



## Bluebirds perceive prey switching by Cooper's hawks across an urban gradient and adjust reproductive effort

Kristen M. Malone, Amanda C. Powell, Fangyuan Hua & Kathryn E. Sieving

To cite this article: Kristen M. Malone, Amanda C. Powell, Fangyuan Hua & Kathryn E. Sieving (2017): Bluebirds perceive prey switching by Cooper's hawks across an urban gradient and adjust reproductive effort, *Écoscience*, DOI: [10.1080/11956860.2017.1346449](https://doi.org/10.1080/11956860.2017.1346449)

To link to this article: <http://dx.doi.org/10.1080/11956860.2017.1346449>



Published online: 10 Jul 2017.



Submit your article to this journal [↗](#)



Article views: 9



View related articles [↗](#)



View Crossmark data [↗](#)

ARTICLE



## Bluebirds perceive prey switching by Cooper's hawks across an urban gradient and adjust reproductive effort

Kristen M. Malone<sup>a</sup>, Amanda C. Powell<sup>b</sup>, Fangyuan Hua<sup>c,d</sup> and Kathryn E. Sieving<sup>a</sup>

<sup>a</sup>Wildlife Ecology and Conservation Department, University of Florida, Gainesville, FL, USA; <sup>b</sup>Avian Research and Conservation Institute, Gainesville, FL, USA; <sup>c</sup>Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, UK; <sup>d</sup>State Key Laboratory of BioControl, College of Ecology and Evolution/School of Life Sciences, Sun Yat-sen University, Guangzhou, China

### ABSTRACT

Urban-adapting carnivorous predators such as the Cooper's hawk appear to be adjusting their diet in urban areas to mostly include larger-bodied adult birds rather than nest contents, compared to Cooper's hawks in natural areas. If adult prey in urban areas are relatively more threatened by predation relative to their offspring and non-urban adults, then life-history theory predicts contrasting shifts in urban vs. non-urban reproductive behavior and effort. We tested whether urban and non-urban Eastern bluebirds exhibited contrasting reproductive effort consistent with shifts in the relative risk perception of adult vs. nest predation. At urban sites, Eastern bluebirds using nest boxes exposed to broadcasts of Cooper's hawk vocalizations exhibited enhanced reproductive parameters compared to controls, whereas the opposite trend occurred in box-nesting bluebirds at non-urban sites. As predicted by theory, given prey life-stage switching by a dominant predator, increased perception of predation risk from hawks led to opposing reproductive strategies in urban vs. non-urban habitats. Results align with increasing evidence that urban predation pressures, prey risk perception, and reproductive investment patterns are distinct from those of natural habitats.

### RÉSUMÉ

Les prédateurs carnivores adaptés à l'environnement urbain, comme l'épervier de Cooper, semblent ajuster leur alimentation pour inclure principalement des oiseaux adultes de plus grande taille plutôt que les contenus de nids, comparativement aux éperviers de Cooper en milieu naturel. Si les proies adultes dans les zones urbaines sont relativement plus menacées par la prédation que leur progéniture ou que les adultes en milieu naturel, la théorie des histoires de vie prédit des comportements et des efforts reproducteurs différents en milieux urbain et naturel. Nous avons testé si les merlebleus de l'Est urbains et non-urbains présentaient des efforts reproducteurs différents, correspondant aux changements de perception du risque relatif de prédation des adultes et des nids. Dans les sites urbains, les merlebleus de l'Est utilisant des nichoirs exposés à des enregistrements de vocalisations d'éperviers de Cooper ont présenté de meilleurs paramètres de reproduction que les témoins, alors que la tendance inverse a été observée pour les merlebleus utilisant les nichoirs en milieu naturel. Comme le prédisait la théorie, le changement de proie par un prédateur dominant a modifié la perception du risque de prédation, conduisant à des stratégies de reproduction opposées dans les milieux urbains et non-urbains. Ces résultats s'ajoutent à ceux d'études précédentes montrant que les pressions de prédation, la perception du risque de prédation par les proies et les patrons d'effort reproducteur diffèrent dans les milieux urbains et naturels.

### ARTICLE HISTORY

Received 14 March 2017  
Accepted 19 June 2017

### KEYWORDS

prey switching;  
non-consumptive effects;  
urban adaptation; *Accipiter cooperii*; Eastern bluebird; *Sialia sialis*

### MOTS CLÉS

changement de proie; effets non-létaux; adaptation urbaine; *Accipiter cooperii*; Merlebleu de l'Est; *Sialia sialis*

## Introduction

Urban wildlife communities are distinctive in their ecology compared to less disturbed ecosystems along the wildland-urban gradient (Adams 2005). Major defining features of urbanized vertebrate communities include fewer but superabundant native (Blair 2001; Kark et al. 2007) and exotic species (McKinney 2002),

many of which can take advantage of superabundant human-provided subsidies (Pickett et al. 2001). High urban songbird density has been attributed to both anthropogenic food subsidies (feeders and irrigation-driven insect foods) and to lower documented nest predation rates in urban habitats (Gering and Blair 1999; Kosinski 2001; Fischer et al. 2012). However, populations of urban-adapting predators such as the

Cooper's hawk (*Accipiter cooperii*; Rosenfield et al. 1995), a predator known to take both adult and nestling passerine birds (Curtis et al. 2006), also occur at higher density in urban areas (Sorace 2002). The incongruity of simultaneously elevated avian predator and prey densities and non-elevated avian predation rates (based primarily on nest predation studies) has distinguished urban wildlife communities as unique (Chiron and Julliard 2007; Fischer et al. 2012).

Prey switching by urban nest predators has been hypothesized to explain decreased nest predation in urban areas. Cooper's hawks in particular are characterized as abundant and efficient killers of both adult (Rosenfield et al. 1995; Roth and Lima 2003; Curtis et al. 2006) and juvenile birds in nests, and can take a wide variety of other small taxa (e.g. Liebezeit and George 2002). However, strong evidence from different North American study sites documents that both urban Cooper's hawks and Eastern screech owls (*Otus asio*) specialize exclusively on adult life-stages of larger-bodied birds; juvenile birds (nestlings, fledglings) and other smaller vertebrate taxa were absent from deliveries to chicks in urban nests (Gehlbach 1994; Estes and Mannan 2003; Newsome et al. 2015). Moreover, in an urban and non-urban comparison of nest predators at passerine nests, Stracey (2011) determined from nest cameras that, while Cooper's hawks were the single most dominant nest predator in non-urban areas, they were never once detected raiding suburban nests. Instead, domestic cats replaced hawks as the top urban nest predator. These patterns strongly suggest that Cooper's hawks switch life-stages and specialize on adult avian prey in urban areas, although parallel data on low urban survival rates of adults of their prey species are lacking (Fischer et al. 2012). If urban predators consume mostly human subsidies (omnivores) or specialize on adult birds (raptors), then this could explain both low urban nest predation rates and thriving, superabundant urban predator populations.

