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## Use of nest boxes by European Starlings (*Sturnus vulgaris*): Effects of perceived nest predation risk

Bradley F. Blackwell,<sup>1\*</sup> Morgan B. Pfeiffer,<sup>1</sup> Joshua L. Hoblet,<sup>1</sup> and Bruce N. Buckingham<sup>1</sup>

**ABSTRACT**—The European Starling (*Sturnus vulgaris*) has expanded beyond its native Eurasian range, exploiting both natural cavities and human structures for nesting. We hypothesized that starling exposure to enhanced risk of nest predation at nest boxes (surrogates for nest sites in other structures), due to predator access, would negatively affect occupancy (establishment of a nest and  $\geq 1$  egg) and subsequent nest success. We also hypothesized that starlings would show no distinction in occupancy between nest boxes relative to the presence/absence of old nest material (i.e., material from the previous season), conditions that can contribute to nest predation risk. We conducted our study from April to June 2021 in Erie County, Ohio, USA, using 120 wooden nest boxes. Our treatments comprised protected/swept (nest boxes protected by a predator guard below the nest box and swept of old nest material), protected/unswept (containing old nest material), and unprotected/unswept nest boxes. To maximize sample size per treatment, we opted to forego use of unprotected/swept nest boxes, thereby preventing assessment of possible, enhanced nest predation (from below the nest box) at unprotected nest boxes due to the presence of old nest material. We used generalized linear models and nonparametric approaches in our comparisons. Starlings occupied and fledged young in unprotected nest boxes and nest boxes containing old nest material through the breeding season, despite possible, elevated perceived predation risk. There was no advantage of protection or disadvantage of presence of old nest material on reproductive metrics in protected/unswept nest boxes, because of predation from raptors (Accipitridae) and arboreal mammals (Sciuridae). The absolute amount of nest predation was, not surprisingly, highest in unprotected/unswept nest boxes across laying, incubation, and brood stages, but occurred primarily during brood rearing for protected boxes. *Received 6 January 2023. Accepted 30 December 2023.*

Key words: nest predator, nest site selection, reproduction, secondary cavity-nesting species.

### Uso de cajas nido por estorninos *Sturnus vulgaris*: Efectos de riesgo percibido de depredación de nido

**RESUMEN** (Spanish)—El estornino *Sturnus vulgaris* se ha expandido más allá de su rango nativo Eurasiático, explotando tanto cavidades naturales como estructuras humanas para anidar. Hipotetizamos que la exposición del estornino a riesgos aumentados de depredación en cajas nido (sustitutos para sitios de anidación en otras estructuras) debido a acceso de depredadores afectaría la ocupación (establecimiento de nido y  $\geq 1$  huevo) y éxito de nido sucesivo. También hipotetizamos que los estorninos no mostrarían diferencia en ocupación entre cajas nido relativas a la presencia/ausencia de material viejo de nido (es decir, material de estaciones anteriores), condiciones que pueden contribuir al riesgo de depredación. Condujimos nuestro estudio de abril a junio del 2021 en el condado Erie, Ohio, Estados Unidos, usando 120 cajas nido de madera. Nuestros tratamientos consistieron en cajas nido protegidas/barridas (cajas nido protegidas por guardián de depredadores bajo la caja nido y barrida de material viejo de nido), protegida/sin barrer (que contenía material viejo de nido) y sin proteger/sin barrer. Para maximizar el tamaño de muestra por tratamiento, optamos por no usar cajas nido sin proteger/barridas, previniendo así la medición de un posible aumento de depredación de nido (desde abajo de la caja nido) a cajas nido sin proteger debido a la presencia de material viejo de nido. Usamos modelos lineales generalizados y un acercamiento no paramétrico para nuestras comparaciones. Los estorninos ocuparon y emanciparon crías en cajas nido sin protección y en cajas nido que contenían material viejo de nido durante la estación reproductiva, a pesar del posible elevado riesgo percibido de depredación. No hubo ventaja en protección o desventaja en presencia de material viejo de nido en métricas reproductivas en cajas nido protegidas/sin barrer, debido a la depredación por rapaces (Accipitridae) y mamíferos arbóreos (Sciuridae). La cantidad absoluta de depredación de nidos fue, sin ninguna sorpresa, mayor en cajas nido sin protección/sin barrer en puesta, incubación y crianza, pero ocurrieron mayormente durante la crianza de los polluelos en cajas protegidas.

Palabras clave: depredación de nidos, selección de sitio de anidación, reproducción, especies que anidan en cavidades secundarias.

Nest predation is a major factor driving the evolution of reproductive strategies and anti-predator responses (Caro 2005) across taxa (Blackwell et al. 2018 and references therein). In birds, for example, nest predation risk contributes to variation in nest site selection, mating behaviors, timing, and degree of nest construction activities,

reproductive physiology, and behaviors associated with incubation, brood rearing, and maintenance of the brood (Ricklefs 1969; Slagsvold 1982; Lima 1987, 2009; Martin 1988, 1993; Bradley and Marzluff 2003; Martin and Briskie 2009).

Cavity-nesting species generally fare better than open-nesting species relative to nest predation (Nice 1957, Martin and Li 1992, Martin 1993, Fontaine et al. 2007), but with tradeoffs associated with cavity construction or competition for existing cavities, as well as lower adult

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survival in secondary cavity-nesting species relative to open-nesting and primary cavity-nesting species (Martin and Li 1992). Still, diverse adaptations to perceived and realized nest predation risk are not necessarily static, nor do they represent wholly innate responses. Behavioral plasticity in response to predation risk, in general, is dependent to some degree on prior experience with predators (Curio 1988, Griffin et al. 2001, Brown et al. 2013, Ghalambor et al. 2013, Hua et al. 2014). Further, effective allocation of nesting activities will be correlated with some certainty about the current environment and associated risks (Lima and Dill 1990, Lima and Bednekoff 1999, Fontaine and Martin 2006a, Laundré et al. 2010, Stanback et al. 2018, Sonnerud 2022).

Bird response to perceived predation risk during site selection is thought to vary with predator type and frequency of encounter (Lima and Dill 1990, Lima 2009), but also the degree of familiarity with risk at alternative nest sites (Martin 1993, Stanback et al. 2018). For example, Fisher and Wiebe (2006) suggested that a single encounter by Northern Flickers (*Colaptes auratus*), a primary cavity nester, with a familiar mammalian predator at the nest site was insufficient to induce site abandonment, given costs associated with cavity construction. By manipulating perceived predation risk over 15 d (via a familiar reptilian predator in model form), Parejo and Avilés (2011) showed that Mediterranean secondary cavity-nesting birds (resident Little Owl [*Athene noctua*], migratory European Roller [*Coracias garrulus*], and Scops Owl [*Otus scops*]) first selected sites absent the predator model, “safe” nest sites within territories occupied the previous year; birds also favored “safe” sites overall. Here, period of predation risk within a territory and familiarity with predator models used in treatments, site availability, costs of nest construction, and cues associated with perceived risk elsewhere informed selection of “safe” sites (Fontaine and Martin 2006a, 2006b).

