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ORIGINAL ARTICLE

A classic question revisited in red-winged blackbirds: disentangling confounding hypotheses surrounding parental investment theory and nest defense intensity

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Abstract
The pattern of increased nest defense effort over the course of a nesting season could result from three distinct (albeit nonexclusive) mechanisms: increased value of offspring to parents with progression toward independence (parental investment theory), decreased opportunity for renesting (renesting potential hypothesis), or decreased perceived costs of defense after repeated encounters with human observers (positive reinforcement hypothesis). To gauge relative empirical support for each of these mechanisms, we disentangle these three often-confounded hypotheses using multimodel inference with mixed-model ordinal regression applied to an extensive red-winged blackbird (*Agelaius phoeniceus*) nesting data set (4518 monitoring visits to 1330 nests). Parent aggression was rated on an ordinal scale (0–4) during repeated monitoring visits. Additionally, we assessed clutch/brood size, nest density, time of day, and nest concealment effects on aggression. In a preliminary analysis, including all three major hypotheses, male and female nest defense was most strongly explained by parental investment (nest age). Positive reinforcement (visit number) and renesting potential (Julian date) were also well-supported predictors in males. The interactions of decomposed nest age (within-individual and between-individual centered) with Julian date were particularly important in the top male model. Additional factors, such as clutch/brood size, nest density, and nest concealment, appeared to have larger predictive roles in explaining female aggression relative to males. These patterns are likely explained by different sexual reproductive roles within a polygynous mating system. Our study highlights the importance of interacting mechanisms involving parental investment theory and the use of within-individual standardization to help disentangle competing and empirically confounded hypotheses.

Significance statement
Avian nest defense generally increases over the course of a nesting season, potentially from the result of three different mechanisms: parental investment theory, renesting potential hypothesis, or positive reinforcement hypothesis from repeated nest visitation. We revisit this classic question through a comprehensive analytical approach with an extensive observational data set with red-winged blackbirds, employing multimodel selection and within-individual and between-individual centering techniques. We found that parental investment (nest age) was the strongest predictor of nest defense for both sexes; however, positive reinforcement and renesting potential also appeared to help explain additional variation in nest defense for males. Competitiveness of models with interactive effects indicated that these mechanisms do not operate

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independently for either sex, and additional covariates (e.g., clutch/brood size) especially aided female model competiveness. Our study highlights the importance of multiple and often interacting factors that influence avian nest defense.

Keywords Nest defense intensity · Red-winged blackbird · Parental investment theory · Renesting potential hypothesis · Positive reinforcement hypothesis · Ordinal regression

Introduction

Parental investment theory predicts that parents will defend offspring more aggressively as they increase in value to the parents (Trivers 1972). Offspring value to the parents increases when offspring progress toward independence, because there is an increasingly higher probability the offspring will reproduce in the future. Thus, any behavioral strategies that can reduce predation risk of offspring without having detrimental impacts on parent survival are likely adaptive and shaped by natural selection (Williams 1966). Avian parents, specifically, can reduce predation risk on nests via distraction displays or direct attacks on potential nest predators (Montgomerie and Weatherhead 1988; Brunton 1990; Weidinger 2002). Such defensive responses are potentially costly, so their occurrence and intensity scale with the potential benefits, which are determined by both the cost of predation and the expected efficacy of defense. Bird studies potentially provide substantial support for the parental investment theory, but only to the extent that the patterns are not driven by other potentially confounding effects of time of year and parent experience with human nest observers as potential predators. Thus, increases in nest defense effort over the course of a nesting season could result from three distinct (albeit non-exclusive) mechanisms: increasing value of offspring to parents with progression toward independence (parental investment theory; Trivers 1972), decreasing opportunity for renesting as time passes (renesting potential hypothesis; Barash 1975), or decreasing perceived costs of defense after repeated encounters with human observers (positive reinforcement hypothesis; Knight and Temple 1986a). Determining which of these three factors, or combination of factors, are most important in driving nest aggression in red-winged blackbirds (*Agelaius phoeniceus*) may provide a framework for behavioral ecologists to better understand the role of nest defense behavior in terms of life history theory.

Nest defense constitutes a form of reproductive effort, and energy allocated toward defense can be a trade-off between current reproduction and future reproduction (William's principle; Williams 1966). Individuals responding too aggressively could face higher rates of adult mortality, thus eliminating future reproduction. An increase in nest defense aggression over the course of the nesting season has been observed in multiple bird species (Brunton 1990; Tryjanowski and Golawski 2004). In general, the value of the clutch to parents increases as young develop toward independence (Redondo and Carranza 1989; Anderson 1990; Palestis 2005; Redmond et al. 2009; Svagelj et al. 2012) and results in increased nest defense (parental investment theory; Trivers 1972). However, a decrease in renesting potential through the season could also affect nest aggression. Renesting potential is a function of (1) time before another breeding attempt can be made and (2) the probability of survival of the parents during that time (Montgomerie and Weatherhead 1988). Renesting potential starts out high early in the breeding season (when there is ample time to renest and replace a clutch) and declines rapidly toward the end of the breeding season (when not enough time remains to successfully breed again). Most importantly, reproductively mature individuals face a non-breeding season where survival to the next breeding season is uncertain and often face higher rates of mortality compared to the breeding season (Burger et al. 1995; Sillet and Holmes 2002). Accordingly, defense behavior should change as the breeding season progresses (renesting potential hypothesis; Barash 1975), with parents investing more in defense later in the season when it becomes more urgent to have a successful clutch because the chances of renesting are greatly reduced later in the breeding season (Regelmann and Curio 1983; Pavel and Bureš 2008).

Even though both the nesting cycle and renesting potential could drive aggression response in parents, it is also possible that an observed increase in defense response might be an artifact of repeated nest visits by observers. Knight and Temple (1986a) first suggested that increased aggression by parents might be due to repeated nest visits by observers resulting in parental habituation to a non-threatening human intruder and, therefore, that the perceived increase in aggression over time may be artifactual rather than representing an actual response to the nest cycle (positive reinforcement hypothesis). In this case, the parents learn that they can be bolder toward the observer, or predator model, without any apparent risk to themselves or their nest. In these repeated situations, parents perceive their effort put into aggressive nest defense as successful in deterring a predator, which leads to a perpetuating cycle of increase aggression without any apparent risk of predation. Conversely, it could be argued that repeated nest visits by observers could result in a potential dilution of aggressive response by parents (Montgomerie and Weatherhead 1988). The problem with these three competing hypotheses is that they are interrelated and thus somewhat confounded. Moreover, if an increase in nest aggression is purely because of habituation to observers, that would mean a strong bias in any recorded nest behaviors.

