMB

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(Brooks et al. 2017), car (Fox & Weisberg 2024), emmeans (Lenth 2025), performance (Lüdecke et al. 2021), and stats]., with $\alpha = 0.05$.

Permits

These studies were approved by the animal ethics committee (IACUC) of Oregon State University (#IACUC-2024-0526), and by USA federal (#MBPER13990444) and Oregon State Fish and Wildlife (#568) agencies.

Results

We presented stimuli at 40 nests (stage: incubation $n = 21$, nestling $n = 19$), resulting in 115 total trials across our 6 treatments: gopher snake (incubation = 10, nestling = 9), ground squirrel (incubation = 11, nestling = 9), rattlesnake (incubation = 10, nestling = 8), scrub jay (incubation = 11, nestling = 11), cowbird (incubation = 8, nestling = 9), and song sparrow (incubation = 10, nestling = 9). For the majority of trials we were able to gather behavioral responses from both focal birds, though there were several trials where only one of the birds from the focal pair was present within the trial radius (Absent birds from trials: incubation = 2M, 2F; nestling = 2M, 3F). Three nests did not receive all 3 trials because they were depredated or abandoned between trials.

PCA

The first 2 principal components explained 78.3% of the total variance. PC1 (eigenvalue = 2.09, 52.2% variance explained) loaded strongly across all 4 behavioral metrics, while PC2 (eigenvalue = 1.04, 26.1% variance explained) loaded positively for physical behaviors (swoops and strikes) but negatively for vocal behaviors (alarm calls and latency to respond, which was nearly always triggered by alarm calls rather than physical behaviors) (Table 2). Therefore, PC1 represents overall aggression toward the stimuli, with larger values indicating greater aggression. In contrast, PC2 reflects aggression type, with larger values indicating more physical aggression relative to vocal aggression.

PC1: general aggression

The GLMM revealed significant effects of stimulus treatment (likelihood ratio test [LRT]: $\chi^2_5 = 99.94$, $P < 0.001$) and the stimulus × nest-stage interaction (LRT: $\chi^2_5 = 28.77$, $P < 0.001$) on aggression scores, whereas nest stage alone was not significant (LRT: $\chi^2_5 = 2.22$, $P = 0.13$). Post hoc pairwise comparisons of least-square means for the stimulus × stage interaction indicated that responses to predator models varied across nesting stages (Fig. 2).

Table 2 Principal component loadings for the 4 included behavioral metrics.

	PC1	PC2
Calls	0.5524	−0.3236
Swoops	0.5633	0.3192
Strikes	0.4506	0.6042
Latency	0.4176	−0.6544

PC1 reflects overall nest defense intensity (general aggression), with high positive loadings for all behaviors. PC2 captures variation in physical aggression (strikes and swoops) versus vocal and latency responses, with opposing signs indicating different defensive behaviors.

During incubation, birds displayed significantly higher aggression toward all nest predator and brood parasitic stimuli than toward the song sparrow control. During nestling stage, aggression remained elevated toward all predator stimuli relative to the control, except for the cowbird. Within this stage, birds showed more aggression toward the gopher snake, ground squirrel, and rattlesnake compared to the cowbird, and more aggression toward the gopher snake than to the scrub jay. All other pairwise comparisons within stages were non-significant (Table S1). Across nesting stages, aggression toward cowbirds was significantly higher during incubation stage, when nests are most vulnerable to parasitism, than during nestling stage ($t(204) = 3.44$, $P < 0.001$). Aggression toward all other stimuli did not vary significantly between stages (Table S2).

Aggression also varied by sex (LRT: $\chi^2_1 = 17.95$, $P < 0.001$), with males displaying higher aggression overall ($t(204) = 4.23$, $P < 0.001$). There was no effect of day in season (LRT: $\chi^2_1 = 0.38$, $P = 0.53$) or trial order (LRT: $\chi^2_2 = 5.36$, $P = 0.06$). However, nest age significantly predicted aggression (LRT: $\chi^2_1 = 4.28$, $P < 0.05$), with birds becoming more aggressive as their nests aged (slope = 0.096 ± 0.046 SE, 95% confidence interval [CI] = 0.004 to 0.188).

