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Increased perception of predation risk to adults and offspring alters avian reproductive strategy and performance

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Predation risk can inflict profound effects on prey by influencing prey behavior and other traits. Prey are often subjected to a diversity of predators, which can exert differential predation pressures on prey life-history strategies. In birds, breeding adults and offspring (as eggs, nestlings, and fledglings) are susceptible to different types of predators, and life-history theory predicts that breeding birds can adjust to adult versus offspring predation risk differentially via allocation of breeding investment. Here, we experimentally tested for the effects of perceived adult versus offspring predation risk on breeding birds' reproductive strategy and performance. On study plots with nest boxes used by the cavity-nesting Eastern bluebird *Sialia sialis*, we manipulated vocal cues of 3 avian predators that preferentially prey on either bluebird adults, or offspring, or both. We found that 1) increased perception of predation risk by all predator treatments reduced bluebird parental investment in egg production and/or post-egg nesting performance, and 2) increased perception of adult and offspring predation risks affected bluebirds differentially, with bluebirds exhibiting shorter nestling rearing periods under offspring, but not adult, predation risk. Our results provide experimental evidence for the nonconsumptive effects of predation risk on avian breeding behavior that can influence demographic vital rates and highlight the mechanisms by which breeding birds can adjust reproductive strategies under different predation risk situations.

Key words: **adult, avian reproduction, life-history theory, offspring, perceived predation risk.**

INTRODUCTION

Predation risk is widely recognized as a key force shaping ecological and evolutionary processes (Reznick and Endler 1982; Lima and Dill 1990; Endler 1991). Predation risk exerts such influences not only through directly killing prey (i.e., "consumptive effects"; Endler 1991) but also through influencing prey behavior and other traits via prey perception of predation risk (i.e., "nonconsumptive effects"; Schmitz et al. 1997; Lima 1998a; Preisser et al. 2005; Creel and Christianson 2008; Peckarsky et al. 2008). Animal sensitivity to predation risk should be particularly acute during breeding because of increased vulnerability of the distracted adults busy with parental care (Lima and Dill 1990; Magnhagen 1991) and the defenselessness of young (e.g., McLennan et al. 1996).

To maximize life-time reproductive success (Magnhagen 1991), breeding animals that detect and respond to cues of predators can choose to avoid high-risk breeding habitats during territory establishment (e.g., Fontaine and Martin 2006; Hua et al. 2013) or oviposition site selection (e.g., Blaustein et al. 2004). Once breeding habitat selection has occurred, life-history theory suggests that breeding animals can adjust to perceived predation risk via allocation of breeding investment and other behaviors (Sih 1987; Lima and Dill 1990). The essential predictions of life-history theory concerning the behavioral adaptation of breeding prey to varying intensities and types of predation risk are supported by an increasing number of empirical studies of a wide variety of taxa. Overall, reductions in current reproductive investment and output are observed when breeding animals perceive increased predation risk to themselves (e.g., in mammals, Koskela and Ylonen 1995; Creel et al. 2007; in birds, Thomson et al. 2006; in fish, Fraser and Gilliam 1992; Candolin 1998; in aquatic invertebrates, Lasley-Rasher and Yen 2012), their offspring (e.g., in birds, Doligez and Clobert 2003; Eggers et al. 2006; Fontaine and Martin 2006; Mönkkönen et al. 2009; in fish, Wisenden 1993), or both (e.g., in birds, Zanette et al. 2011). However, assessments of how breeding animals may differentially respond to perceived adult versus offspring predation risk in the same context are currently rare (but see Ghalambor and Martin 2000).

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Predation risks to adult versus offspring are expected by life-history theory to influence breeding animals by different mechanisms (Pianka and Parker 1975, Lima and Dill 1990; Magnhagen 1991; Templeton and Shriner 2004) because they influence contrasting ends of the fundamental evolutionary trade-off between current versus future reproduction (Magnhagen 1991). In general, on an ecological time scale, iteroparous species perceiving primarily high adult predation risk should minimize exposure to adult predators (e.g., Lima 2009), whereas animals perceiving primarily high offspring predation risk should minimize current offspring predation and/or reduce investment in current reproduction to bet-hedge for future reproduction (e.g., Martin and Briskie 2009). In altricial birds, efforts to minimize adult predation are expected to translate into reduced clutch size and/or offspring feeding rate, thereby reducing exposure during foraging effort (Lima 1987). Efforts to minimize predation on current offspring and reduce investment in current reproduction are expected to lead to reduced clutch size, egg mass, and clutch mass, as well as reduced offspring feeding rate to increase nest crypsis (Skutch 1949; Safriel 1975; Slagsvold 1984; Martin 1995; Martin et al. 2000a; 2000b; Fontaine and Martin 2006). Alternatively, efforts to minimize predation on current offspring may also predict increased offspring feeding rate (hence allowing more active nest defense; Montgomerie and Weatherhead 1988; Martin 1992) and/or speedier offspring development to shorten the high-risk nesting period (Martin 2002; Martin et al. 2011). Therefore, although life-history theory predictions regarding birds' reproductive response to increased perception of adult versus offspring predation risk overlap to some extent, they are based on different mechanisms, and a shortened nestling period is one unique prediction for birds responding to increased risk of offspring predation (Table 1). A simultaneous test of prey responses to increased perception of adult versus offspring predation risk in the same study system can provide the means of comprehensively testing life-history theory predictions and of detecting prey accommodation of the evolutionary trade-off with its behavioral decision-making.

We experimentally tested for reproductive response in a breeding bird species under increased perception of predation risk to adults, or offspring, or both. We specifically asked how birds would respond in their breeding investment, performance, and output at 3 stages of reproduction: egg production, egg hatching, and offspring rearing. We set up nest boxes on experimental plots in pine sandhill forests of the Southeastern United States for free-living pairs of the cavity-nesting Eastern bluebird *Sialia sialis*. We used the vocalizations of three predator species, each conveying different risks to 1) adult bluebirds (Eastern screech-owl *Megascops asio*), 2) offspring (i.e., egg and nestlings; blue jay *Cyanocitta cristata*), and 3) both adults and offspring (Cooper's hawk *Accipiter cooperii*), in addition to control (no calls). We manipulated predator cues over a full breeding season after bluebirds made settlement decisions and monitored bluebird reproduction to quantify their responses.