For secondary cavity-nesting species adapted to nesting in human structures, there is not only the possibility of additional or alternative nest sites (Sandoval et al. 2021) but increased protection against nest predation. This type of adaptability has marked the successful expansion of the

European Starling (*Sturnus vulgaris*; hereinafter, starling), a secondary cavity-nesting species, beyond its native range (Feare 1984). The starling is a facultative, colonial-breeding passerine, recognized as frequently polygynous (Feare 1984, Pinxten et al. 1989, Pinxten and Eens 1990); males defend a nest hole, possibly more cavities within a very small area (<1 m radius) about the main cavity, and a small territory ( $\leq 500$  m radius from main cavity; Feare 1984, but see Bruun and Smith 2003), but without defending food sources therein (Kluijver 1933, Kessel 1957, Verheyen 1980, Feare 1984, Pinxten et al. 1989). In addition to its introduction to the United States in the 1880s, the starling has expanded its distribution to include much of North America (Chapman 1925, Kessel 1957, Linz et al. 2007) as well as South Africa (Winterbottom and Liversidge 1954), Australasia, Pacific and Caribbean islands (Feare 1984), and South America (Pérez 1988, Zufiaurre et al. 2016, Ojeda et al. 2022).

The starling has been considered a competitive threat to native cavity-nesting birds in North America (Kalmbach and Gabrielson 1921, Brush 1983, Kerpez and Smith 1990, Ingold 1994, but see Koenig 2003, Koenig et al. 2017) as well as a pest species and hazard to aviation safety (Bridgman 1962, Feare 1984, Ingold 1994, Jackson 2000, Psiropoulos and Selner 2019, Dolbeer et al. 2022). To date there is no method of deterring starling nesting in human structures, short of manipulating or blocking access (Tyson et al. 2011, Seamans et al. 2015). For example, recent efforts toward manipulating perceived predation risk (via indirect predator cues and direct predation risk via model) in starlings selecting nest boxes, which conceivably could provide a simple, inexpensive approach to preventing starling nesting, have met with no success (Blackwell et al. 2018, 2020, 2021).

We sought to understand the array of predators that might threaten starling nesting in nest boxes, features of that predation (e.g., mammalian vs. avian predators), and starling response. More specifically, we hoped to gain insight as to how predators at our experiment site exploit starling nesting in our nest boxes and whether we might be able to adapt aspects of those behaviors to methods to deter starling nesting. In addition, we questioned

whether our preparation of nest boxes on our experiment site to prevent access by terrestrial, climbing predators and provide a clean nesting space has, over decades of breeding seasons, positively influenced site selection by returning pairs and previous offspring (Dolbeer et al. 1988, Seamans et al. 2015, Blackwell et al. 2021). Rendell and Verbeek (1996), for example, showed that Tree Swallows (*Tachycineta bicolor*) preferred clean nest boxes over treatments involving old nest material. Stanback and Rockwell (2003) expanded beyond simply using old nest material to examine breeding Eastern Bluebirds' (*Sialia sialis*) choice of nest sites. Specifically, these authors found that bluebirds showed nest site fidelity when presented with a choice between occupying their preferred nest box, though containing soiled nest material and associated parasites, versus a clean, less-preferred nest box (based on nest box material composition). In contrast, when presented with the choice of the preferred nest box, though soiled, and an identical but clean nest box, bluebirds selected the clean nest box. Importantly, previous nesting success can influence site fidelity (Ibáñez-Álamo et al. 2015).

Our protection of nest boxes against nest predation by terrestrial, climbing predators has likely reduced the frequency in which recent nesting pairs have observed predation attempts on conspecifics or neighbor nests, instances that can enhance perceived predation risk (Marzluff 1985, Lima and Dill 1990, Ibáñez-Álamo et al. 2015). For example, reuse of cavities or nest boxes over years can attract predators (Sonerud 1985, Nilsson et al. 1991, Sorace et al. 2004), whereas protection of the nest box can reduce the frequency of realized nest predation events and perceived nest predation risk. We note, too, that starlings, whether a given nesting pair or another pair usurping a nest box, showed persistence in use of nest boxes on our site despite a disturbance regimen, and with only a modest effect on date of first egg (Blackwell et al. 2022).

In addition, starlings generally prefer clean nest boxes (Mazgajski 2003, 2007, 2013). Old nest material can contribute to ectoparasite loads (Möller 1989, Rendell and Verbeek 1996), and starlings have shown, depending on effort to remove old

nest material, delayed laying, reduced clutch size, and longer intervals between provisioning in nests containing old material vs. swept nest boxes (Mazgajski 2013). Also, if present in enough volume, old nest material can predispose a nest to greater likelihood of nest predation success (e.g., from placement of eggs and young closer to the entrance; Wesolowski 2002). However, starling pairs will place green vegetation and other material atop of some or all old nest material (Kessel 1957; Feare 1984; Mazgajski 2007, 2013). Further, starlings show preference for, and thus reuse, natural cavities (Ingold 1998, Mazgajski 2003), despite nest material load, hence serving as a terminal species for a cavity (Wiebe et al. 2020). Importantly, metrics associated with cavity quality, including presence of old nest material, and predation risk are not necessarily independent (Wesolowski 2002, Wiebe et al. 2020).

We hypothesized that enhanced risk of nest predation (i.e., not a manipulation of perceived, direct predation risk; Fisher and Wiebe 2006, Parajo and Avilés 2011, Duré Ruiz et al. 2018, Blackwell et al. 2021), as well as experience with nest predation events, would be expressed as a lower amount of occupied nest boxes (starling nest and  $\geq 1$  egg) by starlings and negative effects on nesting parameters. Specifically, recognizing potential predation by an array of species, we predicted that nest boxes unprotected against nest predation by terrestrial, climbing predators would experience a higher rate of nest predation such that starling clutches might be destroyed prior to our twice-weekly observations. The result of clutch loss prior to our observations would be a lower estimate of occupancy and a delay in the ordinal date of first egg (i.e., an increase in estimated ordinal date of first egg), particularly for unprotected boxes. Further, we anticipated that starlings nesting in unprotected nest boxes would show smaller clutch sizes, possibly due to time given to nest defense (Lima 1987, 2009; Martin and Li 1992) or losses to nest predation. We also anticipated decreased hatching and fledging success, as well as increased numbers of nest boxes showing clutch/brood abandonment. Alternatively, if predators accessed nest boxes from above (i.e., raptors [Accipitridae] and arboreal mammals [Sciuridae]),

access that is not easily controlled, we predicted that there would be no distinguishable effect of the predator guard.

We note, too, that natural cavities are preferred by starlings (Ingold 1998, Mazgajski 2003), and previous work indicated that natural cavities on our site were not limited (Pfeiffer et al. 2019). That said, we have no reason to suspect that a high availability of natural cavities limited use of our nest boxes. However, limitation on cavity availability could positively influence use of our nest boxes.

In addition, we hypothesized that starlings would show no distinction in occupancy between nest boxes relative to presence/absence of old nest material. Our reasoning is based on the lack of a clear cost or benefit to starlings associated with the presence of old nest material. First, birds must have sufficient time, relative to competition for nest sites, to assess relative quality of nest sites (Stanback and Rockwell 2003, Stanback et al. 2018, Sonerud 2022). Also, costs to starlings associated with presence of old nest material (e.g., ectoparasite load; Mazgajski 2013) might be balanced to some extent by nest construction behaviors (Kessel 1957; Feare 1984; Mazgajski 2007, 2013). Further, costs must be weighed against effects of unknown, predation pressure at another site (Fontaine and Martin 2006a, Stanback et al. 2018). In contrast, old nest material might also indicate aspects of nest site quality (Olsson and Allander 1995, Rendell and Verbeek 1996, Mazgajski 2003).