If adult prey in urban settings are relatively more threatened with lethal attack from hawks than their offspring, there should be predictable and identifiable shifts in behavioral phenotypes of urban prey (Lima 2002). Variation in kinds (predator species or type) and relative strengths of perceived predation risk can strongly influence prey behavioral responses (anti-predator communication, Hetrick and Sieving 2012; habitat selection, Hua et al. 2013) and even allocation of avian reproductive effort (Eggers et al. 2006; Zanette et al. 2011; Hua et al. 2014). Clutch size and other reproductive parameters can vary considerably with changes in relative predation risks to adult vs. nest predation risks (Martin 2002; Hua et al. 2013;

LaManna and Martin 2016). With respect to differential targeting of adult vs. juvenile prey in urban and non-urban predators, life-history theory predicts that greater adult mortality risk favors increased reproductive effort, whereas relatively greater juvenile mortality favors reduced reproductive effort (Hirshfield and Tinkle 1975; Martin 2002). Prey switching by urban nest predators – both omnivorous and carnivorous species – has been hypothesized to explain decreased nest predation in urban areas, although it is currently unknown how prey perceive and respond to a switch in prey life-stage preference by a single predator species. Metrics of reproductive investment and output could be used to assess the ability of prey to perceive and respond to urban vs. non-urban predation pressures, including predation risk from a single predator species that has adapted to urban environments.

Using an urban-adapting prey species that readily uses nest boxes, the Eastern bluebird (*Sialia sialis*), we conducted an experimental test to determine if urban and non-urban bluebirds perceive contrasting adult vs. juvenile mortality risk consistent with prey life-stage switching by Cooper's hawks (an abundant year-round resident in the study region). Working in the same urban and non-urban locations where Stracey's work (2011) was conducted, we assumed that Cooper's hawks functioned as important nest robbers outside of, but not within, the urban area of Gainesville, FL. In both urban and non-urban sites, we compared bluebird reproductive parameters in treatment plots where we increased bluebird perception of threat from Cooper's hawks by playing their recorded calls at active bluebird nests, to reproductive effort at nests in control plots (no hawk-call playbacks). If bluebirds both perceive and respond to this life-stage switching by Cooper's hawks as we hypothesize, then we predicted the following: Cooper's hawk vocal cues should cause: (1) urban bluebirds to perceive a greater threat to their own lives and invest more in their offspring relative to urban controls; and (2) cause non-urban bluebirds to perceive a greater risk to the lives of their offspring and invest less in their offspring relative to controls.

## Methods

The Eastern bluebird is a small (~30 g) insectivorous bird that prefers open or semi-open habitats (Gowaty and Plissner 2015) and is resident throughout Florida. Bluebirds will nest in naturally occurring or excavated cavities with large entrances or (less commonly) build their own open cup nests, making them susceptible to mammalian and avian nest predators (Reid 1884; Gowaty and Plissner 2015). Open cup nests are

known to occur in longleaf pine, and occasionally on mature oak limbs (Gowaty and Plissner 2015). Pairs will also build nests in shallow burn scars of longleaf pine (Finch et al. 2012). Pairs will raise two or three broods per season (and re-attempt if a nest is lost, e.g. DeLuca 2008), and will readily use artificial nest boxes when provided in urban and non-urban environments. Eastern bluebirds are relatively large passerines whose adults, fledglings, and nest contents are attacked by Cooper's hawks (Gowaty and Plissner 2015). Since both Cooper's hawks and Eastern bluebirds are common across the wildland–urban gradient of North Central Florida, the Eastern bluebird was a good model species for this study. Our previous work has demonstrated that bluebirds are highly responsive to shifts in perceived predation risk; when exposed to playback of recorded vocalizations of Cooper's hawks and other predators' calls, bluebirds reduced parental investment (relative to controls) in egg production and post-egg nest performance in a non-urban study site (Hua et al. 2014). Here, we conducted a paired study that includes data from the non-urban study site as well as an urban study site, and measured bluebird reproductive response as an indicator of life-stage predation risk by the Cooper's hawk.

Non-urban bluebird nest boxes were placed on the Ordway-Swisher Biological Station (OSBS), a 3700 ha managed research preserve in North Central Florida (29.4° N, 82.0° W); its extensive sandhill forest is dominated by longleaf pine (*Pinus palustris*) in the canopy and wiregrass (*Aristida beyrichiana*) in the understory, with a variety of oaks, herbs, and grasses (Florida Natural Areas Inventory 2010; details of nest box placement are in Hua et al. 2014). The forest vegetation composition is maintained through prescribed burns in units of 20 ha every 2–5 years (Hua et al. 2013). Gainesville, FL (29.4° N, 82.2° W) is the largest city in Alachua County (~130,000 people in 2013–2014, covering 162 km<sup>2</sup>) and encompasses the busy urban campus of the University of Florida (UF), where urban nest boxes were placed. UF ranked as the eighth-largest US university in 2013–2014, with nearly 50,000 students enrolled. Despite many buildings and expanses of urban hardscape, the 8 km<sup>2</sup> campus includes a variety of natural areas, open lawns, and agricultural teaching fields with suitable sites for bluebird nest boxes (based on DeLuca 2008). In both study sites (non-urban OSBS and urban UF campus) more nest boxes were placed in suitable sites than were occupied, therefore, birds in this study were able to exercise their own choices of nesting microhabitat.

Artificial nest boxes (Gilbertson design; North American Bluebird Society 2011) were placed during

January at both sites, several weeks prior to the typical first egg-laying date for successful first clutches of bluebirds in the area. March is when nesting typically begins in earnest, but can vary across sites by two weeks in the same year (DeLuca 2008). All nest boxes (Gilbertson style) were mounted on 1.5 m high metal poles and were placed at least 100 m apart to maximize the number of boxes that could become occupied (Eastern bluebirds do not typically nest closer to another pair than 100 m; DeLuca 2008; Nest Box Resource Center 2013). To minimize actual predation events and maximize the number of active pairs that could carry out successful nesting and respond to our manipulation (see below), we greased the poles to limit climbing animals (snakes, raccoons) from destroying clutches (USDA Natural Resources Conservation Science 1999). This did not preclude volant nest predators from attacking the boxes.

