SHORT COMMUNICATIONS

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NEST BOX ENTRANCE HOLE SIZE INFLUENCES PREY DELIVERY SUCCESS BY AMERICAN KESTRELS

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ABSTRACT.—Nest boxes are a popular tool for research and conservation of American Kestrels (*Falco sparverius*; hereafter "kestrel"). The size of nest box entrance holes affects occupancy, interspecific competition, and nest predation for a number of bird species, but effects on prey delivery success are unstudied. We used digital video cameras to monitor kestrels using two nest box designs, one with a small circular entrance hole (8.75 cm in diameter; $n = 8$) and the other with a large U-shaped entrance hole (7.62 cm wide by 12.07 cm high; $n = 6$), to compare the rates at which kestrels failed to deliver large prey (vertebrates) into the nest box while provisioning nestlings. Across 111 d of monitoring, we observed a significantly higher prey delivery failure rate at the boxes with small holes (8.9%) compared to boxes with large holes (1.6%). Boxes with small holes fledged 4.33 nestlings and boxes with large holes fledged 4.5. These results suggest that kestrels nesting in boxes with small entrance holes may have higher costs while provisioning nestlings, compared to kestrels using boxes with larger entrance holes. We conclude that the ideal entrance hole size for kestrel nest boxes may be a compromise between being small enough to minimize predation, yet large enough to allow kestrels with large prey to easily enter. Future research should investigate whether boxes with higher prey delivery failure rates have lower reproductive success.

KEY WORDS: *American Kestrel*; Falco sparverius; *entrance hole*; *nest box*; *prey delivery*; *provisioning*.

EL TAMAÑO DEL HUECO DE ENTRADA DE LA CAJA NIDO INFLUYE SOBRE EL ÉXITO DE APORTE DE PRESAS POR *FALCO SPARVERIUS*

RESUMEN.—Las cajas nido son una herramienta popular para la investigación y conservación de *Falco sparverius*. El tamaño del hueco de entrada de la caja nido afecta la ocupación, la competencia interespecífica y la depredación del nido para un número de especies de aves, pero los efectos en el éxito de aporte de presas no están estudiados. Usamos videocámaras digitales para monitorear a *F. sparverius* usando dos diseños de cajas nido, uno con un hueco de entrada circular pequeño (8.75 cm de diámetro;

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$n = 8$) y otro con un hueco de entrada en forma de U grande (7.62 cm de ancho por 12.07 cm de alto; $n = 6$) con el fin de comparar las tasas de fracaso en el aporte de presas grandes (vertebrados) al interior de las cajas nido de los individuos que aprovisionan a los polluelos. A lo largo de 111 d de monitoreo, observamos una tasa de fracaso de aporte de presas significativamente más alta en las cajas con huecos pequeños (8.9%) en comparación con las cajas con huecos grandes (1.6%). Las cajas con huecos pequeños produjeron 4.33 volantones mientras que las cajas con huecos grandes produjeron 4.5 volantones. Estos resultados sugieren que los individuos de *F. sparverius* que anidan en cajas con huecos de entrada pequeños pueden tener costes más altos mientras aprovisionan a los polluelos, en comparación con los individuos que usan cajas con huecos de entrada más grandes. Concluimos que el tamaño ideal del hueco de entrada de las cajas para *F. sparverius* puede representar un compromiso entre ser lo suficientemente pequeño para minimizar la depredación, pero lo suficientemente grande para permitir que los individuos con presas grandes puedan entrar con facilidad. Las investigaciones futuras deberían investigar si las cajas con mayores tasas de fracaso de aporte tienen menor éxito reproductivo.

