USDA National Wildlife Research Center - Staff Publications

U.S. Department of Agriculture: Animal and Plant Health Inspection Service

2018

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Shave, Megan E.; Shwiff, Stephanie A.; Elser, Julie L.; and Lindell, Catherine A., "Falcons using orchard nest boxes reduce fruit-eating bird abundances and provide economic benefits for a fruit-growing region" (2018). *USDA National Wildlife Research Center - Staff Publications*. 2175.
https://digitalcommons.unl.edu/icwdm_usdanwrc/2175

Received: 17 January 2018 | Accepted: 3 April 2018

DOI: 10.1111/1365-2664.13172

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Falcons using orchard nest boxes reduce fruit-eating bird abundances and provide economic benefits for a fruit-growing region

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Funding information
North Central SARE, Grant/Award Number: GNC15-211; George and Martha Wallace Endowed Scholarship Award, Grant/Award Number: N/A; Division of Environmental Biology, Grant/Award Number: 1518366

Handling Editor: Gavin Siriwardena

Abstract

1. Suppression of pest species via a native predator is a regulating ecosystem service that has the potential to limit crop damage and produce economic benefits. American kestrels *Falco sparverius* are widespread, highly mobile, generalist predators that hunt in human-dominated habitats and have the potential to provide previously undocumented ecosystem services in agricultural landscapes.
2. We hypothesized that kestrel activity associated with nest boxes and artificial perches acts to increase perceived predation risk that, in combination with direct predation, can reduce fruit-eating bird abundances in orchards. We used counts and observations of fruit-eating birds from fixed-width transect surveys to investigate variation in bird abundances and to estimate sweet cherry loss in cherry orchards with and without active kestrel boxes. We also conducted a benefit–cost analysis of nest box installation and used regional economic modelling to estimate macroeconomic impacts of increased sweet cherry production in Michigan, an important US fruit production region.
3. Fruit-eating bird counts were significantly lower at orchards with active kestrel boxes. Although kestrels used the perches in young orchard blocks and may benefit from them, the presence of perches did not have a significant effect on bird counts.
4. Benefit–cost ratios for kestrel nest boxes indicated that for every dollar spent on nest boxes, \$84 to \$357 of sweet cherries would be saved from fruit-eating birds. Regional economic modelling predicted that increased sweet cherry production from reduced bird damage would result in 46–50 jobs created and \$2.2 million to \$2.4 million in increased income for the state of Michigan over a 5-year period.
5. *Synthesis and applications*. Kestrel nest boxes in sweet cherry orchards provide a highly cost-effective ecosystem service with potential reverberating benefits for a regional economy. Box occupancy rates will undoubtedly vary across landscapes and regions. However, costs to install and maintain boxes are small and, even if box occupancy rates are low, boxes can direct kestrel activity to particular places in agricultural landscapes where they can deter pest birds. Thus, the potential benefits for fruit crops greatly outweigh the costs of this pest management strategy.

KEYWORDS
agriculture, artificial perches, benefit–cost ratio, ecosystem services, integrated pest management, kestrel, nest box, regional economic modelling

1 | INTRODUCTION

In response to the agricultural expansion and intensification that threatens biodiversity world-wide (Flynn et al., 2009; Green, Cornell, Scharlemann, & Balmford, 2005), much research focuses on the transition from conventional pesticide-based crop protection to a more sustainable integrated pest management (IPM) framework to manage pest populations (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 can be particularly effective predators of pest insects (Maas et al., 2015), rodents (Labuschagne, Swanepoel, Taylor, Belmain, & Keith, 2016) and other birds (e.g. Kross, Tylianakis, & Nelson, 2012).

Furthermore, conservation and agricultural goals come together with conservation biological control (CBC), which employs modifications of the environment to protect or enhance native predator populations to reduce the impact of pests (Eilenberg, Hajek, & Lomer, 2001). An easily-implemented CBC practice is the installation of artificial nesting and roosting cavities for nest site-limited predators. Nest boxes that attract avian predators can result in increased predation of pest insects (e.g. Jedlicka, Greenberg, & Letourneau, 2011) and rodents (Labuschagne et al., 2016). In addition, installing artificial perches can enhance hunting habitat for avian predators, particularly raptors (Widén, 1994), and previous studies have demonstrated negative effects of perches on rodent abundances (Kay, Twigg, Korn, & Nicol, 1994). However, previous work has not assessed cost-effectiveness of nest boxes (Wenny et al., 2011) or examined effects of nest boxes and artificial perches for predatory birds on abundances of prey birds, which are significant pests in fruit crops (Lindell et al., 2016). In addition, few studies have examined economic benefits in relation to job creation from species providing ecosystem services (e.g. Butler, Radford, Riddington, & Laughton, 2009); none have focused on regional job creation as a function of regulating services provided by native predators.

The first objective of our study was to determine whether installation of nest boxes and perches for American kestrels (*Falco sparverius*; 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 & 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 (M. Shave, PhD dissertation). Although birds comprise only about 2% of prey delivered to kestrel offspring during the breeding season (M. Shave, PhD dissertation), kestrels may reduce fruit-eating bird abundances in orchards through a combination of lethal and nonlethal effects of predation (Cresswell, 2008; Kross et al., 2012). Nonlethal effects include antipredator behaviours 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 to increase perceived 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 kestrel presence 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 potential economic benefits that result from kestrel effects on the presence on fruit-eating birds. We focused our economic analyses on sweet cherries (*Prunus avium*), given their higher sugar content (Serrano, Guillén, Martínez-Romero, Castillo, & Valero, 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 economic 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, Anderson, Cullen, White, & Shwiff, 2013). Estimates of these regional impacts can reveal how potential reduction of crop damage through enhancement of regulating ecosystem services can affect people in the community not directly involved in agriculture or wildlife conservation.

