European starling use of nest boxes relative to human disturbance

- BRADLEY F. BLACKWELL, U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 6100 Columbus Avenue, Sandusky, OH 44870, USA bradley.f.blackwell@usda.gov
- BRUCE N. BUCKINGHAM, U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 6100 Columbus Avenue, Sandusky, OH 44870. USA
- MORGAN B. PFEIFFER, U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 6100 Columbus Avenue, Sandusky OH 44870, USA

Abstract: European starling (Sturnus vulgaris; starling) nesting poses debris hazards within airport hangars and to engine and flight surfaces of moored aircraft. We questioned whether consistent removal of nest material would negatively affect use of a nest site, measured by a reduction in material accumulation. We conducted our study on a 2,200-ha site in Erie County, Ohio, USA (41° 22' N, 82° 41' W), from April 15 through June 2, 2020. We used 120 wooden nest boxes on utility poles, protected by an aluminum predator guard below the box. Our treatments included (1) twice weekly, repeated nest material removal (RMR; n = 40 nest boxes); (2) complete nest removal, but only after nest construction and ≥ 1 starling egg was laid (CNR; n = 40 nest boxes); and (3) a control; n = 40 nest boxes; N = 120 nest boxes). Starlings deposited approximately 50% greater mass of nest material and eggs at RMR than CNR nest boxes, indicating that consistent disturbance failed to dissuade use. Predator guard protection of nest boxes at our site reduced nest predation of starlings; the current starling population is likely adapted to selecting these sites. Similar selection toward low nest-predation risk associated with anthropogenic structures and moored aircraft is also possible. Aside from covering moored aircraft and closing hangar doors, actions not necessarily feasible, removal of starling nesting material more than twice weekly would be necessary to maintain minimum control over material deposition that could affect aircraft function and safety.

Key words: airport hangars, European starling, invasive species, nest disturbance, nest predation risk, nest site selection, Ohio, secondary cavity nester, Sturnus vulgaris

WILDLIFE SPECIES ARE continuously confronted with varying levels of perceived and actual predation risk to which they must adapt or succumb (Laundré et al. 2010). Nest predation, in birds for example, acts as a significant selective force because of its effects on reproduction, influencing nest types and concealment, mating behaviors, and reproductive behavior, and physiology (Ricklefs 1969, 1977; Slagsvold 1982; Lima 1987; Martin 1988, 1993, 1995; Bradley and Marzluff 2003; Lima 2009; Martin and Briskie 2009). However, perception of nest predation risk varies relative to open-cup, primary-, and secondary-cavity nesters (Nice 1957; Nilsson 1984; Martin 1993, 1995); cavity-nesting species generally experience lower nest predation (Nice 1957, Martin 1993, Fontaine et al. 2007, Mouton and Martin 2018).

or otherwise) is influenced by direct experience (Griffin et al. 2001, Brown et al. 2013, Bogrand et al. 2017, Bleicher et al. 2018), chronology or frequency of predation (Lima and Dill 1990; Lima 1998a, b), and observing predation attempts on conspecifics or neighbor nests (Marzluff 1985; Lima and Dill 1990; Lima 1998a, b; Lima 2009; Creel et al. 2017). Manipulation of perceived risk of nest predation by birds has shown both behavioral (i.e., nest site selection, timing of nesting, nest abandonment, changes in provisioning) and physiological responses within a breeding season (i.e., reproductive output, such as clutch size and offspring produced; Fisher and Wiebe 2006, Mönkkönen et al. 2009, Zanette et al. 2011, Amo et al. 2017). Assessments of responses by cavity-nesting bird species to manipulation of perceived nest pre-Also, perceived risk of predation (at the nest dation risk, particularly direct predation (i.e.,

presence of an actual predator or model effecting perception of immediate lethality) prior to reproduction, are few and have varied relative to target bird species, predator model, position, timing of exposure, and behavioral metrics (e.g., enhanced vigilance, site abandonment; Fisher and Wiebe 2006, Parejo and Avilés 2011, Stanback et al. 2018, Blackwell et al. 2021).

We contend that a focus on pre-reproductive enhancement of nest predation risk holds promise in refining means (i.e., integration of methods; Conover 2002, Blackwell et al. 2016) to control invasive bird species. For example, efforts to control nesting by the European starling (Sturnus vulgaris; starling) are numerous (Seamans et al. 2015), but only recently has research focused on possible means to exploit antipredator response during nest-site selection (Blackwell et al. 2018, 2020, 2021). Since 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). The starling has been considered a competitive threat to indigenous cavity-nesting birds (Kalmbach and Gabrielson 1921; Brush 1983; Kerpez and Smith 1990; Cabe 1993; Ingold 1994 [but see Koenig 2003, Koenig et al. 2017]; Cabe 2020). Further, the species is a recognized pest relative to interactions with humans (Feare 1984, Pimentel et al. 2000, Linz et al. 2007, Lewis and Conover 2018), particularly its threat to food (Linz et al. 2007, Homan et al. 2017) and aviation safety (DeVault et al. 2011, 2018; Psiropoulos and Selner 2019; Dolbeer et al. 2021).

Our recent research focusing on enhancing perceived nest predation risk (i.e., indirect and direct predator cues), has failed to deter starling nesting (Blackwell et al. 2018, 2020, 2021). However, there is ample evidence that anthropogenic disturbance (Mouillot et al. 2013) can affect both selection of breeding territory and site in open-cup and cavity-nesting species (Remacha and Delgado 2009, Bötsch et al. 2017), but variably given tolerance of the species to human activity (Remacha and Delgado 2009). Still, even human-tolerant, secondary-cavity nesters can experience reduced reproductive success from disturbance (Strasser and Heath 2013). Further, capture and handling of adult starlings from nest boxes by researchers, and followed by release, can stimulate nest abandonment during incubation and brooding stages (Royall 1966), presumably because of perceived risk. In other words, why would starlings fail to maintain incubation or the brood unless the risk perceived warranted selection of an alternative site or forgoing breeding? Importantly, studies involving direct disturbance of starling nesting by humans acting as predators with the intent of inducing site abandonment are rare (Heusmann and Bellville 1978); we know of no work reporting starling nesting metrics relative to consistent efforts at nest material removal.

