Journal of Raptor Research

Journal of Raptor Research 57(4):563–570
doi: 10.3356/JRR-22-88

American Kestrels Compete with European Starlings over Nest Boxes in Eastern Pennsylvania

Matthew J. Bowers,[1] Paula M. Orozco-Valor,[1,2,3] Rebecca A. McCabe,[1*] and Jean-François Therrien[1]

[1]*Acopian Center for Conservation Learning, Hawk Mountain Sanctuary Association, 410 Summer Valley Road, Orwigsburg, PA 17961 USA*
[2]*Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET), Buenos Aires, Argentina*
[3]*Centro para el Estudio y Conservación de las Aves Rapaces en Argentina (CECARA), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa La Pampa, Argentina*

ABSTRACT.—The American Kestrel (*Falco sparverius*) has been steadily declining throughout most of its eastern North American range, and the cause of this decline is still relatively unknown. As a cavity nesting species, the American Kestrel often competes with other cavity nesters such as the invasive and abundant European Starling (*Sturnus vulgaris*) over nest boxes. The relationship between European Starling presence at nesting sites and American Kestrel occupancy and nesting success is understudied. We analyzed data from nest boxes monitored in eastern Pennsylvania, USA, from 1992 to 2021 to identify changes in occupancy of American Kestrels and competitors, and to examine the relationship between competition at nest boxes and American Kestrel nesting parameters. We found that American Kestrel occupancy decreased while European Starling occupancy increased over the study period. All other species occupying nest boxes (small mammals, passerines, owls, and snakes) showed no significant occupancy trends. On average 21% of nest boxes remained unoccupied annually, and 7% of occupied nest boxes were used by both American Kestrels and competitors in the same breeding season. The presence of these competitors had negative associations with American Kestrel occupancy, clutch size, number of fledglings produced, and overall nesting success. Specifically, the rate of nesting success decreased by 26% when European Starlings used the same nest box within the same breeding season. In recent years, nesting productivity of American Kestrels has decreased, with the average number of nestlings, fledglings, and nesting success rate all declining, while the average clutch size remained constant. Our results suggest that American Kestrel nesting parameters in eastern Pennsylvania are negatively associated with competition for nest boxes during the breeding season. The opposing trends in occupancy for the European Starling and the American Kestrel in this study area coupled with the declining productivity of American Kestrel nests raise concerns over the future of this raptor species in eastern Pennsylvania.

KEY WORDS: *cavity nesting*; *invasive species*; *nesting success*; *occupancy*.

FALCO SPARVERIUS COMPITE CON *STURNUS VULGARIS* POR LAS CAJAS NIDO EN EL ESTE DE PENSILVANIA

RESUMEN.—*Falco sparverius* ha estado disminuyendo constantemente en la mayor parte de su área de distribución oriental en América del Norte, y la causa de esta disminución aún es relativamente desconocida. Como especie que anida en cavidades, *F. sparverius* a menudo compite por las cajas nido con otras que también anidan en cavidades, como *Sturnus vulgaris*, una especie invasora y abundante. La relación entre la presencia de *S. vulgaris* en los lugares de cría y la ocupación y el éxito de cría de *F. sparverius* está poco

* Corresponding author: mccabe@hawkmountain.org

estudiada. Analizamos los datos de cajas nido monitoreadas en el este de Pensilvania, EEUU, desde 1992 hasta 2021, para identificar cambios en la ocupación de *F. sparverius* y competidores, y para examinar la relación entre la competencia en las cajas nido y los parámetros de anidación de *F. sparverius*. Encontramos que la ocupación de *F. sparverius* disminuyó mientras que la ocupación de *S. vulgaris* aumentó durante el período de estudio. Todas las demás especies que ocupan cajas nido (mamíferos pequeños, paseriformes, búhos y serpientes) no mostraron tendencias significativas en la ocupación. En promedio, el 21% de las cajas nido permanecieron desocupadas anualmente, y el 7% de las cajas ocupadas fueron utilizadas por *F. sparverius* y competidores en la misma estación reproductiva. La presencia de estos competidores tuvo asociaciones negativas con la ocupación, el tamaño de la puesta, el número de volantones producidos y el éxito general de cría de *F. sparverius*. Específicamente, la tasa del éxito de cría disminuyó en un 26% cuando *S. vulgaris* utilizó la misma caja nido dentro de la misma estación reproductiva. En los últimos años, la productividad de *F. sparverius* ha disminuido, con una caída en el número promedio de polluelos, volantones y en la tasa de éxito de cría, mientras que el tamaño promedio de la puesta se mantuvo constante. Nuestros resultados sugieren que los parámetros reproductivos de *F. sparverius* en el este de Pensilvania están negativamente asociados con la competencia por las cajas nido durante la estación reproductiva. Las tendencias opuestas en la ocupación para *S. vulgaris* y *F. sparverius* en esta área de estudio, junto con la disminución de la productividad de los nidos de *F. sparverius*, plantean preocupaciones sobre el futuro de esta rapaz en el este de Pensilvania.

