Agriculture, Ecosystems and Environment 223 (2016) 167–174

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Agricultural land use, barn owl diet, and vertebrate pest control implications

Sara M. Kross*, Ryan P. Bourbour, Breanna L. Martinico

Department of Wildlife, Fish & Conservation Biology, University of California, Davis, One Shields Avenue, Davis, CA 95616, United States

ARTICLE INFO

Article history:
Received 27 October 2015
Received in revised form 18 February 2016
Accepted 1 March 2016
Available online xxx

Keywords:
Tyto alba
Pest-control
Land use change
Raptor
Ecosystem services

ABSTRACT

Barn owls (*Tyto alba*) are the most widespread raptor species on Earth, and because they are thought to provide natural vertebrate pest control services, farmers in some agricultural regions have encouraged barn owls to breed and hunt on their farms by installing artificial nest boxes. However, barn owl populations are declining in some agricultural regions, which may be a result of changes in land use and agricultural intensification. We studied barn owl diet and nest box occupancy in an intensive agricultural landscape in the Central Valley of California to measure whether agricultural land use affected barn owl diet. We collected 415 viable pellets from 25 active nest boxes over two breeding seasons and compared these results with agricultural land use types within a 1-km radius of each nest. Mice (*Mus musculus* and *Reithrodontomys megalotis*) were the most numerous prey and the most important by biomass, but their importance in barn owl diet declined with higher proportions of perennial crops in the surrounding landscape. California voles (*Microtus californicus*) were less important by number, but still represented a significant proportion of the biomass consumed by owls in our study area. Pocket gophers (*Thomomys* spp.) were consumed less often but were also an important source of biomass. Furthermore, barn owls nesting in areas with higher proportions of perennial crops consumed more gophers and fewer voles, many of which were juveniles, suggesting that gophers are more abundant and a more important part of barn owl diet in perennial crop areas. Over 99.5% of prey items in barn owl diet were agricultural pests and owls are therefore likely to provide valuable pest control services for growers in our area, although the species consumed may vary with crop types with implications for pest-control.

1. Introduction

Globally, agricultural intensification produces higher yields, but is also associated with a loss of natural habitat, expansion of field sizes, simplification of the overall landscape, loss of crop diversity across large areas, and increased chemical inputs (Foley et al., 2005). Agricultural expansion and intensification has been linked with biodiversity losses worldwide and is an especially significant threat to birds (Green et al., 2005). Some avian species, however, are capable of thriving in agricultural systems. Barn owls (*Tyto alba*), the most widespread owl species on Earth (Taylor, 1994), are likely to be one such species. Barn owls display an astonishing breadth of habitat associations and are capable of nesting in buildings and other areas where human and agricultural activity is high (Marti et al., 2005). Raptors, including barn owls, are not only ecologically important as top predators (Sergio et al., 2006), but may also provide farmers with a natural source of pest control by consuming many vertebrate pest species that cause damage to crops and reduce yields (Smal et al., 1990; Hafidzi and Mohd, 2003; Whelan et al., 2015).

By provisioning nest boxes in areas that have lost significant wildlife habitat due to human activity, barn owl populations can persist where there is abundant prey, yet limited natural nest sites (Taylor, 1994). There is some concern that increasingly industrialized and intensive agricultural practices may be causing regional declines of barn owls in farming areas where they were once abundant (Colvin, 1985; Taylor, 1994; Newton, 2004). Declines in barn owl populations have also been attributed to increased vehicle-collisions due to more roads with higher volumes of traffic (Borda-de-Agua et al., 2014).

There has been contrasting evidence from studies examining the effects of agricultural land use change on barn owl populations. For example, barn owl breeding success was not linked with agricultural land use in England (Meek et al., 2009) or Switzerland (Frey et al., 2011), whereas Leech et al. (2009) found that across the United Kingdom, barn owls breeding in semi-natural habitat and extensive grazing systems had higher breeding success compared

* Corresponding author.
E-mail address: Saramaekross@gmail.com (S.M. Kross).

http://dx.doi.org/10.1016/j.agee.2016.03.002
0167-8809/

to those nesting in arable fields. In Israel, nest box occupancy was higher when boxes were surrounded by a higher proportion of arable fields compared with sites with more natural fields, villages or date plantations, but these landscape factors did not affect breeding success (Charter et al., 2012). To our knowledge, no studies thus far have examined differences between the diets of owls nesting in different types of intensive agriculture in the same region.

Barn owls are natural predators of many rodents, especially species considered agricultural pests (Marti et al., 2005). Barn owls therefore have strong potential to provide farmers with economically valuable vertebrate-pest control services (Whelan et al., 2015). Barn owl populations are relatively cheap to establish: requiring the initial construction and installation of nest boxes and a low annual maintenance. Rodenticides, on the other hand, may have decreasing efficacy as rodents become resistant to certain compounds (Salmon and Lawrence, 2006; Horak et al., 2015), and are likely to cause secondary poisoning to non-target wildlife species (e.g. Erickson and Urban, 2004; Elliott et al., 2014; Thomas et al., 2011). Trapping to control rodents requires continued effort and associated staffing costs in addition to the high initial inputs for purchasing traps.