Our purpose was to assess continued use of a nest site within a breeding season by starlings (not necessarily the same pair of birds) relative to consistent efforts to prevent nest establishment, and whether concerted disturbance would limit build-up of material that can pose hazards to aviation safety via foreign object debris in hangars, aircraft engines, and flight surfaces (Bridgman 1962, Jackson 2000, Psiropoulos and Selner 2019). Hangars, ideally, and moored aircraft, especially, should be routinely inspected for potential foreign object debris sources, but frequency and thoroughness vary (Psiropoulos and Selner 2019). Further, the presence of nesting starlings on an airport likely increases the risk of bird-aircraft collisions, as nesting starlings will forage within 100 m of their nests (Heldbjerg et al. 2017).

We hypothesized that consistent efforts to prevent nest establishment, via material removal, would reduce site use by inducing abandonment of the nest box by affected pairs due to direct disturbance, but also negatively affect usurping of the site by other starlings due to observing our "predation" at the site and neighbor nest boxes (Marzluff 1985; Lima and Dill 1990; Lima 1998*a*, *b*; Lima 2009; Creel et al. 2017). As such, we predicted that our consistent disturbance would result in less material deposited in nest boxes over the course of the experiment. Alternatively, the starling population could show persistence in selection of a nest box, despite frequent disturbance. Specifically, prey likely require a high degree of certainty about their environment and risks to effectively allocate activities (Luttbeg 2017, Stanback et al.

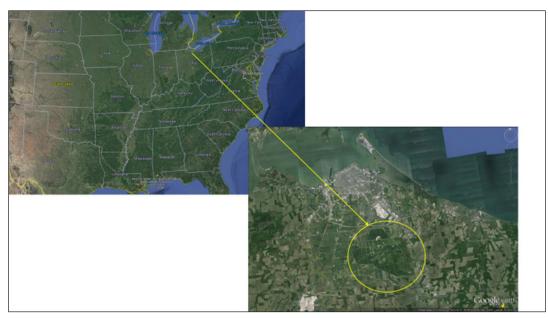


Figure 1. Google Earth Pro 2021 image of the mid-continental and Atlantic coast of the United States with the northcentral Ohio study site shown. The study site was located on the 2,200-ha National Aeronautics and Space Administration Neil Armstrong Test Facility (formerly the Plum Brook Station), Erie County, Ohio, USA (41° 22' N, 82° 41' W), depicted within the circled area. The study site, including 120 nest boxes, was used to evaluate European starling (*Sturnus vulgaris*) response to human disturbance at nest sites during spring and summer 2020.

2018, Meuthen et al. 2019), including shifting to alternative nest sites (Stanback et al. 2018). Importantly, we did not color mark starling pairs; thus, our hypothesis and predictions refer to use of nest boxes on our site by the local starling population.

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; Figure 1), Erie County, Ohio, USA (41° 22' N, 82° 41' W) during spring and summer 2020. The ATF comprises a mix of old field, 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, DeVault et al. 2014). For the month preceding our opening of nest boxes and approximately 1 month thereafter (March through May 2020), the U.S. National Weather Service reported average (SD) temperatures of 9.8 (13.7) °C, as well as 13.6 (4.0) cm of rain and 4.7 (4.7) cm of snow (https://www.weather.gov/ wrh/climate?wfo=cle).

Methods Experimental design

Like Blackwell et al. (2018, 2020, 2021), we used 120 wooden nest boxes (length, depth, width: 28 x 13 x 17 cm with 5.1-cm-diameter entrances) attached to utility poles approximately 2.5-3.0 m above the ground, depending upon slope, and protected with an aluminum predator guard below the box (Figure 2); each box is approximately 60 m (range: between ~50 m and 80 m) from the nearest box. Our study was constrained to no more than 120 boxes from a logistics perspective, which included site availability and personnel. Like previous, similar studies on ATF, these nest boxes had a removable roof for efficient nest checks (Blackwell et al. 2018). Because of pole availability and location, not all boxes faced the same direction. However, previous research has not reported effects of cavity entry orientation on use of boxes (Seamans et al. 2015). Further, we numbered each box sequentially, following road sections of neighbor boxes, up to 120. Our treatment order was randomly assigned over the first 3 nest boxes and continued systematically thereafter over triplets of boxes and through box 120. Thus, nest



Figure 2. Image of a wooden nest box and predator guard below box, 1 of 120 nest boxes located on the 2,200-ha National Aeronautics and Space Administration Neil Armstrong Test Facility (formerly the Plum Brook Station), Erie County, Ohio, USA (41° 22' N, 82° 41' W). These boxes were used to evaluate European starling (*Sturmus vulgaris*) response to human disturbance at nest sites during spring and summer 2020. This image was published originally in Blackwell et al. (2018).

box triplets were distributed spatially across our study area and, subsequently, evenly regarding entrance orientation.

Also, starlings in northern Ohio have been found to overwinter (B. F. Blackwell, B. N. Buckingham, and M. B. Pfeiffer, U.S. Department of Agriculture [USDA], personal observations; see also Kessel 1953), and 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). During Fall 2019, all remnant nest material in nest boxes was removed and all entrances were closed. Though not quantified, anecdotal evidence of starlings visiting closed next boxes during late winter and early spring (B. F. Blackwell, B. N. Buckingham, and M. B. Pfeiffer, USDA, personal observations) indicates sustained interest in our sites.

Our treatments were intended to represent a consistent, twice weekly disturbance of nesting as well as a periodic disturbance more representative of encountering a nest or material within a hangar or within components of a moored aircraft. As such, the treatments comprised (1) repeated, nest material removal, which occurred upon each check and included any starling eggs deposited between checks (RMR; n = 40 nest boxes); (2) complete nest removal, which involved removal of the completed nest structure and eggs, but only after ≥ 1 egg was laid (CNR; n = 40 nest boxes); and (3) a control (no treatments other than nest checks for data collection; n = 40 nest boxes). No eggs of indigenous species were removed.

