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Authors

Carlino, Jaime E. Chavez, Samantha D. Echávez, Laura M. et al.

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Can Barn Owl (*Tyto furcata*) Nest Boxes in Winegrape Vineyards Sustain a Population of Barn Owls?

Jaime E. Carlino, Samantha D. Chavez, Laura M. Echávez, and Matthew D. Johnson Department of Wildlife, California Polytechnic University, Humboldt, Arcata, California

ABSTRACT: Controlling small mammal pests and their damage has always been a challenge for farmers. Farmers and researchers worldwide have been experimenting with deploying nest boxes to attract barn owls to their fields to remove rodent pests. While much research has focused on the potential for nest boxes and barn owls to benefit agriculture, comparatively little work has examined the impact of the practice on owls. In this study, we used a life table analysis and estimates of barn owl reproduction measured in winegrape vineyards in Napa Valley, California coupled with published estimates of survival from long-term studies in Europe to produce a demographic model of a population of barn owls using nest boxes. We then examined how manual perturbations of survival and reproductive rates affect whether the modeled population is stable, increasing, or decreasing. Based on our empirical estimate of reproductive success and literature-sourced estimates of survival, the population appears to be growing. Across all scenarios in which we adjusted survival, there were only five that resulted in the population declining. All scenarios that resulted in population decline occurred when survival was reduced for all ages simultaneously or for adult survival independently. There were no scenarios in which lambda dropped below 1 when modifying reproductive success independent of survival. These results are important for practical pestmanagement reasons, as nest boxes cannot be part of a successful long-term integrated pest management (IPM) plan if they are reliant on continual immigration of adult owls from other source populations to offset mortality. A thorough examination of ecological traps should be conducted using additional information on habitat selection and reproduction in natural nest sites.

KEY WORDS: barn owl, demography, life table analysis, ecological trap, nest box, pest management, reproductive success, survival, *Tyto alba*, *Tyto furcata*

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INTRODUCTION

Controlling small mammal pests has been a challenge for farmers since the dawn of agriculture and is increasingly important in ensuring food security around the world (Witmer and Singleton 2010). Rodents are particularly damaging to winegrapes (McGourty et al. 2011). Gebhardt et al. (2011) conducted a meta-analysis of dozens of studies and ran Monte Carlo simulations to examine damage to crops by vertebrates while accounting for randomness for 19 economically important California crops, including winegrapes. Their simulations estimated that winegrapes suffer the second greatest losses, at 7.2% yield per year, after artichokes at 8.3%. Rodents cause damage by herbivory, especially to young vines (Ross 2009), burrowing, and physical damage to irrigation systems. In a survey of winegrape producers, Anderson et al. (2012) found that over 50% used either toxicants, trapping, or both to control rodents, spending between \$22 and \$28 per acre annually on control efforts. They estimate the net benefit of these efforts (defined as the value of crop saved + reduction in property damage – the cost of control efforts) to be \$390 to \$892 per acre per year.

Rodents in general are notoriously problematic to control with chemicals (via rodenticides such as strychnine, zinc phosphide, anticoagulants) and physical methods (trapping, explosives) due to both the inefficiency of these methods or their documented and potential negative impacts to the environment (Baldwin et al. 2014, van den Brink et al. 2018). The use of rodenticides, especially anticoagulant rodenticides, is increasingly criticized because of their impacts on pets and a wide range

of non-target wildlife, from eagles (family Accipitridae) and owls (order Strigiformes) to foxes (genus *Vulpes*) and mountain lions (*Puma* spp.) (Erickson and Urban 2004, Gabriel et al. 2018, van den Brink et al. 2018). Passed in 2020, the California Ecosystems Protection Act prohibits most uses of second-generation anticoagulant rodenticides (SGARs) until a re-evaluation by the Department of Pesticide Regulation is completed (Harbison 2020). Although SGARs are not used to manage field rodents, the signs are clear: to retain global leadership, the California winegrape industry must find alternatives today that will reduce or replace reliance on toxic chemical rodenticides.