PC2: aggression type

There was no stimulus × nest-stage interaction (LRT: $\chi^2_5 = 2.12$, $P = 0.83$). The model without the interaction revealed that stimulus treatment significantly affected the type of aggression displayed ($\chi^2_5 = 40.51$, $P < 0.001$) (Fig. 3). Post hoc pairwise comparisons revealed birds were more physically aggressive toward all nest predators than the song sparrow control, but that no pairwise comparisons between predator stimuli were significant (Table S3). Trial order also significantly influenced PC2 (LRT: $\chi^2_2 = 7.63$, $P = 0.02$), with birds becoming more physically aggressive by the last trial compared with the first ($z = 2.31$, $P = 0.05$). Neither nest stage (LRT: $\chi^2_1 = 1.69$, $P = 0.19$), sex (LRT: $\chi^2_1 = 0.20$, $P = 0.65$), nest age (LRT: $\chi^2_1 = 0.006$, $P = 0.93$), nor day in season (LRT: $\chi^2_1 = 0.02$, $P = 0.86$) significantly influenced PC2.

Strikes

The model comparing physical strikes directed toward the 2 snake stimuli found that birds struck the gopher snake significantly more often than the rattlesnake ($\chi^2 = 11.23$, $P < 0.001$). Across all trials, blackbirds directed over 80 strikes toward the gopher snake but only a single strike toward the rattlesnake (Fig. 4).

Closest approach

We found no significant stimulus × nest-stage interaction (LRT: $\chi^2_5 = 3.31$, $P = 0.65$); thus, the interaction term was removed and the model re-run. The final model revealed a significant effect of stimulus treatment on how closely birds approached (LRT: $\chi^2_5 = 16.21$, $P < 0.01$). Post hoc pairwise comparisons showed that birds approached more closely when the stimulus was a gopher snake, ground squirrel, or rattlesnake compared with the song sparrow control. All other pairwise comparisons were non-significant (Table S4).

Sex significantly affected approach distance (LRT: $\chi^2_1 = 4.62$, $P < 0.05$), with females approaching more closely than males ($z = -2.14$, $P < 0.05$). Neither nest stage (LRT: $\chi^2_1 = 0.92$, $P = 0.33$), nest age (LRT: $\chi^2_1 = 1.03$, $P = 0.30$), day in season (LRT: $\chi^2_1 = 0.52$, $P = 0.46$), nor trial order (LRT: $\chi^2_2 = 0.13$, $P = 0.93$) significantly influenced approach behavior.

