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Nest Box Cameras Provide Insight into Causes of Nest Failure for American Kestrels

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ABSTRACT.—Although nest failure is a common occurrence in birds, oftentimes the causes, or details, of the failure are unknown because nests cannot be monitored closely or continuously. This inability to monitor nests in ways that allow for a detailed understanding of nest failure can hamper our ability to conserve declining species, such as the American Kestrel (*Falco sparverius*). Here we describe previously unreported observations from continuous video monitoring in kestrel nest boxes and biweekly nest monitoring via an extendable fiber optic endoscopic camera. From continuous video monitoring we observed adult kestrels consume a kestrel egg with little to no development and a European Starling (*Sturnus vulgaris*) pierce and remove an abandoned kestrel egg from a nest box. From biweekly monitoring with a fiber optic camera, we inferred that nest abandonment by kestrels was associated with eggs not developing either from infertility or early-stage embryo death. Although it is unclear how common such occurrences may be across the broader range of kestrels, these observations may provide impetus to explore these causes of nest failure more closely.

KEY WORDS: *camera monitoring*; *cavity-nesting*; *nest abandonment*; *nest failure*; *nest site competition*.

LAS CÁMARAS SITUADAS EN LAS CAJAS NIDO PROPORCIONAN INFORMACIÓN SOBRE LAS CAUSAS DEL FRACASO DEL NIDO EN *FALCO SPARVERIUS*

RESUMEN.—Aunque el fracaso de los nidos es un hecho común en las aves, a menudo se desconocen las causas o los detalles del fracaso, porque los nidos no pueden ser monitoreados de cerca o de forma continua. Esta incapacidad para monitorear los nidos de manera que permita una comprensión detallada del fracaso de los mismos puede obstaculizar nuestra capacidad para conservar especies en declive, como *Falco sparverius*. Aquí presentamos observaciones previamente no reportadas a partir del monitoreo continuo por vídeo de cajas nido utilizadas por *F. sparverius* y del monitoreo quincenal de los nidos mediante una cámara endoscópica de fibra óptica extensible. A partir del monitoreo continuo por vídeo, observamos a individuos adultos de *F. sparverius* consumir un huevo de *F. sparverius* con poco o ningún desarrollo y a un individuo de *Sturnus vulgaris* perforar y retirar de la caja nido un huevo de *F. sparverius* abandonado. A partir del monitoreo quincenal con una cámara de fibra óptica, inferimos que el abandono del nido por parte de *F. sparverius* estaba asociado con el hecho de que los huevos no se desarrollaban, ya sea por infertilidad o por la muerte del embrión en las primeras etapas. Aunque no está claro cuán comunes pueden ser estos sucesos en el área de distribución de *F. sparverius*, estas observaciones pueden proporcionar un aliciente para explorar más de cerca estas causas de fracaso de los nidos.

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INTRODUCTION

The American Kestrel (*Falco sparverius*; hereafter kestrel) is a species of cavity-nesting falcon inhabiting open landscapes including grasslands and agricultural areas throughout the western hemisphere (Smallwood and Bird 2020). Over the past several decades, kestrel populations have declined across much of their North American range (Bird and Smallwood 2023, Oleyar et al. 2023). The primary cause of this decline is under debate, but several factors may contribute concurrently, varying across space and time (McClure et al. 2017). One hypothesized contributing factor is decreased availability of nest sites (i.e., large tree hollows and snags), particularly in areas dominated by intensive agriculture or residential or urban development (Smallwood and Bird 2020). Further aggravating this threat are introduced cavity nesters, including European Starlings (*Sturnus vulgaris*; hereafter starling), which compete with kestrels for nesting cavities (Koenig 2003, Bowers et al. 2023). Competition with starlings for nesting sites can reduce kestrel nesting success (Bowers et al. 2023), although the importance of the role that starlings play in the decline of kestrel populations remains unclear and under debate (e.g., McClure et al. 2017, Smallwood and Bird 2023).