For several decades, farmers and researchers worldwide have been experimenting with deploying nest boxes to attract rodent-eating barn owls (*Tyto alba*, *T. furcata*, *T.* javonica) to their fields to remove rodent pests (Evenden 1995, Kan et al. 2014, Labuschagne et al. 2016). For example, barn owl boxes have been used in Malaysia, where the rice-field rat, Rattus argentiventer, plagues rice paddies and the Malayan wood rat (R. tiomanicus) is a significant pest in oil palm plantations (Hafidzi et al. 1999, Hafidzi and Na'Im 2003). În Israel, barn owls help reduce crop losses in alfalfa (Kan et al. 2014). The practice is particularly common in California's winegrape vineyards (Johnson et al. 2018), where ongoing research is revealing patterns in nest box occupancy (Huysman and Johnson 2021), barn owl hunting habitat selection (Castañeda et al. 2021), and rodent removal (St. George and Johnson 2021). Johnson and St. George (2020) estimated that a family of barn owls in Napa Valley removes 3,466 ±465 rodents per year, and recent work by Hansen and Johnson (Hansen and

Johnson 2022) suggests this removal meaningfully reduces the activity of gophers on vineyards with barn owl nest boxes

While much research has focused on the potential for nest boxes to attract rodent-eating owls to benefit agriculture (Labuschagne et al. 2016, Lindell et al. 2018), comparatively little work has examined the impact of the practice on owls. Agroecology includes the study of reciprocal relationships between native biodiversity and agriculture (Wezel et al. 2009, Altieri 2018), and yet we know relatively little about whether the installation of nest boxes is beneficial for the barn owl populations in winegrape ecosystems. This question has obvious practical application to farmers because a reliable long-term source of barn owls rests on the assumption (not yet tested) that the nest boxes can help maintain a viable local owl population. In addition, addressing whether nest boxes are good for owls will help reveal if the practice is exploitative of wildlife (i.e., good for the farmer but not the owls), or if it represents a truly mutually beneficial management technique. Although American barn owl (*T. furcata*) populations appear stable overall in California, they are declining in southern Canada and in parts of the Midwest and Eastern United States (Marti et al. 2020), and common barn owls (T. alba) are declining in parts of Europe (Roulin 2020). Life table analyses constructed from estimates of survival and reproduction can help indicate whether a population's rate of production is able to offset mortality, and sensitivity analyses can reveal how simulated changes in vital rates affect population viability (Beissinger and McCullough 2002, Manlik et al. 2018). Estimates of barn owl survival are available from the literature, and reproduction is relatively easily measured for owls in nest boxes, but no study has yet examined the viability of barn owl populations nesting in boxes in winegrape vineyards.

In this study, we use estimates of barn owl reproduction measured in winegrape vineyards in Napa Valley, California coupled with published estimates of their survival from long-term studies in Europe to produce a demographic model of a population of barn owls using nest boxes. We then examine how perturbations of survival and reproductive rates affect whether the modeled population is stable, increasing, or decreasing.

METHODS Study System

Napa Valley (Napa County, northern California) is characterized by a Mediterranean climate, with warm, dry summers, and mild winters with moderate levels of precipitation. The Valley is known for its unique geologic history, variety of microclimates, and diverse soils, which support 16 viticultural appellations. With approximately 17,600 of the Valley's 20,000 ha under cultivation, winegrapes are a major economic driver in this region (Stonebridge 2017), and their production in this region alone contributes tens of billions of dollars to the U.S. economy every year (Stonebridge 2017). In addition to winegrapes, the valley is composed of a heterogeneous matrix of grasslands, oak savannas and woodlands, conifer forests, and riparian areas which hosts a high level of biodiversity.

Approximately 300 nest boxes throughout Napa Valley

have been monitored by our research team since 2015 (Wendt and Johnson 2017). The nest boxes included in this study were installed by producers and vineyard managers within vineyards and along vineyard edges prior to and throughout our years of monitoring. The vineyards in our study system vary in acreage, surrounding native uncultivated land, urban development, and farming practices. The nest boxes themselves vary in dimensions, age, orientation, material, etc. (Wendt and Johnson 2017). The number of nest boxes on each vineyard varies from 1 to 37 and the distance between the nearest boxes varies from ~20 m to ~1,353 m.