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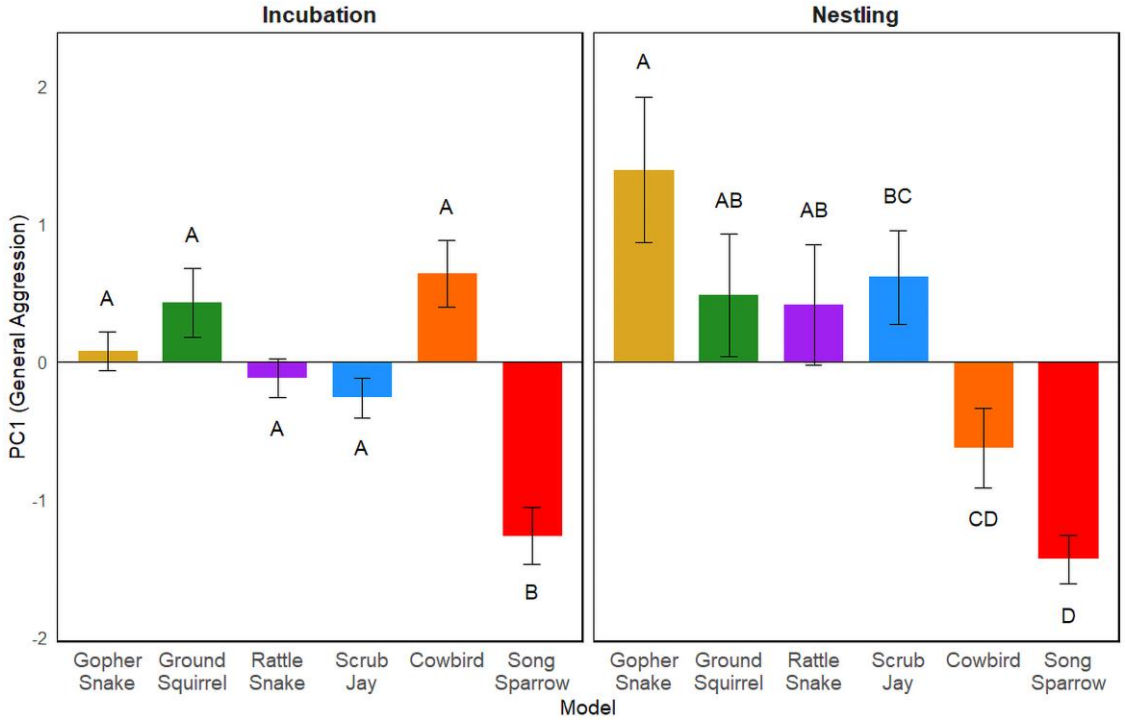

Figure 2 General aggression by breeding blackbirds toward various nest predator models. Model treatment and the model × stage interaction significantly predicted overall aggression. Error bars show ± 1 SE. Letters denote significant differences between treatments *within* each nest stage. Across stages, aggression toward cowbirds significantly declined from incubation to nestling stage.