To mitigate the problem of a lack of nesting sites, many people have resorted to providing kestrels with nest boxes (Smallwood and Collopy 2009). Installing nest boxes in appropriate habitats can increase local populations, especially in areas where suitable nesting sites are limited (Hamerstrom et al. 1973, Toland and Elder 1987, Smallwood and Collopy 2009), including landscapes dominated by intensive agriculture. However, even when nest boxes are provided, kestrels still face challenges to successful reproduction. Nesting attempts by kestrels (and birds in general) may fail for numerous reasons including infertility (Koenig 1982), egg or nestling abandonment (Strasser and Heath 2013), depredation (Chiavacci et al. 2014), cannibalism (Allen et al. 2020), and harsh weather conditions (Harrod and Rolland 2020). Although occasionally researchers can identify the cause of nest failure, often the cause, and details of exactly how the failure occurred, are unknown because nests are rarely monitored continuously. However, when possible, the identification of causes of nest failure can provide valuable details that allow for a better understanding of drivers of population declines (Benson et al. 2010). Here, we describe four observations from kestrel nests in nest boxes located in the intensive row-crop landscape of northeastern Arkansas, USA. These observations, made from both intermittent (via fiber optic endoscopic camera) and continuous video monitoring of nest boxes, provide insight into some causes of reproductive failure for kestrels.

METHODS

These observations were made in nest boxes in Craighead and Poinsett Counties in northeast Arkansas, USA, within the Lower Mississippi Alluvial Valley (LMAV) ecoregion, where industrial row-crop agriculture dominates the landscape (center of study area: 35°79.407′N, 90°68.714′W). The primary crops of this region are soybeans (*Glycine max*), rice (*Oryza sativa*), corn (*Zea mays*), and cotton (*Gossypium hirsutum*; Yasarer et al. 2020). We built kestrel nest boxes from unfinished pine wood and assembled them into a rectangular box (24 cm wide × 18.5 cm deep × 66 cm high) with a 7.5 cm diameter entrance hole and small holes for drainage on the bottom of the box. We installed them on utility poles in the rights-of-way along (mostly dirt) county roads surrounded by agricultural fields. As of 2023, we had installed 37 nest boxes; 19 were installed in 2020 and 18 in 2022. We also monitored three nest boxes that were installed at some point before 2015 by other individuals. On average, boxes were 3.8 m above the ground (range = 2.6–5.7 m). We routinely, and immediately, removed all invasive species' (i.e., starlings or House Sparrows [*Passer domesticus*]) nesting material, eggs, and hatchlings that we found in boxes.

From 2021 to 2023, during the kestrel breeding season (March–July), we monitored these nest boxes in several ways. First, we monitored boxes intermittently by inserting a fiber optic endoscopic camera (Teslong NTC30P-3m, Irvine, California, USA) affixed to a telescoping pole into the entrance hole of the box to view its contents through the USEE application on a smartphone. This intermittent monitoring occurred monthly in 2021 and bi-weekly in 2022 and 2023. From this intermittent monitoring, we observed numerous cases of nest failures that we could not explain, largely because the interval between nest checks was too long. Thus, to better identify the causes of nest failures, during the 2023 breeding season, we installed miniature motion-triggered cameras (Wisepatch SC-1, China, https://www.amazon.com/WisePatch-SC-1-Micro-Camera/dp/B0BHF8RB15) in five of the nine nest boxes that contained active kestrel nests with eggs. We housed the camera and battery in a plastic container affixed to the ceiling of the nest box. We replaced batteries and memory cards every 3–13 d. Kestrels are typically considered to be tolerant of nest site disturbance by researchers, including during nest box camera installation and monitoring (Smallwood 2016, Shave and Lindell 2017).

OBSERVATIONS

Over three breeding seasons, we documented 20 kestrel nesting attempts where eggs were laid in boxes (2021: $n = 4$, 2022: $n = 7$, 2023: $n = 9$). Nine (45%) nests were successful (i.e., producing ≥1 nestling of 22 d post-hatching (Steenhof and Newton 2007, Smallwood and Bird 2020) whereas eleven (55%) nests failed to produce fledglings; of those, nine failed before any eggs hatched. These failures included instances of disappearance of eggs ($n = 6$) or hatchlings ($n = 2$) from the nest box, abandonment of eggs ($n = 2$), and crushed eggshells and yolks in the nest box ($n = 1$). Although some details of these failures remain unknown, camera footage provided insights into the fate of kestrel eggs from some of these failed nesting attempts as described below.

Observation 1. At Box C we removed a starling nest (before any eggs were laid) on 7 April 2023. On our next visit on 20 April, a female kestrel was incubating eggs; we counted at least two at this point, but the female did not leave the nest box to allow for a complete egg count. On 4 May, ≥17 d into incubation, we counted five kestrel eggs and then installed a motion-triggered nest camera in the box.