[Traducción del equipo editorial]

Nest box installation and monitoring have long been used to study cavity-nesting birds and the prevalence of these techniques has steadily increased since they were first employed (Lambrechts et al. 2010). The ability to access and monitor sites in which free-ranging birds roost and reproduce has provided unique insights into avian natural history and ecology (Newton 1994, Visser et al. 2003, Both et al. 2004, Blondel et al. 2006, Griffith et al. 2008, Steenhof and Peterson 2009). Nest box monitoring programs can also serve as a conservation tool for declining species and/or species that are experiencing a decline in natural nest cavities (Hamerstrom et al. 1973, Spring et al. 2001, Wiebe 2011, Libois et al. 2012) with careful consideration of the benefits and limits of such programs (McClure et al. 2017).

Variation in nest box design and placement can significantly influence the results of nest box-based studies (Lambrechts et al. 2010, 2011). Differing nest box features among and within studies include entrance hole orientation and nest box dimensions (Charter et al. 2007, Butler et al. 2009, Rahman et al. 2016). The shape and size of a nest box's entrance hole strongly influence which species or individuals occupy the box (Valdez et al. 2000, López et al. 2010) and which predator species can access the nest (Hakkarainen and Korpimaki 1996). Nest box entrance size could potentially also influence provisioning by parent birds although we are unaware of any studies that have addressed this issue.

The American Kestrel (*Falco sparverius*; hereafter "kestrel") is a popular species for nest box monitoring programs for both research and conservation efforts (Katzner et al. 2005, Eschenbauch et al. 2009, Davis et al. 2017). In addition, kestrels provide ecosystem services in some fruit-producing regions by reducing the abundance of fruit-eating birds (Shave et al. 2018). Despite being the most abundant and widespread North American falcon (Smallwood and Bird 2002), evidence indicates that the kestrel has experienced population declines, particularly in the eastern part of the continent (Farmer et al. 2008, Farmer and Smith 2009, Smallwood et al. 2009a, Sauer et al. 2013). Although kestrels primarily feed on invertebrates, their diet varies from place to place and year to year; they sometimes take mammals, birds, and reptiles approaching their own body size (Smallwood and Bird 2002, Shave 2017). A small entrance hole may present challenges in delivering these larger prey into the nest box.

We conducted an observational study using two kestrel nest box designs to investigate whether the size and shape of a nest box entrance hole affected the rate at which adult kestrels were able to successfully deliver large prey items (vertebrates) into the nest box. If nest boxes with smaller entrance holes showed higher delivery failure rates of large prey, as we expected, then this could potentially have consequences for kestrel energy budgets and reproductive success.

METHODS

Study Area. Between 2012 and 2015 we installed kestrel nest boxes (10 before the 2013 nesting season, 10 more before the 2014 nesting season, and seven more before the 2016 nesting season) within or adjacent to sweet and tart cherry (*Prunus* spp.) orchards in Leelanau County (45°08′N 86°02′W) in northern Michigan. In 2014–2017, we installed boxes (two before the 2015 nesting season, 21 more before the 2016 nesting season, eight more before the 2017 nesting season, and one more before the 2018 nesting season) in blueberry (*Vaccinium corymbosum*) fields in Allegan (42°34′N, 86°15′W) and Van Buren (42°16′N, 86°19′W) Counties in western Michigan (Fig. 1). Both regions are largely agricultural with some forested and residential areas (USDA 2012). The agricultural development in these counties has resulted in large patches of open areas preferred by kestrels (Smallwood et al. 2009b), interspersed with woodlands and largely rural residential areas. Leelanau County (6.3% pastureland, 25.7% woodland, 55.9% cropland) has more pastureland and woodland, and less cropland compared to Allegan (0% pastureland, 7.8% woodland, 82.6% cropland) and Van Buren Counties (0% pastureland, 14.5% woodland, 71.4% cropland; USDA 2012).

Figure 1. Locations of nest box study sites. Sites include cherry orchards in Leelanau County, MI (top right), and blueberry fields in Allegan and Van Buren Counties, MI (bottom left). Large squares indicate nest boxes with larger entrances and small squares indicate nest boxes with smaller entrances.

