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Estimating the Number of Rodents Removed by Barn Owls Nesting in Boxes on Winegrape Vineyards

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ABSTRACT: To mitigate the economic and environmental costs of rodent pests, winegrape producers in Napa Valley, California, have installed nest boxes to attract barn owls to their properties, but their effectiveness to control rodent pests in vineyards has not yet been thoroughly tested. A rigorous estimate of the number of rodents that barn owls remove from the landscape is a necessary step, and this study aimed to produce estimates of rodent removal and prey species composition by using remote nest box cameras. Results indicate that each barn owl chick received 170.2 ± 8.92 rodents before dispersing from the nest box. Combined with the average number of chicks fledged (3.62 ± 1.40), this finding indicates adults deliver on average 616 rodents per nest box, with low and high estimates ranging from 358 to 899 rodents. With conservative assumptions of owl survival and consumption during the non-breeding season, we estimate a barn family could remove 3,466 rodents in a full year (estimates ranged from 1,821 to 7,563). An analysis linking videography to owl telemetry data suggested that 43% of rodents killed were taken from vineyard habitat, which nearly matches the availability of vineyard habitat around the monitored nest boxes (46%). In contrast, more prey were captured from riparian habitat and fewer from grassland habitat than expected given their availabilities. Our results suggest barn owl nest boxes could contribute meaningfully to integrated pest management. Future research should involve rodent surveys in vineyards without and without barn owl nest boxes.

KEY WORDS: barn owl, ecosystem services, gopher, integrated pest management, mice, nest box, pest control, rodent, top-down, *Tyto furcata*, vineyard, vole

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INTRODUCTION

Rodents are economically damaging to winegrapes (McGourty et al. 2011), and environmentally friendly pest management alternatives are urgently needed. Gebhardt et al. (2011) conducted a meta-analysis and Monte Carlo simulations involving dozens of papers to examine damage by vertebrates to 19 economically important California crops, concluding that the winegrape industry suffers the second greatest crop losses, at -7.2% yield per year. Lethal traps and chemical rodenticides can be effective for controlling rodents (Baldwin et al. 2014), but they are expensive and may have decreasing efficacy as rodents become resistant to certain compounds (Salmon and Lawrence 2006); further, some rodenticides can cause secondary poisoning to non-target wildlife species (Gabriel et al. 2018, Van den Brink et al. 2018), prompting increasing scrutiny from the public and heightened environmental regulation (Nagro 2019). Winegrape growers are further incentivized to adopt non-toxic pest management practices by way of winery tourism and consumer preference for environmentally friendly wine (Pomarici et al. 2015). California's famous Napa Valley wine industry is a valuable asset to the United States and California economy with over 300,000 individuals working in production, distribution, or sales of Napa wine and an estimated annual impact of \$13.3 billion (Stonebridge 2012). Using effective integrated pest management (IPM) solutions for rodents in winegrapes can help preserve ecosystem health and longevity while enabling producers to satisfy the environmental demands of consumers and maintain economic profitability for stakeholders.

One alternative rodent pest treatment is the provision-

ing of nest boxes to attract rodent-eating barn owls (*Tyto alba* and *T. furcata*; Labuschagne et al. 2016), which has been practiced in commodity and forage crops such as maize (Ojwang and Ouge 2003) and alfalfa (Motro 2011), as well as luxury crops such as date palms (Charter et al. 2010) and winegrape vineyards (Johnson et al. 2018). Several natural history attributes of barn owls, including their expansive global range, foraging behaviors, and affinity for open habitats, suggest they may be especially effective predators of rodents in agricultural lands (Marti et al. 1979, Meyrom et al. 2009). Barn owls readily occupy human-made structures, allowing them to persist in agricultural settings better than many other bird species (Kasprzykowski and Golawski 2006, Roulin 2020). With diets composed nearly entirely of rodent pests (Kross et al. 2016), barn owls are supremely adapted to be efficient and lethal hunters (Roulin 2020). Moreover, they have fast gut-passage times and incomplete digestion to minimize impacts on their flight from weight gained by ingested prey, and thus demand higher prey numbers than other similarly-sized predators (Roulin 2020). Barn owls are mostly non-territorial and, with sufficient numbers of nest boxes, one km² can accommodate several breeding pairs (Taylor 1994, Meyrom et al. 2009). These factors suggest barn owls may be able to remove large quantities of rodent prey from agricultural lands (Kross and Baldwin 2016, Roulin 2020), but this capacity has received relatively little attention for American barn owls (but see Kross and Baldwin 2016).

