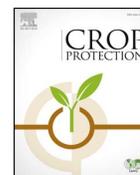




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Impact of field-edge habitat on mammalian wildlife abundance, distribution, and vectored foodborne pathogens in adjacent crops



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ABSTRACT

Field-edge habitat is important for enhancing biodiversity and associated ecosystem services on farms for long term agricultural sustainability. However, there is some concern that this habitat will increase wildlife activity and damage to adjacent crops. Wildlife incursion into production areas may also pose food safety risks. A two-year study in walnut orchards and processing tomato fields in the Sacramento Valley, California, documented variable use of farm fields by mammalian wildlife. This depended on field-edge habitat (restored hedgerows versus conventionally managed field edges where vegetation was mostly controlled), wildlife species present, season, and crop monitored. In walnut orchards, deer mice (*Peromyscus maniculatus* Wagner, 1845) were found throughout the orchard, while house mice (*Mus musculus* Linnaeus, 1758) exclusively used hedgerows. In tomato fields, deer mice were more common in field interiors during spring, but used field-edge habitats more during summer; the opposite was true for house mice. In general, deer mice preferred more open sites, while house mice were most numerous in areas with thick cover. Both desert cottontails (*Sylvilagus audubonii* Baird, 1858) and black-tailed jackrabbits (*Lepus californicus* Gray, 1837) showed affinity to hedgerow portions of fields, although this association was stronger for cottontails. Overall, we documented greater mammalian species richness and abundance associated with hedgerows. However, this increase in diversity did not generally lead to greater wildlife incursion into adjacent crops. In walnut orchards, *Salmonella* and non-O157 STEC were detected from 2 (1%) and 4 (2%) individual rodents, respectively ($n = 218$); no detections occurred in tomato fields. A subset of fecal samples ($n = 87$) from rodents captured in walnut orchards were positive for *Giardia* (25%) and *Cryptosporidium* (24%) but prevalence was not associated with field-edge habitat type. Overall, there does not appear to be a substantially greater risk of crop loss or contamination of foodborne pathogens in crops bordered by hedgerows in our study in the Sacramento Valley, although potential damage could vary by the stage and type of crop and wildlife species present.

1. Introduction

A challenge in the 21st century is to produce food for our growing population, while at the same time, protecting and sustaining our natural resources (Millennium Ecosystem Assessment, 2005). The planting of robust field-border habitats (e.g., hedgerows) is a management practice that has been gaining popularity for enhancing biodiversity on farmlands (Long et al., 2017). These narrow strips of vegetation, often referred to as hedgerows, are planted along crop edges so that no land is taken out of production (Long and Anderson, 2010). Benefits of

hedgerows include enhanced pollination and arthropod pest control in adjacent crops, water quality protection, and habitat for birds (Zhang et al., 2010; Morandin et al., 2016; Rusch et al., 2016; Heath et al., 2017). There is significant policy support behind these plantings through funding from the United States Department of Agriculture (NRCS, 2017; USDA, 2017). However, despite the benefits of hedgerows and financial support, few landholders (growers and landlords) adopt bio-diverse field edges. One reason is the perceived risk of increased damage from wildlife (especially rodents) using these habitat plantings and the potential for transfer of zoonotic enteric foodborne pathogens

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to human food crops by rodent fecal contamination (Jay-Russell, 2013; Karp et al., 2015a; Garbach and Long, 2017). As a result, some landholders have removed habitat on their farms to try to reduce food safety risks, especially following a nationwide outbreak of *Escherichia coli* O157:H7 associated with baby spinach grown in the California Central Coast (Beretti and Stuart, 2008). Since that time, the leafy greens industry and others have adopted a “co-management” strategy to balance food safety and conservation goals during produce production (Bianchi and Lowell, 2016). However, it still remains unclear how habitat modification, including use of hedgerows, may impact food safety risks from wildlife using these agricultural areas.

Mammalian wildlife can be serious agricultural pests, causing millions of dollars in crop losses (Witmer and Singleton, 2010; Gebhardt et al., 2011). Rodents, including mice, voles, and ground squirrels, are some of the most troublesome, as they feed on crops, causing significant yield and quality losses. They also burrow into fields and levees and chew on drip irrigation lines, disrupting and destroying irrigation systems (Baldwin et al., 2014b). Other wild mammals, including wild pigs (*Sus scrofa* Linnaeus, 1758), deer (*Odocoileus* spp.), jackrabbits (*Lepus* spp.), and cottontails (*Sylvilagus* spp.), can likewise either feed on and/or tear up crops, further reducing yields (Baldwin et al., 2014b; Anderson et al., 2016). Mammalian wildlife are also known to be vectors of foodborne pathogens that can cause severe human disease outbreaks (Jay et al., 2007; Laidler et al., 2013). Two groups of pathogens, Shiga toxin-producing *E. coli* (STEC) and *Salmonella enterica*, are responsible for the majority of the bacterial outbreaks in fresh produce (Doyle and Erickson, 2008). Both pathogens are carried by domestic animals (e.g., cattle) and wildlife. However, whereas *S. enterica* is readily isolated from many wildlife hosts (Winfield and Groisman, 2003; Gorski et al., 2011), STEC is generally more prevalent in cattle than in wildlife (Cooley et al., 2013). Other pathogens shed by mammalian wildlife that are more associated with waterborne exposure include the parasites *Giardia* spp. and *Cryptosporidium* spp. (Kilonzo et al., 2013). These may be a concern, particularly when fields are close to streams or irrigation canals.

Managing mammalian vertebrate pests in agricultural systems can include trapping, baiting, shooting, frightening, fencing, and the removal of non-crop habitat around farms (Van Vuren and Smallwood, 1996; Fall and Jackson, 1998; Baldwin et al., 2014b). Although these practices can be effective depending on the vertebrate pest and situation, habitat removal is controversial and with questionable efficacy for several reasons. First, vegetation is critical for providing ecosystem services on farms; filter strips, for example, help protect water quality from pathogens and other sediment associated pollutants (Atwill et al., 2006; Tate et al., 2006; Long et al., 2010). Without habitat, our natural resources degrade, leading to questions about long-term farm sustainability (Tilman, 1999; Hobbs, 2007; Geertsema et al., 2016). Second, wildlife may provide crop protection benefits from arthropod pests. For example, Kross et al. (2016) found greater insect pest control by bird species in alfalfa fields when complex field-edge habitats were present; bats likewise prey on many agricultural pests (Boyles et al., 2011). Third, there is limited information indicating a positive impact of managing habitat for controlling food pathogens. For example, Karp et al. (2015b) found an increase in food pathogens when habitat was reduced on farms. Speculation for this increase included the importance of vegetation for filtering foodborne pathogens, a better breakdown of pathogens in diverse environments, and that removing vegetation may not deter wildlife from entering farm fields.

