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European Starling (*Sturnus vulgaris*) reproduction undeterred by predator scent inside nest boxes

Bradley F. Blackwell, Thomas W. Seamans, Morgan B. Pfeiffer, and Bruce N. Buckingham

Abstract: Indirect predator cues near nests have been shown to enhance perceived predation risk and associated antipredator behaviours in breeding animals across taxa and particularly with birds. We hypothesized that scent from the raccoon (*Procyon lotor* (Linnaeus, 1758)) inside nest boxes would, despite being an evolutionarily unique predator, enhance perceived risk to the European Starling (*Sturnus vulgaris* (Linnaeus, 1758)), thus reducing use of treated sites and reproduction. During early spring, starlings selected from nest boxes treated with equal volumes of predator scent, a novel odour, or water ($n = 40$ boxes per treatment). We evaluated effects of treatment on reproductive traits via generalized linear models. Starlings established nest bowls in 61% of nest boxes (predator scent, $n = 27$ boxes; novel odour, $n = 24$ boxes; control (water), $n = 22$ boxes); clutches were laid in 68 boxes. We observed no effects of treatment on the likelihood of a clutch (≥ 1 egg) or nest failure. Further, we found no treatment effects on date of first egg, clutch size, or hatchling number. We conclude that starling antipredator response to enhanced, indirect risk of nest predation is contingent upon a combination of predator cues, as well as direct or indirect experience with nest predation.

Key words: antipredator behaviour, European Starling, nest box, nest predation, odour, predator scent, *Sturnus vulgaris*.

Résumé : Il a été démontré que les signaux indirects de prédateurs près des nids accroissent le risque de prédation perçu et les comportements antiprédateurs associés chez les animaux reproducteurs de nombreux taxons, particulièrement chez les oiseaux. Nous avons postulé qu'une senteur de raton laveur (*Procyon lotor* (Linnaeus, 1758)) à l'intérieur de nichoirs, même s'il s'agit d'un prédateur singulier sur le plan de l'évolution, rehausserait le risque perçu par des étourneaux sansonnets (*Sturnus vulgaris* (Linnaeus, 1758)), réduisant ainsi leur utilisation des sites traités et leur reproduction. Au début du printemps, des étourneaux ont fait leur choix parmi des nichoirs traités avec des volumes égaux de senteur de prédateur, d'une odeur nouvelle ou d'eau ($n = 40$ nichoirs pour chaque traitement). Nous avons évalué les effets du traitement sur des caractères associés à la reproduction en utilisant des modèles linéaires généralisés. Des étourneaux ont établi des nids dans 61 % des nichoirs (senteur de prédateur, $n = 27$; nouvelle odeur, $n = 24$; témoin (eau), $n = 22$); des œufs ont été pondus dans 68 nichoirs. Aucun effet du traitement sur la probabilité de ponte (≥ 1 œuf) ou d'échec du nid n'a été observé. Nous n'avons en outre observé aucun effet des traitements sur la date de ponte du premier œuf, la taille de la ponte ou le nombre d'oisillons éclos. Nous concluons que la réaction antiprédateur des étourneaux à un risque de prédation indirect accru du nid dépend d'une combinaison de signaux de prédateur, ainsi que de l'expérience directe et indirecte de prédation de nids. [Traduit par la Rédaction]

Mots-clés : comportement antiprédateur, étourneau sansonnet, nichoir, prédation de nids, odeur, senteur de prédateur, *Sturnus vulgaris*.

Introduction

Predation pressure challenges prey to effectively adapt to the perceived or realized level of predation risk by assessing costs and benefits of subsequent behaviours (Lima and Dill 1990; Magnhagen 1991; Lima 1998; Lima and Bednekoff 1999). Risk of nest predation can stimulate antipredator responses (Caro 2005) by breeding adults in the form of site selection, onset of nesting, group living, and effects on propagules (e.g., in insects, Strassmann et al. 1988; Paul et al. 2015; in amphibians, Magnusson and Hero 1991; in fish, Petranksa and Fakhoury 1991; Knapp 1993; Lehtonen et al. 2013; and in reptiles, Refsnider et al. 2015; see also Sih et al. 1985). In birds, nest predation has long been recognized as a significant selective force because of its effects on reproduction, influencing nest types and concealment, mating behaviours, and reproductive behaviour and physiology (e.g., Ricklefs 1969, 1977; Slagsvold

1982; Lima 1987, 2009; Martin 1988, 1993, 1995; Martin and Briskie 2009; contrast Bradley and Marzluff 2003).