METHODS

Study area and species

We conducted fieldwork in the sandhill forest of north-central Florida (29.4°N, 82.0°W), at the Ordway-Swisher Biological Station, a 3700-ha managed research preserve, between late February and mid-August, 2010. Forest vegetation was dominated by longleaf pine *Pinus palustris* and to a lesser extent by turkey oak *Quercus laevis*, with wiregrass *Aristida beyrichiana* in the understory. Other typical species included a variety of oaks, herbs, and grasses (Florida Natural Areas Inventory 2010). These habitats received prescribed burning in units of ~20 ha every 2–5 years to maintain longleaf pine- and wiregrass-dominated conditions (Hua et al. 2013).

The Eastern bluebird is a small (~30 g), insectivorous, resident species at our study site. It depends on naturally occurring or excavated cavities (Gowaty and Plissner 1998), but also readily uses artificial nest boxes when available (DeLuca 2008). At our study site, bluebirds typically exhibit aggressive territorial behavior and defense of selected nest boxes by the end of January (Sieving KE, unpublished data; see also Gowaty and Plissner 1998 for similar territory establishment patterns in Tennessee, which is to the north of our study site). Bluebirds at our study site typically begin egg laying in early April and attempt to raise 2 (sometimes 3) broods per season (DeLuca 2008). Adult birds are susceptible to predation from a variety of predators including hawks, falcons, owls, and snakes. Nest predation is typically from raccoons, snakes, jays, other nest cavity competitors, and *Accipiter* spp. hawks (Gowaty and Plissner 1998; Zimmerman 2013) that are known to depredate passerine nests (McCallum and Hannon 2001; Stracey 2010).

Experimental design

Manipulation of predator cues

On 24 9-ha (300 × 300 m) plots, we broadcast daily vocalization playback of 3 predator species beginning in early March, after most

Table 1

Life-history theory predictions of breeding birds' reproductive response to increased perception of predation risk

Reproductive aspect	Response to increased perception of			
	Adult predation risk	Reference	Offspring predation risk	Reference
Clutch size	↓	A	↓	B
Egg mass	—	—	↓	C
Clutch mass	—	—	↓	D
Offspring feeding rate	↓	A	↓ or ↑	E or F
Nestling development	↓[a]	—	↓[a] or ↑	— or G

—: Life-history theory has no explicit predictions about how the reproductive aspect would respond to increased risk perception. A: Lima 1987; B: Skutch 1949, Safriel 1975, Slagsvold 1984, Martin 1995, Martin et al. 2000a; C: Fontaine and Martin 2006, Martin and Briskie 2009; D: Fontaine and Martin 2006; E: Skutch 1949, Martin et al. 2000b; F: Montgomerie and Weatherhead 1988, Martin 1992; G: Martin 2002, Martin et al. 2011.
[a]Life-history theory has no explicit predictions on the speed of nestling development in these cases, but a slower development should follow based on reduced offspring feeding rate under increased risk perception, provided that the number of nestlings in need of feeding remains largely unchanged. Of these predictions, our study did not test the prediction pertaining to offspring feeding rate.

bluebird territories should have been well established (Gowaty and Plissner 1998) but prior to typical first egg dates (DeLuca 2008). Playback treatments were designed to increase bluebirds' perception of contrasting types of predation risk. We applied vocalizations of 3 species: Eastern screech-owl (owl hereafter; playback at night), blue jay (jay hereafter), and Cooper's hawk (hawk hereafter). In forested parts of the Southeastern United States, all 3 species are important predators of birds and have discernible, relatively frequent vocalizations. Importantly, they represent contrasting types of predation risk to prey including the Eastern bluebird, spanning the gamut of being primarily an adult predator (owl) or offspring predator (jay), or both adult and offspring predator (hawk). The Eastern screech-owl is primarily a predator of adult birds when it preys on birds and less frequently depredates nestlings. It targets mostly small birds including Eastern bluebirds but occasionally attacks larger prey (Gehlbach 1995). The blue jay is an important nest predator of open-cup-nesting birds, whereas its predation on adult birds is infrequently observed (Tarvin and Woolfenden 1999). The Cooper's hawk is a major predator of adult birds (Lima 1993; Curtis et al. 2006), and at our study site also regularly raids open-cup nests of passerines (Stracey 2010). Bluebirds nesting in artificial boxes should not be susceptible to nest predation by blue jay or Cooper's hawk because of the small entry hole sizes of nest boxes (see below: Placement of artificial nest boxes). However, natural nests of bluebirds should be susceptible to these predators because as secondary cavity nesters, bluebirds usually use more open, degraded woodpecker cavities with enlarged entry holes that are accessible to nest predators; under certain cavity-limited situations, bluebirds may even build and use open-cup nests (Gowaty and Plissner 1998). Because bluebirds in our study area do use natural cavities (nest boxes were placed just before the study), we assumed bluebirds would perceive vocal cues of jay and hawk as indications of threat to their offspring.

We assigned plots to 1 of 4 treatments (playback with hawk, jay, or owl vocalizations, or no playback—i.e., control; $N = 6$ plots/treatment) using a randomized block design, where plots within blocks were matched to be in similar postfire recovery stages with similar vegetation features. We delineated a central 4-ha (200×200 m) core within each plot, in which we applied predator vocalization playbacks. Each plot was ≥50 m from habitat edge and spaced ≥200 m apart (≥300 m apart for plot cores). We used 2 automated playback stations on each plot's core area, spaced ~100 m apart and faced toward the plot center. Each playback station consisted of a portable CD player mounted in a box camouflaged in paint at 3 m above ground wired to a deep-cycle marine battery and a timer to provide playback of predator cues (Fletcher 2007; Hua et al. 2013). Control plots had fake stations that looked exactly the same as real playback stations but were silent, to avoid unknown effects from potential procedural control vocalizations (e.g., Nocera et al. 2008; Fletcher 2009). If Eastern bluebirds were responding similarly to playbacks in general (i.e., the rationale for using procedural playback controls), we would expect them to respond to all playback treatments in a similar way, but this was not observed (see Results for details).