Given discrepancies in cost or benefit to starlings, and in contrast to findings by Mazgajski (2007, 2013), we predicted no difference in occupancy, date of first egg, or maximum clutch size (largest clutch size recorded) between nest boxes with or without old nest material. Alternatively, starling efforts to remove old nest material might result in a later date of first egg and smaller clutch size (Mazgajski 2013). We also predicted no difference in hatching success. Consistent with Mazgajski (2007, 2013), we predicted no difference in fledging success between nest boxes with or without old nest material. Finally, we predicted no difference in nest predation or abandonment rates between nest boxes with and without old material. However, if raptors or arboreal mammals were to frequently access nest boxes, we predicted that we

would not be able to distinguish potential effects of the presence/absence of old nest material.

Our objectives were to evaluate differences in starling nesting behavior relative to nest boxes (1) of different nest predation risk levels due to access from below the nest box (i.e., with or without a predator guard installed) and (2) with and without old nest material (i.e., unswept vs. swept). Specifically, we assessed how nest predation risk and presence/absence of old nest material influenced occupancy, date of first egg, clutch size, hatching success, fledging success, nest predation events, and nest abandonment among treatments. Our final 2 objectives were to (3) collect imagery of species at the base of the utility poles on which nest boxes were attached, on the poles, and on the nest boxes, and then (4) assess any effect on nest box occupancy due to our camera mounts.

## Methods

### Study area

We conducted our study on the 2,200 ha National Aeronautics and Space Administration Neil Armstrong Test Facility (ATF; formerly the Plum Brook Station), Erie County, Ohio, USA (41°22'N, 82°41'W), from 24 March to 15 June 2021. We followed this component of our study with a second phase, in March–June 2022, to assess possible bias due to a camera mount system used in 2021 (see below). The ATF comprises a mix of old fields, grasslands, open woodlands, mixed hardwood forest, and anthropogenic structures segmented by numerous access roads (see land cover description by Bowles and Arrighi 2004, Tyson et al. 2011).

Starlings breeding in northern Ohio have been found to overwinter (B. Blackwell, B. Buckingham, and M. Pfeiffer, US Department of Agriculture [USDA], personal observations; see also Kessel 1953, Audubon Christmas Bird Count [<https://netapp.audubon.org/cbcoobservation/>]). Also, resident starlings overwintering on breeding grounds will begin to investigate prior and new, candidate nest sites during late winter through early spring (Kessel 1957, Morrison and Caccamise 1985). For the month preceding our opening of nest boxes (see below) and approximately 1 month thereafter (March through May 2021 and 2022),

the US National Weather Service, Toledo, Ohio, reported average (SD) temperatures of 11.4 (4.2) °C, 7.7 (1.7) cm of rain, and 0.0 cm of snow, as well as 11.3 (6.9) °C, 6.9 (2.6) cm of rain, and 4.7 (7.6) cm of snow in 2021 and 2022, respectively (<https://www.weather.gov/wrh/climate?wfo=cle>).

### Experimental design

We used the same locations and many of the same 120 wooden nest boxes (length, depth, width: 28 × 13 × 17 cm with 5.1 cm diameter entrances) that were used in previous research studies on ATF (Blackwell et al. 2018, 2020, 2021, 2022), each with a removable lid for efficient checks of contents (Blackwell et al. 2018). We note that our nest box design provides 5 cm less depth than the design used by Mazgajski (2003), but Mazgajski (2003) also found no difference in fledging of at least 1 young across manipulated cavity depths (see, however, Tyson et al. 2011). Our nest boxes were attached to utility poles approximately 2.5–3.0 m above the ground, depending upon slope, and protected with an aluminum predator guard, approximately 61 cm in width, below the nest box (figure 1a in Blackwell et al. 2018). Importantly, this predator guard targets only those predators approaching from below the nest box. Each nest box was approximately 60 m (range: ~50–80 m) from the nearest nest box. Because of utility pole availability and location, not all nest boxes faced the same direction. We note that nest boxes are located within grass median areas, within 100 m of agriculture, if possible, and to limit proximity to timber. Previous research has not reported effects of cavity entry orientation on starling use of nest boxes (Seamans et al. 2015). However, there is evidence of cavity entry direction affecting reproductive parameters for the Red-cockaded Woodpecker (*Picoides borealis*, a primary cavity-nesting species; Landler et al. 2022) and the secondary cavity-nesting species American Kestrel (*Falco sparverius*; Butler et al. 2009). That said, our distribution of nest boxes compensated across treatments for entry direction.

A balanced (2 × 2) design was appropriate for our experiment, thus controlling for protection of the nest box and presence/absence of old nest

material. However, availability of nest box sites and history of starling occupancy (typically 75% to <80% of nest boxes; Blackwell et al. 2021) presented logistical challenges, as we opted to provide 40 nest boxes per treatment. We based our necessary sample size per treatment on a recent study and treatments therein (Blackwell et al. 2022) where we used the ordinal date of first egg (mean, SD, and sample size) to estimate a priori an effect size (Cohen 1988, Nakagawa and Cuthill 2007, Lakens 2022), assuming a 7 d delay in laying. Assuming starling occupancy at ≥57.5%, our subsequent power analysis indicated that a sample of 40 nest boxes per treatment allowed us to discern a better than modest effect (Cohen 1988;  $d = 0.59$ ) of treatment (Blackwell et al. 2022).

For the present study, to maximize sample size per treatment, we subsequently assigned treatments as protected/swept (i.e., predator guard installed and nest box swept of old nest material), protected/unswept (i.e., predator guard installed and presence of old nest material), and unprotected/unswept (i.e., no predator guard installed and presence of old nest material), foregoing the unprotected/swept treatment (i.e., no predator guard and swept of old nest material). Under this design, and based on previous years of experiments at ATF, we assumed that predator guards were effective in deterring most nest predation attempts from below the box (e.g., see Blackwell et al. 2018). Further, and despite our unbalanced design, we were able to evaluate starling selection of nest boxes and nesting metrics relative to nest box protection, where boxes contained old nest material (i.e., a comparison between protected/unswept vs. unprotected/unswept nest boxes), as well as the presence or absence of old nest material when nest boxes were protected (i.e., a comparison between protected/swept vs. protected/unswept nest boxes).

However, the design prevented our discerning possible, enhanced nest predation effects in unprotected nest boxes that might be due, in part, to the presence of old nest material (i.e., a comparison between unprotected/swept and unprotected/unswept treatments). Such a difference could be species-specific, wherein terrestrial, climbing predators could benefit not only from access to the unprotected nest box, but potentially

clutch and brood placement closer to the box entrance (Wesolowski 2002; see, however, nest material removal in Kessel 1957, Feare 1984). Further, potential differences in adult activity during nest construction, due to the presence of old nest material, could draw the attention of predators (Lima 2009, Zanette et al. 2011), thereby increasing the likelihood of nest predation. Thus, it is conceivable that nests in unprotected/swept nest boxes might experience fewer losses of clutches, broods, or even adults compared to nests in unprotected/unswept nest boxes. Further, our design prevented the comparison between unprotected/swept and protected/swept nest boxes, examining the effect of nest box protection absent the presence of old nest material. However, as noted above, previous research on ATF indicates limited predator access to nest boxes from below when a predator guard is in place.