Demographic Data

To explore our question, we needed demographic data including estimates of reproductive success and survival. To empirically estimate reproductive success of barn owls in our study area, we monitored 293 boxes in Napa Valley for reproductive occupancy. We conducted occupancy checks monthly from February through July of 2021, the duration of the barn owl breeding season. To monitor nest boxes for occupancy, we used a smartphone-controlled GoPro fixed to a flexible arm attached to the top of a painter's pole (Wendt and Johnson 2017). Occupied nest boxes were then re-visited weekly to obtain an accurate age of nestlings and count the number of young that started to approach fledging age.

The reproductive success of an individual is best measured with long-term reproductive success to capture temporal variation in fecundity and population dynamics. However, given the exploratory nature of this project, annual reproductive success, specifically the number of fledglings, serves as our measure of reproductive success in this analysis. Barn owls reach fledgling age at 62 ± 4 days old (Browning et al. 2016). Based on a pilot study, the number of nestlings present in the nest box when the oldest reached 50 days old served as our measure of the number of fledglings. This allowed us to limit the event of birds fledging before we could obtain an accurate count. Nestling age was estimated using morphological indicators of development and compared to a photographic guide of barn owl nestling development provided by The Barn Owl Trust (BNOW Trust 2020).

Survival estimates were derived from the literature. Altwegg et al. (2007) estimated survival of a population of common barn owls in Switzerland from 1990-2004 using capture-mark-recapture techniques. They used a population matrix model to estimate the effects of changes in fitness components on stochastic population growth rate. Their analysis included three life stages: juveniles (0 -1 years old), yearling (1 -2 years old), and adults (2 - 3+ years old). They also used true survival rates rather than local survival rates, as emigration from the study area is reflected in local survival rates. The mean true survival rate for juveniles was 0.18, 0.543 for yearlings, and 0.768 for adults (Altwegg et al. 2007) (Table 1).

Life Table Analysis

We used a life table analysis to determine the finite rate of population growth, lambda, given our empirical estimates of reproductive success in Napa Valley and estimates of survival from the literature (Altwegg et al.

Table 1. Age, age class, survival rates, and description of survival rates derived from Altwegg et al. 2007.

Age (years)	Age class	Survival	Description
Juvenile (0)	0-1	0.180	Survival from fledging to one years old
Yearling (1)	1-2	0.543	Survival from one years old to two years old
Adult (2+)	2-3+	0.768	Survival from two years old to three-plus years old

Table 2. Life table scenarios of proportional changes in survival or reproductive success.

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Scenario	Juvenile Survival	Yearling Survival	Adult Survival	Female Offspring			
Original	Original	Original	Original	Original			
Juvenile Survival	±5%, 10%, 15%	Original	Original	Original			
Yearling Survival	Original	±5%, 10%, 15%	Original	Original			
Adult Survival	Original	Original	±5%, 10%, 15%	Original			
All Ages	±5%, 10%, 15%	±5%, 10%, 15%	±5%, 10%, 15%	±5%, 10%, 15%			
Reproductive Success	Original	Original	Original	±5%, 10%, 15%			

2007). We then performed a sensitivity analysis using manual proportional perturbation (Mills and Lindberg 2002), also known as conventional sensitivity analysis (Cross and Beissinger 2001), to explore under which scenarios lambda would fall below one, indicating a population in decline. With this approach, vital rates are manually altered by an amount considered relevant to the system and proposed question (Mills and Lindberg 2002). We changed each survival rate independently and collectively by the same percentage, increasing and decreasing the estimate or estimates by 5, 10, and 15% for each scenario. These percentages reflect realistic ranges of survival based on confidence intervals of survival estimates for male and female barn owls in Switzerland (Altwegg et al. 2007).