We began playback on 5th March 2010, at least 1 month after bluebirds were expected to have made territory settlement decisions, and at least 2 weeks before the earliest first egg date of the species that we were aware of from previous experiences (DeLuca 2008; the first bluebird egg of the season was laid almost 1 month after playback began, on 2nd April 2010). We terminated playback on 23rd July 2010, when most breeding had finished. We minimized bluebird habituation to playback by changing playback files

and the location of stations biweekly throughout the manipulation. Further details of playback scheme are provided in Supplementary Appendix A (see also Hua et al. 2013).

Placement of artificial nest boxes
On the core 4-ha area of each plot, we set up 4 artificial nest boxes in early January 2010, well before the recommended nest box placement time for Southern United States (Nest Box Resource Center 2013). Each nest box was mounted on top of a single metal pole ~1.5 m above ground (Supplementary Appendix B), spaced ~100 m from each other in locations with relatively open habitat preferred by bluebirds (Gowaty and Plissner 1998). One hundred meters is the minimum recommended inter-box distance according to Nest Box Resource Center (2013), and bluebird pairs at our study site readily use artificial nest boxes that are ~100 m away from other occupied boxes (DeLuca 2008). We tried to eliminate actual nest predation by live predators in order to maximize sample size of responses to nonconsumptive effects of predation risk, by mounting nest boxes on narrow poles away from trees or shrubs and by greasing the poles to prevent climbing by snakes and meso-mammals such as squirrels and raccoons (USDA Natural Resources Conservation Service 1999). These measures proved largely effective in excluding predation events. In addition, the small entrance hole of nest boxes (~50 mm in diameter) prevented nest predation by most avian nest predators. For example, during the study, we never observed predatory behavior of Cooper's hawks or blue jays on bluebird nest boxes, based on >50 h of video taping during incubation and nestling rearing stages for each of ~20 nests (Hua F, unpublished data). We removed from analyses all nests that were depredated or otherwise failed due to external factors ($N = 6$ nests).

Consideration of alternative factors
To test for bluebirds' reproductive response to increased risk perception, 3 primary alternative factors could explain responses to treatments instead of changes in individual reproductive strategies: variation in habitat quality among treatments (van Horne 1983), individuals that differ in body condition settling in different treatments (Fretwell 1972; Drent and Daan 1980; Pärt 1991, 1994; Thomson et al. 2012), and intraspecific resource competition influencing reproduction due to changes in density among treatments (e.g., Rodenhouse and Holmes 1992). Habitat quality was addressed by the randomized block assignment of study plots, such that we did not expect systematic biophysical habitat quality differences among treatments. Parental body condition was addressed by beginning playback treatment after bluebirds were expected to have made settlement decisions. We, therefore, did not expect systematic body condition differences of breeding bluebirds among treatments; this notion was further supported by the patterns of bluebird nesting habitat selection and nesting initiation phenology (see Results and Discussion for details). Competition for resources was accounted for by including nesting density (i.e., the number of nests/plot) as a nuisance covariate in all analyses.

Data collection

We monitored each nest throughout the breeding season. For each nest, we measured 1) parental investment in egg production and 2) subsequent nesting performance, for both broods when applicable. In addition, we noted the identity of the nest box used, the date when the season's first egg was produced, and the length of the incubation and nestling rearing periods for the first brood. For parental investment in egg production, we measured clutch size and

egg size on the second day following clutch completion (Fontaine and Martin 2006; Martin and Briskie 2009). We derived egg mass from egg size following Hoyt (1979) and in turn calculated clutch mass. For subsequent nesting performance, we recorded egg hatching rate, and the number and body mass of nestlings on the 14th day since hatching (i.e., ~1 day before fledging). We then calculated 14th-day brood mass, the number of fledglings (assuming all 14th-day nestlings fledged), nestling expiration rate (i.e., the probability of nestlings failing to fledge), and the total number of fledglings produced over the breeding season (i.e., seasonal fecundity). All mass and length measurements were accurate to the nearest 0.01 g and 0.01 mm, respectively.

Because bluebirds were not individually marked, we made the following assumptions about the second brood. First, if the same nest box was used for more than 1 brood in sequence, we assumed that the same bluebird pair attempted both broods. On some plots, nests shifted (i.e., 1 box was abandoned after the first brood and a previously empty box was used subsequently to raise a later brood); in no case did more than 1 shift per plot occur. Therefore, we assumed that the new, later, nest belonged to the bluebird pair that left the abandoned box used earlier on the same plot. Both assumptions were realistic given the biology of the Eastern bluebird and our field experiences (e.g., they reuse nest cavities; Stanback and Rockwell 2003). In addition, by considering that the performance of second and first broods was correlated in analysis, statistical inferences were more conservative (see Statistical analyses and Results for details), although they may lead to slightly different interpretations of treatment effect (see Discussion for details). All data are provided in Supplementary Appendix C.

Statistical analyses

To analyze treatment effects on nesting measures across 2 broods, we used generalized linear models (GLMs) with generalized estimation equations (GEEs) to account for the correlated nature of data from repeated broods of the same breeding pairs (Liang and Zeger 1986). We used an identity link, normal error distribution, and exchangeable correlation structure for continuous data, and a logit link, binomial error distribution, and exchangeable correlation structure for binary data (i.e., egg hatching rate, nestling expiration rate, and nest box selection). Except for analysis of nest box selection, all models included treatment, brood identity (i.e., brood 1 or 2), and the number of nests on plot as predictor variables. The model for egg hatching rate additionally included clutch size as a predictor variable because a larger clutch size likely has negative effects on hatching rate (Thomson et al. 1998). For analysis of nest box selection, we included treatment as the only predictor variable and accounted for the correlation of nest boxes on the same plot instead of between broods.