Our treatment order was randomly assigned over the first 3 nest boxes and continued systematically thereafter over triplets of nest boxes and through box 120 (protected/swept = 40 nest boxes; protected/unswept = 40 nest boxes; unprotected/unswept = 40 nest boxes). Our nest box triplets were distributed across our study area and evenly regarding entrance orientation.

From our previous study (Blackwell et al. 2022), conducted in 2020, we knew that 37 control nest boxes likely contained old nest material ( $n = 36$  starling nests;  $n = 1$  Eastern Bluebird nest); the remaining nest boxes ( $n = 74$  nest boxes with nest material or nests with eggs) were subject to nest material removal through 26 May 2020, under the disturbance regimen. During March 2021, we collected old nest material from nest boxes (closed since Fall 2020) designated as protected/swept and distributed the material to randomly selected, unprotected/unswept and protected/unswept nest boxes (Mazgajski 2007). This material was a mix of grasses, broadleaf plants, twigs, feathers, and anthropogenic material. We did not standardize nest material by composition, depth, volume, or mass per nest box (following Mazgajski 2007), but simply distributed enough material to completely cover the bottom of the nest box to approximately 2.5 cm depth, at least. Nest boxes that contained adequate amounts of

old nest material by our standard, or more, were not touched. For example, our nest boxes designated as protected/unswept corresponded with the 37 control sites from our 2020 study (Blackwell et al. 2022) that likely contained nest material, although we did not record presence/absence of old nest material during treatment preparation.

We acknowledge that our approach was not statistically ideal relative to presenting a homogeneous treatment across our nest boxes selected to hold old nest material. However, our objective was to evaluate the potential effects on nest box occupancy and reproductive metrics due to the presence/absence of old nest material. Importantly, attempts to control dimensions of old nest material per nest box would not necessarily control for ectoparasite load. Further, attempting to control for composition, depth, volume, and mass of old nest material assumes an aspect of stasis of these conditions within the nest box until a pair begins nest construction; this assumption is ecologically unrealistic because of investigations by conspecifics and other species, including species removal of nest material prior to closure of nest boxes after a previous study. Also, remaining old nest material inherently differed in condition relative to whether the previous nest had failed or fledged young. For example, nest material in nest boxes where starling young have fledged is typically matted and layered with fecal material. Finally, we could not control for the inherent variability in pair-specific nest construction behaviors (e.g., degree of removal of old nest material relative to individual traits, prior experience, and age; Kessel 1957, Mazgajski 2013). Clearly, this approach resulted in some boxes containing volumes of nest material that might force positioning of the new nest bowl closer to the entrance.

Importantly, we also assumed that there was no breeding pair recognition or avoidance (due to visual or olfactory cues) of old nest material that came from other nest boxes (e.g., see Amo et al. 2014). That said, we assessed for potential differences in nest box occupancy relative to treatment. After preparing our treatments, the entrances to nest boxes were closed again until our checks began (see below).



**Figure 1.** Camera mounting design used during a European Starling nest box study on the National Aeronautics and Space Administration Neil Armstrong Test Facility, Erie County, Ohio, USA, during spring and summer 2021. The mount afforded us ease of camera placement/maintenance and prevented equipment damage or injury to those conducting mowing operations. All 120 nest boxes included the camera mount design, whether the camera was present or not. During spring and summer 2022 we examined the effect of mount relative to enhancing nest predation ( $n = 60$  nest boxes with the mount;  $n = 60$  nest boxes without the mount).

Because of grass mowing operations at ATF, we could not safely position cameras on or near the ground below our utility poles. Instead, on 13 and 14 April 2021, we attached a 1.3 cm diameter, metal conduit approximately 71 cm above each nest box; approximately 84 cm from the center of the utility pole where the conduit was attached, the end was angled downward. On this angled end of the conduit, we affixed a wooden, camera mounting board. The board was positioned 81.7 cm ( $SD = 4.3$  cm) on a diagonal from the nest box roof; the downward angle allowed the camera to capture the utility pole just above the nest box, top of the nest box (and the nest box number), entry, the utility pole below the nest box and to the ground, and ground below the utility pole (Fig. 1).

We used 30 Reconyx HyperFire 2 Cellular Professional cameras (Reconyx, Holmen, Wisconsin, USA) in a systematic placement for 2-week intervals during 2021. We randomly selected the first 30 nest boxes, as opposed to nest boxes 91 through 120, to be initially monitored by cameras.

We set the cameras to record, upon movement detection, every 10 s. Nest boxes not monitored by cameras looked similar in setup, because the camera mounting boards were of equal shape and 2-dimensional area, painted black, and remained in position regardless of camera presence. After 2 weeks, we shifted cameras to the next 30 nest boxes, and followed this succession of placement over the next 6 weeks. Because we could not identify specific individuals in photographs, other than in sequential bursts of images, we provide only descriptive statistics on non-starling visits to nest box sites relative to total images collected (below).

Importantly, the camera mounting poles created potential perches/access above each nest box, potentially enhancing nest predation events (e.g., by raptors and arboreal mammals), as well as perceived predation risk to starling pairs across treatments; we addressed this issue in our 2022 component of this study (below).

### Sampling protocol

Starling breeding phenology has been linked, in part, to midwinter temperatures (in North America), but with mean laying date falling within early to mid April. Specifically, temperatures during midwinter can affect growth and biomass of critical prey for starlings (e.g., Tipulidae larvae; Williams et al. 2015). We opened nest boxes on 19 April 2021. We began nest box checks on 22 April and attempted checks twice weekly, yielding a 2 to 5 d interval between checks; we did not check boxes during intense rain events. Two observers inspected nest boxes each week, at approximately 0830 h and continuing through approximately 1300 h. As in our past efforts (e.g., Blackwell et al. 2018), we randomly selected the direction of nest box inspection (e.g., box 1–120 or the opposite) on the first day and alternated thereafter. The same observers (BFB, JLH, and BNB) collected data through completion of the study.

For all nest boxes, we estimated the ordinal date of first egg and recorded clutch size, number of eggs hatched, and number of young per check. Starlings generally lay 1 egg per day, begin incubation with the next-to-last or last egg laid, and incubate approximately for 12 d; young hatch



asynchronously (Feare 1984). We estimated date of first egg by subtracting the total number of eggs within a nest when first encountered from the date of the observation (Blackwell et al. 2018).

Additionally, we noted whether a nest appeared to have been abandoned, suffered nest predation, or had evidence of infanticide (e.g., eggs or young found at base of the utility pole). We suspect, however, that eggs or young dropped at the base of the pole were subject to scavenging soon after removal. We considered nest predation likely if there was evidence of destroyed eggs inside the box, nest material was disrupted, or complete clutches were missing. When eggs were encountered below the pole and prior to our observation of laying, we continued observations at the box. If eggs were discovered below the pole, but the nest remained active, though with fewer eggs, we continued observations of the nest. In other words, it was possible that intraspecific competition for a nest site (Evans 1988, Lombardo et al. 1989, Romagnano et al. 1990, Feare 1991), conspecific nest parasitism (Pinxten et al. 1991), or nest predation could have disrupted nesting before we made our observations, as well as after a clutch was initiated. We considered nests as abandoned if there was no adult activity apparent over at least 2 checks, eggs were cold (on the second check after no apparent adult activity), and the nest revealed no evidence of recent maintenance or incubation. If a nest was scored as experiencing infanticide (i.e., nest empty and some or all eggs or young found at base of the pole) or abandoned, we discontinued observations at that nest box. Finally, we considered a nest as fledged (per fully feathered young counted on the previous nest check) when the nest was empty, and no sign of nest predation was evident. We ended our observations on 15 June 2021. During Fall 2021 we removed all nest material, closed nest box entrances, and made any necessary repairs.