Antipredator behavioural responses to predation risk during nesting, as well as in other contexts, will generally involve multiple sensory cues beyond the temporality of actual predation events (Kats and Dill 1998; Lima 1998; Lima and Bednekoff 1999). Predator scent, for example, can negatively affect prey activity level, suppress nondefensive behaviours such as foraging, feeding, and grooming, and stimulate shifts to habitats perceived to be less risky (Kats and Dill 1998; Apfelbach et al. 2005; Roth et al. 2008; Lloyd et al. 2009; Parsons and Blumstein 2010; Hegab et al. 2015). In some cases, prey can benefit from “selective eavesdropping” on predators, investigating scent sources so as to avoid costs of unnecessary flight (Garvey et al. 2016; see also Ramp et al. 2005). Interestingly, early work noted a lack of empirical data on the role of chemosensory stimuli in predation risk assessment by birds

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(Kats and Dill 1998; see, however, Mason et al. 1991; Roper 1999). Kats and Dill (1998), however, recognized that odour cues would seem an important component of avian risk assessment, for example, in selection of nest sites. Recent research in this area has yielded a wealth of information on bird response to predator scent, particularly focused on nest predation.

For instance, Godard et al. (2007) suspected that chemosensory capacity in cavity-nesting birds might be particularly acute so as to detect predators (e.g., snakes and small mammals) that have selected cavities as refuges, thus posing immediate risk to breeding adults. The authors exposed Eastern Bluebirds (*Sialia sialis* (Linnaeus, 1758)) via nest boxes to scent from two common nest predators, the Black Rat Snake (*Elaphe obsoleta* (Say in James, 1823)) and the deer mouse (*Peromyscus maniculatus* (Wagner, 1845)), along with a neutral cue (via absorbent paper). Bluebirds showed no antipredator response to cues and were as likely to lay eggs in boxes with predator scent as those with the neutral scent. Godard et al. (2007) suspected that bluebirds were able to discern the predator scents, but that a learning component was possibly involved (see also Johnson et al. 2011). Indeed, behavioural plasticity in response to predation risk is dependent to some degree on prior experience with predators (Barnett 1982; Curio 1988; Griffin et al. 2001; Brown et al. 2013; Chivers et al. 2014). Moreover, predation pressure and subsequent learning might instill greater sensitivity to odours inside nest boxes (Godard et al. 2007; Johnson et al. 2011). However, Amo et al. (2011) showed that recognition of predator scent is innate in the cavity-nesting and -roosting Great Tit (*Parus major* Linnaeus, 1758).

Mönkkönen et al. (2009) also used a nest-box approach in examining effects of perceived predation risk on nest site selection and reproductive investment by the European Pied Flycatcher (*Ficedula hypoleuca* (Pallas, 1764)). The authors used predator scent (mustelid urine), vinegar, or water inside triplets of boxes. In addition, a tuft of least weasel (*Mustela nivalis* Linnaeus, 1766) hair was attached under the nest box entrance for predator-scent treatments, an effect intended to enhance the perceived risk, but one that also confounded effects of the predator scent. This caveat aside, the authors found significant avoidance of predator-treated boxes, and those birds nesting in these “higher risk” sites nested four days earlier and laid 10% larger clutches than birds nesting in boxes with novel odour or water. Further, in application to open-nesting species, Forsman et al. (2013) treated the ground in a farmland bird community at different saturations with either a predator spray solution (from mustelid urine and feces) versus water and mud (control). Migrant passerine birds (17 species) avoided settling in potential breeding habitat patches treated with the predator solution. Also, Eichholz et al. (2012) reported that dabbling ducks (Anatidae) can assess nest predation risk (in the form of predator density) based on artificial scent marks made with urine from a red fox (*Vulpes vulpes* (Linnaeus, 1758)) and relative to water controls.