[Traducción del equipo editorial]

INTRODUCTION

Globally, 18% of all bird species are considered cavity nesters, the majority of which are secondary cavity nesters that use cavities excavated by other species (Van der Hoek et al. 2017). This resource is often limited due to human development and the removal of natural habitat such as decaying and old growth trees (Cockle et al. 2011, Wiebe 2011, Orchan et al. 2013). Interspecific competition for nesting cavities is frequent throughout the world, as several bird and mammal species can adequately use the same type of site (Newton 1994, Valdez et al. 2000, Czeszczewik et al. 2008, Wiebe et al. 2020). Nest box programs have been established and maintained throughout North America to provide supplemental nesting sites for birds in suitable habitats where tree cavities are limited (Smallwood et al. 2009, Bailey et al. 2020). However, nest boxes also frequently invite other—often invasive—cavity nesting species, which can exploit these sites and negatively affect the target species for which the nest box is intended (Newton 1994, Charter et al. 2010, Stojanovic et al. 2021).

Across North America, a frequent nontarget species using nest boxes is the invasive, nonnative European Starling (*Sturnus vulgaris*), which is one of the most abundant bird species on the continent (Koenig 2003, Sauer et al. 2020). European Starlings are fierce competitors for nest sites, often usurping the cavities of other native species such as Northern Flickers (*Colaptes auratus*), Red-bellied Woodpeckers (*Melanerpes carolinus*), and Eastern Bluebirds (*Sialia sialis*), among other woodpecker and songbird species (Ingold 1994, Koenig 2003, Bailey et al. 2020). European Starlings' persistence in renesting and ability to dismantle the nests of competitors means even larger cavity nesters that can prey upon European Starlings are vulnerable to usurpation (Wilmers 1987, McClure et al. 2015, Bailey et al. 2020). Understanding the larger impact of these actions on native bird populations is often challenging because several biotic and abiotic factors can independently or jointly drive change (Colléony and Shwartz 2020). For some native bird species, exploitative competition with an invasive bird species has been associated with declines in body size and subsequently, survival (Freed and Cann 2009). However, in most instances, even when competition for nesting sites is common, this interaction does not have population-level effects on native birds (Koenig 2003, Baker et al. 2014, Martin-Albarracin et al. 2015).

As a secondary cavity nesting species, the American Kestrel (*Falco sparverius*) will readily use artificial wooden nest boxes as nesting sites (Smallwood et al. 2009). Interspecific competition between European Starlings and American Kestrels for nest boxes has been documented throughout their range (e.g., McClure et al. 2015, Kolowski et al. 2022). Some studies have found that American Kestrels outcompete European Starlings for a limited number of nest boxes, potentially due to their larger relative size (50% larger than European Starlings), which may discourage usurpation by this invasive species

(Bechard and Bechard 1996, Koenig 2003). However, other studies have found that harassment by European Starlings has caused American Kestrels to abandon their nests in both artificial and natural cavities and prevented American Kestrels from taking over established European Starling nests (Weitzel 1988, Loftin 1992, Rohrbaugh and Yahner 1997). Additional research suggests European Starlings contribute to the disappearance or predation of American Kestrel eggs and even the decline of local American Kestrel populations (Varland and Loughin 1993, Rohrbaugh and Yahner 1997). Clearly, conclusions regarding the "winner" of this interspecific competition vary, as both species can evict one another from nest boxes (Varland and Loughin 1993). American Kestrels and European Starlings have also been observed successfully using the same nest box within the same breeding season, adding another dimension to this relationship (Wilmers 1987, Klucsarits et al. 1997).