## Year 2

For our second year of the study, our sampling protocol followed that described above, but our first nest box check occurred on 21 April due to a snowstorm earlier in the week. In this component

of our study, we assessed the effect, if any, of the camera mount on loss of starling nests to predation. Specifically, the camera mount could have provided perching/access opportunities for raptors and arboreal mammals, possibly enhancing predation pressure. Using the same site and nest boxes as in our 2021 component, we randomly selected whether nest box 1 would maintain the camera mount or whether we would remove the equipment. We then followed systematically over the remaining 119 nest boxes with treatment assignment. This approach resulted in 60 nest boxes for which we maintained the conduit mounting pole and camera mounting board and 60 nest boxes where we removed the mounting poles and boards; we made these changes in early March 2022, prior to opening nest boxes. Further, our design distributed control and treatments equally across our study area relative to nest box entry direction and nearby vegetation. That said, the design also allowed each nest box absent the camera mount to be bounded by 2 nest boxes with the camera mount in place. We assumed, however, that nest predation attempts by raptors, if different between treatments, would be focused on those nest boxes with the camera mounts and pose negligible effects on neighboring nest boxes for which camera mounts were removed. In addition, we replaced all predator guards that were removed from utility poles for Year 1 of this study. In summary, all nest boxes were protected from predation from below and swept. No cameras were used in this component of the study. To approximate timing from the 2021 component, we opened nest boxes on 14 April 2022. We ended our observations on 28 June 2022.

## Statistical analyses

Again, our unbalanced design prevented us from assessing the potential effect of old nest material on enhanced nest predation (i.e., by mammals and birds) on nests in unprotected nest boxes, an event that could be expressed as a greater number of nest boxes showing clutch and brood loss in unprotected/unswept vs. unprotected/swept nest boxes (i.e., the omitted treatment). For other comparisons, we first examined effects across treatments. Then, to assess specific

**Table 1.** European Starling nesting metrics taken during a nest box study on the 2,200 ha National Aeronautics and Space Administration Neil Armstrong Test Facility, Erie County, Ohio, USA, during spring and summer 2021 and 2022. Nest boxes occupied were defined as containing a starling nest and  $\geq 1$  egg. All reproductive metrics are presented as the mean (SD). For Year 1 (2021), protected nest boxes included a predator guard around the utility pole below the box. Unswep nest boxes contained nest material from the previous season. An unprotected/swep treatment was not included in the design.

Metrics (Year 1)	Nest box treatments		
	Protected/swep	Protected/unswep	Unprotected/unswep
Nest boxes occupied	23	22	24
Ordinal date of first egg	125.6 (6.6)	125.0 (6.0)	126.8 (10.8)
Maximum clutch size	5.1 (6.0)	5.0 (0.7)	4.3 (1.4)
Maximum number of young	3.6 (1.8)	3.5 (2.1)	2.3 (2.3)
Hatching success	0.7 (0.3)	0.7 (0.4)	0.5 (0.5)
Fledging success	0.5 (0.4)	0.4 (0.4)	0.2 (0.4)
Nests lost to predation	1	6	12
Nests lost to infanticide	0	0	1
Nests abandoned	5	5	3
Nest boxes used by native species	10	11	7
Nest boxes unused	7	7	9

effects within the contexts of nest box protection and presence or absence of old nest material, respectively, we conducted pairwise comparisons. For pairwise comparisons associated with results from parametric models, we used *emmeans* with a Bonferroni adjustment. For all analyses we used R 4.2.1 (R Foundation for Statistical Computing, Vienna, Austria).

We first assessed the likelihood of starlings occupying a nest box (i.e., starling nest and  $\geq 1$  egg) by using a generalized linear model (GLM), binomial distribution, and logit link; treatment served as the independent effect. Similarly, we assessed the number of nests lost to nest predation and abandonment; we also examined the number of nests lost to predation relative to incubation vs. brood-rearing stages (i.e.,  $\geq 14$  d after ordinal date of first egg). Next, we examined potential differences in the ordinal date of first egg, maximum clutch size, hatching success, and fledging success via GLM, respectively, with treatment as the independent effect. However, we could not transform our response data (i.e., treatment was categorical) to meet the assumptions of normality for model residuals. Therefore, for each response variable we investigated a GLM via different distributions and links, based on diagnostic plots of the response variables. We fit a GLM via gamma distribution and inverse link to ordinal date of first

egg and maximum clutch size; however hatching and fledging success exhibited bimodal distributions for both years of the study. Again, our independent variable, treatment, was categorical. For hatching and fledging success, we used the Kruskal-Wallis rank sum test and conducted paired comparisons via the Dunn test with Bonferroni correction. We followed these same methods for our Year 2 data, except for using the Wilcoxon rank sum test for comparisons between treatments for hatching and fledging success, respectively.

## Results

### Year 1

We recorded 57.5% starling occupancy of nest boxes in Year 1 (Table 1; Table 2 holds reproductive metric findings for Year 2). In addition, 23.3% of nest boxes were used by native cavity nesters (Table 1), including Eastern Bluebird ( $n = 5$  boxes), House Wren (*Troglodytes aedon*;  $n = 5$  boxes), Tree Swallow ( $n = 14$  boxes), American red squirrel (*Tamiasciurus hudsonicus*;  $n = 1$  box), and southern flying squirrel (*Glaucomys volans*;  $n = 3$  boxes); 19.2% of nest boxes went unused (Table 1).

We observed no differences in likelihood of nest box occupancy or ordinal date of first egg relative to our protected/swep treatment (Tables 1 and 3). Our findings for likelihood of occupancy and ordinal

**Table 2.** European Starling nesting metrics taken during a nest box study on the National Aeronautics and Space Administration Neil Armstrong Test Facility, Erie County, Ohio, USA, during spring and summer 2021 and 2022. Nest boxes occupied were defined as containing a starling nest and  $\geq 1$  egg. All reproductive metrics are presented as the mean (SD). For Year 2 (2022), we investigated the potential effect of the camera mount conduit (present at all boxes during Year 1) in providing a potential perch/access for raptors and arboreal mammals, thereby possibly enhancing perceived predation risk to starlings.

Metrics (Year 2)	Nest box treatments	
	No camera mount	Camera mount present
Nest boxes occupied	33	33
Ordinal date of first egg	127 (9.3)	124 (10.7)
Maximum clutch size	4.4 (1.1)	4.4 (1.5)
Maximum number of young	3.4 (1.7)	3.2 (2.0)
Hatching success	0.7 (0.4)	0.6 (0.4)
Fledging success	0.6 (0.4)	0.6 (0.4)
Nests lost to predation	4	5
Nests lost to infanticide	0	0
Nests abandoned	5	6
Nest boxes used by native species	18	17
Nest boxes unused	9	10

date of first egg indicate, not surprisingly, given proximity in dates across treatments (Table 1), that treatment failed to explain variation beyond the null model for both response variables (Table 3).