Despite the widespread use of artificial nest boxes to attract barn owls into agricultural areas for pest control, very few field studies have been able to correlate these actions with long-term or economically viable control of rodent populations (e.g. Smal et al.,

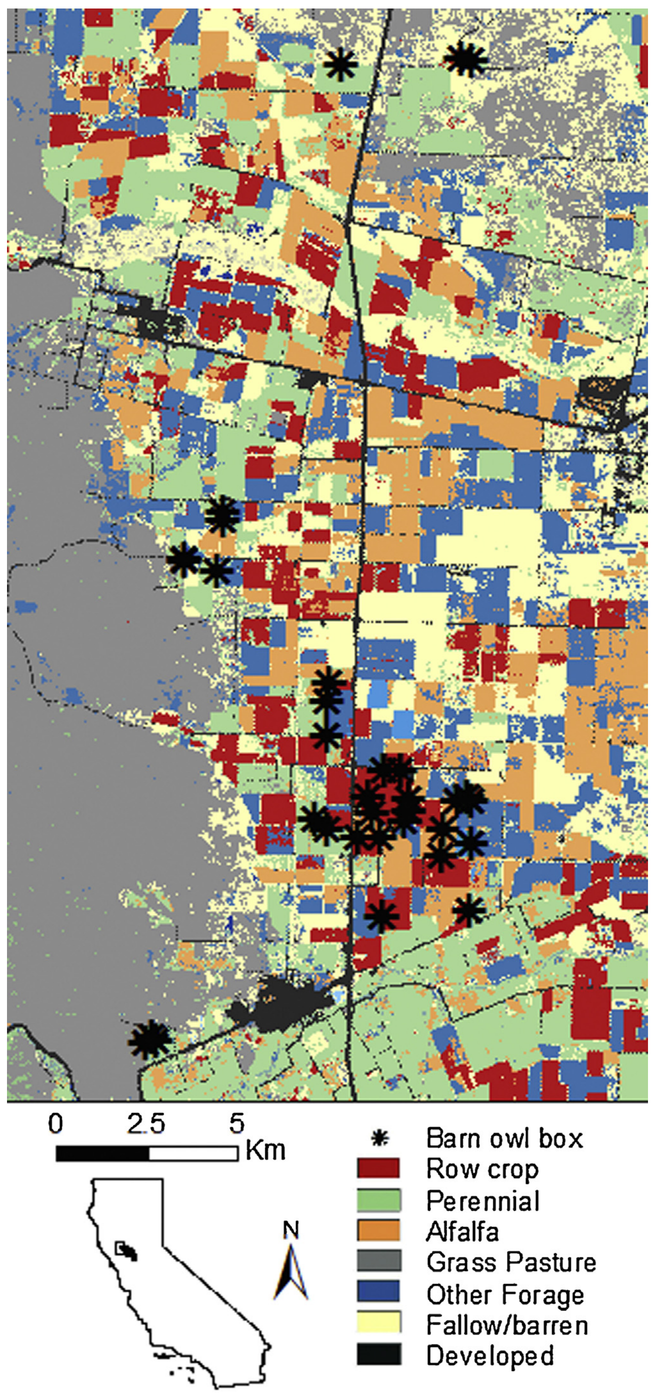

Fig. 1. Map of our study area indicating locations of active barn owl boxes and crop types used for land-use analysis.

1990; Kan et al., 2014). Although the presence of barn owls has been shown to reduce nocturnal rodent activity (Abramsky et al., 1996), it is not fully understood whether a significant reduction in rodent populations is achieved (Van Vuren et al., 1998; Marti et al., 2005). The first step in understanding whether barn owls are able to significantly reduce agricultural pest populations is to describe their diet within the crop types in which farmers are attempting to enhance biological pest control. Here, we investigated the diets of barn owls nesting along a gradient of different high-intensity crops in an intensive agricultural region in California's Central Valley to determine whether owls nesting in areas with more perennial crops differed in their diet from owls nesting in areas with a greater proportion of row or forage crops.

2. Methods

2.1. Study area

In California's Central Valley, one of the world's most productive farming regions, natural habitats were converted to a large diversity of different crop types over the past 200 years, causing the loss of over 90% of the state's wetlands and riparian forests (Dahl, 1990). More recently, market forces have driven the conversion of fields previously growing a rotation of pasture, row, and forage crops into higher value perennial crops, such as vineyards and orchards (Mehta et al., 2013), a trend that has raised concerns over loss of crop diversity and widespread landscape simplification.

Our study area was located within Yolo County, in the Southwestern part of the Sacramento Valley and roughly 120 km Northeast of San Francisco (Fig. 1). Agriculture accounts for roughly 95% of the approximately 1-million acre-feet of the county's water demand (Jackson et al., 2012), and covers over 80% of the county's land area (FMMP, 2010). The dominant crops are alfalfa, tomatoes, wheat/grain, almonds, walnuts, grapes, and rice (Jackson et al., 2012). Westward from the valley floor, cattle grazing occurs in the upland grasslands and oak savannahs (Jackson et al., 2012). Hundreds of owl nest boxes have been installed throughout the agricultural landscape, making this an ideal area to study local barn owl diet.

Owners from three different farm operations with previously erected barn owl nest boxes permitted us to access their private property for the purpose of this study. Barn owl nest boxes were built out of either wood, PVC piping, metal drums, or polyurethane and installed on either a single metal pole, power pole, or trunk of a tree. Nest boxes were mostly evenly spaced along the perimeter of crop fields, with some dispersed throughout a larger area. Growers had installed nest boxes primarily to attract barn owls with the desire to utilize the owls as a natural control for rodent pests; primarily pocket gophers (*Thomomys* spp.) and voles (*Microtus* spp.). Pocket gophers are consistently ranked as one of the most damaging pests of agricultural crops across California because burrows and underground foraging causes loss of vigor or plant death, and chewing can damage expensive buried drip irrigation lines (Baldwin et al., 2011). Voles directly consume vegetation and can damage up to 11% of alfalfa crops in some areas, but are often considered less serious pests than gophers (Baldwin et al., 2011).

2.2. Landscape analysis

In order to determine land cover, we obtained a 2014Crop Data Layer (CDL) from CropScape (USDA-NASS, 2014), a national database that classifies land cover and crop types using remote-sensing for the entire United States (Han et al., 2012). We used ArcGIS (ESRI, 2011) to map the locations of all active barn owl boxes and established a buffer with a radius of 1 km around each nest box (Hindmarch et al., 2014) because it is estimated that barn owls have a home range size of roughly 3 km^2 during the breeding season (Taylor, 1994). We condensed the crop-specific data within CropScape to broad land-cover categories based on crop management and plant types and calculated the proportion of land cover type within each buffer. Our final land use types included eight categories: (1) Alfalfa; (2) other forage (winter wheat, triticale, clover, hay); (3) row crops (tomato, corn, squash, peppers); (4) perennial crops (vineyards and orchards including walnuts, almonds, pistachios, stonefruit, pears, cherries, olives, and citrus); (5) rice; (6) pasture/grassland; (7) fallow/barren; and (8) developed.