In addition to these three major competing hypotheses, many other factors are known to influence nest defense aggression in birds, including individual personality (Hollander et al. 2008; Burtka and Grindstaff 2013), brood size (Fisher and Wiebe 2006; Svagelj et al. 2012), time of day (Burger 1980), nest concealment (Weidinger 2002; Carrillo and González-Dávila 2013), and density of conspecific nests (Anderson and Wiklund 1978; Clark and Robertson 1979; Elliot 1985; Arroyo et al. 2001). Past studies investigating similar hypotheses, although taking an experimental approach, have not accounted for other sources of nest variation, such as inherent individual variation. Controlling for inherent variation, such as individual personality, within a mixed-effects modeling framework can help further elucidate the impacts of competing hypotheses (Zuur et al. 2007).

The main objective of our study was to identify which of the three hypotheses contribute most to explaining nest defense aggression trends in red-winged blackbirds. Using an information theoretic model selection approach, we gauged empirical support for whether (a) parental investment theory, (b) renesting potential hypothesis, or (c) the positive reinforcement hypothesis (or a combination of these hypotheses) provides the best explanation for nest defense aggression of red-winged blackbird parents. Explicitly, our approach allowed us to compare nest defense aggression at various nest ages (parental investment), while simultaneously assessing the importance of, or accounting for, variation in nest initiation date throughout the breeding season (renesting potential) and repeated observer visits to nests (positive reinforcement). Additionally, we assessed the importance of other predictors such as brood size, time of day, nest concealment, and conspecific nest density, all of which have previously been found to influence nest aggression in other species of birds. For instance, we expected that clumped nests may offer improved group nest protection and vigilance (Picman et al. 1988) and predicted lower nest aggression per individual for nests with higher surrounding nest densities, which has been seen in both polygynous and colonial nesting birds (Arroyo et al. 2001; Požgayová et al. 2013).

Methods

Study animal and area

Red-winged blackbirds are ubiquitous in marsh and agricultural landscapes of the midwestern USA and have been one of the most abundant bird species in Illinois within the past century (Walk et al. 2011). Males can be highly polygynous, with up to 15 females nesting in a single male's territory (Yasukawa and Searcy 1995). Because their nests are abundant and generally easy to find, red-winged blackbirds are some of the more commonly studied North American passerines in terms of nesting behavior (Caccamise 1977; Knight and Temple 1986b, 1988; Picman et al. 1988; Gray 1997; Clotfelter 1998; Gillespie and Dinsmore 2014).

We searched for red-winged blackbird nests on 24 grassland fields (12 dominated by smooth brome, *Bromus inermis*, and 12 dominated by native grasses and forbs) located in Stark and Henry counties of northwestern Illinois. All fields were privately owned and enrolled in the federal Conservation Reserve Program (CRP). Common plant species found in these fields included smooth brome, reed canary grass (*Phalaris arundinacea*), little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), Indiangrass (*Sorghastrum nutans*), wild parsnip (*Pastinaca sativa*), goldenrod (*Solidago* sp.), horseweed (*Conyza Canadensis*), poison hemlock (*Conium maculatum*), common milkweed (*Asclepias syriaca*), and yellow coneflower (*Ratibida pinnata*).

We searched each field twice for nests during each breeding season over a 4-year period (2011–2014). The first round of searches was initiated each year during the second week of May, and the second round was initiated during the second week of June. These searches were systematic, where four to six field assistants walked in a line spaced approximately 2–5 m apart. Each person used wooden dowels to disturb vegetation to flush female birds from their nests and marked each nest with a flag approximately 5 m from the nest. We recorded the GPS coordinates for each nest so it could be relocated and monitored twice a week while the nest was active (referred to as a monitoring visit). We conducted nest monitoring visits, during which we assessed nest stage and observed parental behavior, between 0512 and 1926 h during fair weather conditions, and made as little disturbance as possible to the nest area and in the shortest time possible to reduce observer influences on nest survival. Observers rated aggression of each parent on an ordinal scale from 0 to 4 (Table 1; Geupel and Thompson 2013) during each monitoring visit at an individual nest. Because different observers could make monitoring visits to the same nest on different days, we routinely checked and calibrated aggression scores throughout the breeding season to ensure consistency in aggression ratings among observers. It was not possible to record data blind because our study involved focal animals in the field. Nest stage was characterized during each monitoring visit as building (nest structure present but incomplete), laying (eggs present but not yet incubated), incubation, hatching, hatchlings present, or successful. We defined a nest as successful if we observed ≥1 nestling occupant and ≥1 fledgling in the immediate vicinity of the nest during a monitoring visit. Only one observer at a time conducted a nest monitoring visit, with the exception of when the nest was originally found during nest searching. Different observers could potentially conduct monitoring visits at the same nest on different days; however, observers approached nests at a consistent deliberate pace and remained silent during monitoring visits. We excluded inactive nests

Table 1 Predictor variables with definitions used in explaining red-winged blackbird nest defense aggression, an ordinal response (see below), using cumulative link mixed-effects models

Variable group	Variable name	Scale/ levels	Definition
Response	Aggression score		Red-wing blackbird nest defense aggression score on an ordinal scale (0–4)
		0	No bird in the immediate vicinity seen, assume no response
		1	Very little disturbance. Bird is quiet, moves away silently
		2	Little disturbance. A little distress calling
		3	Moderate disturbance. Repeated distress calling and conspicuous perching behavior, single feign
		4	Very disturbed. Loud alarm calling, or repeated feigning
Main hypotheses	InitDate	NA	Estimated Julian date when the first egg of a nest was laid (see text for estimation procedure). Used to evaluate renesting potential
	NestAge	NA	Number of days active from estimated nest initiation date (InitDate = day 0). Used to evaluate parental investment
	Visit Number	NA	The ordered visit number to a monitored nest (first, second, third, etc.). Used to evaluate positive reinforcement
NestAge decomposed	BIC		Between-individual centered NestAge (mean NestAge for an individual nest; $\bar{x}_{j,j}$ = unique nest)
	WIC		Within-individual centered NestAge (NestAge minus NestAgeBIC within an individual nest; $x_{ij} - \bar{x}_j$; x_{ij} = NestAge at visit number i at unique nest j)
Additional covariates	Clutch/brood size	NA	Total number of known viable nest occupants (eggs or chicks, not counting eggs that did not hatch); reflecting the apparent value of the clutch or brood to the parents
	Nest density	NA	Number of active nests within 20, 40, 60, 80, or 100 m for each nest matching the same date of nest monitoring; potential index of polygyny
	Concealment		Sum of below and above nest concealment rated separately from a 0–4 scale, thus a nest concealment score ranged from 0 to 8.
		0	Nothing hiding the nest. Perfectly exposed
		1	Very poorly hidden
		2	Poor to medium hidden
		3	Medium hidden to well hidden
		4	Very well hidden
	Time	NA	Time of day when the nest was visited
Random variable	Nest.ID	NA	Individual nest ID to account for personality differences of parents between different nests

and those nests where stage could not be determined from analysis; these included nests with no change of egg number over subsequent checks and where a flushing female was never detected at the nest.