Upon watching the video footage (Supplemental Material Video S1), the camera had shifted and only part of the nest was visible (one egg), and we observed that on 6 May (≥19 d after incubation began) a female kestrel arrived at the box, pecked open and ate the contents of a kestrel egg. The egg's content appeared to be mostly liquid, suggesting that little to no embryonic development had occurred despite approximately 20 d of incubation (average incubation period of kestrels is 30 d; Smallwood and Bird 2020). After 2 min of eating the contents of the egg, the female kestrel left the nest box. Thirteen min later, a male kestrel entered and immediately pecked at and consumed more of the same egg contents for 2 min. No subsequent visits by a kestrel were recorded at the nest box. Unfortunately, because of the camera shifting, we were unable to observe what happened to the other four eggs in the clutch.

Observation 2. At Box B on 7 April 2023, we observed a female kestrel incubating eggs on top of a starling nest that had been built since our last monitoring visit 17 d prior. On our next visit on 11 April, we observed five kestrel eggs in the nest and installed a motion-triggered nest camera in the box. Subsequent checks on 18 April, 25 April, and 2 May revealed typical incubation behavior. On 9 May, we checked the nest box and a starling flew from the box, which now contained a starling nest that appeared complete, prompting us to remove the nest box camera.

Video footage of this nest showed typical incubation behavior through 2 May (with the full clutch of five eggs present); however, because of a camera malfunction during 3 May and 4 May, the video footage was overwritten. The camera resumed recording on 5 May and showed the kestrel pair taking turns incubating a single egg. There was no sign of the other four eggs in the nest box (e.g., eggshells, dried yolk) suggesting that they were removed on 3 May or 4 May. At 1802 H on 5 May, the female kestrel left the box and 20 min later, a male arrived and appeared to incubate the egg for 2 min before departing. After that, there was no sign of either parent again, suggesting abandonment of the remaining egg (approximately 30 d into incubation). At 0902 H on 6 May, a starling entered the nest box, inspected its contents, briefly pecked at the kestrel egg, then flew out immediately. Then, at 0726 H on 8 May, a starling returned to the box again and briefly pecked at the kestrel egg. At 0921 H on 8 May, a starling came to the box with nesting material and pecked at the kestrel egg multiple times, eventually puncturing and removing it from the nest box (Supplemental Material Video S2). After that, the starling returned to the box repeatedly to add nesting material.

Observation 3. At Box 5, on 6 April 2023, the fiber optic camera showed a female kestrel in the nest box. We checked the nest twice more (on 18 April and 2 May) and a female was incubating during both checks. However, on 16 May, ≥36 d after incubation began, two kestrel eggs remained in the box with no adults observed in the vicinity of the box. Thus, we considered the eggs abandoned and, after confirming that the eggs were cold, we cleaned out the box to accommodate another nesting attempt. To better understand the circumstances around the abandonment, we cracked open the two eggs during cleaning and, despite being incubated for ≥26 d (6 April to 2 May), neither showed any sign of embryonic development to the unaided eye.

Observation 4. In Box 37, on 1 June 2023, we observed two kestrel eggs (none were present during our previous nest check on 17 May) but saw no adults in the vicinity of the box. We monitored the box with the fiber optic camera three more times over the next 2 wk and each time two eggs were present, but no adult was present. On 15 June, we confirmed that the eggs were cold; they broke open during cleaning and they too showed no obvious signs of development.

DISCUSSION

From 2021–2023 we recorded a 45% nest success rate for kestrels using our boxes, which is lower than other kestrel monitoring programs in agricultural areas from nearby regions (70% in Missouri, Toland and Elder 1987; 68.9% in Iowa, Varland and Loughin 1993; 78.9% in Virginia, Kolowski et al. 2023). Our low nest success rate suggests that kestrel populations in this region may be facing challenges to reproduce, in contrast to positive trends (+2.2% annual increase from 1966–2019 in the LMAV; Bird and Smallwood 2023) reported by the Breeding Bird Survey for within the LMAV (Sauer et al. 2020). Most nest failures in our study occurred during incubation as eggs "disappeared" from nest boxes or were putatively abandoned. By using both continuous and intermittent monitoring, we were able to observe previously unreported behaviors that provide insights into the causes of kestrel nest failure.