2.3. Pellet analysis

Barn owls, like many other owls, swallow prey whole and later regurgitate the indigestible material, including fur and bones, as a pellet (Taylor, 1994). During the breeding season, pellets are often regurgitated near the nest box, especially by adults and older chicks. Pellets can be dissected to provide a reliable indicator of diet (Taylor, 1994). Barn owls produce 1–2 pellets per day (Marti, 1973), and because we weren't able to collect pellets from inside nest boxes, our pellets represent a subsample of the diet of barn owls, and each pellet represents at least half of the daily diet of each owl at the nest.

We collected a total of 434 barn owl pellets under 33 different nest boxes at three different farm properties in Yolo County. Only nests sites where $\geq$5 pellets were found were considered in our analysis, resulting in 415 pellets from 25 nest boxes being analyzed. Pellets were collected during the breeding season in 2014 and 2015, and boxes were visited once between 1st April and 31st July each season. Pellets were only collected within 1 meter of nest boxes, with the majority of pellets concentrated directly under the nest box opening. To avoid counting pellets from previous seasons, only whole intact pellets were dissected and analyzed. Because barn owl pellets readily break down once wet, pellets that appeared weathered or fragmented were discarded.

In 2015, to confirm that the pellets collected from under nest boxes were from barn owls, we used a Sony HD digital camera recorder (HDR-AS100 V) attached to an extendable pole to live stream video to a portable tablet/smart phone at 34 nest boxes. Active nests were those that had owl eggs, nestlings, incubating adults, or roosting adults.

We dissected barn owl pellets individually by hand, and used dissection kits and dissecting lenses as needed. After we carefully separated bones and fur, we identified the species composition of each pellet. Due to the degraded nature of diagnostic characteristics, such as teeth and mandibles, we did not distinguish between house mouse (*Mus musculus*) and Western harvest mouse (*Reithrodontomys megalotis*). Instead, we used a single category of "mouse". In addition to vertebrate prey, we also recorded the presence of invertebrates, which can be detected in owl pellets through the presence of exoskeletons (Marti et al., 2007). The only invertebrates we detected in the pellets were field crickets (*Gryllus* spp.) and we quantified the number of field crickets in each pellet by counting each identifiable head.

After prey species were identified, we counted the minimum number of individual prey contained in each pellet (Marti et al., 2007). For mammalian prey, we relied mainly on skulls and dentition for identification, and used limb bones and pelvic girdles when cranial bones were absent. Whenever possible, we quantified the number of individuals contained in each pellet by counting the number of lower mandibles (Van Vuren et al., 1998). The occurrence and quantity of songbirds within a pellet was determined by the diagnostic characteristics of avian skulls, beaks, keels, synsacrums, clavicles, feet, crops, and feathers, but individuals were not identified to species. We used fur or feathers to detect the presence of a species when no bones were contained within a pellet, but could only count a minimum number of one individual, since fur or feathers alone can only detect presence (Marti et al., 2007). Mammalian bones and fur were compared to a museum reference collection from the Museum of Wildlife and Fish Biology, University of California, Davis, and cranial bones were cross-referenced with a North American field guide (Elbroch, 2006).

2.4. Prey biomass

For all complete vole and gopher mandibles that were identified in pellets, we calculated the body mass of the individual animal that was consumed based on mandible length (mm). Gopher mass was calculated from Van Vuren et al. (1998) and is equal to: log (mass) = 3.49 log(mandible length) − 2.73. We calculated a relationship between vole mandible length and body mass by taking mandible measurements from 53 vole skulls stored at the Museum of Wildlife and Fish Biology at the University of California Davis and calculating a regression relationship between the recorded mass of each individual and mandible length. Our regression showed that a mass can be estimated for *Microtus californicus* using mandible length and is equal to the relationship: ln(vole mass) = 3.154 ln (mandible length) −5.015 (see results for model fit). We then used this relationship to estimate the mass of each vole in our pellets. For any incomplete mandibles found in pellets, we used the mean estimated weights based on the complete mandibles in all pellets for *Thomomys bottae* (63.31 g) and for *M. californicus* (37.36 g). For all other prey species, we used the median mass reported in field guides for our area (Table 1).

2.5. Analyses

Using mean values for each nest, we used linear regression in JMP Pro (v. 12.0.1, SAS, 2015) to measure the relationships between the proportion land in perennial crops around each site and the mean mass of voles and gophers consumed at the site. To assess the effects of proportion perennial crop on barn owl diets we used linear mixed effects models in the lme4 (Bates et al., 2015) package in R (v. 3.1.2, R Core Development Team, 2015). We ran separate models for the proportion of each pellet consisting of gophers, voles, or mice by both number and by biomass, and used the proportion perennial crop as our predictor variables in each. Mixed effects models allow for the inclusion of random grouping effects, in this case nest ID and year, to account for multiple observations per site.

3. Results

3.1. Land cover summary

Our habitat analysis showed that row crop was the most abundant land cover type in landscapes around barn owl nest boxes, accounting for an average of 23.7 ± 0.04% (standard error of the mean) of land use. The second most abundant cover type was perennial crops, which accounted for 19.5 ± 0.04%. Other common land use types found in our study area included alfalfa (17.4 ± 0.02%), other forage crops (14.1 ± 0.02%), fallow/barren (10.8 ± 0.02%), grass pasture (9.6 ± 0.03%), developed areas (3.7 ± 0.004%), and rice (1.2 ± 0.005%),

Table 1
Prey identified in 415 pellets from 25 barn owl nests surrounded by varying amounts of perennial crops (orchards and vineyards).