Definition of variables

We modeled the aggression response categories from a "distress" variable described by Geupel and Thompson (2013) with the addition of the "0" category signifying that a parent was not detected during a monitoring visit. The three main variables (relating to the three main hypotheses) used to describe variation in male and female aggression response included nest initiation date (renesting potential hypothesis), nest age (parental investment theory), and visit number (positive reinforcement hypothesis). We also assessed the ancillary variables: clutch/brood size, nest density, nest concealment, and time of day. To account for inherent parental personality variation across nests, we included individual nest (Nest.ID) as a random effect in our analyses.

Nest initiation date (InitDate) was the estimated Julian date when the first egg was laid for a particular nest. We approximated nest initiation date by back-dating from important nesting events and by using information of typical clutch size, incubation, and nestling periods for red-winged blackbirds described by Ehrlich et al. (1988). Thus, we used an average nesting cycle of 28.5 days in our estimation procedure, which represents the number of days between when the first egg was laid (day 1) to when at least one nestling fledged the nest successfully (left the nest unharmed). This number was directly calculated from totaling the average laying (4 days at one egg laid per day), incubation (12 days), and nestling stages (12.5 days) outlined by Ehrlich et al. (1988). We followed a six-step process to estimate nest initiation date. The six steps, in order of most to least informative circumstances, were as follows: (1) back-dated all nests in the suspected laying stage by the number of eggs present during the first visit; (2) forward-dated all nests in the building stage by 2 days from the last build date detected; (3) back-dated all nests hatching or found successful by 16 and 28.5 days, respectively; (4) if no laying, building, or hatching was detected, we took the mid-point between the last incubation and first nestling date and then subtracted 16 days; (5) if a nest was only observed in an incubation stage, we subtracted 10 days from the first observation date; (6) if a nest was only observed in a nestling stage, we back-dated from the first observation date by 22 days. Nest age (NestAge) was calculated from the estimated nest initiation date for each nest and commonly had values less than 28.5 days, which was the average nesting period for red-winged blackbirds accounting for laying, incubation, and nesting periods (Ehrlich et al. 1988). Determining actual clutch size can be difficult without daily nest visits; in order to maintain consistency across all nests when estimating nest age, we assumed that each nest had a four-egg clutch corresponding to a 4-day laying stage. The estimated initiation date of the nest corresponds to a 0-day nest age, and nests detected during the building stage received negative nest age values (Table 1). Empty nests, even if there was evidence of success, were not included in our analysis.

We expected that the clutch/brood size observed during each nest visit would be associated with the perceived value of the clutch or brood to the parents (Table 1). Additionally, because birds in this study were not individually marked, we used a nest density covariate as a proxy for potential degree of polygyny. Nest density was calculated as the total number of active nests at varying concentric distances from each individual nest (20, 40, 60, 80, and 100 m). A higher density of nests, especially at the shorter distance intervals, likely suggests a highly polygynous male territory. During a monitoring visit, each nest was also given a concealment score (0–8, 8 = high nest concealment), which was determined by summing the above and below nest concealment (0–4) estimated within 2 weeks of nest success or failure (Table 1; Geupel and Thompson 2013). Concealment scores across observers were routinely calibrated and checked throughout each field season to ensure consistency. Lastly, during each monitoring visit, time of day was recorded.

Data analysis

We used cumulative link mixed-effects ordinal regression to determine which factors best explained variation in nest aggression. We modeled nest aggression response separately for each sex, and based on our predictions, we considered different combinations of predictor variables. All variables were standardized to a mean of 0 and a standard deviation of 1 across the entire data set after deletion of nests/visits without a full set of measured covariates. Individual nest (Nest.ID) was included as a random intercept to account for repeated measures and inherent variation in nest aggression across parents. We used a flexible threshold modeling structure for the nest aggression response with a logit link function, and maximum likelihood estimates of the parameters were approximated with Laplace approximation methods (Christensen 2015).

We decided to separate our analysis by sex based on strong support for sex interactions among each of the main hypotheses. The interactive model [Sex × (NestAge + Visit Number + InitDate)] was overwhelmingly more supported than to the additive model (Sex + NestAge + Visit Number + InitDate; 183.15 ΔAIC_c), indicating evidence that the hypothesized mechanisms act differently for each sex. Incorporating three-way and four-way interactions including sex would have added another level of complexity to an already complex analytical approach.

Preliminary analysis

In a preliminary analysis, we included all three main hypotheses in the same model (NestAge, Visit Number, InitDate), to disentangle the relative strength of each hypothesis, for both male and female nest aggression. Because nests were found at a variety of nest ages, the effects of nest initiation date and observer visit could be assessed separately from nest age. Incorporating the main hypotheses in a combined additive analysis allowed us to evaluate the relative predictive strength of parental investment theory (in terms of nest age), renesting potential, and positive reinforcement in explaining variation in nest defense aggression. Because all covariates were standardized to a mean of zero, this additive model for both sexes allowed for direct comparison of the three main hypotheses relative to each other. Beta (β) parameter estimates with 95 % confidence intervals for each hypothesis were compared in this preliminary analysis for each sex.

To separate the effects of value of offspring (NestAge) from positive reinforcement (Visit Number) and renesting potential (InitDate), we also performed a separate analysis using cumulative link models with only the first-visit nest data. In this analysis, we included the additive model using both hypotheses (parental investment and renesting potential) to explain parental nest defense aggression on first visits to nests. We were particularly interested in determining if these results corroborated results from the preliminary analysis using all available nest visit data. Here, we also standardized the predictor variables to a mean of zero and standard deviation of 1.

Model building procedure

In addition to our preliminary main hypothesis analysis, we evaluated nest defense aggression in a model building procedure separately for each sex. Within this procedure, NestAge was further decomposed in within-individual and between-individual components by calculating both within-individual centered (NestAgeWIC; $x_{ij} - \bar{x}_j$) and between-individual centered (NestAgeBIC; $\bar{x}_j$) NestAge for all individual nests. Because our study was not experimental in nature, we could not control for the range of nest ages for each nest; thus, nests were found and visited during a range of ages (van de Pol and Wright 2009). Accounting for within-individual and between-individual effects improves inference and reduces problems of falsely generalizing relationships to between and within individuals (van de Pol and Wright 2009).

We used a five-step process to model nest aggression, for each sex separately. For step 1, we compared a NestAge model to a decomposed additive NestAgeWIC plus NestAgeBIC model and used the model with the lowest ΔAIC_c in step 2. This step allowed us to determine if the decomposition of NestAge into within-individual and between-individual components was indeed important in explaining nest aggression. Within this step, if NestAgeBIC and NestAgeWIC together performed better than the non-decomposed NestAge, we tested a random slope model. A more competitive random slope model would suggest that each group of nesting parents responds differently in degree of aggression at different levels of within-individual nest age (van de Pol and Wright 2009). Without a random slope test, we would be assuming that the relationship between nest defense aggression and NestAgeWIC effects would be the same across the range of NestAgeWIC values. For step 2, we combined the variables associated with our three main hypotheses. These included InitDate, NestAge, and the Visit Number variable(s) determined from step 1. Within this a priori set, we included both additive models and suspected interactions of NestAge and InitDate. At the end of this step, we determined the best main hypothesis model. Step 3 involved finding the best nest density model by developing five univariate models with only the five nest density distances (20, 40, 60, 80, 100 m). The highest ranked nest density was carried over to step 4. In step 4, we determined a top modeled using a priori combinations of additional covariates (clutch/brood size, time of day, concealment, and the best nest density model from step 3). Lastly, in step 5, we combined the best model from step 4 and step 2. We developed a candidate set of 25 models for each sex, which included additive models and biologically relevant interactive models.