### Experimental design

Boxes were distributed slightly differently in non-urban and urban sites, but accommodations were made to insure similarly applied playback treatments. In non-urban sites at OSBS, four boxes were placed on the four corners of a square within 200 × 200 m square playback treatment plots (4 ha). Plots were randomly assigned a priori as treatment or control (six of each = 48 boxes) within blocks that were matched for habitat structure and vegetation similarity (Hua et al. 2014). Plots were spaced at a minimum of 300 m apart at the non-urban site. Of the 48 nest boxes placed at OSBS, 18 were occupied by bluebirds. Playbacks of hawk calls at the non-urban site began on 5 March. Nest boxes were distributed more opportunistically on the urban site (campus) due to greater site limitations (i.e. heterogeneous mix of paved and open landscaping). Some plots had up to four boxes, some had fewer, and not necessarily in a square distribution, and plot size varied between 4–18 ha. As at our non-urban sites, a plot at the urban site was a group of nest boxes to which the treatment or control was applied uniformly. At the urban site, we waited until nests were selected by bluebirds (adults seen perching on or defending nest boxes, typically two to three weeks or more prior to egg-laying) to assign active treatment (11) and control (9) nest boxes using a randomized block design, so that in all cases plots within blocks were matched for habitat structure and vegetation similarities. At the urban site, 66 nest boxes were placed, and 20 of them became occupied by bluebirds. Playback of hawk calls on urban plots were initiated when a plot of active nests in a cluster was identified by bluebird nest defense

behaviors. First egg dates in the urban site were in late February (DeLuca 2008) and at a minimum of two weeks following initialization of the playback.

To simulate hawk predation risk, automated playback stations were erected within treatment plots, and each consisted of a portable CD player concealed in a camouflaged plastic box and wired to a deep-cycle marine battery with a timer (see Fletcher 2007; Hua et al. 2013). Each plot in the urban and non-urban sites contained two playback stations that were mounted 3 m above the ground and located at a similar mean distance to the nearest playback station (between ~10–80 m). Playback stations were placed in control and experimental plots alike, but the control stations did not broadcast hawk (or other) vocalizations. To minimize bluebird habituation to the playback, playback audio files (with different sequences and timings of calls; see Hua et al. 2013) and the physical location of the playback stations within the plots (both treatment and control plots) were rotated to new locations (to simulate hawks using different perches) once every two weeks. The average distance between a playback station and a nest was on average 50 m, but varied from 10–100 m. Volume was standardized across playback stations and could readily be heard by humans at all treatment nest sites.

Playback of treatment (or blank) stimuli were initiated at a minimum of two weeks before the earliest expected first-egg date for first broods, and then played throughout second nest attempts. The minimum time allotted prior to first-egg dates allowed ample time to switch choices of nest box, and at both sites unused boxes were available near all occupied boxes to allow birds to switch. For pairs that attempted a second brood, we assumed that if the same nest box was used twice, then it was the same bluebird pair using the nest box. If the nest shifted, i.e. one previously used box was abandoned and a previously unused box nearby became occupied, we assumed the pair that abandoned the earlier box moved into the new, later box (based on DeLuca's 2008 observations).

Experiments at non-urban and urban sites were not carried out in the same year (non-urban in 2010, urban in 2012). In keeping with a variety of avian nesting studies in urban and non-urban sites, non-urban bluebirds began nesting later (early April) than urban bluebirds (March); this difference is repeatedly observed in this region and system and others (due to urban irrigation, fertilization, and earlier insect flush) and was clearly not a year effect (e.g. Rollinson and Jones 2002; Partecke et al. 2004; DeLuca 2008; Stracey and Robinson 2012). Moreover, Alachua Co. (UF campus) nearly always gets more rainfall than Putnam Co. (Ordway). Mean climate measures from mid-March

to Mid-April 2010 (non-urban) and 2012 (urban) were not atypical in either their means or differences from one another (Florida Automated Weather Network; <http://fawn.ifas.ufl.edu/>). Therefore, the difference in nest initiation dates was an expected (and unavoidable) urbanization effect and not a year effect.

### Data collection

Nest boxes were uniquely numbered and visited every three to five days (more frequently at the beginning to catch the first-egg dates) and the length of incubation and brood periods were recorded for the first and second nests. We measured variables associated with: (1) parental investment in egg production; and (2) post-egg nesting performance. For (1) we used clutch size and mass, egg size, and mass on the second day following clutch completion (Fontaine and Martin 2006; Martin and Briskie 2009), and incubation length (total days between first-egg date and hatching date). We used calipers to measure the maximum length and width (to the nearest millimeter) of eggs to calculate egg mass ( $\text{length} \times \text{width}^2 \times 0.51 \times 1.005/1000$ ; Hoyt 1979). Egg mass values for a clutch were summed to calculate clutch mass. For (2) we included egg-hatching rate (number of eggs hatched divided by clutch size), number of 14-day-old nestlings (14 days is the average brood period; video surveillance showed that all broods that were alive on the 14th day in non-urban sites subsequently fledged) and brood period (time between hatching date and fledging date). Seasonal fecundity (total number of fledglings produced over the breeding season) was also calculated.

### Statistical analyses

In all modeling, we used clutch size, clutch mass, average egg mass, incubation length, and hatching rate as response variables for reproductive investment. To control for the effects of clutch size on hatching rate we used clutch size as a covariate (Thompson et al. 1998). We used the number of 14-day-old nestlings, seasonal fecundity, and brood period as response variables for reproductive output. Clutch size was used as a covariate for the number of 14-day-old nestlings. The central test of our hypothesis was determined by the interaction terms between treatment (hawk vs. control) and site (urban vs. non-urban) in all models. If hawk-exposed non-urban birds decreased and hawk-exposed urban birds increased their investment compared to their respective controls, then we could infer that bluebird perception of adult vs. nest predation risk tracked assumed Cooper's hawk predatory behavior.

We used generalized estimating equations (GEE) to estimate the effects of treatment and site on reproductive measures across broods that were produced sequentially in the same boxes using Clutch ID as a covariate in this model. GEE accounts for the correlated nature of data from repeated broods of the same pair (Liang and Zeger 1986). We used a generalized linear model to estimate the effect of treatment and site on seasonal fecundity of a pair. We used a log link, Poisson error distribution, and exchangeable correlation structure for the following response variables: clutch size, number of 14-day-old nestlings, and seasonal fecundity; we used an identity link, normal error distribution, and exchangeable correlation structure for the remaining response variables. The standard error of the GEE estimates was calculated using the robust sandwich variance method, and the significance of predictor terms was inferred using Wald tests. We looked at first and second broods separately using a generalized linear model with the same structure as GEE except that Clutch ID was not used as a covariate. We did not apply model selection because this was a hypothesis testing (not generating) study design. We used the R function `geeglm` in the `geepack` package (Halekoh et al. 2006). We used R\* 3.2.2 (R Core Team 2015).

## Results

Within the urban plots, four nests were depredated by unknown predators and two were abandoned, leading to nest failure. The cause of abandonment is not certain, but we know that nest parasitism was not the cause. Other possible causes could be the death of the parents or infertile eggs. Within non-urban plots, one nest was depredated by an unknown predator species and one nest was abandoned after holes were pecked in some of the eggs (probably by a Carolina chickadee, *Poecile carolinensis*). More than 50 hours of video footage from 20 non-urban nests during incubation and nestling rearing stages (Hua et al. 2014) detected no attempted nest predation by Cooper's hawks (video surveillance was not used in urban sites). We used measurements taken from failed nests where appropriate, and excluded the depredated nests from the calculations of hatching rate and number of 14-day-old nestlings. If we had not excluded depredated nests from our analysis, our results would reflect a combination of lethal and non-lethal effects of predation. However, our focus for this study was only on non-lethal effects. A total of 16 non-urban pairs and 17 urban pairs each had two nesting attempts, while two pairs in the non-urban site and three pairs in the urban site produced only one brood. A total of 34 nesting

attempts were used in our analyses for non-urban plots ( $n = 14$  and  $20$  for control and treatment, respectively) and 37 nesting attempts were used in analyses for urban plots ( $n = 17$  and  $20$  for control and treatment, respectively).