Rigorously evaluating the capacity for the deployment of barn owl nest boxes to contribute to an IPM demands a better understanding of not only how many rodents barn owls consume, but also the habitats from which the rodents

are removed. Barn owls are highly mobile predators with large home ranges (Roulin 2020), and their effect on pest management may be modest if most of their hunting and rodent removal occurs in uncultivated habitats rather than in agricultural fields. Castañeda et al. (in press) showed that barn owls nesting in Napa Valley nest boxes spend about a third of their hunting time in winegrape vineyards, but where they actually capture prey has not yet been confirmed. This study combines videography data on prey delivery rates to nest boxes with data on barn owl diets obtained via videography (St. George 2019) and pellet analysis (Kross et al. 2016) to derive estimates for the total number of rodents killed by adult barn owls for themselves and to provision their nestlings in a nest box. Coupling these figures with estimates of the number of surviving nestlings and their recruitment as adults, we provide one of the firsts estimations of the total number of rodents killed in a year by an American barn owl family. In addition, we combine videography data (St. George 2019) with GPS telemetry data (Castañeda et al. in press) to ascertain the habitats from which rodent prey brought to the nest box were removed.

METHODS

Study System

The Napa Valley is a 50-km long fertile valley between the Vaca and Mayacamas Mountains about 100 km north of San Francisco, California. The Mediterranean climate coupled with rich, diverse soils and microclimates make Napa Valley ideal for growing a variety of wine grapes (Napa Valley Vintners 2014). All nest boxes in the study area were located within vineyards or along their edges. Nest boxes were installed independently by vineyard managers and varied in age, size, structure, orientation, and building materials (see Wendt and Johnson 2017 for a complete description).

We used remote video cameras to document prey delivery at 12 nest boxes in 2017 and 17 in 2018. We selected nest boxes for camera installation to provide a range of habitat conditions and spread camera installations through the nesting season to capture within-season variation. To reduce spatial and temporal autocorrelation of data, we did not add cameras to nest boxes when more than two cameras had been installed within the previous week or if there was another nest box with a camera within approximately 1000 m, the radius within which barn owls spend most of their time hunting within (Castañeda et al. in press). Selection of nest boxes for nest cameras was opportunistic so long as they did not violate these space and time constraints. Risk of abandonment is high during egg incubation (Marti 1994), so to minimize abandonment while maximizing data collection, cameras were installed in nest boxes only after chicks hatched but before they were three weeks of age. The number of nests with cameras varied throughout the season owing to the variable timing of deployment and occasional nest failures.

Videography Installation and Processing

At each focal nest box, we installed a weatherproof, infrared security camera (ZOSI 720P IP66 CCTV Security Camera, ZOSI, Zhong Shan City, Guang Dong Province, China) inside the nest box facing the entrance hole. The

power and AV cables ran out the back of the nest box down to a power source (Interstate Deep Cycle Marine Battery: Group 27), and portable digital video recorder (DVR, 1CH MPEG-4 Mini DVR SD Card Video Recorder) at the base of the nest box pole (see St. George 2019 for details of camera assembly and installation). The DVR was programmed to record 15 min videos continuously starting at 30 min before sunset and ending 30 min after sunrise to ensure that all nightly deliveries were captured. We returned to each focal nest box once per week to check and replace batteries and secure digital (SD) cards as needed and to check the number of adults, chicks, and eggs in the boxes using a GoPro camera. The DVRs recorded video throughout the entirety of the nesting period until the chicks dispersed from the nest box, at which point the cameras and electronics were removed.

To reduce review time, videos were processed using the MotionMeerkat software (Weinstein 2015), which extracts individual frames where motion is detected, allowing the user to skip reviewing video with no motion in frame. Images returned in the MotionMeerkat output were reviewed to document when prey deliveries were made and to identify prey items based on a combination of the following: relative tail length, foot and claw size, overall color, head and mandible shape, ear shape and size, and eye size and orientation.