To be clear, we could not check nest boxes frequently enough to thwart all egg laying at RMR nest boxes. As such, we anticipated the possibility of removing complete nests and eggs from RMR sites. The distinction between RMR and CNR treatments, therefore, relates to the point in the nesting process when disruption of nesting was likely to occur (e.g., nest construction at RMR sites), but also the frequency of disturbance thereafter. In our most recent study (Blackwell et al. 2021), we found on average 10 days between observation of the first nesting material and first egg. Such timing would allow 4 instances (i.e., spanning 14 days by our protocol) of material removal at an RMR site prior to treatment at a CNR nest box.

Also, starling breeding phenology has been linked, in part, to mid-winter temperatures (in North America), but with mean laying date falling within early to mid-April (Williams et al. 2015). We opened nest boxes on April 15.

We inspected each box twice weekly, beginning on April 21. Two observers inspected nest boxes each week at approximately 0800 hours and continuing through approximately 1300 hours. We randomly selected the direction of nest box inspection (e.g., box 1 to 120 or the opposite) on the first day and alternated thereafter. The same observers collected data through completion of the study. We recorded the approximate ordinal date of first nest material (which could be due to starling or, possibly, Eastern bluebird [*Sialia sialis*] activity), appearance of the first nest bowl (Blackwell et al. 2018), and first egg.

The pace of starling nest construction varies by pair, and we had no *a priori* date by which we expected nest bowl formation. Also, starlings generally lay 1 egg per day, begin incubation with the next-to-last or last egg laid, and incubate for approximately 12 days; 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 CNR (i.e., prior to nest removal) or control nest appeared to have been abandoned, suffered predation, or had evidence of infanticide (e.g., eggs or, for control nest boxes, young found at base of the utility pole). We considered nests as abandoned if there was no adult activity apparent over at least 2 checks, eggs were cold, and the nest revealed no evidence of recent maintenance or incubation. Given that we removed all material and any starling eggs from RMR sites upon each check, we could not assess site abandonment by an affected pair.

We considered predation likely if there was evidence of destroyed eggs inside the box, nest material was disrupted, or complete clutches were missing (i.e., control nests only). When eggs were encountered below the pole and prior to our observation of laying (CNR and control nests), 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) or predation could have disrupted nesting before we made our observations as well as after a clutch was initiated. We considered abandonment or predation at CNR nest boxes as potential, indirect effects of our treatment and, therefore, continued our treatments and observations. However, if a control nest suffered abandonment, predation, or infanticide, we ended observations at that nest box.

We quantified the mass of material (i.e., with any starling eggs) collected per nest box at RMR nest boxes upon each check, or upon finding \geq 1 egg at CNR nest boxes, via known-weight plastic bag and Pesola spring scale. We did not weigh individual eggs or the clutch (starling egg mass in the first clutch has been reported to be approximately 7.2 g/egg; Ricklefs 1984). At CNR nest boxes, nests of indigenous cavity-nesting species (identified after an egg was laid) were not removed, and the nest box

was removed from the study. Further, if an indigenous species constructed a nest at any nest box and deposited ≥ 1 egg, or the box was occupied by a mammal (Rodentia), between our site checks, that nest box was removed from the study. We concluded our observations for the experiment with the hatching of the last 2 control nests for which the first clutch was deposited during May.

Statistical analyses

As noted above, we were constrained to 120 nest boxes, but we questioned whether our sample of 40 boxes per treatment would allow us to detect at least a moderate management effect, considering that not all boxes are typically occupied by starlings (Blackwell et al. 2018). Specifically, we were interested in more than discerning a possible statistical effect of our treatments, but whether the observed effects were biologically meaningful to the management of starling nesting, particularly regarding nest material accumulation. Therefore, we conducted a priori sample size estimation and power analyses, based on previous starling research at ATF (Appendix 1). Given our previous research and assumptions regarding a management effect size (Cohen 1988, Nakagawa and Cuthill 2007, Lakens 2022), we considered that our sample of 40 boxes available per treatment, assuming minimum starling occupancy ≥57.5%, would allow us to discern at least a modest effect (per Cohen 1988) of treatment (Appendix 1).

To index possible unmeasured site differences that could affect starling nesting, we compared the likelihood of starling occupancy of a nest box between CNR and control nest boxes via generalized linear model, binomial distribution, and logit link (Proc Genmod, SAS 9.2). To assess the effects of our nest disturbance treatments, we calculated effect sizes (Cohen 1988, and as indicated above) for treatment pairs and relative to a priori, assumed magnitude of effects (i.e., a reasonable management effect) of our RMR treatment on mean ordinal date of first nest bowl formation (i.e., RMR vs. CNR; RMR vs. control; CNR vs. control) and first egg (RMR vs. control only), and mean (across nest boxes within treatment) total mass of material removed (RMR vs. CNR, only). We used Cohen's d (where d = 0.50 is considered

Table 1. Nesting data for 120 wooden nest boxes attached to utility poles and located on the
National Aeronautics and Space Administration Neil Armstrong Test Facility, Erie County, Ohio,
USA, and intended for human disturbance treatments against European starlings (<i>Sturnus vulgaris</i>)
during April through early June 2020. Treatments comprised control or no disturbance, other than
nest checks; CNR, entailing complete nest removal after appearance of an egg; and RMR, involving
repeated removal of nest material upon each check to the nest box.

Treatment	Empty nest boxes	Nest boxes occupied by indigenous species ^a	Nest boxes with nest bowl ^b	Ordinal date nest bowl (SD) ^b	Starling occupied (>1 egg) nest boxes ^c	Ordinal date first egg (SD) ^c
Control	4	2	36	118.0 (6.0)	34	120.7 (6.2)
CNR	6	1	38	118.2 (9.0)	31	119.8 (9.2)
RMR	5	2	36	118.7 (8.8)	33	124.7 (8.4)

^aControl: northern flying squirrel (*Glaucomys volans*), 1 nest box; Eastern bluebird (*Sialia sialis*), 1 nest box; CNR: northern flying squirrel, but also observations of a red squirrel (*Tamiasciurus hudsonicus*), 1 nest box; RMR: tree swallow (*Tachycineta bicolor*), 2 nest boxes.