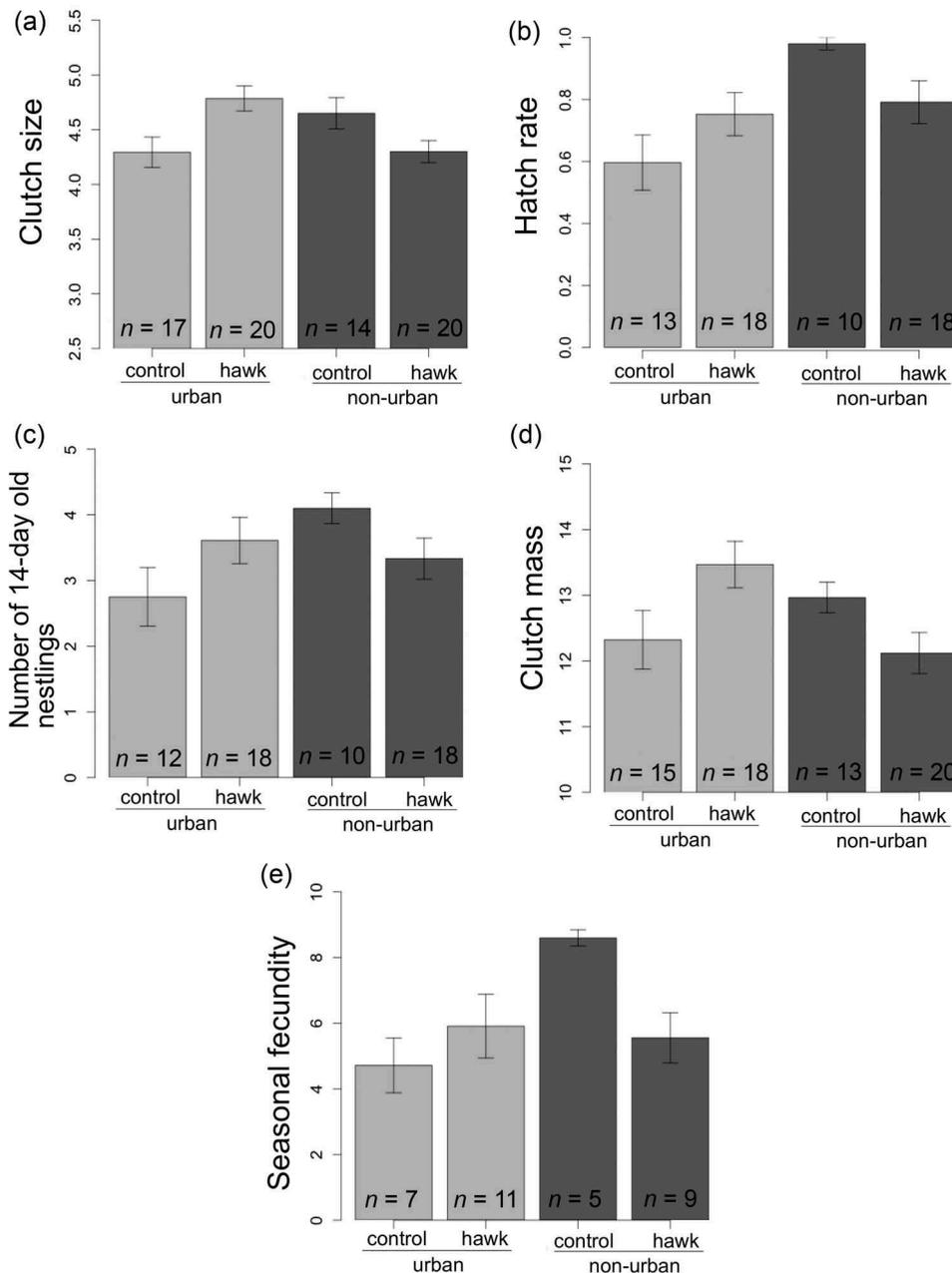
The effect of the treatment on clutch size contrasted between the urban and non-urban sites: the effect was positive at the urban site and negative at the non-urban site (Figure 1). We found the same trend for clutch mass, hatch rate, number of 14-day-old nestlings, and seasonal fecundity per pair; relative to control nests, all were greater at urban nests exposed to the treatment, and lesser at non-urban nests exposed to the treatment (Figure 1). Within control plots only, clutch size was larger at non-urban plots than urban plots but, within treatment plots, clutch size was larger at urban plots than non-urban plots (Figure 1). The interaction effect between treatment and site was statistically significant for clutch size ( $\beta = 0.1853$ ,  $SE = 0.0483$ ,  $p = 0.00012$ ), clutch mass ( $\beta = 1.835$ ,  $SE = 0.7900$ ,  $p = 0.02$ ), hatch rate ( $\beta = 3.2489$ ,  $SE = 1.2327$ ,  $p = 0.0084$ ), and seasonal fecundity ( $\beta = 4.239$ ,  $SE = 1.263$ ,  $p = 0.00138$ ; Table 1), supporting our predictions: reproductive investment in egg production and post-egg nesting performance metrics increased in the urban environment and decreased in the non-urban environment. We did not detect a statistically significant effect of the treatment\*site interaction on the number of 14-day-old nestlings ( $\beta = 0.4789$ ,  $SE = 0.2119$ ,  $p = 0.0239$ ), egg mass ( $\beta = 0.0783$ ,  $SE = 0.1510$ ,  $p = 0.60$ ), incubation period ( $\beta = 0.5630$ ,  $SE = 0.7130$ ,  $p = 0.43$ ), or brood period ( $\beta = 1.1338$ ,  $SE = 0.8241$ ,  $p = 0.169$ ; Table 1).

Clutch ID (first or second clutch) influenced only one of our response variables: brood period. When the data were split into first and second clutches, the treatment\*site interaction had a greater effect in clutch 2 than clutch 1 for hatch rate and the number of 14-day-old nestlings, but no significant effect on other reproductive variables.

