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SHORT-EARED OWL LAND-USE ASSOCIATIONS DURING THE BREEDING SEASON IN THE WESTERN UNITED STATES

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ABSTRACT.—The Short-eared Owl (*Asio flammeus*) is a species of conservation concern in the western USA, with evidence for declining population sizes. Monitoring of Short-eared Owls is complicated because of their low site fidelity and nomadic movements. We recruited community-science participants to implement a multi-year survey of Short-eared Owls across eight states in the western USA, resulting in a program of sufficient temporal and spatial dimensions to overcome many of the challenges in monitoring this species. We implemented both multi-scale occupancy and colonization/extinction modeling to provide insights into land-cover use, and to identify which cover types supported higher occurrence. Short-eared Owls were associated with native and anthropogenic land-cover types, but site occupancy varied among these categories and at different scales. Native grasslands, marsh/riparian, hay/fallow agriculture, and cultivated croplands were occupied most consistently across years. Occupancy rates differed at different scales (e.g., marsh/riparian was the only land-cover type positively associated with occupancy at both transect and point scales). Contrary to expectations, native shrubland was negatively associated with occupancy at the point scale, and exhibited low colonization and high extinction rates. Our results suggest that conserving native landscapes in general, and grasslands, marsh, and riparian areas specifically, would benefit Short-eared Owls. Furthermore, Short-eared Owl occupancy was positively associated with hay/fallow land-cover types, suggesting that some nonnative land-cover types can function as Short-eared Owl habitat. Lastly, our results highlight how developing a broad-scale community science survey can inform conservation for a species not well monitored by existing survey programs.

KEY WORDS: *Short-eared Owl*; Asio flammeus; *colonization/extinction modeling*; *community science*; *habitat use*; *land cover*; *multi-scale occupancy modeling*.

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ASOCIACIONES DE USO DEL SUELO DE *ASIO FLAMMEUS* DURANTE LA TEMPORADA DE CRÍA EN EL OESTE DE ESTADOS UNIDOS

RESUMEN.—*Asio flammeus* es una especie de interés para la conservación en el oeste de los EEUU, que evidencia una disminución de su tamaño poblacional. El seguimiento de esta especie es complicado debido a su baja fidelidad a sus sitios de nidificación y a sus movimientos de carácter nómade. Reclutamos a participantes de ciencia ciudadana para implementar un muestreo de varios años de *A. flammeus* en ocho estados del oeste de EEUU, lo que resultó en un programa de dimensiones temporales y espaciales suficientes como para superar muchos de los desafíos en el seguimiento de esta especie. Implementamos modelos de ocupación a múltiples escalas y de colonización/extinción para proporcionar información sobre el uso de la cobertura del suelo y para identificar qué tipos de cobertura permitieron una mayor ocurrencia. Los individuos de *A. flammeus* se asociaron con tipos de cobertura del suelo nativos y antropogénicos, pero la ocupación del sitio varió entre estas categorías y a diferentes escalas. Los pastizales nativos, los pantanos/áreas ribereñas, la agricultura de heno/barbecho y las tierras de cultivo fueron ocupados de manera más constante a lo largo de los años. Las tasas de ocupación variaron a diferentes escalas (e.g., pantano/área ribereña fue el único tipo de cobertura del suelo asociada positivamente con la ocupación tanto a escala de transecto como de punto). Contrariamente a las expectativas, los matorrales nativos se asociaron negativamente con la ocupación a la escala de punto y exhibieron bajas tasas de colonización y altas tasas de extinción. Nuestros resultados sugieren que la conservación de los paisajes nativos en general, y de los pastizales, los pantanos y las áreas ribereñas en particular, beneficiaría a *A. flammeus*. Además, la ocupación de *A. flammeus* se asoció positivamente con los tipos de cobertura del suelo de heno/barbecho, lo que sugiere que algunos tipos de cobertura del suelo no nativos pueden funcionar como hábitat para la especie. Por último, nuestros resultados destacan cómo el desarrollo de un muestreo a gran escala usando ciencia ciudadana puede apoyar a la conservación de una especie que no está bien monitoreada por los programas de muestreo existentes.

[Traducción del equipo editorial]

INTRODUCTION

Effective conservation requires knowledge of species ecology, including how individuals use habitats across a larger landscape. Of the various factors threatening species in terrestrial ecosystems, changes in land use and land cover are predicted to be the most important for terrestrial species (Sala et al. 2000), potentially having greatest impact on species that use open terrain (Tapia et al. 2017). Efforts to conserve species often rely on protected areas and reserves, but if these locations are limited in their distribution and composition of environmental conditions, they may be insufficient to maintain populations (Margules and Pressey 2000).