In this study, we investigated the association between field-edge habitat, mammalian wildlife, and foodborne pathogens in orchard and row crops. Our objectives were to determine: 1) if mammalian wildlife abundance and richness in crops is influenced by field-edge habitat, 2) if certain habitat features influence the occurrence of mammalian wildlife, and 3) if foodborne pathogen prevalence in rodents is impacted by field-edge habitat. These results will provide much needed information to inform the agricultural industry about the potential

impact of field-edge habitat plantings on wildlife and associated food safety concerns, hopefully allowing producers to balance their ability to maintain biodiversity on farmlands with the need to limit wildlife crop damage and food safety risk.

2. Materials and methods

2.1. Study area

This study was conducted in Yolo and Solano County in California's Sacramento Valley. The study area was intensively farmed, primarily with tree crops such as almonds and walnuts, as well as rotational field crops such as wheat, processing tomato, alfalfa, and seed crops including sunflower. The average size farm in these counties was about 182 ha with a market value of products sold averaging \$400,000. There were 860 farms in Solano County and 1011 farms in Yolo County (Garbach and Long, 2017). This region was characterized by hot, dry summers and cool, wet winters (i.e. Mediterranean climate).

Our study sites included 4 walnut orchards and 5 processing tomato fields with each site approximately 32 ha in area. One side of each field had a hedgerow of California native shrubs and perennial grasses that was approximately 7 m wide × 448 m in length and 10–20-years old. The shrubs mainly included California buckwheat (*Eriogonum fasciculatum* var. *foliolosum* Nutt.), California lilac (*Ceanothus griseus* [Trel.] McMinn), California coffeeberry (*Rhamnus californica* Eschsch.), coyote brush (*Baccharis pilularis* DC.), elderberry (*Sambucus nigra* L.), and toyon (*Heteromeles arbutifolia* [Lindl.] M. Roem.). The other three sides of the fields were conventionally managed for weed control by discing, mowing, and/or the use of herbicides. The field edge on the opposite side of the hedgerow served as our control (minimum of 400 m from the hedgerow). The fields were generally surrounded on all four sides by other crop fields, but for a few sites (2 in walnuts, 1 in tomatoes), a creek ran along one side of the fields. These creeks were located on a field edge perpendicular to the hedgerow and control field edges, equilibrating any potential impact the creeks may have had on mammal response to hedgerow and conventionally managed field edges. Within the crops, weeds were managed similarly to the conventionally managed field edges. Vine training, to open the furrows for harvest, occurred once in each of the tomato fields. No active management for vertebrate species occurred during our study period.

2.2. Small rodent and lagomorph sampling

We monitored small rodent (deer mouse [*Peromyscus maniculatus* Wagner, 1845], house mouse [*Mus musculus* Linnaeus, 1758], western harvest mouse [*Reithrodontomys megalotis* Baird, 1858], California vole [*Microtus californicus* Peale, 1848], Norway rat [*Rattus norvegicus* Berkenhout, 1769], and roof rat [*Rattus rattus* Linnaeus, 1758]) activity seasonally in both walnut orchards (summer, autumn, winter, spring; July 2013 through May 2014) and tomato fields (spring and summer; May through July 2015) with Sherman live traps (HB Sherman Traps, Inc. Tallahassee, Florida, USA; Fig. 1). Trap transects were set at 0, 10, 75 and 175 m from both the conventional and hedgerow field-edge treatments into the adjacent crops. We placed two transects of 10 traps at each distance interval with traps spaced at 10-m intervals; all transects within each distance category were separated by a minimum of 30 m to minimize the likelihood of capturing the same rodent in paired transects. We baited all traps with peanut butter and rolled oats, and we added cotton bedding to provide nesting material and to capture fecal pellets voided during nesting. To minimize daytime exposure, we set traps in the evening before sunset and checked and closed all traps early the following morning for 5 consecutive nights per field site. We identified species, sexed, weighed, and ear tagged (Model 84FF, Salt Lake Stamp Co. Salt Lake City, Utah, USA) all trapped rodents to differentiate between unique and recaptured individuals; all rodents were released at the point of capture.



Fig. 1. Diagram of sampling design using a combination of live traps and remote-triggered cameras to monitor mammalian wildlife in walnut orchards and tomato fields (although cameras were only located within field edges in tomato fields) in the Sacramento Valley, California, 2013–2015.

We monitored lagomorph activity in walnut orchards using 4 remote-triggered cameras (Scoutguard[®] SG550, HCO Outdoor Products, Norcross, Georgia, USA) per trapping transect, with each camera stationed 5-m apart from the two adjacent traps (Fig. 1). We attached all cameras to stakes just above ground level, and focused cameras on wax monitoring blocks (Detex[®], Bell Laboratories, Inc. Madison, Wisconsin, USA) that were held in place with wire flags. The wax monitoring blocks were used to ensure that small wildlife would move close enough to the camera to accurately document presence; cameras were set with a minimum 5-min trigger interval to reduce the impact of repeat visits to the same site (Baldwin et al., 2014a). Lagomorphs were identified to species (black-tailed jackrabbit [*Lepus californicus* Gray, 1837] and desert cottontail [*Sylvilagus audubonii* Baird, 1858]). We did not monitor lagomorphs within tomato fields given limited lagomorph distribution in these fields combined with the risk to cameras from farm operations in an annual crop. However, we did monitor for their activity on field borders.

2.3. Other mammal sampling

We established 4 remote-triggered video cameras in each field-edge habitat to monitor other mammalian species that could not be captured using Sherman live traps (Fig. 1). We left camera sites unbaited so as to minimize the likelihood that we would artificially attract animals to the camera sites. We set cameras to record 10 s of video to maximize our ability to identify the animal to species; video cameras were set with a minimum 5-min trigger interval to reduce the impact of repeat visits to the same site (Baldwin et al., 2014a). We identified all videoed individuals to species when possible.

2.4. Fecal sampling and analysis

We collected fecal samples directly from captured rodents and placed the samples into microcentrifuge tubes with 50 ml of universal

pre-enrichment broth (BD, Sparks, Maryland, USA); fecal pellets from the cotton bedding were also placed into sterile sampling bags. We stored all samples in a cooler and transported them to the University of California, Davis Western Center for Food Safety where we processed for the detection of *E. coli* O157, non-O157 STEC, *Salmonella*, *Cryptosporidium* oocysts, and *Giardia* cysts, using the methodology described by Kilonzo et al. (2013). Genotyping of *Cryptosporidium* and *Giardia* was performed using the methodology described by Kilonzo et al. (2017). Serotyping of *Salmonella* and STEC isolates was conducted at reference laboratories. We sanitized all traps with rodent captures with a 10% bleach solution before resetting in the field. All animal sampling protocols for this study were approved by the Institutional Animal Care and Use Committee at the University of California, Davis (protocol number 17641).

