EVALUATING THE CONSERVATION AND AGRICULTURAL APPLICATIONS OF ORCHARD NEST BOXES FOR A DECLINING RAPTOR

By

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ABSTRACT

EVALUATING THE CONSERVATION AND AGRICULTURAL APPLICATIONS OF ORCHARD NEST BOXES FOR A DECLINING RAPTOR

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Human activities over the past 50 years have caused changes in ecosystems that have led to gains in economic development at the cost of biodiversity loss and degradation of ecosystem services, the functions and processes of ecosystems that benefit human well being. For example, agricultural expansion and intensification has degraded wildlife habitat by removing sources of nesting and roosting cavities, particularly mature trees, which can negatively affect abundance and diversity of animal taxa that provide regulating ecosystem services, such as pest reduction. Many cavity-dependent species will use nest boxes in areas where natural cavities are scarce, thus nest boxes are an easily implemented landscape enhancement. In this dissertation, I drew from theoretical frameworks of population dynamics, foraging ecology, parental care, and predator-prey interactions to assess the potential benefits of nest boxes in terms of conservation of a declining raptor and enhancement of pest reduction services in a fruit-growing region.

Although the American Kestrel (*Falco sparverius*) is the most common falcon in North America, multiple monitoring programs have detected significant and widespread population declines. While the causes of these declines at the continent-wide scale are not yet understood, at the local scale, many breeding kestrel populations are limited by availability of nest sites. In Chapter 1, I monitored 18 new nest boxes installed in cherry orchards (*Prunus* spp.) in northwestern Michigan and found that kestrels made nesting attempts in 100% of the boxes and showed high reproductive rates. Furthermore, models of daily survival rates for nests and brood size at fledging for successful nests indicated that kestrels were highly tolerant of both traditional monitoring techniques (opening the box) and newer camera technologies (a pole-mounted video camera and nest-box video cameras). In Chapter 2, I used roadside transect surveys and multi-season occupancy modeling to determine that the installation of nest boxes has increased the presence of kestrels in the region between 2013 and 2016.

Chapters 1 and 2 indicate that orchard nest boxes can benefit the local conservation of kestrels by increasing breeding populations, which may in turn benefit agriculture by promoting kestrel presence, and therefore predation on pest species, in and around orchards. In Chapter 3, I used nest box video cameras to determine that kestrels provision their nestlings with known orchard pests, including grasshoppers, voles, and frugivorous birds; furthermore, I observed generalizable trends in kestrel prey removal based on nestling age, seasonal timing of prey availability, brood size and sex ratio, weather, and adult female movements relative to the nest box. In Chapter 4, I used transect surveys to determine that fruit-eating bird counts were lower in orchards with active kestrel nest boxes, thus kestrel activity associated with nest boxes likely acts as a reliable cue of predation risk that, in combination with direct consumption, reduces fruit-eating bird abundances in orchards. Finally, in Chapter 5, I used live-trapping to determine that summer small mammal abundances were lower in orchards with active kestrel boxes and orchards that had been more recently mowed; however, these differences did not carry over as differences in winter presence in orchards, when mammal damage to trees is most likely. Based on the results, I recommend that future projects utilize a consistent surveying protocol across seasons, conduct winter surveys in orchards without rodenticide use, and combine small mammal surveys with fruit and tree damage assessments in order to identify which species are responsible for damage throughout the year and under different conditions (e.g., with variation in snowfall).

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CHAPTER 1

AMERICAN KESTRELS OCCUPYING NEST BOXES IN MICHIGAN CHERRY ORCHARDS SHOW HIGH REPRODUCTIVE RATES AND TOLERANCE OF MONITORING

Megan E. Shave and Catherine A. Lindell
(Journal of Raptor Research, 2017, 51: 50-60)

Abstract

Installation of nest boxes for a declining raptor species, the American Kestrel (*Falco sparverius*), in agricultural areas may benefit both local kestrel conservation and management of prey species that cause damage to crops. Kestrels responded quickly to the installation of 18 new nest boxes in northwestern Michigan cherry (*Prunus* spp.) orchards between 2012 and 2013; they made nesting attempts (laid eggs) in 100% of boxes by 2015. In addition, kestrels that made nesting attempts in these boxes in 2013 – 2015 showed high reproductive rates: apparent nesting success was 91%, and mean number of fledglings per box with nesting attempts was 3.8. Also, kestrels were highly tolerant of both traditional monitoring techniques (opening the box) and newer camera technologies (a pole-mounted video camera and nest-box video cameras). Generalized linear modeling indicated that variables related to nest monitoring techniques and effort did not significantly affect daily survival rates for nests or brood size at fledging for successful nests; only hatching date had a small positive effect on brood size at fledging. These results suggest that orchard nest boxes have the potential to sustain or increase the breeding kestrel population in the region while increasing kestrel predation of crop-damaging prey in and around cherry orchards. This is promising for ongoing and future work with nest boxes in agricultural regions.

Introduction

Although the American Kestrel (*Falco sparverius*; hereafter kestrel) is the most common falcon in North America (Smallwood and Bird 2002), multiple monitoring programs have detected significant and widespread population declines (Farmer and Smith 2009, Sauer et al. 2014). These observed declines may be the result of habitat loss on wintering grounds and along migration routes or distribution shifts due to climate change (Smallwood et al. 2009a, Paprocki et al. 2014). At the local scale, human development negatively affects breeding kestrel populations through the removal of tree snags and other sources of natural nesting cavities, which can lead to nest site limitation (Rohrbaugh and Yahner 1997, Smallwood and Bird 2002). However, kestrels readily use nest boxes in areas with valuable hunting habitat, such as open agricultural areas, and box installation can increase local kestrel populations (Smallwood and Collopy 2009).

Nest boxes in agricultural areas are of additional interest because of their potential to promote the reduction of prey species that damage crops. Biological control via a native predator is an appealing management practice that has the potential to limit crop damage by promoting natural predator-prey relationships in agroecosystems (e.g., Jedlicka et al. 2011, Kross et al. 2012). An important step in this type of biological control program is determining whether nest boxes successfully attract the target predator species.

The first objective of this study was to determine occupancy and reproductive rates of kestrels using new nest boxes installed in cherry orchards in northwestern Michigan. High rates of box occupancy and nesting attempts would suggest that kestrels in the region are still limited by nest-site availability and that additional boxes might increase the local population by supporting more breeding pairs within the same area. Determining reproductive rate is important because low nesting success or number of young fledged would be an early indicator that orchards and surrounding areas are not high-quality habitat. For example, kestrel nesting success in southwestern Idaho was lower in areas with high levels of anthropomorphic stressors (e.g., traffic noise; Strasser and Heath 2013). Some human-dominated landscapes may serve as ecological traps by attracting kestrels to areas with favorable hunting resources (e.g., high prey availability along roadsides) but also exposing them to increased mortality and disturbance due to nearby human activity (e.g., road traffic). One concern for our study region is whether the agricultural activities associated with orchards (e.g., mowing, spraying, and harvesting) would lead to low nesting success (Rohrbaugh and Yahner 1997).

Our second objective was to determine whether different methods of monitoring the boxes affected nesting success and productivity. In addition to opening boxes when banding nestlings and capturing adults, we also monitored nests using video cameras. Use of photo and video camera technology for monitoring bird nests is becoming more common (Cox et al. 2012), and we used two such systems: a portable pole-mounted video camera for checking nests and video cameras installed in nest boxes prior to the breeding season for recording adult activity at the boxes. Previous studies of multiple passerine species have indicated that nest cameras do not increase the risk of nest abandonment when deployed at times that minimize disturbance to the adults; furthermore, nest cameras may even reduce depredation risk (Richardson et al. 2009). Previous studies of raptor species have proposed that nest cameras cause minimal disturbance (e.g., Steen 2009, Kross and Nelson 2011), and Dykstra et. al (2002) have quantitatively demonstrated that nest cameras do not significantly affect Bald Eagle (*Haliaeetus leucocephalus*) reproductive rates. However, we have found no quantitative assessments of the effects of nest cameras on kestrel reproductive rates. In addition, previous studies have proposed that checking nests using a pole-mounted camera system also minimizes nest disturbance (e.g., Proudfoot 1996, Eschenbauch et al. 2009), but we have found no quantitative assessments of the effects of pole-mounted camera use on raptor reproductive rates. Adult kestrels are generally tolerant of human activity at their nests (Smallwood and Bird 2002), including the opening of nest boxes and handling of the adults (Smallwood 2016). Thus, we predicted that our box-monitoring efforts would not have significant negative effects on the daily survival rate (DSR) of nests or on the brood size at fledging for successful nests. We predicted that nest features unrelated to monitoring, including seasonal timing of the nesting attempt and status of nest as a first or second attempt in a box, would instead influence nesting success and/or brood size at fledging, as suggested previously (e.g., Steenhof and Peterson 2009).

Methods

Study Area

We conducted this study during the 2013 – 2015 kestrel breeding seasons (April – August) in eastern Leelanau County, MI, an area that produces significant crops of cherries (*Prunus* spp.), as well as apples (*Malus domestica*) and wine grapes (*Vitis vinifera*; USDA. 2012 Census of Agriculture 2014). The region is largely agricultural with some residential and forested areas (USDA 2012 Census of Agriculture 2014). In addition to providing large patches of open habitats preferred by kestrels (Smallwood et al. 2009b), this region also lacks the multi-lane, high-traffic roads that negatively affect kestrel nesting success (Strasser and Heath 2013).

Beginning in the late 1980s, a Boy Scouts of America troop and other groups installed nest boxes on utility poles in this region (F. Otto, *Personal communication*). We found that 24 of these boxes remained intact in 2013. Between 2012 and 2013, we installed 18 new nest boxes within or next to cherry orchards (Fig. 1.1), usually near the edge of an orchard in an open spot where a tree was missing within a row. We installed boxes in five sweet cherry (*Prunus avium*) orchards and 12 tart cherry (*Prunus cerasus*) orchards. We installed one box in an apple orchard adjacent to a tart cherry orchard.

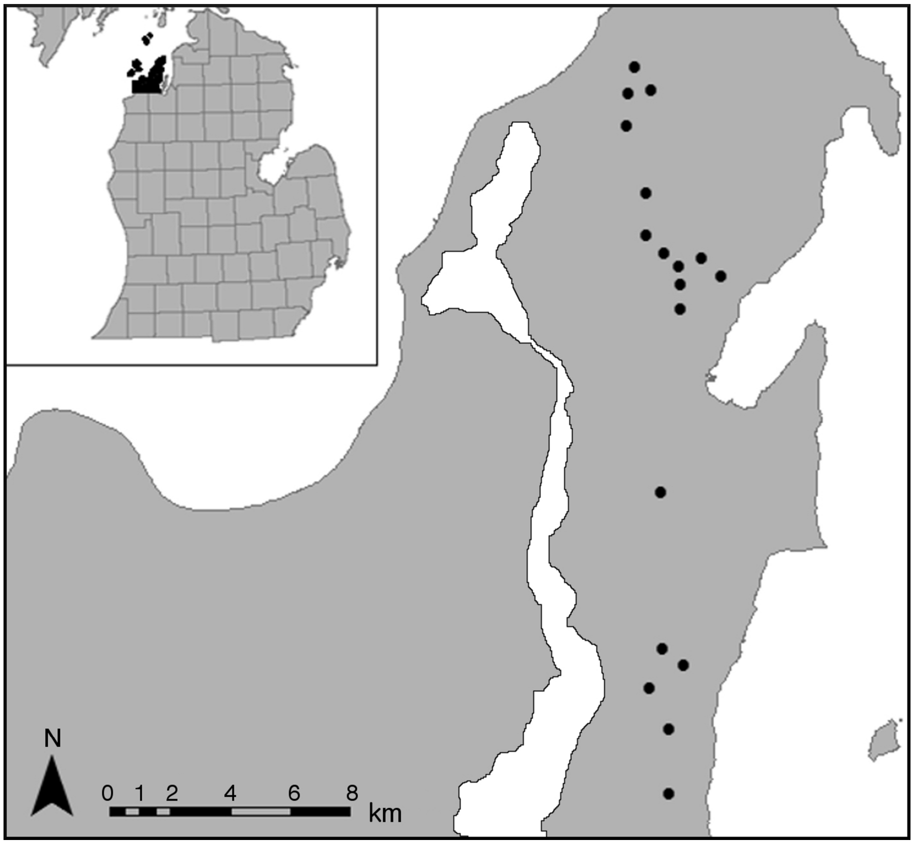

Figure 1.1. **Map of Leelanau County study site.** Points indicate new nest boxes installed in cherry orchards east of Lake Leelanau between 2012 and 2013. Inset: Map of Michigan (Leelanau County shown in black).

Nest Box Design and Maintenance

The nest boxes had a 7.6-cm × 10.2-cm U-shaped entrance hole and a roof shape designed to reduce exposure to sun, rain, and wind (Comfort 2012). We mounted each box on a 5.5-m tower that pivoted to allow two people to lower the box and access it without a ladder (Comfort 2012). We attached the box to the tower using an aluminum turntable bearing that allowed us to keep the box upright when we lowered the tower. We spaced all new boxes at least 800 m apart from each other, and we faced the boxes to the southeast to promote kestrel occupancy and hatching success (Balgooyen 1990, Butler et al. 2009). At the end of each breeding season we cleaned out box contents and refilled boxes with 5 cm of aspen wood shavings.

Nest Monitoring

Starting in 2013, we monitored nest boxes from late April or early May of each year until mid-August. We checked boxes as often as needed to determine the total egg, hatchling, and fledgling counts for each nest. We typically checked each box at least every 7 - 10 d, although we checked as frequently as every other day just prior to hatching to determine hatching date (defined as the date that the first egg hatched). We checked nests using a pole-mounted camera (Fig. 1.2). Our design consisted of an IP56 weatherproof security camera with night vision ($27; Bunker Hill Security, Calabasas, CA U.S.A.) and a 10.2-cm TFT LCD monitor ($15; Sunvalleytek, San Jose, CA U.S.A.) mounted on a telescoping aluminum pole ($14). The camera and screen were powered by a 12-V portable power source ($67; DieHard, Hoffman Estates, IL U.S.A.) with a 300-Watt DC-to-AC power inverter ($25; Bestek, West Chester, OH U.S.A.), both carried in a backpack. This lightweight and inexpensive setup allowed one person to check the box contents quickly. We lowered a box only when handling kestrels or cleaning the box at the end of the season. We banded nestlings at ≥ 14 d old. We captured some adults in the boxes during late incubation or early brood rearing to fit them with radio transmitters or GPS data loggers as part of ongoing research.

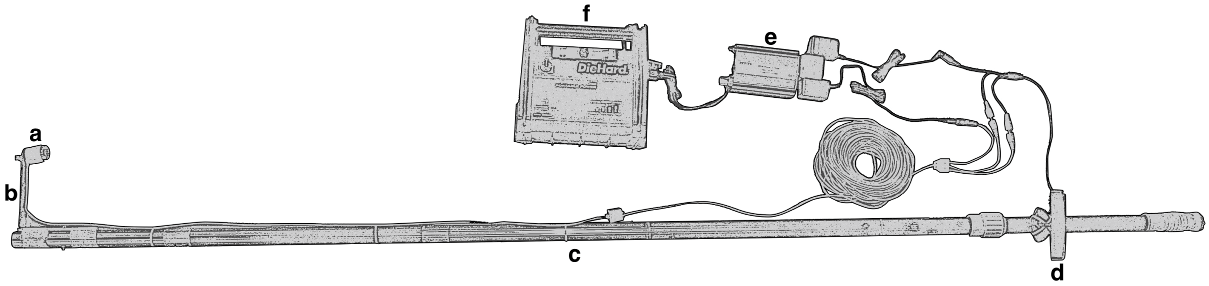

Figure 1.2. **Pole-mounted camera design for checking nest box contents**. Weatherproof security camera (a), 15-cm corner brace (b), telescoping aluminum pole (c), 10.2-cm TFT LCD monitor screen (d), 300-Watt DC-to-AC power inverter (e), and 12-V portable power source (f).

Prior to the start of the 2013 and 2014 breeding seasons, we also installed a weatherproof security camera with night vision ($27 each; Bunker Hill Security) inside each of the boxes. As part of ongoing research, we recorded provisioning of the nestlings at the box using a video recording system consisting of a mini digital video recorder ($80; SecurityMan, Ontario, CA U.S.A.) with an 8 – 32 GB SD card (≥ $4), a 300 W DC-to-AC power inverter ($25; Bestek), and a 12-V, ≥24 Ah rechargeable sealed lead acid deep cycle battery (≥ $60), all housed in a polyethylene plastic storage tote. These cameras and recording systems have proven reliable over the past three years and use less expensive components than similar systems used in the past (e.g. Steen 2009, Kross and Nelson 2011, Cox et al. 2012). We rotated recording systems among multiple nest boxes with cameras as needed. During the 2014 season, we began moving the cameras to the outside of the boxes in cases where nestling excreta had obscured the lens; we found this to be a common problem after nestlings reached 2 wk old. Prior to the 2015 season, we moved most cameras outside of the boxes and attached them to the overhang of the box roof (Fig. 1.3).

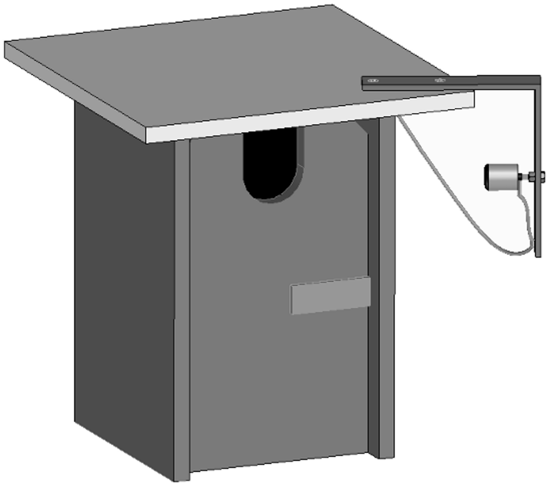

Figure 1.3. **Weatherproof security camera attached to outside of nest box using a 20-cm corner brace.**

Although we did not monitor or maintain the older nest boxes installed in the region by other groups, we opportunistically noted evidence of box occupancy (e.g., kestrels observed entering or exiting a box) to estimate how many of the older boxes were still in use.

Statistical Analysis

We considered a nesting attempt initiated if we found at least one kestrel egg in a box during the monitoring season. We defined apparent nesting success as the percentage of boxes with nesting attempts that produced at least one fledgling (Eschenbauch et al. 2009, Brown et al. 2013). We considered nestlings to be fledglings when they reached 80% of fledging age: > 22 d (Steenhof and Peterson 2009). We defined mean productivity as the total number of fledglings produced divided by the number of boxes with nesting attempts (Eschenbauch et al. 2009). We summarized clutch sizes and numbers of hatchlings and fledglings as means ± SE.

We estimated DSR of nests using logistic-exposure models (Shaffer 2004, Brown et al. 2013). For each observation interval (period between two nest checks), we assigned nest fate as either success or failure. We then built models with nest fate as a binomial response variable and with a modified logit link function that accounts for exposure (length of observation interval in days; Shaffer 2004, Bolker 2014). We included nest-box ID and year as random effects. We included the following variables as fixed effects: whether an adult kestrel from that nest was handled at the start of the observation interval, whether the nest-box camera was moved outside of the box at the start of the observation interval, whether the nest was a first or second attempt in that box, the stage of the nest at the start of the observation interval (incubation or brood rearing; Craft and Craft 1996), and the date of the midpoint of the observation interval (Shaffer 2004). We used a top-down approach for model selection in which we first built models including all fixed effect variables of interest and determined the optimal structure of the random effects using Akaike's Information Criterion (Akaike 1974) corrected for small sample size (AICc; Hurvich and Tsai 1989, Zuur et al. 2009). Using the random effects structure of the highest-ranking model from the first step, we then tested the significance of the fixed effects by comparing nested models using analysis of deviance (Zuur et al. 2009). We used the best-fitting model from the second step to calculate nesting success by taking the product of the estimated DSR across the nesting period (64 d, from Brown et al. 2013): DSR^{64} (Johnson 1979).

We also built Poisson mixed effects and regression models to explain brood size at fledging (number of fledglings produced by successful pairs), with clutch size as an offset to account for differing clutch sizes among nests (Zuur et al. 2009). We did not include failed nests in this analysis because the shorter time window over which we could check these nests biased our monitoring effort. We again included nest-box ID and year as random effects in the mixed effects models. We included the following variables as fixed effects: number of nest checks with the pole-mounted camera, number of times we lowered and opened the box, number of times we flushed an adult during a visit, number of adults handled over the entire monitoring period (0, 1, or 2), location of the box camera during the monitoring period (inside, outside, or both), hatching date (date that first egg hatched), and whether the nest was a first or second attempt in that box. We used the same model selection procedure as described for the logistic-exposure models above. We built all models using package “lme4” in program R (3.1.0)

Results

Kestrels made nesting attempts in all 18 of the new boxes at least once between 2013 and 2015; they made nesting attempts in the eight boxes installed in 2012 during all three years. Nest box use and kestrel reproductive rates were high during all three years (Tables 1.1, 1.2). A total of four nesting attempts failed: two nests with eggs were abandoned due to competition with European Starlings (*Sturnus vulgaris*); another nest with eggs was abandoned for unknown reasons; and one nest failed due to a loss of nestlings, presumably by nocturnal depredation. The case of nest depredation appeared to have occurred during the night following the handling the adult female in the evening: the nest-box video indicated that the female returned to the box the next morning, and the subsequent lack of nestling vocalizations or provisioning by the adults indicated that the nestlings were already dead or missing. Following two of the above cases of nest failure, a kestrel pair initiated a second nesting attempt in the box and produced fledglings. We confirmed that one of these second attempts was made by the same female as the first attempt in that box because we had banded and fitted her with a GPS data logger prior to the failure of the first nest. Hatching dates for all successful nests ranged from 18 May to 22 July, with a median of 4 June.

Table 1.1. **Nesting attempts, apparent nesting success, and mean productivity (number of fledglings per box with nesting attempts) for new nest boxes in Michigan cherry orchards in 2013 – 2015.**

Year	Boxes Available	% Boxes with Nesting Attempts	Nesting Attempts Initiated	% Nesting Success	Mean Productivity
2013	8	100	8	100	4.25
2014	18	83	16	88	3.87
2015	18	100	19	89	3.56
Total	44	93	43	91	3.80

Table 1.2. **Reproductive rates of kestrels using new nest boxes in Michigan cherry orchards, 2013 – 2015.**

Year	Mean Clutch Size ± SE	Mean Hatchlings ± SE	% Hatched	Mean Fledglings ± SE	% Hatchlings Fledged
2013	4.88 ± 0.12	4.75 ± 0.16	97	4.25 ± 0.25	89
2014	4.93 ± 0.071	4.43 ± 0.23	90	4.14 ± 0.31	94

Table 1.2. (cont'd)

2015	4.65 ± 0.15	4.24 ± 0.22	91	3.76 ± 0.30	89
Total	4.82 ± 0.075	4.47 ± 0.13	93	4.05 ± 0.18	91

The best-fitting logistic-exposure model included only the intercept ($\beta_0 = 6.19 \pm 0.50$) without the random effects of box and year (Table 1.3); none of the fixed effect variables had a significant effect on daily survival (Table 4). Using the selected model, the calculated DSR was 0.998 (95% CI: 0.995 – 0.999), and nesting success was 88%.

Table 1.3. **Logistic-exposure models of daily nest survival, with Akaike's Information Criterion corrected for small sample size (AICc) for selection of random effects structure.** Models include all fixed effect variables of interest. The highest-ranking structure was a model without the random effects of box and year.

Model	AICc	ΔAICc	Weight
No random effects	42.4	0.0	0.66
Random slopes	44.5	2.1	0.23
Random intercepts	46.6	4.2	0.080
Random slopes and intercepts	48.7	6.3	0.027

Table 1.4. **Selection of fixed effects in logistic-exposure model of daily nest survival using analysis of deviance.** Asterisks (*) denote fixed effects significant at the 0.05 level. None of the variables of interest, including those related to our monitoring techniques and effort, had a significant effect on daily survival rates of kestrel nests in Michigan cherry orchards.

Fixed Effect	df	χ^2	P
Camera moved[a]	1	0.056	0.81
Nesting attempt[b]	1	0.48	0.49
Midpoint date[c]	1	0.22	0.64
Nesting stage[d]	1	0.92	0.34
Adult handled[e]	1	2.03	0.15

[a] whether we moved the nest box camera outside of the box at the start of the observation interval
[b] whether the nesting attempt was a first or second in that box
[c] date of the midpoint of the observation interval
[d] stage of the nest at the start of the observation interval (incubation or brood rearing)
[e] whether we handled an adult kestrel at the start of the observation interval

The best-fitting model for brood size at fledging did not include the random effects of box and year ($\beta_0 = -6.24 \pm 1.17$; Table 5), but did include the fixed effect of hatching date (Table 6). Later hatching had a small positive effect on brood size at fledging ($\beta_1 = 0.017 \pm 0.007$).

None of the other variables representing our monitoring efforts had a significant effect, nor did the status of the nest as a first or second attempt in that box.

Table 1.5. **Poisson models of brood size at fledging, with Akaike's Information Criterion corrected for small sample size (AICc) for selection of random effects structure.** Models include all fixed effect variables of interest. The highest-ranking structure was a model without the random effects of box and year.

Model	AICc	ΔAICc	Weight
No random effects	167.8	0.0	0.82
Random slopes	171.4	3.7	0.13
Random slopes and intercepts	174.2	6.4	0.034
Random intercepts	175.4	7.6	0.019

Table 1.6. **Selection of fixed effects in Poisson model of brood size at fledging using analysis of deviance.** Asterisks (*) denote fixed effects significant at the 0.05 level. Variables related to nest monitoring techniques and effort did not significantly affect brood size at fledging for successful kestrel nests in Michigan cherry orchards; only hatching date had a small positive effect on brood size at fledging.

Fixed Effect	df	χ^2	*P*
Adults flushed[a]	1	0.0009	0.98
Box camera location[b]	2	0.11	0.94
Box lowered/opened[c]	1	0.017	0.90
Adults handled[d]	1	0.031	0.86
Checks with camera pole[e]	1	0.45	0.50
Nesting attempt[f]	1	0.72	0.40
Hatching date[g]	1	4.42	0.035*

[a] number of times we flushed an adult from the box during a visit
[b] location of the nest box camera during the monitoring period (inside, outside, or both)
[c] number of times we lowered and opened the box
[d] number of adults handled over the entire monitoring period (0, 1, or 2)
[e] number of nest checks with the pole-mounted camera
[f] whether the nesting attempt was the first or second in that box
[g] date that the first egg hatched

Of the 24 intact boxes installed on utility poles by other groups, we opportunistically observed evidence of kestrel occupancy (e.g., kestrels observed entering or exiting a box) at 10 boxes between 2013 and 2015. Of the 14 older boxes at which we never observed occupancy, eight were within 400 m of an occupied box, and four of these were within 400 m of a new box. The shortest observed distance between two occupied boxes was 495 m.

Discussion

The nest box use and reproductive rates observed in this study are similar to or higher than those reported in recent studies (e.g. Rohrbaugh and Yahner 1997, Katzner et al. 2005, Eschenbauch et al. 2009, Smallwood and Collopy 2009, Steenhof and Peterson 2009, Strasser and Heath 2013, Brown et al. 2013, Smallwood 2016) and historical studies (summarized in Eschenbauch et al. 2009). We therefore concluded that the agricultural activities in orchards do not promote nest desertion and lower nesting success rates. Instead, the high rates of nesting attempts and nesting success in the orchard nest boxes may have resulted from the consistency in their placement in suitable habitat. As described in the Methods, we chose the design of the boxes and the mounting orientation to maximize occupancy and success rates. We also installed the boxes away from forested areas, and many of our orchard box locations bordered open fields, pastures, or row crops. Furthermore, the entire study region is predominantly composed of open non-forested habitats. Breeding kestrels prefer, and have higher hunting success, in more open areas (e.g., Smallwood and Collopy 2009, Smallwood, et al. 2009b); thus, the reproductive rates we measured suggested that the nest boxes were placed in high-quality habitat.

We should note that we monitored fewer boxes for fewer years than previous studies. Smallwood et al. (2009a) found that nest box programs of various sizes experienced an increase in occupancy rates during the first 4 – 6 yr after the introduction of boxes, followed by a decrease in later years. Kestrels made nesting attempts in all of the boxes installed during this study, following the expected pattern (Smallwood et al. 2009a), but these new boxes represented an expansion, rather than initiation, of nest-box availability in the region. Thus, the rapid response of kestrels to the ongoing installation of new boxes, combined with the fact that we opportunistically observed occupancy at 41% of the older boxes, may instead indicate that the region has supported a local breeding population that still experienced nest-site limitation more than 25 yr after the introduction of boxes. Because we only observed the older boxes for evidence of occupancy and did not directly monitor nesting attempts, we likely underestimated the actual rates of nesting attempts for the older boxes. In addition, over half of the older boxes with no observed occupancy were within 400 m of an occupied box, which was closer than the observed minimum distance of 495 m between occupied boxes. Some of the older boxes may have been too close to others for all to be occupied and have nesting attempts. In the four cases where a new orchard box was installed within 400 m of an older box, only the new boxes were occupied and had nesting attempts, which may indicate a preference for the new boxes. However, the continued evidence of occupancy at some of the 24 older boxes, combined with the high rates of nesting attempts in the 18 new boxes, suggests an increase in the number of breeding pairs, rather than just a shift of the same or a fewer number of pairs to the new boxes. Overall, our results suggest that additional, properly spaced, and well-maintained orchard nest boxes could sustain or increase the number of breeding pairs in the region in future years.

As predicted, variables related to nest monitoring techniques and effort did not significantly affect the daily survival rate of nests or brood size at fledging. Although the small sample size may have limited our ability to detect significant effects, the lack of a disturbance effect was consistent with findings from a larger, longer-running nest-box monitoring program (Smallwood 2016), supporting the conclusion that kestrels are indeed tolerant of both traditional and video monitoring techniques. Even moving the nest-box cameras from the inside of the box to the outside did not affect kestrels; in fact, video recordings have shown that the adults at most boxes resumed provisioning their nestlings within an hour after camera relocation (M. Shave unpublished data). We therefore concluded that it would be possible to delay camera installation until after nestlings have hatched, which would save effort and resources compared to installing cameras in all boxes prior to the breeding season. This conclusion was further supported by the observation that Eurasian Kestrels (*Falco tinnunculus*) resumed provisioning soon after having their entire box replaced to accommodate a box camera (Steen 2009).

Seasonal timing of the nesting attempt, as measured by the midpoint date of each observation interval in the logistic-exposure models, did not have a significant effect on DSR. Thus, we found no difference in nesting success between early- and late-season nesting attempts. In contrast, Steenhof and Peterson (2009) found that earlier nesting attempts had higher nesting success in southwestern Idaho. One possible explanation for the difference in results is the difference in origins of the breeding populations. Many of the kestrels in southwestern Idaho are year-round residents that breed early (Steenhof and Heath 2009), and lower nesting success observed with later nests may have been due to later-arriving long-distance dispersers that have lower reproductive rates (Steenhof and Peterson 2009). In northwestern Michigan, the kestrel population is considered entirely migratory (Brewer et al. 1991, Smallwood and Bird 2002), and we observed no kestrels in the area during winter (M. Shave, unpublished data). We therefore assume that the breeding population includes no local residents that would have an advantage over later-arriving migrants or immigrants in finding territories or mates (Steenhof and Heath 2009). It is also possible that our sample size was not large enough to detect any differences.