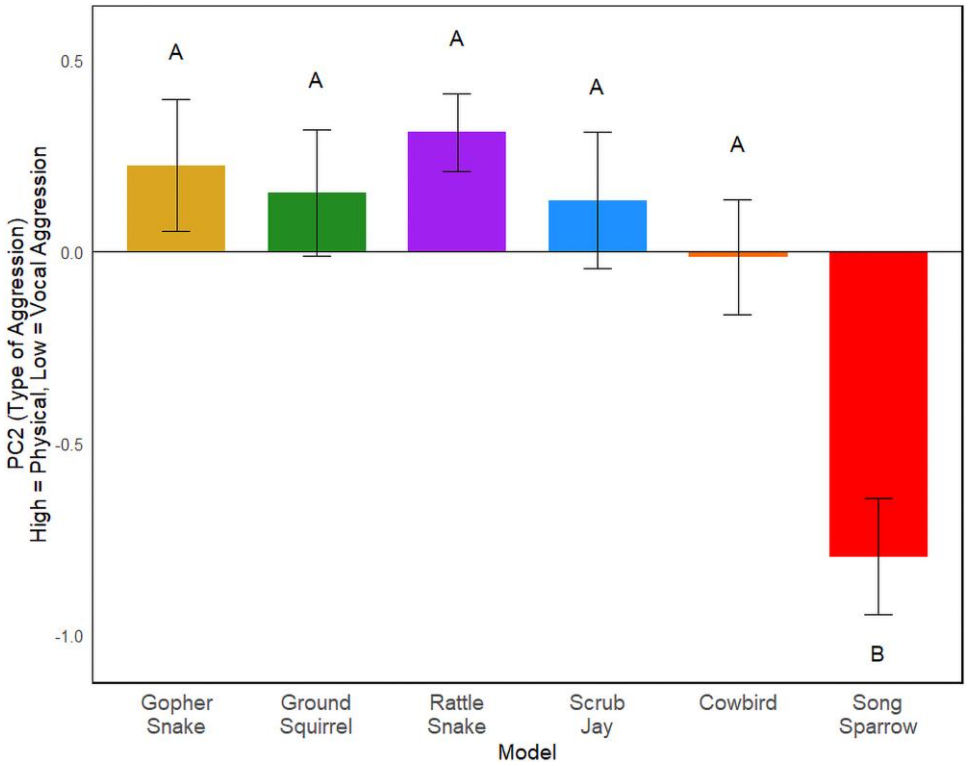

Figure 3 Vocal versus physical aggression by breeding blackbirds toward various nest predator models. Larger values indicate more physical aggression, while smaller values reflect predominantly vocal responses. Model treatment significantly predicted aggression type. Error bars show ± 1 SE. Letters denote significant differences among model treatments in post hoc comparisons.

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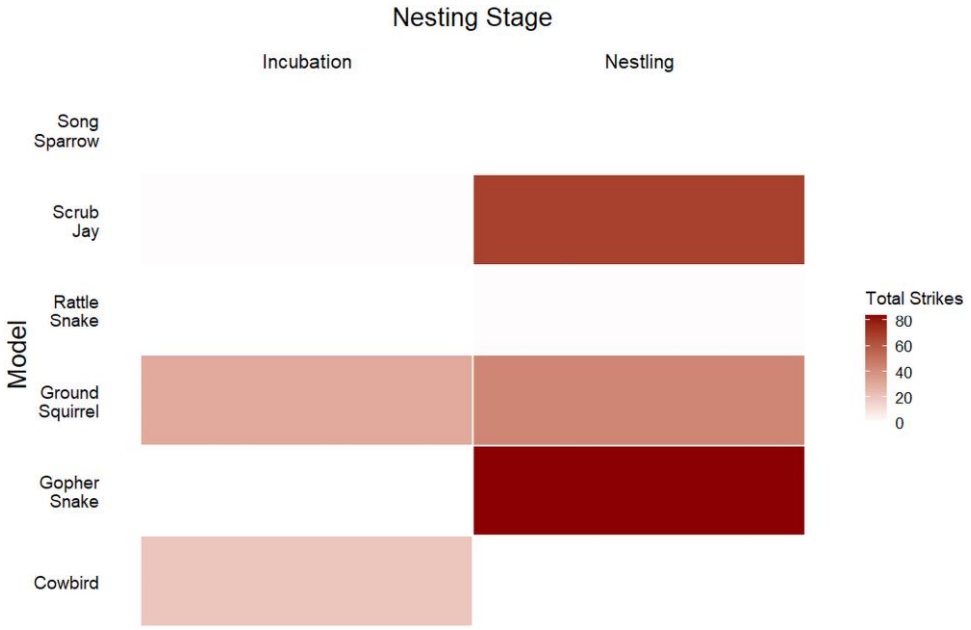

Figure 4 Total number of strikes by focal red-winged blackbirds to different predator models presented at the nest across incubation and nestling stage trials.

Female return rate to nest

We found no stimulus × nest-stage interaction (LRT: $\chi^2_5 = 5.66$, $P = 0.34$). The model without the interaction revealed significant effects of nest stage (LRT: $\chi^2_1 = 6.71$, $P < 0.001$), but not stimulus treatment (LRT: $\chi^2_5 = 9.07$, $P = 0.10$), on whether females returned to the nest during trials. Females were more likely to return to the nest when they had nestlings than when incubating eggs ($z = 2.59$, $P < 0.01$).

Total blackbirds responding

We found no stimulus × nest-stage interaction (LRT: $\chi^2_5 = 4.74$, $P = 0.44$). The model without the interaction found significant effects of stimulus treatment (LRT: $\chi^2_5 = 22.12$, $P < 0.001$) on the number of blackbirds responding, while nest stage was not significant (LRT: $\chi^2_1 < 0.01$, $P = 0.99$). Pairwise comparisons showed that more blackbirds responded to predatory stimuli compared with the song sparrow control, and to the first trial compared to the last ($z = 2.73$, $P < 0.05$). All other comparisons within stages were non-significant (Table S5).