Videography Analysis and Estimate of Number of Rodents Delivered to Chicks

To accommodate for the change in number of chicks throughout the nesting period, we calculated the number of prey deliveries per chick-week, which also dampened extreme day-to-day fluctuations in deliveries and simplified analyses of overall prey delivery rates. This value was produced by first taking the number of deliveries per night divided by the number of chicks for that night to yield a delivery per chick-night value. Next, the delivery per chick-night values were summed for the calendar week, divided by the number of data nights in that week (accounting for occasional nights of DVR failures), and multiplied by seven to produce an estimate of deliveries per chick-week.

The number of weeks included in a box's estimate of nesting prey delivery varied due to the timing of camera deployment. For boxes missing data for week one and/or two due to the variable timing of deployment, we substituted the mean prey delivery per week estimate among all nest boxes with data for those respective weeks. This approach avoided biased-high prey delivery rate estimates for boxes with data only from the latter weeks. Of the 29 focal nest boxes, six boxes were missing data from week one, and two boxes were missing data from week one and week two.

For an overall estimate of the number of rodents delivered to chicks in a nest box over the breeding season, the number of rodent deliveries per chick was multiplied by the average number of chicks fledged in monitored nests (3.62 ± 1.40 ; see Results). This estimate is conservative because in many cases some chicks are fed and only survive a portion of the nesting stage. To obtain the estimate of the number of prey delivered per chick over a breeding season, we took a weighted average of the nightly

estimates of deliveries per chick using the number of deliveries for each respective night as the weight, and multiplied this value by 71 days (mean number of days until chick dispersal) to get an estimate for the entire nestling season for an individual nest box. Since not all prey items were verified as rodents, we then modified this value down slightly by multiplying by the percentage of rodents based on diet data (see below). We used the mean of these values for all nest boxes as our mid estimate, and the mean ± 1 standard deviation as our low and high estimates.

Estimate of Daily Number of Rodents Killed by Adult Barn Owls

To obtain an estimate for the daily number of rodents removed by adult barn owls for self-maintenance, we used published estimates of adult barn owl daily ingestion, rodent body mass, and barn owl prey composition. Specifically, we solved the following formula for the daily total number of all rodent prey nR :

$$\sum_{i=1}^k p_i \times m_i \times nR = mR$$

where p_i is the proportion (by abundance) of rodent species i in the diet, m_i is the estimated mass of rodent species i , nR is the total daily number of all rodent prey, and mR is the total daily mass of rodents consumed, for k rodent taxa. For this analysis, we focused on three rodent taxa [California voles (*Microtus californicus*), mice (*Peromyscus* sp. and *Mus musculus*), and Botta's pocket gophers (*Thomomys bottae*)] that have been shown to comprise nearly all prey in barn owl diets in California agricultural landscapes (Kross et al. 2016, St. George 2019). We used two published sources for the proportion of each rodent taxon in the diet (p_i): St. George (2019) reported proportional diet based on videography of nest boxes (see Methods for details), and Kross et al. (2016) reported diet based on dissection of pellets collected near nest boxes in agricultural areas in Sacramento Valley, California. California voles weigh 36 to 55 g (Verts and Carraway, 1998), mice weigh 15 to 52 g (lower range *M. musculus*, Huminski 1969; upper range *P. californicus*, Merritt 1978), and Botta's pocket gophers weigh 89 to 172 g (Vaughn 1967). We used the lower limit, mid-point, and upper limit of these weights to represent light, medium, and heavy individual prey items for each of the three focal rodent taxa (m_i). To solve the formula for nR we first converted published estimates of daily total mass consumed (Bunn et al. 1982) to daily total mass of rodents consumed (mR) by multiplying a low, middle, and high point estimate of daily total ingestion (100 g, 125 g, and 150 g, respectively; from Bunn et al. 1982) by published estimates of total percentage of diet comprised of our three focal rodent taxa (89.1% and 92.0% from St. George 2019 and Kross et al. 2016, respectively). See Tables 1 and 2 for the values of p_i , m_i , and mR used in our analysis to calculate estimates of the total daily number of rodents consumed (nR).