Although we found no effect of seasonal timing on nesting success, hatching date did have a small positive effect on brood size at fledging for successful nests: later-hatching nests produced significantly more fledglings, regardless of clutch size. A possible reason for the positive effect of hatching date is that the early breeding season in our study region may be a time of lower prey availability, due to factors such as inclement weather. Dawson and Bortolotti

(2000) found that kestrel nests starting with five nestlings produced fewer and smaller fledglings when they experienced inclement weather (decreasing temperatures, increasing wind speeds, and increasing precipitation) during the brood-rearing period. According to data from Michigan State University Enviro-weather stations in the region, eastern Leelanau County experienced increasing monthly average temperatures, decreasing monthly precipitation totals, and decreasing monthly maximum wind speeds between May and July during the years of our study. Thus, kestrel nests hatching earlier in the breeding season were likely exposed to more cold and rainy weather than later nests.

The lack of a significant effect of nesting attempt on DSR or brood size at fledging supports the finding from Smallwood and Collopy (2009) that second nesting attempts did not have significantly different success rates than first attempts. However, Steenhof and Peterson (2009) found a success rate of 46% for second attempts versus a mean success rate of 64% for all attempts. The low frequencies of second attempts by kestrels (10.7% of nests in Smallwood and Collopy 2009, 9.3% in Steenhof and Peterson 2009, and 4.65% in this study) may make comparisons between first and second attempts inconclusive.

Our results supported the conclusion that orchard nest boxes may have important benefits for kestrel conservation and, potentially, agriculture. Kestrels readily occupied and made nesting attempts in the new orchard nest boxes in northwestern Michigan, which indicated that these boxes provide needed nesting cavities with access to favorable hunting habitats. The kestrels using these nest boxes also had consistently high reproductive rates, indicating that the orchards and surrounding areas provide suitable habitat for successful kestrel breeding and fledgling production. Thus, these boxes have the potential to sustain or increase the breeding kestrel population in the region while also increasing kestrel predation of crop-damaging prey in and around cherry orchards. Studies have shown that raptors can reduce the abundance of prey in agroecosystems (e.g., Kay et al. 1994, Kross et al. 2012), but the effect of kestrel predation on prey activity has received limited investigation (e.g., Askham 1990, Sheffield et al. 2001). Our current research program in the fruit-growing regions of Michigan is therefore investigating both the conservation and agricultural benefits of nest boxes installed in fruit crops. Nest-box camera recordings and prey remains collections (Chapter 3) showed that kestrels kill orchard-damaging prey, including grasshoppers (Order Orthoptera; Shane and Wise 2012), meadow voles (*Microtus pennsylvanicus*; Tritten 2014, Wood and Singleton 2015), and fruit-eating birds such as the American Robin (*Turdus migratorius*; Lindell et al. 2012). Ongoing work aims to quantify diet of kestrels using orchard nest boxes and to examine the effects of kestrel predation on prey abundance in orchards. Finally, the kestrels showed high tolerance of various monitoring efforts throughout the nesting period, which makes them appropriate subjects for intensive field research. Overall, these results are promising for ongoing and future work with orchard nest boxes in agricultural regions.

LITERATURE CITED

LITERATURE CITED

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control AC-19:716–723.

Askham, L.R. 1990. Effect of artificial perches and nests in attracting raptors to orchards. Pages 144-148 in L.R. Davis and R.E. Marsh [Eds.], Proceedings of the 14th Vertebrate Pest Conference. University of California Davis Press, Davis, CA, USA.

Balgooyen, T.G. 1990. Orientation of American Kestrel nest cavities: revisited. Journal of Raptor Research 24:27–28.

Bolker, B. 2014. Logistic regression, accounting for differences in exposure. Version 09.30.2014. RPubs. https://rpubs.com/bbolker/logregexp

Brewer, T., G.A. McPeek, and R.J. Adams, Jr. 1991. The atlas of breeding birds of Michigan. Michigan State University Press, East Lansing, MI, USA.

Brown, J.L., K. Steenhof, M.N. Kochert, and L. Bond. 2013. Estimating raptor nesting success: old and new approaches. Journal of Wildlife Management 77:1067–1074.

Butler, M.W., B.A. Whitman, and A.M. Dufty, Jr. 2009. Nest box temperature and hatching success of American Kestrels varies with nest box orientation. Wilson Journal of Ornithology 121:778–782.

Comfort, T. 2012. The Spartan: a nest box for the American Kestrel. NestboxBuilder.com. http://www.nestboxbuilder.com/nestbox-article-spartan.html

Cox, W.A., M.S. Pruett, T.J. Benson, S.J. Chiavacci, and F.R. Thompson, III. 2012. Development of camera technology for monitoring nests. Pages 185–210 in C.A. Ribic, F.R. Thompson, III, and P.J. Pietz [Eds.], Video surveillance of nesting birds. Studies in Avian Biology No. 43. University of California Press, Berkeley, CA, USA.

Craft, R.A. and K.A. Craft. 1996. Use of free ranging American Kestrels and nest boxes for contaminant risk assessment sampling: a field application. Journal of Raptor Research 30:207–212.

Dawson, R.D. and G.R. Bortolotti. 2000. Reproductive success of American Kestrels: the role of prey abundance and weather. Condor 102:814–822.

Dykstra, C.R., M.W. Meyer, and D.K. Warnke. 2002. Bald Eagle performance following video camera placement. Journal of Raptor Research 36:136–139.

Eschenbauch, J.E., E.A. Jacobs, and R.N. Rosenfield. 2009. Nest-box occupancy and reproductive performance of kestrels in central Wisconsin. Journal of Raptor Research 43:365–369.

Farmer, C.J. and J.P. Smith. 2009. Migration monitoring indicates widespread declines of American Kestrels (Falco sparverius) in North America. Journal of Raptor Research 43:263–273.

Hurvich, C.M. and C.L. Tsai. 1989. Regression and time-series model selection in small sample sizes. Biometrika 76:297–307.

Jedlicka, J.A., R. Greenberg, and D.K. Letourneau. 2011. Avian conservation practices strengthen ecosystem services in California vineyards. PLoS ONE 6:e27347.

Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

Katzner, T., S. Robertson, B. Robertson, J. Klucarits, 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 76:217–318.

Kay, B.J., L.E. Twigg, T.J. Korn, and H.I. Nicol. 1994. The use of artificial perches to increase predation on house mice (Mus domesticus) by raptors. Wildlife Research 21:95–106.

Kross, S.M. and X.J. Nelson. 2011. A portable low-cost remote videography system for monitoring wildlife. Methods in Ecology and Evolution 2:191–196.

Kross, S.M., J.M. Tylianakis, and X.J. Nelson. 2012. Effects of introducing threatened falcons into vineyards on abundance of passeriformes and bird damage to grapes. Conservation Biology 26:142–149.

Lindell C.A., R.A. Eaton, E.M. Lizotte, and N.L. Rothwell. 2012. Bird consumption of sweet and tart cherries. Human-Wildlife Interactions 6: 283–290.

Paprocki, N., J.A. Heath, and S.J. Novak. 2014. Regional distribution shifts help explain local changes in wintering raptor abundance: implications for interpreting population trends. PLoS ONE 9:e86814.

Proudfoot, G.A. 1996. Video-board camera used to inspect natural and artificial nest cavities. Wildlife Society Bulletin 24:528–530.

Richardson, T.W., T. Gardali, and S.H. Jenkins. 2009. Review and meta-analysis of camera effects on avian nest success. Journal of Wildlife Management 73:287–293.

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.

Sauer, J.R., J.E. Hines, J. Fallon, K.L. Pardieck, D.J. Ziolkowski, Jr., and W.A. Link. 2014. The North American Breeding Bird Survey, results and analysis 1966-2013. Version 01.30.2015. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, MD, USA. http://www.mbr-pwrc.usgs.gov/bbs

Shaffer, T.L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

Shane, B. and J. Wise. 2012. Increased populations of grasshoppers cause problems in fruit crops. Michigan State University. http://msue.anr.msu.edu/news/increased_populations_of_grasshoppers_cause_problems_in_fruit_crops

Sheffield, L. M., J.R. Crait, W.D. Edge, and G. Wang. 2001. Response of American Kestrels and gray-tailed voles to vegetation height and supplemental perches. Canadian Journal of Zoology 79:380–385.

Smallwood, J.A. 2016. Effects of researcher-induced disturbance on American Kestrels breeding in nest boxes in northwestern New Jersey. Journal of Raptor Research 50:54-59.

Smallwood, J.A. and D.M. Bird. 2002. American Kestrel (Falco sparverius). In A. Poole and F. Gill [Eds.], The birds of North America, No. 602. The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC, USA.

Smallwood, J.A. and M.W. Collopy. 2009. Southeastern American Kestrels respond to an increase in the availability of nest cavities in north-central Florida. Journal of Raptor Research 43:291–300.

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, J.W. Parrish, Jr, T.F. Breen, and K. Boyd. 2009a. Why are American Kestrel (Falco sparverius) populations declining in North America? Evidence from nest box programs. Journal of Raptor Research 43:274–282.

Smallwood, J.A., P. Winkler, G.I. Fowles, and M.A. Craddock. 2009b. American Kestrel breeding habitat: the importance of patch size. Journal of Raptor Research 43:308–314.

Steen, R. 2009. A portable digital video surveillance system to monitor prey deliveries at raptor nests. Journal of Raptor Research 43:69–74.

Steenhof, K. and J.A. Heath. 2009. American Kestrel reproduction: evidence for the selection hypothesis and the role of dispersal. Ibis 151:493–501.

Steenhof, K. and B.E. Peterson. 2009. American Kestrel reproduction in southwestern Idaho: annual variation and long-term trends. Journal of Raptor Research 43:283–290.

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.

Tritten, B. 2014. Mice and vole populations are building in many orchards. Michigan State University Extension. http://msue.anr.msu.edu/news/mice_and_vole_populations_are_building_in_many_orchards

Wood, B.J. and G.R. Singleton. 2015. Rodents in agriculture and forestry. Pages 33–80 in A. Buckle and R. Smith [Eds.], Rodent pests and their control. CAB International, UK.

USDA. 2012 Census of Agriculture. 2014. County profile: Leelanau County, Michigan. United States Department of Agriculture National Agricultural Statistics Service, Washington, DC, USA. http://www.agcensus.usda.gov/Publications/2012/Online_Resources/County_Profiles/Michigan/cp26089.pdf

Zuur, A., E.N. Ieno, N. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed effect models and extensions in ecology with R. Springer Science, NY, USA.

CHAPTER 2

OCCUPANCY MODELING REVEALS TERRITORY-SCALE EFFECTS OF NEST BOXES ON THE PRESENCE, COLONIZATION, AND PERSISTENCE OF A DECLINING RAPTOR IN A FRUIT-GROWING REGION

Megan E. Shave and Catherine A. Lindell

Abstract

Nest boxes for predatory birds in agricultural regions are an easily implemented landscape enhancement with potential benefits for both conservation and agriculture. Although previous studies have demonstrated that nest boxes attract insectivorous passerine birds and increase predation of pest insects, the potential for nest boxes to increase raptor populations in agricultural regions has received limited attention, especially at the fine spatial scale of kestrel territories that is relevant to landowners. This study examined the effects of cherry orchard nest boxes on the local breeding population of a declining species, the American Kestrel (*Falco sparverius*), in a fruit-growing region of Michigan. We conducted temporally-replicated surveys along four roadside transects divided into 1.6 km x 500 m sites. We developed a multi-season occupancy model under a Bayesian framework and found that nest boxes had strong positive effects on first-year site occupancy, site colonization, and site persistence probabilities. The estimated number of occupied sites increased between 2013 and 2016, which reflects the increase in number of sites with boxes. These results support the conclusion that the kestrels in the local breeding population are limited by nest site availability. Furthermore, these results indicate that orchard nest boxes can benefit the conservation of kestrels by maintaining or increasing breeding populations, which may in turn benefit agriculture by promoting kestrel presence, and therefore predation on crop pests, in and around orchards. Finally, this study demonstrates the usefulness of occupancy modeling for measuring the effect of landscape enhancements on predator populations.

Introduction

Changes in land use due to agricultural expansion and intensification pose a significant threat to many species and the functional diversity of species assemblages (Green et al. 2005; Flynn et al. 2009). One form of habitat degradation imposed by agricultural development is the loss of nesting and roosting cavities, particularly those in mature trees (Gibbons et al. 2008), which can negatively affect abundance and diversity of various animal taxa, including birds (Newton 1994). Many cavity-dependent birds species will use artificial cavities, such as nest boxes, in areas where natural cavities are scarce. Installing nest boxes in agricultural regions has increased populations of some species, such as the Eurasian Hoopoe (*Upupa epops*; Arlettaz et al. 2010), European Roller (*Coracias garrulus*; Kiss et al. 2014), and Eurasian Kestrel (*Falco tinnunculus*; Paz et al. 2013). Therefore, nest boxes could potentially play an important role in maintaining biodiversity in agroecosystems.

Nest boxes may also benefit agriculture by increasing the strength of ecosystem services provided by predators. For example, birds can depress the abundances of herbivorous insects and increase plant performance through cascading trophic effects (Whelan et al. 2008). Nest boxes can attract insectivorous birds to orchards and vineyards, resulting in increased predation on pest insects (e.g., Jedlicka et al. 2011) and reduced insect damage (e.g., Mols and Visser 2007).

Raptors are potentially important predators in agriculture (Whelan et al. 2008). For example, artificial perches can attract multiple raptor species to agricultural fields, and the increased raptor presence can decrease the abundance of mice (Kay et al. 1994). Introduction of a native falcon into New Zealand vineyards decreased frugivorous bird abundances and reduced grape damage (Kross et al. 2012). Multiple raptor species use nest boxes (Lambrechts et al. 2012), and recent studies have reported high rates of box use by Barn Owls (*Tyto alba*) and

Eurasian Kestrels that consume pest rodents (e.g., Meyrom et al. 2009, Paz et al. 2013, Kross et al. 2016).

American Kestrels (*Falco sparverius*; hereafter "kestrels") are of interest as predators in fruit-growing regions because their diet typically consists of insects, small mammals, and birds (Smallwood and Bird 2002) and can include a variety of orchard pests (Chapter 3). Furthermore, they are a species of conservation concern; multiple monitoring programs have detected significant and widespread population declines in recent decades (Farmer and Smith 2009, Smallwood et al. 2009a, Sauer et al. 2014). The removal of tree snags and other sources of natural nesting cavities can lead to nest site limitation of local breeding populations, but kestrels readily use nest boxes in open areas with appropriate hunting habitat (Rohrbaugh and Yahner 1997, Smallwood and Bird 2002).

Previous studies have compared regions with and without nest boxes to demonstrate that nest boxes can increase the densities of American and Eurasian kestrels (Smallwood and Collopy 2009, Paz et al. 2013). However, few studies of nest site limitation in birds have explored the relationship between nest boxes and breeding bird presence at the scale of individual territories (e.g., Loman 2006), and no previous studies have investigated the effect of nest boxes on kestrel presence at the fine scale of potential kestrel territories. A nest box potentially enhances the landscape for one breeding kestrel pair, so measuring change at a spatial scale equivalent to the size of potential kestrel territories would allow for stronger conclusions regarding nest site limitation in a region and the effect of nest boxes on the local breeding kestrel population. Also, few studies have focused on kestrel populations in agroecosystems, and previous research has found inconclusive evidence of the effects of nest boxes on kestrel presence in fruit orchards (Askham 1990). The effect of nest boxes on kestrel presence and predation at this finer scale in an agricultural region could therefore provide useful information for farmers and landowners on whose properties nest boxes might be installed.

Fine scale population surveys may result in low numbers of detections at each survey site, and some survey designs may also risk violating assumptions of spatial and temporal independence. However, modern statistical techniques, such as occupancy modeling, can effectively use data to identify patterns from these surveys. The ability to use detection-nondetection data in occupancy modeling is particularly useful for assessing populations of predators that are difficult to detect, are territorial, or occur at low densities, such as raptors (MacKenzie et al. 2006). The ease of including covariates in both the ecological and observation processes allows researchers to test the relative influence of different factors on site occupancy, as well as tailor the model to account for sources of detection variability in their system, including any logistical constraints in their survey design that could result in temporal or spatial dependence (e.g., Aing et al. 2011, Whittington et al. 2015).

This study used surveys of kestrel presence and multi-season occupancy modeling to determine whether nest boxes in a fruit-growing region of northwestern Michigan (Fig. 2.1) increased the presence of breeding kestrels, as defined by the number of potential territories (sites) occupied by kestrels. Although previous work has used occupancy modeling to investigate kestrel nest box use (Brown et al. 2014), this is the first study to use occupancy modeling to test the relative influence of nest boxes on kestrel site occupancy throughout a landscape. Our hypothesis was that this region offers appropriate hunting habitat, but lacks natural nesting cavities, thus that kestrels are limited by nest cavity availability. We therefore predicted that sites (1.6 km x 500 m areas) with nest boxes would have higher kestrel occupancy than sites without, and that increasing the number of sites with nest boxes would in turn increase the number of sites occupied by kestrels.

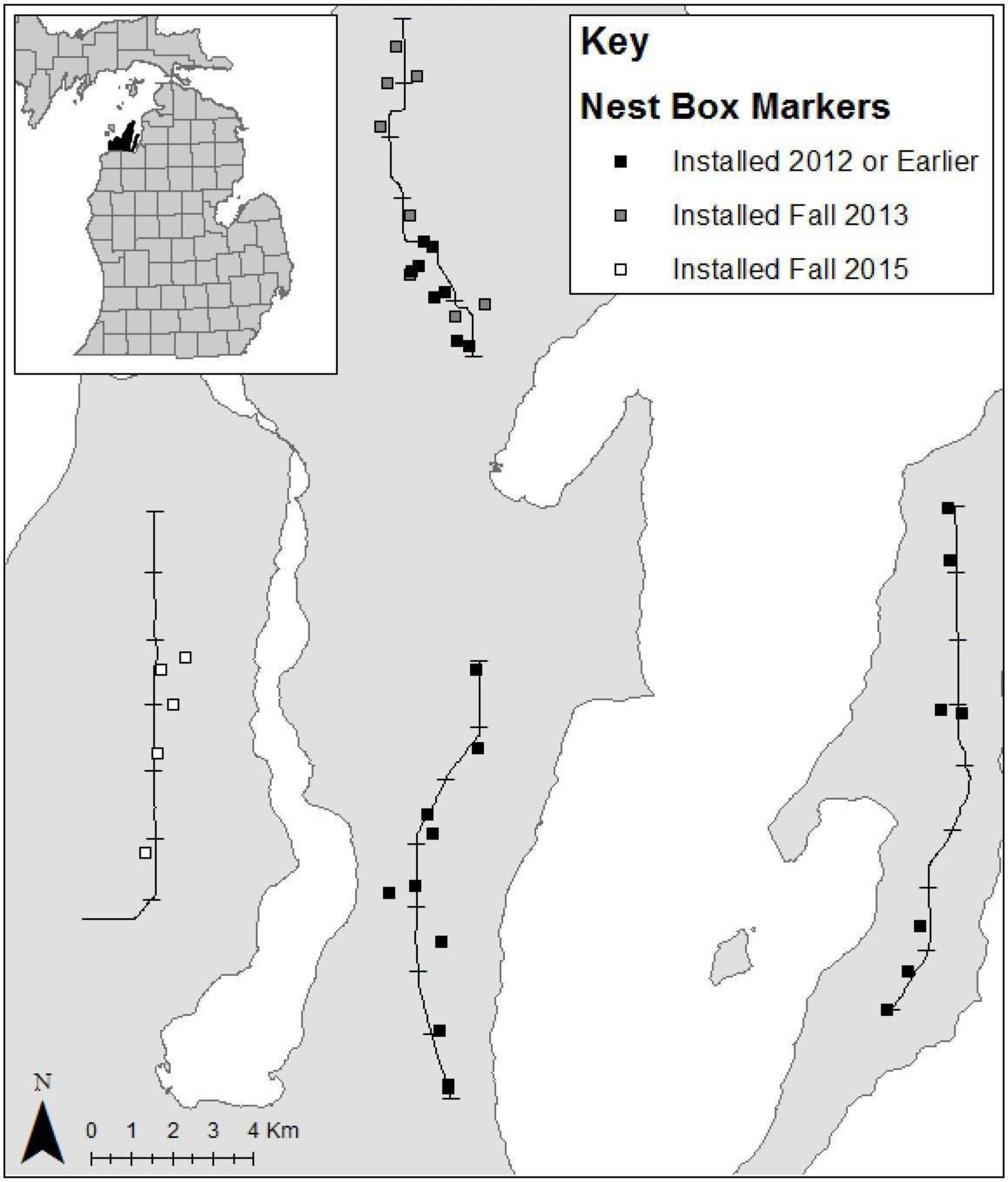

Figure 2.1. **Map of the Michigan study region and survey sites.** Lines indicate the four kestrel survey transects (divided into 28 1.6 km-long survey sites); markers indicate nest boxes located within 0.8 km of transects. Inset: Map of Michigan with Leelanau and Old Mission peninsulas in black.

Methods

Kestrel Surveys in a Fruit-growing Region of Michigan

We conducted surveys on the Leelanau and Old Mission peninsulas of northwestern Michigan (45.0751°N–44.8365°N, 85.5032°W–85.7758°W), a major cherry-growing region that also produces apples and wine grapes, among other crops (USDA 2012 Census of Agriculture 2014). The region is largely agricultural with some residential and forested areas (USDA 2012 Census of Agriculture 2014). Kestrel nest boxes have been present in this region since the late 1980s (F. Otto, *Personal communication*); we installed additional boxes in cherry orchards in 2012, 2013, and 2015 (Fig. 2.1).

Our survey design consisted of four roadside transects (9.6 km – 12.8 km long) divided into 1.6 km survey sites (Fig. 2.1). We placed the starting point of each transect randomly, but we purposefully placed transects along roads in predominately non-forested areas with high densities of cherry orchards, so that each survey site consisted of mostly open habitat with orchards, matching kestrel habitat preferences (Smallwood et al. 2009b).

We conducted temporally-replicated surveys in 2013 – 2016 during the kestrel breeding season. The surveys began each year between 9 - 21 June, after eggs in most of the known kestrel nests had hatched, so that kestrels would no longer be incubating eggs and would therefore be available for detection. The surveys ended each year by 12 August, prior to fall migration; the kestrel population in this region is considered entirely migratory (Brewer et al. 1991, Smallwood and Bird 2002). We assumed temporal and geographical population closure for each year because kestrel pairs hold territories for the entire breeding season (Smallwood and Bird 2002).

During a survey round, we surveyed a site on foot from south to north (initial survey), waited for 5 min, and then surveyed the site again from north to south (return survey). Each survey round therefore yielded two surveys. We surveyed each site six times in 2013 and 12 times in 2014 – 2016. We conducted all surveys between 0830 and 1230 EST (AM period) or 1600 and 2000 EST (PM period) on days without precipitation or fog. During each survey we recorded whether we detected adult kestrels within 250 m of the transect.

Potential Factors Affecting Kestrel Presence

We predicted that kestrel presence would be more likely at sites with nest boxes. We therefore characterized each survey site based on whether it had nest boxes within 0.8 km of the transect (*site boxes*). We chose this distance given that a typical kestrel territory is 0.5 km – 2.4 km in diameter (Bird and Palmer 1988, Smallwood and Bird 2002) and that nest boxes are typically spaced 0.8 km apart (Rohrbaugh and Yahner 1997); we therefore assumed that a kestrel pair using a nest box would have a home range that included a large proportion of the survey site. We searched the landscape within 0.8 km of the transects each year in order to locate any nest boxes installed by other groups or landowners.

We also considered the potential spatial dependence of sites along a transect. We included a random effect of transect ID to account for the possibility that kestrel presence was more similar at sites within the same transect compared to sites from other transects (*transect*; Saracco et al. 2011). In addition, we predicted that some kestrel territories could overlap two neighboring sites, thus potentially violating the assumption of independence. We therefore determined whether kestrel presence was more likely at a site if adjacent sites had nest boxes (*neighbor box*) as a measure of this spatial dependence.

Potential Factors Affecting Kestrel Detectability

We first considered the potential effects of survey timing on kestrel detections. Kestrels exhibit conspicuous hunting behaviors, such as hover-hunting and use of elevated, exposed perches (Bird and Palmer 1988). We predicted that kestrel detections would be higher during the brood rearing period of the breeding season because this period should correspond to higher hunting activity due to nestling provisioning. We used Julian date (*date*) as a measure of the timing of the breeding season to determine whether kestrels became more or less conspicuous as the breeding season progressed. We also considered whether detection rates differed between AM and PM survey periods (*time*).

We also addressed the potential temporal dependence between initial and return surveys of a site during a survey round, as defined above. We investigated whether observer presence during an initial survey of a site influenced kestrel behavior and affected detection during the return survey (*survey*). We predicted that kestrels might avoid the survey area after the initial survey, thus decreasing the detection probability during return surveys.

Finally, kestrel activity at known nest sites can bias survey detections (Smallwood and Collopy 2009). We addressed this potential source of bias in detectability by determining whether detection rates were higher when nest boxes with active nesting attempts were close to a transect. We therefore characterized each site based on whether it had an active nest box within 250 m of the transect (*nest distance*).

Occupancy Modeling

We investigated the effects of these factors on kestrel presence and detectability using multi-season occupancy modeling under a Bayesian framework (Kéry and Schaub 2012).

This modeling approach included the following ecological processes:

$z_{i,1} \sim \text{Bernoulli}(\psi_{i,1})$ at initial state (t =1)

$z_{i,t} \sim \text{Bernoulli}\,(z_{i,(t-1)} * \varphi_{i,t} + (1 - z_{i,(t-1)}) * \gamma_{i,t})$ for years t > 1

where the occurrence state $z_{i,t} = 1$ if at least one kestrel was present at site *i* in year *t*. The first year site occupancy probability $\psi_{i,1}$ determined the initial occurrence state at site *i*; the site colonization probability $\gamma_{i,t}$ and site persistence probability $\varphi_{i,t}$ determined the occurrence state in subsequent years. We modeled the site occupancy, colonization, and persistence probabilities as follows:

$$\text{logit}(\psi_{i,j,1}) = \alpha_0 + transect_j + \alpha_1(site\ box_{i,j,1}) + \alpha_2(neighbor\ box_{i,j,1})$$

$$\text{logit}(\gamma_{i,j,t}) = \alpha_3 + transect_j + \alpha_4(site\ box_{i,j,t}) + \alpha_5\,(neighbor\ box_{i,j,t})$$

$$\text{logit}(\varphi_{i,j,t}) = \alpha_6 + transect_j + \alpha_7(site\ box_{i,j,t}) + \alpha_8\,(neighbor\ box_{i,j,t})$$

where $transect_j$ represented a random effect of transect *j*, and $\alpha_{1,2,4,5,7,8}$ represented the logit-linear coefficients for model covariates (Saracco et al. 2011).

The multi-season occupancy model also included the following observation process:

$$y_{i,k,t}|z_i \sim \text{Bernoulli}(z_{i,t} * p_{i,k,t})$$

where detection state $y_{i,k,t} = 1$ if a kestrel was detected at site *i* during survey *k* in year *t*. The occurrence state $z_{i,t}$ and the detection probability $p_{i,k,t}$. determined whether a kestrel was detected at site *i* during survey *k* in year *t*. We modeled the detection probability as follows:

$$\text{logit}(p_{i,k,t}) = \beta_0 + \beta_1(date_{i,k,t}) + \beta_2(time_{i,k,t}) + \beta_3(survey_{i,k,t}) + \beta_4(nest\ distance_{i,k,t})$$

We estimated model parameters using Markov Chain Monte Carlo (MCMC) methods. For each model we used uninformative priors and ran two chains for 30,000 iterations, discarding the first 20,000 runs as burn-in and thinning by 2. We ran all models using package “R2jags” in Program R (3.3.1). We assessed convergence by visually inspecting model trace plots and confirming that values for the potential scale reduction factor were <1.1 for all model parameters (Gelman et al. 2003). We identified a covariate effect as important if the 95% credible interval (CRI) for the posterior mean of the parameter coefficient did not overlap zero (Kéry and Schaub 2012). We also generated estimates for two derived parameters: the estimated number of occupied sites each year and the annual occupancy-based population growth rate λ (Kéry and Schaub 2012).

Results

Over the four years of this study, we detected kestrels at 22 of the 28 survey sites and during 133 out of 1176 total surveys. We detected kestrels at sites along all four transects; however, we observed kestrels along the western transect in 2016 only, after we had installed nest boxes during the fall of 2015 (Fig. 2.1). The number of sites occupied by kestrels increased between 2013 and 2016, as the number of boxes we installed increased, with positive occupancy-based growth occurring between 2013 and 2014, as well as between 2015 and 2016 (Fig. 2.2).

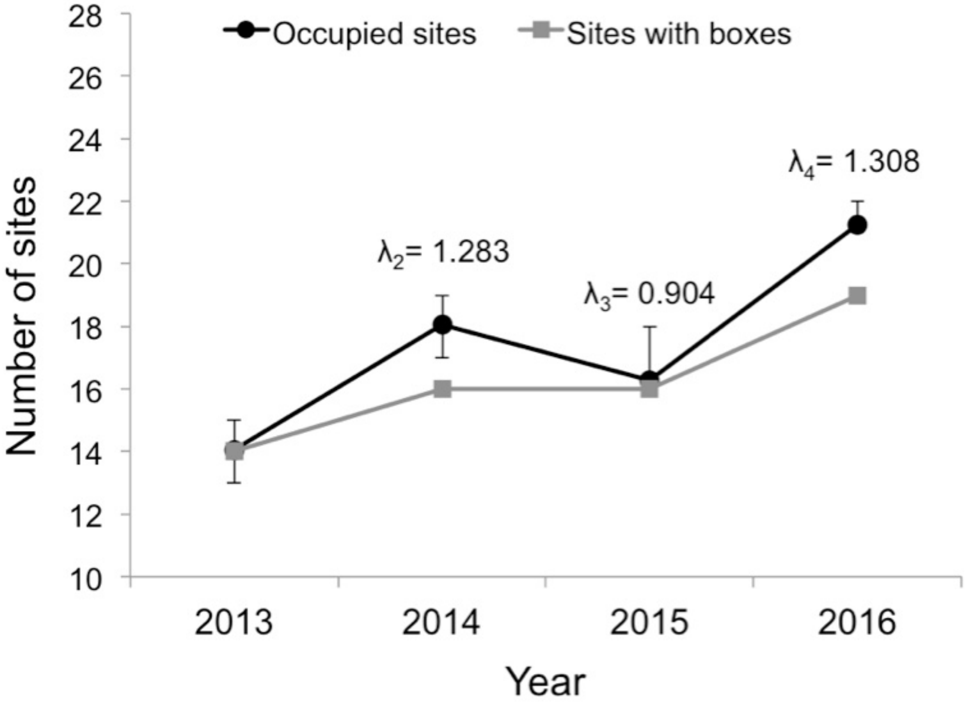

Figure 2.2. **Number of sites with nest boxes and mean estimates of number of sites occupied by kestrels between 2013 – 2016.** Error bars indicate 95% credible intervals. Occupancy-based population growth rates $\lambda_{2\text{-}4}$ refer to changes since previous year.

The covariate coefficient for *site box* in all ecological process models had 95% CRIs that did not overlap zero, indicating that nest boxes were an important predictor of first-year site occupancy, site colonization, and site persistence (Table 2.1). Furthermore, *neighbor box* had an important effect on site colonization: sites were more likely to become occupied if an adjacent site had nest boxes. The random effect of *transect* did not appear to have an important effect. Only *date* had an important effect on detection probability: kestrel detectability decreased between June and August (Fig. 2.3).

Table 2.1. **Multi-season occupancy modeling results for kestrel presence.** Posterior summaries for intercepts, covariate coefficients, and random effect coefficients from the multi-season models for kestrel first-year site occupancy, site probability, site colonization, site persistence, and detection probabilities. Important covariate effects are indicated in bold (95% CRI does not overlap zero; Kéry and Schaub 2012).