However, maximum clutch size for unprotected/unswept nest boxes was approximately 16% smaller than other treatments (Table 1) and differed relative to nests under the protected/swept treatment (Table 3). Further, our comparison indicates that old nest material imparted no negative effect on maximum clutch size, given that the nest boxes were protected (Table 3). A pairwise comparison to examine the effect of nest box protection, given that the nest boxes contained old nest material, revealed no positive effect on maximum clutch size (Estimate:  $-0.029$ ,  $df = 66$ ,  $t$  ratio =  $-2.099$ ,  $P = 0.119$ ).

We found no difference in hatching success across treatments ( $\chi^2 = 2.877$ ,  $df = 2$ ,  $P = 0.237$ ; Table 1). However, we observed a difference across treatments in fledging success ( $\chi^2 = 6.444$ ,  $df = 2$ ,  $P = 0.0399$ ; Table 1). Specifically, we found a reduction ( $\sim 30\%$ ) in fledging success for

nests in unprotected/unswept vs. protected/swept nest boxes (protected/unswept vs. protected/swept:  $Z = 0.845$ ,  $adj P = 1.000$ ; protected/unswept vs. unprotected/unswept:  $Z = 1.613$ ,  $adj P = 0.320$ ; unprotected/unswept vs. protected/swept:  $Z = 2.496$ ,  $adj P = 0.038$ ; Table 1). Similar to our findings for maximum clutch size, we found no positive effect of nest box protection on fledging success when nest boxes contained old nest material. Further, there was no negative effect of old nest material on fledging success when nest boxes were protected.

We observed that 28.0% of nests suffered predation, with nests lost to predation increasing by 6- and 12-fold relative to protected/swept nest boxes (Table 1). We found a difference in likelihood of nests lost to predation for our unprotected/unswept relative to the protected/swept treatment (Table 3). In addition, our findings indicate that protected nest boxes were unaffected by enhanced perceived predation risk that might be due to the presence of old nest material (Table 3). Moreover, a pairwise comparison to examine the effect of the nest box protection, when boxes contained old nest material, revealed no benefit against enhanced predation (Estimate =  $-0.981$ ,  $P = 0.264$ ).

Also, we found that nest predation occurred primarily  $\geq 14$  d after the ordinal date of first egg ( $\bar{x} = 17.9$  d,  $SE = 4.2$  d, range = 7–32 d), thus during brood rearing, and represented 65% of nests lost to predation (protected/swept:  $n = 1$  nest lost, protected/unswept:  $n = 5$  nests lost, unprotected/unswept:  $n = 7$  nests lost; Table 1). Specifically, unprotected/unswept nests were depredated through incubation and brood rearing, while protected/unswept nest boxes were depredated primarily during brood rearing. Recognizing that the 1 instance of nest predation on a protected/swept nest box occurred during brood rearing and that we had unequal sample sizes across treatments for nests lost to predation during brood rearing (see above; Table 1), the likelihood of nest predation during this stage still did not differ among treatments (Table 3). As such, nest box protection did not reduce predation, when nest boxes contained old nest material, and the presence of old nest material did not enhance

**Table 3.** Results from generalized linear model analyses of the likelihood of nest box occupancy by European Starlings, potential differences in ordinal date of first egg and maximum clutch size, and likelihood of nest predation and abandonment; comparisons were made relative to a control. Likelihood values represent probabilities from estimated marginal means. The data and analyses stem from a nest box study on the National Aeronautics and Space Administration Neil Armstrong Test Facility, Erie County, Ohio, USA, during spring and summer 2021 and 2022. Nest boxes occupied were defined as containing a starling nest and  $\geq 1$  egg. For Year 1 (2021), protected nest boxes included a predator guard around the utility pole below the box. Unswep nest boxes contained nest material from the previous season. Protected/swep nest boxes served as controls. An unprotected/swep treatment was not included in the design. For Year 2 (2022), we investigated the potential effect of the camera mount conduit (present at all boxes during Year 1) in providing a potential perch/access for raptors and arboreal mammals, thereby possibly enhancing perceived predation risk to starlings. Nest boxes with a camera mount present served as controls in our analyses.

Year	Response variable	Treatment	Likelihood	Estimate (SE)	Z	t	P
1	Nest box occupancy <sup>a</sup>	Protected/swep (control)	0.575	NA	NA	NA	NA
		Protected/unswep	0.550	-0.102 (0.451)	-0.225	NA	0.822
		Unprotected/unswep	0.600	0.103 (0.454)	0.227	NA	0.820
1	Ordinal date of first egg <sup>b</sup>	Protected/unswep	NA	3.586e-05 (1.535e-04)	NA	0.234	0.816
		Unprotected/unswep	NA	-7.169e-05 (1.492e-04)	NA	0.480	0.632
1	Maximum clutch size <sup>c</sup>	Protected/unswep	NA	0.007 (0.013)	NA	0.541	0.590
		Unprotected/unswep	NA	0.036 (0.013)	NA	2.667	0.010
1	Nests lost to predation <sup>d</sup>	Protected/swep	0.044	NA	NA	NA	NA
		Protected/unswep	0.273	2.110 (1.129)	1.896	NA	0.062
		Unprotected/unswep	0.500	3.091 (1.101)	2.808	NA	0.005
1	Nests lost predation during brood stage <sup>e</sup>	Protected/swep	1.000	NA	NA	NA	NA
		Protected/unswep	0.833	-15.96 (3956.18)	-0.004	NA	0.997
		Unprotected/unswep	0.583	-17.23 (3956.18)	-0.004	NA	0.997
1	Nests lost to abandonment <sup>f</sup>	Protected/swep	0.217	NA	NA	NA	NA
		Protected/unswep	0.227	0.057 (0.717)	0.080	NA	0.936
		Unprotected/unswep	0.125	-0.665 (0.798)	-0.833	NA	0.405
2	Nest box occupancy <sup>g</sup>	Camera mount present (control)	0.550	NA	NA	NA	NA
		No camera mount	0.550	4.074e-16 (3.670e-01)	0.000	NA	1.000
2	Ordinal date of first egg <sup>h</sup>	No camera mount	NA	0.000 (0.000)	NA	-1.126	0.264
2	Maximum clutch size <sup>i</sup>	No camera mount	NA	0.002 (0.017)	NA	0.092	0.927
2	Nests lost to predation <sup>j</sup>	Camera mount present	0.152	NA	NA	NA	NA
		No camera mount	0.121	-0.258 (0.721)	-0.358	NA	0.720

Table 3. Continued.

Year	Response variable	Treatment	Likelihood	Estimate (SE)	Z	t	P
2	Nests lost to abandonment <sup>k</sup>	Camera mount present	0.182	NA	NA	NA	NA
2		No camera mount	0.152	-0.219 (0.663)	-0.330	NA	0.741

<sup>a</sup> Year 1 nest box occupancy: null deviance (intercept only) = 163.65 df on 119 df; residual deviance (model) = 163.44 on 117 df.

<sup>b</sup> Year 1 ordinal date of first egg: null deviance = 0.262 on 68 df; residual deviance = 0.260 on 66 df.