Antipredator response by nesting birds to indirect predator cues can vary relative to reproductive investment. For example, Amo et al. (2008) showed that Blue Tits (*Cyanistes caeruleus* (Linnaeus, 1758)), using nest boxes and caring for eight-day-old hatchlings, exhibited antipredator behaviour when exposed to mustelid scent inside the box (via absorbent paper), including delayed entry into the nest box, refusal to enter the box, and decreased time spent inside the box. Adults exposed to water or Japanese Quail (*Coturnix japonica* Temminck and Schlegel, 1849) scent exhibited fewer of these responses. Also, Amo et al. (2017) investigated breeding Blue Tit response to mammalian predator (mustelid) scent and visual cues (taxidermy mounts) versus the nonpredatory, European rabbit (*Oryctolagus cuniculus* (Linnaeus, 1758)) scent and taxidermy mount or artificial model, with water as the chemical control. In this experiment, treatments and control were placed on the ground, 4 m below nest boxes. Birds attending eight-day-old nestlings minimized time inside boxes associated

with predator cues, decreased nonessential activities with nestlings (e.g., fecal sac removal), but maintained provisioning levels. There was no difference in behaviours between predator scent and visual predator treatments (see also Ekner and Tryjanowski (2008) on effects of visual predator cues on cavity use by roosting birds).

The variety of behavioural and life-history implications on nesting birds of indirect predator sign, particularly scent, leave open the question of whether exploitation of this sensory pathway might prove beneficial in targeted applications against species whose nest site selection can pose problems for human health and safety or in scenarios of competition with indigenous species. For example, the European Starling (*Sturnus vulgaris* (Linnaeus, 1758); hereafter “starling”) has been considered a competitive threat to indigenous cavity-nesting birds in the United States (Kalmbach and Gabrielson 1921; Brush 1983; Kerpez and Smith 1990; Cabe 1993; Koenig 2003), as well as a pest species and hazard to aviation safety (Bridgman 1962; Feare 1984; Ingold 1994; Jackson 2000; Dolbeer et al. 2016). Efforts to deter starlings from nesting have, for the most part, proven ineffective (Seamans et al. (2015) and citations therein; but see Tyson et al. 2011).

Our primary purpose for this study was to investigate recent findings with regard to response of nesting birds, including cavity-nesting species, to the presence of mammalian predator scent near or in potential nest sites (e.g., Amo et al. 2008, 2011; Mönkkönen et al. 2009; Forsman et al. 2013; Stanbury and Briskie 2015). We were also interested as to whether our findings might provide an avenue for development of a scent-based product to deter nesting by starlings. We note that starlings have a relatively high level of olfactory acuity that peaks during the breeding season, possibly related to the selection of green nesting materials that might serve an antimicrobial-parasite function (Clark and Mason 1987; Clark and Smeraski 1990; De Groof et al. 2010) but more so to the mate selection process (Fauth et al. 1991; Brouwer and Komdeur 2004). Starlings in Europe are exposed to a variety of mammalian nest predators (Feare 1984), and they have been shown to respond to carnivore scent in the foraging context (Mason et al. 1991). Further, starlings have shown a latency to enter nest boxes treated with black rat (*Rattus rattus* (Linnaeus, 1758)) urine, but these boxes also housed 10- to 15-day-old young (Stanbury and Briskie 2015). However, no work has examined starling response to predator scent relative to nest-site selection and subsequent reproductive effort.

We hypothesized that indirect predator sign in a nest box would enhance perceived risk to adult starlings, thus effecting reduced use of treated sites (i.e., exposure of adults to predation mortality) and reduced reproduction. We predicted the following: (i) if availability of natural cavities was not limiting (see below), starlings and other cavity-nesting birds would avoid nest boxes pretreated with predator scent (i.e., show plasticity; e.g., Martin and Briskie 2009; Mönkkönen et al. 2009; Zanette et al. 2011; Hua et al. 2013) but readily nest in boxes with a novel odour treatment or control (water treatment); (ii) alternatively, starlings might limit antipredator behaviour if additional evidence of the predator (e.g., visual sign) was absent (Mönkkönen et al. 2009); and (iii) if natural cavities were limited, starlings would use boxes treated with predator scent, but nest initiation would be delayed; clutch size would be smaller than for novel odour treated boxes (suggesting more time given to perceived need for nest defense (Lima 1987) or to allow for increased investment in renesting (see Martin and Li (1992) and citations therein; Martin 1995; Eggers et al. 2006; Fontaine and Martin 2006; Hua et al. 2014; LaManna and Martin 2016; but see Mönkkönen et al. 2009).