				95% CRI	
Parameter		Mean	SD	2.5%	97.5%
ψ (first year occupancy)	α0 (intercept)	2.16	3.63	-4.94	8.69
	α1 (*site box*)	**7.88**	**1.67**	**3.88**	**9.93**
	α2 (*neighbor box*)	1.04	2.73	-4.17	6.53
γ (colonization)	α3 (intercept)	2.15	3.61	-4.96	8.49
	α4 (*site box*)	**5.45**	**2.68**	**0.85**	**9.78**
	α5 (*neighbor box*)	**5.25**	**2.63**	**0.92**	**9.73**
φ (persistence)	α6 (intercept)	3.74	3.20	-2.30	9.50
	α7 (*site box*)	**7.62**	**1.88**	**3.09**	**9.91**
	α8 (*neighbor box*)	0.22	3.38	-6.96	6.82
p (detection)	β0 (intercept)	-1.64	0.11	-1.87	-1.43
	β1 (*date*)	**-0.43**	**0.10**	**-0.64**	**-0.23**
	β2 (*time*)	-0.09	0.098	-0.28	0.052
	β3 (*survey*)	-0.138	0.097	-0.33	0.10
	β4 (*nest distance*)	0.036	0.097	-0.15	0.23
	transect				
	Western	-0.066	1.37	-3.15	2.79
	Eastern	-0.66	1.38	-4.33	1.22
	Northern	0.87	1.93	-1.02	5.54
	Southern	1.41	2.4	-2.76	5.82

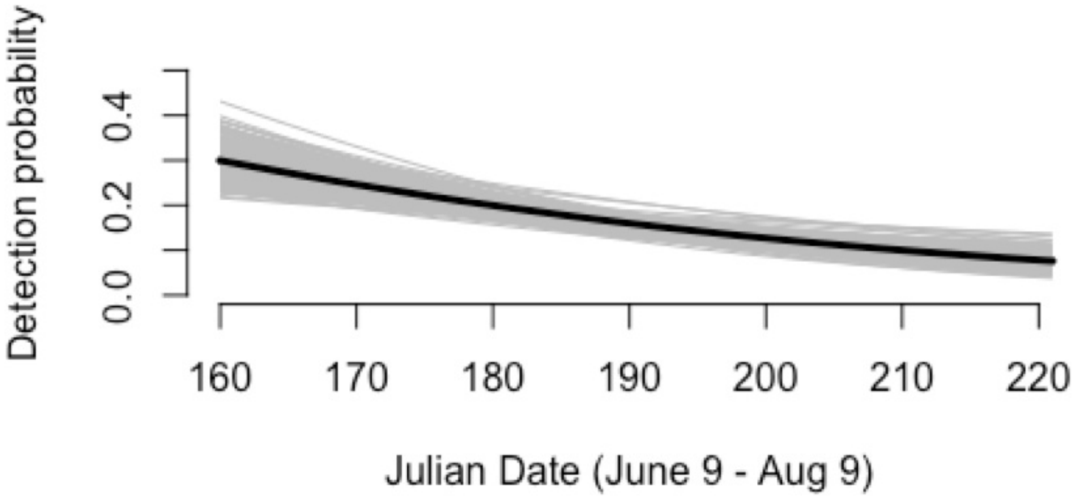

Figure 2.3. **Predictions of the relationship between Julian date and kestrel detection probability *p*.** Black line shows posterior mean, and gray lines show the relationship based on a random posterior sample of size 200 to visualize estimation uncertainty (Kéry and Schaub 2012).

Discussion

As predicted, the probability of kestrel presence was higher at sites with nest boxes compared to those without. The lack of an important effect of transect further suggests that nest boxes, more so than other potential sources of variation in the landscape, determined kestrel site occupancy. Combined with the high rates of orchard nest box use in this region (Shave and Lindell 2017), these results indicate that kestrels in the local population are indeed limited by nest site availability.

Installing additional nest boxes in 2013 and 2015 resulted in an overall increase in kestrel presence between 2013 and 2016. Additionally, as predicted, sites neighboring those with boxes were more likely to become occupied, probably due to home ranges overlapping the two sites. Installing boxes at additional sites during the falls of 2013 and 2015 therefore increased the potential for neighboring sites to also become occupied the following summers. As a result, the number of occupied sites in 2014 and 2016 exceeded the number of sites with boxes. However, the lack of an important effect of *neighbor box* on site persistence suggests that boxes in neighboring sites do not have as strong of an influence on kestrel site occupancy as boxes in the site itself. One explanation for the lack of an important effect of *neighbor box* on site persistence is that the sizes and shapes of kestrel home ranges likely vary each year. Thus, a site without boxes that becomes occupied by kestrels using a new nest box in the neighboring site may not remain occupied the following year if the kestrel pair using the box has a smaller or differently-shaped home range that does not include the neighboring site. Given the strong relationship between the presence of nest boxes at a site and kestrel site occupancy, installing additional boxes at the sites that still lack them would be necessary to potentially ensure kestrel presence at all sites, regardless of kestrel pair home range sizes. Future work is therefore needed to determine the saturation point for increasing kestrel presence using nest boxes in this region.

Julian date had a negative effect on kestrel detectability; kestrel detections decreased between June and August. One explanation is that kestrels are less conspicuous later in the breeding season due to lower hunting activity, as we predicted. Prey consumption requirements for breeding kestrels increase when the eggs hatch because the adults must provision their young (Balgooyen 1976), and although prey requirements for the family remain high after fledging, the adults cease provisioning the young within 3 weeks after fledging (Varland and Klaas 1991). Thus, adult kestrel hunting activity is likely highest during the brood rearing period (June – July in our study) and may decrease during the postfledging period (July - August).

None of the remaining covariates had important effects on kestrel detectability. The lack of an effect of *time* suggests that kestrels are equally conspicuous in the morning and afternoon.

This conclusion is supported by previous observations that kestrels hunt throughout the day without apparent peaks in activity (Balgooyen 1976). The lack of an effect of *survey* suggests that observer presence during the initial survey did not affect kestrel detectability during the return survey. Finally, *site distance* did not have an important effect, which indicates that detections were not biased towards kestrel activity at boxes with active nesting attempts within 250 m of the transect. This conclusion is further supported by the fact that we made no kestrel sightings at a nest box. The results from the detectability model indicate that kestrel researchers have flexibility in the timing of their surveys and the placement of transects with regard to nest boxes.

Our results indicate that orchard nest boxes can benefit the conservation of kestrels in fruit-growing regions by providing cavities for nest-site limited kestrels in the local breeding population, which may in turn benefit agriculture by promoting kestrel presence, and therefore predation on pest species, in and around orchards. Kestrels using orchard nest boxes in northwestern Michigan kill known orchard pests (Chapter 3), including grasshoppers (Order Orthoptera; Shane and Wise 2012), meadow voles (*Microtus pennsylvanicus*; Tritten 2014, Wood and Singleton 2015), and frugivorous birds such as the American Robin (*Turdus migratorius*; Lindell et al. 2012). Ongoing work aims to examine the effects of kestrel presence and predation on prey abundances in orchards; previous studies of raptors in agroecosystems have focused mainly on Barn Owls and their diets (Labuschagne et al. 2016). Nest box programs are relatively easy to implement compared to other methods of enhancing predator populations, such as species reintroduction (e.g., MacDonald 2009) and land cover management (e.g., Tscharntke et al. 2011). Thus, boxes are a useful and widely applicable tool for increasing local population sizes and, potentially, the ecosystem services provided by species that use cavities and are also important predators of pests in agroecosystems, such as birds and bats (Whelan et al. 2008, Maas et al. 2015).

Finally, this study demonstrates the usefulness of occupancy modeling for measuring the effect of landscape enhancements on predator populations. The ease of including covariates in our model allowed us to account for potential sources of spatial and temporal dependence in our surveys in order to investigate the effect of nest boxes on site occupancy at a finer spatial scale than demonstrated in previous studies of kestrel species (Smallwood and Collopy 2009, Paz et al. 2013). Working at the scale of potential kestrel territories allows us to more confidently conclude that nest boxes, and not unmeasured sources of landscape variation, were responsible for the observed increase in kestrel presence. This spatial scale is also highly relevant to the farmers and landowners on whose properties the boxes were installed, for we can conclude that installing a nest box in an orchard resulted in a high probability of kestrels occupying that orchard or the areas adjacent to it. Modern statistical tools such as occupancy modeling may therefore play an important role in future research on landscape enhancements for previously understudied vertebrate predators in agroecosystems, including raptors.

LITERATURE CITED

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Aing, C., S. Halls, K. Oken, R. Dobrow, and J. Fieberg. 2011. A Bayesian hierarchical occupancy model for track surveys conducted in a series of linear, spatially correlated sites. Journal of Applied Ecology 48: 1508 – 1517.

Arlettaz, R., M. Schaub, J. Fournier, T.S. Reichlin, A. Sierro, J.E.M. Watson, and V. Braunisch. 2010. From publications to public actions: When conservation biologists bridge the gap between research and implementation. BioScience 60:835-842.

Askham, L.R. 1990. Effect of artificial perches and nests in attracting raptors to orchards. Pages 144-148 in L.R. Davis and R.E. Marsh [Eds.], Proceedings of the 14th Vertebrate Pest Conference. University of California Davis Press, Davis, CA, USA.

Balgooyen, T.G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius*) in the Sierra Nevada of California. University of California Publications in Zoology 103: 1-83.

Bird, D.M. and R.S. 1988. Handbook of North American birds. Volume 5. Yale University Press, New Haven, CT, USA.

Brewer, T., G.A. McPeek, and R.J. Adams Jr. 1991. The atlas of breeding birds of Michigan. Michigan State University Press, East Lansing, MI, USA.

Brown, J.L., M.W. Collopy, and J.A. Smallwood. 2014. Habitat fragmentation reduces occupancy of nest boxes by an open-country raptor. Bird Conservation International 24:364-378.

Farmer, C.J. and J.P. Smith. 2009. Migration monitoring indicates widespread declines of American Kestrels (*Falco sparverius*) in North America. Journal of Raptor Research 43:263–273.

Flynn, D.F.B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B.T. Richers, B.B. Lin, N. Simpson, M.M. Mayfield, and F. DeClerck. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12:22-23.

Gelman, A., J.B. Carlin, H.S. Stern, and D.B. Rubin. 2003. Bayesian Data Analysis, Second Edition. Chapman & Hall, Boca Raton, FL, USA.

Green, R.E., S.J. Cornell, J.P.W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. Science 307:550-555.

Gibbons, P., D.B. Lindenmayer, J. Fischer, A.D. Manning, A. Weinberg, J. Seddon, P. Ryan, and G. Barret. 2008. The future of scattered trees in agricultural landscapes. Conservation Biology 22:1309-1319.

Jedlicka, J.A., R. Greenberg, and D.K. Letourneau. 2011. Avian conservation practices strengthen ecosystem services in California vineyards. PloS ONE 6(11):e27347.

Kay, B.J., L.E. Twigg, T.J. Korn, and H.I. Nicol. 1994. The use of artificial perches to increase predation on house mice (*Mus domesticus*) by raptors. Wildlife Research 21:95-105.

Kéry, M. and M. Schaub. 2012. Bayesian Population Analysis Using WinBUGS. Elsevier, New York, NY, USA.

Kiss, O., Z. Elek, and C. Moskát. 2014. High breeding performance of European Rollers *Coracias garrulus* in a heterogeneous farmland habitat of southern Hungary. Bird Study 61:496-505.

Kross, S.M., J.M. Tylianakis, and X.J. Nelson. 2012. Effects of introducing threatened falcons into vineyards on abundance of passeriformes and bird damage to grapes. Conservation Biology 26:142-149.

Kross, S.M., R.P. Barbour, and B.L. Martinico. 2016. Agricultural land use, Barn Owl diet, and vertebrate pest control implications. Agriculture, Ecosystems and Environment 223:167-174.

Labuschagne, L., L.H. Swanepoel, P.J. Taylor, S.R. Belmain, and M. Keith. 2016. Are avian predators effective biological control agents for rodent pest management in agricultural systems? Biological Control 101:94-102.

Lambrechts, M.M., K.L. Wiebe, P. Sunde, T. Solonen, F. Sergio, A. Roulin, A. P. Møller, B.C. López, J.A. Fargallo, K-M. Exo, G. Dell'Omo, D. Costantini, M. Charter, M. W. Butler, G. R. Bortolotti, R. Arlettaz, and E. Korpimäki. 2012. Nest box design for the study of diurnal raptors and owls is still an overlooked point in ecological, evolutionary and conservation studies: A review. Journal of Ornithology 153:23-34.

Lindell C.A., R.A. Eaton, E.M. Lizotte and N.L. Rothwell. 2012. Bird consumption of sweet and tart cherries. Human-Wildlife Interactions 6:283-290.

Loman, J. 2006. Does nest site availability limit the density of hole nesting birds in small woodland patches? Web Ecology 6:37-43.

Maas, B., D.S. Karp, S. Bumrungsri, K. Darras, D. Gonthier, J.C-C. Huang, C.A. Lindell, J.J. Maine, L. Mestre, N.L. Michel, E.B. Morrison et al. 2015. Bird and bat predation services in tropical forests and agroforestry landscapes. Biological Reviews 91:1081-1101.

Macdonald, D.W. 2009. Lessons learnt and plans laid: Seven awkward questions for the future of reintroductions. Pages 411 – 488 in M.W. Hayward and M.J. Somers [Eds.], Reintroduction of Top-Order Predators. Wiley-Blackwell, Oxford, UK.

MacKenzie, D.I., J.D. Nichols, J.A. Royle, K.H. Pollock, L.L. Bailey and J.E. Hines 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier, New York, NY, USA.

Meyrom, K., Y. Motro, Y. Leshem, S. Aviel, I. Izhaki, F. Argyle, and M. Charter. 2009. Nest-box use by the Barn Owl *Tyto alba* in a biological pest control program in the Bei She'an valley, Israel. Ardea 97:463-467

Mols, C.M.M. and M.E. Visser. 2007. Great Tits (*Parus major*) reduce caterpillar damage in commercial apple orchards. PloS ONE 2:e202.

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

Paz, A., D. Jareño, L. Arroyo, J. Viñuela, B. Arroyo, F. Mougeot, J. J. Luque-Larena, and J. A. Fargallo (2013). Avian predators as a biological control system of common vole (*Microtus arvalis*) populations in north-western Spain: Experimental set-up and preliminary results. Pest Management Science 69:444–50.

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.

Saracco, J.F., R. B. Siegel, and R.L. Wilkerson. 2011. Occupancy modeling of Black-backed Woodpeckers on burned Sierra Nevada forests. Ecosphere 2:art31.

Sauer, J.R., J.E. Hines, J. Fallon, K.L. Pardieck, D.J. Ziolkowski, Jr., and W.A. Link. 2014. The North American Breeding Bird Survey, results and analysis 1966-2013. Version 01.30.2015. U.S.G.S. Patuxent Wildlife Research Center, Laurel, MD, USA. http://www.mbr-pwrc.usgs.gov/bbs.

Shane, B. and J. Wise. 2012. Increased populations of grasshoppers cause problems in fruit crops. Michigan State University. http://msue.anr.msu.edu/news/increased_populations_of_grasshoppers_cause_problems_in_fruit_crops

Shave, M.E. and C.A. Lindell. 2017. American Kestrels occupying cherry orchard nest boxes show high reproductive rates and tolerance of monitoring. Journal of Raptor Research 51: 50-60.

Smallwood, J.A. and D.M. Bird. 2002. American Kestrel (*Falco sparverius*). In A. Poole and F. Gill [Eds.], The Birds of North America 602. Academy of Natural Sciences, Philadelphia, PA, USA, and American Ornithologists' Union, Washington, DC, USA.

Smallwood, J.A. and M.W. Collopy. 2009a. Southeastern American Kestrels respond to an increase in the availability of nest cavities in north-central Florida. Journal of Raptor Research 43:291-300.

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, J. W. Parrish Jr, T. F. Breen, and K. Boyd. 2009b. Why are American Kestrel (*Falco sparverius*) populations declining in North America? Evidence from nest box programs. Journal of Raptor Research 43:274–282.

Smallwood, J.A., P. Winkler, G.I. Fowles, and M.A. Craddock. 2009. American Kestrel breeding habitat: The importance of patch size. The Journal of Raptor Research 43:308–314.

Tritten, B. 2014. Mice and vole populations are building in many orchards. Michigan State University Extension. http://msue.anr.msu.edu/news/mice_and_vole_populations_are_building_in_many_orchards

Tscharntke, T., Y. Clough, S.A. Bhagwat, D. Buchori, H. Faust, D. Hertel, D. Hölscher, J. Juhrbandt, M. Kessler, I. Perfecto, C. Scherber, G. Schroth, E. Veldkamp, and T.C. Wanger. 2011. Multifunctional shade-tree management in tropical agroforestry landscapes—a review. Journal of Applied Ecology 48:619-629.

USDA 2012 Census of Agriculture. 2014. County profile: Leelanau County, Michigan. United States Department of Agriculture National Agricultural Statistics Service, Washington, DC, USA. http://www.agcensus.usda.gov/Publications/2012/Online_Resources/County_Profiles/Michigan/cp26089.pdf

Varland D.E. and T.M. Klaas. 1991. Development of foraging behavior in the American Kestrel. Journal of Raptor Research 25:9-17.

Whelan, C.J., D.G. Wenny, and R.J. Marquis. 2008. Ecosystem services provided by birds. Annals of the New York Academy of Sciences 1134:25-60.

Whittington, J., K. Heuer, B. Hunt, M. Hebblewhite, and P.M. Lukacs (2015). Estimating occupancy using spatially and temporally replicated snow surveys. Animal Conservation 18:92-101.

Wood, B.J. and G.R. Singleton 2015. Rodents in agriculture and forestry. Pages 33-80 in A. Buckle and R. Smith [Eds.], Rodent Pests and their Control. CAB International, UK.

CHAPTER 3

ASSESSING THE POTENTIAL FOR CROP PEST REDUCTION: QUANTIFYING PREY REMOVAL BY RAPTORS USING ORCHARD NEST BOXES IN A FRUIT-GROWING REGION

Megan E. Shave

Abstract

Extensive human-caused changes to ecosystems over the past 50 years have led to gains in economic development at the cost of biodiversity loss and degradation of ecosystem services, including regulating services, such as crop pest reduction. Quantifying the prey removal efforts of predators is a first step in assessing pest regulation services. American Kestrels (*Falco sparverius*) are widespread generalist predators that may be important providers of regulating services in agricultural regions. However, kestrel diet varies geographically and seasonally, thus my objective was to quantify the prey removal efforts of kestrels using nest boxes installed in cherry orchards in the fruit-growing region of northwestern Michigan. I used nest box video camera and GPS data logger data to 1) determine proportions of different prey types delivered to kestrel nests; 2) develop models to predict kestrel prey removal efforts; and 3) identify patterns in kestrel space use in relation to prey removal. Arthropods and mammals were the two most common prey types delivered. The best-fitting models for numbers of prey delivered and prey type include nestling age, seasonal timing of prey availability, brood size and sex ratio, weather, and adult female movements relative to the nest box. The low marginal R^2 values for models of total prey deliveries indicate low predictive ability beyond the nest boxes and years included in this study; the models would likely benefit from variables that capture habitat variation at smaller spatial and temporal scales. Nevertheless, model parameter estimates suggest some generalizable trends in prey removal; for example, kestrels should remove more total prey during warmer summers with less precipitation. Finally, kestrels delivered more representative pest and neutral prey compared to potentially beneficial prey; I propose cases where prey removal by kestrels is potentially valuable for pest reduction.

Introduction

Human activities over the past 50 years have caused changes in ecosystems that have led to gains in economic development at the cost of biodiversity loss and degradation of ecosystem services, the functions and processes of ecosystems that benefit human well being (Millennium Ecosystem Assessment 2005). Classification and valuation of ecosystem services is therefore important to facilitate greater consideration of ecosystem services in policy and decision-making processes for natural resource management (Chee 2004, Fisher et al. 2009). Regulating services, such as pest regulation, are one class of ecosystem service that has generally been degraded by human activities (e.g. pesticide use in agroecosystems; Millennium Ecosystem Assessment 2005). Enhancement of pest regulation services through reintroduction or encouragement of native predators has received attention in recent decades as a possible key component in integrated pest management (IPM; Lamichhane et al. 2017). Quantifying the prey removal efforts of predators is a first step in assessing the regulating ecosystem services provided by predation in an agricultural region.

The American Kestrel (*Falco sparverius*; hereafter “kestrel”) is a widespread, highly-mobile generalist predator that hunts in a variety of open habitats, including human-dominated landscapes (Smallwood and Bird 2002). Kestrels are therefore potentially important predators in agricultural regions, especially during the summer breeding season, when many crops are susceptible to pests, and kestrel hunting activity is highest due to the increased energetic demand of provisioning nestlings (Bird and 1988). However, kestrel diet varies geographically and seasonally (Sherrod 1978, Bohall-Wood and Collopy 1987). Furthermore, the types and amounts of prey provided to nestling kestrels may vary within the breeding season due to factors such as nestling age and weather. Thus, in order to estimate prey removal, I must understand the mechanisms that predict kestrel prey choice and provisioning effort and relate these predictions to generalizable temporal and spatial features.

This study quantifies the prey removal efforts of kestrels using nest boxes installed in cherry orchards in the fruit-growing region of northwestern Michigan. Michigan is the largest US producer of tart cherries (*Prunus cerasus*) and the third-largest producer of sweet cherries (*Prunus avium*; USDA NASS 2016). Kestrels using these nest boxes have shown high reproductive rates (Chapter 1; Shave and Lindell 2017), and nest boxes have increased kestrel presence in the region (Chapter 2). The kestrel diet potentially includes a variety of orchard pests, including grasshoppers (Shane and Wise 2012), voles (Wood and Singleton 2015), and fruit-eating birds (Lindell et al. 2012). Furthermore, timing of kestrel breeding in the region coincides with orchard vulnerability to many of these pests, particulary fruit-eating birds. My objectives were therefore to 1) determine proportions of different prey types, including proportions of orchard pests and potential beneficial prey, delivered to kestrel nests; 2) develop models to predict kestrel prey removal efforts in terms of numbers and types of prey delivered to kestrel nests; and 3) identify patterns in kestrel space use in relation to prey removal.

I used a multiyear record of prey deliveries from nest box video cameras to identify prey delivered to kestrel nests and determine how the numbers of total deliveries and proportions of mammal deliveries changed with time-dependent variables (Dawson and Bortolotti 2000, Steen 2010). Previous studies have analyzed pellets (e.g. Kross et al. 2016) and fecal samples (Jedlicka et al. 2017) to investigate the diets of avian predators using nest boxes in agricultural regions; however, these methods cannot be used to estimate exact numbers of prey removed, nor can they be easily used to examine changes in diet composition over time. Furthermore, analysis of raptor pellets can underestimate diet diversity when pellets do not include small or rare prey items

(Lewis et al. 2004). Finally, pellet or fecal analysis cannot be used to relate kestrel diet to space use at the level of individual prey deliveries.

I predicted that the numbers of total prey and/or mammal prey would increase with nestling age as energy requirements increased (Balgooyen 1976, Steen et al. 2012). Specifically, I predicted that either 1) total numbers of prey deliveries would increase and proportions of mammal prey would decrease if kestrels switched to more frequent deliveries of smaller prey later in the nestling period (Steen 2010); or 2) proportions of mammal deliveries would increase if kestrels met the increase in demand in part by increasing deliveries of larger, higher-quality prey (Bohall-Wood and Collopy 1987). I also expected kestrels to respond to increased availability of large arthropods over the season; Balgooyen (1976) noted that kestrels switched rapidly from vertebrates to insects with the emergence of winged adult grasshoppers. Thus, the total number of deliveries would increase with accumulated growing degree days (GDDs), which are often used as a measure of arthropod development and can be used to predict the timing of adult insect emergence (Nugent and Rothwell 2005). In particular, I predicted that the total number of deliveries would increase rapidly between 100 and 300 GDD, which corresponds to the adult emergence of multiple grasshopper species (Nufio et al. 2010). Furthermore, I predicted that numbers of deliveries would be lower on days with inclement weather due to decreased prey availability (Dawson and Bortolotti 2000).

In addition, I expected prey removal efforts to vary between nests in relation to brood size and sex ratio. Previous research has demonstrated that total nest provisioning does not increase with brood size during the nestling period (Dawson and Bortolotti 2003), but rather brood size at fledging is determined by provisioning during the nestling period because fledgling production is food limited (Wiehn and Korpimäki 1997). I therefore predicted that larger brood sizes at fledging would correspond to greater provisioning in terms of higher numbers of prey deliveries and/or higher proportions of mammal deliveries. Previous research has also demonstrated that raptors do not adjust their provisioning efforts based on the sex ratio of nestlings (Newton and Marquiss 1979, Laaksonen et al. 2004), and that female-biased broods are more negatively affected by lower provisioning in food poor situations because females are the larger, more expensive sex to raise (Olsen and Cockburn 1991, Laaksonen et al. 2004). However, there is instead evidence that kestrels produce female-biased broods when they are in good condition and spring prey availability is high (Wiebe and Bortolotti 1992) because the larger, more expensive sex benefits more from greater investment (Olsen and Cockburn 1991, Trivers and Willard 1973). Thus, I predicted that female-biased sex ratios in full broods (five fledglings) would correspond to higher numbers of prey deliveries and/or higher proportions of mammal deliveries because higher prey availability and parental condition would result in increased provisioning.

I also considered the effect of land cover variation by looking at the relationship between available hunting habitat and number of deliveries. Kestrels use woodlots and other forested areas for hunting less than expected based on availability, and kestrel hunting success is lower in forested areas than in more open land cover types (Toland 1987). Thus, I expected higher numbers of prey deliveries to nests with lower proportions of forested area within a 1 km^2 potential kestrel home range surrounding a nest box (Smallwood et al. 2009).

Finally, I considered kestrel space use by looking at the relationship between kestrel distance from the nest box and the size of prey subsequently delivered to the nest. The load-size effect in the patch model for central place foragers predicts an increase in load size with increasing distance from the foraging patch and the central location (Orians and Pearson 1979);

in other words, if a parent has traveled farther to find prey, it is expected to bring back larger prey given its large effort. The load-size effect has been observed in multiple raptor species (Sonerud 1992), thus I predicted that kestrels would be more likely to deliver vertebrate prey as their distance from the nest box increased.

Methods

Recording Prey Deliveries to Kestrel Nests

I conducted this study using nest boxes installed in eastern Leelanau County, MI, which has the highest acreage of cherry orchards in the state (Dunckel 2011). Leelanau County is predominantly agricultural with some residential and forested areas (USDA 2012 Census of Agriculture 2014). I had installed these nest boxes in or next to sweet cherry or tart cherry orchard blocks, usually in an open spot where a tree was missing near the end of a row. I installed one box (Box 5) in an apple (*Malus domestica*) orchard block adjacent to a tart cherry block. I installed Boxes 1 – 8 prior to the summer of 2013; I installed Boxes 9 – 18 prior to the summer of 2014. I moved one box (Box 7a) to a new block (Box 7b) between the 2013 and 2014 seasons at the request of the orchard manager. My analyses included 15 of these boxes, which kestrels occupied during at least two breeding seasons between 2013 and 2016 (Fig. 3.1).

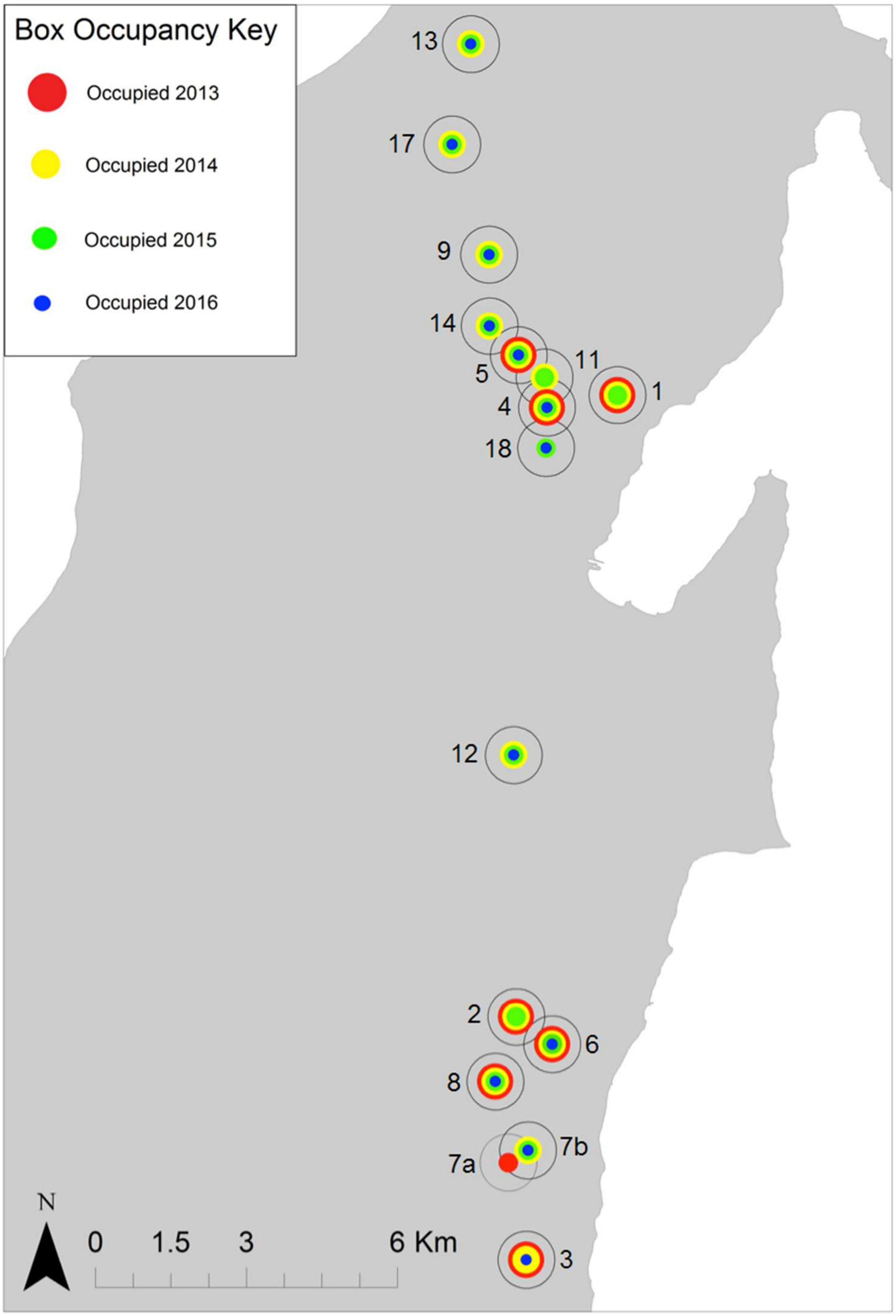

Figure 3.1. **Map of kestrel nest boxes in Leelanau County, MI, included in the analysis of prey delivery video data between 2013 and 2016.** Black circles represent 564 m radius buffers used to delineate potential kestrel home ranges.

Prior to the start of the 2013 and 2014 breeding seasons, I installed a weatherproof security camera with night vision ($27 each; Bunker Hill Security) inside each of the boxes.