Next, we multiplied estimates of nR by the number of adults and number of days in a year. We assumed a stable population of barn owls, wherein two adults survive a single year (365 days) and are replaced by two hatch-year

birds recruiting as adults. Adult lifespan comprises a 103-day breeding season (32 days incubation + 71 days chick-rearing) and a 262-day non-breeding season. This approach is very conservative because in most years some adults will raise a second brood; our estimates of consumption assume only a single brood. Chicks of first broods nearly always fledge by early June (unpubl. data), so we conservatively estimated the number of days for hatch-year birds as 200 (15 June through December 31), which effectively assumes the nestlings in excess of the two that recruit into adults die immediately after leaving the nest.

Estimate of Total Rodent Removal by a Family of Barn Owls in a Year

Finally, we obtained estimates for the total number of rodents killed by a family of barn owls in a year by summing our low, middle, and high estimates of the number of rodents delivered to chicks in a nest box ($nR_{nestlings}$), the number killed by two surviving hatch-year birds ($nR_{hatch-years}$), and the number killed by two adults in a year (nR_{adults}). Since these low, middle, and high estimates each depended on the proportional diet of prey species (p_i), and we used two sources of diet information (St. George 2019 and Kross et al. 2016), our analysis yielded a total of six estimates for the total number of rodents killed by a family of barn owls in a year.

GPS Telemetry of Adult Owls

During the 2017 and 2018 breeding season, female nesting barn owls were fitted with Uria 300 Global Positioning System (GPS) transmitters (Ecotone Telemetry, Gdynia, Poland) as part of an ongoing study of hunting habitat selection (Huysman 2019, Castañeda et al. in press). GPS tags were deployed on females known to have chicks due to sensitivity to disturbance in earlier stages of nesting (i.e., laying and incubation). Barn owl sex was determined by the presence of a brood patch. Birds were selected if their oldest young were approximately 10 to 15 days old at the beginning of tag deployment (aging guide from Barn Owl Trust 2015). This stage was selected because it is after brooding, when females are actively hunting to provision the chicks, but when chicks are still young enough to increase likelihood the tagged female would still be using the nest box for diurnal roosting three to eight days later. This allowed for tag retrieval after the battery on the tag had drained and was no longer collecting locations.

Barn owls were captured in their nest box and fitted with a 13.5 g GPS tag that did not exceed 3% of the owls' mass. Transmitters were attached via a small backpack harness constructed of Teflon ribbon that was designed not to impede the bird's natural mobility (Humphrey and Avery 2014). After the transmitter was attached, the owl was placed back in the nest box and the entrance blocked for 10 minutes to reduce risk of the owl flushing from the box. Total handling time did not exceed 20 minutes per bird. Telemetry tracking began the night after attaching the transmitter, 8-12 hours after handling (see Castañeda et al. in press for full details). Only females were tagged because they roost diurnally in the nest box for several weeks after the chicks hatch, increasing the likelihood of retrieving the transmitter at a later time. Whether male and female barn

owls in this system show different hunting habitat selection remains unresolved and awaits future research. Each telemetry tag was set to record a location once per minute to provide fine temporal scale data on hunting habitat use. All monitoring and handling was approved by Humboldt State University's Institutional Animal Care and Use Committee (IACUC No.15/16.W.43-A).

Ascertaining the Habitats from which Prey Deliveries were Captured

We combined the telemetry data and nest videography data to ascertain the habitats from which prey delivered to the nest box were captured. Specifically, there were five barn owls fitted with a GPS tag whose nest boxes were simultaneously outfitted with a remote video camera. For these cases, we noted the timestamp (see Figure 1) and rodent species of each prey delivery by a female owl (sex determined by coloration and/or observation of the telemetry tag). After capturing prey for nestlings, barn owls make immediate and direct flights back to their nesting sites (Roulin 2020). Therefore, we examined GPS locations associated with a tagged female for ~15 minutes preceding each timestamped prey delivery, backtracking through the data until we found the location from which she made an immediate and direct return flight back to the nest box; this was taken to be the location of prey capture. Data points were only included for analysis if a clear capture location was discernible. For example, since barn owls usually hunt by slow flight (Roulin 2020), if a tagged owl was stationary for a long period prior to a direct flight back to the nest, we omitted this datapoint due to uncertainty from where the prey item was removed. Further, when untagged males delivered prey items (confirmed by cross-referencing female GPS location at time of delivery), no location of prey removal was discerned.