To analyze treatment effects on nesting measures of only the first brood and seasonal fecundity, all of which were continuous data, we used analysis of covariance with treatment and the number of nests per plot as predictor variables. In case the assumptions we made about the second brood did not hold, we also analyzed data across 2 broods without assuming that second broods came from the same nesting pair and used GLMs with the same model structure as the GEE models specified above to analyze treatment effects. Results from GEEs analysis should be more conservative than the corresponding GLMs analysis (Stout and Papandonatos 2002), although the 2 analysis framework entail different interpretations (see Discussion for details). Finally, because raw data seem to suggest bluebirds had more pronounced reproductive responses to

treatment during the second brood than the first brood, we additionally analyzed data from the 2 broods separately using corresponding GLM analyses. Because this was an experimental test of predator treatment, and due to the simplicity of model structure and the biological reasons to include the other predictor variables as explained previously, we utilized only the full models and did not apply model selection (e.g., Pan 2001). We conducted all statistical analyses using R.3.0.2 (R Core Team 2013) with package "geepack" (for GEE analyses; version 1.1–6).

RESULTS

A total of 35 bluebird pairs nested in nest boxes on our plots during the breeding season. Thirty pairs produced 2 broods (N = 7, 7, 7, and 9 for control, owl, jay, and hawk treatments, respectively). The other 5 pairs produced 1 brood (N = 1, 2, and 2 for owl, jay, and hawk treatments, respectively), all on treatment plots. Four pairs (N = 2, 1, and 1 for control, owl, and hawk treatments, respectively) failed 1 or more broods because of external factors (i.e., nest predation, prescribed burning, and probable parent infertility). Two additional nests (1 for owl and hawk treatments each) sustained partial egg predation possibly by Carolina chickadee *Poecile carolinensis* competing for nest cavities (Gowaty and Plissner 1998; Maier and DeGraaf 2000). We excluded these nests from analyses accordingly.

We detected a weak tendency for nest boxes on plots under hawk treatment to be preferred by bluebirds, with a 42.8% increase in the odds of being selected compared with those on control plots ($0.05 < P < 0.1$, Table 2). No preference/avoidance of nest boxes on other treatment plots were detected.

Treatments negatively affected bluebird reproductive performance. All 3 treatments reduced bluebirds' clutch size ($P < 0.05$; Table 2, Figure 1a). Owl treatment reduced clutch mass, whereas there was a weak tendency for reduced clutch mass under hawk treatment (Table 2). Hawk and jay treatments reduced egg hatching rate (Table 2, Figure 2). By the 14th-day after hatching, hawk treatment nests had a reduced number of nestlings, whereas jay treatment nests had heavier nestlings and exhibited a tendency toward fewer nestlings (Table 2, Figure 3). Owl treatment did not affect the number, body mass, or brood mass of 14th-day nestlings. No treatment effects were detected for egg mass, 14th-day brood mass, nestling expiration rate, the date of the first egg, or the length of incubation period. Overall, by the end of the breeding season, nests under the hawk treatment produced 42.3% fewer fledglings (Table 2, Figure 4a).

Perceived predation risk to offspring only (jay) but not to adults (hawk or owl) appeared to have shortened the nesting cycle. First, jay treatment shortened nestling rearing period for the first brood by 10.2% compared with control (Table 2, Figure 4b). This result is corroborated by the finding that 14th-day nestlings under jay treatment were significantly heavier than control (Figure 3b; see results above). Second, birds under jay treatment appeared to have produced heavier eggs (Figure 1b) such that clutch mass was unchanged despite significantly smaller clutches, a possible risk response to speed up offspring growth (see Discussion for details).

Results of analyses where we did not assume which breeding pairs the second broods belonged to were generally more significant but did not qualitatively differ from those reported above with 2 exceptions: hawk treatment was found to result in heavier eggs and heavier 14th-day nestlings (Supplementary Appendix D). In addition, seasonal fecundity should be a breeding parameter at

Table 2

Bluebirds' reproductive responses to different types of perceived predation risk

Reproductive response	Treatment effect (over control)				
	Treatment	Mean	Standard error	Odds ratio[a]	*P*-value
Nest box selection	Owl	0.099	0.195	1.104	0.613
	Jay	0.194	0.201	1.214	0.334
	Hawk[b]	0.551	0.284	1.735	0.052
Clutch size	**Owl**	**−0.473**	**0.205**	**NA**	**0.021**
	Jay	**−0.449**	**0.167**	**NA**	**0.007**
	Hawk	**−0.508**	**0.183**	**NA**	**0.006**
Clutch mass	**Owl**	**−1.360**	**0.681**	**NA**	**0.046**
	Jay	−0.714	0.659	NA	0.278
	Hawk[b]	−1.320	0.731	NA	0.071
Hatching rate	Owl	−1.326	1.077	0.266	0.218
	Jay	**−2.445**	**1.078**	**0.087**	**0.023**
	Hawk	**−2.695**	**1.200**	**0.068**	**0.025**
14th-day nestling number	Owl	−0.197	0.316	NA	0.534
	Jay[b]	−0.518	0.301	NA	0.085
	Hawk	**−0.794**	**0.342**	**NA**	**0.020**
14th-day nestling mass	Owl	0.455	0.666	NA	0.494
	Jay	**1.567**	**0.529**	**NA**	**0.003**
	Hawk	1.172	0.751	NA	0.119
Seasonal fecundity	Owl	−1.756	1.299	NA	0.191
	Jay	−2.086	1.233	NA	0.105
	Hawk	**−3.442**	**1.356**	**NA**	**0.019**
Nestling rearing period	Owl	−0.845	0.876	NA	0.350
	Jay	**−1.667**	**0.758**	**NA**	**0.044**
	Hawk	−1.306	0.951	NA	0.190

Table shows treatment effects for response variables that responded to at least 1 treatment (i.e., *P* < 0.1, Wald test). Statistically significant treatment effects with *P* < 0.05 are highlighted in bold.
[a]Odds ratios are provided for variables that were analyzed with a logit link; they are not applicable to, and are thus marked NA (not applicable) for, variables that were not analyzed using a logit link.
[b]Indicates treatment effects with 0.05 < *P* < 0.1.

the level of plots rather than individual breeding pairs. When we tested broods separately, bluebirds' reproductive responses to treatment were more pronounced for the second brood (Supplementary Appendix E). Finally, nesting density showed no correlation with most response variables except for a positive correlation with egg mass (see Supplementary Appendices C and D), which was contrary to what might be expected if bluebirds' reproductive responses were driven by resource competition.