2 | MATERIALS AND METHODS

2.1 | 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). Between 2012 and 2016, we installed 25 new boxes within or next to cherry orchards (Figure 1; Shave & Lindell, 2017a). Kestrels quickly occupied these new boxes and showed high reproductive rates (Shave & Lindell, 2017a). In 2015, we randomly chose five orchards with active kestrel nest boxes for installation of artificial perches (see Appendix S1 for details on perch installation and use).

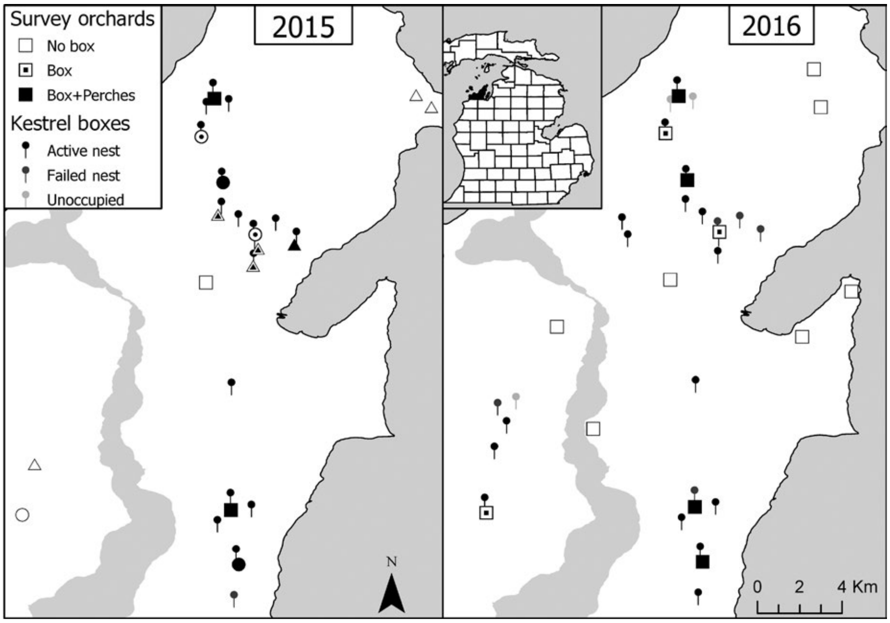

FIGURE 1 Map of 25 kestrel nest boxes installed and 21 cherry orchards surveyed for prey bird abundance during this study in Leelanau County, MI. Square, triangle, and circle markers indicate orchards where we conducted surveys in sweet blocks, tart blocks, and both sweet and tart blocks respectively. Inset: Map of MI with Leelanau County highlighted in black

2.2 | Fruit-eating bird abundances

We conducted fruit-eating bird surveys along 200-m-long fixed-width transects within cherry orchard blocks in 2015 and 2016 (Kross et al., 2012). We chose a fixed width of six orchard rows (32 m) 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 and 8:30 EST on days without precipitation or fog 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 before and after harvest because some cherries remain on the trees and ground following harvest (Eaton, Lindell, Homan, Linz, & Maurer, 2016). One observer conducted all surveys. The observer recorded all birds detected visually during surveys and 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 observations (described below), or if our previous study documented them eating cherries (Lindell, Eaton, Lizotte, & Rothwell, 2012). A list of bird species observed during surveys but excluded from analysis based on these criteria are listed in Appendix S2.

In 2015, we conducted surveys at 27 transects in 15 cherry orchards: five orchards with an active kestrel box, five orchards with an active kestrel box and perches and five orchards with no active box within 1.6 km (Figure 1). At orchards with active boxes, we placed transects within 150 m of the box. At orchards with boxes and perches, we placed transects within 100 m of a perch and 150 m of the boxes. In orchards comprising both sweet and tart cherry blocks, we placed one transect in a block of each crop type; in large orchards comprising 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). We placed the two transects in each orchard at least 150 m apart to reduce the chance of observing the same individuals at both transects during a survey. In 2016, we surveyed 14 transects within sweet cherry blocks in 14 orchards: three orchards with an active box, four orchards with an active box and perches, and seven orchards with no active box within 1.6 km (Figure 1). We focused on sweet cherry blocks in 2016 because the 2015 results and our previous work (Lindell et al., 2012) suggested a substantial preference by birds for sweet cherries, and we wanted to insure sufficient sample sizes for robust economic analyses. Orchard block areas ranged from 1.2 to 38.2 ha, with a mean of 6.3 ± 1.4 (*SE*) ha.

2.3 | Statistical analyses

2.3.1 | 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 (Johnson, 2008; Kross et al., 2012). We built Poisson mixed effects and regression models to explain the number of fruit-eating birds observed at orchard survey transects. We included orchard ID as a random effect 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 within 100 m of the transect (perch), whether the transect was in a sweet or tart cherry block (crop), survey year (year), whether the transect was at the edge or interior of the 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, year, edge and harvest to potentially explain more variation in fruit-eating bird counts beyond the focal effects of boxes 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 included the quadratic effect of harvest date because we also predicted that bird counts would level out or decrease after harvest. We also predicted that bird counts would be higher at edge transects, given that edges were adjacent to windbreaks or wooded areas that may facilitate bird entry into the block (Lindell et al., 2016).

We used a top-down approach for model selection; 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 corrected for small sample size (Hurvich & Tsai, 1989; Zuur, Ieno, Walker, Saveliev, & Smith, 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 (Type II Wald chi-squared tests; 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 (Nakagawa & Schielzeth, 2013). We built all models using package "lme4" (Bates, Maechler, Bolker, & Walker, 2015) in program R (3.1.0; R Core Team, 2017).