During the 2014 season, I began moving the cameras and attaching them to the overhang of the nest box roof in cases where nestling feces had obscured the lens. Prior to the 2015 season, I had moved most cameras outside of the boxes. I found that camera location did not affect kestrel nest success or productivity (Shave and Lindell 2017). I recorded prey deliveries to a box using a video recording system consisting of a mini digital video recorder (DVR, $80; SecurityMan, Ontario, California, U.S.A.) with an 8 – 32 GB SD card (≥ $4), 300 W DC-to-AC power inverter ($25; Bestek), and a 12-V rechargeable sealed lead acid deep cycle battery (≥ $60), all housed in a polyethylene plastic storage tote. In 2013, I used two UB12120 12 Ah batteries run in parallel in each recording setup; in 2014 – 2016, I used a 24MDC marine battery with 75 Ah capacity in each setup.

My recording system used lower cost components than similar systems (e.g. Steen 2009, Kross and Nelson 2011, Cox et al. 2012) and allowed us to easily rotate a setup among multiple nest boxes. I deployed a recording setup at a nest box prior to the start of the target recording day. I synchronized time and date for the DVR at each deployment. A recording day lasted from 09:00 – 17:00 EST in 2013, from either 07:00 – 19:00 or 06:00 – 21:00 in 2014, and from 06:00 – 21:00 in 2015 and 2016. I recorded each nest box at least twice per season during the four week nestling period; I recorded a box once per week when possible. In 2013, I programmed the DVRs to record continuously during recording day hours. In order to reduce file size and review time in 2014 – 2016, I programmed the DVRs to record using motion capture. I set the motion target window around the box entrance so that prey deliveries would trigger the recording. I also included at 2 s pre-record that captured the kestrel as it approached the box entrance.

I reviewed video files in QuickTime Player 7. I recorded the time of each prey delivery and the sex of the kestrel making the delivery (if one kestrel passed a prey item to the other at the box, then I recorded the sex of the first kestrel). I classified each delivery as one of the following prey types: arthropod, mammal, bird, herptile, annelid, mollusc, unidentifiable invertebrate, or unidentifiable vertebrate.

I also selected a random subset of recording days to review more intensively to identify pest, neutral, and potentially beneficial arthropod and mammal prey. For arthropods, I chose three suborders/families (grasshoppers, crickets, and ground beetles, respectively) as representatives of the three categories based on their expected presence in the deliveries and my ability to identify them from the video. For mammals, I attempted to identify individuals to species. Finally, I also collected prey remains from inside the nest box after banding the kestrel nestlings and when cleaning out the box at the end of the season. I used these remains to qualitatively identify additional prey species, particularly birds. I classified the representative arthropods, mammal species, and bird species as pests, neutral, or potentially beneficial based on accounts of their diet and roles in agricultural from the literature (see Table 3.1 for citations).

Recording Kestrel Movements Using GPS Data Loggers

I used a protocol successfully tested in 2015 to deploy GPS data loggers on adult female kestrels in 2016. I trapped kestrels in the nest boxes within the first 10 d post nest hatching by blocking the box entrance with a sponge on an extendable pole (Bloom et al. 2007); if the kestrel flushed before I could place the sponge, I would temporarily install a remote controlled trap door in the box (Plice and Balgooyen 1999). I collected standard measurements, including weight, for each kestrel and fitted her with a USGS metal leg band. I fitted kestrels weighing at least 130 g with a 3.0 g GiPSy-5 GPS data logger (TechnoSmArt, Italy), weatherproofed with 0.5 g of either self-sealing tape or a mixture of baking soda and cyanoacrylate glue, attached to a 1 g Teflon ribbon diagonal-loop backpack-style harness (Kenward 1985, Rodriguez et al. 2012), so that the weight did not exceed 3.5% of the bird's weight (Kenward 1985). I attached the harness straps to the data logger using rivets made from 80 lb test monofilament (Smallwood and Natale 1987). Other methods designed for permanent harness attachment to falcons include copper tubing or other coverings to protect the attachment points and prevent the falcon from removing the harness (e.g. Steenhof et al. 2006); I did not protect the monofilament rivets on the harness, and observed in 2015 that kestrels would begin destroying the rivets within a five day deployment. I therefore assumed that the harness would remain attached for the four day deployments in 2016 but would not remain attached indefinitely if I were unable to recapture the kestrel. I also tested a polyester ribbon harness on three female kestrels in 2016 as an option for an even lighter and less permanent attachment method for male kestrels. After releasing the kestrel, I observed her until she flew out of sight to confirm that she was moving normally. Finally, I recaptured the kestrel three days later to remove the GPS data logger and download the data.

I programmed the GPS data loggers with a 9 – 12 hr delay and treated the first day of deployment as an acclimatization period (Rodriguez et al. 2012). I then programmed the data loggers to record a locational fix every 30 s or 1 min between 06:00 – 21:00 EST. I screened the data to first remove fixes with a Position Dilution of Precision (PDOP) >1.5 in order to remove grossly imprecise locations (Frair et al. 2010). I then removed fixes with timestamps corresponding to periods when the kestrel was inside the nest box, as determined from the nest box video recordings. Finally, I calculated the distance between each remaining locational fix and the nest box.

Statistical Analyses

Models of total deliveries and proportion of mammal deliveries

I built Poisson mixed effects regression models to explain the number of total deliveries made to a nest box in a day, with recording hours included as an offset to account for the differing lengths of recording days (Zuur et al. 2009). I also built logistic mixed effects and regression models to explain the proportion of mammal deliveries made to a nest box in a day. I included box ID and year as random effects in the mixed effects models. I built two sets of these models: one that included all nests and one that included only nests that produced five fledglings (as determined by the number of nestlings reaching 80% of fledging age, 22 d; Steenhof and Peterson 2009).

In all models I considered the following standardized covariates as potential fixed effects: the linear (nestling age) and quadratic (nestling age^2) effects of nestling age measured as days post nest hatch initiation (the day the first egg hatched; Shave and Lindell 2017), the linear (GDD) and quadratic (GDD^2) effects of accumulated growing degree days, daily precipitation in mm (precipitation), max daily wind speed in m/s (wind), max daily air temperature in °C (temp), latitude, proportion forested area within a 1 km^2 potential kestrel home range centered on the nest box (forested; Smallwood et al. 2009). In models with all nests I also included the brood size at fledging (brood size); in models with nests that produced five fledglings I included the proportion of female fledglings (brood sex ratio).

I generated weather measurements for each box using data from the closest MSU Enviroweather station. I generated accumulated GDDs via numerical integration of hourly data from MSU Enviroweather stations using Jan 1st as the starting date for each year and 10° C as the base temperature (Nugent and Rothwell 2005). I calculated forested area proportions in

ArcMap (10.2.2) using a forest cover shapefile layer drawn from interpretation of 2014 and 2016 USDA NAIP imagery. I tested for multicollinearity between covariates using Pearson’s correlation coefficients. I found correlations of 0.60 and 0.75 between nestling age and GDD for all nests and nests that produced five nestlings, respectively; I kept both covariates in the models with all nests because I considered them biologically distinctive and the correlation was below the threshold of 0.7 at which model estimates become significantly distorted (Dormann et al. 2013).

Models of kestrel locations preceding deliveries

I also built logistic mixed effects regression models to explain a prey delivery as either invertebrate (0) or vertebrate (1). I included box ID as the random effect in the mixed effects models. I included the following standardized covariates as fixed effects: nestling age (nestling age) and mean distance of the kestrel from the nest box in m (distance). I generated a mean distance for each prey delivery by averaging the distances with timestamps preceding the delivery.

Model selection

For all models I used a top-down approach for model selection in which I first built models including all fixed effect variables of interest and determined the optimal structure of the random effects using Akaike's Information Criterion (Akaike 1974) corrected for small sample size (AICc; Hurvich and Tsai 1989, Zuur et al. 2009). Using the random effects structure of the highest-ranking model from the first step, I then tested the significance of the fixed effects by comparing nested models using analysis of deviance (Zuur et al. 2009). I calculated marginal R^2

(associated with fixed effects) and conditional R^2 (associated with fixed and random effects) values for the best model to assess goodness of fit of the fixed effects and overall model (Nakagawa and Schielzeth 2013). I also assessed goodness of fit visually by plotting observed values against fitted values. I built all models using package “lme4” in program R (3.1.0).

Results

Kestrel Prey Deliveries

Overall, the video recording system performed well, with few cases of malfunction (see Appendix A). I analyzed video from 179 recording days and documented 7,778 prey deliveries; overall, arthropods and mammals were the two most common prey types delivered (Fig. 3.2). I attempted to identify representative pest, neutral, and beneficial arthropods during 33 of the recording days; crickets were most commonly identified out of 489 identifiable individuals from 986 arthropod deliveries during those days (Table 3.1). I attempted to identify pest, neutral, and beneficial mammal species during 63 of the recording days; voles were most commonly identified out of 310 identifiable individuals from 381 mammal deliveries during those days (Table 3.1). I identified several bird species from the video recordings and remains collections (Table 3.1); I could not calculate proportions of species because most bird deliveries were unidentifiable due to the removal of heads and feathers.

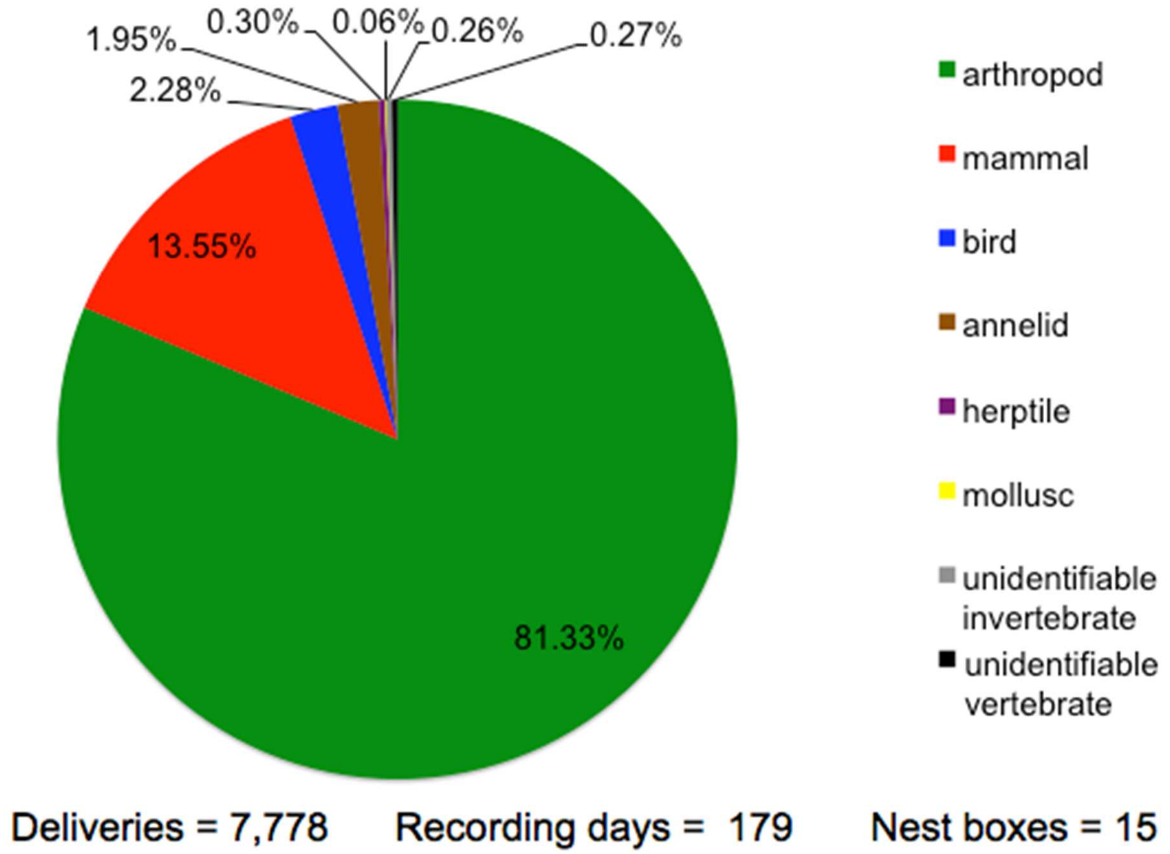

Figure 3.2. **Summary of prey types delivered to kestrel nest boxes during the 2013 – 2016 breeding seasons.**

Table 3.1. **Identities and proportions of representative pest, neutral, and beneficial prey delivered to kestrel nest boxes.**

	Arthropod (n = 986 total; 489 identifiable)		Mammal (n = 381 total; 310 identifiable)		Bird
		% identified as		% identified as	
Pest (herbivore/ frugivore)	grasshopper [a] (Suborder Caelifera)	14.9	meadow vole[c,d] (*Microtus pennsylvanicus*) *Peromyscus* spp.[d]	56.9 7.6	American Robin[f,g] (*Turdus migratorius*) European Starling[f,g] (*Sturnus vulgaris*) Blue Jay[g] (*Cyanocitta cristata*)

Table 3.1 (cont'd)

Neutral (omnivore/ granivore)	cricket (Family Gryllidae)	28.1	meadow jumping mouse (*Zapus hudsonius*) thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	7.3 3.9	Sparrows (Family Emberizidae)
Potential beneficial (insectivore/ omnivore)	ground beetle[b] (Family Carabidae)	5.9	short-tailed shrew[e] (*Blarina brevicauda*)	3.4	Eastern Bluebird[h] (*Sialia silias*) Downy Woodpecker[i] (*Picoides pubescens*) Black-capped Chickadee[e] (*Poecile atricapillus*)

a Shane and Wise (2012)
b Jones et. al (2013)
c Wood and Singleton (2015)
d Irish-Brown (2016)
e McCollough et al. (2001)
f Lindell et al. (2012)
g M. Shave, *Personal observation*
h Jedlicka et al. (2017)
i Flower et al. (2014)

Models of Total Deliveries and Proportion Mammal Deliveries

The best-fitting model for the total number of prey deliveries ($\beta_0 = -8.93 \pm 1.57$) in a day for all nests included the random effects of box and year with random intercepts and slopes (Appendix B, Table 3.2) and the fixed effects of nestling age, nestling age^2, GDD, GDD^2, precipitation, temp, and brood size (Appendix B, Table 3.3.). Age had a positive effect on total deliveries ($\beta_1 = 0.72 \pm 0.20$), while age^2 had a negative effect ($\beta_2 = -0.40 \pm 0.017$); thus, the total number of deliveries increased with nestling age at a decreasing rate over the nestling period (Fig. 3.3). The coefficients for GDD (β_3 = -0.56 ± 0.032) and GDD^2 (β_4 = -0.056 ± 0.014) were both negative; thus, the relationship between GDD and the total number of deliveries was a concave curve with a peak around 200 - 300 GDD (Fig. 3.4). Deliveries decreased with increasing precipitation (β_5 = -0.11 ± 0.015) and increased with increasing temperature (β_6 = 0.24 ± 0.016). The marginal and conditional R^2 values for the model were 0.024 and 0.58, respectively. The model predicted lower numbers of deliveries better than higher numbers of deliveries (Appendix B, Fig. 3.8); in particular, the model seemed to underestimate the highest numbers of deliveries (Appendix B, Fig. 3.9).

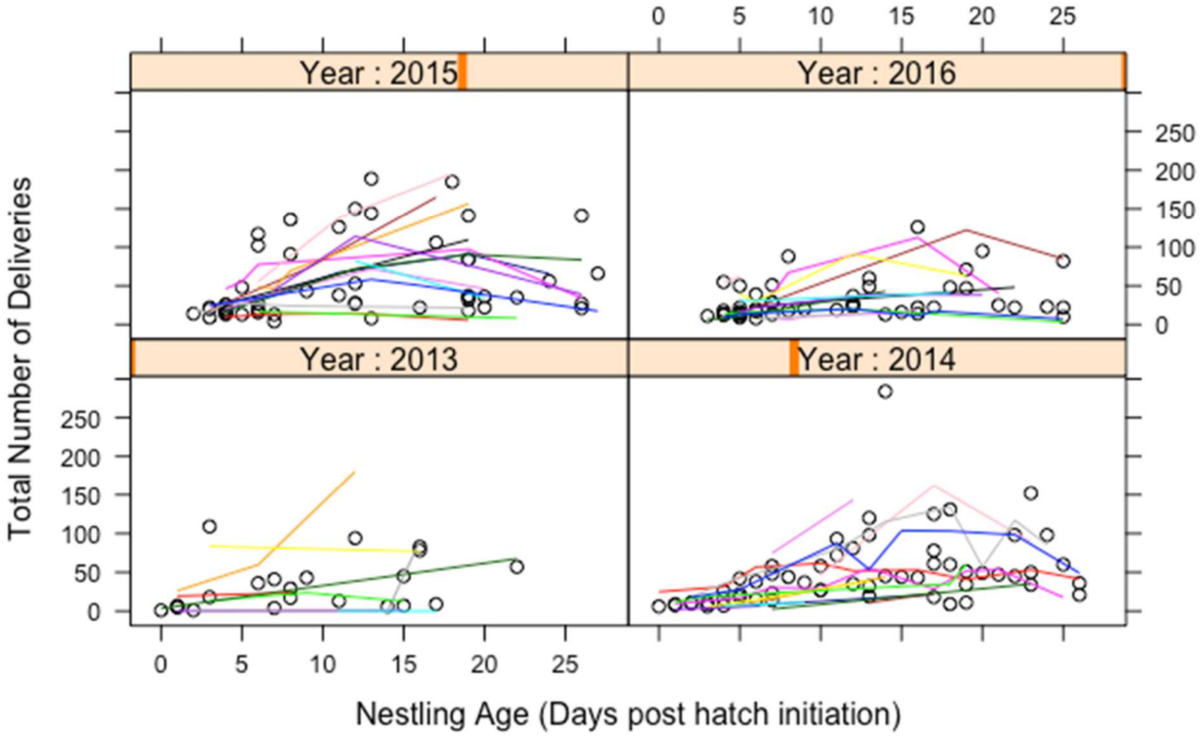

Figure 3.3. **Total number of deliveries to a nest box in a day increased at a decreasing rate with nestling age.** Black circles represent observed values; colored lines represent fitted values (estimated conditional means from Poisson mixed effects model) for each box.

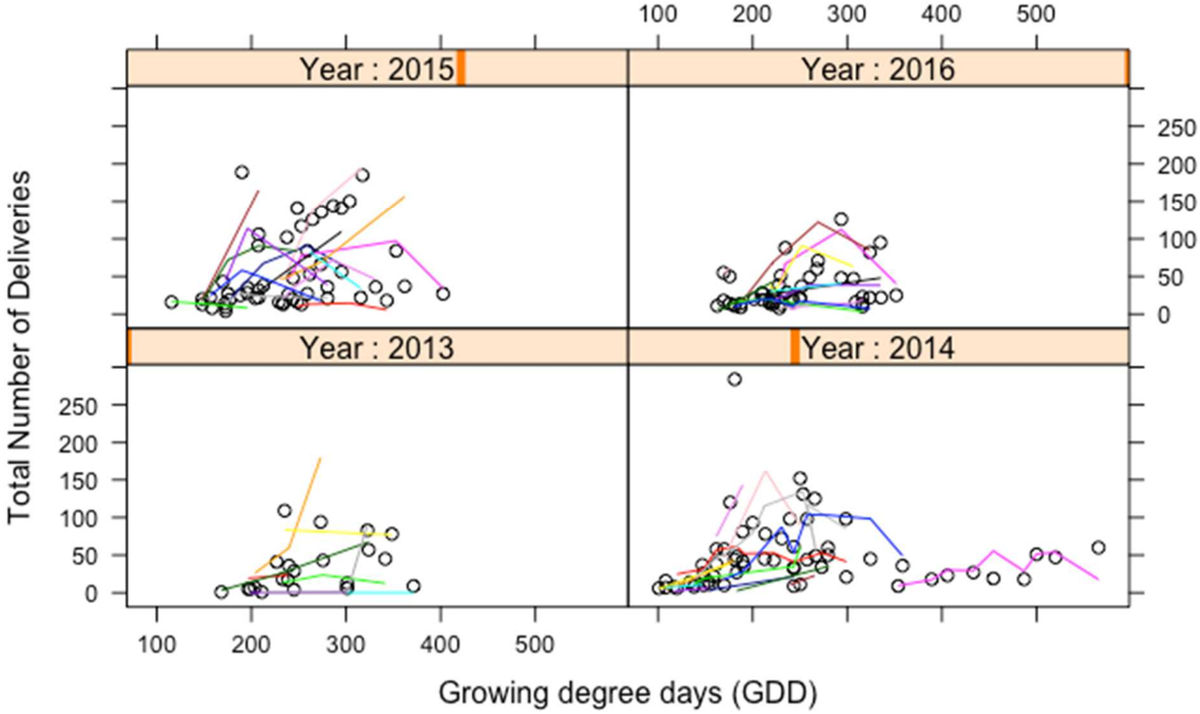

Figure 3.4. **Total number of deliveries to a nest box in a day increased and then decreased (concave curve) with accumulated GDD.** Black circles represent observed values; colored lines represent fitted values (estimated conditional means from Poisson mixed effects model) for each box.

The best-fitting model for proportion of mammal deliveries (β_0 = -2.44 ± 0.50) in a day for all nests included the random effects of box and year with random slopes and intercepts (Appendix B, Table 3.4) and the fixed effects of nestling age, nestling^2, GDD, precipitation, wind, and temp (Appendix B, Table 3.5). Nestling age had a negative effect (β_1 = -1.09 ± 0.26), while nestling age^2 had a positive effect (β_2 = 0.56 ± 0.050); thus, the proportion of mammals decreased with nestling age at a decreasing rate over the nestling period (Fig. 3.5). The proportion of mammal deliveries decreased with GDD (β_3 = -0.31 ± 0.075) and temp (β_4 = -0.14 ± 0.048), and increased with precipitation (β_5 = 0.15 ± 0.043) and wind speed (β_6 = 0.09 ± 0.045). The marginal and conditional R^2 values for the model were 0.14 and 0.36, respectively. Again the model predicted lower proportions better than higher proportions of mammal deliveries (Appendix B, Fig. 3.10); in particular, the model seemed to underestimate higher proportions of mammal deliveries (Appendix B, Fig. 3.11).

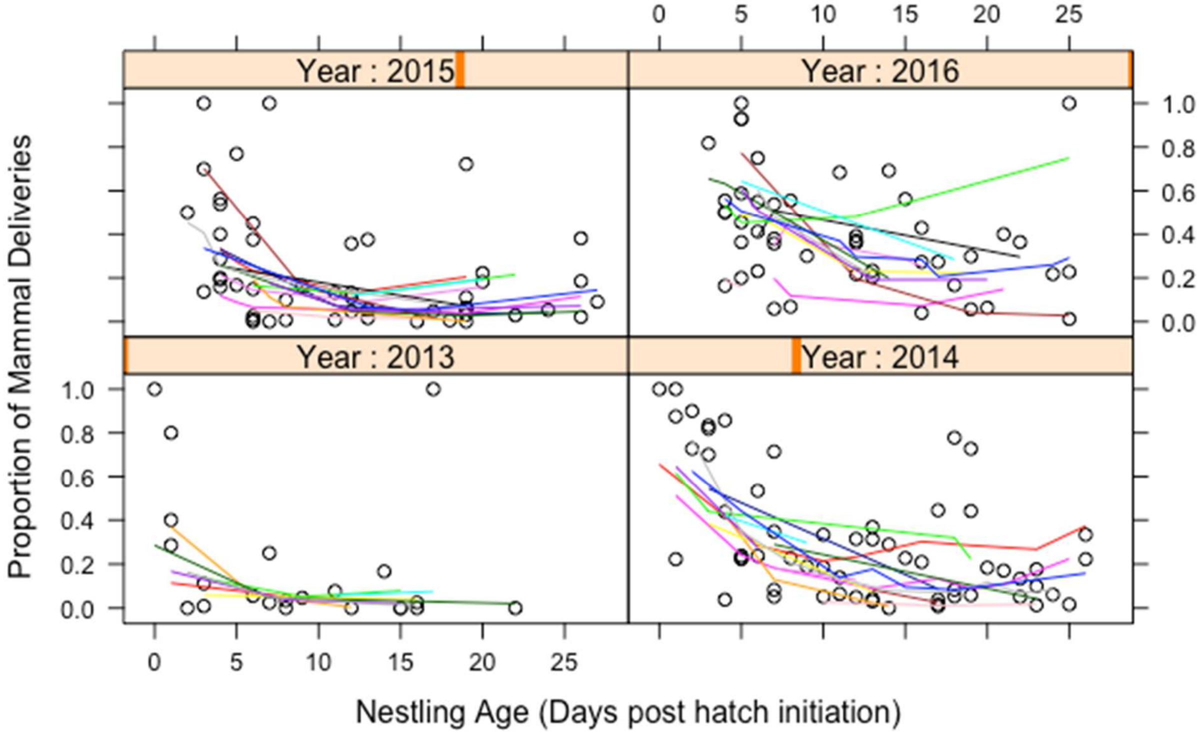

Figure 3.5. **Proportion of mammal deliveries to a nest box decreased at a decreasing rate with nestling age.** Black circles represent observed values; colored lines represent fitted values (estimated conditional means from logistic mixed effects model) for each box.

The best-fitting model for the total number of prey deliveries ($\beta_0 = -8.67 \pm 1.50$) in a day for nests producing five fledglings included the random effects of box and year with random intercepts and slopes (Appendix B, Table 3.6) and the fixed effects of nestling age ($\beta_1 = 0.32 \pm 0.28$), nestling age^2 ($\beta_2 = -0.59 \pm 0.026$), precipitation ($\beta_3 = -0.03 \pm 0.020$), temp ($\beta_4 = 0.41 \pm 0.029$), and brood sex ratio ($\beta_5 = -0.49 \pm 0.035$; Appendix B, Table 3.7). Directions of included fixed effects were the same as in the model with all nests. The total number of deliveries decreased with higher proportions of female nestlings. The marginal and conditional R^2 values for the model were 0.022 and 0.62, respectively.

The best-fitting model for the proportion of mammal deliveries (β_0 = -2.39 ± 0.41) in a day for nests producing five fledglings included the random effects of box and year with random intercepts and slopes (Appendix B, Table 3.8) and the fixed effects of nestling age (β_1 = -0.57 ± 0.32), nestling age^2 (β_2 = 0.73 ± 0.027), precipitation (β_3 = 0.16 ± 0.022), temp (β_5 = -0.44 ± 0.076), and brood sex ratio (β_6 = 0.25 ± 0.095; Appendix B, Table 3.9). Directions of fixed effects were the same as in the model with all nests. The proportion of mammal deliveries increased with higher proportions of female nestlings. The marginal and conditional R^2 values for the model were 0.14 and 0.33, respectively.

Model of Kestrel Locations Preceding Deliveries

I fitted 13 female kestrels with GPS data loggers during the 2016 season. Two of the three kestrels fitted with a lighter polyester harness removed the harness and data logger prior to the start of recording on the second day of deployment. The third kestrel removed the harness on the second day of recording; I recovered the data logger in the nest box and included the locational data from the first day of recording in my analysis. I were unable to retrieve the data logger from one female whose nest failed between the second and third days of deployment; she did not make a second nesting attempt. I were not able to capture any male kestrels; they did not enter the nest box while I were present with the remote controlled trap door installed in the box. My analysis therefore included locational data from 10 female kestrels.

The best-fitting model for prey type delivered (β_0 = 0.81 ± 0.46) included the random effects of box and time with random intercepts and slopes (Appendix B, Table 3.10) and the fixed effects of age and distance (Appendix B, Table 3.11). The probability of a vertebrate delivery decreased with nestling age (β_1 = -1.08 ± 0.45) and increased with mean kestrel distance from the box (β_2 = 0.67 ± 0.26; Fig. 3.6). The marginal and conditional R^2 values for the model were 0.23 and 0.49, respectively. Figure 3.7 maps the locations preceding vertebrate and invertebrate deliveries.

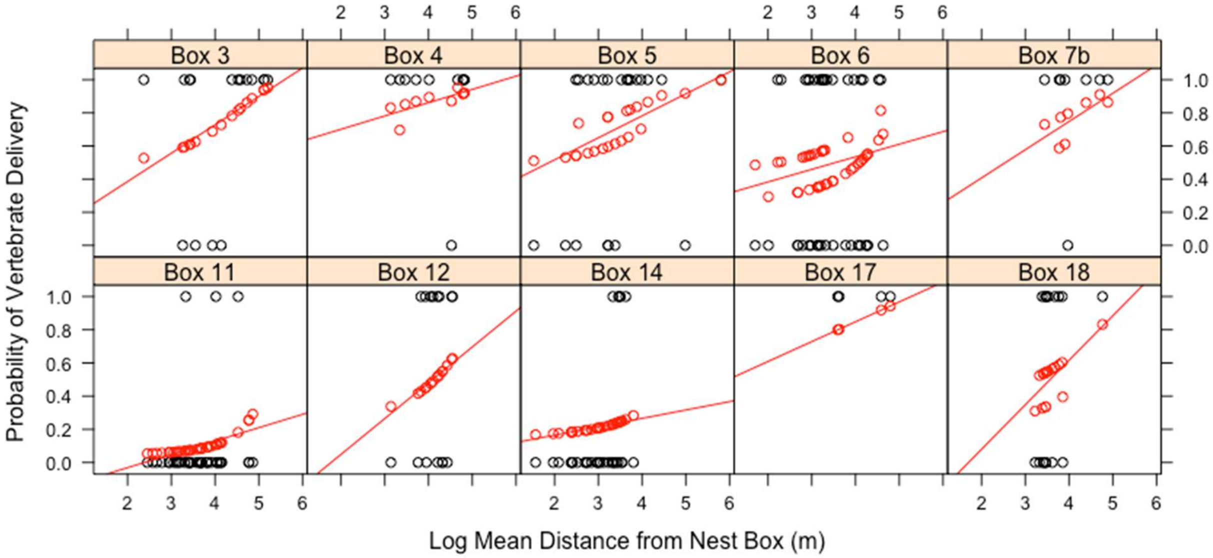

Figure 3.6. **Probability of delivery of vertebrate prey increased with mean distance of female kestrel from the nest box prior to delivery.** Observed values shown in black (0 = invertebrate delivery; 1 = vertebrate delivery). Fitted values (estimated conditional means from logistic mixed effects model) with subject-level regression lines shown in red. X-axis shown on log scale for improved visualization.