DISCUSSION

By simultaneously comparing Eastern bluebirds' reproductive response to perceived adult versus offspring predation risk, we found that increased perception of predation risk negatively affected bluebird reproductive performance, and that adult and offspring predation risks affected bluebird reproduction differentially. Given our research design and findings (see discussion below), these reproductive responses were most likely attributable to individual adjustments in reproductive strategy and alterations in reproductive performance. Our findings provide empirical support to life-history theory predictions pertaining to breeding birds' reproductive response under elevated perception of predation risk (Lima 2009; Martin and Briskie 2009) and provide the first evidence of an accelerated nestling rearing period under increased offspring predation risk in birds as predicted by theory (Martin 2002; Martin et al. 2011). Overall, our results demonstrate the strong impacts of the nonconsumptive effects of predation risk on avian reproduction (Fontaine and Martin 2006; Zanette et al. 2011) and highlight the different mechanisms by which breeding

bluebirds may adjust reproductive strategies under different predation risk situations.

To maximize life-time reproductive success under the trade-off between current and future reproduction (Williams 1966), breeding animals should adjust reproductive effort in response to shifts in perceived adult and offspring predation risk (Lima and Dill 1990). Bluebirds' smaller clutch size under perceived adult predation risk suggests an adaptive response that can reduce nesting-related activities and thus exposure to adult predation (Lima 1987, 2009). This result is corroborated by other experimental studies on various taxa (e.g., mammals: Koskela and Ylonen 1995; Creel et al. 2007; Maron et al. 2010; birds: Thomson et al. 2006; fish: Fraser and Gilliam 1992, Candolin 1998; aquatic invertebrates: Lasley-Rasher and Yen 2012). Bluebirds' simultaneously reduced clutch size and nestling production, and a shortened nestling stage in response to increased perception of offspring predation risk, appropriately serve to reduce predation risk for current offspring while saving investment for future nesting (Martin and Briskie 2009). Reduced clutch size and investment have been experimentally recorded in breeding birds (Eggers et al. 2006; Fontaine and Martin 2006; Mönkkönen et al. 2009, Greenwood and Dawson 2011) and are consistent with results from experimental studies on fish (Wisenden 1993). However, to our knowledge, a speedier nestling rearing period in response to increased perception of offspring predation risk has not had previous empirical support in birds (accelerated egg hatching in amphibians under increased egg predation risk occurs via phenotypic plasticity of offspring rather than the behavioral plasticity of attending adults; Warkentin 1995). Our study thus provides unique evidence supporting the life-history
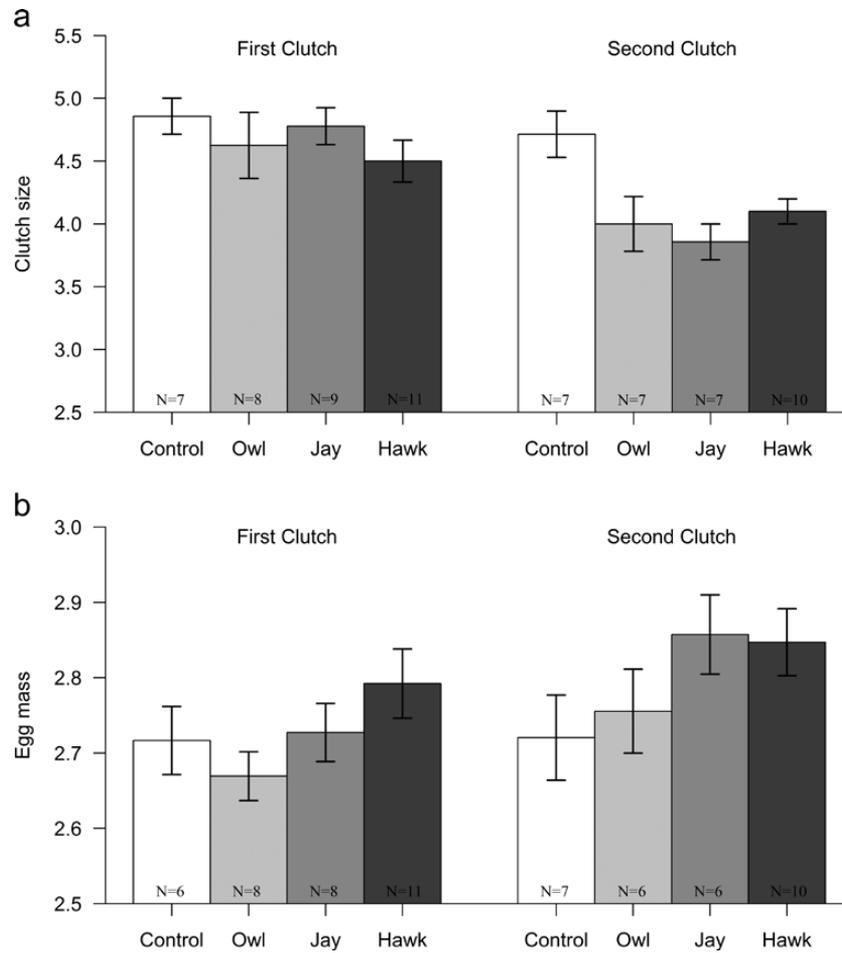
Figure 1