For decades, the American Kestrel population has been steadily declining throughout most of the species' eastern North American range (Bird 2009, Sauer et al. 2020). The cause of this decline is still relatively unknown, as various hypotheses—including habitat loss, increased predation by Cooper's Hawks (*Accipiter cooperii*), pesticides, climate change, and pathogens like West Nile Virus—have not definitively explained this trend (Smallwood et al. 2009, McClure et al. 2017b). With the uncertainty surrounding the cause(s) of this decline, it is important to address all factors that could be affecting the population. Despite being fierce competitors for nesting cavities, European Starlings are rarely addressed as a possible factor influencing American Kestrel declines via their effect on American Kestrel reproductive success (Bird 2009, Kolowski et al. 2022). McClure et al. (2017b) recommend that research should investigate drivers of nest success within nest boxes, noting nest box design and placement in relation to cover type and landscape, but not directly mentioning competition. Here, we correlate long-term trends of nest box occupancy and nesting success in American Kestrels with European Starling and other competitor (small mammals, passerines, owls, and snakes) presence over 30 yr. In turn, this study addresses whether European Starlings and other competitors could play a role in the sustained decline of the American Kestrel in eastern North America. We predict that American Kestrels encountering European Starlings at nest boxes will have lower nesting success. We also predict that European Starlings will have the highest nest box occupancy of all competitor species, as the European Starling is often the most common nontarget species at American Kestrel nest boxes (Loftin 1992, Klucsarits et al. 1997, Valdez et al. 2000).

METHODS

Study Area and Data Collection. From 1992 to 2021, researchers and volunteers from Hawk Mountain Sanctuary (Pennsylvania, USA) consistently monitored 60 nest boxes designed for American Kestrels within a 40-km radius of the sanctuary. Nest boxes all had the same shape and size, described by Rusbuldt et al. (2006), and were located on utility poles, trees, and buildings in open habitats, often on or near agricultural land. All nest boxes were checked in early May and again in early June for occupancy, defined as the presence of at least one egg (for American Kestrels) or nesting material or eggs (for European Starlings and other species). If occupied by American Kestrels, clutch size (the number of eggs) was determined. Unoccupied nest boxes (empty throughout the breeding season) and nest boxes with nontarget species were recorded, and nesting material and content from nonnative species (e.g., European Starlings) were removed. Nest boxes occupied by American Kestrels were checked regularly around the estimated hatch date (approximately 30 d after the last egg was laid or every 14 d if laying date was unknown). After hatching, the nestlings were counted and measured at approximately 7 d and 21 d of age, and if feasible, at 14 d of age. For nest boxes occupied by American Kestrels, a nesting attempt (a nest with at least one egg) was considered successful (i.e., nesting success) if at least one nestling reached 80% of fledging age (approximately 21 d; Griggs and Steenhoff 1993, Steenhof and Newton 2007). Multi-species occupancy was recorded if both species occupied the same nest box within the same breeding season, irrespective of the order of occupancy.

Statistical Analyses. First, we used generalized linear models (GLM) to assess (1) changes in nest box occupancy over time (with year as a continuous variable) by American Kestrels, European Starlings, and other species, (2) trends in the percentage of unoccupied nest boxes, and (3) trends in the percentage of nest boxes occupied by both American Kestrels and competitors in the same breeding season. Models were built using occupancy as a binomial variable (1 = occupied, 0 = not occupied) and logit links functions.

Second, we used generalized linear mixed models (GLMM) to evaluate the relationship between European Starling and other species occupancy on the response variables of American Kestrel occupancy, clutch size, number of fledglings, and nesting success. Nesting success and occupancy models were built using a binomial distribution and logit links functions with the response variable being 1 (successful/occupied) or 0 (not successful/not occupied), and nest box ID was included as a random factor and year as a covariate in all analyses. The clutch size model was built using a Conway-Maxwell-Poisson distribution with a log link function. The number of fledglings model was built using a Poisson distribution with a log link function.

Third, we used GLMs to assess overall American Kestrel nest productivity using clutch size, number of nestlings, and number of fledglings produced annually as the response variables. The clutch size model was built using a Conway-Maxwell-Poisson distribution with a log link function. The number of nestlings and number of fledglings models were built using a Poisson distribution and a log link function. We did these analyses on both the entire study period (1992–2021) and post-2005 (2006–2021). A previous study (Rusbuldt et al. 2006) within the same study area and nest box network, ending in 2005, suggested competition with European Starlings for limited nest cavities was high and could be impacting American Kestrel productivity and nesting success, which were decreasing at the time. Therefore, we analyzed data post-2005 to determine whether these trends continued. Likewise, we used GLMs using a binomial distribution and logit links functions to identify trends in the nesting success, both for the entire study period and post-2005. Values reported in the results are means ± standard deviation (SD) except where noted as standard error (SE), and a level of significance of $P < 0.05$ was used for all statistical tests. All statistical analyses were conducted in R version 4.1.1 (R Core Team 2021).