We evaluated models using an information theoretic approach and compared models by calculating Akaike's information criterion corrected for small sample size (AIC_c) for each model (Burnham and Anderson 2002). The model with the lowest AIC_c was considered most parsimonious. The AIC_c weight of a model (w_i) provides evidence of the relative likelihood that the specified model was the best given the candidate model set and the data set. Statistical analyses were done using the "clmm" function within the "ordinal package" (Christensen 2015) in R programming software (R Development Core Team version 3.0.3, 2014).

Because longitudinal studies can sometimes have highly correlated variables relating with progression of time, we assessed essential multicollinearity with a correlation matrix of all possible standardized predictor variables (Cohen et al. 2003). Pairs of predictor variables with a correlation of $r > 0.55$ were not used within the same model to avoid multicollinearity issues (Online Resource 1, Table A1). Multicollinearity problems arise in multiple regression when predictor variables are *highly* correlated; often, issues can be detected with thoughtful investigation of slope parameter estimates and standard errors between univariate and full predictor models (Cohen et al. 2003).

Results

We found 1330 red-winged blackbird nests and monitored them over 4518 separate visits; thus, 29.4 % of visits were first visits. Of the first nest visits, 12.2 % were building, 19.1 % laying, 55.3 % incubating, 2.7 % hatching, 10.7 % nestling, and 0.1 % were confirmed successful. Over all nest visits, 3.8 % of nests were in the building stage, 8.1 % were in the laying stage, 53.3 % were being incubated, 4.1 % were hatching, 30.1 % had nestlings, and 0.7 % were confirmed successful. The mean number of visits per nest was 3.40 ± 1.88 SD, with a maximum of 10 visits for a single nest. Of the 4528 separate monitoring visits, males and females were not present (aggression score 0) during 48.6 % and 55.61 % of total monitoring visits, respectively. This was the most common class recorded for both sexes. The next most frequently scored aggression classes for males were three (24.2 %) and two (19.83 %), and two (17.7 %) and one (12.8 %) for females. Mean male aggression per visit was higher (1.39 ± 0.042, 95 % CI) than females (0.92 ± 0.034, 95 % CI).

Males

The preliminary analysis of the three main hypothesis revealed that NestAge was explaining the greatest amount of variation in nest aggression response followed by Visit Number and then InitDate (Fig. 1). We found similar results in the first-visit only analysis with NestAge ($\beta = 0.69$, 95 % CI = 0.57, 0.82) showing a stronger relationship than InitDate ($\beta = 0.25$, 95 % CI = 0.13, 0.37). When testing NestAge decomposition hypotheses, the additive NestAgeWIC and BIC model had overwhelming support over NestAge ($\Delta AIC_c = 33.25$). This suggested the importance of distinguishing both within-individual and between-individual effects of NestAge on male blackbird nest aggression. Because nest age decomposition was important for males, we further tested the inclusion of a random slope model across various values

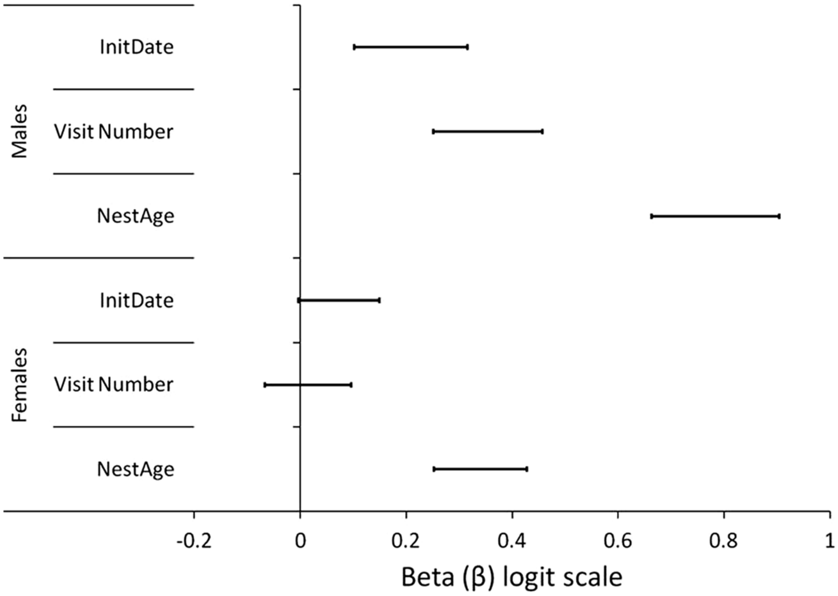

Fig. 1 Beta slope parameter estimates with 95 % confidence intervals of the three main hypotheses, showing the relative strength of the covariate (hypotheses) relationships to nest defense aggression for separate analyses for each sex. Main hypotheses were included in a three-covariate additive model, and original covariates were standardized to a mean of zero and standard deviation of 1 to allow for relative comparison among each hypothesis

of NestAgeWIC, and we found strong support for this model over the decomposed model (NestAgeWIC + NestAgeBIC; $\Delta AIC_c = 17.84$). Because male NestAgeWIC was highly correlated with Visit Number ($r = 0.82$), we did not test any models with these two covariates together in the main hypothesis analysis (step 2). However, the interactive models of InitDate with both NestAgeWIC and BIC with random slope inclusion had overwhelming support compared to Visit Number and InitDate interaction ($\Delta AIC_c = 190.80$).

The best supported model for male red-winged black bird aggression (Table 2; $w_i = 1.00$) included NestAgeWIC and NestAgeBIC (main effects $\beta = 1.34$, 95 % CI = 1.20, 1.49; $\beta = 0.80$; 95 % CI = 0.65, 0.94; respectively) each interacting with InitDate (main effect $\beta = 0.32$, 95 % CI = 0.20, 0.44) (step 2) plus the top model covariates from the additional covariate model (step 4). These interactions were both negative and represented higher magnitude betas compared to any additional covariates (NestAgeWIC × InitDate $\beta = -0.35$, 95 % CI = −0.47, −0.23; NestAgeBIC × InitDate $\beta = -0.30$, 95 % CI = −0.44, −0.15). Earlier initiated nests (InitDate), especially with 0–3 aggression scores (Fig. 2a, c), were generally defended more aggressively up to mid-June for nests with greater within-individually centered NestAge values. However, this trend appeared to reverse after mid-June,

Table 2 Summary of model selection results for cumulative link mixed-effects models of male red-winged blackbird nest defense aggression in northwest Illinois (2011–2014), with individual nest (Nest.ID) included as a random effect

Model rank	Candidate models	K	ΔAIC_c	w_i
1[b]	C/B size + Nest density (100 m) + Concealment + Time + NestAgeWIC × InitDate + NestAgeBIC × InitDate	16	0.00	1.00
2[c]	NestAgeWIC × InitDate + NestAgeBIC × InitDate	12	41.49	0.00
3	NestAgeBIC + NestAgeWIC × InitDate	11	54.39	0.00
6[d]	NestAge + Visit Number + InitDate	8	87.06	0.00
7	NestAgeBIC + NestAgeWIC	9	98.50	0.00
8	Visit Number × InitDate	8	282.29	0.00
11[a]	C/B size + Nest density (100 m) + Concealment + Time	9	686.95	0.00
23	Nest.ID	5	828.10	0.00

Models were ranked from lowest to highest Akaike information criterion (AIC_c) value. K represents the number of parameters in the model, and w_i represents the Akaike weighting factor of the model.