^bEvidence of a completed nest structure.

^cMetric affected by removal of CNR nests from study due to error in treatment application (2 nests removed for starling-occupied nest boxes and ordinal date of first egg, n = 31 nests; 3 nests removed for maximum clutch size, n = 30 nests).

as a medium effect size, and values >0.50 indicate a larger effect; Cohen 1988, Nakagawa and Cuthill 2007, Lakens 2022). Cohen's (1988) formula is expressed as a ratio of the difference between 2 means (i.e., a comparison mean that might be derived from related research and a mean representing the desired management effect) to the pooled sample standard deviation.

Although we had no data to reference for starling nest material from similar prior studies, we anticipated the magnitude of treatment effects would be expressed as at least a 7-day delay in the mean ordinal date of formation of the first nest bowl at RMR nest boxes, as well as a 7-day delay in mean ordinal date of first egg. Also, we anticipated a 50% reduction in mean total weight of nest material at RMR versus CNR nest boxes (i.e., per our primary prediction).

Our methods (Protocol QA-3190) were reviewed and approved by the U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center Institutional Animal Care and Use Committee. Other than starling eggs, no animals were injured or killed during our study.

Results

We monitored boxes twice weekly from April 21 through June 2, 2020, following all control nests through hatching or nest termination due to clutch loss or abandonment. Because we assumed that our treatments would also affect nesting at control nest boxes (e.g., egg dumping; Evans 1988, Power et al. 1989, Stouffer and Power 1991, Blackwell et al. 2020), we ceased treatments at RMR and CNR nest boxes by May 26, when only 2 control nests remained for monitoring of hatching success (recorded on June 2). We found that 91% of nest boxes (n =109) had some nest material deposited by April 21, only 6 days after opening the boxes (control: 37 nest boxes; CNR: 37 nest boxes; RMR: 35 nest boxes). Starlings eventually occupied 100 nest boxes (83%) over the period of the study (Table 1). Only 5 nest boxes (4.2%) were used by indigenous species, and we omitted 3 nest boxes under the CNR due to error in treatment application in the field (Table 1); 15 nest boxes were not used for nesting by any species (Table 1). Additionally, 8 nests in control boxes were likely depredated (disappearance of entire clutch = 7 nests; disappearance of hatchling = 1 nest), while no abandonments or instances of infanticide were noted. We found no evidence of predation for CNR nests.

Relative to our *a priori* planning concerning necessary sample size and power (Appendix 1), our sample size of occupied boxes per treatment exceeded findings reported by Blackwell et al. (2021; Table 1). Further, our observed variability in ordinal date of first egg for RMR nests (the metric used in our sample size estimation; Appendix 1) was 44% lower than our assumption of twice the variability reported by Blackwell et al. (2020) or SD = 15.0 days (Table 1). As a result, we realized Power ≈ 0.97 to detect a management effect of the RMR treatment on ordinal date of first egg (G*Power, https://www.psychologie.hhu. de/arbeitsgruppen/allgemeine-psychologie-und-arbeitspsychologie/gpower.html).

Regarding potential unmeasured site differences, we found no difference between control and CNR nest boxes relative to the likelihood of starling occupancy (Table 1; control, likelihood = 1; CNR, likelihood = 0.94; treatment effect: df = 1, χ^2 = 2.9, *P* = 0.09). We note that our removal of CNR nests from the study (noted earlier relative to treatment error in the field), affected our metric for ordinal date of first egg (2 nests removed from study; Table 1), contributing to the absolute difference (6%) in likelihood.

Contrary to our prediction, our effect sizes, *d*, across treatments for ordinal date of first nest bowl (Table 1) were <0.1, thus indicating no management effect (Cohen 1988) of the RMR treatment on rate of construction of the nest. Further, at RMR nest boxes, we found on average 37 boxes per check (SE = 1.8 boxes; n = 10 checks) that contained some amount of nest material.

We encountered our first starling-occupied (i.e., completed nest and ≥ 1 egg) nest box, an RMR treatment, on the first check, 6 days after opening next boxes. However, after our fourth next box check (April 30), we had removed 17 starling nests with eggs. Despite our consistent, repeated removal of nest material at RMR next boxes, we found on average 8.4 starling-occupied nest boxes (with $\geq 1 \text{ egg}$) per check (SD = 8.4 nests; maximum for any single check = 23 nests; n = 10 checks; Table 1). At control nest boxes, we found an average 20.7 starling-occupied nest boxes per check (SD = 14.6 nests; maximum for any single check = 33 nests; n = 10 checks; Table 1). Also, we found approximately a 4-day delay in date of first egg at RMR versus control nest boxes (Table 1), yielding an effect size d = 0.54. In other words, our treatment at RMR sites had only a modest effect on date of first egg, but less than our predicted management effect.

Further, within the group of RMR nest boxes that had been noted as starling-occupied at any point during the experiment, we recorded on average 2.8 starling nesting attempts (SD = 1.4 nesting attempts) per nest box; as noted above, we could not discern pair-specific attempts. We removed on average 53.4 g (SE = 29.9 g) of nest material and eggs per nest box/check at RMR nest boxes. We removed on average 530.12 g of nest material and eggs per box (SD = 308.20 g), and a cumulative total of 19,117 g of nest material and eggs during the study, across 40 RMR nest boxes.

At CNR nest boxes, we removed 33 starling nests as of April 30 (approximately 50% more nests than at RMR nest boxes). Further, we found on average 11.0 starling-occupied nest boxes per check (SD = 6.9 nests; n = 10 checks). Within starling-occupied CNR nest boxes, we recorded on average 3.9 starling nesting attempts (SD = 1.9 nesting attempts) per nest box.