Pellets	Prop. perennial crops	Total consumed							Biomass Consumed						
		Mouse	Vole	Gopher	Bird	Cricket	Shrew	Rat	Mouse	Vole	Gopher	Bird	Cricket	Shrew	Rat
39	0.01	96	17	1	1	0	0	1	1598.4	660.2	62.4	60.5	0	0	355
5	0.01	22	0	0	0	1	0	0	366.3	0.0	0.0	0	2	0	0
34	0.01	59	21	2	8	0	0	0	982.4	771.4	157.1	484	0	0	0
35	0.01	108	15	2	1	29	1	1	1798.2	682.4	110.7	60.5	58	5.8	355
10	0.01	32	1	0	0	1	0	1	532.8	60.2	0.0	0	2	0	355
28	0.02	44	14	4	6	3	0	0	732.6	612.2	199.5	363	6	0	0
6	0.02	22	3	0	1	0	0	0	366.3	112.1	0.0	60.5	0	0	0
13	0.02	14	17	0	0	1	1	0	233.1	635.1	0.0	0	2	5.8	0
15	0.03	0	19	0	2	1	0	0	0.0	490.7	0.0	121	2	0	0
5	0.11	1	3	0	1	0	0	0	16.7	114.5	0.0	60.5	0	0	0
7	0.15	14	1	3	1	0	0	0	233.1	41.7	164.7	60.5	0	0	0
38	0.18	53	19	5	1	0	1	0	882.5	709.8	316.6	60.5	0	5.8	0
8	0.19	2	8	0	2	0	0	0	33.3	285.4	0.0	121	0	0	0
21	0.22	42	7	0	0	0	2	0	699.3	167.2	0.0	0	0	11.6	0
20	0.25	32	17	2	1	0	1	0	532.8	614.4	145.5	60.5	0	5.8	0
8	0.25	0	5	5	0	1	0	0	0.0	211.9	288.9	0	2	0	0
6	0.28	0	2	4	0	0	0	0	0.0	82.2	297.6	0	0	0	0
23	0.28	0	34	5	7	0	0	0	0.0	1113.5	344.9	423.5	0	0	0
23	0.31	22	20	6	0	0	0	0	366.3	714.9	382.4	0	0	0	0
6	0.33	0	5	1	0	0	0	0	0.0	193.7	92.3	0	0	0	0
5	0.38	6	3	3	0	0	0	0	99.9	112.1	189.9	0	0	0	0
17	0.38	15	25	2	4	0	0	0	249.8	883.8	75.8	242	0	0	0
21	0.41	33	9	0	0	0	0	0	549.5	270.5	0.0	0	0	0	0
6	0.44	0	3	5	0	0	0	0	0.0	69.6	303.4	0	0	0	0
16	0.56	6	15	5	1	0	0	0	99.9	494.1	317.6	60.5	0	0	0
Total		623	283	55	37	37	6	3	10,373	10,104	3,449	2,239	74	35	1,065
Relative Importance in diet		0.597	0.271	0.053	0.035	0.035	0.006	0.003	0.379	0.370	0.126	0.082	0.003	0.001	0.039

Mass values were based on regression estimates from jaw bone length for gophers (Van Vuren et al., 1998) and voles (this paper). When mandibles were damaged or missing from pellets, we used the mean mass of voles or gophers based on the results of this paper. Mass for other species are based on the median of reported mass values for common species in the central valley-Mouse: Western-harvest mouse (*Reithrodontomys megalotis*) 7–15 g (Smithsonian, 2015) and house mouse (*Mus musculus*) 15.6–26.3 g (Berry, 1970); Shrews: ornate shrew (*Sorex ornatus*), 2.9–8.7 g (Smithsonian, 2015); Rats were all Norway rat (*Rattus norvegicus*) 200–510 g (Timm et al., 2011). Bird biomass was taken as the mean between Western meadowlark (*Sturnella neglecta*) 106 g (Davis and Lanyon, 2008) and lazuli bunting (*Passerina amoena*) 15 g (Greene et al., 2014). Crickets (*Gryllus spp.*) were assigned a weight of 2 g.

3.2. Nest box use

Of the 34 nest boxes that we checked for owl activity using our video system, 19 (55.88%) had barn owl chicks and/or adults inside them. Fourteen of the active boxes (41.18% of all boxes checked) contained chicks and/or eggs. The remaining five active boxes had one or two roosting adults. One American Kestrel (*Falco sparverius*) was found incubating 5 eggs in one box, but pellets were never collected from this site, and we did not consider this box as 'active'. Kestrel pellets are significantly smaller than barn owl pellets. Five of the eight boxes constructed from PVC were active, and one contained the kestrel nest. Fourteen of the twenty-six boxes constructed from wood were active.

3.3. Prey consumption

We detected 1044 individual prey species from 415 pellets collected from active barn owl boxes. Mice were the most frequently consumed prey item by barn owls (59.7% of 1,044 prey items) and were also the most important prey by biomass (37.9% of the total biomass of prey items; Table 1). Voles were less important by number (27.1%) but equally important for their contribution to biomass (37.0%). Gophers were consumed less frequently across the whole population (5.3% of all prey items), but were an important source of biomass (12.6%). Other prey groups identified in pellets included birds (3.5% by number, 8.2% by biomass), crickets (3.5% by number, 0.3% by biomass), shrews (*Sorex ornatus*, 3.5% by number, 0.1% by biomass), and Norway rats (*Rattus norvegicus*, 0.3% by number, 3.9% by biomass; Table 1).

Voles were consumed by the greatest proportion of nests, with evidence of voles in at least one pellet from 96% of nests. Mice were found in 76% of nests, gophers in 64%, birds in 56%, crickets in 28%, rats in 12%, and shrews in 2% of nests.