2.4 | Economic analyses

2.4.1 | Estimating sweet cherry loss

In 2016, we conducted observations of foraging birds in each sweet cherry block ($n = 14$) during a minimum of 5 and maximum of 11 days starting several weeks before harvest and continuing until 1–2 weeks after harvest. One observer conducted all observations. The observer walked through a 32 × 200 m area (0.64 ha; the same area covered by 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 30 min or until he observed 10 birds foraging for a minimum of 20 s each. When a bird of any species was detected, it was kept in sight as long as possible; the following information was recorded with a digital recorder: time the bird was encountered, species, number of fruits eaten/damaged and 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 had not foraged after 2 min. We used these observations ($n = 158$) to calculate the mean number of sweet cherries eaten/damaged per min by fruit-eating birds. We excluded observations when the bird showed some obvious response to the observer, such as an alarm call. We initially calculated the mean number of cherries eaten/damaged per min for each species separately for transects with and without active kestrel nests. These calculations all produced means of less than 1 cherry per min with one exception. Species-specific values for ten species combining kestrel and no-kestrel transects ranged from 0 to 0.28 fruits eaten/damaged per min. Two additional species had higher values: European starlings with 0.79 fruits eaten/damaged per min and Baltimore orioles with 0.46 fruits eaten/damaged per min. Given the low variability of the means, we calculated one mean for all species and transects (0.18 cherries per min).

We then calculated the number of cherries min^{-1} ha^{-1} lost to fruit-eating birds in orchards with and without active nests by combining the abundance survey data with the observational data. Previous telemetry data (R. A. Eaton and C. A. Lindell, unpubl. data) document that American robins and cedar waxwings, two of the most common frugivore species, were present in sweet cherry orchards more often between 06:00 and 11:00 hr (39% of the time) and between 16:00 and 21:00 hr (39% of the time), than from 11 a.m. to 4 p.m. (22% of the time; see Appendix S3). Therefore, we multiplied the number of cherries min^{-1} ha^{-1} lost to fruit-eating birds by (600 min + 300 min × 0.56) to estimate the number of cherries per ha lost to fruit-eating birds day^{-1} ha^{-1}. (The 600 min is the number of min per day in the hours between 06:00 and 11:00 and 16:00 and 21:00 hr, and the 300 min × 0.56 accounts for the hours between 11:00 and 16:00 hr when, based on the percentages above, robin and waxwing activity is only 0.56 as much as during the other two time periods). The resulting values were the estimated numbers of sweet cherries lost to fruit-eating birds per ha over the course of the ripening period in orchards with and without active kestrel boxes.

2.4.2 | Benefits of kestrel nest boxes

We measured the benefits of kestrel nest boxes in terms of additional sweet cherry production from reduced bird damage. We translated the estimated numbers of cherries lost to fruit-eating birds to weight by multiplying numbers by 7.5 and 8 g, typical weights for sweet cherries in the study region (Whiting, Lang, & Ophardt, 2005; G. Lang, pers. comm.). We calculated the value of the additional cherries using a 5-year price average (USDA Economic Research Service, 2016) and then multiplied by the number of bearing-age hectares of sweet cherries in Michigan and Leelanau, Antrim, and Grand Traverse Counties (USDA Census of Agriculture, 2012) to provide the total values of cherries saved, if kestrel boxes were installed across all sweet cherry hectarage and experienced a 90% occupancy rate by kestrels (Shave & Lindell, 2017a).

2.4.3 | Costs of kestrel nest boxes

Costs for each nest box included a pre-made box as well as lumber and hardware for the tower and installation. We included labour costs for installation and annual cleaning: we valued labour at $25 per hour and assumed a 90% box occupancy rate for cleaning (Shave & Lindell, 2017a). We determined the number of nest boxes needed to cover all sweet cherry hectarage based on kestrel territory size.

The average kestrel territory ranges from 500 m to 1 km in diameter, or 19.6–78.5 ha (Bird & Palmer, 1988; Rohrbaugh & Yahner, 1997). We assumed installation of enough nest boxes to cover the bearing-age hectares in the first year; we included only cleaning costs in subsequent years. We calculated costs and benefits for a total of 5 years.

2.4.4 | 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; Boardman, Greenberg, Vining, & Weimer, 2005). 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; a discount rate accounts for people generally placing a higher value on resources in the present that in the future. We performed a sensitivity analysis using the ranges of cherry weights and kestrel territory sizes, through which we obtained a low and high estimate for net benefits and BCRs.

2.4.5 | Macroeconomic impacts

We constructed a county-level regional economic model of the state of Michigan based on 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. We aggregated county-level results from Leelanau County, Antrim County, and Grand Traverse County to represent the state; these three counties contained nearly 80% of sweet cherry-bearing hectarage in Michigan in 2012. All models were built in the REMI PI+ software package.

Macroeconomic changes arising from increased cherry production due to reduced bird damage were analysed using REMI PI+ software (Regional Economic Models, Inc.). We input into the REMI model the additional tons of sweet cherries expected to be produced in each of the three counties if nest boxes were installed across all sweet cherry hectarage; we estimated the additional tons based on our field data (see Section 3.2.1 and Section 2.4.2 above). REMI is a computer-based simulation model of the US economy that allows modelling at both the national and subnational scales. This structural economic forecasting model uses a nonsurvey based input–output table, which models the linkages among industries and households of a regional economy (Shwiff et al., 2013; Figure 2). Using the REMI model, we can generate forecasts that detail behavioural responses to changes in price, production and other economic factors (Treyz, Rickman, & Shao, 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