We removed on average 105.2 g (SE = 26.6 g) of nest material and eggs per nest box/check. Also, we removed on average 420.20 g of nest material and eggs per nest box (SD = 210.7 g), and a total of 12,730 g of nest material and eggs during the study, across 31 CNR nest boxes (i.e., RMR nest boxes realized approximately 50% more material than CNR nest boxes). Given these findings, our effect size (Cohen's *d* = 0.41) indicated no management effect of the RMR treatment on diminishing nest material deposition relative to CNR nest boxes, where starlings could complete nest construction and lay \geq 1 egg undisturbed. We observed no abandonment of CNR nest boxes.

Discussion

Removal of starling nests and nest material can, over years, diminish starling use of artificial cavities, but use will vary with starling population density (Heusmann and Bellville 1978). Ours is the first study, however, to assess a starling population's use and occupancy of nest boxes relative to consistent removal of nest material, within a breeding season.

Importantly, we found no indications of unmeasured site differences that could have affected starling use of our nest boxes. Although our RMR treatment necessarily excluded those nest boxes from assessment of likelihood of occupancy, we found relatively equal likelihoods of starling occupancy of CNR and control nest boxes. Further, there was no difference in the ordinal date of first egg between CNR and control nest boxes.

In contrast to expectations, we found that disturbance of nesting efforts involving repeated nest material removal, which occurred upon each check and included any eggs deposited between checks (RMR nest boxes), had no detectable management effect on deposition of nest material in nest boxes. Although multiple species can deposit or remove nest material during and after construction of a nest, starlings were likely the major contributors of nest material at our first detection. Again, individuals will overwinter in northern Ohio, the species is an early nester, and it is generally dominant to indigenous cavity-nesting species in competition for nest sites (Koch et al. 2012), except for mammals that roost and nest in cavities (e.g., southern flying squirrel [Glaucomys Volans]; Linz et al. 2007; Table 1) and American kestrels [Falco sparverius]; McClure et al. 2017). Starlings eventually deposited approximately 50% more nest material at RMR nest boxes than CNR nest boxes.

Certainly, a limited availability of natural cavities could result in focused attention by starlings on nest boxes and despite our disturbance. However, findings by Pfeiffer et al. (2019) relative to availability of natural cavities on ATF do not support this hypothesis. Further, we found that approximately 13% of our boxes (across control and CNR nest boxes; Table 1) went unused. Our findings of a lack of management effect on nest material deposition at RMR versus CNR nest boxes suggest a tendency by individuals in the ATF starling population toward selection for nest boxes within a breeding season, despite disturbance, whether by the same or different pair. We note, too, that RMR sites showed only a modest negative effect of treatment on ordinal date of first egg relative to control nest boxes.

Still, continued starling nesting attempts at RMR nest boxes (both suspected and confirmed, when eggs were found) were somewhat unexpected. We repeatedly removed nest material and partial and near-complete clutches (up to 5 eggs) twice weekly at RMR nest boxes, and we found that on average 20% of RMR nest boxes were occupied (i.e., nest structure and ≥ 1 egg) upon each check. Again, absent marked birds, we could not determine whether eggs laid in RMR or CNR boxes were deposited by females that had initially nested (including females attempting to complete clutches in RMR nest boxes), competing females, or brood parasites.

Further, this consistent use of nest boxes on ATF by starlings, despite disturbance, is particularly notable from an antipredator behavior perspective. Relative predation risk at natural sites and selection for individuals that prefer nest boxes are not mutually exclusive. For example, Stanback et al. (2018) suggested that remaining at a cavity site where a predator was recently observed was less costly and no riskier than locating a new cavity where predator presence was unknown. Although starlings generally prefer freshly excavated cavities (Ingold 1998; Mazgajski 2003, 2007) over nest boxes (Planck 1967), natural cavities might be more susceptible to predation (Nilsson 1984). But, nest box placement relative to proximity to shrub or timber can increase access by predators (Gibo et al. 1976), as can absence of predator guards (Miller 2002).

Starlings nesting in ATF nest boxes (protected by predator guards) are, however, infrequently subject to nest predation (Seamans et al. 2015; Blackwell et al. 2018, 2020, 2021; findings herein). As such, pairs returning to an ATF nest box in a subsequent breeding season or new pairs occupying a nest box and observing infrequent predation attempts on neighbor nest boxes (Marzluff 1985; Lima and Dill 1990; Lima 1998a, b; Lima 2009) might not abandon a site simply due to our disturbance. Specifically, it is conceivable that our protection of nest boxes on ATF (i.e., including the removal of old nest material prior to a breeding season; Møller 1989, Mazgajski 2003, Seamans et al. 2015) enhanced selection of and fidelity to our sites (sensu Martin and Clobert 1996). We suggest that similar selection toward low nest predation risk associated with anthropogenic structures and moored aircraft is also possible.

Management implications

Aside from covering moored aircraft and closing doors of aircraft hangars, which are not necessarily feasible options, removal of nest material more than twice weekly would be necessary to maintain minimum control over material deposition that could affect aircraft function and safety. The persistence of the problem, however, underscores the need for a combination of frequent removal of nesting material and development of means to effectively deter starlings (e.g., manipulation of risk of adult mortality at select sites) when site closure or lethal control are not acceptable options.

Supplemental material

Supplemental material can be viewed at https://digitalcommons.usu.edu/hwi/vol16/ iss1/11.

Acknowledgments

We thank B. Collier, P. Klug, G. Linz, and H. Streby for reviews and helpful comments of earlier versions of this manuscript. We also appreciate comments provided by G. Linz, HWI associate editor, and 2 anonymous reviewers, which improved our final manuscript. Funding for data collection was provided by the National Wildlife Research Center. The U.S. Federal Aviation Administration provided support for B. Buckingham and M. Pfeiffer via Interagency Agreement between Wildlife Services and the Federal Aviation Administration (APH-HQ-19-0122) under Contract No. 692M15-19-T-00017.