RESULTS

Annually, American Kestrels were the most frequent occupants of nest boxes ($\bar{x} = 49.4 \pm 14.9\%$), followed by European Starlings ($\bar{x} = 25.7 \pm 8.0\%$), and all other species ($\bar{x} = 7.6 \pm 4.4\%$). We found that American Kestrel nest box occupancy decreased over time ($\beta = -0.056 \pm 0.006$ [SE], $Z = -9.45$, $P < 0.001$) whereas European Starling occupancy increased over time ($\beta = 0.037 \pm 0.007$ [SE], $Z = 5.58$, $P < 0.001$; Fig. 1). We found no difference in other species occupancy over time at nest boxes ($\beta = -0.013 \pm 0.011$ [SE], $Z = -1.186$, $P = 0.236$; Fig. 1).

The percentage of unoccupied nest boxes averaged 20.7 ± 10.7% (range: 0–45%), and increased over the 30-yr period ($\beta = 0.0398 \pm 0.007$ [SE], $Z = -5.582$, $P < 0.001$). On average 7.0 ± 8.0% of occupied nest boxes had both American Kestrels and competitors (i.e., European Starlings and other species) using the same nest box within the same breeding season.

GLMM results revealed that European Starling occupancy had a negative association with American Kestrel occupancy ($\beta = -3.413 \pm 0.216$ [SE], $Z = -15.835$, $P < 0.001$), clutch size ($\beta = -0.206 \pm 0.043$[SE], $Z = -4.766$, $P < 0.001$), number of fledglings ($\beta = -0.689 \pm 0.149$ [SE], $Z = -4.634$, $P < 0.001$), and nesting success ($\beta = -1.044 \pm 0.374$ [SE], $Z = -2.789$, $P = 0.005$). Specifically, nesting success decreased by 26% (from 77.9% to 51.9%) when European Starlings used the same nest box within the same breeding season. In addition, other species' occupancy was also negatively associated with American Kestrel occupancy ($\beta = -1.360 \pm 0.244$ [SE], $Z = -5.564$, $P < 0.001$), and number of fledglings ($\beta = -0.313 \pm 0.133$ [SE], $Z = -2.348$, $P = 0.02$), but did not influence clutch size ($\beta = -0.085 \pm 0.045$ [SE], $t = -1.905$, $P = 0.06$) or nesting success ($\beta = -0.532 \pm 0.411$ [SE], $Z = -1.295$, $P = 0.195$).

Overall, we found no trend in American Kestrel nesting productivity throughout the 30-yr study period, with no difference in clutch size ($\beta = -0.0013 \pm 0.008$ [SE], $t = -1.710$, $P = 0.087$), number of nestlings ($\beta = -0.0029 \pm 0.0023$ [SE], $Z = -1.25$, $P = 0.208$), number of fledglings ($\beta = -0.0019 \pm 0.0024$ [SE], $Z = -0.79$, $P = 0.429$), or nesting success ($\beta = -0.0082 \pm 0.0094$ [SE], $Z = -0.876$, $P = 0.381$; Fig. 2). However, in recent years (2005 to 2021) the average number of nestlings ($\beta = -0.029 \pm 0.006$ [SE], $Z = -4.556$, $P < 0.001$), number of fledglings ($\beta = -0.029 \pm 0.006$ [SE], $Z = -4.478$, $P < 0.001$), and nesting success significantly decreased ($\beta = -0.085 \pm 0.025$ [SE], $Z = -3.316$, $P < 0.001$), while the average clutch size remained constant ($\beta = -0.003 \pm 0.002$ [SE], $t = -1.39$, $P = 0.16$; Fig. 2).

DISCUSSION

Although we did not explicitly study interspecific interactions at nest boxes, our results support our prediction that American Kestrel reproductive rate in eastern Pennsylvania is negatively associated with