<sup>c</sup> Year 1 maximum clutch size: null deviance = 4.045 on 68 df; model residual deviance = 3.676 on 66 df.

<sup>d</sup> Year 1 nests lost to predation (65% during brood stage): null deviance = 82.216 on 68 df; residual deviance = 67.280 on 66 df.

<sup>e</sup> Year 1 nests lost to predation during brood stage (only 1 control nest lost to predation overall, and during brood rearing): null deviance = 23.699 on 18 df; residual deviance = 21.707 on 16 df.

<sup>f</sup> Year 1 nests lost to abandonment: null deviance = 66.779 on 68 df; residual deviance = 65.752 on 66 df.

<sup>g</sup> Year 2 nest box occupancy: null deviance = 165.150 on 119 df; residual deviance = 165.150 on 118 df.

<sup>h</sup> Year 2 ordinal date of first egg: null deviance = 0.411 on 65 df; model residual deviance = 0.403 on 64 df.

<sup>i</sup> Year 2 maximum clutch size: null deviance = 9.443 on 65 df; model residual deviance = 9.442 on 64 df.

<sup>j</sup> Year 2 nests lost to predation: null deviance = 52.577 on 65 df; model residual deviance = 52.448 on 64 df.

<sup>k</sup> Year 2 nests lost to abandonment: null deviance = 59.474 on 65 df; model residual deviance = 59.365 on 64 df.

nest predation, when nest boxes were protected. However, our findings relative to the effects of the presence/absence of the predator guard and old nest material are likely linked to raptor and arboreal mammal access to our nest boxes (see below).

Further, 18.8% of starling-occupied nest boxes were abandoned (Table 1). However, relative to the likelihood of abandonment for our protected/swept treatment we found no difference across treatments (Table 3). Here, treatment failed to explain variation in our response variable (nest abandonment) beyond the null model (Table 3).

In addition, our cameras recorded animal visits to the area below nest boxes, the utility pole, and nest box from 21 April to 15 June 2021; we recorded nests lost to predation between 11 May and 10 June. We obtained 785 images distributed across treatments as protected/swept (28.4%), protected/unswept (12.6%), and unprotected/unswept nest boxes (59.0%) (Table 4). Again, because we could not identify individuals, and our cameras recorded bursts of sequential images based on the set time interval, these percentages represent simple indices of species activity at our sites. Eight species of mammals and 6 species of birds (in addition to starlings) were observed on the ground near the utility pole, on the utility pole below the nest box, or on the nest box; 3 species of mammals and 3 species of birds were observed on nest boxes (Table 4). Interestingly, our camera also recorded the removal by an adult starling of a nestling approximately 9 d old and 2 d prior to our check; that nest box, a protected/swept nest box, was recorded as abandoned with young decomposing in the box.

Raccoons (*Procyon lotor*), a species active primarily during crepuscular and nocturnal hours (Sharp and Sharp 1956), were apparently deterred by the predator guard, accessing the nest box for unprotected/unswept treatments only. However, the species appeared in 51% of photographs ( $n = 399$  photographs; Table 4). The southern flying squirrel, a nocturnal species (Bendel and Gates 1987), was observed on utility poles or on nest boxes across treatments, and it was observed in 29.7% ( $n = 233$  photographs) of 785 collected images (Table 4). American red squirrels, diurnally active (Larsen and Boutin 1994), were

**Table 4.** Species, other than the European Starling, photographed at nest boxes, via Reconyx HyperFire 2 Cellular Professional cameras mounted to utility poles above nest boxes, during a starling nest box study on the National Aeronautics and Space Administration Neil Armstrong Test Facility, Erie County, Ohio, USA, during spring and summer 2021. Protected nest box treatments included a predator guard around the utility pole below the box. Unswept nest boxes contained nest material from the previous season. An unprotected/swept treatment was not included in the design. Photographs were categorized relative to the species on the ground near the utility pole, on the pole, or on the nest box. Species noted by an asterisk (\*) were observed at nest boxes that suffered nest loss to predation (not necessarily by the species photographed).

Treatment ( <i>n</i> images)	Location and species <sup>a</sup> observed		
	Ground	Pole	Nest box
Protected/swept (223)	Turkey Vulture	Northern Flicker Red-bellied Woodpecker	Northern Flicker Red-tailed Hawk
	Domestic cat	Southern flying squirrel	Southern flying squirrel
	Opossum	American red squirrel	American red squirrel
	Raccoon*		
Protected/unswept (99)		Northern Flicker Red-bellied Woodpecker	Red-tailed Hawk*
	Domestic cat*	Southern flying squirrel*	Southern flying squirrel*
	Southern flying squirrel	Raccoon*	
	Raccoon*		
	Striped skunk		
Unprotected/unswept (463)	Sharp-shinned Hawk*	Northern Flicker	American Kestrel*
	Turkey Vulture	Red-bellied Woodpecker*	
	Fox squirrel	Fox squirrel	Southern flying squirrel
	Opossum*	Southern flying squirrel	Raccoon
	Raccoon*	American red squirrel	American red squirrel
	Striped skunk	Raccoon	
	White-tailed deer		

<sup>a</sup> American Kestrel (*Falco sparverius*), Northern Flicker (*Colaptes auratus*), Red-bellied Woodpecker (*Melanerpes carolinus*), Red-tailed Hawk (*Buteo jamaicensis*), Sharp-shinned Hawk (*Accipiter striatus*), Turkey Vulture (*Cathartes aura*), American red squirrel (*Tamiasciurus hudsonicus*), domestic cat (*Felis domesticus*), fox squirrel (*Sciurus niger*), opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), southern flying squirrel (*Glaucomys volans*), striped skunk (*Mephitis mephitis*), white-tailed deer (*Odocoileus virginianus*).

photographed on poles or nest boxes for protected/swept and protected/unswept treatments and present in 11.8% ( $n = 93$  photographs) of our images (Table 4). For raccoons and southern flying squirrels, 77% of these images were obtained between 2100 h and 0600 h, thus encompassing primarily crepuscular and nocturnal periods. The remaining 11 species (Table 4) appeared in <3% of photographs, respectively.

We also witnessed nest predation events. We observed a raccoon below a box entrance and the leg of a nestling, approximately 10 d of age, hanging outside the box; the brood was lost to predation. At another nest box we observed a southern flying squirrel exiting a box with a nestling starling approximately 9 d of age (Figure 2); that nest failed because of predation. Also, 1 adult starling was photographed taken in the talons of

a Sharp-shinned Hawk (*Accipiter striatus*) on the ground near a utility pole hosting a nest box. However, the starling nest in that box had suffered a loss to predation, likely by a southern flying squirrel, approximately 20 d earlier.

In addition, we observed a Red-tailed Hawk (*Buteo jamaicensis*) with a talon inserted into the opening of a protected/swept nest box (just prior to the clutch hatching); we estimate that this nest fledged 2 young. At the adjacent nest box, a protected/unswept site, we observed a similar attempt (Figure 3); this nest was lost to predation, with young between 10 and 13 d old.

## Year 2

In Year 2, we recorded 55.0% starling occupancy (Table 2). Also, 29.2% of nest boxes were used by native cavity nesters (Table 2), including Eastern



**Figure 2.** Southern flying squirrel exiting a nest box with a European Starling nestling approximately 9 d old. The image was taken via Reconyx HyperFire 2 Cellular Professional camera mounted to the utility pole above the nest box, during a starling nest box study on the National Aeronautics and Space Administration Neil Armstrong Test Facility, Erie County, Ohio, USA, during spring and summer 2021.