Literature cited

- Amo, L., G. Tomás, and A. López-García. 2017. Role of chemical and visual cues of mammalian predators in nest defense in birds. Behavioral Ecology and Sociobiology 71:49.
- Blackwell, B. F., T. L. DeVault, E. Fernández-Juricic, E. Gese, L. Gilbert-Norton, and S. Breck. 2016. No single solution: application of conservation behaviour principles in mitigating human–wildlife conflict. Animal Behaviour 120:245–254.
- Blackwell, B. F., T. W. Seamans, M. B. Pfeffer, and B. N. Buckingham. 2018. European starling reproduction undeterred by predator scent inside nest boxes. Canadian Journal of Zoology 96:980–986.
- Blackwell, B. F., T. W. Seamans, M. B. Pfeiffer, and B. N. Buckingham. 2020. Predator scent and visual cue applied to nest boxes fail to dissuade European starlings from nesting. Wilson Journal of Ornithology 132:113–123.
- Blackwell, B. F., T. W. Seamans, M. B. Pfeiffer, and B. N. Buckingham. 2021. European starling nest-site selection given enhanced direct nest predation risk. Wildlife Society Bulletin 45:62–69.
- Bleicher, S. S., H. Ylönen, T. Käpylä, and M. Haapakoski. 2018. Olfactory cues and the value of information: voles interpret cues based

on recent predator encounters. Behavioral Ecology and Sociobiology 72:187.

- Bogrand, A. L., D. L. Neudorf, and P. Matich. 2017. Predator recognition and nest defense by Carolina wrens *Thryothorus ludovicianus* in urban and rural environments: does experience matter? Bird Study 64:211–221.
- Bötsch, Y., Z. Tablado, and L. Jenni. 2017. Experimental evidence of human recreational disturbance effects on bird-territory establishment. Proceedings of the Royal Society B 284(1858):20170846.
- Bowles, M. D., and R. S. Arrighi. 2004. NASA's nuclear frontier: the Plum Brook Reactor Facility, 1941–2002. Monographs in Aerospace History Series. Vol. 33. National Aeronautics and Space Administration History Division, Office of External Relations, Washington, D.C., USA.
- Bradley, J. E., and J. M. Marzluff. 2003. Rodents as nest predators: influences on predatory behavior and consequences to nesting birds. Auk 120:1180–1187.
- Bridgman, C. J. 1962. Bird nesting in aircraft. Breeding Birds 55:461–470.
- Brown, G. E., M. C. O. Ferrari, C. K. Elvidge, I. Ramnarine, and D. P. Chivers. 2013. Phenotypically plastic neophobia: a response to variable predation risk. Proceeding of the Royal Society B 280(1756):20122712.
- Brush, T. 1983. Cavity use by secondary cavitynesting birds and response to manipulations. Condor 85:461–466.
- Cabe, P. R. 1993. European starling (*Sturnus vulgaris*). Version 2.0. *In* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Cabe, P. R. 2020. European starling (*Sturnus vul-garis*). Version 1.0. *In* S. M. Billerman, editor. The birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA, https://birdsoft-heworld.org/bow/species/eursta/cur/introduction>. Accessed March 30, 2021.
- Chapman, F. M. 1925. The European starling as an American citizen. Natural History 25:480–485.
- Cohen, J. 1988. Statistical power analysis for the behavioral sciences. Second edition. Lawrence Erlbaum Associates, Hillsdale, New Jersey, USA.
- Conover, M. R. 2002. Resolving human–wildlife conflicts: the science of wildlife damage management. CRC Press, Boca Raton, Florida, USA.
- Creel, S., E. Dröge, J. M'soka, D. Smit, M. Becker,

D. Christianson, and P. Schuette. 2017. The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey. Ecology 98:2081–2092.

- DeVault, T. L., J. L. Belant, B. F. Blackwell, and T. W. Seamans. 2011. Interspecific variation in wildlife hazards to aircraft: implications for airport wildlife management. Wildlife Society Bulletin 35:394–402.
- DeVault, T. L., B. F. Blackwell, T. W. Seamans, M. J. Begier, J. D. Kougher, J. E. Washburn, and P. R. Miller. 2018. Estimating interspecific economic risk of bird strikes with aircraft. Wildlife Society Bulletin 42:94–101.
- DeVault, T. L., B. F. Blackwell, T. W. Seamans, S. L. Lima, and E. Fernández-Juricic. 2014. Effects of vehicle speed on flight initiation by turkey vultures: implications for bird-vehicle collisions. PLOS ONE 9(2): e87944.
- Dolbeer, R. A, M. J. Begier, P. R. Miller, J. R. Weller, and A. L. Anderson. 2021. Wildlife strikes to civil aircraft in the United States 1990–2020. Serial report 27. Department of Transportation, Federal Aviation Administration, Office of Airport Safety and Standards, Washington, D.C., USA.
- Evans, P. G. H. 1988. Intraspecific nest parasitism in the European starling *Sturnus vulgaris*. Animal Behavior 36:1282–1294.
- Feare, C. 1984. The starling. Oxford University Press, New York, New York, USA.
- Feare, C. 1991. Intraspecific nest parasitism in starlings *Sturnus vulgaris*: effects of disturbance on laying females. Ibis 133:75–79.
- Fisher, R. J., and K. L. Wiebe. 2006. Breeding dispersal of northern flickers *Colaptes auratus* in relation to natural nest predation and experimentally increased perception of predation risk. Ibis 148:772–781.
- Fontaine, J. J., M. Martel, H. M. Markland, A. M. Niklison, K. L. Decker, and T. E. Martin. 2007. Testing ecological and behavioral correlates of nest predation. Oikos 116:1887–1894.
- Gibo, D. L., R. Stephens, A. Culpeper, and H. Dew. 1976. Nest-site preferences and nesting success of the starling *Sturnus vulgaris* L. in marginal and favorable habitats in Mississauga, Ontario, Canada. American Midland Naturalist 95:493–499.
- Griffin, A. S., C. S. Evans, and D. T. Blumstein. 2001. Learning specificity in acquired predator recognition. Animal Behaviour 62:577–589.