## Discussion

### Bluebird reproductive effort tracks Cooper's Hawk predatory strategy

Addition of the same cues for the same species of predator in both urban and non-urban environments led to opposing reproductive strategies by Eastern bluebird parents, supporting our hypothesis that urban and non-urban bluebirds perceived Cooper's hawks as functionally different kinds of predators. The reproductive responses of bluebirds in this study fit classic life-history predictions for adaptive reproductive investment under



**Figure 1.** Reproduction of Eastern bluebirds relative to treatment (Cooper's hawk playback) and site (urban and non-urban): (a) mean clutch size; (b) mean hatch rate; (c) mean number of 14-day-old nestlings; (d) mean clutch mass (grams); (e) mean number of offspring produced per female (seasonal fecundity). Bars represent the data rather than model estimates. Error bars represent  $\pm 1$  SE.

threat of predation on adults vs. offspring (Hirshfield and Tinkle 1975; Martin 2002). Relative to paired controls, urban bluebirds increased clutch size, clutch mass, hatch rate, and fledged more offspring; whereas non-urban bluebirds reduced clutch size and productivity under threat of predation by Cooper's hawks (Gadgil and Bossert 1970; Zera and Harshman 2001). To our knowledge, this is the first evidence of a single predator species' (simulated) presence generating contrasting reproductive investments in different environments where other confounding factors were controlled. The

extent and general direction of reproductive adjustment we observed in bluebirds have been observed in other prey and ecosystems when the same predators (or reliable cues for their presence) are added or subtracted from prey environments (invertebrates, Stoks et al. 2006; birds, Eggers et al. 2006; Fontaine and Martin 2006; Lima 2009; Zanette et al. 2011; Hua et al. 2014; fish, Mukherjee et al. 2014). Moreover, the effectiveness of acoustic cues in evoking non-consumptive behavioral or physiological changes observed in this study has been demonstrated previously (Hua et al. 2014; Ibanez-

**Table 1.** Effects of treatment (hawk playback or control) and site (urban or non-urban) on reproductive responses of Eastern bluebirds based on generalized estimation equations (GEE). TRT represents the effect of the hawk treatment relative to the control baseline. Site represents the effect of urban site relative to the non-urban baseline.

Reproductive response	Model results			
	Estimate	Standard error	Wald statistic	P-value
Clutch size (log(clutch size) ~ TRT*Site + clutch ID)				
Intercept	1.5821	0.0488	1051.14	$<2 \times 10^{-16}$
TRT	-0.1053	0.0261	16.23	$5.6 \times 10^{-5*}$
Site	-0.1109	0.0287	14.96	0.00011*
TRT:Site	0.1853	0.0482	14.77	0.00012*
Clutch ID	-0.0110	0.0310	0.13	0.72320
Clutch mass (clutch mass ~ TRT*Site + clutch ID)				
Intercept	12.890	0.304	1801.63	$2 \times 10^{-16}$
TRT	-0.754	0.484	2.42	0.12
Site	-0.563	0.535	1.11	0.29
TRT:Site	1.835	0.790	5.39	0.02*
Clutch ID	0.027	0.504	0	0.96
Egg mass (egg mass ~ TRT*Site + clutch ID)				
Intercept	2.6782	0.1054	645.27	$<2 \times 10^{-16}$
TRT	0.0585	0.1209	0.23	0.63
Site	0.0312	0.1071	0.08	0.77
TRT:Site	0.0783	0.1510	0.27	0.60
Clutch ID	0.0515	0.0401	1.65	0.20
Hatch rate (logit(hatch rate) ~ TRT*Site + clutch size + clutch ID)				
Intercept	4.4164	2.5024	3.11	0.0776
TRT	-2.5441	1.0735	5.62	0.0178*
Site	-3.4889	0.9562	13.31	$2.6 \times 10^{-4*}$
TRT:Site	3.2489	1.2327	6.95	0.0084*
Clutch Size	0.0007	0.4795	0	0.9988
Clutch ID	-0.3541	0.4060	0.76	0.3832
Incubation period (incubation period ~ TRT*Site + clutch ID)				
Intercept	16.600	0.724	525.56	$<2 \times 10^{-16}$
TRT	0.533	0.431	1.53	0.22
Site	-0.346	0.738	0.22	0.64
TRT:Site	0.563	0.713	0.62	0.43
Clutch ID	0.200	0.642	0.10	0.76
Brood period (brood period ~ TRT*Site + clutch ID)				
Intercept	18.4888	0.7037	690.26	$<2 \times 10^{-16}$
TRT	-0.4857	0.6827	0.51	0.477
Site	-0.0193	0.7022	0	0.978
TRT:Site	1.1338	0.8241	1.89	0.169
Clutch ID	-1.2888	0.5507	5.48	0.019*
Number of 14-day-old nestlings (log(number of 14-day-old nestlings) ~ TRT*Site + clutch size + clutch ID)				
Intercept	1.0420	0.6212	2.81	0.093
TRT	-0.1656	0.1305	1.61	0.205
Site	-0.3754	0.1656	5.14	0.023*
TRT:Site	0.3976	0.2503	2.52	0.112
Clutch Size	0.1124	0.1176	0.91	0.339
Clutch ID	-0.1085	0.0956	1.29	0.256
Seasonal fledgling output (log(seasonal fledgling output) ~ TRT*Site)				
Intercept	8.600	0.765	11.24	$<2 \times 10^{-16}$
TRT	-3.044	0.955	-3.19	0.00227*
Site	-3.886	1.002	-3.88	0.00026*
TRT:Site	4.239	1.263	3.36	0.00138*

\**p*-values less than 0.05.

Alamo et al. 2015). Additionally, bluebirds (and other oviparous prey more generally) are known to distinguish predator species that function differently as either offspring or adult predators based on acoustic cues (Bonnington et al. 2013, 2015; Hua et al. 2013, 2014). In essence, Eastern bluebird responses in our study bolster confidence in Stracey's (2011) hypothesis (and other evidence, e.g. Estes and Mannan 2003), that Cooper's hawks are prey life-stage switching across wildland-urban gradients they inhabit, and that they

are functioning as adult bird specialists in urban environments.

We assumed that nest predation pressure by Cooper's hawks, in particular, is generally (for all passerines) greater in non-urban than urban sites, and in particular quite high at our specific non-urban site (Curtis et al. 2006; Stracey 2011; Smith 2013). Indeed, Stracey et al. (2011) video-taped a large sample of open cup nests in both of our study areas; Cooper's hawks were the most frequent nest raiders at the Ordway-Swisher Biological

Station (our non-urban site), and were never detected at a nest in the much larger urban sample of nests videotaped in Gainesville (our urban site). We observed four depredated nests in urban plots compared to none in non-urban plots during our study, and this may seem contradictory to Stracey's (2011) conclusion that urban Cooper's hawks are probably ignoring nests to specialize on superabundant adults in urban areas. However, we note first that such low numbers of nest losses cannot be used to critically confirm actual patterns of nest loss, as this study was not designed to determine lethal predation patterns. We did not survey for predators or videotape nest boxes in both areas, nor did we enhance the sample size such that nest-loss rates could be large enough to achieve statistical power; all aspects of designing a rigorous nest predation study (Sieving and Willson 1998; Major and Kendal 1996). In contrast, we suppressed ground predators of bluebirds (Gowaty and Plissner 2015) by greasing the nest-box poles, to maximize the number of successful nests available for tracking reproductive allocation by adults with successful nests. On the other hand, bluebird nest boxes are traditionally placed in open microsites, are easy to spot, and can be readily harassed by avian predators (KES, personal observations). It is likely that superabundant urban Cooper's hawks or other hawks, attracted to the nest boxes by adult bluebird activity, may have more often attempted to take nest contents and been successful on our urban plots. However, we can only speculate about actual patterns of nest predation. We designed the study to detect reproductive allocation shifts in response to a manipulated perception of Cooper's hawk abundance that, in turn, would confirm whether Cooper's hawks represent functionally different risks to Eastern bluebirds.