C/B size clutch/brood size

[a] Top additional covariate model

[b] Combined top models from main hypotheses and additional covariate analyses

[c] Top main hypothesis model with NestAgeWIC random slope incorporation

[d] Preliminary main hypothesis additive analysis (NestAge + Visit Number + InitDate)

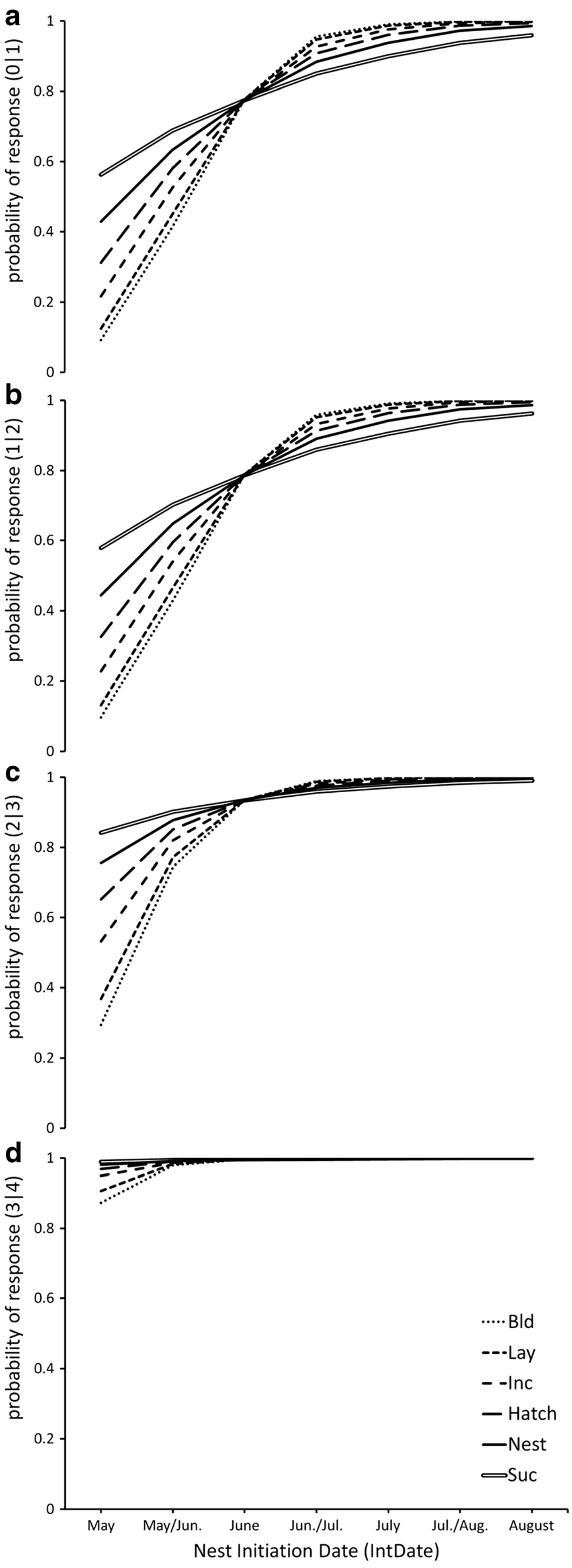

Fig. 2 Probability of nest aggression response of male red-winged blackbirds, at distinct thresholds (0–4), predicted from increasing nest initiation dates and within-individually centered nest ages (NestAgeWIC). Nest age was grouped by nest stage, which was determined from the mid-points for general nesting periods (Ehrlich et al. 1988). Blackbird nests were monitored over 2011–2014 breeding seasons in northwestern Illinois, USA. *Bld* building, *Lay* laying, *Inc* incubation, *Hatch* hatching, *Nest* nestling, *Suc* successful

especially for males with 0–2 aggression scores, as lower NestAgeWIC values (younger nests) generally had males with increased aggression scores (Fig. 2a, b). Males appeared to most consistently increase their aggression response with nesting cycle but also showed higher aggression at nests visited multiple times compared to the first visits to nests (Fig. 3a). In addition, clutch/brood size (β = 0.28, 95 % CI = 0.19, 0.37), time of day (β = 0.12, 95 % CI = 0.05, 0.20), and nest concealment (β = 0.037, 95 % CI = −0.079, 0.15) all had positive effects on nest aggression. Nest aggression seemed to decrease with an increase in nest density within 100 m of a specified nest (β = −0.047, 95 % CI = −0.15, 0.60).

Females

The preliminary analysis of the three main hypotheses for females revealed that NestAge has the strongest influence on female nest defense aggression compared with the other main hypotheses (Fig. 1). NestAge (β = 0.57, 95 % CI = 0.46, 0.69) also had a much greater positive effect on aggression compared to InitDate (β = 0.056, 95 % CI = −0.051, 0.16) with the first-visit only analysis for females and supported our preliminary analysis results. Unlike males, female model competitiveness did not improve with nest age decomposition. Female best main hypothesis model (step 2) included the NestAge by Visit Number interaction plus InitDate (ΔAIC_c = 45.57).