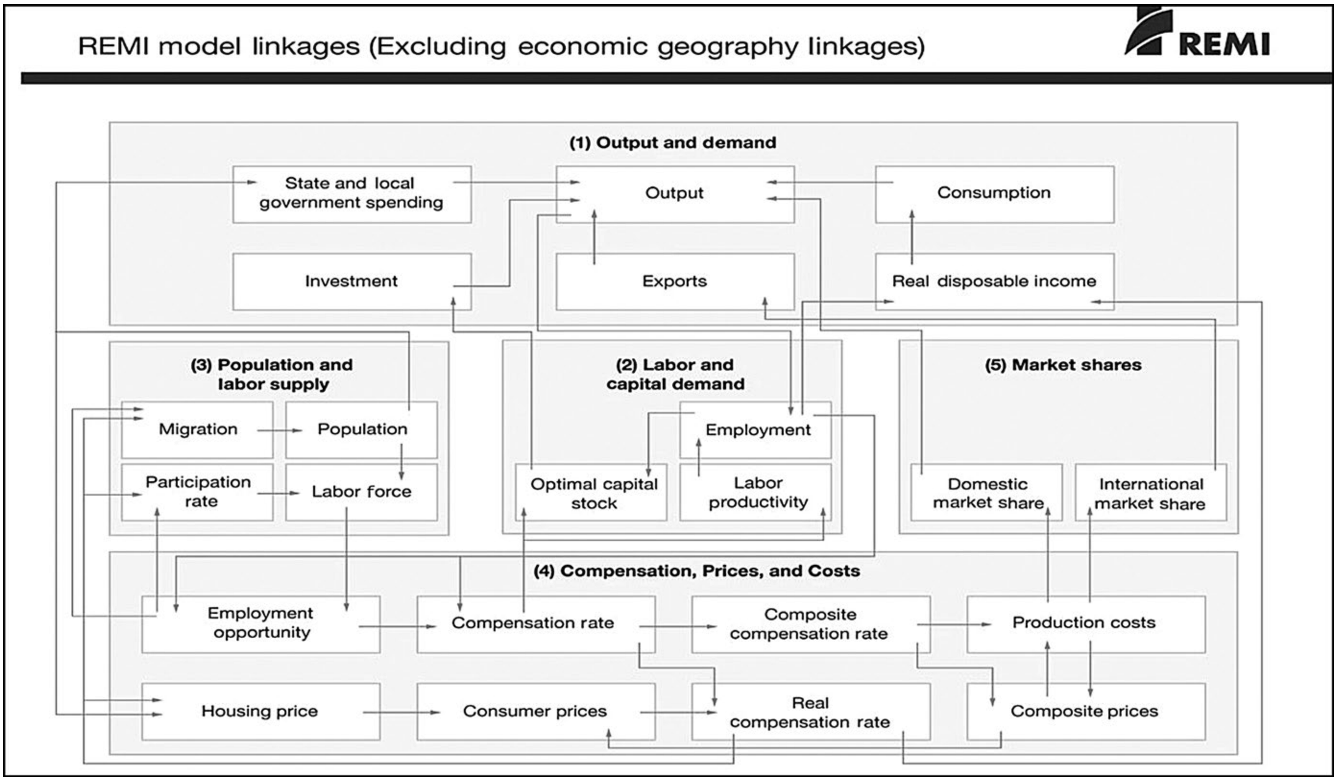

FIGURE 2 Linkages among industries and households of the regional economy included in the REMI model to predict macroeconomic impacts of decreased sweet cherry damage in Michigan

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 & Blair, 2009).

3 | RESULTS

3.1 | Fruit-eating bird abundances

We conducted a total of 268 surveys over both years. In 2016, the kestrel nests failed at two orchards with active kestrel nest boxes; the surveys from transects at these orchards were dropped from analyses because they no longer matched the distance criterion for the active nest box treatment (active nest within 150 m). Also, we discovered a kestrel nest in an abandoned house near an orchard; the surveys from the transect at this orchard were dropped from analyses because they no longer matched the criteria for the no active 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 13 fruit-eating species during surveys (Figure 3). We saw or heard a kestrel during or prior to 64 surveys (35%) at transects in orchards with active kestrel nests; we did not detect any kestrels during or prior to surveys at transects in orchards without active kestrel nests.

The best-fitting model for total fruit-eating bird abundance ($\beta_{\text{intercept}} = 1.50 \pm 0.27$ *SE*) included the random effect of orchard ID (see Appendix S4) and the fixed effects of box, crop, year and a quadratic effect of harvest (Table 1). Transects in orchards with active kestrel boxes had significantly lower fruit-eating bird counts compared to transects in orchards without ($\beta_{\text{box}} = -2.03 \pm 0.34$; Figure 4). Tart orchard blocks had significantly lower fruit-eating bird counts compared to sweet blocks ($\beta_{\text{crop}} = -0.77 \pm 0.22$; Figure 4). Surveys conducted in 2016 had significantly lower counts than in 2015 ($\beta_{\text{year}} = -0.73 \pm 0.26$). Finally, counts initially increased as the harvest date approached and then decreased after harvest ($\beta_{\text{harvest}} = -0.062 \pm 0.046$; $\beta_{\text{harvest}^2} = -0.024 \pm 0.012$). The marginal and conditional R^2 values for the model were 0.35 and 0.50 respectively.

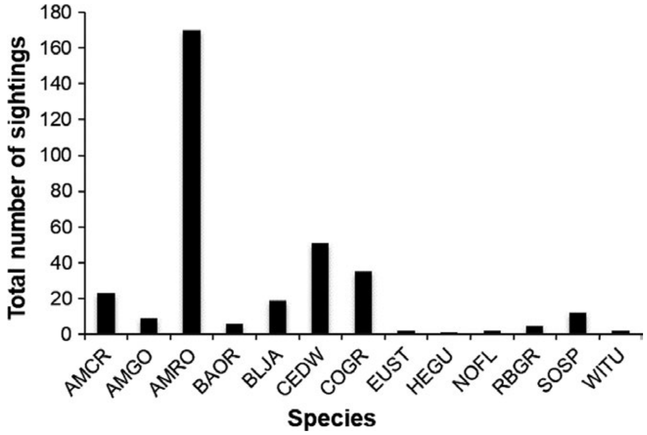

FIGURE 3 Total number of sightings of fruit-eating birds during 2015–2016 surveys. We identified 13 species during surveys: American crow (*Corvus brachyrhynchos*; AMCR), American goldfinch (*Spinus tristis*; AMGO), American robin (*Turdus migratorius*; AMRO), Baltimore oriole (*Icterus galbula*; BAOR), 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), northern flicker (*Colaptes auratus*; NOFL), rose-breasted grosbeak (*Pheucticus ludovicianus*; RBGR), song sparrow (*Melospiza melodia*; SOSP) and wild turkey (*Meleagris gallopavo;* WITU)