Discussion

We found that blackbirds consistently responded more aggressively to predatory stimuli than to innocuous controls. Over time responses to certain threats shifted—most notably, aggression toward the cowbird decreased from incubation to nestling stages as risk of successful parasitism decreased, which is commonly seen in blackbirds and other hosts of brood parasites (Neudorf and Sealy 1992; Gill and Sealy 1996; Fasanella and Fernández 2009; Lawson et al. 2021b; see Lawson et al. 2021a for meta-analysis). Although we did not observe changes in aggression across stages or seasons, aggression *did* increase with nest age. Thus, defense effort scaled with the incremental value of a brood, rather than with discrete stage boundaries or renesting potential, supporting the offspring value hypothesis. This is consistent with other studies of red-winged blackbirds, where nest age was found to be a strong predictor of defensive intensity (eg Shew et al. 2016).

Aggression type (PC2) did not vary with nest stage or nest age, only with predator type. Combined with PC1 results, this suggests that blackbirds respond to increasing brood value not by changing tactics, but by amplifying total aggression intensity, increasing both vocal and physical responses in tandem. This pattern implies a general escalation in parental motivation rather than a fine-tuned adjustment of risk-taking strategies. Interestingly, however, birds approached snake and ground-squirrel threats more closely than avian threats (scrub jay, cowbird). This could reflect strategic inspection of visual and/or tactile risk cues to identify predators, or broader recognition categories for non-avian predators (Lima and Dill 1990; Ferrari et al. 2010). Differences in approach distance may also reflect predator mobility and attack dynamics. Avian predators are capable of rapid multidirectional movement, potentially requiring defending parents to maintain greater spacing to allow sufficient time to assess and respond to attacks, whereas terrestrial predators such as snakes may be perceived as more spatially constrained during defensive encounters.

Blackbirds did not treat the snake stimuli more cautiously than other predator types, even though snakes generally pose greater potential danger to adults. Passerines typically display heightened caution toward predators that directly endanger adults (eg raptors) but strong, direct aggression toward those that threaten primarily offspring (eg corvids, mammals), including small-to-medium sized snakes (Kleindorfer et al. 2005; Mahr et al. 2015; Eggleston et al. 2025; Liu et al. 2025). In our experiment, both snake models represented medium adult-sized individuals—unlikely to pursue healthy adult blackbirds but capable of injuring them during close-range nest defense—while the rattlesnake's venom made it inherently more dangerous to engage with. Although blackbirds responded similarly to the 2 snake models across most aggregate behavioral metrics, 1 particularly risky defensive behavior revealed a pronounced difference: physical strikes. Neither snake was struck during incubation, but

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during the nestling stage focal birds delivered over 80 strikes toward the gopher snake (not including dozens of strikes from neighboring blackbirds), compared with only a single strike toward the rattlesnake. This suggests that while blackbirds did not strongly alter overall aggression toward the 2 snakes, they may have selectively modulated their riskiest form of defense.

Whether this hesitation to strike the rattlesnake reflects recognition of greater danger or caution toward unfamiliar visual features (ie the rattle, triangular head) remains unclear. Responses between the gopher snake and rattlesnake were otherwise statistically indistinguishable across aggregate measures of aggression, aggression type, and approach distance. Thus, differences between the snake stimuli were reflected primarily by specific, high-risk behaviors rather than broad changes to defensive strategy. This ambiguity represents a limitation of our study, as the rattlesnake model is largely allopatric in our system and therefore unlikely to be a familiar threat. Consequently, we cannot determine whether reduced striking behavior reflected sensitivity to venom-associated cues, novelty, or both. Future experiments should isolate specific snake features (eg head shape, body thickness, rattle, posture, movement; see Yin et al. 2025) to determine which cues drive recognition and whether any are innately encoded.