Effects of perceived adult or offspring predation risk on bluebird parental investment in egg production. (a) Compared with control, owl, jay, and hawk treatments reduced bluebird clutch size by 9.44%, 8.96%, and 10.14%, respectively. (b) Although there was no significant treatment effect on egg mass, jay (and hawk) treatment appeared to have resulted in heavier eggs. Values are mean ± standard error. "N=" in bars indicates the number of nests included in the analysis.
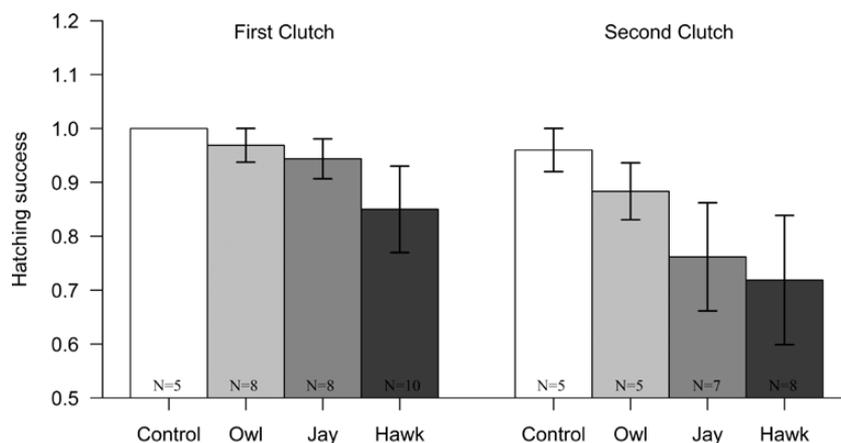

Figure 2

Effects of perceived adult or offspring predation risk on bluebird egg hatching success. Compared with control, jay, and hawk treatments reduced the odds of egg hatching probability by 91.33% and 93.25%, respectively. Values are mean ± standard error. "N=" in bars indicates the number of nests included in the analysis.

prediction of a speedier nestling rearing period as a result of breeding adults' behavioral adjustment (Martin 2002; Martin et al. 2011). Additionally, we detected decreased egg hatching rate under hawk and jay treatments. Reduced egg hatching success under increased predation risk has earlier been suggested by Zanette et al. (2011),

although to our knowledge, life-history theory does not have specific predictions on this aspect of avian reproduction. The impaired hatching success was possibly due to increased level of stress parent birds experienced during the egg-forming and egg-laying stages (Lima 1998b), which is known to be detrimental to body condition
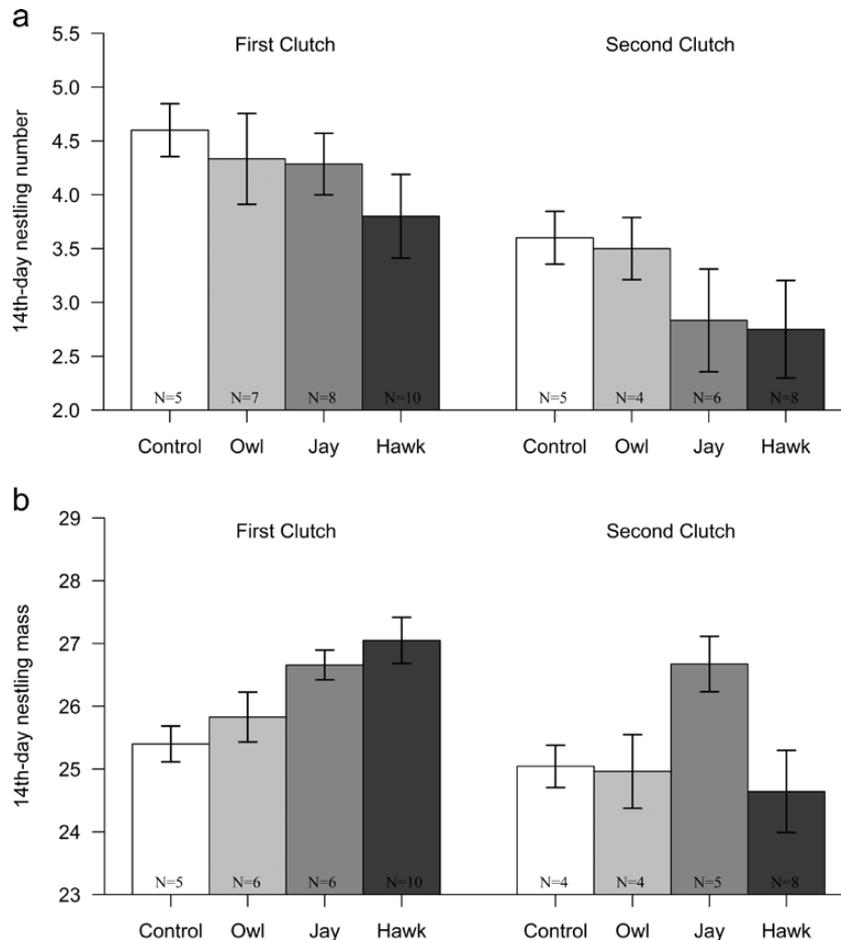
Figure 3
Effects of perceived adult or offspring predation risk on bluebird nestling number and body mass on the 14th day since hatching. (a) Compared with control, hawk treatment reduced the number of 14-day nestlings by 16.91%. (b) Compared with control, jay treatment increased the body mass of 14-day nestlings by 5.89%. Values are mean ± standard error. "*N*=" in bars indicates the number of nests included in the analysis.

and performance in a variety of reproductive tasks including fertility rate (Siegel 1980, Wingfield and Silverin 1986, Scheuerlein et al. 2001, Creel et al. 2009). The culmination of these impaired reproductive performances was the over 40% reduction in seasonal reproductive output under the hawk treatment (Figure 4b), a magnitude similar to that reported in song sparrows *Melospiza melodia* by Zanette et al. (2011). Taken together, our results 1) provide experimental evidence for multiple theoretical predictions, 2) highlight the different behavioral mechanisms by which breeding bluebirds adjust reproductive strategies under different risk situations, and 3) suggest the potential demographic implications of the nonconsumptive effects of predation risk through effects on avian reproductive performance.