3.4. Habitat associations

The relative importance of gophers by number of prey items in the diet of barn owls increased as the amount of perennial crop in the surrounding habitat increased ($t = 2.89$, $p = 0.009$, Fig. 2), as did the relative importance of gophers as a source of prey biomass ($t = 2.65$, $p = 0.02$). Conversely, the relative importance of mice by number of prey items ($t = -2.66$, $p = 0.01$) and by the biomass of prey items ($t = -2.80$, $p = 0.01$) decreased with increasing perennial crop (Fig. 2). Similarly, as the amount of forage crop in the surrounding landscape increased, the relative importance of mice in barn owl diet by prey number ($t = -3.21$, $p = 0.004$) and by biomass increased ($t = -2.68$, $p = 0.01$). The relative importance of voles in the diet of barn owls was not affected by surrounding crop type ($t = -2.18$, $p = 0.08$).

Mean vole mass for all measurable mandible lengths in our study area was 37.36 g ± 0.79 g. Voles reach adult size at a minimum of 35 g for females (Greenwald, 1957), and 145 (60.67%) of the vole mandibles that we measured corresponded with adult voles. Mean vole mass declined with increasing perennial habitat in the landscape surrounding each nest ($R^2 = 0.26$, $t = -2.75$, $p = 0.01$), and owls foraging in habitats with more perennial habitat were more likely to consume juvenile voles (Fig. 3). Mean gopher mass for all measurable mandible lengths in our study area was 63.31 g ± 2.80 g. There was no clear relationship between gopher size and the proportion of perennial habitat surrounding nests ($R^2 = 0.008$, $t = 0.35$, $p = 0.73$, Fig.4). Gophers reach adult size at a minimum of 90 g for females (Daly and Patton, 1986), and only seven of the 51 mandible lengths (13.73%) that we measured corresponded with adult gophers.

4. Discussion

Our study provides a primary example on the effects of land-use changes within an intensive agricultural landscape on barn owl diets, and its implications for vertebrate pest control. We show that barn owl diet changes along a gradient of increasing orchard and vineyard crops, which suggests that these habitats may have tradeoffs for both pest control and barn owl breeding. Of the 1,044 prey items we identified in barn owl pellets, 99.5% were from species that are considered agricultural pest species (Gebhardt et al., 2011). Gophers and voles are consistently listed as key agricultural pests across California and are estimated by farmers to cause economic losses of over 5% in all crops, but can cause losses as high as 8.8% (gophers) and 11.3% (voles) in alfalfa (Baldwin et al., 2011). While mice are often considered less important pests than gophers and voles (Baldwin et al., 2011), they can carry food-borne pathogens that are considered a food-safety risk in fresh-to-market crops (Kilonzo et al., 2013). Farmers targeting rodents utilize poison baits, fumigants, traps, and/or habitat modification to reduce pest populations on their land, although these methods may be less effective than their costs warrant (Baldwin et al., 2011) and can have severe ecological implications (e.g. Erickson and Urban, 2004; Elliott et al., 2014; Gennet et al., 2013).

Barn owls in the study area are likely to occupy over half of artificial nest boxes available to them, so installing nest boxes on farms may therefore enhance the natural vertebrate-pest control services provided by barn owls. With the Central Valley's poor

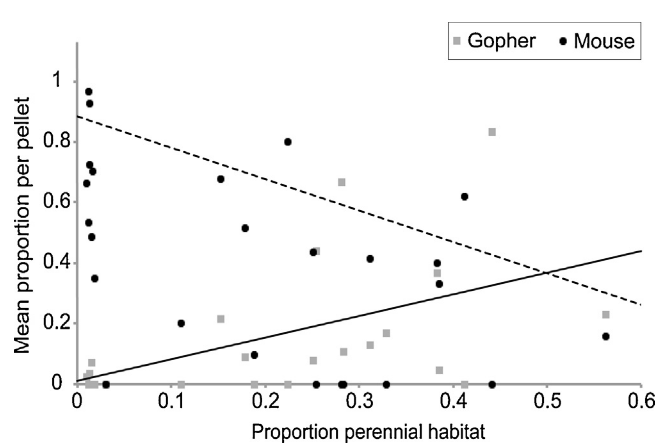

Fig. 2. Mean proportion prey items in each pellet at 24 barn owl nests that were gophers (grey squares) and mice (black circles) compared to the proportion of land use within a 1-km radius of each nest that was used for growing perennial crops including vineyards and orchards. Line shows the model predictions from linear mixed effects models for gophers (solid line) and mice (dotted line) as a function of increasing perennial habitat.

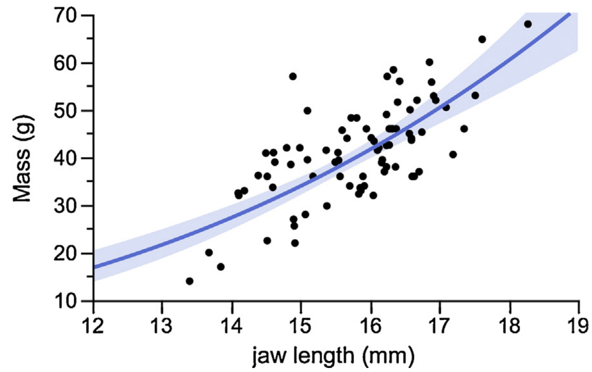

Fig. 3. The relationship between mandible length and body mass for California voles *Microtus californicus* based on measurements from 53 specimens in a museum collection.

riparian health and soil quality (Young-Mathews et al., 2010) and the increasing incidences of secondary poisonings of non-target species (Erickson and Urban, 2004; Elliott et al., 2014; Thomas et al., 2011), the implementation of biological control in pest management is potentially a step toward reducing environmental toxicants. There is growing interest from farmers toward attracting barn owls to their properties (Van Vuren et al., 1998), therefore, future targeted studies will need to measure whether attracting owls can reduce the economic and ecological costs of conventional pest management methods such as rodenticides, trapping, and habitat modification.