Materials and methods

We conducted our study on the 2200 ha National Aeronautics and Space Administration Plum Brook Station (PBS), Erie County,

Fig. 1. Example of (a) nest box placement and (b) construction and treatment placement used in a study of European Starling (*Sturnus vulgaris*) response to predator scent, novel odour, or water inside boxes. A total of 120 nest boxes (28 × 13 × 17 cm; 5.1 cm diameter entrance) were attached to utility poles 2.5 to 3.0 m above the ground with an aluminum predator guard below the box; each box was approximately 60 m from the nearest box. The study was conducted during March through July 2017 on the U.S. National Aeronautics and Space Administration's Plum Brook facility in Erie County, Ohio, USA. See text for further details on the study area, experimental design, and treatments.

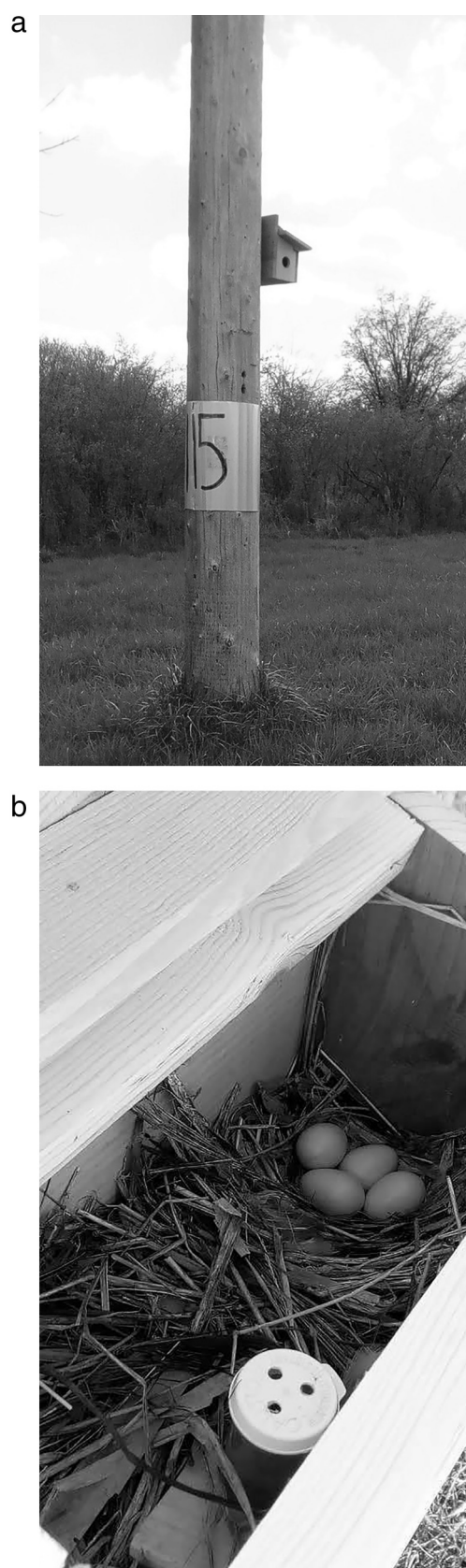
Ohio, USA (41°22'N, 82°41' W), during spring–summer 2017 (for a detailed description of PBS, see [Bowles and Arrighi 2004](#)). In prior studies completed at PBS, nest boxes were attached to 50 to 100 utility poles ([Seamans et al. 2015](#)). We attached 120 wooden nest boxes (28 × 13 × 17 cm; 5.1 cm diameter entrance) to utility poles 2.5 to 3.0 m above the ground and with an aluminum predator guard below the box; each box was approximately 60 m from the nearest box ([Fig. 1](#)). As in previous studies on PBS ([Seamans et al. 2015](#)), these nest boxes were designed to include a removable roof for efficient nest checks ([Fig. 1](#)); the roof fit within a groove and was held in place by a removable nail. Given pole availability and location, not all boxes faced the same direction; however, previous research ([Seamans et al. 2015](#)) has not reported effects of cavity entry direction on starling use of boxes. Further, treatment assignments to boxes controlled for this potential bias.