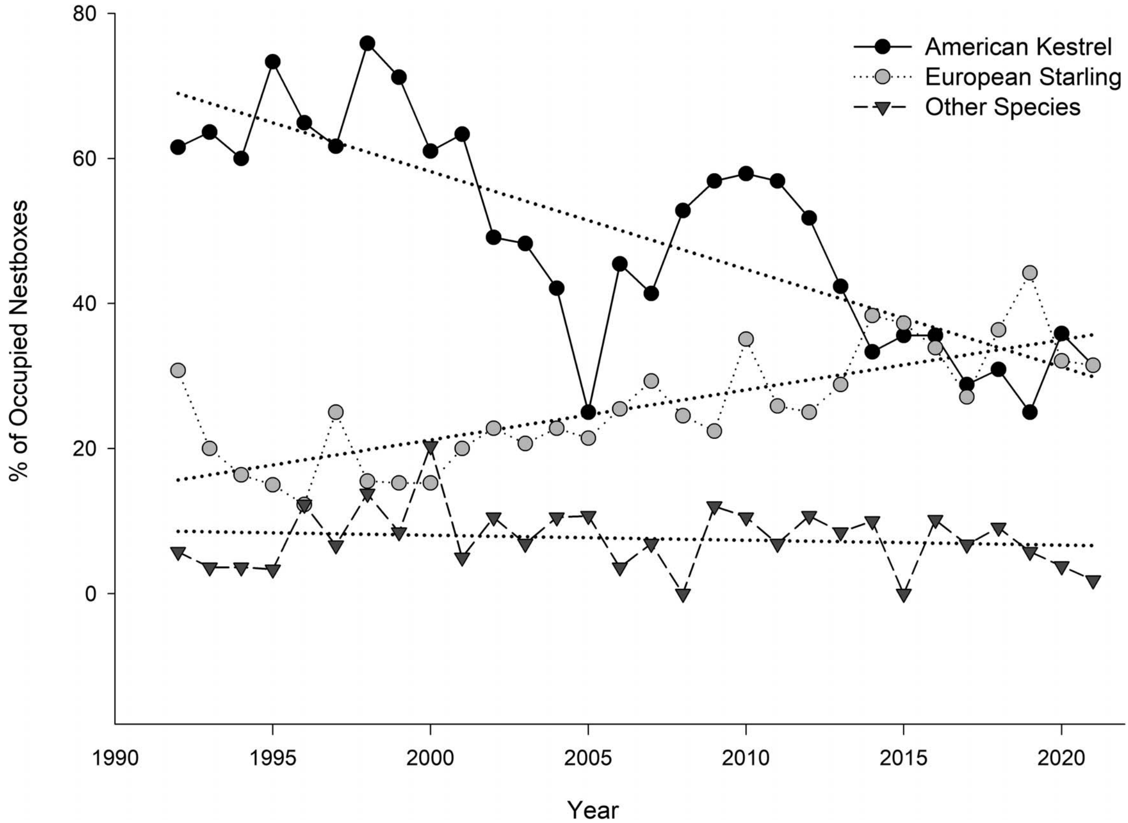

Figure 1. Species occupancy of American Kestrel nest boxes ($n = 60$) from 1992–2021 near Hawk Mountain Sanctuary, PA, USA. Dotted lines represent logistic regressions for each species group.

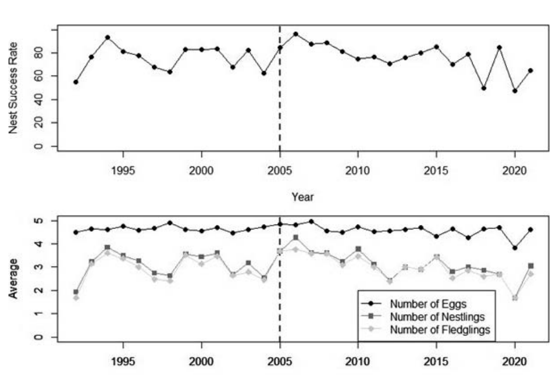

Figure 2. Average nesting success (top panel) and average nest productivity (number of eggs, nestlings, and fledglings; bottom panel) of American Kestrels at nest boxes ($n = 60$) from 1992–2021 near Hawk Mountain Sanctuary, PA, USA. Vertical dotted lines represent the starting point of the post-2005 analysis.

competition for nest boxes during the breeding season. When competitors (regardless of species) used the same nest box as American Kestrels within the same breeding season, American Kestrel occupancy, clutch size, and number of fledglings decreased compared to nest boxes without competitors. In addition, American Kestrel nesting success was 26% lower in nest boxes that were also occupied by European Starlings during the breeding season, a value that is comparable to that documented in an earlier study in eastern Pennsylvania (i.e., 28%; Rohrbaugh and Yahner 1997). However, because the majority of analyses indicate negative associations between competitor presence and American Kestrel reproductive parameters, regardless of the competitor species, the conclusion that American Kestrel reproductive rate is also negatively associated with the presence of other (non-European Starling) species is plausible. Temporal differences in the association between European Starling presence and

American Kestrel nesting success (whether success is greater when American Kestrels occupy a nest box before versus after European Starlings) needs further research.