2.5. Habitat sampling

We measured 8 habitat variables to determine their impact on mammal activity in both crop systems at every site. In walnut orchards, data collected from habitat assessments in autumn (October 2013) were also used for winter analyses given that no substantive new vegetative growth occurred during those two sampling seasons (mainly due to a lack of rain associated with drought conditions). Spring (April–May 2014) was the final walnut habitat sampling season due to time constraints (i.e. we did not collect data during summer). We conducted two habitat assessments in the tomato study: about a month after transplanting seedlings (May–June 2015, hereafter spring) and again pre-harvest (June–July 2015, hereafter summer).

We estimated the percentage of ground cover including thatch, grasses, forbs, woody plants, and bare ground to the nearest 5% measurement at 5 randomly selected 1-m² habitat sampling plots per trapped transect. Forbs were herbaceous dicots that did not contain a woody stem, grasses were monocots, woody species were dicots that contained a woody stem, bare soil was devoid of vegetation, while

thatch referred to dead vegetation and leaf litter. We used a spherical densiometer to measure mean canopy cover (4 times per sampling plot, once per cardinal direction) for each 1-m² habitat sampling plot (Lemmon, 1956). A Robel pole was used to measure mean vertical cover (4 times per sampling plot, once per cardinal direction; measurements were taken from a 1-m vantage point 4 m from the Robel pole) for each 1-m² sampling plot (Robel et al., 1970). We recorded vertical cover at the ground level (0–50 cm) and across a higher vertical threshold (0–150 cm) in case the mammals perceived the importance of vertical cover across different ranges. All measurements were recorded across each sampled transect with average values calculated per habitat sampling plot, and then again averaged for each transect for inclusion in all analyses. All transects were measured at the 0- and 10-m intervals. Because of extreme uniformity in habitat measurements in our large-scale monoculture cropping systems at the 75- and 175-m intervals, we only collected habitat measurements for one randomly-selected transect at both the 75- and 175-m distance intervals for each field-edge habitat type, with results of these habitat measurements repeated in analyses for the second trapped or photographed transect at that distance.

2.6. Data analysis

We used data collected from Sherman live traps and remote-triggered cameras to assess relative measures of mammalian abundance and richness within respective halves (0–175 m from field edge) of each walnut orchard and tomato field associated with hedgerow and conventionally managed field borders. For live-trapped individuals, we only used uniquely identified individuals for our relative measure of abundance (i.e. no recaptures). For rabbits monitored with remote-triggered cameras (excluding video cameras), we used the number of camera sites where a species was recorded to provide a relative index of activity for each area.

We calculated general index values for unique small rodent captures by dividing the composite number of unique captures for each transect by the sum of the number of nights that all traps on that transect were operated (Engeman, 2005; Baldwin et al., 2014a). Unique captures for analysis of variance (ANOVA) tests were defined as the initial capture of an individual within a field edge-distance category per season. If an individual was captured within both transects of the same field edge-distance category, we only used the initial capture to reduce concerns of pseudoreplication. However, if an individual was captured during a subsequent season or within a separate field edge-distance category, we considered the first capture during this subsequent season or field edge-distance category a unique capture as well.

We analyzed general index values derived from unique mouse captures in a three-factor repeated measure ANOVA with site as the blocking effect that received all combinations of season, treatment (hedgerow vs. conventionally managed border), and distance from field edge (0, 10, 75, 175 m; Zar, 1999) for walnut orchards and tomato fields separately. If a model resulted in a $P < 0.10$, we used Fisher's least significant difference *post hoc* test to determine which categories were different ($\alpha = 0.05$ for *post hoc* test). The two transects that we sampled per distance classification at each site were considered subsamples of each field edge-distance combination (sample unit) each season. Analyses were conducted separately between walnut orchards and tomato fields given the large difference in habitat type between the two crops. Given fewer observations of house mice, desert cottontails, and black-tailed jackrabbits in walnut orchards, we used the exact multinomial test to determine if the number of observations differed between distance categories from hedgerow and conventionally managed field borders (Zar, 1999). If an exact multinomial test resulted in a $P < 0.10$, we used multiple exact binomial tests to determine which categories differed. Our assumption for the multinomial and binomial tests was that these observations would be uniform across the different field edge-distance categories.

We compared habitat variables averaged across each transect to trapping index values and photograph index values (number of photographs taken of a species per camera site per 24-hr period; Engeman, 2005; Bengsen et al., 2011; Baldwin et al., 2014a) averaged across these same transects using Spearman's ranked correlation analysis to determine how strongly habitat factors were related to mammal activity (Zar, 1999). For correlation analyses, each transect served as the sampling unit given the potential for habitat variables to vary between transects at the 0- and 10-m distance from field-edge categories. Data were analyzed seasonally to determine potential differences in correlations between habitat variables and mammal activity across seasons.

We compared proportion of positive samples of foodborne pathogens between hedgerow and conventionally managed field-edge halves of fields using Fisher's exact test (Zar, 1999). We provided descriptive results for pathogens that were not detected at a high enough rate to statistically analyze.

3. Results

3.1. Species richness and relative abundance

Overall, we documented 16 mammal species during this study (Table 1). We observed substantial overlap in species richness and abundance across the two crop systems, with the principle difference reflected by broader representation of mesopredators and mule deer (*Odocoileus hemionus* Rafinesque, 1817), but fewer house mice, in walnut orchards as compared to tomato fields (Table 1). We observed greater species richness in hedgerow portions of sampled fields across all seasons for both crop systems (Table 1). Relative abundance generally mirrored species richness with California ground squirrels (*Otospermophilus* spp.; 15 vs. 1), desert cottontails (34 vs. 0), black-tailed jackrabbits (37 vs. 17), and Virginia opossums (*Didelphis virginiana* Linnaeus, 1758; 15 vs. 2) substantially more numerous in the half of the field associated with a hedgerow versus the conventionally managed field edge (Table 1). Species richness was greatest in summer and least in spring in walnut orchards; we observed little difference in species richness between spring and summer in tomato fields (Table 1).