### **Urban predator–prey ecology: Unique but not paradoxical?**

A current theme guiding the analysis of urban wildlife ecology is the 'urban predator paradox' based on observations that terrestrial predators of small vertebrates are more abundant in urban habitats, but per capita predation on urban prey appears unchanged or lower (Haskell et al. 2001; Sorace 2002; Chiron and Julliard 2007; Fischer et al. 2012). This is apparently despite the addition of domestic cats (*Felis domesticus*) to the line-up of urban-adapting native predators that consume small urban vertebrates (Bolger et al. 1997; Tratalos et al. 2007; van Heezik 2010; Stracey 2011; Loss et al. 2013). In order to fully address the validity of the urban predator paradox, many more paired non-urban and urban analyses of predator–prey food webs and behaviors will be needed;

most such efforts are rare to date and biased (first) toward predators of passerine birds (Chamberlain et al. 2009) rather than other vertebrates and (second) even more narrowly toward bird nests and their predators (eggs, nestlings, and artificial nests). Indeed, the quantity of avian nest predation data far outweighs information on other key factors (e.g. adult mortality, food habits; Stracey 2011; Rodewald et al. 2011) that may be more important in defining avian population viability (Saether and Bakke 2000; Dinsmore et al. 2010; Mortensen et al. 2016). Because urban nest depredation rates are most often the same or lower than in paired non-urban settings (Fischer et al. 2012), the 'paradox' may, therefore, exist because it rests solely on avian nest data patterns.

We predict that the paradox will be fully resolved when the question of what superabundant urban predators feed on is answered, along with comparisons of prey survival rates in urban and non-urban areas (Fischer et al. 2012). For carnivorous predatory birds that adapt to urban environments, all of the data we could find support prey life-stage switching. In addition to data suggesting that urban Cooper's hawks specialize on adult birds (Estes and Mannan 2003; Stracey 2011; this study), Gehlbach (1994) confirms that Eastern screech owls (*Megascops asio*), another abundant urban-adaptor (Gehlbach 1995), also specializes on adult birds in urban habitats. Adult songbirds and columbids (pigeons and doves) are typically the largest prey items available and are preferred (Gehlbach 1995; Curtis et al. 2006). Many passerines thrive in suburbia because of the availability of nest predator-free niches and supplemental foods (Marzluff 2001). Some species (Northern Mockingbirds, *Mimus polyglottos*; Northern Cardinals, *Cardinalis cardinalis*; Blue Jays, *Cyanocitta cristata*) become superabundant making them highly attractive to urban raptors. Raptor distribution and abundance is driven by the distribution and abundance of their prey (Tornberg et al. 2005; Millon et al. 2009; Thorup et al. 2010). Therefore, predator specialization in the face of hyperabundance of preferred prey provides a parsimonious route to explain away the urban predator paradox (Fischer et al. 2012).

In sum, the focus of this study was to test the validity of a novel cause of variation in non-consumptive (fear- or perception-mediated) behavioral effects within a common prey species: specifically, a previously indicated gradient in predator life-stage specialization. Hormonal or population genetic differences affecting bluebird behavior between our study sites are potential mediating factors influencing differential reproductive effort (Cox et al. 2016). Hormone titers may well vary between urban and non-urban sites (Huang 2016), and hormonal

fluctuations are likely involved in many non-consumptive behavioral changes observed to date. However, given the wide-ranging nature of Eastern bluebirds (natal dispersal documented = 93 km; distance between our study areas = 30 km), strong genetic differences between the populations studied here are unlikely (Lang 2013). Differential risk perception and behavioral flexibility caused by our experimental manipulation and by actual variation in Cooper's hawk predatory behavior are the most parsimonious explanations of our results. There is a strong body of evidence that prey, including songbird species, are phenotypically plastic with respect to reproductive traits and can respond on short temporal scales to changes in predation risk (Lima and Dill 1990; Lima 2009; Hua et al. 2014; LaManna and Martin 2016). Behavioral flexibility, rather than behavioral stasis, in the face of changing predation risk is likely an extremely important trait under strong selection (Nussey et al. 2005). And beyond direct killing, we now know that predators – by their activity and encounter rates with prey – strongly influence the behavior, physiology, population vital rates, and, ultimately, demographic trajectories and fitness of individuals of surviving prey (Preisser et al. 2005; Eggers et al. 2006; Creel et al. 2007; Creel and Christianson 2008; Cresswell 2008; Zanette et al. 2011; Elliott et al. 2016; LaManna and Martin 2016). Finally, while there may be a paucity of adult mortality data on many wild species, perhaps the increasingly predictable behavioral responses of prey to their predators' behaviors could help fill the gaps in our understanding of unique or unexpected predation pressures within urban landscapes of fear (Gill and Brumm 2014; Donihue and Lambert 2015). Advances in understanding and managing urban wildlife should anticipate both the effects of non-lethal selection on species' life histories (Isaksson and Hahs 2015) and also their potential utility in reducing human–wildlife conflicts (McManus et al. 2015; Götz and Janik 2016) in urban environments.

## Funding

Funding came from the University of Florida, Department of Wildlife Ecology and Conservation, and School of Natural Resources and Environment, which had no input on the content of the manuscript nor required approval of the manuscript before submission.

## Ethics statement

Research was conducted with approval by, and in full compliance with, the University of Florida Institute for Food and Agricultural Sciences' Animal Research Committee for studies fitting their criteria for 'non-regulatory animal research' (see <http://www.wec.ufl.edu/research/arc.php>).

## Author contributions

KES and FH conceived the idea for the study; ACP and FH collected the data; KMM executed statistical analysis; KMM, ACP, FH, and KES wrote or substantially edited the manuscript.