European Starlings occupied a quarter of nest boxes available, more than all other species combined, supporting our prediction that European Starlings would have the highest occupancy of nontarget species. The opposing trends of American Kestrel and European Starling occupancy are concerning, as European Starlings will soon surpass American Kestrels as the most common occupant of Hawk Mountain Sanctuary nest boxes if this trend continues. This trend differs from that reported earlier, i.e., stable occupancies for both species from 1992–1997 within the same study area (Valdez et al. 2000). Occupancy trends of these two species suggest that European Starlings are actively taking sites from American Kestrels over time. Breeding Bird Survey data further highlight the significance of these trends, as European Starlings have been declining in Pennsylvania yet their occupancy of nest boxes has been increasing (Sauer et al. 2020). Conversely, the decline of American Kestrel occupancy in our nest boxes coincides with the decline of American Kestrel populations in much of eastern North America (Sauer et al. 2020). However, a decline in occupancy at monitored nest boxes or a negative correlation between American Kestrel and European Starling occupancy does not necessarily mean that the population is declining (McClure et al. 2017a) or impacted solely by competition. Given stable habitat conditions and reproductive rates at nesting sites over time, a decline in American Kestrel occupancy at nest boxes could reflect increased mortality during the nonbreeding season (Smallwood et al. 2009), or be influenced by immigration and adult survival (McClure et al. 2021). Another consideration is that increased European Starling occupancy could be a result of, rather than a contributor to, American Kestrel occupancy declines and nest failures. Bridging the gap between correlation and causation is needed to better understand the dynamic between these two species.

The high variability in the number of unoccupied nest boxes is also noteworthy and could be due to variability in nest box/cavity availability at sites not monitored within this study (McClure et al. 2017a). This study attempted to reduce this bias by analyzing a stable number of nest boxes that have existed throughout the entire study period. Indeed, the abundance of surrounding nest boxes has changed through time (i.e., Hawk Mountain Sanctuary monitored more nest boxes in the 1990s than today; Katzner et al. 2005), but one would expect unoccupied nest box frequency to be higher in the early years (opposite of our findings) because there were likely more potential cavities in the study area. In most years the percentage of unoccupied nest boxes was >10%, and this percentage increased over time, suggesting that American Kestrel-European Starling competition exists not due to a lack of nesting cavities, rather, because American Kestrels and European Starlings fight over the highest-quality sites. American Kestrels may compete with European Starlings over prime sites rather than settle for an unoccupied, poorer-quality site. Further research on this topic is warranted.

The declining trend of American Kestrel nest productivity (i.e., number of nestlings and fledglings per occupied nest) and nesting success in recent years is interesting as the average clutch size has remained constant. The cause of this apparent decline in nestling survival needs further research. Additionally, it is important to note that American Kestrel productivity and nesting success started to noticeably decline in 2005 in our study area (Fig. 2), contrary to Rusbuldt et al. (2006) who reported a decline in earlier years in the same study area. However, 2005 was the year with the lowest recorded American Kestrel occupancy (i.e., 25%), which was consistent with Rusbuldt et al. (2006). It is possible that multiple threats arose and subsided since 2005 to produce an apparently steady decline in American Kestrel productivity and nesting success through time (McClure et al. 2017b).

Based on our results, future studies should monitor the decline of American Kestrel occupancy while implementing strategies that discourage European Starling occupancy at American Kestrel nest boxes. For example, the frequency of usurpation by European Starlings may be less at nest boxes with low concealment, larger entrance holes, and a higher light intensity inside the box (Curley et al. 1987, Wilmers 1987, Rohrbaugh and Yahner 1997). Avoiding habitats preferred by nontarget species is a similar management strategy (Stojanovic et al. 2021), but might be difficult in this situation considering the ability of European Starlings to adapt to a large variety of habitats (Higgins et al. 2006). An additional obstacle involves the heterospecific habitat copying hypothesis, in which competitors use public information (such as breeding success) of other species to indicate habitat quality

(Parejo et al. 2005). Under this scenario, highly successful American Kestrel sites could be favored by European Starlings because of their success, which could lead to increased competition. Looking forward, the opposing trends of European Starling and American Kestrel occupancy coupled with the declining productivity of American Kestrel nests in this study area raise concerns over the future of this raptor species in eastern Pennsylvania, with potential implications for other areas experiencing American Kestrel declines. Taking actions to reduce competition at sites could aid in slowing down or reversing these trends.

ACKNOWLEDGMENTS

We are extremely grateful to all the people who contributed to Hawk Mountain Sanctuary's (HMS) long-term kestrel project including private landowners, HMS staff, interns and trainees, graduate students, and volunteers, and especially Chris Farmer, Bob and Sue Robertson, and Jim Klucsarits. Funding for this research was provided by HMS supporters of Adopt-a-Nest box and generous private donors, and the Pennsylvania Game Commission, Pennsylvania Department of Conservation and Natural Resources, the Giorgi Family Foundation, the Robert F. Schumann Foundation, and Christina Clayton and Stanley Kolber. We thank the three reviewers and the *Journal of Raptor Research* Associate Editor for their insightful comments and suggestions. This is Hawk Mountain conservation science contribution number 380.

LITERATURE CITED

Bailey, R. L., H. A. Faulkner-Grant, V. Y. Martin, T. B. Phillips, and D. N. Bonte (2020). Nest usurpation by non-native birds and the role of people in nest box management. Conservation Science and Practice 2(5):e185. doi:10.1111/csp2.185.