Mice and California voles were the most common species found in the barn owl pellets and there was a negative correlation between the importance of mice in owl diets and the proportion of perennial habitat in the surrounding landscape. Conversely, while pocket gophers were less abundant in barn owl diets, their importance as prey increased as the proportion of perennial habitat increased. Perennial agriculture around the nest boxes in this study included vineyards, nut and fruit orchards and olive groves, which are managed differently but all consider gophers and voles to be detrimental pests. Previous studies in California have shown that gophers are the most abundant prey species in owl diets (Browning et al., unpublished data; Van Vuren et al., 1998), although these studies were centered in predominantly perennial habitats (vineyards). We found fewer voles in the diet of owls compared with other studies in North America, where voles normally make up 71.2% of the total diet biomass of owls (Taylor, 1994). However, many of the studies reviewed by Taylor were not focused on intensive agricultural systems.

This leads to further questions about why mice were so common in owl diet within our study area and whether this trend was due to suppressed mice populations in perennial crops or due to barn owls in predominantly annual crops types having less access to larger prey (gophers). Barn owls have been shown to

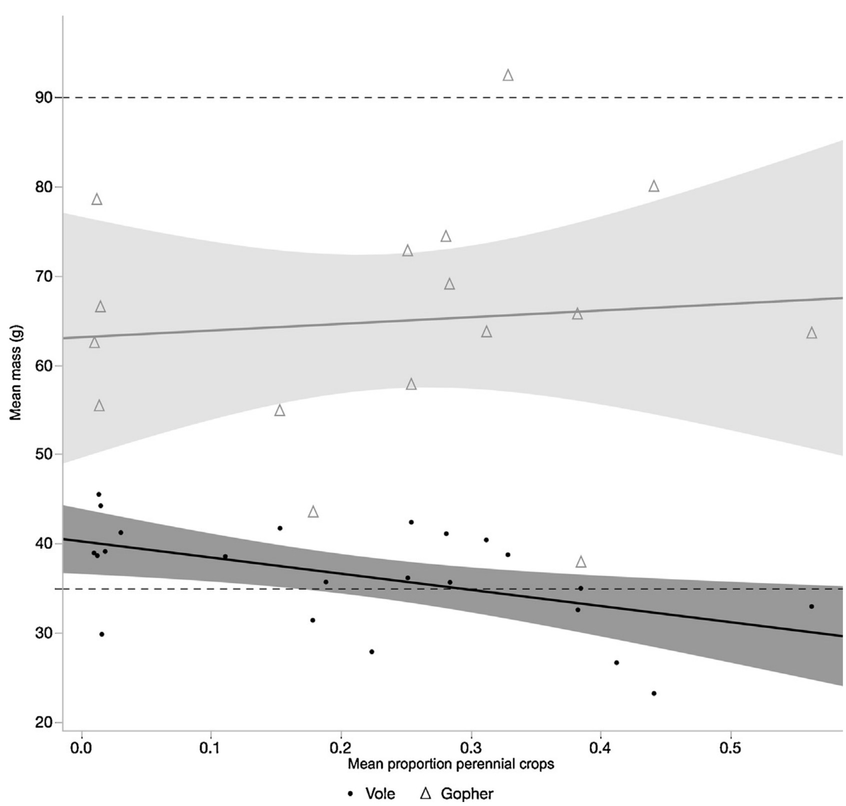

Fig. 4. The average size of vole (circles) and gopher (triangles) prey items found in the pellets of barn owl nests surrounded by varying amounts of perennial crops (orchards and vineyards). There was a significant negative effect of proportion perennial crop on the mean size of voles (black line, $R^2 = 0.26$, $t = -2.75$, $p = 0.01$), but no effect on the mean size of gophers (grey line, $R^2 = 0.008$, $t = 0.35$, $p = 0.73$). Horizontal dashed lines show the minimum adult size for voles (lower line) and gophers (upper line).

preferentially hunt for larger prey when available (Tores et al., 2005), but vegetation structure and ground cover can prevent owls from accessing favored prey in some situations even when those prey are abundant (Arlettaz et al., 2010). There are many factors that influence the selective and opportunistic hunting behavior of barn owls, such as prey size, time of year, habitat, and the anti-predator strategies of potential prey (Marti et al., 2005). Pocket gophers are fossorial herbivores and spend the majority of their time within extensive underground burrow systems (Jones and Baxter, 2004). In our study area row crops are ploughed annually at a depth that would destroy most gopher tunnels and forage crops are flooded repeatedly over the spring and summer months which may keep gopher populations in check. We were not able to take into account ongoing rodent control methods on our study farms, and therefore cannot be sure that gopher numbers were not reduced due to rodenticide applications. Competition with other carnivores could also influence the low number of gophers found in barn owl diets within row and forage crops in this study. Gophers are important prey items for Swainson's hawks (*Buteo swainsoni*), Northern harriers (*Circus cyaneus*), and white-tailed kites (*Elanus lecurus*), and are often seen hunting in Yolo County agricultural fields (Smallwood et al., 2001).

Our study took place exclusively during the spring and summer months, so did not capture the diet of barn owls during fall or winter. Van Vuren et al. (1998) found that a population of barn owls nesting in primarily vineyard-dominated landscapes in California consumed gophers more in the spring and summer and that voles became a more important component of barn owl diet in winter, so it is likely that the habitat associations we found change seasonally.

5. Conclusions

For farmers to be able to take advantage of the potential pest control benefits derived from attracting barn owls to their land, it is important to consider the crop types around nest box sites. Here, we demonstrated that farmers cannot rely on diet studies from single crops to guide assumptions about the potential pest control benefits from barn owls, since diet can change drastically across different crops located within the same landscape. Our results suggest that barn owls eat more gophers when their nests are surrounded by vineyards or orchard crops. The implications for these results for both pest control and barn owl breeding success need further investigation, as this trend may be due to increased gopher populations in perennial agricultural habitats, or it may be due to increased hunting efficiency for barn owls in perennial agricultural habitats. However, these results indicate that studies predicting the pest-control value of predators such as barn owls should account for variability in both prey numbers and predator behavior across crop types, even within a small region.