Of the rodent species trapped, deer mice were the species we most frequently captured in walnut orchards ($n = 372$ individuals, 94%) and tomato fields ($n = 180$, 52%). House mice were the second most common rodent in both crop systems, although they were far more prevalent in tomato fields ($n = 160$, 46%) than walnut orchards ($n = 13$, 3%). We rarely captured California voles (walnut: $n = 7$; tomato: $n = 3$); in walnut orchards, we captured 6 California voles directly within hedgerows, with one additional vole trapped 75 m from the conventionally managed field edge. Similarly, we captured two California voles 10 m from the hedgerow in a tomato field, with one additional vole captured 10 m from the conventionally managed field edge. We also captured two western harvest mice in walnut orchards, and two rats in tomato fields, all of which were located within the hedgerow. Because of limited observations of most species, we only included deer mice, house mice, desert cottontails, and black-tailed jackrabbits in statistical analyses.

3.2. Deer mice

We observed a difference in deer mouse activity across seasons ($F_{3,27} = 3.6$, $P = 0.061$) with activity greatest in winter and lowest in autumn (Fig. 2). We did not identify any effect of field-edge habitat ($F_{1,27} = 4.7$, $P = 0.118$) or distance from field edge ($F_{3,27} = 1.2$, $P = 0.358$) on deer mouse activity in walnut orchards, nor were any two- ($F_{3,27}$ and $F_{9,27} \leq 2.3$, $P \geq 0.143$) or three-way interactions ($F_{9,27} = 1.8$, $P = 0.109$) significant. For tomato fields, deer mice were 2 times more abundant during spring than summer ($F_{1,12} = 20.9$, $P = 0.010$; Table 1). We did not observe any effect of field-edge habitat ($F_{1,12} = 0.1$, $P = 0.814$) or distance from field edge ($F_{3,12} = 0.6$,

Table 1

Measures of relative abundance for all mammalian species identified across various seasons (Sum = summer, Aut = autumn, Win = winter, Spr = spring) at 4 walnut orchards (2013–2014) and 5 tomato fields (2015) in the Sacramento Valley, California (CA). Data were collected on halves of orchards and fields bordered by hedgerows and conventionally managed field edges. Species richness is provided for comparison.

Species	Walnut orchards								Tomato fields				
	Hedgerow				Conventional				Hedgerow		Conventional		
	Sum	Aut	Win	Spr	Sum	Aut	Win	Spr	Spr	Sum	Spr	Sum	
Deer mouse ^a	43	18	97	45	48	24	80	17	61	31	58	30	
House mouse ^a	0	6	7	0	0	0	0	0	34	63	8	55	
California vole ^a	0	1	4	1	0	0	1	0	1	1	0	1	
Western harvest mouse ^a	0	0	0	2	0	0	0	0	0	0	0	0	
Norway rat ^a	0	0	0	0	0	0	0	0	1	0	0	0	
Roof rat ^a	0	0	0	0	0	0	0	0	1	0	0	0	
CA ground squirrel ^b	6	1	0	0	1	0	0	0	1	7	0	0	
Western gray squirrel ^b	1	0	0	0	0	0	0	0	0	0	0	0	
Desert cottontail ^b	13	7	1	0	0	0	0	0	5	8	0	0	
Black-tailed jackrabbit ^b	2	7	18	8	0	10	6	1	0	2	0	0	
Raccoon ^b	7	2	1	0	5	4	1	0	0	0	0	0	
Striped skunk ^b	3	1	2	0	3	0	1	1	0	0	1	0	
Virginia opossum ^b	6	5	4	0	2	0	0	0	0	0	0	1	
Mule deer ^b	4	0	0	1	3	0	0	0	0	0	0	0	
Domestic cat ^b	25	4	9	7	25	10	17	4	0	1	1	0	
Domestic dog ^b	2	0	0	1	1	0	1	0	0	0	0	1	
Species richness	11	10	9	7	8	4	7	4	7	7	4	5	

^a Number of unique individuals captured using Sherman live traps.

^b Number of remote-triggered camera locations with a photograph documenting the presence of the listed species.

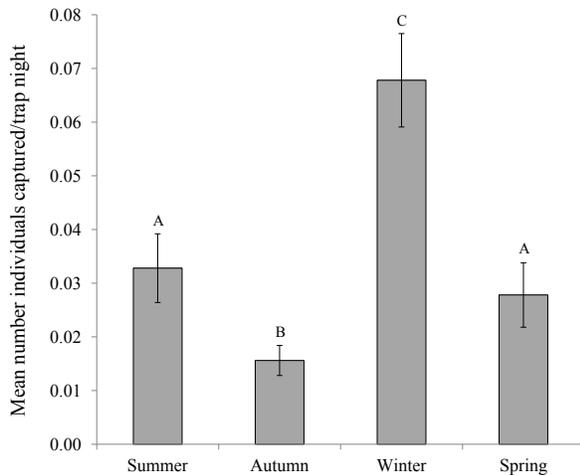


Fig. 2. Mean number of unique deer mice captured per trap night and associated standard errors across four seasons in walnut orchards in the Sacramento Valley, California during 2013–2014. Differences in mean captures are denoted by different letters ($P \leq 0.05$).

$P = 0.649$) on deer mouse activity in tomato fields, but we did observe an interaction between season and distance from field edge ($F_{3,12} = 4.6$, $P = 0.022$), with deer mice observed more frequently toward field interiors during spring and more frequently toward field edges during summer (Fig. 3). No other two- ($F_{1,12}$ and $F_{3,12} \leq 0.9$, $P \geq 0.495$) or three-way interactions ($F_{3,12} = 2.0$, $P = 0.169$) were significant.

We did not observe a consistent trend in deer mouse habitat preference across seasons or crop types. In walnut orchards, deer mice were captured more frequently in areas with abundant forb cover ($r_s = 0.30$, $n = 64$, $P = 0.016$) but less thatch cover ($r_s = -0.45$, $n = 64$, $P < 0.001$) during autumn. No variables strongly influenced deer mouse presence during winter or spring in walnut orchards, but we did see a correlation with habitat variables reflective of more open and sparsely vegetated areas in tomato fields during spring (grass cover: $r_s = -0.43$, $n = 79$, $P < 0.001$; thatch cover: $r_s = -0.42$, $n = 79$,

$P < 0.001$; woody cover: $r_s = -0.29$, $n = 79$, $P = 0.010$; canopy cover: $r_s = -0.32$, $n = 79$, $P = 0.004$). No variables were correlated with deer mouse presence in tomato fields during summer.