Nest Box Design. We used two models of boxes in both regions. The larger model had dimensions of 23.5 cm wide by 28.58 cm long by 43.18 cm high with a U-shaped entrance hole measuring 7.62 cm wide by 12.07 cm high (85.7 cm^2; Comfort 2012). The smaller model had dimensions of 22.5 cm wide by 21 cm long by 45 cm high with a circular entrance hole measuring 8.75 cm in diameter (60.1 cm^2; Coveside Conservation Products [2019]; Fig. 2). We mounted each box on a 4.5 or 5.5 m tower with a hinge allowing the box to be lowered to the ground (Comfort 2013). We mounted the box on the tower using a 9.5 cm $\times$ 9.5 cm, square-shaped aluminum turntable bearing attached to the upper back of the box. When we needed to examine the contents of the box, we kept the box upright as it was lowered using a rope attached via an eye hook to the bottom of the box. We spaced boxes at least 800 m apart and positioned them so that the entrance holes faced southeast to promote occupancy and hatching success (Balgooyen 1990, Butler et al. 2009, Shave and Lindell 2017a).

Nest Monitoring. We monitored boxes during the nesting season (April–August) of 2016. We began checking boxes on 23 April in the cherry orchards and 13 April in the blueberry fields at 7–10-d intervals and then as often as every other day in the week prior to hatching in order to determine hatch date (date that the first egg hatched). We used a pole-mounted camera to see inside the boxes without lowering them (Proudfoot 1996; see Shave and Lindell 2017a for design details). We defined a nestling as "fledged" once it reached 22 d (80% of fledging age), which is typical for kestrel studies (Steenhof and Peterson 2009, Shave and Lindell 2017a).

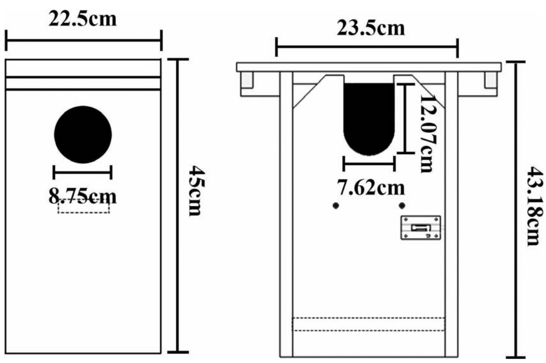

Figure 2. Scaled diagram of nest boxes used to assess the associations between delivery success of large prey items by American Kestrels and nest box entrance size. The smaller box (left) has a volume of 21,263 cm^3 and the larger box (right) 29,001 cm^3. The larger box is 7.6 cm longer front-to-back. The smaller box's circular entrance hole has an area of 60.1 cm^2 and the larger box's U-shaped entrance hole has an area of 85.7 cm^2.

Provisioning of Nestlings. We equipped the boxes with waterproof security cameras attached to an overhang on the box exterior (Shave and Lindell 2017a). We aimed the cameras at the entrance hole to record the adults arriving at the box and provisioning the nestlings. We recorded video from the cameras using a digital video recorder powered by a rechargeable sealed lead deep cycle battery, all housed within a plastic storage tote (Shave and Lindell 2017a). We used video data from six boxes (one with a large entrance hole and five with small entrance holes) on the blueberry farms and eight boxes (five with large entrance holes and three with small entrance holes) located in the cherry orchards. We rotated cameras among boxes to roughly match amounts of video recordings from both regions, box designs, and nestling age measured as days from the date that the first egg hatched. Nestling ages ranged from 3–32 d of age when video data were recorded, with a majority of recordings from 12–25 d.

We employed the motion activation function of the digital video recorders so that recording started when an adult kestrel arrived and entered or exited the box. During video review we documented and identified all prey deliveries and noted if a delivery was dropped. We defined a delivery as a "drop" if a kestrel failed to deposit the prey item within the box and the prey item fell to the ground. These drops generally appeared to be a result of the food item being larger than what the adult could effectively handle and transfer into the box, given the size of the entrance hole, presumably because the entrance hole was small. We predominantly observed kestrels bringing large prey to the box in their feet, not in their bills. We often observed kestrels falling to the ground with their prey item. Prey items that were retrieved and successfully deposited after dropping were counted as successful deliveries. We defined a "retrieval"' as any delivery within 30 sec of a drop as long as the prey species matched that of the dropped delivery.