Acknowledgements

This work was funded by the David H. Smith Conservation Research Fellowship, hosted by John Eadie and the department of Wildlife, Fish & Conservation Biology at UC Davis. We thank J. Haight, S. Remmes, J. Heasell, E. Barry, and M. Pelagio for help with collecting and dissecting owl pellets. D. Van Vuren provided guidance on pellet analysis and study design. The UC Davis Museum of Wildlife & Fish Biology provided museum reference collections. Lastly, this study would not have been possible without the permission and support from the three land managers, Turkovich Farms, Citrona Farms, and Dunnigan Hills Ranch, who allowed access to their private property for the purpose of wildlife research. The protocol for checking nest box occupancy was approved by the Institutional Animal Care and Use Committee (IACUC #18717) at the University of California, Davis. Entomologists at the Bohart Museum of Entomology at University of California, Davis helped us identify the cricket remains.

References

Abramsky, Z., Strauss, E., Subach, A., Kotler, B.P., Riechman, A., 1996. The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and G-pyramidum. Oecologia 105 (3), 313–319. doi:http://dx.doi.org/10.1007/bf00328733.PubMedPMID:WOS:A1996TV85000005.

Arlettaz, R., Krahenbuhl, M., Almasi, B., Roulin, A., Schaub, M., 2010. Wildflower areas within revitalized agricultural matrices boost small mammal populations but not breeding Barn Owls. J. Ornithol. 151, 553–564.

Baldwin, R.A., Salmon, T.P., Schmidt, R.H., Timm, R.M., 2011. Vertebrate Pest "Research Needs" Assessment for California Agricultural Commodities. Report for the Vertebrate Pest Control Research Advisory Committee. http://ucanr.edu/sites/CEprogramevaluation/files/147383.pdf.

Bates, D., Maechler, M., Bolkerr, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48.

Berry, R.J., 1970. The natural history of the house mouse. Field Stud. 3, 219–262.

Borda-de-Agua, L., Grilo, C., Pereira, H.M., 2014. Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using age-structured models. Ecol. Model. 276, 29–37. doi:http://dx.doi.org/10.1016/j.ecolmodel.2013.12.022. PubMedPMID:WOS:000333854500004.

Colvin, B.A. 1985. Common barn-owl population decline in Ohio and the relationship to agricultural trends. J. Field Ornithol. 56(3): 224–235. PubMed PMID: WOS:A1985AVW5000002.

Charter, M., Leshem, Y., Meyrom, K., Peleg, O., Roulin, A., 2012. The importance of micro-habitat in the breeding of Barn Owls *Tyto alba*. Bird Study 59, 368–371.

Dahl, T.E. 1990. Wetland losses in the United States 1780's to 1980's. In: U.S. Department of the Interior FaWS, editor. Washington, D.C. p. 13.

Daly, J.C., Patton, J.L., 1986. Growth, reproduction, and sexual dimporphism in *Thomomys bottae* pocket gophers. J. Mammal. 67, 256–265.

Davis, S.K., Lanyon, W.E., 2008. Western Meadowlark (*Sturnella neglecta*). In: Poole, A. (Ed.), The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY.

Elbroch, M., 2006. Animal Skulls: A Guide to North American Species. Stackpole Books, Mechanicsburg, PA.

Elliott, J.E., Hindmarch, S., Albert, C.A., Emery, J., Mineau, P., Maisonneuve, F., 2014. Exposure pathways of anticoagulant rodenticides to nontarget wildlife. Environ. Monit. Assess. 186 (2), 895–906. doi:http://dx.doi.org/10.1007/s10661-013-3422-x.

Erickson, W., Urban, D., 2004. Potential risks of nine rodenticides to birds and nontarget mammals: a comparative approach. United States Environmental Protection Agency. United States Environmental Protection Agency, Office of Pesticide Programs p230pp.

ESRI, 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

ESRI, 2011. FMMP, 2010. Farmland Mapping and Monitoring Program. 2008–2010 Yolo County Important Farmland Data. California Department of Conservation. Available online at: http://redirectconservationcagov/DLRP/fmmp/product_pageasp2010.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., et al., 2005. Global consequences of land use. Science 309 (5734), 570–574. doi:http://dx.doi.org/10.1126/science.1111772.

Frey, C., Sonnay, C., Dreiss, A., Roulin, A., 2011. Habitat, breeding performance, diet and individual age in Swiss Barn Owls (Tyto alba). J. Ornithol. 152, 279–290.

Gebhardt, K., Anderson, A.M., Kirkpatrick, K.N., Shwiff, S.A., 2011. A review and synthesis of bird and rodent damage estimates to select California crops. Crop Prot. 30 (9), 1109–1116. doi:http://dx.doi.org/10.1016/j.cropro.2011.05.015.

Gennet, S., Howard, J., Langholz, J., Andrews, K., Reynolds, M.D., Morrison, S.A., 2013. Farm practices for food safety: an emerging threat to floodplain and riparian ecosystems. Front. Ecol. Environ. 11, 236–242.

Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. Science 307 (5709), 550–555. doi:http://dx.doi.org/10.1126/science.1106049.

Greene, E., Muehter, V.R., Davison, W., 2014. Lazuli Bunting (*Passerina amoena*). In: Poole, A. (Ed.), The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY.

Greenwald, G.S., 1957. Reproduction in a coastal California population of the field mouse, *Microtus californicus*. Univ. Calif. Publ. Zool. 57, 421–446.

Hafidzi, M.N., Mohd, N.I., 2003. The use of the barn owl, *Tyto alba*, to suppress rat damage in rice fields in Malaysia. In: Singleton, G.R., Hinds, L.A., Krebs, C.J., Spratt, D.M. (Eds.), Rats, Mice and People: Rodent Biology and Management. Australian Centre for International Agricultural Research, Canberra, pp. 274–276.

Han, W., Yang, Z., Di, L., Cropscape, Mueller R., 2012. A web service based application for exploring and disseminating US conterminous geospatial cropland data products for decision support. Comput. Electron. Agric. 84, 111–123.

Hindmarch, S., Krebs, E.A., Elliott, J., Green, D.J., 2014. Urban development reduces fledging success of Barn Owls in British Columbia, Canada. Condor 116, 507–517.