The best additional covariate model (ΔAIC_c = 61.65) when combined to best main hypothesis model greatly improved the competitiveness of the top model (Table 3). The top-ranked model for female aggression response (w_i = 1.0; Table 3) included the combination of all main hypothesis covariates and the additional covariates. NestAge (β = 0.28, 95 % CI = 0.19, 0.37), InitDate (β = 0.090, 95 % CI = 0.0074, 0.17), Visit Number (β = 0.036, 95 % CI = −0.59, 0.13), and negative interaction of NestAge and Visit Number (β = −0.039, 95 % CI = −0.12, 0.39) represented the best main hypothesis covariate combination. In terms of the additional covariates, aggression response was negatively related to nest concealment (β = −0.0088, 95 % CI = −0.089, 0.071), time of day (β = −0.035, 95 % CI = −0.10, 0.030), and nest density within 100 m of a specified nest (β = −0.11, 95 % CI = −0.19, −0.030). After the main effects of NestAge, clutch/brood size was the second most influential predictor of female nest defense aggression (β = 0.23,

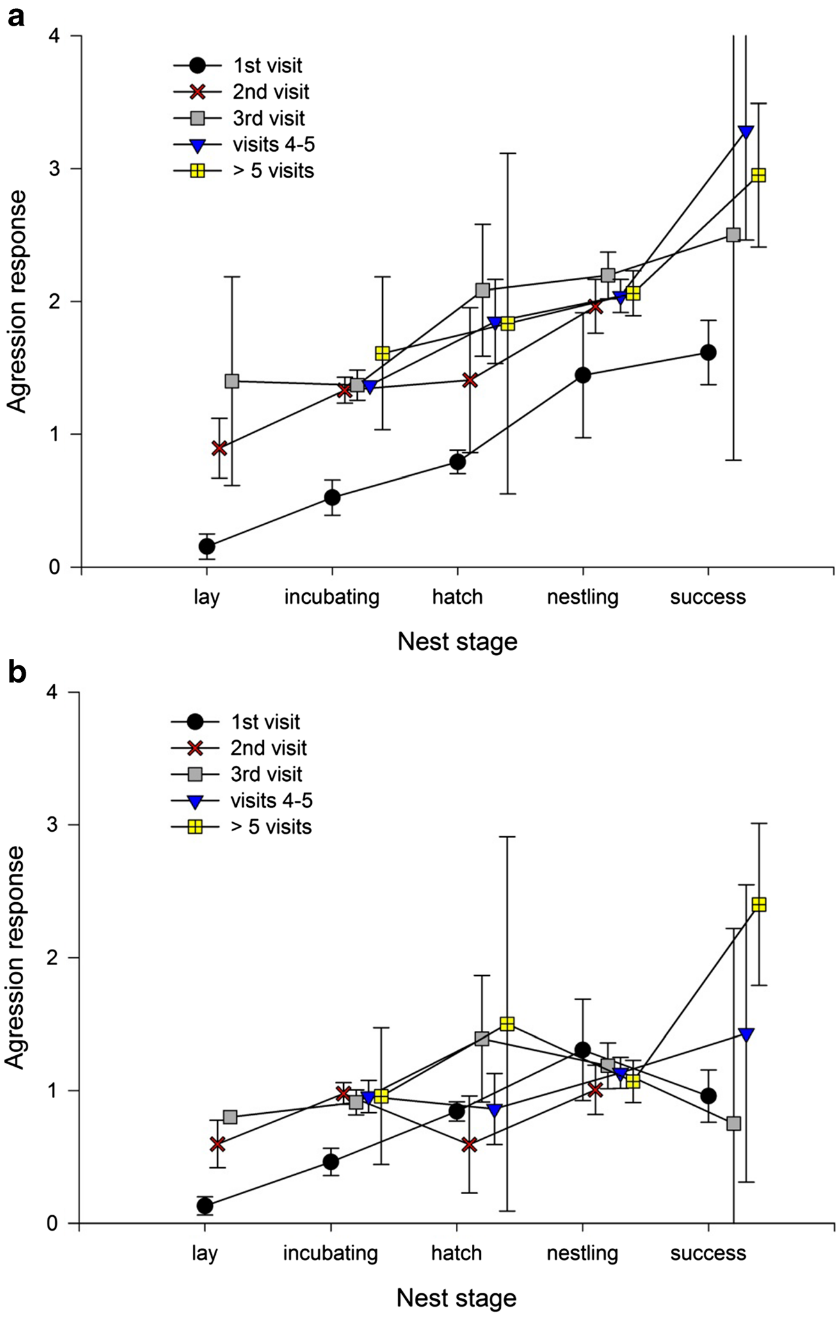

Fig. 3 Mean nest defense response by nesting stage with 95 % confidence intervals of male (**a**) and female (**b**) red-winged blackbird separated by nest monitoring visit numbers (first, second, third, fourth to fifth, >5). Nests were monitored during the breeding seasons of 2011–2014 in northwestern Illinois, USA

95 % CI = 0.15, 0.33) followed by interaction between clutch/brood size and nest concealment (β = 0.13, 95 % CI = 0.055, 0.20; Fig. 4). Nests with higher clutch/brood sizes generally experienced higher nest defense aggression by females, especially for females scored between 0 and 3, as nest concealment increased (Fig. 4). The opposite effect was seen for more concealed nests with low clutch/brood sizes. Females generally increased aggression with the progression of the nesting cycle, and an increase in female aggression to multiple visits was most apparent during the laying and incubation stages (Fig. 3b).

Discussion

From our preliminary analysis of the three main hypotheses, we found most support for parental investment theory (NestAge) for both sexes; however, for males, the two other hypotheses, positive reinforcement (Visit Number) and renesting potential (InitDate) also received support. Thus, overall, parental investment theory was explaining most of the variation in nest defense aggression for red-winged blackbirds in our study area. However, when these same hypotheses were considered in our comprehensive model building analysis, the effects of these

Table 3 Summary of model selection results for cumulative link mixed-effects models of female red-winged blackbird nest defense aggression in northwest Illinois (2011–2014), with individual nest included as a random effect

Model rank	Candidate models	k	ΔAIC_c	w_i
1[b]	C/B size × Concealment + Nest density (100 m) + Time + NestAge × Visit Number + InitDate	14	0.00	1.00
2[c]	NestAge × Visit Number + InitDate	9	45.57	0.00
3	NestAge × Visit Number	8	47.57	0.00
5	NestAge	6	54.90	0.00
7[d]	NestAge + Visit Number + InitDate	8	55.10	0.00
11[a]	C/B size × Concealment + Nest density (100 m) + Time	10	61.65	0.00
12	C/B size + Nest density (100 m)	7	68.28	0.00
23	Nest.ID	5	152.93	0.00

Models are ranked from lowest to highest Akaike information criterion (AIC_c) value. K represents the number of parameters in the model, and w_i represents the Akaike weighting factor of the model

C/B size clutch/brood size

[a] Top additional covariate model

[b] Combined top models from main hypotheses and additional covariate analyses

[c] Top main hypothesis model

[d] Preliminary main hypothesis additive analysis (NestAge + Visit Number + InitDate)

hypotheses were not so straightforward. We reveal that interactions among these hypotheses were also important to consider. Our study revisits these classic questions, first brought forward by Knight and Temple (1986a), in a direct manner.

Based on the parental investment theory (Trivers 1972), nest defense should increase concomitant with nest age and clutch/brood size (e.g., Redondo and Carranza 1989; Anderson 1990; Wiklund 1990; Tryjanowski and Golawski 2004; Palestis 2005; Redmond et al. 2009). We found support for this theory, as nest age was positively related to both male and female nest aggression and consistently had higher slope parameter estimates (β) compared to the two other main hypotheses and additional covariates. Our results mirror studies with indigo buntings (*Passerina cyanea*) and mourning doves (*Zenaida macroura*) which also found nest defense increased with age of nest (Westmoreland 1989; Westneat 1989). With eastern kingbirds (*Tyrannus tyrannus*) however, Siderius (1993) found that eggs were defended just as aggressively as young to a repeatedly displayed American crow predator model. Here, the author suspected that the population's natural history traits, such as low within-season renesting potential, might make eggs just as important as nestlings within this kingbird population (Siderius 1993).