We occasionally observed the adult male, adult female, and nestling kestrels aggressively interacting with each other at the entrance hole, resulting in dropped prey items. We did not define these situations as drops.

Data Analysis. Only large prey items (mammals, birds, and reptiles) that were essentially intact when delivered to boxes were included in analyses. We defined large prey as any intact chordate delivered into the box. Invertebrates and pieces of large prey (organs and tissue) were excluded because the size of the entrance hole did not appear to present any challenges in delivering these smaller items. We totaled all large prey delivery attempts and drops for each box. We used logistic regression modeling to evaluate the effect of nest box entrance hole size on the proportion of dropped large prey items. We fit two nested models using the glm function in Program R (version 3.1.0; R Core Team 2017): an intercept-only null model and a model with hole size (small or large) as an explanatory variable. Both models included the proportion of dropped large prey items as the response variable, weighted by the number of large prey delivery attempts observed per box. We used an analysis of deviance test to compare the nested models and determine the significance of the hole size variable (Zuur et al. 2009).

We calculated mean productivity as the total number of fledglings divided by the number of boxes of each design with nesting attempts (i.e., a nest where eggs were laid; Eschenbauch et al. 2009, Shave and Lindell 2017a).

RESULTS

We recorded 938 large prey item deliveries (Table 1) and 3726 small prey deliveries across approximately 111 d of monitoring 14 kestrel nest boxes with young. We recorded 564 large prey deliveries over 67 d from boxes with small entrance holes (n = 8) and 374 large prey deliveries over 44 d from boxes with large entrance holes (n = 6). Small-entrance-hole boxes had 514 large prey delivery successes and 50 drops (8.9%), while boxes with large entrance holes had 368 successes and 6 drops (1.6%). Comparison of the nested logistic regression models via analysis of deviance indicated that hole size was significant (df = 1, $\chi^2 = 25.06$, $P < 0.001$). Proportions of dropped large prey were greater for boxes with small entrance holes ($\beta_{small} = 1.79 \pm 0.44$). We observed a 28% retrieval rate of dropped large prey, usually by the individual that dropped the prey but we also observed one incident where the adult male retrieved a large prey item dropped by the female.

We checked 10 nest boxes (six with small entrance holes and four with large entrance holes) often enough to determine whether the nest fledged young; all ten of these boxes successfully fledged young. Nest boxes with small

Table 1. Large-prey delivery attempts and the number of large prey dropped by American Kestrels using nest boxes with small and large entrances. Nest boxes were placed in agricultural areas producing primarily blueberries or cherries. The age of nestlings is a range estimate for each brood during the duration of monitoring.

Box	Design	Crop	Nestling Ages (d)	Days Of Monitoring	Prey Delivery Attempts	Drops
1	Small	Blueberry	15–32	7	33	10
2	Small	Cherry	4–25	11	81	18
3	Small	Blueberry	19–23	3	18	0
4	Small	Blueberry	12–32	20	195	11
5	Small	Cherry	3–20	6	67	1
6	Small	Cherry	3–26	12	102	7
7	Small	Blueberry	19–24	5	39	3
8	Small	Blueberry	16–18	3	29	0
9	Large	Cherry	4–25	8	68	2
10	Large	Cherry	16–22	7	58	0
11	Large	Blueberry	12–24	7	54	0
12	Large	Cherry	7–20	7	56	0
13	Large	Cherry	4–24	8	64	0
14	Large	Cherry	11–21	7	74	4

entrance holes ($n = 6$) fledged 4.33 individuals, while nest boxes with large entrance holes ($n = 4$) had a mean productivity of 4.5 fledglings.