Horak, K.E., Volker, S.F., Campton, C.M., 2015. Increase diphacinone and chlorophacinone metabolism in previously exposed wild caught voles *Microtus californicus*. Crop Prot. 78, 35–39.

Jackson, L., Haden, V.R., Hollander, A.D., Lee, H., Lubell, M., Mehta, V.K., et al., 2012. Adaptation strategies for agricultural sustainability in Yolo County, California. In: Commission CE, editor. p. 183.

Jones, C.A., Baxter, C.N., 2004. Thomomys bottae. Mammalian Species 742, 1–14.

Kan, I., Motro, Y., Horvitz, N., Kimhi, A., Leshem, Y., Yom-Tov, Y., et al., 2014. Agricultural rodent control using barn owls: is it profitable? Am. J. Agric. Econ. 96 (3), 733–752. doi:http://dx.doi.org/10.1093/ajae/aat097.
Leech, D.I., Shawyer, C.R., Barimore, C.J., Crick, H.Q.P., 2009. The Barn Owl Monitoring Programme: establishing a protocol to assess temporal and spatial variation in productivity at a national scale. Ardea 97 (4), 421–428. doi:http://dx.doi.org/10.5253/078.097.0404.
Marti, C.D., 1973. Food consumption and pellet formation rates in four owl species. Wilson Bull. 85, 178–181.
Marti, C.D., Alan, F.P., Bevier, L.R., 2005. Barn owl (*Tyto alba*). Cornell Lab of Ornithology, Ithaca. http://bna.birds.cornell.edu/bna/species/001.
Marti, C.D., Bechard, M.J., Jaksic, F.M., 2007. Food habits. In: Bird, D.M., Bildstein, K.L. (Eds.), Raptor Research and Management Techniques. Hancock House, Blaine, WA p. 464.
Meek, W.R., Burman, P.J., Nowakowski, M., Sparks, T.H., Hill, R.A., Swetnam, R.D., et al., 2009. Habitat does not influence breeding performance in a long-term Barn Owl *Tyto alba* study. Bird Study 56, 369–380. doi:http://dx.doi.org/10.1080/00063650902937339.
Mehta, V.K., Haden, V.R., Joyce, B.A., Purkey, D.R., Jackson, L.E., 2013. Irrigation demand and supply, given projections of climate and land-use change, in Yolo County, California. Agric. Water Manag. 117, 70–82. http://dx.doi.org/10.1016/j.agwat.2012.10.021.
Newton, I., 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146 (4), 579–600. doi:http://dx.doi.org/10.1111/j.1474-919X.2004.00375.x.
R Core Development Team. R: A language and environment for statistical computing. In: Computing RFfS, editor. Vienne, Austria: R Foundation for Statistical Computing; 2015.
Salmon TP, Lawrence SJ, editors. Anticoagulant resistance in meadow voles (*Microtus californicus*). Proceedings of the 22nd Vertebrate Pest Conference; 2006: University of California, Davis.
SAS Institute Inc. JMP Pro. 2015.
Sergio, F., Newton, I.A.N., Marchesi, L., Pedrini, P., 2006. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. J. Appl. Ecol. 43 (6), 1049–1055. doi:http://dx.doi.org/10.1111/j.1365-2664.2006.01218.x.
Smal CM, Halim AH, Amiruddin M. Predictive modeling of rat populations in relation to use of rodenticides or predators for control. PORIM occasional paper. 1990; 25: 1–55.
Smallwood, K.S., Geng, S., Zhang, M., 2001. Comparing pocket gopher (*Thomomys bottae*) density in alfalfa stands to assess management and conservation goals in northern California. Agric. Ecosyst. Environ. 87 (1), 93–109. http://dx.doi.org/10.1016/S0167-8809(00)00300-5.
Smithsonian, 2015. North American Mammals. In: Costello, R., Rosenberger, A. (Eds.), Smithsonian National Museum of Natural History, Washington, DC. http://www.mnh.si.edu/mna/main.cfm.
Taylor, I.R., 1994. Barn Owls: Predator–Prey Relationships and Conservation. Cambridge University Press, Cambridge, UK p. 304.
Thomas, P.J., Mineau, P., Shore, R.F., Champoux, L., Martin, P.A., Wilson, L.K., et al., 2011. Second generation anticoagulant rodenticides in predatory birds: probabilistic characterisation of toxic liver concentrations and implications for predatory bird populations in Canada. Environ. Int. 37 (5), 914–920. doi:http://dx.doi.org/10.1016/j.envint.2011.03.010.
Timm, R.M., Salmon, T.P., Marsh, R.E., Pest notes: Rats. University of California Statewide IPM Program. 2011.
Tores, M., Motro, Y., Motro, U., Yom-Tova, Y., 2005. The barn owl- A selective opportunist predator. Israel J. Zool. 51 (4), 349–360. doi:http://dx.doi.org/10.1560/7862-9E5G-RQJJ-15BE.
USDA-NASS. Cropland Data Layer [Internet]. 2014 [cited 25 May 2015]. Available from: http://nassgeodata.gmu.edu/CropScape/.
Van Vuren, D., Moore, T.G., Ingels, C.A., 1998. Prey selection by barn owls using artificial nest boxes. Calif. Fish Game 84 (3), 127–132.
Whelan, C.J., Wenny, D.G., Marquis, R.J., 2015. Ecosystem services provided by birds. In: Ostfeld, R.S., Schlesinger, W.H. (Eds.), Year in Ecology and Conservation Biology 2008. Annals of the New York Academy of Sciences, pp. 25–60 11342008.
Young-Mathews, A., Culman, S., Sánchez-Moreno, S., Toby O'Geen, A., Ferris, H., Hollander, A., et al., 2010. Plant-soil biodiversity relationships and nutrient retention in agricultural riparian zones of the Sacramento Valley, California. Agrofor. Syst. 80 (1), 41–60. doi:http://dx.doi.org/10.1007/s10457-010-9332-9.