3.3. House mice

House mice were not evenly distributed throughout the walnut orchards (exact multinomial test, $P < 0.001$), with all individuals ($n = 13$) observed within the hedgerow itself. House mice were present only during winter ($n = 7$) and autumn ($n = 6$). In tomato fields, we did not observe a significant effect of season ($F_{3,12} \leq 2.3$, $P \geq 0.208$), field-edge habitat ($F_{1,12} \leq 2.8$, $P \geq 0.169$), or distance from field edge ($F_{3,12} \leq 2.4$, $P \geq 0.124$) on house mouse activity, nor did we observe any significant two-factor interactions ($F_{1,12}$ and $F_{3,12} \leq 1.4$, $P \geq 0.286$). However, we did observe a season \times field edge \times distance interaction ($F_{3,12} = 3.4$, $P = 0.053$) with house mice generally more common closer to the hedgerow during spring and in the field interior during summer (Fig. 4). House mice were never found in the conventionally managed field border regardless of season (Fig. 4), and in contrast to deer mice, their overall abundance across all sites and field-edge habitats was 2.8 times greater during summer than in spring (Table 1).

In contrast to deer mice, we observed relatively consistent relationships between house mice and several habitat features in walnut orchards during both autumn (woody cover: $r_s = 0.48$, $n = 64$, $P < 0.001$; bare ground cover: $r_s = -0.26$, $n = 64$, $P = 0.036$; grass cover: $r_s = 0.24$, $n = 64$, $P = 0.052$; ground level vertical cover: $r_s = 0.25$, $n = 64$, $P = 0.049$; total vertical cover: $r_s = 0.26$, $n = 64$, $P = 0.035$) and winter (woody cover: $r_s = 0.58$, $n = 64$, $P < 0.001$; bare ground cover: $r_s = -0.33$, $n = 64$, $P = 0.008$; grass cover: $r_s = 0.32$, $n = 64$, $P = 0.010$; ground level vertical cover: $r_s = 0.32$, $n = 64$, $P = 0.009$; total vertical cover: $r_s = 0.33$, $n = 64$, $P = 0.007$), likely reflective of their exclusive use of relatively dense hedgerow habitats. We observed similar results in tomato fields in spring (bare ground cover: $r_s = -0.28$, $n = 79$, $P = 0.012$; forb cover: $r_s = 0.23$, $n = 79$, $P = 0.045$; ground level vertical cover: $r_s = 0.37$, $n = 79$, $P < 0.001$; total vertical cover: $r_s = 0.32$, $n = 79$, $P = 0.004$), but saw a different trend in summer with their movement out of hedgerows and into more interior portions of the fields (forb cover: $r_s = 0.32$, $n = 79$,

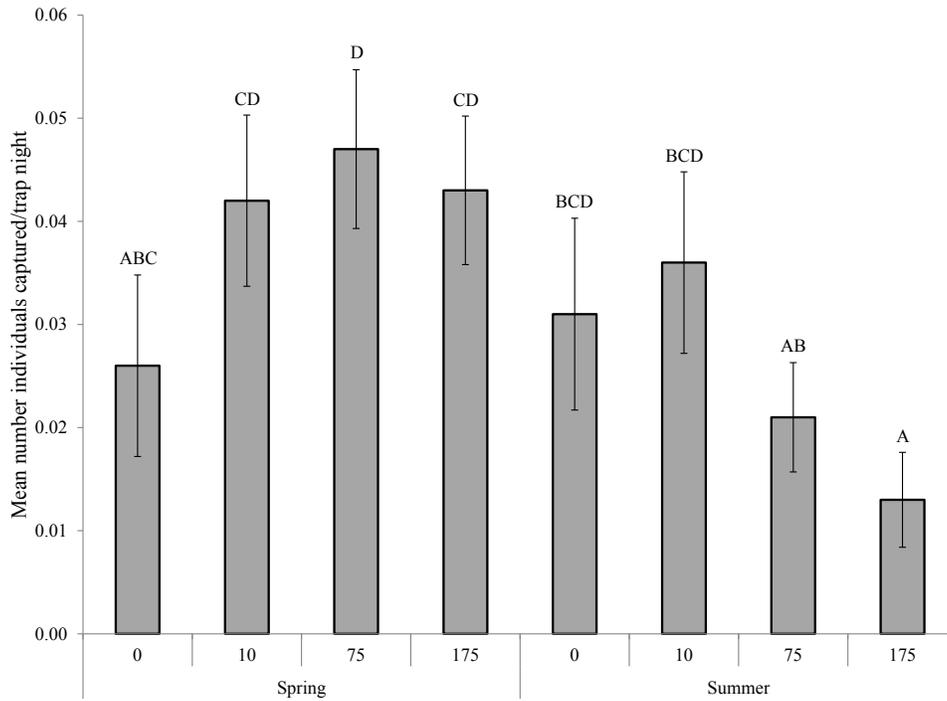


Fig. 3. Mean number of unique deer mice captured per trap night, as well as their respective standard errors, across four distances (0, 10, 75, and 175 m) from tomato field edges in the Sacramento Valley, California during spring and summer 2015. Differences in mean captures as defined by distance from field edge and season are denoted by different letters ($P \leq 0.05$).

$P = 0.004$).

3.4. Desert cottontails

We observed an unequal distribution of desert cottontails in walnut orchards (exact multinomial test, $P = 0.020$), with all cottontail

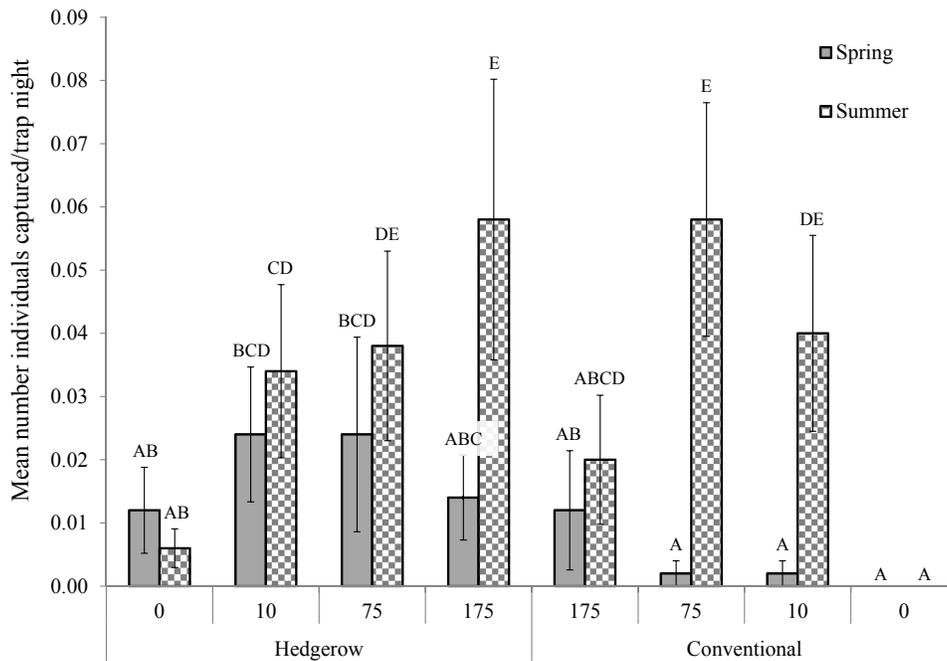


Fig. 4. Mean number of unique house mice captured per trap night, as well as their respective standard errors, across four distance intervals from hedgerow and conventionally managed field edges in tomato fields in the Sacramento Valley, California during spring and summer 2015. Differences in mean captures as defined by field-edge habitat, distance from field edge, and season are denoted by different letters ($P \leq 0.05$).