Approximately 50 boxes were in place for six years prior to this experiment, with each box entrance closed for the previous two years. The older nest boxes were cleaned, repaired, or replaced as necessary and 70 new boxes were positioned by the end of February 2017. We did not attempt to balance the number of new and old boxes. A balanced design by box age would have required relocating older boxes that were in good repair, thus potentially damaging boxes and introducing possible added variability due to winter monitoring of candidate nest sites by starlings. Specifically, nest site “age” relative to starling selection of potential nest sites during the winter preceding a breeding season ([Kessel 1957](#)) can effect box use. This effect was not found in previous studies ([Seamans et al. 2015](#)), but we included box age in our analyses (see below).

Experimental design

A single nest box was selected at random and assigned as a predator-scent treatment. We then randomly selected the travel direction (right or left) from that box, and the subsequent two next boxes were assigned as control and novel odour. We maintained a systematic assignment of treatments in this order to triplets of boxes (e.g., [Mönkkönen et al. 2009](#)). Treatments were placed in each box and all boxes were opened in early March 2017, thus allowing exposure to treatment upon investigation of the site and prior to a reproductive commitment by the birds.

Our treatments included (i) a commercial, male raccoon (*Procyon lotor* (Linnaeus, 1758)) urine- and glandular-based product as the predator scent (WCS™ Raccoon Eviction Fluid, Wildlife Control Supplies, East Granby, Connecticut, USA); (ii) a novel odour (Febreze Extra Strength Fabric Refresher, original scent, Procter and Gamble, Cincinnati, Ohio, USA); and (iii) distilled water as the control. We selected scent from the raccoon, a native North American mesocarnivore and evolutionarily unique predator of the starling (see, however, phylogeny of canoid families; [MacClintock 1981](#)), for several reasons. First, the starling was introduced to North America in the late 19th century and is a successful species well adapted to anthropogenic resources ([Feare 1984](#)). The raccoon is also adapted to anthropogenic resources ([Vantassel et al. 2013](#)) and will prey upon accessible cavity nests ([Hamilton 1936](#); [Dolbeer et al. 1988](#); [Christman and Dhondt 1997](#); [Begg 2009](#)). We assumed that starlings nesting during our study had some experience with



raccoons (T.W. Seamans, personal observation; [Dolbeer et al. 1988](#)). Further, the combination of odour cues and experience with a predator can serve to elicit antipredator behaviours ([Kats and Dill 1998](#)), and there is evidence of non-native prey selectively

Table 1. Most frequently observed species nesting and associated statistics for nest boxes occupied (No. of nests: a nest bowl was evident) during an experiment on the U.S. National Aeronautics and Space Administration's Plum Brook facility in Erie County, Ohio, USA, during March through July 2017, relative to the effect of predator scent in enhancing perceived predation risk.

Species	Treatment	No. of nests (with ≥ 1 egg)	First egg, days	Clutch size	No. of hatchlings
European Starling (<i>Sturnus vulgaris</i>)	Predator scent	27 (26)	23.8 (9.4)	4.9 (1.4)	3.3 (1.6)
	Novel odour	24 (21)	19.7 (8.08)	4.4 (1.8)	3.4 (1.9)
	Control	22 (21)	22.0 (10.3)	4.8 (1.5)	3.7 (1.5)
Tree Swallow (<i>Tachycineta bicolor</i>)	Predator scent ^a	11 (11)	43.7 (5.6)	5.1 (1.9)	4.6 (1.3)
	Novel odour	12 (12)	45.8 (6.0)	5.4 (1.1)	4.5 (1.9)
	Control	9 (9)	41.6 (3.6)	4.4 (2.8)	3.7 (2.7)

Note: Data shown include number of eggs (number of nests begun, with the number of nests that produced ≥ 1 egg in parentheses), first egg (mean (SD) days since the nest box was opened for appearance of first egg), and mean (SD) clutch size and number of hatchlings. See text for details on experimental design.