It is worth noting that much of the bluebirds' reproductive responses were driven by the second brood (Figures 1–3): responses were more pronounced in the second brood than in the first brood (Supplementary Appendix E). Apart from possible changes in seasonal resources that could constrain breeding and account for bluebirds' stronger risk responses (Martin 1987), the difference in parents' breeding costs-and-benefits balance between the first and second broods may be a main driver of such differential response. For 2-brooded species, offspring produced from the second brood are generally thought to be of lower fitness value to parents than offspring from the first brood (Hochachka 1990). This derives from

the fact that second broods tend to have lower chances of survival, thus recruitment, into the breeding population (e.g., Kluyver et al. 1977). Given that predation risk constitutes a significant reproductive cost for animals (Magnhagen 1991), the theory of maximizing life-time reproductive success predicts reduced willingness by parents to pay such costs for offspring with lower fitness value, that is, offspring from the second brood, and a higher willingness for offspring from the first brood (Kluyver et al. 1977; Drent and Daan 1980). This prediction may explain bluebirds' stronger reproductive responses to perceived predation risk during the second brood than the first brood. Additionally, because of energy expenditure during the first brood, bluebirds may likely have a lower energy reserve during the second brood attempt (Smith et al. 1987). This may, in turn, impair their ability and/or willingness to engage in costly reproductive activities under predation risk, thereby intensifying their reproductive responses to perceived predation risk. Bluebirds' differential reproductive responses between the first and second broods suggest that including multiple broods (if they occur) in assessing birds' reproduction is not only necessary for obtaining an adequate assessment of the demographic implications of reproduction (Zanette et al. 2011) but can also reveal potentially important patterns that may be missed if only the first brood was studied (e.g., Fontaine and Martin 2006). It should be noted, however, that the above interpretations were based on our assumptions
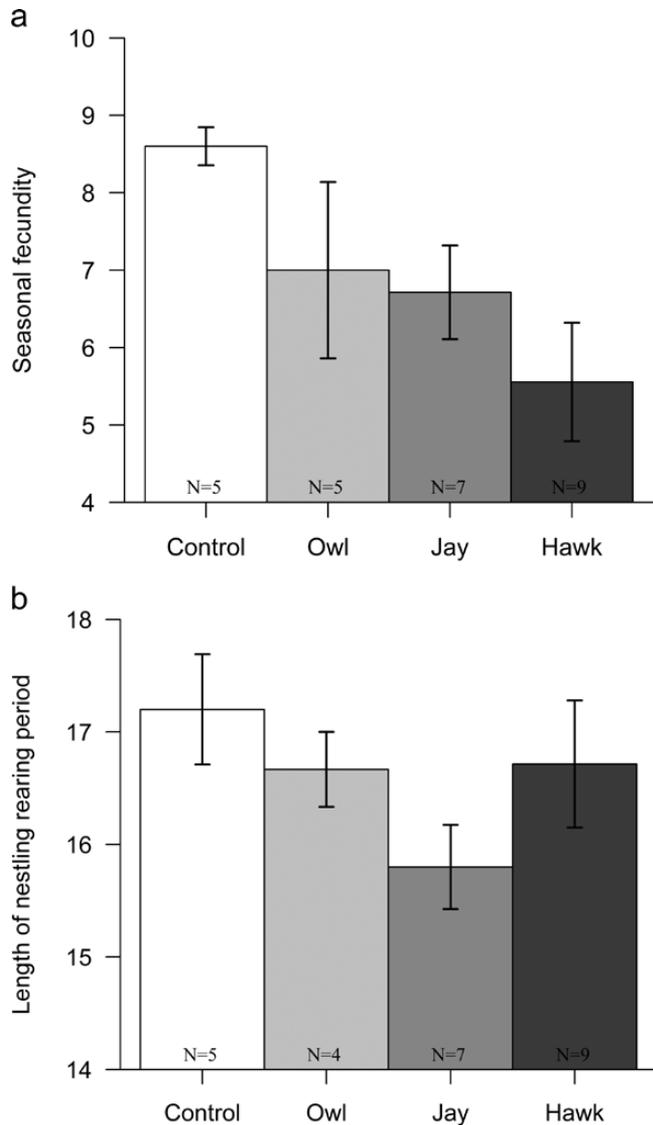
Figure 4

(a) Effects of treatments on bluebird seasonal fecundity. Compared with control, hawk treatment reduced bluebird seasonal fecundity by 42.30%. Values are mean ± standard error. (b) Effects of treatments on the length of bluebird nestling rearing period of the first brood. Compared with control, jay treatment shortened bluebirds' nestling rearing period of the first brood by 10.2%. Values are mean ± standard error. "*N*=" in bars indicates the number of nests included in the analysis. .

of assigning the second broods (see Data collection in Methods). If these assumptions did not hold, treatment effects on the first versus second broods should then be interpreted as seasonally different effects (with stronger risk effects later in the season) at the level of treatment plots, rather than between-brood different effects at the level of individual breeding pairs. Similarly, treatment effects on bluebird seasonal fecundity should be interpreted at the level of treatment plots (e.g., as a measure of a plot's habitat value for bluebird reproduction) rather than individual breeding pairs. Still, our conclusion remains unaffected that bluebird reproduction responded to the nonconsumptive effects of different types of predation risk strongly and differentially.