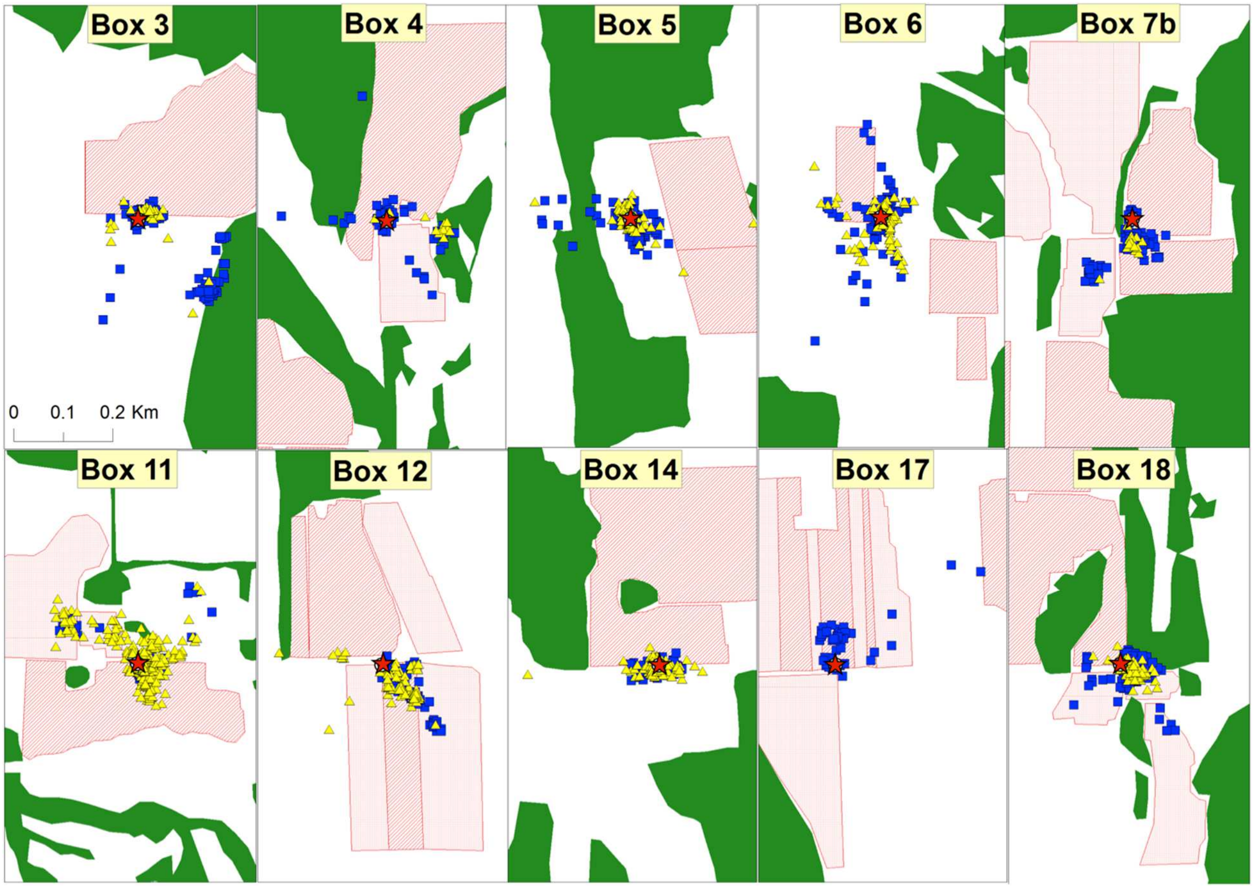

Figure 3.7. **Maps of female kestrel locations (GPS data logger fixes) preceding deliveries of invertebrate (yellow triangles) and vertebrate (blue squares) prey.** Red stars represent nest box locations, green polygons represent forested areas, and red hatched and stippled polygons represent mature and young orchard blocks, respectively.

Discussion

The total number of prey deliveries to the nest box increased with nestling age; however, the proportion of mammal deliveries decreased with nestling age, which indicates that the adult kestrels met the increasing energetic need of the nestlings by delivering arthropods in both greater numbers and proportions. One explanation for this switch is that, during the first two weeks of the nestling period, the adult kestrel (usually the female) enters the nest box with a prey delivery to dismember and feed it to the nestlings. For this period during which the nestlings require assistance for all feeding, it is more efficient for the adult to spend time in the nest box dismembering mammals and other vertebrate prey; however, once the nestlings can feed on small prey unassisted, it may become more efficient for both parents to provide more frequent deliveries of arthropods and spend less time in the box preparing prey (Steen et al. 2012).

The increase in arthropod deliveries may also be a functional response to the increase in arthropod availability due to the emergence of large adult insects. My model of total prey deliveries indicates that the relationship between accumulated GDD and total number of deliveries was a concave curve that peaked around 200 – 300 GDD, which corresponds to the adult emergence of early insects, such as some grasshopper species (Pfadt 1994, Nufio et al. 2010). Also, the proportion of mammal deliveries decreased with GDD, which further suggests a switch to arthropod prey as more large insects became available. This switch is likely facilitated by the formation of a specific search image (SSI) for insect prey. Laboratory studies have shown that kestrels will form SSIs and focus on specific prey for long intervals (Mueller 1987); furthermore, field studies have shown that bal-chatri traps baited with mice are more effective at catching kestrels in the winter, when insect prey are absent, compared to the summer (Berger and Mueller 1959).

Additional variation in prey deliveries occurred in relation to brood size and sex ratio. As predicted, total prey deliveries were higher for nests with larger broods at fledging. The median and mode clutch size in my study area was five eggs, and 93% of all eggs hatched (Shave and Lindell 2017), which suggests that parents that provisioned more maintained more nestlings and produced larger broods at fledging. This result complements the finding that kestrel pair provisioning rates were independent of experimental manipulations in brood size, indicating that parental effort instead determines brood size (Dawson and Bortolotti 2003). Also, the total number of prey deliveries decreased with increasingly female-biased sex ratios in nests that produced five fledglings, while the proportion of mammal deliveries increased. Broods are more likely to be female-biased when prey availability is high and/or when parents are in good condition (Wiebe and Bortolotti 1992). Also, females are the more expensive sex to raise, thus it is unlikely that parents facultatively changed their provisioning rates to provide more prey to male-biased broods. Instead, female-biased sex ratios were likely the result of conditions that also lead to parents providing more mammal prey. For example, high spring prey availability may relate specifically to availability of mammals, thus kestrels produced female-biased broods when mammals were more abundant and consequently provisioned their nests with greater proportions of mammals. Another possible explanation is that adults that produce female-biased broods are also more efficient at capturing mammal prey; in particular, second-year and older breeders may be more likely to produce female-biased broods and be more experienced and effective hunters compared to yearling breeders (Wiebe and Bortolotti 1992).

Also as predicted, weather affected prey deliveries in various ways. The number of total deliveries increased with increasing daily temperature, which likely corresponds to the increase in activity of insects (e.g. grasshoppers; Pfadt 1994) over the range of temperatures observed during this study (14 - 32° C). The number of total deliveries decreased with increasing precipitation, which likely corresponds to decreased activity of flying insects (e.g., adult grasshoppers; Beirne 1970). While previous research has indicated that mammal activity, and therefore availability, decreases with inclement weather (Dawson and Bortolotti 2000), proportions of mammal deliveries increased in my study with increasing precipitation and wind speeds and decreasing temperature, which suggests that mammal availability is less affected by inclement weather than arthropod availability. Furthermore, the increase in proportions of mammal deliveries with increasing wind speed may be a result of increased hover hunting, because kestrels are more likely to hover hunt during periods of moderate wind (3 – 8 m/s), and kestrels tend to capture more mammals while hovering than while perching (Bildstein and Collopy 1987). Max wind speeds rarely exceeded 12 m/s in my study region, supporting the conclusion that increasing wind speeds were more likely to enable kestrel hover hunting than preclude it.

Potential Implications for Agriculture

Within the two most common prey types, arthropods and mammals, kestrels delivered more representative pest and neutral prey compared to potentially beneficial prey (Table 3.1.). These results suggest that kestrel predation is more likely to have a net positive impact on orchards rather than a negative impact. In particular, the consumption of fruit-eating bird species is promising for potential impacts on fruit-eating birds and fruit loss in orchards (Chapter 4). I did identify remains of insectivorous species such as the fiery hunter beetle (*Calosoma calidum*) and Eastern Bluebird (*Sialia sialis*) in kestrel box contents, which suggests a possibly complicated relationship between kestrel predation and insect herbivory in orchards, because some these prey species may be beneficial as consumers of crop pests. Sampling of herbivorous insects and leaf damage in orchards with and without kestrel nest boxes would be needed to examine this relationship. Also, avoiding use of conflicting pest management practices could reduce the potential for negative interactions. For example, I found the Eastern Bluebird remains in a kestrel nest box near which bluebird boxes were installed that summer, and a trail camera captured images of a female kestrel at one of the bluebird boxes (S. Wieferich, *Personal communication*). Thus, I would recommend that orchards with active kestrel nest boxes not provide additional nest boxes or other landscape enhancements for species that may be kestrel prey.

The low marginal R^2 values for models of total and proportion mammal prey deliveries, especially the models of total prey deliveries, indicate low predictive ability beyond the nest boxes and years included in this study. Any spatial variation between nests is currently explained by the random effect of box ID only, due to the lack of generalizable spatial or habitat variables in the models. Proportion forest cover and latitude were not significant in any of my models of prey deliveries. One explanation is that these spatial factors did not vary enough in my study region to result in significant differences in prey selection or provisioning rates among kestrels at different nest boxes. Broad land cover variables might still be useful when comparing regions with significantly different land cover compositions, but when attempting to explain variation in prey deliveries within a region, I may need to consider how kestrels respond to habitat variation occurring at smaller spatial and temporal scales. For example, field studies have noted that hunting kestrels quickly cued in on recently harvested, plowed, irrigated, or mowed crop and hay fields, likely due to increased prey vulnerability from loss of vegetative cover (Rudolph 1982, Toland 1987). Thus, data on the timing and locations of human disturbance activities could improve the models and their predictive ability; in particular, these activities may correspond to the highest observed numbers of total prey deliveries that were underestimated by my models (Appendix B, Tables 3.5 and 3.6).

Although my models for number of prey deliveries have not identified important and generalizable spatial variables in terms of habitat surrounding the nest box, my model of prey delivery type revealed a significant relationship to kestrel movements relative to the nest box. As predicted by the load size effect for central place foragers, female kestrels were more likely to deliver vertebrate prey as their mean distance from the nest box increased, which coincides with a previous finding that kestrel flight time increased with prey size (Rudolph 1982). This result suggests the importance of nest box placement for arthropod removal in particular, because the female kestrel will remove arthropods from areas in close proximity to the nest box.

In addition, although my models of prey deliveries could not be used to make precise predictions of daily numbers of prey removed outside of my study system, I can still use the model parameter estimates to suggest some generalizable trends in prey removal by a kestrel pair over the breeding season. First, based on the observed relationships of prey deliveries to GDD, kestrels with nests that hatch just before or during the 200 – 300 GDD range should remove more total prey than the earliest- and latest-hatching nests, while kestrels with nests that hatch earliest in the growing season should remove higher daily proportions of mammals and may therefore remove more mammals over the entire season. Kestrels should remove more total prey during warmer summers with less precipitation; however, they may remove more mammal prey during colder summers with more wind and precipitation. Also, kestrels with nests that ultimately produce more fledglings should remove more total prey. Finally, kestrels with nests with higher proportions of female nestlings should remove fewer total prey but more mammals. Thus, I can make qualitative comparisons of kestrel prey removal efforts based on easily-obtainable information from weather stations and nest box monitoring.

To conclude, I can use these results to propose cases where prey removal by kestrels is potentially valuable for pest reduction. For example, in drought years when young fruit trees are especially susceptible to grasshopper damage (Shane and Wise 2012), nest boxes in young orchard blocks would encourage predation of grasshoppers and other large herbivorous insects in the block by the female kestrel. Furthermore, the lack of precipitation should increase the number of prey captured. In another case, a mild winter or peak in vole populations that results in high spring vole abundance may also result in kestrels producing female-biased broods and provisioning them with greater proportions of mammal prey. Thus, kestrels may dampen vole cycles and reduce peak vole abundances, as expected for generalist predators (Andersson and Erlinge 1977, Korpimäki and Krebs 1996), which may help mitigate the risk of high vole damage during the following winter. Finally, high levels of kestrel activity in and around an orchard due to the female provisioning the nest with frequent arthropod deliveries may have indirect effects on other potential prey species that exhibit predator avoidance behaviors, such as birds (Cresswell 2008). Thus, if the high rates of prey delivery later in the nestling period coincide with the timing of fruit-eating birds feeding in ripening orchards, then the kestrel activity may deter enough birds to reduce abundances in orchards.

APPENDICES

APPENDIX A

Video Recording System Performance

Overall, the video recording system performed with few cases of malfunction. In 2013, I found that three cameras were faulty and would overheat after a few hours, resulting in a loss of the video feed to static. I therefore adjusted the recording hours for those nest boxes to reflect the duration of recording before the loss of video. I replaced the three cameras for the 2014 season and tested all subsequent cameras for this fault before installation. One other camera needed replacement at the start of the 2015 season after condensation in the unit permanently clouded the lens. In 2014, I lost two recording days at one nest box due to a loose AV connection; I avoided this issue going forward by always checking the video feed with a portable screen during each recording setup deployment. In 2015, I lost one recording day at one nest box after the DVR failed to record during the set recording hours and instead recorded during the preceding hours (00:00 – 6:00); resetting the recording settings fixed the issue. I also noted that when I left a recording setup at a box for several days after the target recording day, the DVR would sometimes begin recording blank (zero bytes) files on the day when the battery voltage became low (~11.9 V, below which the DVR would turn off completely).

APPENDIX B

Model Selection and Assessment

Table 3.2. **Selection of random effects structure in Poisson model of the total number of prey deliveries to a nest in a day (all nests).** Models include all fixed effect variables of interest.

Model	AICc	ΔAICc	Weight
Random intercepts + slopes (box + year)	6213.4	0.0	1
Random slopes (box + year)	6892.1	678.8	<0.001
Random intercepts (box + year)	15484.9	9271.6	<0.001
No random effects	18639.8	12426.5	<0.001

Table 3.3. **Selection of fixed effects in Poisson model of the total number of prey deliveries to a nest in a day (all nests).** Asterisks (*) denote fixed effects significant at the 0.05 level.

Fixed effect	df	χ^2	*P*
nestling age	1	6.86	0.0088*
nestling age^2	1	559.54	<0.001*
GDD	1	414.58	<0.001*
GDD^2	1	56.30	<0.001*
precipitation	1	50.26	<0.001*
temp	1	229.36	<0.001*
wind	1	1.16	0.57
forest	1	2.14	0.10
latitude	1	2.48	0.23
brood size	1	147.77	<0.001*

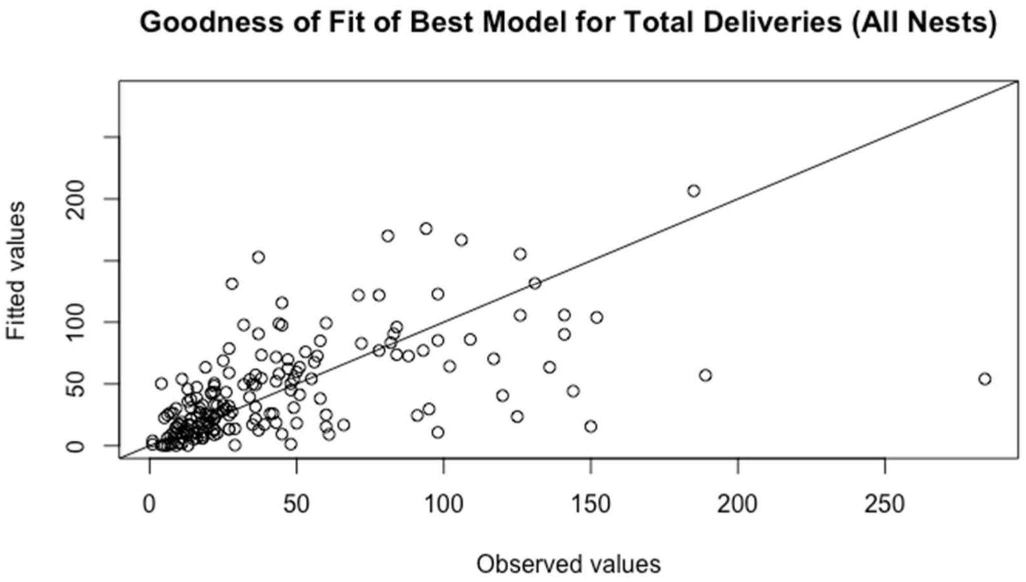

Figure 3.8. **Observed values plotted against fitted values (estimated conditional means) from Poisson mixed effects model for total deliveries to all nests.**

Figure 3.9. **Fitted values (estimated conditional means) from Poisson mixed effects model for total deliveries to all nests overlaid (in red) on observed values (bars).**

Table 3.4. **Selection of random effects structure in logistic model of proportion of mammal prey deliveries to a nest in a day (all nests).** Models include all fixed effect variables of interest.

Model	AICc	ΔAICc	Weight
Random intercepts + slopes (box + year)	1417.8	0.0	1.0
Random intercepts (box + year)	1541.2	123.4	<0.001
Random slopes (box + year)	1788.3	370.5	<0.001
No random effects	1922.1	504.3	<0.001

Table 3.5. **Selection of fixed effects in logistic model of proportion of mammal prey deliveries to a nest in a day (all nests).** Asterisks (*) denote fixed effects significant at the 0.05 level.

Fixed effect	df	χ^2	P
nestling age	1	8.59	<0.001*
nestling age^2	1	120.90	<0.001*
GDD	1	12.69	<0.001*
GDD^2	1	1.29	0.26
precipitation	1	11.26	<0.001*
temp	1	8.34	0.0039*
wind	1	5.57	0.018*
forest	1	0.45	0.50
latitude	1	0.023	0.88
brood size	1	2.43	0.12

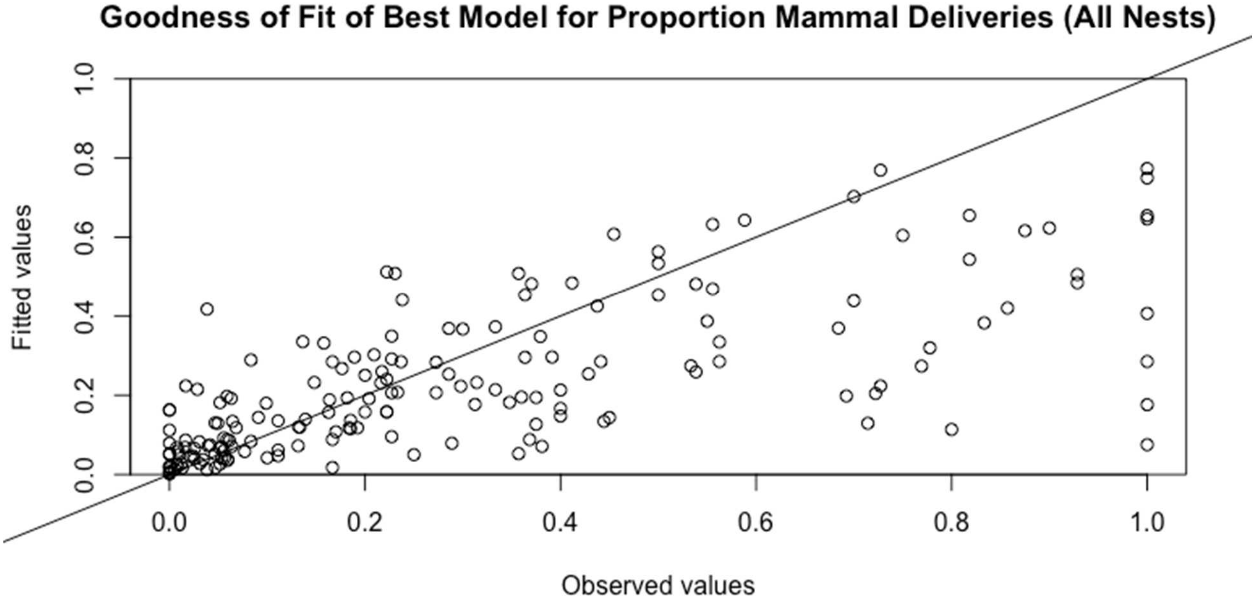

Figure 3.10. **Observed values plotted against fitted values (estimated conditional means) from logistic model of proportion of mammal prey deliveries to all nests.**

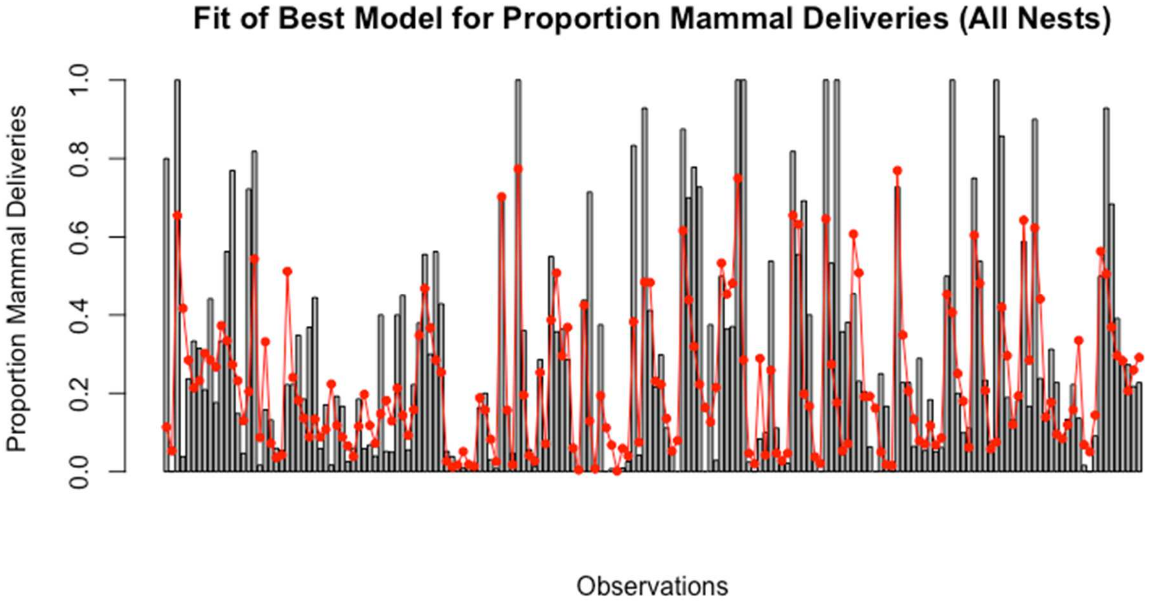

Figure 3.11. **Fitted values (estimated conditional means) from logistic model of proportion of mammal prey deliveries to all nests overlaid (in red) on observed values (bars).**

Table 3.6. **Selection of random effects structure in Poisson model of the total number of prey deliveries to a nest in a day (nests with five fledglings).** Models include all fixed effect variables of interest.

Model	AICc	ΔAICc	Weight
Random intercepts + slopes (box + year)	1611.5	0.0	1
Random intercepts (box + year)	1836.5	225.1	<0.001
Random slopes (box + year)	6178.0	4566.5	<0.001
No random effects	9299.7	7688.2	<0.001

Table 3.7. **Selection of fixed effects in Poisson model of the total number of prey deliveries to a nest in a day (nests with five fledglings).** Asterisks (*) denote fixed effects significant at the 0.05 level.

Fixed effect	df	χ^2	*P*
nestling age	1	1.03	0.31[a]
nestling age^2	1	582.54	<0.001*
precipitation	1	5.02	0.025*
temp	1	204.73	<0.001*
wind	1	1.15	0.69
forest	1	3.61	0.057
latitude	1	0.45	0.50
brood sex ratio	1	191.39	<0.001*

[a] Although nestling age was not significant, I included it in the model because nestling age^2 was significant.

Table 3.8. **Selection of random effects structure in logistic model of proportion of mammal prey deliveries to a nest in a day (nests with five fledglings).** Models include all fixed effect variables of interest.

Model	AICc	ΔAICc	Weight
Random intercepts + slopes (box + year)	636.0	0.0	1.0
Random intercepts (box + year)	736.7	100.7	<0.001
Random slopes (box + year)	830.7	194.8	<0.001
No random effects	919.4	283.4	<0.001

Table 3.9. **Selection of fixed effects in logistic model of proportion of mammal prey deliveries to a nest in a day (nests with five fledglings).** Asterisks (*) denote fixed effects significant at the 0.05 level.

Fixed effect	df	χ^2	*P*
nestling age	1	2.40	0.12[a]
nestling age^2	1	84.35	<0.001*
precipitation	1	6.28	0.012*
temp	1	32.92	<0.001*
wind	1	0.15	0.70
forest	1	0.42	0.51
latitude	1	0.63	0.43
brood sex ratio	1	7.50	0.0062*

[a] Although nestling age was not significant, I included it in the model because nestling age^2 was significant.

Table 3.10. **Selection of random effects structure in logistic model of prey type delivered.** Models include all fixed effect variables of interest.

Model	AICc	ΔAICc	Weight
Random intercepts (box)	227.8	0.0	0.87
Random intercepts + slopes (box)	231.7	3.8	0.13
Random slopes (box)	239.8	12.0	0.0022
No random effects	249.6	21.8	<0.001

Table 3.11. **Selection of fixed effects in logistic model of prey type delivered**. Asterisks (*) denote fixed effects significant at the 0.05 level.

Fixed effect	df	χ^2	*P*
nestling age	1	7.72	0.0055*
distance	1	8.01	0.0047*

LITERATURE CITED

LITERATURE CITED

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control AC-19:716-723.

Andersson, M. and S. Erlinge. 1977. Influence of predation on rodent populations. Oikos 3:591–597.

Bildstein, K.L. and M.W. Collopy. 1987. Hunting behavior of Eurasian (*Falco tinnunculus*) and American Kestrels (*F. sparverius*): a review. Pages 66 – 82 In D.M. Bird and R. Bowman [Eds.], The Ancestral Kestrel. Raptor Research Foundation and Macdonald Raptor Research Center, McGill University, Ste. Anne de Bellevue, Quebec.

Balgooyen, R.G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius*) in the Sierra Nevada of California. University of California Publications Zoology 103:1-87.

Beirne, B. P. 1970. Effects of precipitation on crop insects. The Canadian Entomologist 102:1360–1373.

Berger, D.D. and H.C. Mueller. 1959. The bal-chatri: a trap for birds of prey. Bird-Banding 30:18-26.

Bird, D.M. and R.S. 1988. Handbook of North American birds. Volume 5. Yale University Press, New Haven, CT, USA.

Bloom, P.H., W.S. Clark., and J.W. Kidd. 2007. Capture Techniques. Pages 193 – 219 in Bird, D.M., Bildstein, K.L. [Eds.], Raptor Research Management and Techniques. Hancock House Press, WA, USA.

Bohall-Wood, P.G. and M.S. Collopy. 1987. Foraging behavior of Southeastern American Kestrels in relation to habitat use. Pages 58-65 in D.M. Bird and R. Bowman [Eds.], The Ancestral Kestrel. Raptor Research Foundation and Macdonald Raptor Research Center, McGill University, Ste. Anne de Bellevue, Quebec.

Chee, Y. E. 2004. An ecological perspective on the valuation of ecosystem services. Biological Conservation 120:549–565.

Cox, W. A., M. S. Pruett, T. J. Benson, S. J. Chiavacci, and F. R. Thompson III. 2012. Development of camera technology for monitoring nests. Pages 185–210 in C.A. Ribic, F. R. Thompson III, and P. J. Pietz [Eds.], Video surveillance of nesting birds. Studies in Avian Biology No. 43. University of California Press, Berkeley, CA, USA.

Cresswell, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3–17.

Dawson, R., and G. Bortolotti. 2000. Reproductive success of American kestrels: the role of prey abundance and weather. The Condor 102:814–822.

Dawson, R. D., and G. R. Bortolotti. 2003. Parental effort of American kestrels: the role of variation in brood size. Canadian Journal of Zoology 81:852–860.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. Mcclean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Dunckel, M. 2011. Michigan leads the nation in the production of blueberries and tart cherries. Michigan State University Extension. http://msue.anr.msu.edu/news/michigan_leads_the_nation_in_the_production_of_blueberries_and_tart_cherrie

Fisher, B., R. K. Turner, and P. Morling. 2009. Defining and classifying ecosystem services for decision-making. Ecological Economics 68:643–653.

Flower, C. E., L. C. Long, K. S. Knight, J. Rebbeck, J. S. Brown, M. A. Gonzalez-Meler, and C. J. Whelan. 2014. Native bark-foraging birds preferentially forage in infected ash (*Fraxinus* spp.) and prove effective predators of the invasive emerald ash borer (*Agrilus planipennis Fairmaire*). Forest Ecology and Management 313:300–306.

Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2187–2200.

Hurvich, C. M. and C. L. Tsai. 1989. Regression and time-series model selection in small sample sizes. Biometrika 76:297-307.

Irish-Brown, A. 2016. Rodent management in commercial apple orchards requires an integrated approach. Michigan State University Extension. http://msue.anr.msu.edu/news/rodent_management_in_commercial_apple_orchards_requires_an_integrated_appro

Jedlicka, J. A., A.-T. E. Vo, and R. P. P. Almeida. 2017. Molecular scatology and high-throughput sequencing reveal predominately herbivorous insects in the diets of adult and nestling Western Bluebirds (*Sialia mexicana*) in California vineyards. The Auk 134:116–127.

Jones, A., S. Birthisel, R. Jabbour, F. Drummond and D. Yarborough. 2013. Insects - 196-Beneficial Insect Series 2: Carabidae (Ground Beetles) on Maine Farms. University of

Maine Extension. https://extension.umaine.edu/blueberries/factsheets/insects/insects-196-beneficial-insect-series-2-carabidae-ground-beetles-on-maine-farms/

Kenward, R.E. 1985. Raptor radio-tracking and telemetry. ICBP Technical Publication No. 5, 409 – 420.

Korpimäki, E., and C. J. Krebs. 1996. Predation and population cycles of small mammals: a reassessment of the predation hypothesis. Bioscience 46:754–764.

Kross, S.M. and X.J. Nelson. 2011. A portable low-cost remote videography system for monitoring wildlife. Methods in Ecology and Evolution 2:191-196.

Kross, S. M., R. P. Bourbour, and B. L. Martinico. 2016. Agricultural land use, barn owl diet, and vertebrate pest control implications. Agriculture, Ecosystems & Environment 223:167–174.

Laaksonen, T., J. a Fargallo, E. Korpimaki, S. Lyytinen, J. Valkama, and V. Poyri. 2004. Year- and sex-dependent effects of experimental brood sex on fledging condition of Eurasian ratio manipulation kestrels. Journal of Animal Ecology 73:342–352.

Lamichhane, J.R., M. Bischoff-Schaefer, S. Bluemel, S. Dachbrodt-Saaydeh, L. Dreux, J.P. Jansen, et al. 2017. Identifying obstacles and ranking common biological control research priorities for Europe to manage most economically important pests in arable, vegetable and perennial crops. Pest Management Science 73:14–21.

Lewis, S. B., M. R. Fuller, and K. Titus. 2004. A comparison of 3 methods for assessing raptor diet during the breeding season. Wildlife Society Bulletin 32:373–385.

Lindell C.A., R.A. Eaton, E.M. Lizotte and N.L. Rothwell. 2012. Bird consumption of sweet and tart cherries. Human-Wildlife Interactions 6:283-290.

McCullough, D.G., K.A. Raffa, R.C. Williamson. 2001. Natural enemies of gypsy moth. MSU Extension. http://www.entomology.wisc.edu/raffa/Research/AllPubs/Extension%20Manuals/McCullough.Raffa.Williamson.GypsyMothGoodGuys.pdf

Millennium Ecosystem Assessment. 2005. Summary for decision makes. Pages 1 – 24 in Ecosystems and Human Well-being: Synthesis. Island Press, Washington DC, USA.

Mueller, H.C. 1987. Prey selection by kestrels: a review. Pages 83 – 106 In D.M. Bird and R. Bowman [Eds.], The Ancestral Kestrel. Raptor Research Foundation and Macdonald Raptor Research Center, McGill University, Ste. Anne de Bellevue, Quebec.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133-142.

Newton, I. and M. Marquiss. 1979. Sex ratio among nestlings of the European sparrowhawk. American Naturalist 113:309-315.

Nufio, C. R., C. R. McGuire, M. D. Bowers, and R. P. Guralnick. 2010. Grasshopper community response to climatic change: Variation along an elevational gradient. PLoS ONE 5: e12977.

Nugent, J. and N. Rothwell. 2005. Calculating degree days. Michigan State University Extension. http://agbioresearch.msu.edu/uploads/files/Research_Center/NW_Mich_Hort/General/CalculatingGrowingDegreeDays.pdf

Olsen, P. D., and A. Cockburn. 1991. Female-biased sex allocation in peregrine falcons and other raptors. Behavioral Ecology and Sociobiology 28:417–423.

Orians, G.H. and N.E. Pearson. 1979. On the theory of central place foraging. In D.J. Horn, R.D. Mitchell, and G.R. Stairs [Eds.], Analysis of Ecological Systems, Ohio State University Press, Columbus, OH, USA.