We ran a total of 31 scenarios (Table 2). Our first scenario included our empirical estimate of average reproductive success in 2021 and the literature-sourced estimates of survival (Altwegg et al. 2007). For scenarios two through seven, we increased and decreased juvenile survival by 5, 10, and 15% from its original literature-sourced estimate of 0.18 while holding yearling and adult survival rates constant at the literature-sourced estimates. We then repeated this process but for yearlings and then adults (scenarios eight through 19). We also ran scenarios in which we increased and decreased survival rates across all ages simultaneously, each by 5, 10 and 15% (scenarios 20 through 25). Lastly, we kept survival rates constant at their original values while increasing and decreasing reproductive success from our empirically measured estimate by 5, 10, and 15% (scenarios 26 through 31).

Altwegg et al. (2007) found that survival rates for males and females differed but followed the same patterns over time. They also found that all males in their study system bred by 2 years of age, whereas all females bred by 5 years of age. However, approximately 80% of males and approximately 70% of females bred by 1 year of age. There was no evidence of senescence as it relates to reproductive success. Results of Altwegg et al. (2007) indicated the sex ratio of nestlings in their study system was very close to 1:1 and did not vary significantly from 1996-2003. Therefore, they assumed an equal sex ratio over the rest of their study period. For the sake of simplicity, we kept the survival rates constant between sexes and for all ages of

adults. A life table uses the expected number of female offspring, so assuming the sex ratio in our study area is 1:1, we reduced the number of fledglings per year by half and held it constant for all ages, starting at 1 year of age.

RESULTS

In 2021, the range of fledglings per occupied nest was 0 to 7 (Figure 1) with an average of 4.02 ± 1.75 , 0.19 (mean \pm SD, SE). Approximately 42% of nests fledged the modal values of 4 or 5 offspring. Based on our empirical estimate of reproductive success and literature-sourced estimates of survival, the population appears to be growing (lambda = 1.05).

Adjusting survival rates in our sensitivity analysis (scenarios 2-25) resulted in lambdas ranging from 0.88 to 1.16, with the minimum and maximum values obtained when decreasing and increasing survival across all ages simultaneously by 15% (Figure 2). Across all 24 scenarios in which we adjusted survival, there were only five that resulted in the population declining. All these scenarios resulting in population decline occurred when reducing survival across all ages simultaneously (by 5, 10, or 15%; 3 scenarios) or when reducing adult survival independently (by 10 or 15%; 2 scenarios).

Finite population growth was highest when increasing survival across all ages by 10%, and 15%, with lambda equal to 1.13 and 1.16, respectively. An increase in survival across all ages by 5% resulted in population growth equal to increasing adult survival by 10% while keeping juvenile and yearling survival at their original literature-sourced values. When independently modifying age classes, a reduction in adult survival had the greatest effect on the population going into decline and resulted in the greatest range of values for lambda (Figure 2).

Reducing reproductive success (scenarios 26-31) had a very similar effect on lambda as reducing juvenile survival. When modifying reproductive success independent of survival, finite population growth ranged from 1.00 to 1.09 across scenarios. There were no scenarios in which lambda dropped below 1 when modifying reproductive success independent of survival. However, as was the case with a reduction in juvenile survival, lambda rounded to 1.00 when reproductive success was reduced by 15%, indicating no population growth or decline. When reproductive

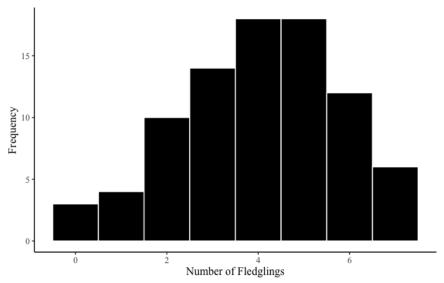


Figure 1. Frequency distribution of the number of fledglings produced by barn owls nesting in nest boxes in Napa Valley winegrape vineyards.