^aOne tree swallow nest followed the loss of a starling clutch to predation; however, the predator scent treatment was still present.

responding to native predators (Naddafi et al. 2007; Castorani and Hovel 2016), behaviours that can serve invasion success (Castorani and Hovel 2016; Carthey and Blumstein 2018). Also, our predator-scent treatment is a commercial product used to deter female raccoons (pregnant or with young) from human structures (Vantassel et al. 2013).

Each treatment (~3 mL) was placed in an equal-volume container (i.e., not spread or dispersed within the nest box), sealed with a perforated, plastic cap, and secured within a bored, wooden block placed inside and in the middle of the nest box (Fig. 1). During weekly nest checks, we ensured that treatments were still present in unused boxes and those for which nesting material was present. We were also interested in the possibility of a deterrent application, therefore we refilled treatments as necessary (e.g., because of vials overturned or evaporation) to ensure an equal-volume point source for each treatment. However, we refilled vials only to the point at which we detected the first egg (or early clutch if first egg was not detected) of a starling or another species. Because treatments in all boxes did not require refilling, we assessed the likelihood that refilling treatments dissuaded birds from nesting or were less likely to host starling nests (see below).

We inspected each box once weekly and recorded the stage of nest completion (i.e., whether a nest bowl was evident), ordinal date for first egg, species, clutch size, and number of hatchlings (number of eggs hatched). A nest bowl connotes that nesting material has been manipulated into a circular form and shows evidence of finer material at the centre (Feare 1984). Starlings generally lay one egg per day, and young hatch asynchronously (Feare 1984). To estimate date of first egg, we subtracted the total number of eggs within a nest when first encountered from the date of the observation. We followed nests through fledging, but we could not accurately estimate fledging success given our inspection protocol. We noted, however, whether a nest appeared to have suffered predation.

As noted above, availability of natural cavities plays a potential role in starling use of nest boxes. Seamans et al. (2015) speculated that cavity availability on PBS might not be limiting because of the 2003 invasion of the Emerald Ash Borer (*Agrilus planipennis* Fairmaire, 1888; Ohio Department of Natural Resources 2015), an insect pest that causes tree death, and the presence of cavity-excavating species that could take advantage of increased tree mortality. In this study, however, we could not directly measure cavity availability, but we assumed that if a majority of control boxes were used by starlings, given the species' competitive dominance against indigenous cavity nesters (see above), such a scenario would be indicative of increased competition for nesting space. Alternatively, if control boxes went unused by starlings or were used infrequently, we assumed that natural cavities were likely abundant and available. We note, also, that starling popu-

lations in the lower Great Lakes region of the United States and in Ohio are slightly declining (North American Breeding Bird Survey, BBS; <https://www.pwrc.usgs.gov/bbs/>), but BBS relative abundance indices indicate >300 birds per route in these regions.

Statistical analyses

We first evaluated whether boxes with treatments that were refilled were more likely to be found without nests (i.e., no eggs recorded) than boxes with treatments not refilled. We also assessed the likelihood that boxes with vials refilled would be used by starlings for nesting (≥ 1 egg recorded). For both questions, we used a generalized linear model, a binomial distribution, and logit link (PROC GENMOD, SAS 9.2, SAS Institute Inc., Cary, North Carolina, USA). Generalized linear models use the distribution of the observations, the linear predictor(s), variance function, and a link function (Ngo 2016). Next, we evaluated whether treatment affected starling establishment of a clutch (≥ 1 egg) and nest failure. Again, for both questions, we used a generalized linear model, a binomial distribution, and logit link (PROC GENMOD, SAS 9.2, SAS Institute Inc.).

We then evaluated treatment, box age, and treatment \times box age interaction effects on date of first egg, clutch size, and maximum number of hatchlings (i.e., the maximum number of hatchlings detected, including dead and alive) via generalized linear model analysis. Our model residuals were not normally distributed. Instead, we assumed a Poisson distribution and used a log link.

Our methods for this study were approved by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center Institutional Animal Care and Use Committee under protocol 2744.