Pfadt, R.E. 1994. Field guide to western grasshoppers. Wyoming Agricultural Experiment Station Bulletin 912, University of Wyoming, Laramie, WY, USA.

Plice, L., and T. G. Balgooyen. 1999. A remotely operated trap for American Kestrels using nestboxes. Journal of Field Ornithology 70:158–162.

Rudolph, S. G. 1982. Foraging strategies of American Kestrels during breeding. Ecology 63:1268–1276.

Rodríguez, A., J.J. Negro, M. Mulero, C. Rodríguez, J. Hernández-Pliego, and J. Bustamante. 2012. The eye in the sky: combined use of unmanned aerial systems and GPS data loggers for ecological research and conservation of small birds. PLoS ONE 7(12): e50336.

Shane, B. and J. Wise. 2012. Increased populations of grasshoppers cause problems in fruit crops. Michigan State University. http://msue.anr.msu.edu/news/increased_populations_of_grasshoppers_cause_problems_in_fruit_crops

Shave, M.E. and C.A. Lindell. 2017. American Kestrels occupying cherry orchard nest boxes show high reproductive rates and tolerance of monitoring. Journal of Raptor Research 51: 50-60.

Sherrod, S. K. 1978. Diets of North American Falconiformes. Journal of Raptor Research 12:49–121.

Smallwood, J. A., and C. Natale. 1987. The effect of patagial tags on breeding success in American Kestrels. North American Bird Bander 23: 73–78.

Smallwood, J.A. and D.M. Bird. 2002. American Kestrel (*Falco sparverius*). In A. Poole and F. Gill [Eds.], The Birds of North America 602. Academy of Natural Sciences, Philadelphia, PA, USA, and American Ornithologists' Union, Washington, DC, USA.

Smallwood, J. A., P. Winkler, G. I. Fowles, A. Craddock, G. R. I. F. Owles, and M. E. A. C. Raddock. 2009. American Kestrel breeding habitat : the importance of patch size. 43:308–314.

Sonerud, G.A. 1992. Functional responses of birds of prey: biases due to the load-size effect in central place foragers. Oikos 63:223–232.

Steen, R. 2009. A portable digital video surveillance system to monitor prey deliveries at raptor nests. Journal of Raptor Research 43:69-74.

Steen, R., G.A. Sonerud, and T. Slagsvold. 2012. Parents adjust feeding effort in relation to nestling age in the Eurasian Kestrel (*Falco tinnunculus*). Journal of Ornithology 153:1087–1099.

Steenhof, K., K.K. Bates, M.R. Fuller, M.N. Kochert, J.O. McKinley, and P.M. Lukacs. 2006. Effects of radiomarking on Prairie Falcons: attachment failures provide insights about survival. Wildlife Society Bulletin 34:116-126.

Steenhof, K., and B. E. Peterson. 2009. American Kestrel reproduction in Southwestern Idaho: annual variation and long-term trends. Journal of Raptor Research 43:283–290.

Toland, B. R. 1987. The effect of vegetative cover on foraging strategies, hunting success and nesting distribution of American Kestrels in central Missouri. Journal of Raptor Research 21:14–20.

Trivers, R.L., D.E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 191:249-263

USDA 2012 Census of Agriculture. 2014. County profile: Leelanau County, Michigan. United States Department of Agriculture National Agricultural Statistics Service, Washington, DC, USA. http://www.agcensus.usda.gov/Publications/2012/Online_Resources/County_Profiles/Michigan/cp26089.pdf

USDA NASS. 2016. Cherry Production. United States Department of Agriculture National Agricultural Statistics Service, Washington, DC, USA. http://usda.mannlib.cornell.edu/usda/current/CherProd/CherProd-06-22-2016.pdf

Wiebe, K. L., and G. R. Bortolotti. 1992. Facultative sex ratio manipulation in American kestrels. Behavioral Ecology and Sociobiology 30:379–386.

Wiehn, J., and E. Korpimäki. 1997. Food limitation on brood size: Experimental evidence in the Eurasian Kestrel. Ecology 78:2043–2050.

Wood, B.J. and G.R. Singleton. 2015. Rodents in agriculture and forestry. Pages 33-80 *in* A. Buckle and R. Smith [Eds.], Rodent pests and their control. CAB International, UK.

Zuur, A., E.N. Ieno, N. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed effect models and extensions in ecology with R. Springer Science, NY, USA.

CHAPTER 4

FALCONS USING ORCHARD NEST BOXES REDUCE FRUIT-EATING BIRD ABUNDANCES AND PROVIDE ECONOMIC BENEFITS FOR A FRUIT-GROWING REGION

Megan E. Shave, Stephanie A. Shwiff, Julie L. Elser, and Catherine A. Lindell

Abstract

Reduction of pest species via a native predator is a regulating ecosystem service that has the potential to limit crop damage and produce regional economic benefits. American kestrels (*Falco sparverius*) are widespread, highly-mobile, generalist predators that hunt in human-dominated habitats, thus they are potentially important predators providing previously undocumented ecosystem services in agricultural landscapes. hypothesized that kestrel activity associated with nest boxes and perches acts as a reliable cue of predation risk that, in combination with kestrel consumption of prey birds, can reduce fruit-eating bird abundances in orchards. We used counts and observations of fruit-eating birds from fixed-width transect surveys in cherry orchards to investigate sources of variation in bird abundances and to estimate sweet cherry loss in orchards with and without active kestrel boxes. We also conducted a benefit-cost analysis of installing kestrel nest boxes and used regional economic modeling to estimate macroeconomic impacts of increased sweet cherry production in Michigan, an important US fruit-production region. Fruit-eating bird counts were significantly lower at transects with active kestrel boxes. Perches did not have a significant effect on bird counts, although perches were used by kestrels, with peak use after the offspring fledged from the nest, particularly in young orchards. Benefit-cost ratios for kestrel nest boxes ranged from 131 to 557, indicating that for every dollar spent on nest boxes, $131 to $557 of sweet cherries is saved from fruit-eating birds. Regional economic modeling predicted that increased production of sweet cherries from reduced bird damage would result in 72 to 77 jobs created and $3.5 million to $3.8 million in increased income for the state of Michigan over a five-year period. *Synthesis and application*. Kestrel nest boxes in sweet cherry orchards provide a highly cost-effective ecosystem service in fruit crops with reverberating benefits for a regional economy. Some kestrel populations are not limited by

availability of nest sites, thus saturating a region with nest boxes may not result in the high occupancy rates observed in our study area. We therefore recommend that farmers prioritize installations of nest boxes in high-risk orchards that would benefit most from a reduction in fruit-eating birds.

Introduction

In response to the agricultural expansion and intensification that threatens biodiversity worldwide (Green et al. 2005, Flynn et al. 2009), much current research focuses on the transition from conventional pesticide-based crop protection to a more sustainable integrated pest management (IPM) framework to manage pest populations rather than eradicate them (Lamichhane et al. 2017). Enhancing the regulating ecosystem services provided by native predators is an appealing management strategy that has the potential to limit crop damage by promoting natural predator-prey relationships in agroecosystems. Avian predators in particular can be effective predators of pest insects (Maas et al. 2015), rodents (Labuschagne et al. 2016), and even other birds (e.g., Kross et al. 2012).

The ecosystem services of predators can be augmented through the practice of conservation biological control (CBC), which employs modifications of the environment to protect or enhance native predator populations to reduce the impact of pests (Eilenberg et al. 2001). An example of an easily-implemented practice for CBC is the installation of artificial nesting and roosting cavities for nest site-limited predators. Previous studies have demonstrated that nest boxes attract avian predators, resulting in increased predation of pest insects (e.g., Mols and Visser 2007, Jedlicka et al. 2011) and rodents (Labuschagne et al. 2016). In addition, installing artificial perches can enhance the hunting habitat for avian predators, particularly raptors (Widén 1994), and previous studies have demonstrated effects on rodent abundances (Kay et al. 1994). However, no previous studies have examined the effects of nest boxes and artificial perches for predatory birds on the abundances of prey birds, which are significant pests in fruit crops (Lindell et al. 2016). In addition, the cost-effectiveness of nest boxes needs investigation (Wenny et al. 2011).

The first objective of our study was to determine whether installation of nest boxes and perches for American kestrels (hereafter "kestrel"), a declining raptor species (Smallwood et al. 2009), leads to reduced fruit-eating bird abundances in orchards. Kestrels are widespread, highly-mobile, generalist predators that hunt in open habitats, including human-dominated landscapes (Smallwood and Bird 2002), thus they are potentially important for sustainable biological control at local and landscape scales (Tscharntke et al. 2007). Kestrels using orchard nest boxes in the fruit-growing region of northwestern Michigan consume insects, mammals, and fruit-eating birds (Chapter 3). Although birds comprise only about 2% of prey delivered to kestrel offspring during the breeding season (Chapter 3), kestrels may reduce fruit-eating bird abundances in orchards through a combination of the lethal (direct consumptive) and non-lethal effects of predation (Cresswell 2008, Kross et al. 2012). Non-lethal effects include the antipredator behaviors of prey birds, such as avoiding areas of high predation risk (Cresswell 2008). Our first hypothesis was that active nest boxes are sites of high kestrel activity that act as reliable cues of predation risk for fruit-eating birds. We also hypothesized that a lack of suitable perches limits orchard use by kestrels, so artificial perches would increase the presence of the kestrels in the orchards. Thus, we predicted that fruit-eating bird abundances would be lower in orchards with active nest boxes and perches compared to orchards without.

Our second objective was to quantify the economic benefits that result from the total effects of kestrel presence on fruit-eating birds. We focused our economic analyses on sweet cherries (*Prunus avium*), given their higher sugar content (Serrano et al. 2005) and expected greater risk of bird damage compared to tart cherries (*Prunus cerasus*; Lindell et al. 2016). We predicted that kestrel nest boxes have a very low cost of implementation compared to the benefit of decreased sweet cherry loss due to reduced fruit-eating bird abundances. Furthermore, we employed regional economics analysis to translate the costs and benefits of kestrel nest boxes into county- and state-level metrics that are important to the general public, such as changes in income (gross domestic product) and employment (Shwiff et al. 2013). Estimates of these regional impacts can reveal how crop damage and its potential reduction through enhancement of regulating ecosystem services can affect people in the community who are not directly involved in agriculture or wildlife conservation.

Author Contributions

M. Shave conducted the statistical analyses of perch use and fruit-eating bird abundances. C. Lindell calculated the sweet cherry loss to fruit-eating birds. S. Shwiff and J. Elsner conducted the benefit-cost analysis and regional economics modeling. This chapter will be submitted as a manuscript when finalized.

Methods

Kestrel Nest Boxes in Northwestern Michigan

We conducted this study in eastern Leelanau County, MI, an important US fruit-growing region that is predominantly agricultural with some residential and forested areas (USDA Census of Agriculture 2014). Beginning in the late 1980s, a Boy Scouts of America troop and other groups installed kestrel nest boxes on utility poles in this region (F. Otto, personal communication). Between 2012 and 2016, we installed 25 new boxes within or next to cherry orchards, usually near the edge of an orchard in an open spot where a tree was missing within a row (Shave and Lindell 2017). We installed boxes in eight sweet cherry (*Prunus avium*) orchard blocks and 16 tart cherry (*Prunus cerasus*) orchard blocks. We installed one box in an apple (*Malus domestica*) orchard block adjacent to a tart cherry block. Kestrels have quickly occupied these new boxes and have shown high reproductive rates (Shave and Lindell 2017).

Kestrel Perch Use

We randomly chose five orchards with active kestrel nest boxes in 2015 in which to install artificial perches. We built the perches from 6.4 m of steel pipe mounted on 1.2 m of rebar buried 0.9 m underground, resulting in a 5.5 m perch height. The perches themselves were 45 cm lengths of 2.54 cm-wide pine dowel attached to the pipe with a floor flange (Hall et al. 1981). We installed three perches per orchard; we placed perches within the orchard rows, usually in an open spot where a tree was missing. In 2015, we recorded each perch during daylight hours (06:00 – 21:00 EST) once per week using a weatherproof color security camera ($33; Bunker Hill Security) and a video recording system that could be rotated between orchards (Shave and Lindell 2017). We used the video recordings to measure kestrel use of the perches (proportion of daylight hours in which a kestrel was recorded on the perch during the hour) starting the second week following the nest hatching (week 2) and continuing for three weeks after nest fledging (week 7). We estimated mean tree height in each orchard block with a perch by measuring five randomly selected trees in each block using a rangefinder (Nikon Forestry PRO).

Fruit-Eating Bird Abundances In Cherry Orchards

We conducted fruit-eating bird surveys along 200 m-long fixed-width transects in 2015 and 2016. We chose a fixed width of six orchard rows (32 m) in order to minimize variation in bird detectability between transects. Each survey lasted 10 min, with 20 m of the transect length travelled each min. We conducted all surveys between 06:30 – 8:30 EST on days without precipitation or fog in order to minimize variation in bird detectability due to time of day or weather. We conducted at least six surveys per transect between early June and mid July. We conducted surveys both before and after harvest because some cherries remain on the trees and ground following harvest (Eaton et al. 2016). One observer conducted all surveys. The observer recorded all birds detected visually during surveys and also recorded any visual or aural detections of kestrels during or in the min prior to the survey. We classified species as fruit-eating birds if they ate cherries during surveys, or if previous studies documented them eating cherries (e.g., Lindell et al. 2012).

In 2015, we conducted surveys at 30 transects in 15 orchards: five orchards with an active kestrel box, five orchards with an active kestrel box and perches, and five orchards with no kestrel box within 1.6 km. At orchards with active kestrel boxes, we placed transects within 150 m of the box. At orchards with perches, we placed transects within 100 m of a perch and 150 m of the boxes. In orchards with sweet and cherry blocks, we placed one transect in a block of each crop type; in orchards with blocks of one crop type only, we placed one transect at the orchard edge and one in the interior (at least six rows in from the edge row). We placed the two transects in each orchard at least 150 m apart to reduce the chance of observing the same individual birds at both transects during a survey visit. In 2016, we conducted surveys at 14 transects in 14 orchards: three orchards with an active kestrel box, four orchards with an active kestrel box and perches, and seven orchards with no kestrel box within 1.6 km or perches. We placed all transects in sweet cherry blocks in 2016.

Statistical Analyses

Analysis of perch use

We built binomial mixed effects and regression models to explain kestrel perch use. We included perch nested within orchard as random effects in the mixed effects models. We included the following variables as fixed effects: average height of trees in orchard block (tree height), and the linear (age) and quadratic (age^2) effects of kestrel offspring age in weeks. We used a top-down approach for model selection in which we first built models including all fixed effect variables of interest and determined the optimal structure of the random effects using Akaike's Information Criterion (Akaike 1974) corrected for small sample size (AICc; Hurvich and Tsai 1989, Zuur et al. 2009). Using the random effects structure of the highest-ranking model from the first step, we then tested the significance of the fixed effects by comparing nested models using analysis of deviance (Zuur et al. 2009). We calculated marginal (fixed effects) and conditional (fixed and random effects) R^2 values for the best model to assess goodness of fit of the fixed effects and overall model (Nakagawa and Schielzeth 2013). We built all models using package “lme4” in program R (3.1.0).

Analysis of fruit-eating bird abundances

We used bird counts as an index of abundance with the assumption that our survey design minimized potential sources of variation in detectability and the chance of observing individual birds more than once during a survey. We built Poisson mixed effects and regression models to explain the number of fruit-eating birds observed at orchard survey transects. We included orchard and year as random effects in the mixed effects models. We included the following variables as fixed effects: whether the orchard had an active kestrel box within 150 m of the transect or no active box within 1.6 km (box), whether the orchard had artificial perches installed within 100 m of the transect (perch), whether the transect was in a sweet or tart cherry orchard block (crop), whether the transect was at the edge or interior of the orchard block (edge), and the linear (harvest) and quadratic (harvest^2) effects of weeks from harvest (where 0 represented the week of harvest). We included the effects of crop, edge, and harvest to potentially explain more variation in fruit-eating bird counts beyond the focal effects of box and perches. We predicted that bird counts would be higher in sweet cherry blocks and during weeks closer to harvest due to higher sugar content in the cherries (Serrano et al. 2005). We also predicted that bird counts would be higher in edge transects, given that edges were adjacent to windbreaks or wooded areas that may facilitate bird entry into the orchard block (Lindell et al. 2016). We used the same model selection procedure as described for the models of perch use above.

Economic Analyses

Estimating sweet cherry loss to fruit-eating birds

In 2016, we conducted observations of foraging birds in each sweet cherry block ($n = 14$) on between five and 11 days from three to five weeks before harvest until one to two weeks after harvest. One observer conducted all observations. The observer walked through a 32 x 200 m area (0.64 ha; the same area covered by the fixed-width transects for the bird abundance surveys) during the following time blocks: 6:30-8:30 EST, 8:30-10:30 EST, 10:30-12:30 EST, or 18:00-20:00 EST. Orchard blocks were observed during different time blocks to the extent possible.

The observer walked through the area for a maximum of one half hour or until he observed 10 birds foraging for a minimum of 20 s each. When a bird was detected, it was kept in sight for as long as possible and the following information was recorded with a digital recorder: the time the bird was encountered, whether it was on the ground or in a tree, how many meters above the ground if in a tree, the species, the number of fruits eaten, and the time the observation ended. The observer followed foraging birds until they were lost from view or flew out of the block. The observer ended the observation if an individual bird was observed for 2 min and did not forage.

We used these foraging observations to calculate the mean number of cherries eaten min^{-1} by fruit-eating birds. We estimated the mean number of fruit-eating birds min^{-1} ha^{-1} for sweet cherries from the fruit-eating bird abundance surveys, because each survey covered 0.064 ha min^{-1} during the 10 min survey. We then calculated the number of cherries min^{-1} ha^{-1} lost to fruit-eating birds in orchards with and without active kestrel nests. We multiplied these values by 900 min (the approximate daily min of daylight in the study region at harvest times) and 21 days (to represent the three weeks before sweet cherry harvest, when the fruit is ripening) to estimate the total loss to fruit-eating birds in a growing season.

Benefits of kestrel nest boxes

We estimated the benefits of kestrel nest boxes in terms of additional sweet cherry production from reduced loss to fruit-eating birds. We translated the calculated numbers of cherries lost to fruit-eating birds to weight by multiplying cherry numbers by 7.5 and 8 g, typical weights for sweet cherries in the study region (G. Lang, *Personal communication*). We calculated the value of the additional cherries using a five-year price average (USDA Economic Resource Service 2016) and then multiplied by the number of bearing age hectares in Michigan, Leelanau County, Antrim County, and Grand Traverse County (USDA Census of Agriculture 2012) to provide the total value of cherries saved in each region, if kestrel boxes were installed across all sweet cherry hectarage.

Costs of kestrel nest boxes

Costs for each kestrel nest box included a pre-made nest box as well as lumber and hardware for the tower and installation. We also included labor costs for installation and annual cleaning. We determined the number of nest boxes needed to cover each region based on kestrel territory size. The average kestrel territory ranges from 500 m to 1 km in diameter, or 19.6 to 78.5 ha (Bird and Palmer 1988, Rohrbaugh and Yahner 1997). We assumed installation of enough nest boxes to cover the bearing age hectares in each region in the first year; we included only cleaning costs in subsequent years. We calculated costs and benefits for a total of five years.

Benefit-Cost analysis

We measured the value of kestrel nest boxes as an enhancement of crop pest reduction via net benefits and benefit-cost ratios (BCRs). Net benefits are simply the difference between the total benefits and total costs. We calculated BCRs by dividing the total benefits by the total costs. A BCR of greater than one indicates an efficient use of resources because the benefits outweigh the costs. We applied a discount rate, based on the real interest rate, of 1% to both benefits and costs to account for the fact that current benefits and costs are more valued than future benefits and costs. We performed a sensitivity analysis using the ranges of cherry weights and kestrel territory sizes. We obtained a low and high estimate for net benefits and BCRs.

Macroeconomic impacts

We estimated macroeconomic impacts arising from increased cherry production due to reduced bird damage using regional economic analysis with REMI PI+ (Regional Economic Models, Inc.). REMI is a computer-based simulation model of the US economy that allows modeling at both the national and sub-national scales. This structural economic forecasting model uses a non-survey based input-output (I-O) table, which models the linkages among industries and households of a regional economy (Shwiff et al. 2013). Using the REMI model, we can generate forecasts that detail behavioral responses to changes in price, production, and other economic factors (Treyz et al. 1991). In other words, REMI can model the impact that changes in the agricultural sector might have on other sectors of the economy and predict changes in employment and income in those sectors. For example, an increase in cherry production may result in increased spending at local restaurants and retail shops, which in turn generates jobs at those businesses. This increased income among workers then translates into further spending. Capturing these ripple effects, or multiplier effects, is vital to understanding the total impact a change in one sector has on the entire regional economy (Miller and Blaire 2009).

We constructed the REMI model used in this analysis from national, state, and county level data from the Bureau of Economic Analysis, Bureau of Labor Statistics, and the Bureau of the Census, as well as forecasts from the Research Seminar in Quantitative Economics at Michigan State University. The model was a county-level model of the state of Michigan. We then aggregated county-level results from Leelanau County, Antrim County, and Grand Traverse County to represent the state.

Results

Fruit-Eating Bird Abundances In Cherry Orchards

We conducted a total of 268 surveys over both years. In 2015, we conducted surveys at four transects in young orchard blocks that were not harvested that year; the surveys from transects in these blocks were dropped from the analyses due to sparse fruit development (non-bearing blocks). In 2016, the kestrel nests failed at two orchards with active kestrel nest boxes; the surveys from transects at these orchards were dropped from the analyses because they no longer matched the distance criterion for the active kestrel nest box treatment (active nest within 150 m). Also, we discovered a kestrel nest in an abandoned house near an orchard with no kestrel box within 1.6 km; the surveys from the transect at this orchard were dropped from the analyses because they no longer matched the distance criteria for the no active kestrel nest box treatment (no active nest within 1.6 km). Finally, we lost access to two orchards after three surveys each; we kept these surveys in the analyses.

We identified 11 fruit-eating species during surveys (Fig. 4.1). We saw or heard a kestrel during or prior to 64 surveys (35%) at transects with active kestrel nest boxes; we did not detect any kestrels during or prior to surveys at transects without active kestrel nests.

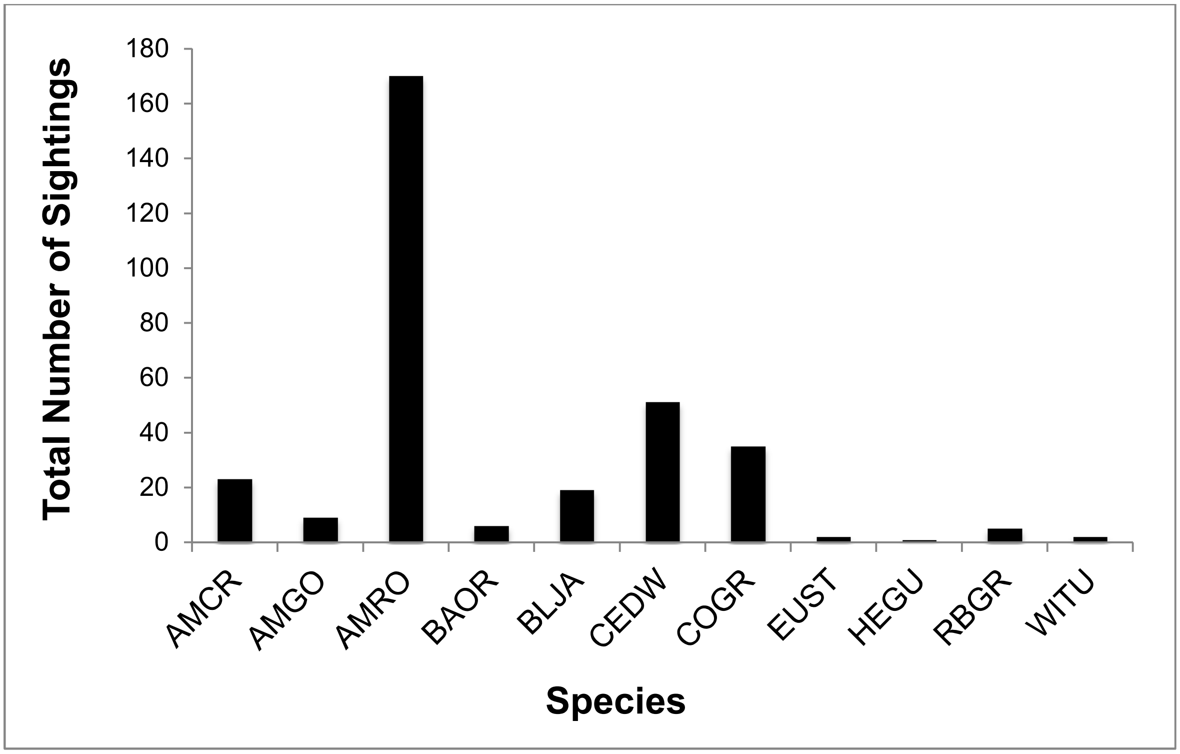

Figure 4.1. **Total number of sightings of fruit-eating birds during 2015 – 2016 surveys.** We identified 11 species during surveys: American crow (*Corvus brachyrhynchos*; AMCR), American goldfinch (*Spinus tristis*; AMGO), American robin (*Turdus migratorius*; AMRO), Baltimore oriole (*Icterus galbula*; BAOR), blue jay (*Cyanocitta cristata*; BLJA), cedar waxwing (*Bombycilla cedorum*; CEDW), common grackle (*Quiscalus quiscula*; COGR), European starling (*Sturnus vulgaris*; EUST), herring gull (*Larus argentatus*; HEGU), rose-breasted grosbeak (*Pheucticus ludovicianus*; RBGR), and wild turkey (*Meleagris gallopavo*; WITU).

We originally built models for three different groups of fruit-eating birds expected to have similar detection rates within groups but potentially vary among groups, based on size and behavior; however, models for the three groups all included the same fixed effects, so we then pooled data from the three groups. The best-fitting model for total fruit-eating bird abundance ($\beta_0 = 0.93 \pm 0.29$) included the random effects of orchard and year (Appendix, Table 4.1) and the fixed effects of box and crop (Appendix, Table 4.2). Transects with active kestrel boxes had significantly lower fruit-eating bird counts compared to transects without ($\beta_1 = -1.89 \pm 0.39$; Fig. 4.2). Tart orchard blocks had significantly lower fruit-eating bird counts compared to sweet blocks (β_2 = -0.70 ± 0.21). The marginal and conditional R^2 values for the model were 0.29 and 0.52, respectively.

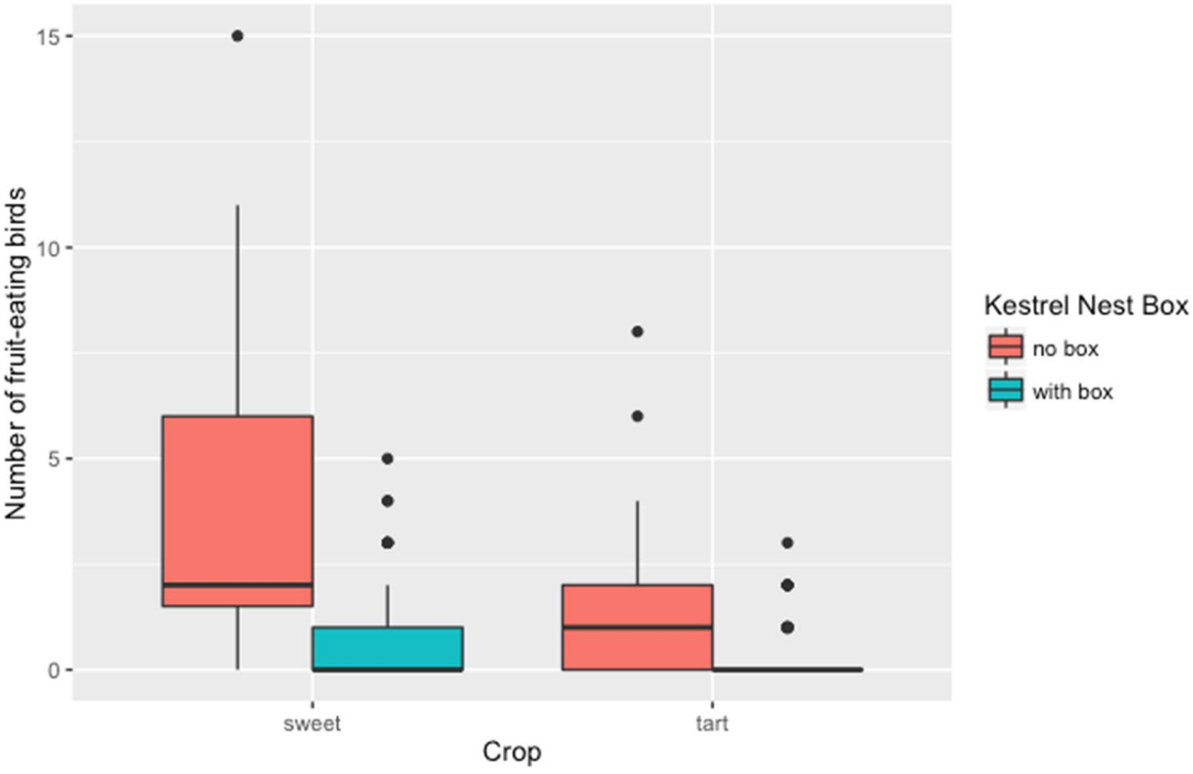

Figure 4.2. **Numbers of fruit-eating birds (medians and interquartile ranges [IQRs]) observed per 10 min survey at sweet and tart orchard block transects with and without active kestrel boxes.** Boxplot whiskers extend 1.5 IQRs.

Economic Analyses

Estimating sweet cherry loss to fruit-eating birds

We excluded observations of foraging birds that were less than 20 s or when the bird showed some obvious response to the observer, such as an alarm call. We also excluded observations of bird species that never or only occasionally eat fruit during the summer, for example black-capped chickadees, *Poecile atricapillus*. After these exclusions, 90 total observations remained for the following species: AMCR, AMGO, AMRO, BAOR, BLJA, CEDW, COGR, EUST, RBGR, and WITU. We initially calculated the mean number of cherries eaten min^{-1} for each species separately for transects with and without active kestrel nests. These calculations all produced means of less than 1 cherry min^{-1} with the exception of one 45 s observation of a BAOR that produced a cherry-eating rate of 1.3 min^{-1}. Given the low variability of the means, we calculated one mean for all species and transects (0.21 cherries min^{-1}).

The numbers of fruit-eating birds min^{-1} per 0.064 ha observed at transects in orchards with and without active kestrel nests were 0.04 and 0.29, respectively. We therefore calculated 0.63 (rounded up to 1) birds min^{-1} ha^{-1} and 5.43 (rounded to 5) birds min^{-1} ha^{-1} for orchards with and without active kestrel nests, respectively. We then calculated that 0.21 cherries min^{-1} ha^{-1} were lost to fruit-eating birds from orchards with active kestrel nests (1 fruit-eating bird min^{-1} ha^{-1} * 0.21 cherries min^{-1}), while 1.05 cherries min^{-1} ha^{-1} were lost from orchards without active kestrel nests (5 fruit-eating birds min^{-1} ha^{-1} * 0.21 cherries min^{-1}). We therefore estimated that a total of 3,969 cherries ha^{-1} (0.21 cherries min^{-1} ha^{-1} * 900 min * 21 days) and 19,845 cherries ha^{-1} (1.05 cherries min^{-1} ha^{-1} * 900 min * 21 days) were lost to fruit-eating birds in orchards with and without active kestrel nests, respectively.