## References

- Adams LW. 2005. Urban wildlife ecology and conservation: a brief history of the discipline. *Urban Ecosyst.* 8:139–156.
- Blair RB. 2001. Birds and butterflies along urban gradients in two ecoregions of the US. In: Lockwood JL, McKinney ML, editors. *Biotic homogenization*. USA: Springer; p. 33–56.
- Bolger DT, Scott TA, Rotenberry JT. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conserv Biol.* 11:406–421.
- Bonnington C, Gaston KJ, Evans KL. 2015. Ecological traps and behavioural adjustments of urban songbirds to fine-scale spatial variation in predator activity. *Anim Conserv.* 18:529–538.
- Bonnington C, Gaston KJ, Evans KL, Whittingham M. 2013. Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. *J Appl Ecol.* 50:15–24.
- Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ. 2009. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis.* 151:1–18.
- Chiron F, Julliard R. 2007. Responses of songbirds to magpie reduction in an urban habitat. *J Wildl Manage.* 71:2624–2631.
- Cox RM, McGlothlin JW, Bonier F. 2016. Hormones as mediators of phenotypic and genetic integration: an evolutionary genetics approach. *Integr Comp Biol.* 56:126–137.
- Creel S, Christianson D. 2008. Relationships between direct predation and risk effects. *Trends Ecol Evol.* 23:194–201.
- Creel S, Christianson D, Liley S, Winnie JA Jr. 2007. Predation risk affects reproductive physiology and demography of elk. *Science.* 315:960.
- Cresswell W. 2008. Non-lethal effects of predation in birds. *Ibis.* 150:3–17.
- Curtis OE, Rosenfield RN, Bielefeldt J. 2006. Cooper's hawk (*Accipiter cooperii*). In: Poole A, editor. *The birds of North America online*. Cornell lab of ornithology. Ithaca (NY). <http://bna.birds.cornell.edu/bna/species/075>
- DeLuca J. 2008. Reproduction of Eastern bluebirds (*Sialia sialis*) in relation to farmland and management and food resources in north-central Florida [master's thesis]. Gainesville (FL): University of Florida.
- Dinsmore SJ, Wunder MB, Dreitz VJ, Knopf FL. 2010. An assessment of factors affecting population growth of the mountain plover. *Avian Conserv Ecol.* 5:5.
- Donihue CM, Lambert MR. 2015. Adaptive evolution in urban ecosystems. *Ambio.* 44:194–203.
- Eggers S, Griesser M, Nystrand M, Ekman J. 2006. Predation risk induces changes in nest-site selection and clutch size in the siberian jay. *Proc R Soc B.* 273:701–706.
- Elliott KH, Betini GS, Dworkin I, Norris DR. 2016. Experimental evidence for within- and cross-seasonal effects of fear on survival and reproduction. *J Anim Ecol.* 85:507–515.

- Estes WA, Mannan RW. 2003. Feeding behavior of Cooper's hawks at urban and non-urban nests in southeastern Arizona. *Condor*. 105:107–116.
- Finch B, Young B, Johnson R, Hall JC. 2012. Longleaf, as far as the eye can see. Chapel Hill: University of North Carolina Press.
- Fischer JD, Cleeton SH, Lyons TP, Miller JR. 2012. Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *Bioscience*. 62:809–818.
- Fletcher RJ Jr. 2007. Species interactions and population density mediate the use of social cues for habitat selection. *J Anim Ecol*. 76:598–606.
- Florida Natural Areas Inventory. 2010. Guide to the natural communities of Florida: 2010 edition. Tallahassee (FL): Florida Natural Areas Inventory.
- Fontaine JJ, Martin TE. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol Lett*. 9:428–434.
- Gadgil M, Bossert WH. 1970. Life historical consequences of natural selection. *Am Nat*. 104:1–24.
- Gehlbach FR. 1994. The Eastern screech owl: life history, ecology, and behavior in the suburbs and countryside. College Station (TX): Texas A. and M. University Press.
- Gehlbach FR. 1995. Eastern screech-owl (*Megascops asio*). In: Poole A, editor. The birds of North America online. Cornell lab of ornithology. Ithaca (NY). <http://bna.birds.cornell.edu/bna/species/165>.
- Gering JC, Blair RB. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? *Ecography*. 22:532–541.
- Gill D, Brumm H. 2014. Avian urban ecology: behavioural and physiological adaptations. Oxford (UK): Oxford University Press.
- Götz T, Janik VM. 2016. Non-lethal management of carnivore predation: long-term tests with a startle reflex-based deterrence system on a fish farm. *Anim Conserv*. 19:212–221.
- Gowaty PA, Plissner JH. 2015. Eastern bluebird (*Sialia sialis*). In: Poole A, editor. The birds of North America Online. Cornell lab of ornithology. Ithaca (NY). <http://bna.birds.cornell.edu/bna/species/381>
- Halekoh U, Højsgaard S, Yan J. 2006. The R package geepack for generalized estimating equations. *J Stat Softw*. 15:1–11.
- Haskell DG, Knupp AM, Schneider MC. 2001. Nest predator abundance and urbanization. In: Marzluff J, Bowman R, Donnelly R, editors. Avian ecology and conservation in an urbanizing world. USA: Springer; p. 243–258.
- Hetrick SA, Sieving KE. 2012. Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. *Behav Ecol*. 23:83–92.
- Hirshfield MF, Tinkle DW. 1975. Natural selection and the evolution of reproductive effort. *P Natl Acad Sci USA*. 72:2227–2231.
- Hoyt DF. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk*. 96:73–77.
- Hua F, Fletcher RJ Jr., Sieving KE, Dorazio RM. 2013. Too risky to settle: avian community structure changes in response to perceived predation risk on adults and offspring. *Proc R Soc B*. 280:20130762.
- Hua F, Sieving KE, Fletcher RJ Jr., Wright CA. 2014. Increased perception of predation risk to adults and offspring alters avian reproductive strategy and performance. *Behav Ecol*. 25:509–519.
- Huang P. 2016. Behavioral syndrome, stress hormone, melanin-based morphological trait and urban–rural variation of Northern cardinals (*Cardinalis cardinalis*) [PhD dissertation]. Gainesville (FL): University of Florida.
- Ibanez-Alamo JD, Magrath RD, Oteyza JC, Chalfoun AD, Haff TM, Schmidt KA, Thomson RL, Martin TE. 2015. Nest predation research: recent findings and future perspectives. *J Ornithol*. 156:S247–S262.
- Isaksson C, Hahs A. 2015. Urbanization, oxidative stress and inflammation: a question of evolving, acclimatizing or coping with urban environmental stress. *Funct Ecol*. 29:913–923.
- Kark S, Iwaniuk A, Schalimtzek A, Banker E. 2007. Living in the city: can anyone become an 'urban exploiter'? *J Biogeogr*. 34:638–651.
- Kosinski Z. 2001. Effects of urbanization on nest site selection and nesting success of the Greenfinch (*Carduelis chloris*) in Krotoszyn, Poland. *Ornis Fennica*. 78:175–183.
- LaManna JA, Martin TE. 2016. Costs of fear: behavioural and life-history responses to risk and their demographic consequences vary across species. *Ecol Lett*. 19:403–413.
- Lang JD. 2013. Eastern bluebird (*Sialia sialis*) survival and dispersal in areas with high and low densities of red imported fire ants (*Solenopsis invicta*) [master's thesis]. Athens (GA): University of Georgia.
- Liang KY, Zeger SL. 1986. Longitudinal data-analysis using generalized linear-models. *Biometrika*. 73:13–22.
- Liebezeit JR, George TL. 2002. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed Ponderosa Pine forest. *Condor*. 104:507–517.
- Lima SL. 2002. Putting predators back into behavioral predator–prey interactions. *Trends Ecol Evol*. 17:70–75.
- Lima SL. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biol Rev*. 84:485–513.
- Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool*. 68:619–640.
- Loss SR, Will T, Marra PP. 2013. The impact of free-ranging domestic cats on wildlife of the United States. *Nat Commun*. 4:1396.
- Major RE, Kendal CE. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis*. 138:298–307.
- Martin TE. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proc R Soc B*. 269:309–316.
- Martin TE, Briskie JV. 2009. Predation on dependent offspring: a review of the consequences for mean expression and phenotypic plasticity in avian life history traits. *Ann NY Acad Sci*. 1168:201–217.
- Marzluff J. 2001. Worldwide urbanization and its effects on birds. In: Marzluff J, Bowman R, Donnelly R, editors. Avian ecology and conservation in an urbanizing world. USA: Springer; p. 19–47.
- McKinney ML. 2002. Urbanization, biodiversity, and conservation. *Bioscience*. 52:883–890.
- McManus JS, Dickman AJ, Gaynor D, Smuts BH, Macdonald DW. 2015. Dead or alive? Comparing costs and benefits of lethal and non-lethal human–wildlife conflict mitigation on livestock farms. *Oryx*. 49:687–695.
- Millon A, Nielsen JT, Bretagnolle V, Møller AP. 2009. Predator–prey relationships in a changing environment:

- the case of the sparrowhawk and its avian prey community in a rural area. *J Anim Ecol.* 78:1086–1095.
- Mortensen JL, Reed JM, Margalida A. 2016. Population viability and vital rate sensitivity of an endangered avian cooperative breeder, the white-breasted thrasher (*Ramphocinclus brachyurus*). *PLoS One.* 11:e0148928.
- Mukherjee S, Heithaus MR, Trexler JC, Ray-Mukherjee J, Vaudo J. 2014. Perceived risk of predation affects reproductive life-history traits in *Gambusia holbrooki*, but Not in *Heterandria formosa*. *PLoS One.* 9(2):e88832.
- Nest Box Resource Center. 2013. Nest box placement. <http://nestwatch.org/learn/nest-box-resource-center/nest-box-placement/>.
- Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR. 2015. The ecological effects of providing resource subsidies to predators. *Global Ecol Biogeogr.* 24:1–11.
- North American Bluebird Society, Inc: Nest Box Plans. 2011. [accessed 2017 July 4]. <http://www.nabluebirdsociety.org/nestboxes/gilbertson.htm>
- Nussey DH, Postma E, Gienapp P, Visser ME. 2005. Selection on heritable phenotypic plasticity in a wild bird population. *Science.* 310:304–306.
- Pardecke J, Van't Hof T, Gwinner E. 2004. Differences in the timing of reproduction between urban and forest European blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? *Proc R Soc B.* 271:1995–2001.
- Pickett STA, Cadenasso ML, Grove JM, Nilon CH, Pouyat RV, Zipperer WC, Costanza R. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socio-economic components of metropolitan areas. *Annu Rev Ecol Syst.* 32:127–157.
- Preisser E, Bolnick D, Benard M. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology.* 86:501–509.
- R Core Team. 2015. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. <http://www.R-project.org>.
- Reid S. 1884. The birds of Bermuda. *Bull US Nat Mus.* 24:163–279.
- Rodewald AD, Kearns LJ, Shustack DP. 2011. Anthropogenic resource subsidies decouple predator–prey relationships. *Ecol Appl.* 21:936–943.
- Rollinson DJ, Jones DN. 2002. Variation in breeding parameters of the Australian magpie *Gymnorhina tibicen* in suburban and rural environments. *Urban Ecosyst.* 6:257–269.
- Rosenfield RN, Bielefeldt J, Affeldt JL, Beckmann DJ. 1995. Nesting density, nest area reoccupancy, and monitoring implications for Cooper's hawks in Wisconsin. *J Raptor Res.* 29:1–4.
- Roth TC, Lima SL. 2003. Hunting behavior and diet of Cooper's hawks: an urban view of the small-bird-in-winter paradigm. *Condor.* 105:474–483.
- Saether BE, Bakke O. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology.* 81:642–653.
- Sieving KE, Willson MF. 1998. Nest predation and avian species diversity in northwestern forest understory. *Ecology.* 79:2391–2402.
- Smith EZ. 2013. Sialis.org, Woodstock CT. <http://www.sialis.org/predatorid.htm>.
- Sorace A. 2002. High density of bird and pest species in urban habitats and the role of predator abundance. *Ornis Fennica.* 79:60–71.
- Stoks R, De Block M, Slos S, Van Doorslaer W, Rolff J. 2006. Time constraints mediate predator-induced plasticity in immune function, condition, and life history. *Ecology.* 87:809–815.
- Tracey CM. 2011. Resolving the urban nest predator paradox: the role of alternative foods for nest predators. *Biol Conserv.* 144:1545–1552.
- Tracey CM, Robinson SK. 2012. Does nest predation shape urban bird communities? In: Lepczyk CA, Warren PS, editors. *Urban bird ecology and conservation*. USA: University of California Press; p. 49–70.
- Thomson DL, Monaghan P, Furness RW. 1998. The demands of incubation and avian clutch size. *Biol Rev Camb Philos.* 73:293–304.
- Thorup K, Sunde P, Jacobsen LB, Rahbek C. 2010. Breeding season food limitation drives population decline of the little owl *Athene noctua* in Denmark. *Ibis.* 152:803–814.
- Tornberg R, Korpimäki E, Jungell S, Reif V. 2005. Delayed numerical response of goshawks to population fluctuations of forest grouse. *Oikos.* 111:408–415.
- Tratalos J, Fuller RA, Evans KL, Davies RG, Newson SE, Greenwood JJ, Gaston KJ. 2007. Bird densities are associated with household densities. *Global Change Biol.* 13:1685–1695.
- USDA Natural Resources Conservation Service. 1999. Eastern bluebird (*Sialia sialis*). In: Fish and wildlife habitat management leaflet no. 2. Madison (WI): USDA Natural Resources Conservation Services. p. 12.
- van Heezik Y. 2010. Pussyfooting around the issue of cat predation in urban areas. *Oryx.* 44:153–154.
- Zanette LY, White AF, Allen MC, Clinchy M. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. *Science.* 334:1398–1401.
- Zera AJ, Harshman LG. 2001. The physiology of life history trade-offs in animals. *Annu Rev Ecol Syst.* 32:95–126.