Results

During April and early May, we refilled vials in 16 boxes. Vials in 14 of these boxes were refilled only once, but we refilled vials in one novel-odour box and one predator-scent box twice. Boxes treated with the novel odour or water required more refilling (vials containing the novel-odour treatment involved eight boxes: overturned, seven instances; treatment evaporated, two instances; water vials involved five boxes: overturned, four instances; evaporated, one instance; predator-scent vials involved three boxes: overturned, three instances; evaporated, one instance). Starlings laid clutches in nine of these boxes, and Tree Swallows (*Tachycineta bicolor* (Viellot, 1808)) laid clutches in another four boxes; two boxes were not used for nesting. We found no effect of refilling on the likelihood that a box would not be used for nesting by any species (likelihood ratio (LR): $df = 1$, $\chi^2 = 0.11$, $P = 0.7364$), and there was no effect of refilling on the likelihood that starlings would nest in a box (≥ 1 egg detected; LR: $df = 1$, $\chi^2 = 0.33$, $P = 0.5647$).

We observed a 90% rate of nest bowl completion ($n = 108$ boxes) across species. Starlings completed nest bowls in 73 of the avail-

Table 2. Results of generalized linear model analysis, assuming a Poisson distribution, of nest box treatment and age on phases of reproduction in European Starling (*Sturnus vulgaris*) nesting on U.S. National Aeronautics and Space Administration's Plum Brook facility in Erie County, Ohio, USA, during March through July 2017.

Response variable	Model df	Independent variable	df	χ^2	P
Date of first egg	62	Treatment	2	2.03	0.3630
		Age	1	3.58	0.0585
		Treatment \times age	2	0.30	0.8623
		Dispersion = 0.6967	1		
Clutch size	67	Treatment	2	0.86	0.6502
		Age	1	0.00	0.9745
		Treatment \times age	2	0.64	0.7262
		Dispersion = 0.8274	1		
No. of hatchlings	63	Treatment	2	0.74	0.6911
		Age	1	0.04	0.8433
		Treatment \times age	2	1.35	0.5103
		Dispersion = 1.2960	1		

Note: Model dispersion was estimated based on the Pearson chi-square (χ^2) statistic divided by the degrees of freedom (df). Model df varied per response variable because of failure to lay, thus yielding no ordinal date of first egg and a score of zero for clutch size, as well as nests without hatchlings. See text for experimental design and methods.

able 120 boxes (61%) but laid clutches in only 68 nests (Table 1). Tree Swallows nested in 32 boxes (Table 1), while Eastern Bluebirds and House Wrens (*Troglodytes aedon* Vieillot, 1809) nested in four boxes. Only 10 starling nests were lost to apparent predation, likely by other cavity-nesting birds; we found one instance of possible infanticide, likely due to loss of a mate and subsequent remating (predator scent treated box nest losses, three instances; novel odour, five instances; control, two instances). We observed no treatment effect on the likelihood of a clutch (≥ 1 egg) in starling nests (LR: df = 2, χ^2 = 0.55, P = 0.7589) or nest failure (LR: df = 2, χ^2 = 2.21, P = 0.3309; Table 1). Further, we found no effect of treatment, box age, or treatment \times box age interaction on date of first egg for starlings, clutch size, or number of hatchlings (Table 2).

Discussion

Animals vary behavioural and life-history responses to the level of perceived and realized risk (Lima and Dill 1990; Creel and Christianson 2008; Martin and Briskie 2009; LaManna and Martin 2016; Minnie et al. 2016). In the context of a nest-box experiment, we tested the hypothesis that predator scent in a nest box will enhance perceived risk to adult starlings, thus affecting use of the site, as well as reproduction. We found that predator scent (raccoon) had no effect on starling use of predator scent treated nest boxes or reproduction. We note, also, that our maintenance of treatment volume, via refilling vials where evaporation or overturning affected volumes (an action intended to simulate what one would expect if a scent product was used in a nesting-deterrent application), had no effect on nesting by any species or by starlings. Previous work with starlings suggests that detection of odour treatments was likely (sensu Clark and Mason 1987; Mason et al. 1991; Stanbury and Briskie 2015). For instance, Stanbury and Briskie (2015) evaluated starling antipredator behavior in response to predator versus control scent at nest boxes that housed 10- to 15-day-old young. The authors video-recorded each nest over a 30 min period, immediately after placement of a rat urine treated sachet or a water-treated, control sachet. Starlings showed latency to enter nest boxes treated with rat urine.