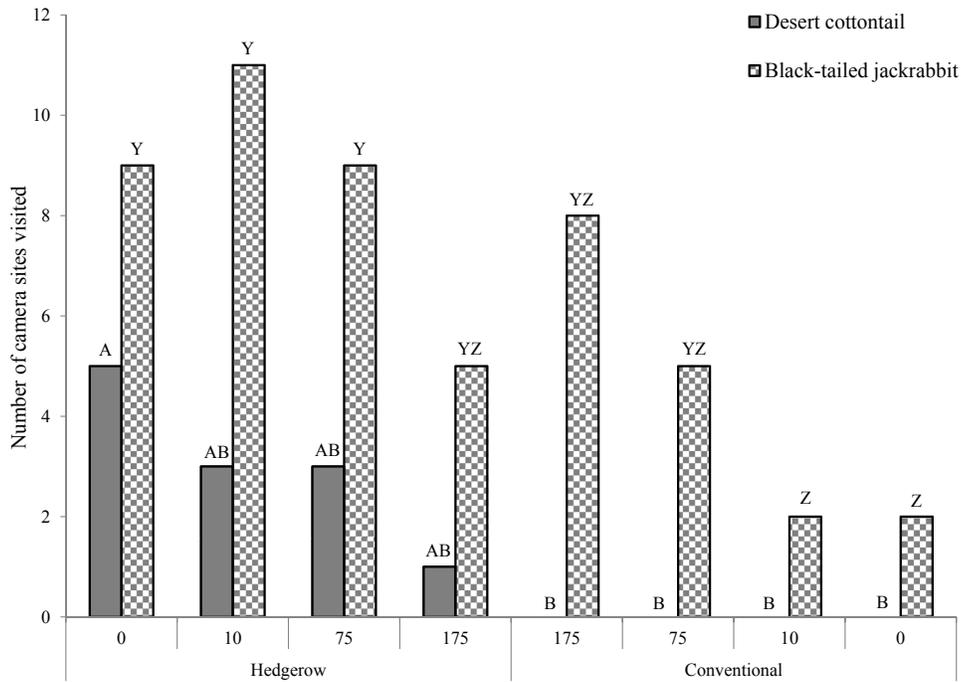


Fig. 5. Total number of photographic camera sites (excluding video cameras) visited by desert cottontails and black-tailed jackrabbits across four distances (0, 10, 75, and 175 m) from hedgerow and conventionally-managed field edges in walnut orchards in the Sacramento Valley, California during 2013–2014; sampling occurred across all four seasons. Differences in the number of visited camera sites as defined by field-edge habitat and distance from field edge for each species are denoted by different letters ($P \leq 0.05$ except for cottontails where $P = 0.06$ due to low number of observations).

Table 2

Incidence of *Salmonella*, *Escherichia coli* O157, Non-O157 Shiga toxin-producing *E. coli* (STEC), *Giardia*, and *Cryptosporidium* from rodent feces (from individual live trapped deer mice, house mice, and voles) in walnut orchards (2013–2014) and processing tomato fields (2015) in the Sacramento Valley, California. Data were collected on halves of orchards and fields (Field edge) bordered by hedgerows and conventionally managed field edges.

Crop	Field edge	Incidence in individual rodent feces				
		<i>Salmonella</i>	<i>E. coli</i> O157	Non-O157 STEC	<i>Giardia</i>	<i>Cryptosporidium</i>
Walnut	Hedgerow	2/125	0/125	2/125 ^a	15/49	12/49
	Conventional	0/93	0/93	2/93 ^b	7/38	9/38
	Total percentage	1	0	2	25	24
Tomato	Hedgerow	0/141	0/141			
	Conventional	0/118	0/118			
	Total percentage	0	0			

^a Serotype O3 and O137.

^b Serotype O137.

observations occurring exclusively on the hedgerow side of the orchard and generally closer to hedgerow habitats (Fig. 5). Almost all observations occurred during autumn ($n = 6$) and summer ($n = 5$), although we did photograph a cottontail at one site in winter (Table 1).

Desert cottontails exhibited consistently high use of areas with abundant woody cover in walnut orchards ($r_s = 0.30$, $n = 64$, $P = 0.016$) and tomato fields ($r_s = 0.61$, $n = 20$, $P = 0.004$) across all seasons for which we had sufficient visitation data to analyze (excluded winter and spring seasons in walnut orchards). No other attributes were strongly correlated to cottontail use in walnut orchards during autumn, but we did observe strong fidelity to sites with abundant vertical and canopy cover during both spring (canopy cover: $r_s = 0.55$, $n = 20$, $P = 0.012$; total vertical cover: $r_s = 0.52$, $n = 20$, $P = 0.019$) and summer (canopy cover: $r_s = 0.71$, $n = 20$, $P < 0.001$; ground level vertical cover: $r_s = 0.47$, $n = 20$, $P = 0.035$; total vertical cover: $r_s = 0.69$, $n = 20$, $P < 0.001$) sampling periods in tomato fields.

3.5. Black-tailed jackrabbits

As with desert cottontails, black-tailed jackrabbits were not evenly distributed throughout walnut orchards (exact multinomial test, $P = 0.086$). However, jackrabbits used a substantial proportion of the orchard, although use was minimal toward the conventionally managed field edge (Fig. 5). Jackrabbits used the orchards most frequently during winter ($n = 25$) and autumn ($n = 17$); observations were less frequent during spring ($n = 7$) and summer ($n = 2$).

Black-tailed jackrabbits showed a consistent avoidance of areas with abundant thatch cover (autumn: $r_s = -0.35$, $n = 64$, $P = 0.005$; winter: $r_s = -0.39$, $n = 63$, $P = 0.002$; spring: $r_s = -0.30$, $n = 64$, $P = 0.015$) across all seasons in walnut orchards. We also observed a negative correlation between canopy cover and black-tailed jackrabbit use of sites during autumn ($r_s = -0.26$, $n = 64$, $P = 0.035$). We had insufficient visitations at tomato fields for analysis.