Although nest age was the main parental investment hypothesis addressed in our research, parental investment theory also predicts that clutch or brood size should positively affect nest defense intensity. Many studies have supported this idea (Knight and Temple 1986b; Wiklund 1990), and we found that clutch or brood size positively influenced both male and female nest defense and appeared to be an important predictor of nest aggression for both sexes. Research on American goldfinches (*Carduelis tristis*) showed a positive relationship with call rates and artificially increased brood sizes (Knight and Temple 1986b). This positive relationship between parental female nest defense intensity and brood size was also observed in merlins (*Falco columbarius*), though original clutch size did not seem to be as important as brood size after alteration (Wiklund 1990). For females in our study, clutch/brood size was second to nest age in terms of magnitude of slope parameter estimate, and this variable interacted with nest concealment.

The renesting potential hypothesis predicts that later-season nests will be defended more intensely because there is reduced renesting potential as the breeding season progresses (Barash 1975). In our study, we showed that both male and female aggression responses were higher for nests that were initiated later in the breeding season, although, males, compared to females, appeared to have a much stronger aggression response to nest initiation date. Previous studies have shown parental aggression to be either positively or negatively correlated with Julian date (Biermann and Robertson 1981; Regelmann and Curio 1983), but these trends were confounded with nest stage. The survival uncertainty of the upcoming non-breeding season is driving this hypothesis; in one study, male annual mortality was estimated at 52 % with 29 % of the mortalities associated with the non-breeding season (Yasukawa 1987). Despite similar reported annual mortality rates for females, parental investment covariates, such as nest age and clutch/brood size, appear to be more important than renesting potential in females (Fankhauser 1971; Searcy and Yasukawa 1981; Martin and Li 1992). Potentially high annual male mortality rates may be driving some of the variation we observed in nest defense aggression; however, it appeared that the interaction between renesting potential and parental investment offered a better explanation of variation in nest dense aggression. Particularly for males, the renesting potential hypothesis was most supported for nests with lower nest ages.

Our results contradict Biermann and Robertson (1981), who found that red-winged blackbird nest defense increased through the breeding season for nests with nestlings but decreased for nests with eggs. They suggested that seasonal predation risk (e.g., higher predation later in season) and parental investment might be driving these patterns. We found that early in breeding season, males were more aggressive at older nests, but late in the breeding season, males were generally more aggressive for younger nests (lay/incubation stages). We suspect that nesting attempts earlier in the season may actually have more value to parents; thus, they may be defended more vigorously, especially if the nest is at a later stage. Similarly, first broods of merlins (*F. columbarius*) in Sweden were defended more vigorously than second broods (Wiklund 1990). Also, several studies have documented higher nest success earlier in the breeding season compared to later (Grant et al. 2005; Adams et al. 2013), and earlier fledged broods often have a greater chance of survival compared to later fledged broods (Wiklund 1990; Møller and Nielsen 2014). However, within males, positive reinforcement or variables highly correlated with positive reinforcement appeared to have stronger relationships with aggression.

After accounting for all three main hypotheses in the same model, positive reinforcement (Visit Number) was explaining variation in male nest aggression but not for females. The problem is to disentangle the effect of nest age and repeated visits by human observers. As Knight and Temple (1986a) suggested, an increase in aggression response by red-winged blackbirds might be an artifact of repeated nest monitoring visits through “positive reinforcement” of repeated success in driving away non-threatening human observers. This would suggest that the perceived cost of defensive aggression (threat to adult) is reduced and perceived effectiveness is increased. In our study, males appeared to respond more aggressively after nests were visited at least two times across most nest stages, whereas females appeared more aggressive during second visits if nests were at the incubation stage. A limited number of studies suggest that the positive reinforcement hypothesis explains nest defense intensity of passerines better than parental investment (Knight and Temple 1986a; Hobson and Sealy 1989). Other studies, despite experimental approaches, have not found conclusive support for the positive reinforcement hypothesis (Westmoreland 1989; Westneat 1989; Siderius 1993; Viñuela et al. 1995). In a study on nest defense of willow tits, *Parus montanus*, revisitation of nests by the same individual was not associated with increased nest defense intensity (Rytkönen et al. 1990). However, our results offer some support for Knight and Temple’s (1986a) positive reinforcement hypothesis, especially for male red-winged blackbirds.

There are several potential explanations for the commonly witnessed patterns of positive reinforcement in nest defense intensity in birds. Potential mechanisms include repeated successful human intruder deterrence, elevated perceived predation risk, past experience of parent with an individual human observer or nest predator, and even the reinforcement of reciprocal altruism by neighbors (Knight and Temple 1986a; Olendorf et al. 2004; Krams et al. 2010; Langmore et al. 2012). Knight and Temple (1986a) argue that human and predator models used in studies routinely can be successfully defended against and may lead to results supporting positive reinforcement. Although not investigated in our study, repeated nest visits by the same individual observer and parental past experience with a nest predator, opposed to a naïve parents, have increased nest defense intensity (Knight and Temple 1986c; Levey et al. 2009; Langmore et al. 2012). Increased perceived risk of blackbird nest predation in our study may especially have been the case, because certain study fields often had multiple observers simultaneously present to improve the nest monitoring efficiency. Also, neighboring male red-winged blackbirds seem to cooperate in nest defense in what appears to be a form of reciprocal altruism (Olendorf et al. 2004). It has been shown that heightened male nest defense attracts conspecific neighbors to assist, and Olendorf et al. (2004) contends that this may be a direct reason to develop and reinforce cooperative relationships with neighbors. Although visit number was not included in the male top model, its high correlation with within-individually centered nest age suggests that positive reinforcement was a driver of nest aggression in males but not conclusive for females. For both sexes, the additional covariates, such as nest concealment and nest density, improved model competitiveness when added to best main hypothesis models.