Baker, J., K. J. Harvey, and K. French (2014). Threats from introduced birds to native birds. Emu-Austral Ornithology 114(1):1–12. doi:10.1071/MU12122.

Bechard, M. J., and J. M. Bechard (1996). Competition for nest boxes between American Kestrels and European Starlings in an agricultural area of southern Idaho. In Raptors in Human Landscapes: Adaptation to Built and Cultivated Environments (D. M. Bird, D. E. Varland, and J. J. Negro, Editors). Academic Press, Cambridge, MA, USA. pp. 155–162.

Bird, D. M. (2009). The American Kestrel: From common to scarce? Journal of Raptor Research 43:261–262. doi:10.3356/0892-1016-43.4.261.

Charter, M., I. Izhaki, and Y. Leshem (2010). Effects of the risk of competition and predation on large secondary cavity breeders. Journal of Ornithology 151:791–795. doi:10.1007/s10336-010-0514-z.

Cockle, K. L., K. Martin, and T. Wesołowski (2011). Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Frontiers in Ecology and the Environment 9:377–382. doi:10.1890/110013.

Colléony, A., and A. Shwartz (2020). When the winners are the losers: Invasive alien bird species outcompete the native winners in the biotic homogenization process. Biological Conservation 241:e108314. doi:10.1016/j.biocon.2019.108314.

Curley, E. M., R. Bowman, and D. M. Bird (1987). Nest site characteristics of boxes occupied by starlings and kestrels. In The Ancestral Kestrel (D. M. Bird and R. Bowman, Editors). Raptor Research Foundation Inc. and Macdonald Raptor Research Center of McGill University, St. Anne de Bellevue, Quebec, Canada. pp. 160–164.

Czeszczewik, D., W. Walankiewicz, and M. Stańska (2008). Small mammals in nests of cavity-nesting birds: Why should ornithologists study rodents? Canadian Journal of Zoology 86:286–293. doi:10.1139/Z07-139.

Freed, L. A., and R. L. Cann (2009). Negative effects of an introduced bird species on growth and survival in a native bird community. Current Biology 19:1736–1740. doi:10.1016/j.cub.2009.08.044.

Griggs, G. R., and K. Steenhof (1993). Photographic Guide for Aging Nestling American Kestrels. USDI Bureau of Land Management. Raptor Research Technical Assistance Center, Boise, ID, USA.

Higgins, P. J., J. M. Peter, and S. J. Cowling (2006). Handbook of Australian, New Zealand, and Antarctic Birds, Vol. 7: Boatbill to Starlings. Oxford University Press, Melbourne, Australia.

Ingold, D. J. (1994). Influence of nest-site competition between European Starlings and woodpeckers. Wilson Bulletin 106:227–241.

Katzner, T., S. Robertson, B. Robertson, J. Klucsarits, K. McCarty, and K. L. Bildstein (2005). Results from a long-term nest-box program for American Kestrels: Implications for improved population monitoring and conservation. Journal of Field Ornithology 76:217–226. doi:10.1648/0273-8570-76.3.217.

Klucsarits, J. R., B. Robertson, and S. Robertson (1997). Breeding success of American Kestrels nesting in boxes in eastern Pennsylvania, 1987–1994. Pennsylvania Birds 11:138–140.

Koenig, W. D. (2003). European Starlings and their effect on native cavity-nesting birds. Conservation Biology 17:1134–1140. doi:10.1046/j.1523-1739.2003.02262.x.

Kolowski, J., L. Morrow, and J. Morrow (2022). Factors associated with American Kestrel (*Falco sparverius*) nest box occupancy and reproductive success in an agricultural landscape. Journal of Raptor Research 57:220–237. doi:10.3356/JRR-21-64.

Loftin, R. W. (1992). Use of nest boxes by the Florida Kestrel. Florida Field Naturalist 20:57–64.

Martin-Albarracin, V. L., G. C. Amico, D. Simberloff, and M. A. Nuñez (2015). Impact of non-native birds on native ecosystems: A global analysis. PLoS ONE 10(11):e0143070. doi:10.1371/journal.pone.0143070.

McClure, C. J. W., J. L. Brown, S. E. Schulwitz, J. Smallwood, K. E. Farley, J.-F. Therrien, K. E. Miller, K. Steenhof, and J. A. Heath (2021). Demography of a widespread raptor across disparate regions. Ibis 163:658–670. doi:10.1111/ibi.12916.