3.2 | Economic analyses

3.2.1 | Estimating sweet cherry loss

The numbers of fruit-eating birds per min per 0.064 ha observed at transects in orchards with and without active kestrel nests were 0.05 and 0.30, respectively, ranging from 0 to 0.4 fruit-eating birds detected per min per 0.064 ha for transects with active nests, and from 0 to 0.9 fruit-eating birds detected per min per 0.064 ha for transects without active nests. We therefore calculated 0.78 birds min^{-1} ha^{-1} and 4.69 birds min^{-1} ha^{-1} for orchards with and without active kestrel nests respectively. We then calculated that 0.14 cherries min^{-1} ha^{-1} were lost to fruit-eating birds from orchards with active kestrel nests (0.78 fruit-eating bird min^{-1} ha^{-1} × 0.18 cherries per min), while 0.84 cherries min^{-1} ha^{-1} were lost from orchards without active kestrel nests (4.69 fruit-eating birds min^{-1} ha^{-1} × 0.18 cherries per min). We therefore estimated that a total of 2,258 cherries per ha (0.14 cherries min^{-1} ha^{-1} × (600 min + (300 min × 0.56)) × 21 days) and 13,548 cherries per ha (0.84 cherries min^{-1} ha^{-1} × (600 min + (300 min × 0.56)) × 21 days) were lost to fruit-eating birds in orchards with and without active kestrel nests respectively.

3.2.2 | 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

TABLE 1 Analysis of deviance table (Type II Wald chi-squared tests) for selection of fixed effects in Poisson model of fruit-eating birds

Fixed effect	*df*	χ^2	*p*
Box	1	25.23	<0.0001[a]
Crop	1	12.14	0.0005[a]
Year	1	7.55	0.006[a]
Harvest	1	1.83	0.18[b]
Harvest^2	1	4.08	0.043[a]
Perch	1	0.00	0.99
Edge	1	0.037	0.85

[a] Fixed effects significant at the 0.05 level.

[b] Although the linear term is not significant, we retained it in the selected model (Faraway, 2002).

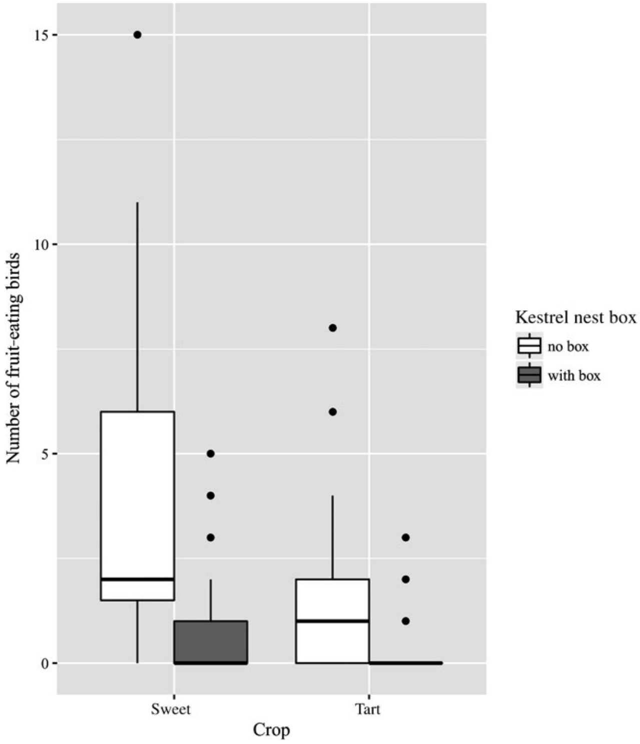

FIGURE 4 Numbers of fruit-eating birds (medians and interquartile ranges [IQRs]) observed per 10-min survey in fixed-width survey areas at sweet and tart orchard blocks with and without active nest boxes. Boxplot whiskers extend 1.5 IQRs

minus the costs of the next boxes, their installation and maintenance, totalled over 5 years. The majority of the costs arise in the first year from purchase and installation of the nest box ($114.79 per box). Years 2 through 5 consist of only maintenance (cleaning) costs ($22.50 per box yearly). Costs for the state of Michigan range from $8,021 to $32,124 and benefits range from $2.6 million to $2.9 million (Table 2). Costs were low enough that net benefits are approximately equal to the benefits. BCRs ranged from 84 to 357, indicating that for every dollar spent on kestrel nest boxes, $84 to $357 of cherries is saved. To provide some context for these values, Michigan sweet cherry production for 2014, 2015, and 2016 was 4.46, 2.07, and 3.37 tons per acre, respectively, and prices received by growers were $2,430, $2,650 and $2,420 per ton (USDA National Agricultural Statistics Service, 2017).

3.2.3 | Macroeconomic impacts

Regional economic modelling predicted that increased production of cherries from reduced bird damage from kestrel activity at nest boxes would result in 46–50 jobs created and $2.2 million to $2.4 million in increased income for the state of Michigan over a 5-year period (Table 3).

4 | DISCUSSION

As predicted, fruit-eating bird abundances were significantly lower at transects in orchards with active nest boxes compared to transects in orchards 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 significantly decreased counts between transects in orchards 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 to increase perceived predation risk that, in combination with kestrel consumption of prey birds, reduce fruit-eating bird abundances in orchards.

Although kestrels used the perches installed in cherry orchards (see Appendix S1), 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 (see Appendix S1). Kestrels mostly used the perches in the youngest blocks; meanwhile, we conducted the fruit-eating bird surveys in mature 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. 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, Herzog, & Smith, 2011).