Nest concealment has been suggested as driving aggression response in some birds (Carrillo and González-Dávila 2013). Nest concealment may especially be important to deter visual predators such as avian predators, but well-concealed nests may generally suffer greater depredation to olfactory base predators such as mice and snakes (Weidinger 2002; Colombelli-Négrel and Kleindorfer 2009). We found that increased nest concealment predicted increased aggression in males but decreased aggression in females; however, for both sexes, concealment confidence intervals overlapped zero. For males, the common explanation of the observed pattern is a behavioral compensation for more exposed nests, but this pattern, across both sexes, has not been supported previously in other species (Onnebrink and Curio 1991; Weidinger 2002). Most interestingly, for females, there was a strong interactive aggression response depending on the size of the clutch/brood and nest concealment. Females in laying situations with smaller clutch sizes (zero to two eggs), may have to balance the trade-off between physical nest concealment and defense intensity, which can be a form of nest concealment behavior. Females may rely more on concealment in these

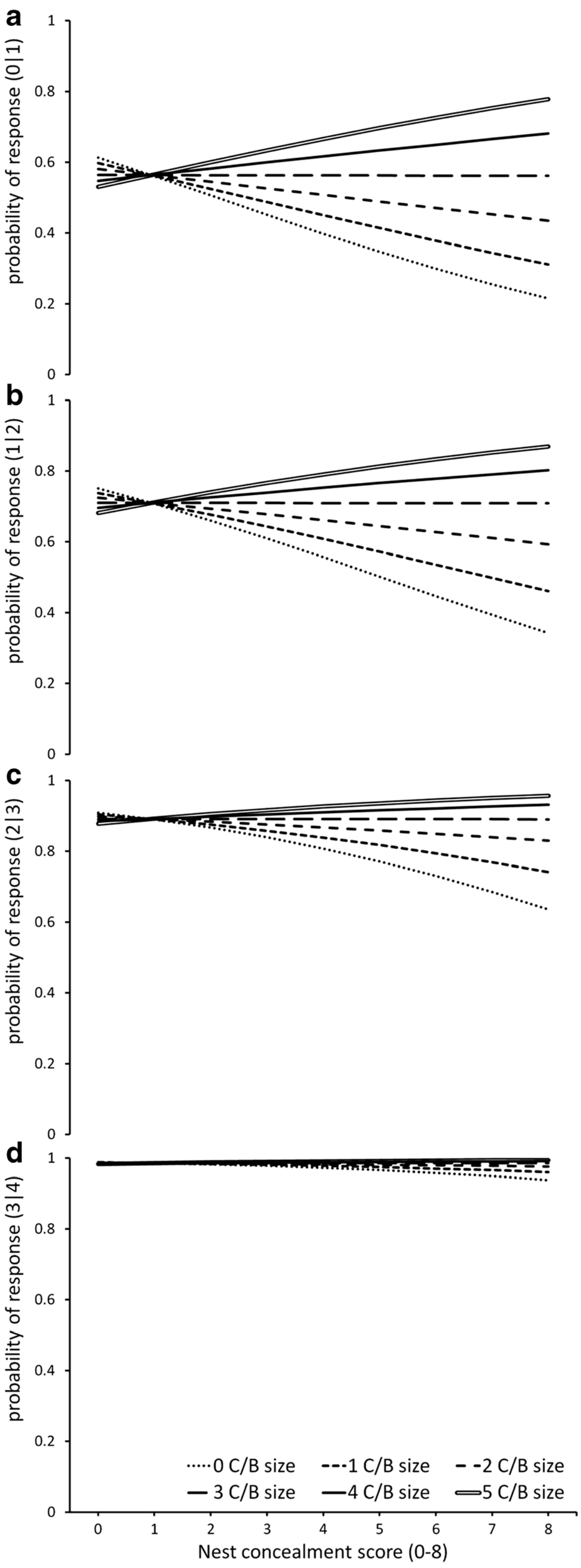

Fig. 4 Probability of nest aggression response of female red-winged blackbirds, at distinct response thresholds (0–4), predicted from increasing nest concealment scores and clutch/brood size (C/B size). Blackbird nests were monitored during the 2011–2014 breeding seasons in northwestern Illinois, USA

cases, as can be seen in great tits (*Parus major*) that responded more aggressively to a predator model at less vulnerable nests (Onnebrink and Curio 1991). These results generally support the patterns we found, and the authors contend that when nests are more vulnerable, less concealed in our case, offspring survival is reduced as is their potential for future reproduction and parents may be responding accordingly.

Our analysis did not compare males and females in the same analysis, and we decided against this approach in order to simplify already complex models, avoiding a sex interaction term. However, differences between results of males and females can be implied. In general, males had higher aggressive ratings than females, likely because females are investing more effort into reproductive activities such as nest building, egg development and laying, incubation, and feeding young resulting in less energy and time available for nest defense (Yasukawa and Searcy 1995). Male red-winged blackbirds, which do not share many of the reproductive responsibilities of females, have more time and energy to devote to nest defense. On the other hand, additional factors such as clutch/brood size and nest density relatively were more supported within females when added to top main hypothesis models compared to males. In terms of clutch/brood size, which was especially important for females, a clutch increase from four to five eggs represents a 20 % increase in reproductive potential for females (and monogamous males), and the loss of one nest represents a potential 100 % loss of reproduction for a female. This may partly explain why clutch/brood size effects seem more important in driving female aggression. Conversely, a polygynous male has risk of nest lost spread out over multiple nests, and therefore, aggressively defending nests with larger clutches would only have marginal payoff compared with females.

Polygynous male-nesting situations will lead to greater nest densities within a given area, a covariate which we measured. In lieu of marked birds, nest density served as our proxy for degree of polygyny. Nest defense for females significantly decreased with increasing nest density surrounding a particular nest. One explanation for this pattern is likely due to increased group vigilance and cooperative nest defense through the dilution explanation (Arroyo et al. 2001). In dense nesting situations, nest defense aggression can be spread out over multiple parents, both males and females, allowing aggression intensity per individual to decrease. Why females responded more to nest density compared to males might be explained by greater variability in female numbers across different polygynous male territories. In a marsh habitat, it was an increased female density that reduced nest depredation rates (Picman et al. 1988). For males, the issue of parental uncertainty likely becomes more prevalent in dense nesting situations as extra-pair copulations increase (Westneat and Sherman 1997), and males appear to be able to discriminate between faithful and unfaithful females (Gray 1997). These studies likely corroborate the decreasing nest defense intensity trend with increasing nest density result we found for males.

Conclusions

We found the strongest evidence supporting the parental investment theory (Trivers 1972) for both sexes. Positive reinforcement hypothesis (Knight and Temple 1986a) followed by the renesting potential hypothesis (Barash 1975) also appeared to be influencing male nest defense aggression. This suggests that an answer to this classic question is not straightforward, and it appeared that male aggression was driven by interactive combinations of the three main hypotheses, whereas female aggression was explained by parental investment plus additional factors such as clutch/brood size, nest density, and nest concealment.

Although controlled experimental approaches are typically desirable when addressing research questions, large-scale observational data sets remain useful and can assist in developing ecological generalizations and compliment experimental approaches (Martin 2002). Much remains to be clarified about nest defense intensity in birds, which sometimes may be positively reinforced by frequent nest visitations. Our approach elucidates some of the complexities, namely the potential interaction between different hypotheses and the importance accounting for within-individual and between-individual standardization, involved in explaining nest defense aggression. In the future, consistent methodological and statistical approaches across multiple species with varying life history traits would be useful in further clarifying factors affecting nest defense intensity

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Compliance with ethical standards

Ethical approval For this type of study, formal consent is not required. Birds were not handled during this study, and nest monitoring was conducted in a manner to minimize disturbance to the area and blackbird parents. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

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Conflict of interest The authors declare that they have no competing interests

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