Bluebird ( $n = 7$  boxes), House Wren ( $n = 8$  boxes), Tree Swallow ( $n = 18$  boxes), American red squirrel ( $n = 1$  box), and southern flying squirrel ( $n = 1$  box); 15.8% of nest boxes went unused (Table 2).

We observed no differences in likelihood of nest box occupancy or in ordinal date of first egg relative to our treatment involving the camera mount present (Tables 2 and 3). Further we found no difference between treatments in maximum clutch size (Table 3), hatching success ( $W = 481$ ,  $P = 0.404$ ), or fledging success ( $W = 507.5$ ,  $P = 0.622$ ; Table 2). For each of the responses in our GLMs, treatment added little to no explanation of variance relative to our null model (Table 3).

We also observed that 13.6% of starling nests suffered predation and 16.7% of nests were abandoned (Table 2). However, we saw no difference in likelihood of nest loss to predation or abandonment between treatments (Table 3). For both metrics, our model added little to explaining variance in the response metrics beyond that of the null (Table 3).

## Discussion

Nest predation risk and cavity quality (including presence of old nest material) are not necessarily independent (Wesolowski 2002, Wiebe et al. 2020). Also, the effects of perceived predation risk are dependent upon context and experience (Curio 1988, Lima 2009; see also references, above), and likely expressed differentially relative to specific reproductive metrics (Lima 2009). In our study (Year 1), our comparisons across treatments, intended to elevate perceived nest-predation risk, revealed negligible difference in likelihood of nest box occupancy, ordinal date of first egg, or hatching success. We found that maximum clutch size was smaller and fledging success was less for nests in unprotected/unswept nest boxes, and that predation losses were greater for this treatment than for protected/swept nest boxes. Nest abandonment did not differ across treatments.

In addition, nest box protection appeared to impart little positive effect to maximum clutch size or fledging success, but conditional upon nest boxes containing old nest material. We also found



**Figure 3.** Red-tailed Hawk attempting to depredate a nest box with European Starling young, approximately 9–13 d old. The image was taken via Reconyx HyperFire 2 Cellular Professional camera mounted to the utility pole above the nest box, during a starling nest box study on the National Aeronautics and Space Administration Neil Armstrong Test Facility, Erie County, Ohio, USA, conducted in Spring and summer 2021.

that, during brood rearing, nest box protection did not reduce predation, but, again, only when nest boxes contained old nest material. Further, the presence of old nest material posed little to no negative effect on reproductive metrics, given that nest boxes were protected. We contend, however, that these findings reflect the confounding effects of predator access to nest boxes from above; again, this is an issue that is not easily controlled. Notably, our Year 2 results revealed no effect of our camera mount in enhancing nest predation, a scenario that could have imparted bias to our interpretation of predation effects observed during Year 1.

Also important to our findings is the fact that predation events might not result in immediate nest loss and, if partial predation goes undetected, estimates of reproductive parameters can be affected. For example, we note that our calculation of hatching success, unaffected by treatment, was based on maximum clutch size; we found a smaller maximum clutch size at unprotected/unswept nest boxes. However, egg loss could

have occurred prior to our accounting for a full clutch or clutch size might have been adjusted relative to perceived nest predation risk (Lima 1987, 2009; Martin and Li 1992). In other words, an underestimation of maximum clutch size could impart a positive bias to estimates of hatching success in depredated nests. Similarly, an adjusted (i.e., reduced) clutch size might also improve estimated hatching success in these same nests. Both scenarios, therefore, could favor hatching success on par with that observed for our protected/swept treatment.

In addition, we calculated fledging success based on the maximum number of young. As noted, we observed that unprotected/unswept nest boxes fledged fewer young. Loss of young to potential, periodic predation is consistent with our findings for this metric.

Further, we observed a progressive increase in nests lost to predation relative to protective status, with our unprotected/unswept nest boxes, not surprisingly, realizing more nest losses to predation than those under the protected/swept treatment. Timing of nest losses to predators also varied.



Nest predation at unprotected/unswept nest boxes occurred across the reproductive period, whereas nests in protected/unswept nest boxes were lost to predation primarily during brood rearing; only 1 protected/swept nest box experienced nest predation.

More frequent visits by the breeding pair during nest construction (Mazgajski 2013) might alert predators (e.g., via activity of pairs dealing with nest boxes containing old nest material), and nest predation attempts could be chronic thereafter (Fontaine and Martin 2006b, Fontaine et al. 2007). However, the brood-rearing stage also necessitates more adult visits to the nest box to provision young (Kessel 1957), might draw increased visits by conspecifics (Schuett et al. 2017), and is characterized by increased noise from the brood over time, all factors that can draw the attention of predators (Lima 2009).

Given that we found no difference across treatments in likelihood of nest abandonment, one can assume, then, no differential adult loss to predation, a factor that can lead to clutch or brood abandonment by the surviving adult (typically if the survivor is the male starling; Kessel 1957). If the male of the pair is lost and replaced, one would not necessarily expect abandonment, but infanticide (i.e., destruction of the entire clutch or brood; Smith et al. 1996). We found only a single instance of possible infanticide, with 3 of 4 eggs, approximately 11 d old, located at the base of the utility pole. Further, along with our findings of no difference among treatments in ordinal date of first egg, our findings on nest abandonment could imply that nesting experience or adult quality (Komdeur et al. 2005) was distributed well among our 3 treatments.

Regarding predator identification and tactics to access our nest boxes, the raccoon, southern flying squirrel, and Red-tailed Hawk were the only species that we observed actively depredate a nest box (see also red squirrel predation of open nests in Martin 1988). Blackwell et al. (2018) noted prior starling research on ATF that was disrupted by raccoon nest predation because of lack of predator guards positioned on utility poles below the nest boxes. As noted above, our photographs revealed raccoons below and on utility poles, as well as on nest boxes. We also saw

what appeared to be active raccoon depredate of a nest.

The southern flying squirrel, a species photographed exiting a nest box with a nestling, can access our nest boxes (protected or unprotected) when the utility lines (serving as a pathway to a utility pole) and poles are within gliding distance from timber that exceeds either the nest box or line height. For example, the similar-sized northern flying squirrel (*G. sabrinus*) can achieve approximately 16.6 m of horizontal glide distance from a 9.8 m height (Vernes 2001; see also Bishop 2006 for arena-based, experiment evidence for horizontal glide distance by southern flying squirrels).

Our series of images showing a Red-tailed Hawk extending a talon into the entry hole of at least 2 nest boxes was, admittedly, most surprising. However, this species has been observed to flush gray squirrels (*S. carolinensis*) from dreys, pursue them along tree limbs, and then perch above cavities used as shelter by the squirrel and continue the predation effort (Tumlinson 2012).

In summary, we found no difference in starling occupancy of nest boxes across treatments, however implications for perceived risk relative to our treatments are unclear. Specifically, enhanced predation risk achieved by our removal of predator guards from below the nest box, allowing access by terrestrial predators, and perceived risk associated with the presence of old nest material, were likely confounded by predation from above the nest box involving raptors and squirrels. Based on frequency of appearances in our image database, the raccoon and southern flying squirrel were predominant predation threats.

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