McClure, C. J. W., D. M. Hilleary, and D. P. Spurling (2015). American Kestrels actively exclude European Starlings from using a nest box. Journal of Raptor Research 49:231–233. doi:10.3356/0892-1016-49.2.231.

McClure, C. J. W., B. P. Pauli, and J. A. Heath (2017a). Simulations reveal the power and peril of artificial breeding sites for monitoring and managing animals. Ecological Applications 27:1155–1166. doi:10.1002/eap.1509.

McClure, C. J. W., S. E. Schulwitz, R. Van Buskirk, B. P. Pauli, and J. A. Heath (2017b). Commentary: Research recommendations for understanding the decline of American Kestrels (*Falco sparverius*) across much of North America. Journal of Raptor Research 51:455–464. doi:10.3356/JRR-16-73.1.

Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: A review. Biological Conservation 70:265–276.

Orchan, Y., F. Chiron, A. Shwartz, and S. Kark (2013). The complex interaction network among multiple invasive bird species in a cavity-nesting community. Biological Invasions 15:429–445. doi:10.1007/s10530-012-0298-6.

Parejo, D., E. Danchin, and J. M. Avilés (2005). The heterospecific habitat copying hypothesis: Can competitors indicate habitat quality? Behavioral Ecology 16:96–105. doi:10.1093/beheco/arh136.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rohrbaugh, R. W., Jr., and R. H. Yahner (1997). Effects of macrohabitat and microhabitat on nest-box use and nesting success of American Kestrels. Wilson Bulletin 109:410–423.

Rusbuldt, J. J., J. R. Klucsarits, S. Robertson, and B. Robertson (2006). Reproductive success of American Kestrels using nest boxes in eastern Pennsylvania, 1992–2005. Pennsylvania Birds 20:112–117.

Sauer, J. R., W. A. Link, and J. E. Hines (2020). The North American Breeding Bird Survey, analysis and results 1966–2019. U.S. Geological Survey data release. doi:10.5066/P96A7675.

Smallwood, J. A., M. F. Causey, D. H. Mossop, J. R. Klucsarits, B. Robertson, S. Robertson, J. Mason, M. J. Maurer, R. J. Melvin, R. D. Dawson, G. R. Bortolotti, et al. (2009). Why are American Kestrel (*Falco sparverius*) populations declining in North America? Evidence from nest-box programs. Journal of Raptor Research 43:274–282. doi:10.3356/JRR-08-83.1.

Steenhof, K., and I. Newton (2007). Assessing raptor reproductive success and productivity. In Raptor Research and Management Techniques (D. M. Bird and K. L. Bildstein, Editors), Hancock House, Blaine, WA, USA and Surrey, BC, Canada. pp. 181–192.

Stojanovic, D., G. Owens, C. M. Young, F. Alves, and R. Heinsohn (2021). Do nest boxes breed the target species or its competitors? A case study of a critically endangered bird. Restoration Ecology 29(3):e13319. doi:10.1111/rec.13319.

Valdez, U., S. Robertson, B. Robertson, and K. L. Bildstein (2000). Nest box use by American Kestrels (*Falco sparverius*) and European Starlings (*Sturnus vulgaris*) in eastern Pennsylvania. Pennsylvania Birds 14:150–153.

Van der Hoek, Y., G. V. Gaona, and K. Martin (2017). The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world. Diversity and Distributions 23:1120–1131. doi:10.1111/ddi.12601.

Varland, E. D., and T. J. Loughin (1993). Reproductive success of American Kestrels nesting along an interstate highway in central Iowa. Wilson Bulletin 105(3):465–474.

Weitzel, N. H. (1988). Nest-site competition between the European Starling and native breeding birds in northwestern Nevada. The Condor 90:515–517.

Wiebe, K. L. (2011). Nest sites as limiting resources for cavity-nesting birds in mature forest ecosystems: A review of the evidence. Journal of Field Ornithology 82:239–248. doi:10.1111/j.1557-9263.2011.00327.x.

Wiebe, K. L., K. L. Cockle, M. K. Trzcinski, A. B. Edworthy, and K. Martin (2020). Gaps and runs in nest cavity occupancy: Cavity "destroyers" and "cleaners" affect reuse by secondary cavity nesting vertebrates. Frontiers in Ecology and Evolution 8:1–11. doi:10.3389/fevo.2020.00205.

Wilmers, T. J. (1987). Competition between Starlings and Kestrels for nest boxes. In The Ancestral Kestrel (D. M. Bird and R. Bowman, Editors). Raptor Research Foundation Inc. and Macdonald Raptor Research Center of McGill University, St. Anne de Bellevue, Quebec, Canada. pp. 156–159.

Received 9 August 2022; accepted 25 February 2023
Associate Editor: Christopher J. W. McClure