Previous work argues that the mere presence of predators can elicit strong antipredator behaviour in birds (Cresswell, 2008). In our study region, the presence of active kestrel boxes as cues of predation risk should be reinforced by actual predation events. Birds made up a regular, if low, proportion of the prey items delivered by adult kestrels to nestlings in the study region; American robins, European starlings and blue jays were all documented as prey items of kestrels either through video recordings at boxes or through the discovery of remains in boxes at the end of the season (M. Shave, PhD dissertation). These predation events should reduce the likelihood of habituation of fruit-eating birds to kestrel presence in orchards over time.

Although previous studies have estimated yield gains (e.g. Gras et al., 2016) and/or economic benefits to farmers of vertebrate predation of crop-damaging pests (e.g. Karp et al., 2013), ours is the first study to estimate potential job creation from this ecosystem service. Assuming statewide nest box installation, and similar patterns of nest site limitation and high box occupancy rates (90%) as those observed in our study region, the increased fruit production would be substantial enough to result in a roughly $2.3 million increase in the GDP of Michigan and the creation of up to 50 jobs. Insuring economic benefits for local communities is increasingly seen as a key component of improving ecosystem service provisioning (e.g. Raes, Aguirre, D'Haese, & Van Huylenbroeck, 2014). The results here, along with

TABLE 2 Benefit–cost analysis of reduced sweet cherry damage due to active kestrel boxes. Analyses are for Michigan overall and for the three counties in the state that account for nearly 80% of the sweet cherry-bearing hectarage in Michigan

	Benefits Cherry weight		Costs Kestrel Territory		Net benefits	
Year	7.5 g	8.0 g	19.6 ha	78.5 ha	High	Low
Michigan						
2016	$547,125	$583,600	$18,202	$4,545	$579,055	$528,923
2017	$541,708	$577,822	$3,532	$882	$576,940	$538,175
2018	$536,344	$572,101	$3,498	$873	$571,227	$532,847
2019	$531,034	$566,436	$3,463	$865	$565,572	$527,571
2020	$525,776	$560,828	$3,429	$856	$559,972	$522,348
Total	$2,681,988	$2,860,787	$32,124	$8,021	$2,852,766	$2,649,864
Leelanau County						
2016	$263,581	$281,153	$8,769	$2,189	$278,964	$254,812
2017	$260,971	$278,369	$1,702	$425	$277,945	$259,270
2018	$258,387	$275,613	$1,685	$421	$275,193	$256,702
2019	$255,829	$272,884	$1,668	$417	$272,468	$254,161
2020	$253,296	$270,183	$1,652	$412	$269,770	$251,644
Total	$1,292,065	$1,378,203	$15,476	$3,864	$1,374,339	$1,276,589
Antrim County						
2016	$61,243	$65,326	$2,037	$509	$64,817	$59,206
2017	$60,637	$64,679	$395	$99	$64,581	$60,241
2018	$60,036	$64,039	$392	$98	$63,941	$59,645
2019	$59,442	$63,405	$388	$97	$63,308	$59,054
2020	$58,854	$62,777	$384	$96	$62,681	$58,470
Total	$300,212	$320,226	$3,596	$898	$319,328	$296,616
Grand Traverse County						
2016	$105,732	$112,781	$3,518	$878	$111,902	$102,214
2017	$104,685	$111,664	$683	$170	$111,494	$104,002
2018	$103,649	$110,558	$676	$169	$110,390	$102,973
2019	$102,622	$109,464	$669	$167	$109,297	$101,953
2020	$101,606	$108,380	$663	$165	$108,215	$100,944
Total	$518,294	$552,847	$6,208	$1,550	$551,297	$512,086

Discount rate = real interest rate = 1%.

TABLE 3 Jobs created and increase in Michigan GDP due to reduced sweet cherry damage

	2016	2017	2018	2019	2020	Total
Low						
Jobs created	9	10	9	9	9	46
GDP (2013 USD)	$403,829	$441,347	$452,832	$452,383	$452,383	$2,202,774
High						
Jobs created	10	10	10	10	10	50
GDP (2013 USD)	$442,104	$473,866	$485,852	$485,123	$485,123	$2,372,068

previous work demonstrating consumer willingness to pay more for fruit produced with predator nest boxes (Oh, Herrnstadt, & Howard, 2014), build the case that a variety of real economic benefits can accrue to regions where farmers employ native predators as part of their pest management strategies.

5 | CONCLUSIONS

Our bird survey results, combined with the high kestrel reproductive rates observed for boxes in the study region (Shave & Lindell, 2017a), indicate that orchard nest boxes are effective tools that can enhance regulating ecosystem services while also sustaining or increasing the local kestrel breeding population (Shave & Lindell, 2017b). Kestrel presence was particularly valuable in deterring fruit-eating birds in sweet cherry orchards and also significantly reduced fruit-eating bird abundance in tart cherries. Perch presence did not significantly influence fruit-eating bird abundance; however, perches were used as a safe spot by kestrel fledglings and so may enhance fledgling survivorship (see Appendix S1). We conclude that kestrel nest boxes in orchards are an easily-implemented and valuable addition to IPM practices in fruit crops. Finally, 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.

As expected with any IPM strategy, kestrel nest boxes did not eliminate pest birds from the orchards. In addition, some local kestrel populations are not limited by availability of nest sites (McClure, Pauli, & Heath, 2017). For this and other reasons, box occupancy rates will undoubtedly vary across landscapes and regions (Smallwood et al., 2009). However, costs to install and maintain boxes are small and, even if box occupancy rates are low, boxes can direct kestrel activity to particular places in agricultural landscapes (Shave & Lindell, 2017b) where they can reduce pest bird activity. Thus, the potential benefits in fruit crops greatly outweigh the costs of this pest management strategy.