Figure 1. Example individual frame of remote infrared video deployed showing prey delivery (a California vole) by a barn owl to a wooden nest box in Napa Valley, California, 2017.

Each location of prey capture was ascribed a habitat using a GIS vegetation type map created with high-resolution (<1 m) National Agriculture Imagery Data provided by the United States Department of Agriculture (2018) and fine-scale elevation LiDAR (Light Detection and Ranging) data from the National Center for Airborne Laser Mapping (NCALM). Vegetation and habitat were classified into seven dominant categories: water/wetland, urban, vineyard, grassland, oak savanna, mixed-forest, and riparian (see Castañeda et al. in press for detailed description of each habitat category). Non-vineyard row crops were virtually absent (<0.5% of the landscape) and were small plots adjacent to urban areas with which they were lumped. Managed pastures (<2%) were combined with grasslands.

We used a chi-squared test of independence to test whether different rodent taxa were obtained disproportionately from certain habitat categories. Due to a limited sample size of known prey capture locations (see Results), we combined locations from riparian and forest habitats (i.e., wooded habitats), and we combined locations from oak savanna and grassland (i.e., mostly open habitats); we had no prey capture locations from water/wetland or urban categories. We also combined smaller rodent prey (voles and mice) into a single category separate from gophers, yielding a statistical analysis of two rodent taxa categories \times three habitat categories. We used a chi-squared goodness of fit test to determine whether prey were captured (combining all rodent taxa) from habitat categories out of proportion to the availability of those habitat categories around a nest box. The availability of habitats was obtained in the GIS as the total m² of each habitat category within a 2.74 km radius of each of the five nest boxes fitted with both a video camera and used by a GPS-tagged owl; 2.74 km is the mean maximum distance moved by GPS-tracked barn owls in this population (Huysman 2019).

RESULTS

In total 29 nest boxes were video-monitored in 2017-2018, with 1,781 nights of videography, 20,487 total hours of video, and 11,404 observed prey deliveries. As reported in St. George (2019), of all prey deliveries, 92.0% were identifiable, with voles being the most common prey items (49.6%), followed by mice (22.0%), and gophers (17.5%) which combined to 89.1% of all items (Table 1). Only 3% of identified prey items were identified as something other than these three taxa, and included frogs, insects, rats, young squirrels, and young rabbits. Videography analysis indicated an individual chick who is in the nest box for 10 weeks received on average 191 ± 10.01 prey items, of which 89.1% were one of the three focal rodent taxa (i.e., 170.2 ± 8.92 rodents per nestling). In this study, the mean number of nestlings raised to fledging was 3.62 ± 1.40 .

Combining proportional diet data, estimates of daily mass of rodents ingested by barn owls, and the reported mass of individual voles, mice, and gophers (from Table 1), we used the summation formula (see Methods) to estimate the daily number of rodents consumed by an adult barn owl. Estimates ranged from 1.295 to 3.639 based on diet information from this study (St. George 2019), which included comparatively more voles and gopher prey, or

Table 1. Rodent species proportions (pi) and mass estimates (mi) for rodents in American barn owl diets in California agriculture.

Species <i>i</i>	<i>p_i</i>		<i>m_i</i> (g)		
	St. George (2019)	Kross et al. (2016)	Light	Medium	Heavy
Mouse	0.220	0.597	15 ¹	33.5	52
Vole	0.496	0.271	36 ²	45.5	55
Gopher	0.175	0.053	89 ³	130.5	172
Total	0.891	0.921	-	-	-

¹ Lower range for *Mus musculus* (Huminski 1969); upper range for *Peromyscus californicus* (Merritt 1978)

² From Verts and Carraway (1998)

³ From (Vaughn 1967)

Table 2. Estimates of daily mass of rodents (mR) and daily number of rodents (nR) consumed by adult barn owls in Napa vineyards derived from proportional diet composition provided in St. George (2019) and Kross et al. (2016).