We documented the first reported case of adult kestrels eating the contents of an undeveloped conspecific egg (or any egg) in the wild. We did not band or otherwise mark the adults, so it is unknown if the kestrels consuming the egg were in fact the parents or an unrelated pair. Although cannibalism of young by raptors is known to occur (Allen et al. 2020), few studies report adult raptors eating their own eggs, or the contents of their eggs (but see Stanback and Koenig 1992). In general, avian parents may eat their own eggs for a few reasons: adaptively, if the parents have reason to believe the egg is not developing properly, an egg could serve as a source of nutrition (Stanback and Koenig 1992); or maladaptively, parents may eat the egg as a stress displacement response (Chardine and Morris 1983). Porter and Wismeyer (1970) observed kestrels eating their eggs and nestlings during captive propagation, a behavior that they attributed to nutritional deficiencies. Additionally, the Cornell Bird Cams (2018) recorded a female kestrel feeding a developed unviable egg to her young as a potentially adaptive response to ensure the fledging of at least one offspring. During our Observation 1, the egg in question did not appear to have developed despite a period of incubation of ≥19 d, so if the adults that ate the egg were in fact the parents, they may have still been acting adaptively (making the best of a bad situation). However, it is unclear why the egg did not develop appropriately or how the parents may have determined this.

We also documented, for the first time, a starling removing a kestrel egg (albeit an abandoned one) from a nest (Observation 2), which may provide evidence of the negative impact starlings can have on kestrels, at least in the LMAV. This instance of egg removal was likely an act of sanitation by the starling to prepare its new nest (Guigueno and Sealy 2011). However, at the very least, this observation demonstrates that starlings are capable of removing kestrel eggs from a nest. It has been thought that although starlings compete with kestrels for nesting sites (Koenig 2003), this competition was generally limited to the front-end of breeding (i.e., cavity acquisition). This observation, however, suggests that starlings may be able to decrease productivity even after a kestrel pair has occupied a nesting cavity for weeks. In this case, we cannot say for sure why the kestrels abandoned their remaining egg, nor do we know exactly what happened to the other four eggs that vanished from the box. Starlings are known to remove conspecific eggs from nests (Lombardo et al. 1989) and can be aggressive interspecific nest usurpers (Cabe 2020), but to our knowledge, there has not been any documentation of starlings removing a heterospecific egg from a nest (however, there have been anecdotal reports of such behavior; e.g., Kelly 2016). However, given the highly aggressive and competitive behavior of starlings, egg removal has likely occurred but has just not been documented in the literature (at least partly because of the challenge of continuously monitoring cavity nests). More studies with continuously monitored nest boxes would be needed to determine how often this behavior occurs and the consequences for kestrels at the population (or species) scale.

In total, our observations suggest inadequate early embryo development may be an underlying issue that eventually led to the negative outcomes for all these kestrel nests. This apparent lack of development could be caused by either fertilization failure or early-stage embryo death (Assersohn et al. 2021). Fertilization failure, although thought to be relatively rare in the wild, can arise from poor sperm quality or abundance, female-mediated post-copulatory sperm selection, or (as seen in domesticated poultry) factors such as poor female condition, reproductive organ disorders, and various environmental factors such as diet and stress (Lifjeld et al. 2007, Assersohn et al. 2021). Early-stage embryo death is likely the more common cause of egg failure in the wild and is typically the result of lethal genetic abnormalities of the embryo, poor female condition, and/or environmental factors including exposure to extreme temperatures (Assersohn et al. 2021, Savage et al. 2021). Another environmental factor that may be implicated in either case is exposure to contaminants (e.g., organic pollutants, non-halogenated pesticides, and toxic metals), which may negatively impact egg and embryo viability (Giesy et al. 2009, Assersohn et al. 2021). Agricultural areas such as the LMAV may be particularly affected by such contaminants (Kröger et al. 2011), which adult kestrels may have been exposed to directly or indirectly through contaminated prey. Understanding the ultimate cause of hatching failures and nest abandonment in kestrels could be important for effective conservation management for this declining species. Finally, our observations highlight the importance (and challenge) of properly assigning the cause of nest failure when intermittently monitoring avian nests. When eggs disappear from bird nests we often blame predators as a default; however, our observations via nest cameras clearly show that conspecifics or nest competitors may in fact be to blame. Thus, in the future, these alternative explanations of missing eggs should be considered when determining the causes of failed nesting attempts for kestrels and other bird species.

SUPPLEMENTAL MATERIAL (available online). Video S1: Observation 1–A female and male American Kestrel eating an undeveloped kestrel egg (https://youtu.be/YuAnPx2vTxo). Video S2: Observation 2–A European Starling piercing and removing an abandoned American Kestrel egg from a nest box (https://youtu.be/GruoN_GFPj0).

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