ACKNOWLEDGEMENTS

We thank L. Clark and E. Oja for field assistance. We thank the growers of Leelanau County for allowing us to install nest boxes and perches and conduct surveys on their properties. We thank R. Eaton for telemetry data for fruit-eating bird activity. We thank Gavin Siriwardena and two anonymous reviewers whose comments greatly improved the manuscript. Grants from the George and Martha Wallace Endowed Scholarship Award, NCR SARE Program (GNC15-211) and NSF CNH Program (DEB – 1518366) funded this work. The Institutional Animal Care and Use Committee at Michigan State University approved this study.

AUTHORS' CONTRIBUTIONS

M.S., C.L. and S.S. conceived the ideas and designed methodology; M.S., C.L., J.E. and S.S. collected the data; M.S., C.L., J.E. and S.S. analysed the data; M.S. and C.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.3356t85 (Shave, Shwiff, Elser, & Lindell, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Shave ME, Shwiff SA, Elser JL, Lindell CA. Falcons using orchard nest boxes reduce fruit-eating bird abundances and provide economic benefits for a fruit-growing region. *J Appl Ecol*. 2018;55:2451–2460. https://doi.org/10.1111/1365-2664.13172

Appendix S1. Perch installation and use

Perch installation and monitoring

In 2015, we randomly chose five orchards with active kestrel nest boxes for installation of 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, placing perches within 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 (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).

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Statistical analysis

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 predicted that kestrel perch use would be higher in orchard blocks with shorter trees due to increased visibility. We predicted that perch use would increase with kestrel offspring age due to the female spending more time outside of the box (M. Shave, PhD dissertation) and the offspring using the perches after fledgling; we also predicted that use may decrease towards the end of the season due to fledgling dispersal (Olea, 2001).

We used a top-down approach for model selection; 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 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).

Results

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 (β_0 = -1.84 ± 0.51) included the random effect of perch nested within orchard (Table S1) and the fixed effects of tree height, age, and age^2 (Table S2). Increasing mean tree height in an orchard block had a negative effect on perch use (β_1 = -1.84 ± 0.51). The linear effect of offspring age was positive (β_2 = 0.67 ± 0.32); the quadratic effect was negative (β_3 = -0.16 ± 0.038), thus kestrel use of the perches first increased and then decreased (Fig. S1). The marginal and conditional R^2 values for the model were 0.46 and 0.71, respectively.

Discussion

As predicted, perch use was higher in younger orchard blocks with shorter trees. Although perch use was not high in mature orchard blocks where kestrel presence could benefit prey bird deterrence, we found that perches in the young blocks could provide benefits to the kestrels themselves. Kestrel use of the perches first increased and then decreased with increasing age of the offspring. The increase in use likely corresponded as predicted to the adult female spending increasingly more time outside the box as the offspring aged (M. Shave, PhD dissertation); 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 near the nest box could be a valuable resource for young fledglings.

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Table S1. 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 S2. 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	X^2	P
tree height	1	13.24	0.00028*
age	1	3.94	0.047*
age^2	1	17.28	<0.0001*

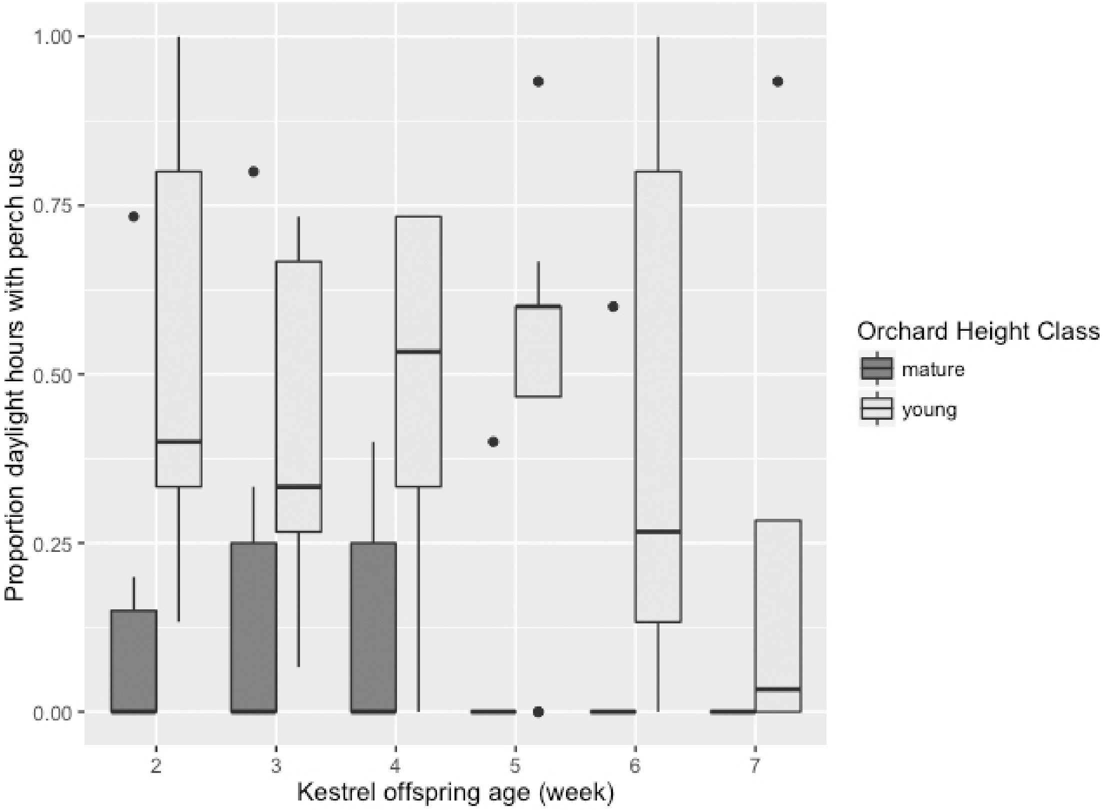

Fig. S1. Kestrel perch use (medians and interquartile ranges [IQRs]) in mature (mean tree height >3.5 m) and young (mean tree height <3.5 m) orchard blocks during kestrel nestling (weeks 2 – 4) and post-fledging (weeks 4 – 7) periods. Boxplot whiskers extend 1.5 IQRs.