Estimate	St. George (2019)		Kross et al. (2016)	
	<i>mR</i> (g) ¹	daily <i>nR</i>	<i>mR</i> (g)	daily <i>nR</i>
Low	89.10	1.295 ²	92.10	1.673 ²
Mid	111.38	2.110 ³	115.13	2.933 ³
High	133.65	3.639 ⁴	138.15	5.897 ⁴

¹ Estimated as the total proportion of mice, voles, and gophers in the diet from St. George (2019) and Kross et al. 2016 (from Table 1) × three estimates of daily mass ingestions for American barn owls from Bunn et al. (1983): 100 g (low), 125 g (mid), 150 g (high)

² Calculated as $mR(\text{low}) / (p_{\text{mouse}} \cdot m_{\text{mouse}}(\text{heavy}) + p_{\text{vole}} \cdot m_{\text{vole}}(\text{heavy}) + p_{\text{gopher}} \cdot m_{\text{gopher}}(\text{heavy}))$

³ Calculated as $mR(\text{mid}) / (p_{\text{mouse}} \cdot m_{\text{mouse}}(\text{medium}) + p_{\text{vole}} \cdot m_{\text{vole}}(\text{medium}) + p_{\text{gopher}} \cdot m_{\text{gopher}}(\text{medium}))$

⁴ Calculated as $mR(\text{high}) / (p_{\text{mouse}} \cdot m_{\text{mouse}}(\text{light}) + p_{\text{vole}} \cdot m_{\text{vole}}(\text{light}) + p_{\text{gopher}} \cdot m_{\text{gopher}}(\text{light}))$

Table 3. Estimates of total number of rodent prey (nR) for a family of barn owls over one year, comprised of estimates of rodent prey delivered to nestlings in the nest box (nRnestlings), consumed by nestlings surviving as hatch-year adults (nR_{hatch-years}), and parental adults (nR_{adults}).

	<i>nR</i> per Nestling	# Nestlings	St. George (2019)				Kross et al. (2016)		
			<i>nR</i> _{nestlings} ¹	<i>nR</i> _{hatch-years} ²	<i>nR</i> _{adults} ³	<i>nR</i> _{total} ⁴	<i>nR</i> _{hatch-years} ²	<i>nR</i> _{adults} ³	<i>nR</i> _{total} ⁴
Low	161.3	2.22	358	518	945	1821	669	1221	2248
Mid	170.2	3.62	616	844	1541	3001	1173	2141	3931
High	179.1	5.02	899	1455	2656	5011	2359	4305	7563

¹ Estimated as *nR* per nestling × the number of nestlings

² Estimated as 2 nestlings surviving as hatch-year adults and consuming adult daily *nR* (from Table 2) for 200 days (from 15 June to 31 Dec)

³ Estimated as 2 adults consuming adult daily *nR* (from Table 2) for 365 days

⁴ Estimated as *nR*_{nestlings} + *nR*_{hatch-years} + *nR*_{adults}

1.674 to 5.897 based on diet information from Kross et al. (2016), who reported a higher proportion of small mice as prey (Table 2).

The total number of rodents captured to deliver to nestlings (*nR*_{nestlings}) was the product of rodents per chick and the number of chicks raised to fledging, and was estimated at 691 (with low and high estimates of 402 and 1,010, respectively, Table 3). The total number of rodents consumed by two hatch-year owls after dispersing (*nR*_{hatch-years}) was estimated to be 844 and 1,173 depending on proportional diet (St. George 2019 and Kross et al. 2016, respectively), with low and high estimates ranging from 518 to 2,359 (Table 3). The total number of rodents consumed by two adult owls (*nR*_{adults}) was estimated to be 1,541 and 2,141 depending on proportional diet (St. George 2019 and Kross et al. 2016, respectively), with low and high estimates ranging from 945 to 4,305 (Table 3). Together, the number of rodents removed by an entire family over a year (*nR*_{nestlings} + *nR*_{hatch-years} + *nR*_{adults}) was estimated to be 3,001 and 3,931 depending on proportional diet (St. George 2019 and Kross et al. 2016, respectively). The average of these two mid-estimates was 3,466 and is

our current best estimate for the number of rodents removed per barn owl family in this system per year. Low and high estimates ranged from 1,821 to 7,563 (Table 3).