Heldbjerg, H., A. D. Fox, P. V. Thellesen, L. Dalby,

and P. Sunde. 2017. Common starlings (*Sturnus vulgaris*) increasingly select for grazed areas with increasing distance-to-nest. PLOS ONE 12(8): e0182504.

- Heusmann, H. W., and R. Bellville. 1978. Effects of nest removal on starling populations. Wilson Bulletin 90:287–290.
- Homan, H. J., R. J. Johnson, J. R. Thiele, and G. M. Linz. 2017. European starlings. Wildlife Damage Management Technical Series. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services National Wildlife Research Center, Fort Collins, Colorado, USA.
- Ingold, D. 1994. Influence of nest-site competition between European starlings and woodpeckers. Wilson Bulletin 106:227–241.
- Ingold, D. J. 1998. The influence of starlings on flicker reproduction when both naturally excavated and artificial nest boxes are available. Wilson Bulletin 110:218–225.
- Jackson, J. A. 2000. Rapid nest-site selection and initiation of nests on commercial aircraft by European starlings. Migrant 71:97–99.
- Kalmbach, E. R., and I. N. Gabrielson. 1921. Economic value of the European starling in the United States. Bulletin of the U.S. Department of Agriculture, No. 868.
- Kerpez, T. A., and N. S. Smith. 1990. Competition between European starlings and native woodpeckers for nest cavities in saguaros. Auk 107:367–375.
- Kessel, B. 1953. Distribution and migration of the European starling in North America. Condor 55:49–67.
- Kessel, B. 1957. A study of the breeding biology of the European starling (*Sturnus vulgaris* L.) in North America. American Midland Naturalist 58:257–331.
- Koch, A. J., K. Martin, and K. E. H. Aitken. 2012. The relationship between introduced European starlings and the reproductive activities of mountain bluebirds and tree swallows in British Columbia, Canada. Ibis 154:590–600.
- Koenig, W. D. 2003. European starlings and their effect on native cavity-nesting birds. Conservation Biology 17:1134–1140.
- Koenig, W. D., E. L. Walters, and P. G. Rodewald. 2017. Testing alternative hypotheses for the cause of population declines: the case of the red-headed woodpecker. Condor 119:143–154.

Lakens, D. 2022. Sample size justification. Col-

labra: Psychology 8:33267.

- Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology Journal 2010:1–7.
- Lewis, R. J., and M. J. Conover. 2018. Feeding a hungry world. Pages 99–105 in W. C. Pitt, editor. Ecology and management of terrestrial vertebrate invasive species in the United States. Taylor and Francis, Boca Raton, Florida, USA.
- Lima, S. L. 1987. Clutch size in birds: a predation perspective. Ecology 68:1062–1070.
- Lima, S. L. 1998a. Nonlethal effects in the ecology of predator–prey interactions. BioScience 48:25–34.
- Lima, S. L. 1998b. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215–290.
- Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews of the Cambridge Philosophical Society 84:485–513.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.
- Linz, G. M., J. H. Homan, S. M. Gaukler, L. B. Penry, and W. J. Bleier. 2007. European starlings: a review of an invasive species with far-reaching impacts. Pages 378–386 *in* G. W. Witmer, W. C. Pitt, and K. A. Fagerstone, editors. Symposium 24. Managing Vertebrate Invasive Species. National Wildlife Research Center, Fort Collins, Colorado, USA.
- Lombardo, M. P., H. W. Power, P. C. Stouffer, L. C. Romagnano, and A. S. Hoffenberg. 1989. Egg removal and intraspecific brood parasitism in the European starling. Behavioral Ecology and Sociobiology 24:217–223.
- Luttbeg, B. 2017. Re-examining the causes and meaning of the risk allocation hypothesis. American Naturalist 189:644–656.
- Martin, T. E. 1988. Habitat and area effects on forest bird assemblages: is nest predation an influence? Ecology 69:74–84.
- Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. BioScience 43:523–532.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food.

Ecological Monographs 65:101-127.

- Martin, T. E., and J. V. Briskie. 2009. Predation on dependent offspring: a review of the consequences for mean expression and phenotypic plasticity in avian life history traits. Annals of the New York Academy of Science 1168:201–217.
- Martin, T. E., and J. Clobert. 1996. Nest predation and avian life-history evolution in Europe versus North America: a possible role of humans? American Naturalist 147:1028–1046.
- Marzluff, J. M. 1985. Behavior at a pinyon jay nest in response to predation. Condor 87:559–561.
- Mazgajski, T. D. 2003. Nest site choice in relation to the presence of old nests and cavity depth in the starling *Sturnus vulgaris*. Ethology Ecology & Evolution 15:273–281.
- Mazgajski, T. D. 2007. Effect of old nest material in nest boxes on ectoparasite abundance and reproductive output in the European starling (*Sturnus vulgaris* L.). Polish Journal of Ecology 55:377–385.
- McClure, C. J. W., S. E. Schultz, R. V. Buskirk, B. B. Pauli, and J. A. Heath. 2017. Commentary: research recommendations for understanding the decline of American kestrels (*Falco sparverius*) across much of North America. Journal of Raptor Research 51:455–464.
- Meuthen, D., M. C. O. Ferrari, T. Lane, and D. P. Chivers. 2019. High background risk induces risk allocation rather than generalized neophobia in the fathead minnow. Behavioral Ecology 30:1416–1424.
- Miller, K. E. 2002. Nesting success of the great crested flycatcher in nest boxes and in tree: are nest boxes safer from nest predation? Wilson Bulletin 114:179–185.
- Møller, A. P. 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? Oikos 56:421–423.
- Mönkkönen, M., J. T. Forsman, T. Kananoja, and H. Ylönen. 2009. Indirect cues of nest predation risk and avian reproductive decisions. Biology Letters 5:176–178.
- Morrison, D. W., and D. F. Caccamise. 1985. Ephemeral roosts and stable patches? A radio-telemetry study of communally roosting starlings. Auk 102:793–804.
- Mouillot, D., N. A. J. Graham, S. Villé, N. W. H. Mason, and D. R. Bellwood. 2013. A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution 28:167–177.