Benefit-Cost analysis for kestrel nest boxes

Net benefits from installing kestrel next boxes across all sweet cherry hectarage in Michigan were the value of cherries saved minus the costs of the next boxes, their installation, and maintenance, totaled over five years. The first year sees the majority of the costs that arise from purchase and installation of the nest box (Table 4.3). Years two through five consist of only maintenance (cleaning) costs. Costs for the state of Michigan range from \$8,000 to \$32,000 and benefits range from \$4.2 million to \$4.5 million (Table 4.4). Costs were low enough that net benefits are approximately equal to the benefits. BCRs ranged from 131 to 557, indicating that for every dollar spent on kestrel nest boxes, $131 to $557 of cherries is saved.

Table 4.3. **Cost of a kestrel next box in the first year.**

Nest box, lumber, and hardware		$67.29
1 hour of labor to install box		$25.00
1 hour of labor to clean box		$22.50
	Total	$114.79

Labor is valued at $25 per hour; a 90% occupancy rate is assumed for cleaning.

Table 4.4. **Benefit cost analysis of reduced damage to cherry orchards.**

		Benefits		**Costs**		**Net Benefits**	
		Cherry weight		**Kestrel Territory**			
	Year	**7.5 g**	**8.0 g**	**19.6 ha**	**78.5 ha**	**High**	**Low**
Michigan	2016	$854,852	$911,843	$18,202	$4,545	$907,298	$836,650
	2017	$846,389	$902,814	$3,532	$882	$901,932	$842,856
	2018	$838,008	$893,876	$3,498	$873	$893,002	$834,511
	2019	$829,711	$885,025	$3,463	$865	$884,161	$826,248
	2020	$821,496	$876,263	$3,429	$856	$875,407	$818,068
	Total	**$4,190,457**	**$4,469,821**	**$32,124**	**$8,021**	**$4,461,800**	**$4,158,333**
Leelanau County	2016	$411,831	$439,286	$8,769	$2,189	$437,097	$403,062
	2017	$407,753	$434,937	$1,702	$425	$434,512	$406,051
	2018	$403,716	$430,630	$1,685	$421	$430,210	$402,031
	2019	$399,719	$426,367	$1,668	$417	$425,950	$398,051
	2020	$395,761	$422,145	$1,652	$412	$421,733	$394,110
	Total	**$2,018,780**	**$2,153,366**	**$15,476**	**$3,864**	**$2,149,502**	**$2,003,304**
Antrim County	2016	$95,689	$102,068	$2,037	$509	$101,560	$93,652
	2017	$94,742	$101,058	$395	$99	$100,959	$94,346
	2018	$93,804	$100,057	$392	$98	$99,959	$93,412
	2019	$92,875	$99,067	$388	$97	$98,970	$92,487
	2020	$91,955	$98,086	$384	$96	$97,990	$91,572
	Total	**$469,065**	**$500,336**	**$3,596**	**$898**	**$499,438**	**$465,469**
Grand Traverse County	2016	$165,200	$176,214	$3,518	$878	$175,335	$161,683
	2017	$163,565	$174,469	$683	$170	$174,298	$162,882
	2018	$161,945	$172,741	$676	$169	$172,573	$161,269
	2019	$160,342	$171,031	$669	$167	$170,864	$159,672
	2020	$158,754	$169,338	$663	$165	$169,172	$158,092
	Total	**$809,806**	**$863,793**	**$6,208**	**$1,550**	**$862,243**	**$803,598**

Discount rate = real interest rate = 1%

Macroeconomic impacts

Regional economic modeling predicted that increased production of cherries from reduced bird damage from kestrel activity at nest boxes would result in 72 to 77 jobs created and \$3.5 million to \$3.8 million in increased income for the state of Michigan over a five year period (Table 4.5).

Table 4.5. **Jobs created and increase in GDP due to reduced damage.**

	2016	**2017**	**2018**	**2019**	**2020**	**Total**
Jobs created	14	15	15	14	14	**72**
GDP (2013 USD)	\$640,716	\$693,811	\$711,629	\$710,757	\$698,705	**\$3,455,617**
Jobs created	16	16	15	15	15	**77**
GDP (2013 USD)	\$743,172	\$761,912	\$760,730	\$747,674	\$747,674	**\$3,761,161**

Kestrel Perch Use

The video recordings of perches indicated that both adult and fledgling kestrels used the perches; we observed up to four kestrels on a perch simultaneously. The best-fitting model for kestrel perch use ($\beta_0 = -1.84 \pm 0.51$) included the random effect of perch nested within orchard (Appendix, Table 4.6) and the fixed effects of tree height, age, and age^2 (Appendix, Table 4.7). Increasing mean tree height in an orchard block had a negative effect on perch use ($\beta_1 = -1.84 \pm 0.51$). The linear effect of offspring age was positive ($\beta_2 = 0.67 \pm 0.32$); the quadratic effect was negative ($\beta_3 = -0.16 \pm 0.038$), thus kestrel use of the perches first increased and then decreased (Fig. 4.3). The marginal and conditional R^2 values for the model were 0.46 and 0.71, respectively.

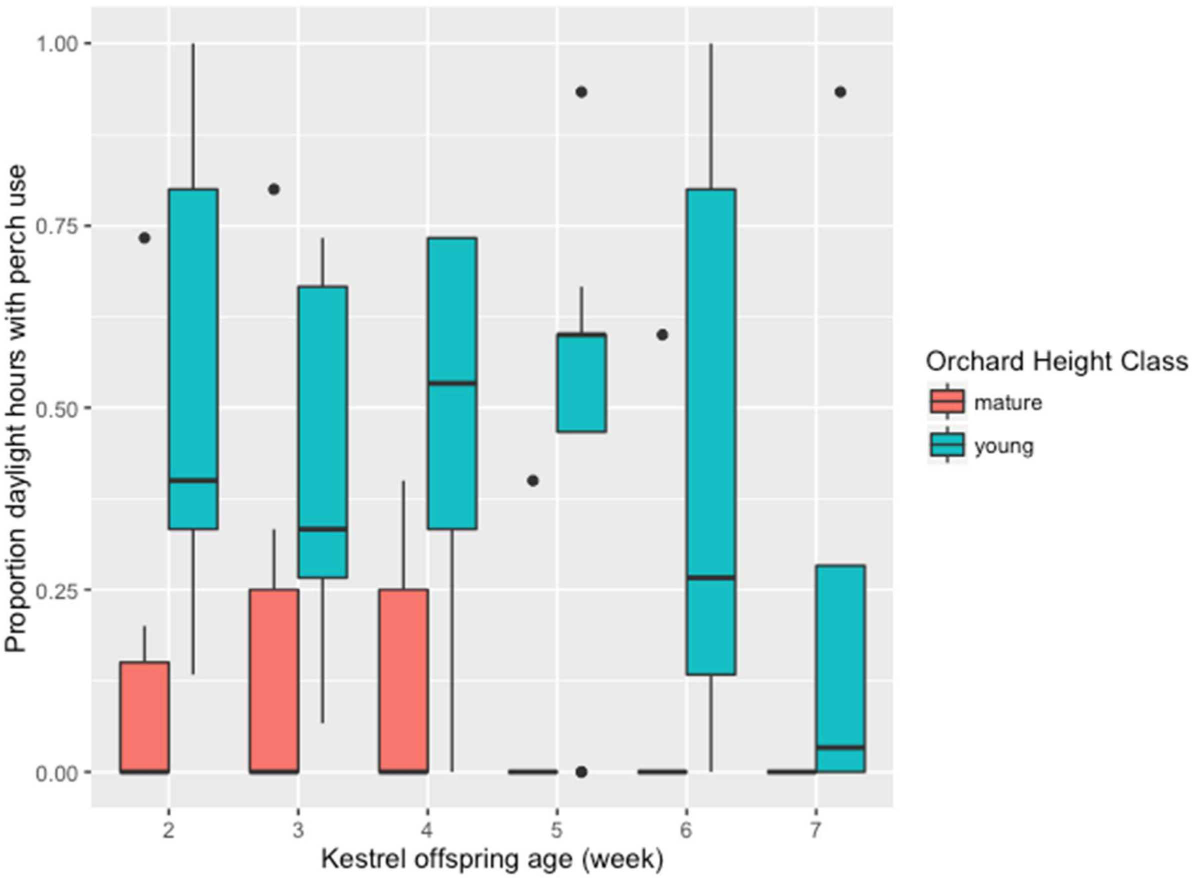

Figure 4.3. **Kestrel perch use (medians and interquartile ranges [IQRs]) in mature (mean tree height >3.5 m) and young (mean tree height <3.5 m) orchard blocks during kestrel nestling (weeks 2 – 4) and post-fledging (weeks 4 – 7) periods.** Boxplot whiskers extend 1.5 IQRs.

Discussion

As predicted, fruit-eating bird abundances were significantly lower at transects with active nest boxes compared to transects without. The reduction was greatest in sweet cherry blocks, which had significantly higher bird counts than transects in tart cherry blocks, but tart blocks also showed decreased counts between transects with and without kestrel boxes. These results, combined with our detections of kestrels only at transects with active nests, support the idea that active kestrel nest boxes act as reliable cues of predation risk that, in combination with kestrel consumption of prey birds directly, reduces fruit-eating bird abundances in orchards.

We also found that perches in young blocks could provide benefits to kestrels. Kestrel use of the perches first increased and then decreased with increasing age of the offspring. The increase in use likely corresponded to the adult female spending increasingly more time outside the box as the offspring aged (M. Shave, *unpublished data*); the peak in use occurred soon after the offspring fledged from the nest and began using the perches. Kestrel mortality is high during the post-fledging period (Stupik et al. 2015): kestrels are not yet proficient fliers during the first days after fledging, and they are exposed to mammalian predation when on the ground (Varland and Klaas 1993). Thus, artificial perches in young orchard blocks and other open areas near the nest box could be a valuable resource for fledglings. The subsequent decrease in perch use would correspond with the dispersal of the offspring away from the nest box in later weeks post fledging (Smallwood and Bird 2002).

However, fruit-eating bird abundances were not significantly lower at transects with perches and active nest boxes compared to those with active nest boxes only. The lack of a perch effect coincides with our finding that kestrel use of the perches was significantly greater in orchard blocks with shorter trees. Kestrels mostly used the perches installed in the youngest orchard blocks; meanwhile, we conducted the fruit-eating bird surveys in mature orchard blocks where kestrels rarely used the perches. Although the artificial perches were still taller than the trees in mature blocks, the mature trees form a denser canopy cover that limits visibility of the ground, which could reduce the quality of mature orchards as hunting habitat for kestrels compared to young orchards, despite the potential abundance of prey in mature orchards. This conclusion is supported by studies of kestrel habitat use on the wintering grounds, which have found that kestrels are more positively associated with more open land cover types compared to orchards (Pandolfino et al. 2011).

Also in contrast to our prediction, edge transects did not have significantly higher counts of fruit-eating birds compared to interior transects. While orchard edges may generally be at greater risk of bird damage, this pattern has not been consistent within and across fruit-growing regions (Lindell et al. 2016). In addition, weeks-from-harvest did not have a significant effect on counts of fruit-eating birds. This result coincides with findings from a telemetry study of cherry orchard use by American robins and cedar waxwings (Eaton et al. 2016), which indicates that harvest date, a human industry-based measure of fruit ripening, does not accurately predict how fruit-eating birds respond to fruit availability. For example, birds may target early-ripening blocks heavily early in the season, but as harvest approaches, more blocks have suitably ripened, thus diluting the bird activity in any particular orchard as it is spread across the landscape (Tobin et al. 1991).

Conclusions and Management Implications

Our bird survey results, combined with the high kestrel reproductive rates observed for boxes in the study region (Shave and Lindell 2017), indicate that orchard nest boxes are effective tools for CBC that can enhance regulating ecosystem services through reduction of pest bird abundances in the orchards throughout the fruit-ripening season while also sustaining or increasing the local kestrel breeding population (Chapter 2). We conclude that kestrel nest boxes in orchards are an easily-implemented and valuable addition to IPM practices in fruit crops. The estimated benefits in terms of increased sweet cherry production from reduced fruit-eating bird abundances in orchards greatly outweigh the low costs of installing and maintaining nest boxes. Furthermore, assuming installation of nest boxes in sweet cherry orchards statewide and high box occupancy rates (90%), the increased fruit production would be substantial enough to result in job creation and an increase in the GDP of Michigan. While previous research has shown how biological control can increase agricultural yield (e.g., Cleveland et al. 2006, Kross et al. 2012), our study demonstrates how adopting a CBC IPM strategy in agriculture can provide economic benefits for people beyond those directly involved in agriculture or wildlife conservation.

Nevertheless, as expected with any IPM strategy, kestrel nest boxes did not completely eliminate pest birds from the orchards. Also, some local kestrel populations are not limited by availability of nest sites (Smallwood et al. 2009, McClure et al. 2017), thus saturating a region with nest boxes may not result in the high occupancy rates observed in our study area, even if boxes are spaced to account for kestrel territoriality. We would therefore recommend that farmers first prioritize installations of nest boxes in high-risk orchards that would benefit most from a reduction in fruit-eating birds.

APPENDIX

APPENDIX

Model Selection

Table 4.1. **Akaike's Information Criterion corrected for small sample size (AICc) table for selection of random effects structure in Poisson model of fruit-eating birds.** Models include all fixed effect variables of interest.

Model	AICc	ΔAICc	Weight
Random intercepts (orchard + year + interaction)	665.9	0.0	0.957
Random intercepts (orchard + year)	673.1	7.3	0.0251
Random intercepts (orchard)	674.9	9.0	0.0106
Random intercepts + slopes (orchard + year + interaction)	676.6	10.7	0.0045
Random intercepts + slopes (orchard + year)	677.6	11.7	0.0027
Random slopes (orchard + year)	717.4	51.5	<0.001
Random slopes (orchard + year + interaction)	718.9	53.1	<0.001
No random effects	740.7	74.8	<0.001

Table 4.2. **Analysis of deviance tests for selection of fixed effects in Poisson model of fruit-eating birds.** Asterisks (*) denote fixed effects significant at the 0.05 level.

Fixed effect	df	χ^2	*P*
box	1	11.25	0.0008*
crop	1	10.72	0.001*
perch	1	0.019	0.89
edge	1	0.19	0.66
harvest	1	1.82	0.18
harvest^2	1	2.62	0.11

Table 4.6. **Akaike's Information Criterion corrected for small sample size (AICc) table for selection of random effects structure in binomial model of kestrel perch use.** Models include all fixed effect variables of interest.

Model	AICc	ΔAICc	Weight
Random intercepts + slopes (orchard/perch)	400.5	0.0	1
Random slopes (orchard/perch)	421.4	20.8	<0.001
Random intercepts (orchard/perch)	427.3	26.8	<0.001
No random effects	569.8	169.4	<0.001

Table 4.7. **Analysis of deviance tests for selection of fixed effects in binomial model of kestrel perch use**. Asterisks (*) denote fixed effects significant at the 0.05 level.

Fixed effect	df	χ^2	*P*
tree height	1	13.24	0.00028*
age	1	3.94	0.047*
age^2	1	17.28	<0.0001*

LITERATURE CITED

LITERATURE CITED

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control AC-19:716-723.

Bird, D.M. and R.S. 1988. Handbook of North American birds. Volume 5. Yale University Press, New Haven, CT, USA.

Cleveland, C.J., Frank, J.D., Federico P, T. G. Hallam, J. Horn, J. D. Lopez, G. F. Mccracken, R. A. Medellin, A. Moreno-Valdez et al. 2006. The economic value of pest control services provided by the Brazilian free-tailed bat in south-central Texas. Frontiers in Ecology & Environment 4:238–43

Cresswell, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3–17.

Eaton, R.A., Lindell, C.A., Homan, H.J, Linz, G.M, & Maurer, B.A. 2016. American Robins (*Turdus migratorius*) and Cedar Waxwings (*Bombycilla cedorum*) vary in use of cultivated cherry orchards. Wilson Journal of Ornithology 128:97-107.

Eilenberg, J., A. Hajek, and C. Lomer. 2001. Suggestions for unifying the terminology in biological control. BioControl 46:387–400.

Flynn, D.F.B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B.T. Richers, B.B. Lin, et al. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12:22-23.

Green, R.E., S.J. Cornell, J.P.W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. Science 307:550-555.

Hall, T.R., W.E. Howard, and R.E. Marsh. 1981. Raptor use of artificial perches. Wildlife Society Bulletin 9:296-298.

Hurvich, C. M. and C. L. Tsai. 1989. Regression and time-series model selection in small sample sizes. Biometrika 76:297-307.

Jedlicka, J.A., R. Greenberg, and D.K. Letourneau. 2011. Avian conservation practices strengthen ecosystem services in California vineyards. PloS ONE 6:e27347.

Kay, B.J., L.E. Twigg, T.J. Korn, and H.I. Nicol. 1994. The use of artificial perches to increase predation on house mice (Mus domesticus) by raptors. Wildlife Research 21:95–106.

Kross, S.M., J.M. Tylianakis, and X.J. Nelson. 2012. Effects of introducing threatened falcons into vineyards on abundance of passeriformes and bird damage to grapes. Conservation Biology 26:142-149.

Labuschagne, L., L.H. Swanepoel, P.J. Taylor, S.R. Belmain, and M. Keith. 2016. Are avian predators effective biological control agents for rodent pest management in agricultural systems? Biological Control 101:94-102.

Lamichhane, J.R., M. Bischoff-Schaefer, S. Bluemel, S. Dachbrodt-Saaydeh, L. Dreux, J.P. Jansen, et al. 2017. Identifying obstacles and ranking common biological control research priorities for Europe to manage most economically important pests in arable, vegetable and perennial crops. Pest Management Science 73:14–21.

Lindell, C.A., R.A. Eaton, E.M. Lizotte and N.L. Rothwell. 2012. Bird consumption of sweet and tart cherries. Human-Wildlife Interactions 6:283-290.

Lindell, C.A., K.S. Steensma, P.D. Curtis, J.R. Boulanger, J.E. Carroll, C. Burrows, et al. 2016. Proportions of bird damage in tree fruits are higher in low-fruit-abundance contexts. Crop Protection 90: 40-48.

Maas, B., D.S. Karp, S. Bumrungsri, K. Darras, D. Gonthier, J.C-C. Huang, et al. 2015. Bird and bat predation services in tropical forests and agroforestry landscapes. Biological Reviews 91:1081-1101.

McClure, C. J. W., B. P. Pauli, and J. A. Heath. 2017. Simulations reveal the power and peril of artificial breeding sites for monitoring and managing animals. Ecological Applications 0:1–12.

Miller, R.E. and P.D. Blair. 2009. Input-output analysis: foundations and extensions. Cambridge University Press, Cambridge, UK.

Mols, C.M.M. and M.E. Visser. 2007. Great Tits (Parus major) reduce caterpillar damage in commercial apple orchards. PloS ONE 2: e202.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133-142.

Pandolfino, E. R., M. P. Herzog, and Z. Smith. 2011. Sex-related differences in habitat associations of wintering American Kestrels in California's Central Valley. Journal of Raptor Research, 45:236–243.

Rohrbaugh Jr., R.W. 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.

Serrano, M., F. Guillén, D. Martínez-Romero, S. Castillo, and D. Valero. 2005. Chemical constituents and antioxidant activity of sweet cherry at different ripening stages. Journal of Agricultural and Food Chemistry 53: 2741–2745.

Shave, M.E. and C.A. Lindell. 2017. American Kestrels occupying cherry orchard nest boxes show high reproductive rates and tolerance of monitoring. Journal of Raptor Research 51:50-60.

Shwiff, S.A., Anderson, A., Cullen, R., White, P.C.L., and Shwiff, S.S. 2013. Assignment of measurable costs and benefits to wildlife conservation projects. Wildlife Research 40:134-141.

Smallwood, J.A. and D.M. Bird. 2002. American Kestrel (*Falco sparverius*). In A. Poole and F. Gill [Eds.], The Birds of North America 602. Academy of Natural Sciences, Philadelphia, PA, USA, and American Ornithologists' Union, Washington, DC, USA.

Smallwood, J.A., M. F. Causey, D. H. Mossop, J. R. Klucsarits, B. Robertson, S. Robertson, J. 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.

Stupik, A.E., T. Sayers, M. Huang, T.A.G. Rittenhouse, and C.D. Rittenhouse. 2015. Survival and movement of post-fledging American kestrels hatched from nest boxes. Northeastern Naturalist 22:20-31.

Tobin, M.E., R.A. Dolbeer, C.M. Webster, and T.W. Seamans. 1991. Cultivar differences in bird damage to cherries. Wilson Society Bulletin 19:190-194.

Treyz, G.I., D.S. Rickman, G. Shao. 1991. The REMI economic-demographic forecasting and simulation model. International Regional Science Review 14:221-253.

Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, et al. 2007. Conservation biological control and enemy diversity on a landscape scale. Biological Control 43:294–309.

USDA Census of Agriculture. 2012. Table 31. Fruits and Nuts: 2012 and 2007. United States Department of Agriculture National Agricultural Statistics Service, Washington, DC USA. https://www.agcensus.usda.gov/Publications/2012/Full_Report/Volume_1,_Chapter_2_County_Level/Michigan/st26_2_031_031.pdf

USDA Census of Agriculture. 2014. County profile: Leelanau County, Michigan. United States Department of Agriculture National Agricultural Statistics Service, Washington, DC USA. http://www.agcensus.usda.gov/Publications/2012/Online_Resources/County_Profiles/Michigan/cp26089.pdf

USDA Economic Research Service. 2016. Fruit and Tree Yearbook. United States Department of Agriculture National Agricultural Statistics Service, Washington, DC USA. http://usda.mannlib.cornell.edu/usda/ers/89022/2016/FruitandTreeNutYearbook2016.pdf

Varland, D.E. and E.E. Klaas. 1993. Use of habitat and perches, causes of mortality and time until dispersal in post-fledging American Kestrels. Journal of Field Ornithology 64:169-178.

Wenny, D.G., Devault, T.L., Johnson, M.D., Kelly, D., Sekercioglu, C.H., Tomback, D.F, & Whelan, C.J. 2011. The need to quantify ecosystem services provided by birds. Auk 128:1-14.

Widén, P. 1994. Habitat quality for raptors: a field experiment. Journal of Avian Biology 35:219–223.

Zuur, A., E.N. Ieno, N. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed effect models and extensions in ecology with R. Springer Science, New York, USA.

CHAPTER 5

EFFECTS OF AMERICAN KESTREL NEST BOXES ON SMALL MAMMAL PREY IN CHERRY ORCHARDS

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Abstract

In order to potentially reduce use of environmentally damaging rodenticides, integrated Pest Management (IPM) for rodents, or Ecologically Based Rodent Management (EBRM), proposes a more sustainable management approach using strategies informed by an increased understanding of rodent population and community ecology, including interactions with important predators, such as raptors. Nest boxes and perches can encourage raptor presence in agricultural areas and potentially enhance the regulatory ecosystem services provided by raptor predation of agricultural pests. To assess this idea, we studied American Kestrels, widespread, generalist predators that readily use nest boxes, in a fruit-growing region of northwestern Michigan. The most common mammal prey in the diets of these kestrels from 2013 through 2016 were voles, which are considered the most important rodent pests in temperate fruit orchards. We utilized live trapping to measure small mammal abundances and activity during the summer at sites with and without active kestrel nest boxes; furthermore, we utilized camera trapping to measure small mammal presence during the winter, when damage to trees is most likely. As predicted, small mammal abundance and activity was lower at orchards with active kestrel boxes and at orchards that had been more recently mowed; however, these differences did not carry over as differences in winter presence in orchards. Our sampling demonstrated that voles were absent from orchards during both summer and winter, which suggests that orchards offer insufficient cover except under certain conditions, such as sustained snow cover. Instead, *Peromyscus* spp. were the most abundant small mammals in most orchards during the summer and were also present during the winter. More evidence is therefore needed to determine the extent of orchard damage attributable to *Peromyscus* spp. and whether indirect effects of kestrels on *Peromyscus* spp. may reduce damage. We provide recommendations for future research on

the effects of raptor predation in orchards.

Introduction

Small mammals, particularly rodents, are worldwide agricultural pests with widespread distributions and high adaptive and reproductive potentials (Leirs 2003). Anticoagulant and zinc phosphide rodenticides are commonly used as effective rodent control agents (Stone et al. 1999, Proudfoot 2009); however, these chemicals can cause secondary poisoning of predators (e.g. Brakes and Smith 2005, Hughes et al. 2013) and pollute soil and groundwater (Arias-Esteves et al. 2008). Integrated Pest Management (IPM) for rodents, or Ecologically Based Rodent Management (EBRM; Singleton et al. 1999) proposes a more environmentally sustainable rodent pest control approach using strategies informed by an increased understanding of rodent population and community ecology, including interactions with important predators, such as raptors.

Previous research has investigated the use of artificial perches and nest boxes to attract raptors to agricultural areas and encourage predation of rodents. The majority of studies have focused on the Barn Owl (*Tyto alba*), a specialist predator that uses nest boxes (Labuschagne et al. 2016). However, generalist predators may also be important rodent predators; generalists can show a functional response to peak densities of rodents with cyclical population dynamics such as voles by increasing the proportion of rodents in their diet, and may stabilize and dampen rodent population cycles (Andersson and Erlinge 1977, Korpimäki and Krebs 1996). Perches can increase hunting activity of a variety of raptor species, which reduces growth of rodent populations and limits maximum rodent densities (e.g. Kay et al. 1994, Sheffield et al. 2001). Thus, encouraging raptor presence in agricultural areas can enhance the regulatory ecosystem services provided by predation on agricultural pests.

American Kestrels (*Falco sparverius*; hereafter "kestrel") are widespread generalist raptors that include a variety of small mammal species in their diets. In the fruit-growing region of northwestern Michigan, mammals were the second most common prey type in the diet of nestling kestrels, comprising 13% of 7,778 deliveries made over a total of 179 days to nestlings by breeding kestrels using 15 cherry orchard nest boxes (Chapter 3). Voles, particularly *Microtus pennsylvanicus* in northern North America, are the most important rodent pests in temperate fruit orchards (Wood and Singleton 2015). Voles can damage and even kill young trees by girdling the bark and roots (Tritten 2014, Wood and Singleton 2015). *Microtus pennsylvanicus* was the most common mammal prey of kestrels using the orchard nest boxes (57% of mammal deliveries; Chapter 3). Kestrels may be able to reduce peak vole abundances, which would benefit orchards if vole densities are kept below the threshold for tree damage (Tritten 2014).

A previous study of kestrel nest boxes in apple orchards did not find a significant effect of boxes on rodent activity (Askham 1990); however, the nest box occupancy rates in that study were much lower than those observed in northwestern Michigan (Shave and Lindell 2017). Our objective was therefore to investigate the effects of active kestrel nest boxes on small mammals, especially voles, in cherry orchards. We utilized live-trapping to measure small mammal abundances and activity during the summer at sites with and without active kestrel nest boxes. We predicted small mammal abundance and activity would be lower at orchards with active kestrel boxes and at orchards that had been recently mowed because mowing exposes small mammals to greater predation risk (Tritten 2013), and hunting kestrels will cue in on recently mowed or plowed areas (Rudolph 1982, Toland 1987).

We used camera-trapping to measure small mammal presence during the winter, when damage to trees is most likely. Although the kestrels in our study region are migratory and not present during the winter (Brewer et al. 1991), we predicted that the probabilities of small mammal presence would be lower at trapping sites in orchards that had active kestrel boxes during the summer if kestrel predation, combined with rodenticide application, reduced small mammal populations below the threshold for presence in the orchard. We also predicted that trapping sites in orchards with perches would have lower probabilities of small mammal presence because breeding kestrels and their offspring used the perches in young orchards (Chapter 4), thus they may have further reduced small mammal density in the orchard due to facilitation of hunting (Sheffield et al. 2001). Additionally, we predicted higher small mammal presence at orchard edges because small mammals from adjacent woodlots, drainage ditches, and other agricultural fields may move into orchards after exhausting available resources (e.g. residual crop in corn and soybean fields; Irish-Brown 2016). Finally, we predicted that small mammal presence would be more likely in orchards with snow because small mammals, particularly voles, use snow cover as protection from most predators (Hansson and Hettonen 1985, Tritten 2014).

Methods

Summer Surveys of Small Mammal Abundance and Activity

Live trapping in orchards

We conducted small mammal live trapping in cherry orchards between late June and early Aug during the 2014 kestrel breeding season in Leelanau County, MI (45.0751°N–44.8365°N, 85.5032°W–85.7758°W). Orchards consisted of blocks of sweet and/or tart cherries of varying ages. Rodent management in these orchards included mowing the grass lanes between the tree rows during summer and applying rodenticides to young (three years old or younger) blocks in the fall. We trapped in six orchards with an active kestrel box and three orchards that were at least 800 m from the nearest active kestrel box. At orchards with active kestrel boxes, we trapped in the block closest to the nest box. We considered orchards 800 m from the nearest active box to have significantly less exposure to hunting kestrels based on the average kestrel territory diameter of 500 m (Rohrbaugh and Yahner 1997). At each orchard site we set up a grid of 100 small mammal traps (2 x 2.5 x 9" aluminum Sherman traps) arranged across five orchard rows with 20 traps per row (with the exception of one 10 by 10 trap arrangement due to orchard shape). We spaced traps approximately 12 m apart in the orchard rows, and we faced the trap openings towards the grass lanes in between rows. We baited traps with rolled oats (Barnett and Dutton 1995). We opened traps at 21:00 EST at each orchard and then checked traps three times per day (06:00 – 07:00, 14:00 – 15:00, and 21:00) for three days. We identified each captured small mammal to species. We weighed and measured tail length of each small mammal when possible; for *Peromyscus* spp., we also measured ear length to distinguish between *Peromyscus maniculatus bairdii* and *Peromyscus leucopus* (Jones and Birney 1988). In order to identify mammals as new versus recaptured individuals, we cut away a small patch of the outer coat to expose the contrasting color of the underfur (Barnett and Dutton 1995). We released all small mammals following processing.

Vegetative cover in orchards

We measured vegetation height in the lanes between rows in order to estimate vegetative cover in orchards. We sampled vegetation in four lanes within the trapping grid at each orchard.

We used the step-point method of vegetation sampling in which we started at a random point within a lane and measured the height of vegetation touching a flag stake stuck into the ground every 10 steps (Evans and Love 1957). We collected 25 measurements per lane and calculated the mean vegetation height for each orchard. We found that mean heights were either < 100 mm or > 150 mm. We therefore created two vegetation height categories: recently mowed (mean height < 100 mm) or not recently mowed (mean height > 150 mm).

Statistical analysis

Because our trapping protocol was consistent across orchards, we used the number of new small mammal captures as an index of relative abundance (Hopkins and Kennedy 2004). Similarly, we also used total number of small mammal captures as an index of relative activity. We built Poisson regression models to explain the variation in small mammal abundance and activity between orchards. We included the following variables as fixed effects: whether the orchard had an active kestrel box (box) and whether the grass lanes in the orchard had been recently mowed (mow). We ranked models using Akaike's Information Criterion (Akaike 1974) corrected for small sample size (AICc; Hurvich and Tsai 1989, Zuur et al. 2009). We built all models using package “lme4” in program R (3.1.0). We calculated model-averaged parameter estimates based on the 95% confidence set of models (Buckland et al. 1997).

Winter Surveys of Small Mammal Presence

Camera trapping in orchards

We surveyed small mammal presence in orchards during winter using camera traps. Camera trap surveys allow for species identification without the added monitoring effort and trap myopathy risk associated with traditional live trapping methods (McCleery 2014). We therefore considered camera trapping the appropriate choice for surveying small mammals during winter fieldwork, when time constraints made regular trap checks unfeasible. Camera trap stations consisted of a modified Hunt trap, designed to prevent disturbance by larger non-target animals (McCleery 2014), containing a weatherproof security camera connected to a portable video recording system (Shave and Lindell 2017). We baited camera traps with peanut butter and oats.