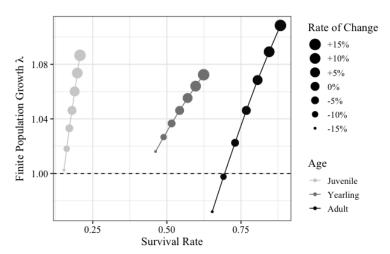


Figure 2. The relationship between survival rates for juvenile, yearling, and adult survival rates on finite population growth. Each point is increasing and decreasing in size with the proportional changes in survival.

success was decreased by 5% and 10%, lambda equaled 1.03 and 1.02, respectively. When we increased reproductive success by 5%, 10% and 15%, lambda equaled 1.06, 1.07, and 1.09, respectively.

DISCUSSION

Our modeling suggests that under most scenarios, deploying wooden nest boxes in winegrape vineyards in Napa Valley California should be able to support a viable local population of barn owls. Using our own empirically measured estimates of reproduction from the field coupled with published estimates of survival from long-term studies in Europe, our modeled estimate of lambda was 1.046. Manual perturbations of survival and reproduction suggested lambda remained greater than one even after reducing reproduction, juvenile survival, or yearling survival by even up to 15% while keeping the other

parameters at their original estimates. Lambda fell below 1.00 if adult survival was reduced by more than ~10% (Figure 2), or if survival was reduced for multiple age classes simultaneously.

These results are important for practical pestmanagement reasons. For nest boxes to be part of a successful long-term integrated pest management (IPM) plan, they should not be reliant on continual immigration of adult owls from other source populations to offset mortality (Johnson et al. 2018, Lindell et al. 2018). Numerous studies have documented that wooden nest boxes are attractive to nesting barn owls throughout the world (Hafidzi et al. 2003, Meyrom et al. 2009, Labuschagne et al. 2016, Bank et al. 2019, Huysman and Johnson 2021, Meaney et al. 2021). This study is among the first to suggest that reproduction in nest boxes is

good enough to avoid causing an "ecological trap" (Robertson and Hutto 2006) in which owls are attracted to nest sites in which they cannot offset their own mortality. However, a thorough examination of ecological traps would require additional information on habitat selection and reproduction in natural nest sites. In Hungary, Klein et al. (2007) found that owlets developing in nest boxes had significantly lower post-fledging survival than those hatched in church towers. Though they did not examine whether reproduction in nest boxes was sufficient to offset mortality, they cautioned that recently fledged owlets could be vulnerable when fledging from nest boxes. In addition, our results have several important caveats explained in more detail below, and more study is needed especially in other regions and years to better understand the durability and generalizability of these results. Our estimate of reproduction from Napa Valley, California $(4.02 \pm 0.19 \text{ young fledged per nest attempt})$ was lower than that reported from Israel (4.61 ± 0.15 , Charter et al. 2015) and from Hungary (4.45 ± 0.07 ; Bank et al. 2019) suggesting nest boxes may be even better for barn owls in those regions unless they also experience markedly lower survival rates. It should also be noted that juvenile dispersal for most barn owl populations appears to be substantial, with dispersed yearlings detected an average of 36 km away from their natal sites (Roulin 2020). Thus, even with sufficient local reproduction, recruitment of new adult barn owls into a farmland ecosystem is likely affected by their reproduction in the region overall, underscoring the importance of broad-scale conservation of owls.

Our findings also have ethical implications. Arguably, attracting sentient vertebrate animals into human-occupied habitats with nest boxes or feeders introduces a responsibility to ensure they are not lured into an environment unhealthy or evolutionarily maladaptive to them (Marris 2021). Indeed, Donaldson and Kymlicka (2011) articulated a relational animal rights theory that clarifies the unique ethical considerations of "liminal" animals that are wild but live within human settlements. Additional considerations may extend to wild species that benefit from or even become reliant on human activities, including commensal or synanthropic species (Johnston 2001, Cochrane 2013, Von Essen and Allen 2016). Our results suggest the use of nest boxes in Napa Valley winegrape vineyards can be a "win-win" situation that is mutually beneficial to both farmers and owls. In our view, this outcome elevates the practice from a simple utilization of a natural enemy for pest control to a reciprocal relationship between a landowner and wildlife on the land. Such recognition could help recast animal-provided ecosystem services from a transactional to a relational economy (Johnson et al. 2016), in this case, one in which farmers help owls and owls help farmers.