3.6. Pathogens

A minimal number of *Salmonella* (2 out of 218) and non-O157 STEC (4 out of 218) were detected from individual rodents in walnut orchards (Table 2). We did not observe any noticeable trend based on species, location, or season. For example, *Salmonella* was detected in 1 house mouse during autumn and 1 California vole during spring, both of which were captured in the hedgerow field edge. For non-O157 STEC, 2 infected individuals were located 10 m from the hedgerow field edge, while the other 2 positive tests occurred 10 m and 175 m from the conventionally managed field edges; of these positive samples, 3 occurred during winter and 1 during autumn, all of which were deer mice. We never detected *E. coli* O157 in any samples. Furthermore, we did not detect any foodborne pathogens from rodent samples collected from tomato fields.

We detected *Giardia* cysts and *Cryptosporidium* oocysts in 22 and 21 individual deer mice ($n = 87$), respectively, in walnut orchards (Table 2). We did not detect *Giardia* or *Cryptosporidium* in any other rodent species, nor did we detect any difference in *Giardia* or *Cryptosporidium* positive samples between hedgerow and conventionally managed portions of sampled orchards (*Giardia* = Fisher's exact test, $P = 0.223$; *Cryptosporidium* = Fisher's exact test, $P = 1.0$; Table 2). Due to the limited numbers of (oo)cysts obtained from positive samples, only 2 samples of *Cryptosporidium* and 3 samples of *Giardia* from deer mice were genotyped. Genotyping results suggested *Cryptosporidium* and *Giardia* in these deer mice were Deer mouse genotypes.

4. Discussion

Hedgerows along field-crop edges have the potential to provide valuable refuge and food resources for wildlife in intensively farmed landscapes (Benton et al., 2003; Rodríguez-Pastor et al., 2016). Our study supports this important ecological role of hedgerows for many wildlife species in orchard and vegetable fields in Northern California. For example, lagomorphs and all rodents except deer mice were more common on the hedgerow side of fields, with several species only found within or immediately adjacent to hedgerows. However, by design, hedgerows are narrow, linear patches that exhibit a high edge to interior ratio, potentially limiting their attractiveness to some wildlife species (Danielson, 1990; Tilman, 1999). Although these linear habitats are structurally more heterogeneous than nearby fields and conventionally managed field borders, they do not have a large enough insular area to permit substantial population growth or high diversity without support from adjacent crop systems. In particular, it is habitat generalists that maximize the benefits of these hedgerow habitats by expanding out into crop fields (Mineau and McLaughlin, 1996; Butet and Leroux, 2001; Tattersall et al., 2002), although such expansion is dependent on the crop available (e.g., house mice did not expand into walnut orchards but readily expanded into tomato fields). Likewise, the current crop influences the species potentially present in the field regardless of field-edge composition (e.g., mule deer and raccoon [*Procyon lotor* Linnaeus, 1758] were present only in walnut orchards), and should be considered when determining potential wildlife damage and food safety risk to crops.

While species richness was greatest in and around hedgerows, we still observed large numbers of small rodents in field interiors both in walnut orchards and tomato fields. Deer mice were the principle species found in walnut orchard interiors. These interiors often had minimal vegetative cover, particularly when compared to hedgerow habitats. Deer mice are pioneering species that will inhabit vacated areas regardless of surrounding field-edge habitat (Burt and Stirton, 1961). They do well in habitats with more open space and less vegetative cover (Geier and Best, 1980; Wolf et al., 2017) which illustrates why they were distributed throughout the orchard.

Furthermore, we observed a difference in deer mouse activity within walnut orchards seasonally, with the greatest activity observed

in winter; activity was substantially lower in autumn. Reasons for the seasonal disparity are likely driven by the prevailing climatic conditions in our study areas. Central California experiences a Mediterranean climate defined by cool, wet winters and hot, dry summers. Winter through early spring is when most of the vegetation grows in California, likely providing more abundant food and cover resources for deer mice at this time (Jameson, 1952). Conversely, autumn represents the end of the hot, dry season with little natural food available within the orchard. Additionally, harvest of walnuts occurred prior to autumn sampling, thereby reducing the availability of this food source as well.

This seasonal disparity in usage of orchards by deer mice is worth noting, as it provides insight into key times for monitoring and managing deer mice in orchards. Although winter is the season with the greatest deer mouse activity, winter also coincides with the dormant season for tree crops. This allows the grower to predict potential damage and food safety concerns that may arise later in the year (i.e. large numbers of deer mice in winter could predict greater damage and food safety risk during the crop growing season). Effective removal of abundant deer mouse populations from orchards during winter should lower this potential risk later in the year. Furthermore, the dormant season is the only time that some treatment options can legally be used (e.g., rodenticide applications; Baldwin et al., 2014a). Therefore, effective early-season monitoring is essential for limiting potential damage concerns from deer mice during the growing season.

Although deer mice were widely distributed throughout the walnut orchards, house mice were relegated exclusively to the hedgerows, and were only found during autumn and winter. House mice generally prefer sites with denser vegetation (Lorenz and Barrett, 1990; Wolf et al., 2017) as was found in hedgerow habitats. In particular, house mice were more attracted to sites with abundant vertical cover, woody cover, and less bare ground. Nonetheless, house mouse numbers were quite low, suggesting that crop systems with minimal cover will likely be monopolized by deer mice rather than house mice regardless of the field-edge habitat.

In contrast, tomato fields were far more desirable for house mice. When initially planted, tomato fields consist mostly of bare ground which deer mice prefer and house mice avoid (Geier and Best, 1980; Lorenz and Barrett, 1990; Wolf et al., 2017). As tomato plants mature, the field essentially becomes a solid vegetative mass that benefits house mice. As such, we would expect greater use of field interiors by house mice as the plants matured, which was the exact trend that we observed in this study. Interestingly, the type of edge habitat did not influence deer mouse distribution, but hedgerow field-edges were utilized more frequently than conventionally-managed field edges by house mice, particularly during spring. Again, this is likely driven by a difference in cover needs between the two species. House mice were strongly attracted to sites with more vertical cover, more forb cover, and less bare soil during spring, while deer mice utilized sites with less grass, woody, thatch, and canopy cover. This allowed deer mice to use most of the field, but relegated house mice mostly to the hedgerows and immediately adjacent portions of the fields during spring. This changed in summer when house mice were able to expand out into the middle of tomato fields given abundant vegetative growth, which was further reflected by the strong correlation to forbs (i.e. tomato plants) during summer.