DISCUSSION

The specific designs (e.g., size, dimensions, material) of artificial nest boxes are rarely reported in methodologies. Lambrechts et al. (2011) noted that 65.2% of nest box studies published after 1994 ($n = 221$) lacked detailed information on nest box design. Our results show that boxes with smaller entrance holes had a significantly higher rate of dropped large prey. These results support the idea that a larger nest box entrance hole facilitates a higher rate of successful large prey delivery. This likely means that a larger entrance hole also results in less wasted energy when adult kestrels provision nestlings. After a large prey item was dropped, kestrels ignored it 72% of the time and returned with a different prey item as their next delivery.

An alternative explanation for more drops at boxes with small entrance holes is that the most fit kestrels were able to occupy and defend the larger-holed boxes. This may have resulted in the less-competent kestrels occupying the boxes with smaller entrance holes and could potentially explain the higher drop rates at those boxes. However, dates of occupancy of boxes with large holes were not consistently earlier than boxes with small holes at either of the two study regions, indicating that there is not a preference for boxes with large holes that might have resulted in more-competent kestrels occupying boxes with large holes. In the cherry orchards, both nest box designs were first occupied between 30 April and 17 May. In the blueberry fields, the one large entrance nest box was first occupied on 25 April and the small entrance nest boxes were first occupied between 15 April and 1 June. Our sample sizes are small but suggest similarly competent kestrels occupied boxes with large and small holes.

The rate of failed large prey deliveries at boxes with small holes could potentially affect reproductive success; however, we could not detect significant differences in fledgling rates or productivity from boxes with small and large holes with our small sample sizes. It is possible that we would have detected productivity differences with larger sample sizes. It is also possible that energy costs associated with dropped large prey could have hard-to-detect effects on adults, such as altered short-term movement or survival patterns. Repeatedly dropping large prey may result in kestrels switching to providing more small prey. Increased parental workloads associated with experimentally increased brood sizes resulted in significantly lower local survival rates in the following year for European Kestrels (*Falco tinnunculus*; Deerenberg et al. 1995). Nest box size itself may not be a critical aspect of box design for kestrels. Bortolotti (1994) found no difference in productivity of kestrels based on box size. Our box size covaried with our entrance hole sizes, with boxes with larger entrance holes being 26.7% larger in volume.

Dropped large prey likely occurs with other cavity-nesting raptors that use nest boxes with entrance holes not much wider than the species' girth. Small entrance holes may minimize predation for nest-box-using passerines, which deliver food stored in the bill or throat. Raptors, however, sometimes deliver larger prey items into the nest box with their feet (Gill 2007). In areas with low predation at nest boxes, such as our study regions in Michigan (Shave and Lindell 2017b, C. Lindell et al. unpubl. data), boxes with larger entrance holes likely have few costs and we recommend they be used for kestrels. In areas with more predation, the costs of boxes with large entrance holes may be higher, and boxes with smaller entrance holes could benefit kestrels by reducing predation, even though adults will drop more large prey when provisioning nestlings. Thus, the ideal entrance hole size for nest boxes in an area may be a compromise between that needed to minimize predation and minimize dropped prey. A focused larger-scale study could address these types of questions.

Nest box programs can be used to monitor abundance and population trends (Bloom and Hawks 1983). Kestrel nest box programs alone have provided information on a number of topics including breeding phenology, carotenoid variation, and the influence of agriculture on habitat selection (Sassani et al. 2016, Smith et al. 2016, Touihri et al. 2019). Kestrel nest boxes are also promoted to landowners for birdwatching, conservation, and pest management (Comfort 2012, Shave and Lindell 2017b, Lindell et al. 2018, Shave et al. 2018). Considering the popularity of kestrel nest box programs (American Kestrel Partnership 2019), the potential for nest boxes to play a role in the conservation of kestrels, and the value of kestrels in delivering ecosystem services in fruit-producing systems (Shave et al. 2018), identifying nest box designs that optimize kestrel reproductive success and survival should be a priority in future work.

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