While we did not conduct a thorough sensitivity analysis, our modeling did make clear that the viability of the modeled population was most strongly affected by perturbations to adult survival (Figure 2). Therefore, environmental factors that could suppress adult survival may be especially important to investigate in this and other populations of barn owls. In particular, increased mortality from vehicle collisions, poisoning, or elevated predation risk could render some owl populations unable to sustain themselves even if reproduction remained high in wooden nest boxes. Road mortality can be significant for barn owls, who have the highest road mortality rates among raptors (Borda-de-Água et al. 2014), with estimates ranging from 0.07 owls/km/year (Illner 1992) to 2.61 owls/km/year (Boves and Belthoff 2012). Using an age-structured model and empirical evidence from southern Portugal, Borde-de-Agua et al. (2014) showed that even an annual road mortality rate of 5% would reduce barn owl populations to half of their original size. Arnold et al. (2019) studied barn owl road mortality in Idaho, and they offer some practical recommendations to help mitigate risks, including roadside vegetation management. The effect of proximity of nest boxes to roads on barn owl mortality, to our knowledge, has not been rigorously examined, and merits future study. Barn owls may also be exposed and potentially vulnerable to secondary poisoning from rodenticides (Hindmarch et al. 2017). Evidence of short-term direct lethal toxicity is limited (e.g., Gray et al. 1994, Newton et al. 1990), but sublethal effects could impact reproduction (Naim et al. 2011, Salim et al. 2014) or long-term survival (Huang et al. 2016). Great-horned owls (*Bubo virginianus*) are among the most important predators of American barn owls, and habitat conditions such as large trees, forests, or telephone poles that facilitate the use of farmland by horned owls could enhance predation risk for barn owls and should be considered when placing barn owl nest boxes

Our study has several important limitations, which we hope will prompt future work in our study region and elsewhere to help clarify the robustness and generalizability of these preliminary results. First, like many demographic models, our work relied on empirical estimates of reproduction and survival, and if these are unrepresentative, then our findings may not be reliable. Our survival estimates were from a long-term study in Europe because similar estimates are not yet available from our study region in Napa Valley. Second, our estimate of reproduction from Napa Valley was obtained using a single year of data (2021). Similar work we have cited here from Hungary (Bank et al. 2019) and Israel (Charter et al. 2015) involved multi-year datasets of 24 and 4 years, respectively. Rodent populations are notoriously variable from year to year, and barn owl fecundity and survival are strongly correlated with vole abundance (Taylor 2003), which in turn can link long-term owl population growth or decline to rodent abundance (Hone and Sibly 2002, Klok and Roos 2007). Whether the rate of reproduction we used in this study is high or low relative to other years in Napa Valley awaits analysis of long-term monitoring, which is ongoing. Third, our modeling approach was deterministic (static vital rates) rather than stochastic (variable vital rates), which results in generally more optimistic estimates of lambda. Thus, temporal variation in survival or reproduction, even if the long-term averages are precisely what we modeled, would likely yield lower estimates of population growth (Altwegg et al. 2007). Lastly, we made several assumptions in our demographic model that, if severely invalid, would affect results. We used a standard proportion perturbation, assuming vital rates may vary similarly, but some measures may be more dynamic than others. We assumed survival rates were similar between males and females. We also assumed that the age of first reproduction is at one year of age, and that each pair only produced a single brood each year. Our estimates of lambda could be biased if reproduction is delayed for some birds (biased high) or if a significant proportion of pairs raise a second brood (biased low).

In short, our simple modeling results provide a preliminary analysis indicating that the use of barn owl nest boxes in vineyards appears able to sustain a local population. This is an encouraging result because it suggests the practice of deploying nest boxes to aid in rodent pest removal can be mutually beneficial to owls and farmers. However, additional research is needed, especially in other areas and years to better understand how generalizable these initial findings are.

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