Although bluebirds in our study had most likely established breeding territories before playback treatments began (see

Experimental design), and we should thus not expect systematic body condition differences of breeding pairs among treatments, we did not have definitive data on birds' body condition. Therefore, we could not completely rule out the alternative explanation that the observed reproductive responses may have been caused by birds with poorer body conditions occupying treatment plots due to dominance-related habitat selection (Fretwell 1972; Drent and Daan 1980; Pärt 1991, 1994; Thomson et al. 2012). However, several pieces of information pertaining to the patterns of bluebirds' breeding habitat selection and nesting initiation phenology combine to argue against this alternative explanation. First, nest boxes on control plots were not preferred over those on treatment plots as might be expected under condition-dependent habitat sorting. Quite to the contrary, the only possible signal of habitat selection suggested by our data was a weak tendency for bluebirds to prefer nest boxes on hawk plots (see Results), which might have been related to the avoidance of these plots by other nest cavity competitors such as Carolina chickadees that subsequently freed up nesting resources for bluebirds (Hua et al. 2013; we did have 2 chickadee nests in our nest boxes, 1 on an owl plot, the other on a jay plot). Considering that bluebird territories can be very small (2 ha in New York and South Carolina; Gowaty and Plissner 1998), and that our control plots had mostly only 1 nesting pair (only 1 control plot had 2 pairs) while many treatment plots had 2 nesting pairs, it is likely that control plots were generally below the resource carrying capacity for breeding bluebird pairs. Therefore, if bluebirds were competing for breeding territories on control plots such that more dominant (and better conditioned) birds occupied them preferentially (Gauthreaux 1978), we should expect to see higher nest box occupancy of control plots than that on treatment plots because pairs on treatment plots should also preferentially opt to occupy control plots before treatment plots. Second, repeated surveys found no difference in plot-level bluebird abundance among treatments (Supplementary Data S6 in Hua et al. 2013), further suggesting that bluebirds did not prefer control plots as breeding habitat over treatment plots. Third, bluebirds' reproductive responses differed among treatments, with distinct responses under jay treatment compared with hawk and owl treatments. If the observed responses were driven by bluebirds having generally poorer body condition on treatment plots compared with control plots, we should not expect to see differential reproductive responses under different treatments. Finally, first egg date did not differ among treatments. If there was preferential occupancy of nesting territories on control plots, we might expect to see earlier nest initiation for pairs on control plots (Alatalo et al. 1984; but see Stutchbury and Robertson 1987). Therefore, despite the lack of data on bluebirds' body condition, these pieces of information taken together argue against the possibility that our observed reproductive responses were an artifact of bluebirds' habitat selection and resultant body condition differences among treatments. Rather, the observed reproductive responses are more parsimoniously explained as being the direct consequence of bluebirds' reproductive behavioral adjustments.

There is one potential caveat about interpreting our results on bluebird reproductive allocation and performance as deriving only from the nonconsumptive effects of predation risk. Because we did not mark the breeding individuals and could not eliminate or detect adult predation events, post-egg-laying reproductive responses to perceived adult predation risk could potentially involve consumptive effects resulting from the predation of 1 parent. This situation is conceivable as a result of conspecific attraction (Reed and

Dobson 1993) of owls and hawks to owl and hawk plots, respectively, followed subsequently by treatment-related predation losses of bluebird adults. However, video camera surveillance data on nest boxes during the incubation ($\geq$25 day-light-h/nest; N = 5, 5, and 7 for control, owl, and hawk, respectively) and offspring rearing ($\geq$25 day-light-h/nest; N = 4, 6, and 6 for control, owl, and hawk, respectively) stages of the first brood detected only 1 incidence of a single parent attending nest (in hawk treatment during incubation; Hua F, unpublished data). Such extremely low incidence of nest attendance by a single parent suggests that the observed reduction in reproductive performance was not an artifact of lone parents raising their broods. On another hand, loss of 1 parent could have occurred and gone undetected by cameras if birds rapidly replaced lost mates. This raises another possibility that such pairs could suffer reduced reproductive performance due to a period of adjusting to a new mate. However, within-season mate switching is not known to have immediate or dramatic reproductive costs or benefits (e.g., Drilling and Thompson 1991), nor do we have any reason to believe that mate loss patterns did or should vary with treatment.

Predation risk constitutes a reproductive cost for breeding animals by posing a "survival cost" through adult predation and a "fecundity cost" through offspring predation (Magnhagen 1991). Despite the fact that these 2 risk types pose very different fitness consequences and are expected to influence animals' reproduction via distinct mechanisms (Lima and Dill 1990; Magnhagen 1991), most empirical studies to date have focused on testing a single risk type (e.g., Wisenden 1993; Koskela and Ylonen 1995; Candolin 1998; Fontaine and Martin 2006; Thomson et al. 2006; Creel et al. 2007; Lasley-Rasher and Yen 2012) or a single treatment of a mix of risk types (e.g., Zanette et al. 2011). To our knowledge, only 2 previous studies have simultaneously tested for the effects of perceived adult versus offspring predation risk on animal reproduction, both in relation to avian risk-taking behavior around the nest (Ghalambor and Martin 2000; Schneider and Griesser 2013). By experimentally testing a comprehensive suite of avian reproductive traits across contrasting types of perceived predation risk, our study thus provides the most direct assessment to date of how animals may respond differentially to these different risk types via reproductive adjustments that can directly translate into fitness and demographic consequences. It should be noted, however, that we used only 1 species of predator for each type of predation risk, leaving open the potential issue that the observed reproductive responses may be particular to the specific predator species, rather than the type of predation risk the predator species was intended to represent. Although the 3 predator species we used posed distinct types of predation risk to breeding bluebirds, future studies that test multiple species of predators for each type of predation risk would help generalize our understanding of prey responses to different predator types.

Our study suggests that nonconsumptive effects of predation risk can strongly affect the reproduction of animals (Fontaine and Martin 2006; Creel and Christianson 2008; Zanette et al. 2011; Orrock et al. 2013). Our findings add to the increasing body of evidence demonstrating that prey can respond to predation risk phenotypically with plastic traits on short temporal scales (e.g., Schmitz et al. 1997; reviewed in Lima 1998a; Agrawal 2001; Creel and Christianson 2008; Cresswell 2008). Given that prey are under constant threat of mortality and, in turn, selection pressures have crafted keen perceptions of predation risk in prey individuals, our results demonstrate that birds can exhibit a high degree of nuance in their behavioral flexibility toward changing perceptions of predation risk. We conclude that our understanding of the nonconsumptive effects of predation risk will benefit from an understanding of how different types of predators can differentially impact prey behaviors and exert selection pressures (Templeton and Shriner 2004; Preisser et al. 2007; Maron et al. 2010).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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