A total of 136 prey deliveries was recorded by videography at the five nest boxes while the female of the box was simultaneously GPS-tracked. Of these deliveries, 44 were by the female and included voles (32%), mice (9%), and gophers (57%). Back-tracking from the delivery timestamp to locate the habitat from which the prey item was captured revealed that prey items were taken from vineyard (43%), oak savanna (25%), and mixed forest (20%), with fewer prey taken from riparian (11%) and none from the other habitats (grassland, urban, water/wetland). The proportion of different rodent taxa delivered did not differ significantly among habitats from which they were captured ($\chi^2 = 2.88$, *df* = 2, *P* = 0.24). The proportion of rodents delivered that were from vineyard habitat (43%) closely matched the availability of vineyard habitat around the nest boxes (46%; Figure 2). In contrast, more prey were killed from riparian habitat and fewer from grassland habitat than expected given their availabilities ($\chi^2 = 55.0$, *df* = 4, *P* < 0.01).



Figure 2. Distribution of habitats from which rodent prey were captured by barn owls compared to the availability of those habitats around barn owl nest boxes. Data were obtained using infrared videography coupled with GPS tracking of tagged owls and comprised 44 prey deliveries by four female barn owls nesting in wooden nest boxes in Napa Valley, California, 2017-2018.

DISCUSSION

This study is one of the first to estimate the total number of rodents removed by a family of American barn owls nesting in an agricultural setting. In our Napa Valley vineyard ecosystem, we estimated that 3,466 rodents are removed each year per barn owl family, though this estimate ranged widely from 1,821 to 7,563, depending mainly on the proportion and weights of different rodent species in the owls' diet (Table 3). If barn owls eat more small rodent prey, for example by taking more mice and fewer gophers, or by eating mostly juvenile and subadult rodents, the total number of rodents consumed will be toward our higher estimates. Ingestion of juveniles is especially likely for gophers, whose upper limit body masses may be inaccessible for most barn owls. Indeed, Moore et al. (1998) found that barn owls took juvenile gophers especially in spring and summer in an agricultural landscape comprised mainly of vineyards, orchards, and alfalfa. Likewise, a diet of proportionally larger prey such as gophers will lead to lower estimates of the total number of rodents consumed annually. We made several conservative assumptions in our estimates: we assumed adults survive only one year, we assume only two nestlings survive fledging as hatch-year birds to recruit as adults, we ignored rodents killed for chicks that die early in the nestling period, and we assume no increased adult ingestion during courtship or egg-formation. Thus, our estimates of rodent removal are likely less than the actual number removed and could be refined as more empirical data become available to improve our calculations.

With sufficient nest boxes, barn owls can nest in high densities in agricultural settings (Meyrom et al. 2009, Wendt and Johnson 2017), and our data indicate that the use of barn owl nest boxes can lead to substantial rodent removal from winegrape vineyards. For example, one 80-ha (200 acre) vineyard in our study system had 27 nest boxes, of which at least 20 were typically occupied by breeding barn owls (Huysman 2019). Based on our estimates, annual rodent removal by owls in these boxes is

estimated to be over 69,000 rodents. Importantly, our study is the first to investigate the source of rodents delivered by barn owls to their nest boxes in an agricultural setting, offering vital information about the potential for owls to remove rodents from cropland habitat specifically. Although our sample size of owls that were simultaneously GPS tracked and video-monitored was small (five females tending chicks in five nest boxes), we found that 43% of all rodents taken by females were captured from vineyard habitat (Figure 2). This suggests that 29,670 rodents could be removed annually from the 80-ha vineyard mentioned above. Additional telemetry data, including of male barn owls, linked to simultaneous videography of nest deliveries would help establish how robust this finding is.