The possibility exists, however, that scent from a native, North American mesocarnivore has negligible effect on perceived risk in the invasive starling. Still, starling populations in North America have been exposed to raccoon predation for approximately 120 years (Feare 1984; see also Hamilton 1936; Dolbeer et al. 1988; Christman and Dhondt 1997; Begg 2009), and there is evidence that experience with predation will elicit antipredator behaviours

in naïve prey (Naddafi et al. 2007; Castorani and Hovel 2016). Below, we summarize our findings relative to our predictions and draw conclusions with regard to starling antipredator behaviour in the context of nest-site selection and breeding relative to an indirect predator cue.

Our finding that starlings occupied (i.e., a nest bowl was evident) only 61% of available nest boxes falls at the lower end of previous studies (58%–97% occupancy; Tyson et al. 2011) and is suggestive that either nest box availability was not a limiting factor or natural cavities were not limited; however, that starlings in North American prefer natural cavities (Planck 1967; Ingold 1998) favors the availability of natural cavities as the more reasonable explanation.

Given cavity availability, we predicted that starlings would show plasticity in site selection by avoiding sites with enhanced perceived risk (Martin and Briskie 2009; Mönkkönen et al. 2009; Zanette et al. 2011; Hua et al. 2013) effected by predator scent treatments, but we also questioned whether predator scent alone, particularly applied prior to laying or hatching, would be sufficient to deter nesting. Specifically, the lack of a visual cue associated with the predator scent upon access to the box interior (Mönkkönen et al. 2009) might have resulted in birds accepting some level of perceived risk for the breeding opportunity.

Prey sensitivity to multiple indirect predator cues that impart greater saliency can serve to stimulate different enhanced levels of antipredator response (Griffin et al. 2001). For example, slimy sculpins (*Cottus cognatus* Richardson, 1836) display antipredator behaviours in response to chemical cues from sympatric, predatory brook trout (*Salvelinus fontinalis* (Mitchell, 1814)), but when sculpins can visually assess trout size, smaller trout stimulate no threat-sensitive response (Chivers et al. 2001). Also, Brown et al. (2013) argued that prey experience with predators can inform adaptability in antipredator responses such as neophobia whereby animals from high-risk environments might show stronger antipredator responses to novel predator scent (see, also, Chivers et al. (2014) and LaManna and Martin (2016)). Similarly, the observed avoidance by migratory Passeriformes of areas treated with predator urine (Forsman et al. 2013) is likely indicative of a learned susceptibility to nest predation for these open-cup nesters. Open-cup nesters are generally more vulnerable to nest predation than cavity-nesting species (Martin and Li 1992; Martin 1995).

In our experiment, the fact that we found no evidence of predator-scent effects on deposition of a clutch, timing of laying, clutch size, or hatchling number (in contrast to Martin and Li (1992), Martin (1995), Eggers et al. (2006), Fontaine and Martin

(2006), and Hua et al. (2014)) underscores the likelihood that starlings perceived little enhancement of predation risk. We also suggest that the potential lack of experience of starlings with direct nest predation at nest boxes on PBS or indirectly through observations of other pairs (see Tobler and Smith (2004) and Aitken and Martin (2008)) could have detracted from overall perceived risk associated with predator scent treatments (*sensu* Lima and Dill 1990).

We conclude, therefore, that the effects of an indirect predator cue in the form of scent inside nest boxes or near nest sites varies by species, reproductive investment, and likely experience with nest predation. Although raccoons will prey upon starlings in nest cavities (Dolbeer et al. 1988), direct experience with a predation attempt might serve to enhance perceived risk associated with a predator scent cue (Godard et al. 2007). Future research to assess starling response to enhanced nest predation risk should investigate a combination of indirect predator cues and consider both scent and predator hair (Mönkkönen et al. 2009) in experimental designs. We caution, however, that designs incorporating predator hair as a visual cue must also consider that pelage samples might introduce odour cues that could confound results.

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