Of the two lagomorph species present in the study area, desert cottontails were most impacted by the presence of hedgerows; all cottontail activity occurred on the hedgerow side of fields for both walnut and tomato crops (Table 1) likely due their strong need for sufficient vertical and canopy cover to avoid predators, as well as woody vegetation for both cover and food (Chapman and Litvaitis, 2003). Black-tailed jackrabbits also showed a moderate preference for hedgerow habitats, although this effect was definitely muted when compared to desert cottontails. Black-tailed jackrabbits are more accustomed to using open habitats (Brown and Krausman, 2003; Flinders and Chapman, 2003), as indicated by greater use of sites with less canopy

cover during autumn. Interestingly, most desert cottontail activity occurred during summer through autumn while black-tailed jackrabbit activity was greatest from autumn through winter. Both cottontails and jackrabbits will differentially use surrounding landscapes across varying seasons (Brown and Krausman, 2003; Chapman and Litvaitis, 2003; Flinders and Chapman, 2003), which clearly was the case in walnut orchard study sites. It is also worth noting that black-tailed jackrabbits underutilized sites with greater thatch cover across all seasons in walnut orchards. Reasons for this apparent avoidance are unknown but thatch would provide no nutritive or concealment value, so we would not expect a positive relationship between thatch and black-tailed jackrabbit occurrence.

Because wildlife species use various cropping systems differently, a case-by-case assessment may be needed to address potential impacts of field-edge habitats on crop damage by each species. In our study, we did not observe any notable damage by deer mice or house mice, but they can cause substantial damage in some crops (Pearson et al., 2000; Brown and Singleton, 2002). Other species cause more significant and consistent losses in crop fields (e.g., ground squirrels, pocket gophers [*Thomomys* spp.], and lagomorphs; Lewis and O'Brien, 1990; Marsh, 1992, 1998; Baldwin et al., 2014b). For example, newly planted trees and annual field crops in the seedling stage (e.g., sunflowers) can be highly susceptible to damage from lagomorphs (Johnson, 1964; Schlegel, 2016). For tree crops, the presence of a hedgerow along the field edge may increase the likelihood of damage for a few years until the trees are old enough to withstand damage from rabbits and hares. Therefore, managers may seek to delay the implementation of a hedgerow in these situations, or alternatively, they will need to be ready to actively manage lagomorphs in these fields. Still, the impact of hedgerows on crop damage seems to be minimal in many settings, and when not, the impact can be negated through effective wildlife management programs.

Greater rodent abundance and diversity in hedgerow habitats did not lead to a greater food safety risk in our monitored crop systems. For example, *Salmonella* prevalence was low, and we did not find *E. coli* O157 in rodent fecal samples during this study, supporting other surveys showing a low presence of foodborne pathogens in wild rodents (Gennet et al., 2013; Jay-Russell, 2013; Kilonzo et al., 2013; Langholz and Jay-Russell, 2013). Furthermore, the prevalence of non-O157 STEC in feces from rodents captured in this study was also low and the serogroups (O3 and O137) were not among those that account for a majority of human illness as defined by the Centers for Disease Control and Prevention (Hughes et al., 2006; Luna-Gierke et al., 2014).

Due to resource limitations, we only tested for *Giardia* and *Cryptosporidium* in rodents in walnut orchards and determined that background levels of oocyst shedding in our study were similar to other areas of California (Kilonzo et al., 2013). Only deer mice tested positive for these parasites. This may be because the majority of captured rodents were deer mice (94%), thereby limiting our opportunities for detecting these protozoans in other rodent species. Genotyping analysis of limited available isolates of *Cryptosporidium* (2 isolates) and *Giardia* (3 isolates) indicated that the two parasites carried by deer mice both were Deer mouse genotypes that are not infectious to humans. In addition, movement of *Giardia* and *Cryptosporidium* into waterways can be mitigated through the use of vegetated filter strips along field edges, including hedgerows on drainage ditches. This would help trap and breakdown pathogens to reduce the prevalence of these protozoal parasites in our water supply (Atwill et al., 2006; Tate et al., 2006). Furthermore, we observed no increase in deer mouse activity associated with hedgerows, again indicating that hedgerow habitats should have little negative impact on protozoal distribution throughout walnut orchards. In short, the prevalence of hedgerow habitats adjacent to walnut orchards does not appear to increase prevalence of *Giardia* and *Cryptosporidium*, and may in fact reduce their risk to humans and the surrounding environment through increased filtration of potential pathogens.

4.1. Management implications

Field-edge habitat in intensively farmed landscapes promotes important ecosystem services of pollination, pest control, and water quality protection (Kremen and Miles, 2012). However, concerns about damage from wildlife and associated food safety in adjacent crops emphasize the importance of a co-management approach (Langholz and Jay-Russell, 2013; Bianchi and Lowell, 2016). This approach is important to prevent a loss of biodiversity and degradation of our natural resources and ecosystem services (Costanza et al., 1997; Kennedy et al., 2013; Holland et al., 2016). Notably, guidelines from the Leafy Green Marketing Agreement (LGMA, 2016), a well-established commodity-specific set of food safety best practices, include a definition of co-management. Although we did not examine leafy green fields in this study, our approach could be adapted to conduct future research for these crops or other produce commodities. Through its new regulations, the U.S. Food and Drug Administration (FDA) also addresses the application of practices that can enhance food safety and sustainable conservation, as described in the Food Safety Modernization Act (FSMA) Produce Safety Rule preamble (FDA, 2015).

Results from this study, although limited in cropping systems studied, showed a relatively minimal impact of hedgerow field-edge plantings on increasing mammalian wildlife incursions within adjacent crops, although locations closer to hedgerows did somewhat increase house mouse presence in tomato fields during spring when crop coverage was minimal. Still, when combined with the observed low incidences of bacterial pathogens and the fact that genotypes of *Cryptosporidium* and *Giardia* that we observed were not human-infectious, this study reinforces a growing body of literature (Langholz and Jay-Russell, 2013; Karp et al., 2015b) suggesting that vegetated field-edge habitats do not substantially increase intrusion of most wildlife species and associated transfer of fecal-borne pathogens. Hedgerows and similar field-edge habitats are generally too linear and small relative to the larger landscape to serve as a source population for mammalian pests in adjacent crops, compared to the larger agricultural landscape. Future studies are warranted to assess other commodities and geographical regions. There is also a need to examine the human clinical importance of *Cryptosporidium* and *Giardia* isolated from rodent feces through additional genotyping.

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