Blackbirds may therefore adopt a generalized anti-snake response while selectively modifying particularly costly behaviors. However, it is also possible that blackbirds *do* possess a visual template for the ecologically relevant gopher snake based on coloration or pattern, and that they misidentified the rattlesnake either due to mimicry, or lack of experience with the extirpated species. By contrast, mammals that coevolved and have extensive experience with venomous snakes show highly specialized recognition. California ground squirrels, which frequently encounter rattlesnakes, can assess threat based on snake size and temperature, and modulate their defenses appropriately—tail-flagging more vigorously but approaching less closely when snakes are larger, warmer, or encountered during the pup-rearing period (Rowe and Owings 1996; Swaisgood et al. 2003). Birds in regions where venomous snakes are common may likewise experience stronger and more consistent selection to distinguish among snake types, potentially leading to finer-scale recognition of venom-associated cues. Comparative studies across taxa and populations with differing exposure to venomous snakes would be valuable for determining whether such discrimination is learned, innate, or requires ongoing selection to be maintained.

Although the type of aggression used did not differ by sex, males exhibited higher overall aggression than females (PC1), similar to other findings in the red-winged blackbird system (Knight and Temple 1988; Shew et al. 2016; Lawson et al. 2020), and females approached stimuli more closely than males, consistent with their greater proximity to the nest and primary role in incubation and provisioning. Females also returned more frequently to the nest when chicks were present than during incubation, indicating a need to resume parental care despite the risk to self. This pattern reflects a trade-off between defensive behavior and the time and energetic demands of provisioning, as females must balance predator avoidance with the necessity of caring for their offspring.

Blackbirds frequently used alarm calling to warn partners and recruit neighboring conspecifics, and in our study many nearby individuals joined the defense. More blackbirds responded when the stimulus was a threat compared with the control, mirroring responses of the focal parents, even though the threat was localized to focal nests. Mobs were likely drawn in by alarm calls produced by the focal pair, which are known to encode some information about general risk (conveyed via call switching by males: Beletsky et al. 1986; chit calls by females: Yasukawa 1989). Because red-winged blackbirds often breed synchronously, nearby nests are typically at similar stages and equally vulnerable to predators, and such coordination could enhance colony-level protection through cooperation—consistent with a "neighborhood watch" model of communal defense (Ligon 1983; Olendorf et al. 2004; Lawson et al. 2023).

Taken together, our findings demonstrate that blackbirds adjust the intensity, but not the nature, of nest defense in relation to brood value and perceived threat. They do not shift toward riskier physical aggression over time, but instead, both sexes intensify aggression as investment increases. Furthermore, the widespread recruitment of neighboring birds underscores that alarm communication serves not only immediate defense but also collective risk management, possibly enhancing reproductive success. Finally, our work contributes to the broader understanding of predator recognition by showing that even highly aggressive species like red-winged blackbirds may respond similarly to visually comparable predators across many defensive behaviors, while still modulating behaviors that involve the greatest personal risk.

Acknowledgments

We thank Oregon State University, Benton County Parks, City of Corvallis Parks & Recreation, and Oregon State Parks services for granting permission to conduct this study on their managed lands. We are especially grateful to Elena Gasiorowski for providing the spectral scans of snakes used to spectrally match the paint coloration of our models. We also thank Benjamin Sonnenberg for his assistance in the field. Finally, we thank reviewers for their suggestions which strengthened the manuscript.

Author contributions

Shelby L. Lawson (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing—original draft, Writing—review & editing [lead], Supervision [equal]), Angela H. Zbaracki (Data curation [supporting], Methodology, Writing—review & editing [supporting]), Russell M.L. Campbell (Data curation [supporting], Writing—review & editing [supporting]), Eleanor M. Fraser (Data curation, Writing—review & editing [supporting]), and David W. Kikuchi (Conceptualization, Writing—review & editing [equal], Formal analysis, Methodology [equal], Funding acquisition, Resources, Supervision [lead])

Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

Funding

None declared.

Conflict of interest

None declared

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Data availability

Analyses reported in this article can be reproduced using the data provided by Lawson et al. (2026).

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