We conducted surveys between Nov 2015 and Mar 2016, following fall rodenticide application, in nine orchards with blocks of trees that were three years old or younger: three orchards had active kestrel boxes during the summer, three orchards had active boxes and 5.5 m-tall supplemental perches (Hall et al. 1991) installed during the summer of 2015, and three orchards had no active box within 1.63 km and no supplemental perches. Five of these orchards were included in the summer of 2014 surveys. We conducted surveys in one or two blocks per orchard. In orchards with more than two young blocks, we conducted surveys in two randomly chosen blocks. We set up three camera trap stations in each block: one in a randomly chosen spot in an interior tree row, and two in randomly chosen edge rows that had continuous non-orchard edge habitat. Each camera trap station served as a trapping site ($n = 51$). We placed the camera traps in the orchard rows, and during surveys with snow on the ground, we dug out spaces for the traps so that the entrances opened into the subnivean space. We left the camera traps at each site for 24 h. We conducted one to three surveys per trapping site over three survey rounds (Nov, Dec, Mar surveys).

Occupancy modeling

We recorded small mammal presence or absence during 15 min intervals (events) within the 24 h surveys (Rendall et al. 2014). We then built a dynamic occupancy model of small mammal presence under a Bayesian framework (Kéry and Schaub 2012). Small mammal populations in seasonal northern environments experience population declines during the winter (Fairbairn 1978, Hansen et al. 1999); furthermore, summer territories break down as dispersal occurs in the fall (Fairbairn 1978), so we considered populations open between surveys.

We modeled trapping site occupancy ($\psi_{i,1}$), colonization ($\gamma_{i,t}$), and persistence ($\varphi_{i,t}$) probabilities as follows:

$$\text{logit}(\psi_{i,1}) = \alpha_0 + \alpha_1(box_{i,1}) + \alpha_2(perch_{i,1}) + \alpha_3(edge_{i,1}) + \alpha_4(snow_{i,1})$$

$$\text{logit}(\gamma_{i,t}) = \alpha_5 + \alpha_6(box_{i,t}) + \alpha_7(perch_{i,t}) + \alpha_8(edge_{i,t}) + \alpha_9(snow_{i,t})$$

$$\text{logit}(\varphi_{i,t}) = \alpha_{10} + \alpha_{11}(box_{i,t}) + \alpha_{12}(perch_{i,t}) + \alpha_{13}(edge_{i,t}) + \alpha_{14}(snow_{i,t})$$

where $\alpha_{1\text{-}4,6\text{-}9,11\text{-}14}$ represented the logit-linear coefficients for model covariates (Saracco et al. 2011): whether the trapping site *i* was in an orchard with an active kestrel box during the summer (*box*), whether the trapping site *i* was in an orchard with perches (*perch*), whether the trapping site *i* was at an orchard edge (*edge*), and whether the trapping site *i* was in an orchard with > 10 cm of snow cover on the ground during survey *t* (*snow*).

We modeled the detection probability, $p_{i,k,t}$, as follows:

$$\text{logit}(p_{i,k,t}) = \beta_0 + \beta_1(night_{i,k,t}) + \beta_2(lag_{i,k,t})$$

where $\beta_{1,2}$ represented the logit-linear coefficients for model covariates: whether event *k* at site *i* occurred during daylight hours or night (*night*), and whether we detected a small mammal at trapping site *i* during the previous event (*lag*). We predicted that detection probabilities would be higher at night due to the nocturnal behavior of most small mammal species (Jones and Birney

1988). We included the *lag* variable to account for the potential spatial dependence between consecutive events within a 24 h survey.

We estimated model parameters using Markov Chain Monte Carlo (MCMC) methods. For each model we used uninformative priors and ran two chains for 30,000 iterations, discarding the first 20,000 runs as burn-in and thinning by two. We ran all models using package "R2jags" in Program R (3.3.1). We assessed convergence by visually inspecting model trace plots and confirming that values for the potential scale reduction factor were < 1.1 for all model parameters (Gelman et al. 2003). We identified a covariate effect as important if the 95% credible interval (CRI) for the posterior mean of the parameter coefficient did not overlap zero (Kéry and Schaub 2012). We also generated estimates for two derived parameters: the estimated number of occupied sites during each round of surveys and the occupancy-based population growth rate λ between survey rounds (Kéry and Schaub 2012).

Results

Summer Surveys of Small Mammal Abundance and Activity

We had a total of 122 small mammal captures, including 52 new captures (Fig. 5.1). The captures represented seven species, including one capture of the mustelid *Mustela nivalis*. Hereafter, we group *Peromyscus maniculatus bairdii* and *Peromyscus leucopus* as *Peromyscus* spp. because the species identity of some captures was ambiguous based on tail and ear length. We also removed the Box 11 orchard from our statistical analyses because we expected the presence of *Mustela nivalis*, a specialist predator of rodents, to potentially confound the effect of kestrel predation on small mammals.

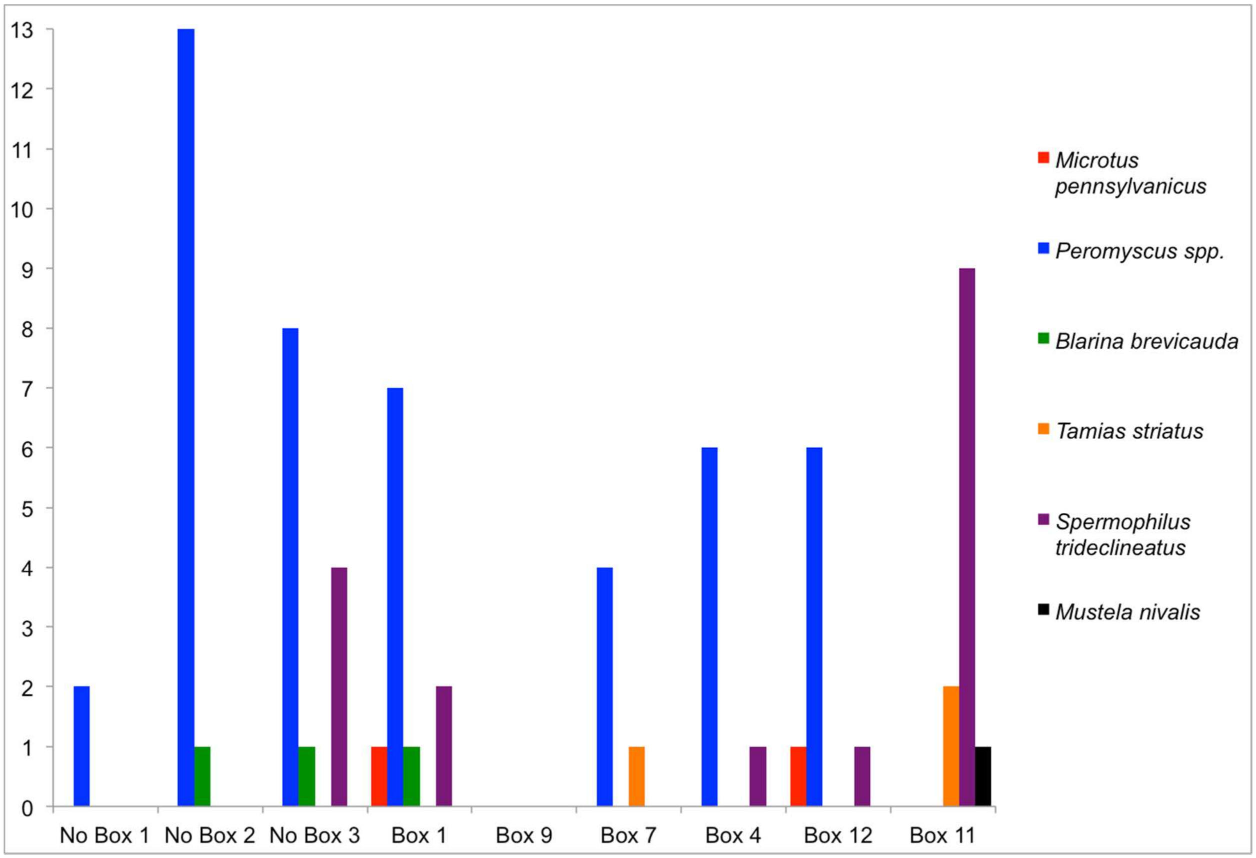

Figure 5.1. **Number of new small mammal captures in each orchard by species during the summer of 2014.** Orchards identified by their nest box ID (or "No Box" for orchards without a nest box). *Peromyscus* spp. includes *Peromyscus maniculatus* (*bairdii*) and *Peromyscus leucopus*.

According to the model-averaged parameter estimates based on the 95% confidence set of models for small mammal abundance (β_0 = 1.60; Table 5.1), new small mammal captures were greater in orchards without active kestrel boxes than in those with boxes (β_1 = 0.10), and new small mammal captures were greater in orchards that had not been recently mowed than in those recently mowed (β_2 = 0.69; Fig. 5.2).

Table 5.1. **Akaike's Information Criterion corrected for small sample size (AICc) table for Poisson models of summer small mammal abundance.** Bold indicates the 95% confidence set of models used for parameter estimation via model averaging.

Model	AICc	ΔAICc	Weight
Mow	**56.4**	**0.0**	**0.681**
Box + Mow	**58.7**	**2.4**	**0.209**
Intercept only	**60.9**	**4.6**	**0.0688**
Box	62.1	5.8	0.0381
Box * Mow	67.7	11.4	0.0023

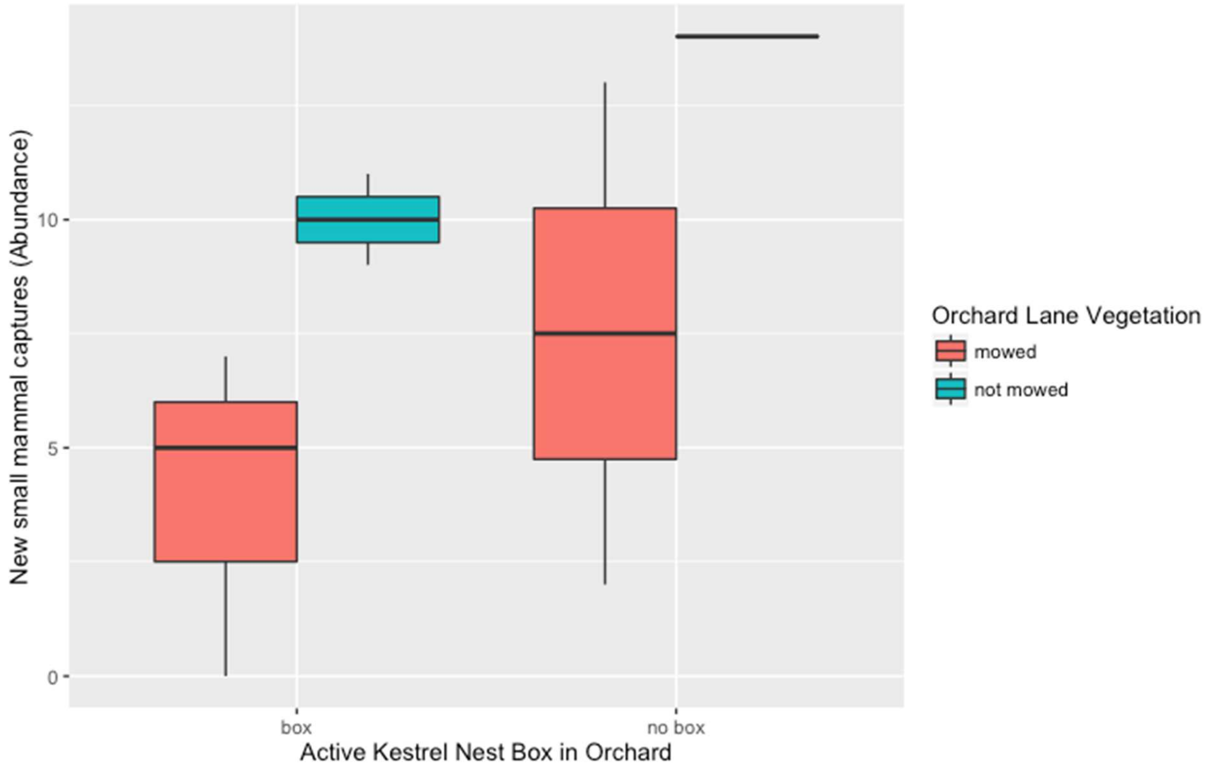

Figure 5.2. **New small mammal captures (abundance) in recently and not recently mowed orchards with and without active kestrel boxes.** Boxplots show medians and interquartile ranges (IQRs); boxplot whiskers extend 1.5 IQRs.

According to the model-averaged parameter estimates based on the 95% confidence set of models for small mammal activity (β_0 = 1.90; Table 5.1), total small mammal captures were greater in orchards without active kestrel boxes than in those with boxes (β_1 = 0.36), and total small mammal captures were greater in orchards that had not been recently mowed than in those recently mowed (β_2 = 0.66; Fig. 5.3).

Table 5.2. **Akaike's Information Criterion corrected for small sample size (AICc) table for Poisson models of summer small mammal activity.** Bold indicates the 95% confidence set of models used for parameter estimation via model averaging.

MODEL	AICc	ΔAICc	WEIGHT
Box + Mow	**77.0**	**0.0**	**0.672**
Mow	**78.4**	**1.5**	**0.320**
Box * Mow	85.8	8.9	0.008
Box	93.7	16.7	<0.001
Intercept only	95.4	18.5	<0.001

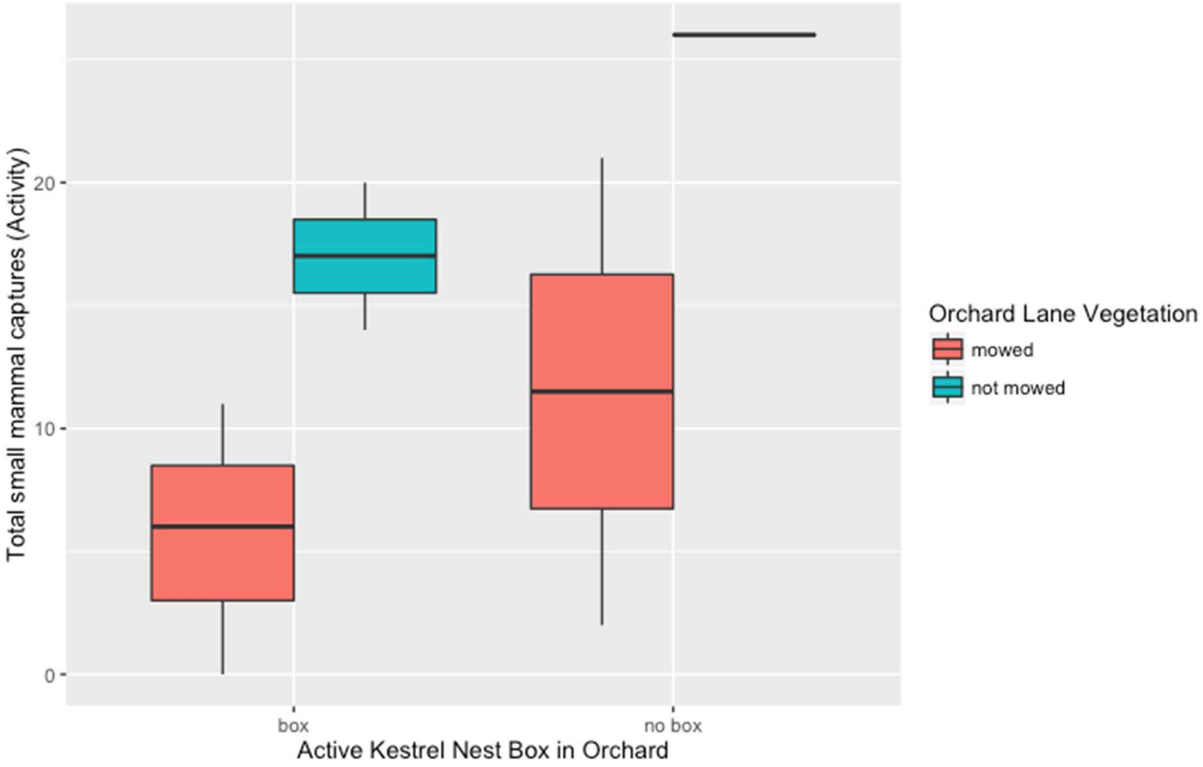

Figure 5.3. **Total small mammal captures (activity) in recently and not recently mowed orchards with and without active kestrel boxes.** Boxplots show medians and interquartile ranges (IQRs); boxplot whiskers extend 1.5 IQRs.

Winter Surveys of Small Mammal Presence

We detected small mammals at 17 of the 51 trapping sites and during 19 of 135 surveys across all trapping sites during the three trapping rounds. All detections appeared to be of *Peromyscus* spp. based on relative tail, ear, and eye sizes (Fig. 5.4).

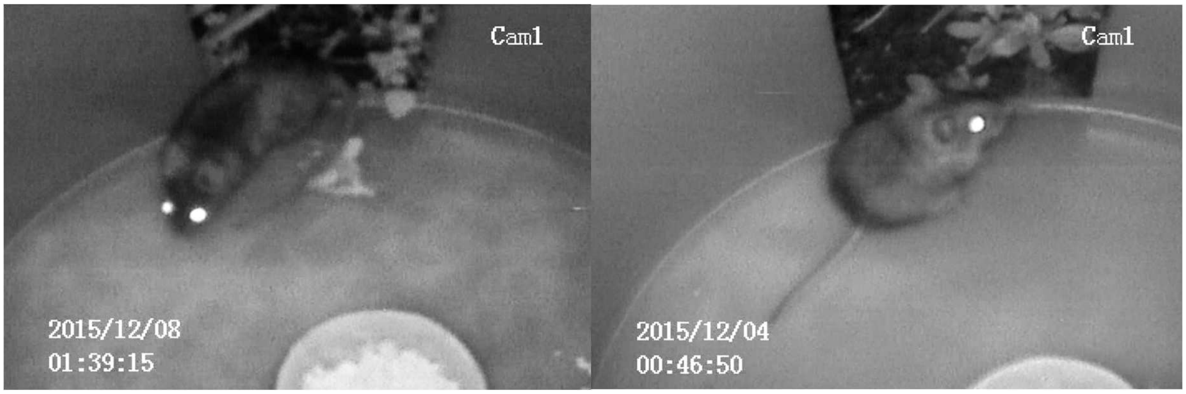

Figure 5.4. **Example *Peromyscus* spp. detections at camera traps**. Camera trap stills show examples of rodents identified as *Peromyscus leucopus* (left) and *Peromyscus maniculatus bairdii* (right).

Because we detected only *Peromyscus* spp., we hereafter refer to the occupancy model as a model of deer mouse presence (Table 5.3). *Edge* had an important positive effect on the colonization probability; *Peromyscus* spp. were more likely to colonize trapping sites in edge rows. *Night* and *lag* had a positive effect on detections; we were more likely to detect a deer mouse during an event at night and if we had detected a deer mouse during the preceding event. The estimated number of occupied sites decreased between the Nov and Mar survey rounds; furthermore, the occupancy-based population growth rates were less than 1.0, which indicates that deer mouse presence decreased as the winter progressed.

Table 5.3. **Posterior summaries for parameter coefficients and derived parameters from the model of *Peromyscus* spp. presence at a trapping site (n = 51) in orchards in winter**. Important covariate effects are indicated in bold (95% CRI does not overlap zero; Kéry and Schaub 2012).

				95% CRI	
Parameter		Mean	SD	2.5%	97.5%
ψ (first survey occupancy)	α0 (intercept)	-2.12	1.71	-4.64	1.46
	α_1 (*box*)	0.01	0.49	-0.96	0.95
	α_2 (*perch*)	0.18	0.46	-0.71	1.11
	α_3 (*edge*)	-0.19	0.38	-0.93	0.56
	α_4 (*snow*)	-2.31	5.37	-9.68	8.98
γ (colonization)	α_5 (intercept)	-7.76	1.61	-9.91	-4.17
	α_6 (*box*)	-3.00	2.32	-7.84	0.64
	α_7 (*perch*)	4.31	2.23	-0.93	9.01
	α_8 (*edge*)	**4.12**	**2.27**	**0.57**	**5.74**
	α_9 (*snow*)	-2.48	2.80	-9.19	0.25
φ (persistence)	α_{10} (intercept)	-6.42	2.38	-9.83	-1.13
	α_{11} (*box*)	0.58	4.49	-7.53	9.12
	α_{12} (*perch*)	4.25	2.70	-0.11	9.51
	α_{13} (*edge*)	-0.21	0.98	-2.10	1.72
	α_{14} (*snow*)	3.29	4.75	-8.16	9.68
p (detection)	β0 (intercept)	-7.47	1.43	-9.85	-4.17
	β1 (*night*)	**5.37**	**1.61**	**2.32**	**8.05**
	β2 (*lag*)	**0.24**	**0.02**	**0.22**	**0.28**
Number of occupied sites	Nov survey round (1)	11.44	1.70	10	16
	Dec survey round (2)	6.61	0.59	6	8
	Mar survey round (3)	3.19	1.04	2	5
λ (occupancy-based growth rate)	Survey 1 to 2	0.59	0.09	0.40	0.73
	Survey 2 to 3	0.48	0.16	0.29	0.83

Discussion

As predicted, summer small mammal abundance and activity was lower at orchards with active kestrel boxes and at orchards that had been more recently mowed. These results suggest that kestrel boxes enhance the regulatory ecosystem services provided by kestrel predation and should therefore be further considered as a potential tool for biological control of orchard-damaging rodents. Our results also indicate that mowing the lanes between orchard rows is effective for rodent reduction.

However, differences in summer abundances and activity did not translate into differences in winter presence in orchards. One explanation is that rodenticides reduced small mammal populations to low enough levels that any additional effects of kestrel predation could not be detected by our survey method.

Another unexpected result was the detection of voles on only two occasions total during summer and winter small mammal surveys. We expected to capture voles regularly because they were the most common small mammal prey in the kestrel diet (Chapter 3), and they are the most well-documented rodent pest in orchards (Wood and Singleton 2015). One explanation for our results is that voles are typically absent from orchards during the summer because of the general lack of sufficient ground cover; furthermore, they are only present in the winter during periods of sustained snow cover. We were unable to adequately investigate this possible relationship because of the lack of sustained snow cover during the winter of 2015 – 2016: snow cover > 10 cm was only present in two orchards during one survey visit, and that cover was likely not present long enough prior to our surveys for voles to have moved into those orchards. Furthermore, a lack of sufficient snow fall during the winter of 2016 – 2017 again prevented us from investigating the effect of snow cover on vole presence.

Unlike voles, *Peromyscus* spp. mice were present in the orchards during the summer and winter, which suggests that their requirements for cover are lower. Thus, *Peromyscus* spp. are apparently less deterred by removal of ground cover in orchards or by years of limited snow fall. *Peromyscus* spp. damage in orchards may therefore be more difficult to control than vole damage. Our occupancy model of winter presence further indicates that *Peromyscus* spp. are more likely to move into edge rows, which supports the conclusion that orchard edges may be particularly vulnerable to damage (Tritten 2013). The question remains of whether *Peromyscus* spp. are as important an orchard pest as voles. Many farmers refer to “mice and voles” when discussing orchard damage (e.g., Tritten 2013, Tritten 2014, Irish-Brown 2016), but there is little evidence in the literature that *Peromyscus* spp. in particular are responsible for the same tree girdling damage usually attributed to voles (Irish-Brown 2016). *Peromyscus* spp. are associated with consumption of seeds and newly-emerged seedlings in agricultural fields and forest regeneration sites (Witmer and Moulton 2012). However, research has also identified *Peromyscus* spp. as a “lesser known” consumer of crop in almond orchards (Pearson et al. 2000), which raises the question of whether *Peromyscus* spp. may damage cherries and other tree fruit. *Peromyscus leucopus* in particular will climb trees (Kaufman et al. 1985); we observed a few individuals climbing cherry trees upon release during the summer live-trapping surveys. Thus, more evidence is needed to determine the extent of orchard damage attributable to *Peromyscus* spp..

Overall, our results prompt us to propose three recommendations for future research on the effects of raptor predation in orchards. First, we recommend utilizing a consistent surveying protocol across seasons if possible in order to facilitate seasonal comparisons and detect potential carry-over effects of predation by migratory predators. Next, we suggest conducting surveys in orchards without rodenticide use in order to detect effects of predation that were potentially masked in the present study by the reductions of small mammal populations following rodenticide application. Finally, we recommend combining small mammal surveys with fruit and tree damage assessments in order to identify which species are responsible for damage throughout the year and under different conditions (e.g., with variation in snowfall).

LITERATURE CITED

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Andersson, M., and S. Erlinge. 1977. Influence of predation on rodent populations. Oikos 3:591–597.

Arias-Estévez, M., E. López-Periago, E. Martínez-Carballo, J. Simal-Gándara, J. C. Mejuto, and L. García-Río. 2008. The mobility and degradation of pesticides in soils and the pollution of groundwater resources. Agriculture, Ecosystems and Environment 123:247–260.

Askham, L.R. 1990. Effect of artificial perches and nests in attracting raptors to orchards. Pages 144-148 in L.R. Davis and R.E. Marsh [Eds.], Proceedings of the 14th Vertebrate Pest Conference. University of California Davis Press, Davis, CA, USA.

Brakes, C. R., and R. H. Smith. 2005. Exposure of non-target small mammals to rodenticides: Short-term effects, recovery and implications for secondary poisoning. Journal of Applied Ecology 42:118–128.

Brewer, T., G.A. McPeek, and R.J. Adams Jr. 1991. The atlas of breeding birds of Michigan. Michigan State University Press, East Lansing, MI,USA.

Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. Biometrics 53:603–618.

Evans, R.A. and R.M. Love. 1957. The step-point method of sampling – a practical tool in range management. Journal of Range Research 10:208-212.

Fairbairn, D. J. 1978. Dispersal of deer mice, *Peromyscus maniculatus*. Oecologia 32:171–193.

Gelman, A., J.B. Carlin, H.S. Stern, and D.B. Rubin. 2003. Bayesian Data Analysis, Second Edition. Chapman & Hall, Boca Raton, FL, USA.

Hall, T.R., W.E. Howard, and R.E. Marsh. 1981. Raptor use of artificial perches. Wildlife Society Bulletin 9:296-298.

Hansen, T. F., N. C. Stenseth, and H. Henttonen. 1999. Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. American Naturalist 154:129–139.

Hansson, L., and H. Henttonen. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. Oecologia 67:394–402.

Hopkins, H. L., and M. L. Kennedy. 2004. An assessment of indices of relative and absolute abundance for monitoring populations of small mammals. Wildlife Society Bulletin 32:1289–1296.

Hughes, J., E. Sharp, M. J. Taylor, L. Melton, and G. Hartley. 2013. Monitoring agricultural rodenticide use and secondary exposure of raptors in Scotland. Ecotoxicology 22:974–984.

Irish-Brown, A. 2016. Rodent management in commercial apple orchards requires an integrated approach. Michigan State University Extension. http://msue.anr.msu.edu/news/rodent_management_in_commercial_apple_orchards_requires_an_integrated_appro

Jones, J., and E. Birney. 1988. M. Davis [Ed.], Handbook of Mammals of the North-Central States, University of Minnesota Press, MN, USA.

Kaufman, D.W., M.E. Peak, and G.A. Kaufman. 2016. *Peromyscus leucopus* in riparian woodlands: use of trees and shrubs. Journal of Mammology 66:139–143.

Kay, B.J., L.E. Twigg, T.J. Korn, and H.I. Nicol. 1994. The use of artificial perches to increase predation on house mice (*Mus domesticus*) by raptors. Wildlife Research 21:95 – 106.

Kéry, M. and M. Schaub. 2012. Bayesian population analysis using WinBUGS. Elsevier, New York, NY, USA.

Korpimäki, E., and C. J. Krebs. 1996. Predation and population cycles of small mammals: a reassessment of the predation hypothesis. Bioscience 46:754–764.

Labuschagne, L., L.H. Swanepoel, P.J. Taylor, S.R. Belmain, and M. Keith. 2016. Are avian predators effective biological control agents for rodent pest management in agricultural systems? Biological Control 101:94-102.

Leirs, H. 2003. Management of rodents in crops: the pied piper and his orchestra. Pages 180-190 in Singleton, G., Hinds, L.A., Krebs, C.J., Spratt, D.M. [Eds.], Rats, Mice and People: Rodent Biology and Management, ACIAR Monograph No. 96. Australian Centre for International Agricultural Research, Canberra.

McCleery, R.A., C. Zweig, M.A. Desa, R. Hunt, W.M. Kitchens and H.F. Percival. 2014. A novel method for camera-trapping small mammals. Wildlife Society Bulletin 38:1-5.

Pearson, A.B., W.P. Gorenzel, and T.P. Salmon. 2000. Lesser-known vertebrate pests of almonds in California. Proceedings of the Vertebrate Pest Conference 19:365-376.

Proudfoot, A. T. 2009. Aluminum and zinc phosphide poisoning. Clinical Toxicology 47:89–100.

Rendall, A.R., D.R. Sutherland, R. Cooke and J. White. 2014. Camera trapping: a contemporary approach to monitoring invasive rodents in high conservation priority ecosystems. PLoS One 9:e86592.

Rudolph, S. G. 1982. Foraging strategies of American Kestrels during breeding. Ecology 63:1268–1276.

Saracco, J.F., R. B. Siegel, and R.L. Wilkerson. 2011. Occupancy modeling of Black-backed Woodpeckers on burned Sierra Nevada forests. Ecosphere 2:art31.

Shave, M.E. and C.A. Lindell. 2017. American Kestrels occupying cherry orchard nest boxes show high reproductive rates and tolerance of monitoring. Journal of Raptor Research 51: 50-60.

Sheffield, L. M., J. R. Crait, W. D. Edge, and G. Wang. 2001. Response of American kestrels and gray-tailed voles to vegetation height and supplemental perches. Canadian Journal of Zoology 79:380–385.

Singleton, G.R., H. Leirs, L.A. Hinds, and Z. Zhang. 1999. Ecologically-based management of rodent pests – re-evaluating our approach to an old problem. Pages 17-30 in Singleton, G.R., H. Leirs, L.A. Hinds, and Z. Zhang [Eds.], Ecologically-based management of rodent pests, ACIAR Monograph No. 59. Australian Centre for International Agricultural Research, Canberra.

Stone, W.B., J.C. Okoniewski, and J.R. Stedelin. 1999. Poisoning of wildlife with anticoagulant rodenticides in New York. Journal of Wildlife Disease 35:187–193

Toland, B. R. 1987. The effect of vegetative cover on foraging strategies, hunting success and nesting distribution of American Kestrels in central Missouri. Journal of Raptor Research 21:14–20.

Tritten, B. 2013. Fall mice and vole control is critical to reduce potential damage in orchards. Michigan State University Extension. http://msue.anr.msu.edu/news/fall_mice_and_vole_control_is_critical_to_reduce_potential_damage_in_orchar

Tritten, B. 2014. Mice and vole populations are building in many orchards. Michigan State University Extension. http://msue.anr.msu.edu/news/mice_and_vole_populations_are_building_in_many_orchards

Witmer, G.W. and R. S. Moulton. 2012. Deer mice (*Peromyscus* spp.) biology, damage and management: a review. Pages 213 – 219 in R.M. Timm [Ed.], Proceedings of the 25th Vertebrate Pest Conference. University of California, Davis, CA, USA.

Wood, B.J. and G.R. Singleton. 2015. Rodents in agriculture and forestry. Pages 33-80 in A. Buckle and R. Smith [Eds.], Rodent pests and their control. CAB International, UK.