Mouton, J. C., and T. E. Martin. 2018. Fitness con-

sequences of interspecific nesting associations among cavity-nesting birds. American Naturalist 192:389–396.

- Nakagawa, S., and I. C. Cuthill. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biological Reviews 82:591–605.
- Nice, M. M. 1957. Nesting success in altricial birds. Auk 74:305–321.
- Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scandinavica 15:167–175.
- Parejo, D., and J. M. Avilés. 2011. Predation risk determines breeding territory choice in a Mediterranean cavity nesting bird community. Oecologia 165:185–191.
- Pérez, J. H. 1988. El estornino pinto en la capital federal. Nuestra Aves 17:13.
- Pfeiffer, M. B., T. W. Seamans, B. N. Buckingham, and B. F. Blackwell. 2019. Landscape factors that influence European starling (*Sturnus vulgaris*) nest box occupancy in northern Ohio. Ohio Journal of Science 119:38–47.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53–65.
- Planck, R. J. 1967. Nest site selection and nesting of the European starling (*Sturnus vulgaris*) in California. Dissertation, University of California, Davis, Davis, California, USA.
- Power, H. W., E. D. Kennedy, L. C. Romagnano, M. P. L. Lombardo, A. S. Hoffenberg, P. C. Stouffer, and T. R. McGuire. 1989. The parasitism insurance hypothesis: why starlings leave space for parasitic eggs. Condor 91:753–765.
- Psiropoulos, J. L., and L. A. Selner. 2019. European starlings fly before they fledge. Human–Wildlife Interactions 13:356–359.
- Remacha, C., and J. A. Delgado. 2009. Spatial nestbox selection of cavity-nesting bird species in response to proximity to recreational infrastructures. Landscape and Urban Planning 93:46–53.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.
- Ricklefs, R. E. 1977. Reactions of some Panamanian birds to human intrusion at the nest. Condor 79:376–379.
- Ricklefs, R. E. 1984. Variation in the size and composition of eggs of the European starling. Condor

86:1–6.

- Romagnano, L., A. S. Hoffenberg, and H. W. Power. 1990. Intraspecific brood parasitism in the European starling. Wilson Bulletin 102:279–291.
- Royall, W. C, Jr. 1966. Breeding of the starling in central Arizona. Condor 68:196–205.
- Seamans, T. W., B. F. Blackwell, and L. A. Tyson. 2015. Low occupancy rates of artificial nest cavities by European starlings. Ohio Journal of Science 115:53–55.
- Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. Oecologia 54:159–169.
- Stanback, M. T., N. A. DiLuzio, A. N. Mercadante, and E. S. Diamant. 2018. Eastern bluebirds (*Sialia sialis*) do not abandon their chosen nest site in response to a single visit by a nest predator. Wilson Journal of Ornithology 130:568–573.
- Strasser, E. H., and J. A. Heath. 2013. Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. Journal of Applied Ecology 50:912–919.
- Stouffer, P. C., and H. W. Power. 1991. Brood parasitism by starlings experimentally forced to desert their nests. Animal Behaviour 41:537–539.
- Tyson, L. A., B. F. Blackwell, and T. W. Seamans. 2011. Artificial nest cavity used successfully by native species and avoided by European starlings. Wilson Journal of Ornithology 123:827–830.
- Williams, T. D., S. Bourgeon, A. Cornell, L. Ferguson, M. Fowler, R. R. B. Fronstin, and O. P. Love. 2015. Mid-winter temperatures, not spring temperatures, predict breeding phenology in the European starling *Sturnus vulgaris*. Royal Society Open Science 2: 140301.
- Winterbottom, J., and R. Liversidge. 1954. The European starling in the south west Cape. Ostrich 25:89–96.
- Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. Science 334:1398–1401.
- Zufiaurre, E., A. Abba, D. Bilenca, and M. Codesido. 2016. Role of landscape elements on recent distributional expansion of European starlings (*Sturnus vulgaris*) in agroecosystems of the Pampas, Argentina. Wilson Journal of Ornithology 128:306–313.

Associate Editor: George M. Linz

BRADLEY F. BLACKWELL (photo unavailable) serves as the USDA/APHIS Wildlife Services, National Wildlife Research Center (NWRC) project and field station leader at the Ohio Field Station in Sandusky, Ohio. He focuses his research toward understanding and exploiting animal sensory ecology and antipredator behavior relative to human-wildlife interactions. He works primarily in the area of aviation safety but is also interested in applications of sensory ecology and animal behavior in the broader perspectives of animal response to vehicle approach and other forms of human disturbance to wildlife populations. He received his B.S. and M.S. degrees from North Carolina State University and his Ph.D. degree from the University of Maine. He served as a National Oceanic and Atmospheric Administration Cooperative Marine Education and Research Fellow at the University of Massachusetts, Amherst, prior to transitioning to the NWRC.

BRUCE N. BUCKINGHAM joined the USDA/APHIS Wildlife Services, National Wildlife Re-



e Services, National Wildlife Research Center, Ohio Field Station, in Sandusky, Ohio, after retiring from the Ohio Division of Wildlife in 2009. He has held a Master Bird Banding permit since 1973, and his research interest includes colonial nesting species, especially herring gulls.

MORGAN B. PFEIFFER is a research wildlife biologist within the USDA/APHIS Wildlife



n the USDA/APHIS Wildlife Services, National Wildlife Research Center at the Ohio Field Station in Sandusky, Ohio. Her research interests include understanding species plasticity, movements, and behaviors in anthropogenic landscapes. She applies these interests to understanding and preventing wildlife collisions with aircraft. Her current research involves evaluating uncrewed aircraft systems technology for wildlife

hazard management. She is a member of The Wildlife Society (TWS), the Secretary/Treasurer for the TWS Drone Working Group, and is a Certified Wildlife Biologist. She received her B.S. degree in wildlife and fisheries science from The Pennsylvania State University and her M.S. and Ph.D. degrees from the University of KwaZulu-Natal in South Africa. Her focus in South Africa was on the ecology and conservation of endangered African vultures.