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Appendix S2. Excluded bird species

The following bird species were observed during surveys but not included in models of fruit-eating bird abundance in sweet or tart cherries because they weren't observed eating fruit during surveys or observations in this study or in our previous study (Lindell, C.A. et al. 2012. Bird consumption of sweet and tart cherries. *Human-Wildlife Interactions* 6:283-290).

Species	No. times detected during surveys
Black-capped chickadee, *Poecile atricapillus*	16
Brown thrasher, *Toxostoma rufum*	1
Chipping sparrow, *Spizella passerina*	33
Downy woodpecker, *Picoides pubescens*	4
Eastern bluebird, *Sialia sialis*	6
Eastern kingbird, *Tyrannus tyrannus*	8
Tufted titmouse, *Baeolophus bicolor*	3
Hairy woodpecker, *Picoides villosus*	3
Red-headed woodpecker, *Melanerpes erythrocephalus*	1
Red-bellied woodpecker, *Melanerpes carolinus*	1
Vesper sparrow, *Pooecetes gramineus*	16

Appendix S3. Time of day and fruit-eating bird activity

Description of data collection to determine differences in activity levels of fruit-eating birds in sweet cherry orchard blocks at different times of day (Eaton and Lindell, unpubl. data) for use in calculations of cherries *day*$^{-1}$ ha^{-1} lost to fruit-eating birds (*Estimating sweet cherry* loss section of manuscript).

We placed stationary receivers in four sweet cherry orchards on the Leelanau Peninsula, Michigan, in June 2013 and retrieved them in September 2013. Receivers scanned continuously for the frequencies of transmitters attached to 42 robins and waxwings combined. Of all detections of these two species in orchards between 6 am and 9 pm (n = 281), 39% were in the period from 6-11 am, 22% were in the 11 am to 4 pm period, and 39% were in the 4-9 pm period. Based on these percentages, birds were in the orchards from 11 am to 4 pm about 0.56 times as often as in the other two time periods.

We used observations of frugivorous birds foraging in sweet cherry orchards (see manuscript for details) to calculate the mean number of cherries eaten min^{-1} by fruit-eating birds. We estimated the mean number of fruit-eating birds present in a sweet cherry orchard min^{-1} ha^{-1} from the fruit-eating bird abundance surveys conducted in 2016; each survey covered 0.064 ha min^{-1} during a 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 by using both the foraging and survey data described in this paragraph. To then obtain the number of cherries *day*$^{-1}$ ha^{-1} lost to fruit-eating birds in orchards we multiplied the number of cherries min^{-1} ha^{-1} lost to fruit-eating birds by (600 minutes + 300 minutes* 0.56) to account for the lower activity in the five hours in the middle of the day. The 600 minutes is the number of minutes per day in the hours between 6 and 11 am and 4 and 9 pm, and the 300 minutes * 0.56 accounts for the hours between 11 am and 4 pm when, based on the percentages above, robin and waxwing activity is only 0.56 as much as during the other two time periods. The approximate daylight hours in the study region in July run from 6 am to 9 pm.

More details of the methods and results of the full telemetry study are in:

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

Appendix S4. Random effects in models of fruit-eating bird abundance

Table S1. 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 (birds ~ box + crop + year + perch + harvest + I(harvest^2) + edge).

MODEL	AICC	ΔAICC	WEIGHT
Random intercepts (orchard)	685.9	0.0	0.99
Random intercepts + slopes (orchard)	694.6	8.7	0.0013
Random slopes (orchard)	717.4	31.5	<0.001
No random effects	731.8	45.8	<0.001

#

Table S2. Intercepts and slopes for each orchard from best-fitting model of fruit-eating birds (birds ~ box + crop + year + harvest + I(harvest^2) + (1|orchard)).#

ORCHARD	INTERCEPT (FIXED + RANDOM EFFECTS)	INTERCEPT (RANDOM EFFECTS)	SLOPE				
			BOX	CROP	YEAR	HARVEST	HARVEST^2
1	1.71	0.21	-2.03	-0.77	-0.73	-0.062	-0.024
2	2.32	0.82	-2.03	-0.77	-0.73	-0.062	-0.024
3	0.73	-0.77	-2.03	-0.77	-0.73	-0.062	-0.024
4	1.86	0.36	-2.03	-0.77	-0.73	-0.062	-0.024
5	2.21	0.71	-2.03	-0.77	-0.73	-0.062	-0.024
6	0.65	-0.85	-2.03	-0.77	-0.73	-0.062	-0.024
7	0.60	-0.90	-2.03	-0.77	-0.73	-0.062	-0.024
8	1.56	0.05	-2.03	-0.77	-0.73	-0.062	-0.024
9	2.31	0.81	-2.03	-0.77	-0.73	-0.062	-0.024
10	2.02	0.52	-2.03	-0.77	-0.73	-0.062	-0.024
11	1.18	-0.32	-2.03	-0.77	-0.73	-0.062	-0.024
12	1.96	0.46	-2.03	-0.77	-0.73	-0.062	-0.024
13	1.22	-0.28	-2.03	-0.77	-0.73	-0.062	-0.024
14	1.25	-0.25	-2.03	-0.77	-0.73	-0.062	-0.024
15	1.24	-0.26	-2.03	-0.77	-0.73	-0.062	-0.024
16	0.72	-0.78	-2.03	-0.77	-0.73	-0.062	-0.024
17	2.13	0.64	-2.03	-0.77	-0.73	-0.062	-0.024
18	0.61	-0.89	-2.03	-0.77	-0.73	-0.062	-0.024
19	2.09	0.59	-2.03	-0.77	-0.73	-0.062	-0.024
20	2.61	1.10	-2.03	-0.77	-0.73	-0.062	-0.024
21	1.30	-0.20	-2.03	-0.77	-0.73	-0.062	-0.024

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