While our data are suggestive, whether the removal of rodents by a barn owl family is sufficient to meaningfully reduce rodent numbers in vineyards is uncertain. Barn owl predation on rodents could be the proverbial “drop in the bucket” if rodent densities are extremely high in winegrape vineyards. Alternatively, removal of rodents by barn owl predation could be offset by density dependent increases in rodent reproduction or reductions in other forms of mortality (e.g., starvation), such that the long-term average rodent population could remain similar with and without the top-down effect of barn owl predation (*sensu* Ford and Goheen 2015). Heske (1987) provided estimates of vole density in a high vole year in a grassland about 50 km from our study area, ranging 685-1,077 voles per ha. If vineyard habitat supports similar numbers, then the example 80-ha vineyard mentioned above could house up to 86,000 voles, of which we estimate 34.5% could be removed by barn owls each year, which in theory could be sufficient for top-down regulation of some prey species (Borer et al. 2005). Kross and Baldwin (2016) modeled the removal of rodents by barn owls against published estimates of rodent productivity, concluding that, at least for gophers, barn owl predation could offset annual productivity of gophers in average years, but not at peak gopher densities and reproductive rates. These calculations are suggestive, but confirming or

refuting whether removal of rodents by barn owls is sufficient to reduce total rodent numbers awaits surveying rodent numbers on vineyards with and without barn owl nest boxes, ideally with experimental installation of nest boxes in a before-after-control-impact (BACI) experiment (Johnson et al. 2018). A recent BACI experiment in alfalfa and fruit-tree crops in Spain (Luna et al. 2020) showed reduced numbers of voles, based on indirect measures of burrows and tunnels, in experimental areas relative to control sites after the addition of barn owl nest boxes.

Kross and Baldwin (2016) also used published estimates of barn owl diet, prey delivery, owl energetic requirements, and rodent body mass to estimate the number of rodents removed annually by a family of barn owls. Though their mathematical methods differed somewhat from ours, and they used different data for some key assumptions, they concluded that a barn owl family would remove 2,961 prey items (~28% gophers, 20% voles, and 52% other prey comprised mostly of mice). It is encouraging that their figure is similar to our estimate, especially since their use of a comparatively higher proportional ingestion of gophers would lead to our lower estimates of annual removal. In fact, substituting their proportion of gophers, mice, and voles (p_i) into our summation formula, we arrive at a mid-estimate of 2,856 rodents removed per year, a figure only 3.5% below their estimate, despite several remaining differences in their and our assumptions, calculation methods, and selection of empirical data. In our view, additional empirical data on barn owl diet in winegrape vineyards throughout the year is very valuable, enabling the calculations to accommodate variation in prey consumption through the annual cycle, as done by Kross and Baldwin (2016). In addition, both Kross and Baldwin (2016) and our own calculations rely heavily on the estimated daily energetic requirement of barn owls. This parameter needs to be better assessed empirically; we used 100, 125, and 150 g per day (per Bunn et al. 1982) for our low, mid and high estimates, respectively. Collaboration with raptor rehabilitation centers, which often feed adult and juvenile barn owls for extended periods, may provide useful data. Roulin (2020) used simple assumptions and empirical data to estimate the total number of rodents consumed by a family of European barn owls (*T. alba*), arriving at a figure of 5,000-7,000 rodents per year. European barn owls are smaller than American barn owls (*T. furcata*), with correspondingly lower energetic requirements (~75 g of rodents per day), but they also consume smaller prey (Roulin 2020 used 20-25 g for voles), which increases the estimate of the total number of rodents consumed.

In conclusion, the data and analyses presented here suggest a family of American barn owls nesting in winegrape vineyards can remove large numbers of rodents, and that many of these prey are captured directly from within vineyard habitat. Our results confirm and refine previously published estimates in other settings, and they highlight the need to continue examining barn owl diets and daily energetic requirements to further refine our estimates. Rodent surveys and BACI experiments are the next steps to examine the impact of barn owls on rodent pests in vineyards (Johnson et al. 2018). It is also vital to carefully examine whether barn owls can successfully replace them

selves demographically while nesting in boxes imbedded within vineyard ecosystems, to ensure the boxes are not ecological traps (Robertson and Hutto 2006). This work will require investigating reproduction and survival as well as possible lethal or sub-lethal effects of rodenticides that nest boxes are intended to partially or entirely replace.

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