Short-eared Owls (*Asio flammeus*) have a near-global distribution and occupy tundra, marsh, grassland, and shrubland (Holt et al. 1999, Wiggins et al. 2020). In North America, Short-eared Owls breed in the northern USA and Canada, and mostly overwinter in the USA and Mexico (Wiggins et al. 2020). Booms et al. (2014) argued that Short-eared Owls have experienced a long-term, range-wide decline in North America. They based this claim on trends in indices of abundance derived from the Breeding Bird Survey and Christmas Bird Count from across North America (Sauer et al. 2017, National Audubon Society 2020), and state/regional conservation designations (e.g., threatened, endangered, and species of concern). Most BBS indices at the state and regional level suggest a substantial decline, exceeding 50% over the past 40 years, but only those with the largest sample sizes (e.g., regional or national), or most substantial estimated decline (e.g., California), have confidence intervals to support the projection. Langham et al. (2015), also using Christmas Bird Count data, considered Short-eared Owls as "climate endangered" and predicted a 30% loss of range and corresponding population declines. Booms et al. (2014) acknowledged that neither the Breeding Bird Survey nor Christmas Bird Count adequately sampled the Short-eared Owl population in North America, as the species is not highly vocal and is most active during crepuscular periods and at night, resulting in very few detections. Nonetheless, the Breeding Bird Survey and Christmas Bird Count represent the best broad-scale and long-term data available and provide a useful index of possible trends in Short-eared Owl abundance.

Booms et al. (2014) and Langham et al. (2015) highlighted the apparent disconnect between estimated declining population trends of Short-eared Owls, which is suggested by the Breeding Bird Survey and Christmas Bird Count, and current conservation programs underway within states and provinces in North America. To address this disconnect, Booms et al. (2014) proposed several measures to better understand and prioritize actions associated with the conservation of this species, the first of which is to better define and protect important habitats. Although Swengel and Swengel (2014) described habitat used by Short-eared Owls in the Midwest USA and Miller et al. (2016) described habitat use in Idaho, little is known about how Short-eared Owls use landscapes and habitats across western North America (i.e., information needed to direct conservation actions).

Several aspects of Short-eared Owl ecology further complicate the development of effective monitoring strategies. First, Short-eared Owls respond numerically and functionally to prey populations that undergo large fluctuations (Korpimäki and Norrdahl 1991). Numerical fluctuations of prey species vary in their synchrony, with prey populations being in or out of phase both temporally and spatially. As prey cycles can be moderated by predation pressure, the presence or absence of Short-eared Owls may influence the amplitude and period of prey cycles, resulting in temporal or spatial changes in habitat suitability (Ims and Andreassen 2000, Myers 2018). Furthermore, the timing and amplitude of prey cycles tend to vary between temperate and more northerly regions. Short-eared Owls appear to respond to these complex changes by adopting an irruptive or nomadic movement strategy whereby they regularly move across landscapes and regions—sometimes involving great distances—to settle in areas with suitable food resources (Village 1987, Korpimäki and Norrdahl 1991). Second, Short-eared Owls do not always return to previous breeding locations and may spend consecutive summers in areas great distances apart (Johnson et al. 2017). This high variability in movement both within and between years means that population monitoring at local scales provides little knowledge about population status; observed change could reflect either a change in population size or movement of owls beyond the boundaries of local monitoring efforts. Because of these aspects of Short-eared Owl ecology, and because the Breeding Bird Survey and Christmas Bird Count do not adequately monitor Short-eared Owl populations at scales relevant to conservation, it may be necessary to develop different approaches to assessing their population status and trends at a regional spatial scale.

To address the need for assessing population status and habitat use of Short-eared Owls in the western USA, we formed the Western *Asio flammeus* Landscape Study (hereafter WAfLS) in 2015. We used 5 yr of data (2016–2020) from that coordinated survey effort across the western USA to (1) quantify breeding-season habitat use by evaluating associations of Short-eared Owl presence and land-cover types in the western United States, and (2) quantify how land-cover types are associated with annual site occupancy. Based on existing descriptions of Short-eared Owl–habitat relations (Swengel and Swengel 2014, Miller et al. 2016), we expected Short-eared Owls in western USA to occupy native grasslands, marshlands, and shrublands, with greater annual occupancy in the most productive land-cover types.

Methods

Study Area. Our study area evolved over the period of this project. We began surveys in Idaho and Utah in 2015 (Miller et al. 2016), added Nevada and Wyoming in 2017, and in 2018 added California, Montana, Oregon, and Washington. Our 2018–2020 study area included those eight western states (Fig. 1).

We randomly located survey areas within a grid-cell network distributed across our study area. We placed a 10-km^2 grid across our study area, and within grid cells, quantified land-cover types using Landfire data (US Geological Survey [USGS] 2019), or in the case of California, using Vegetation Classification and Mapping Program (VegCAMP; California Department of Fish and Wildlife 2020) data (not available in other states). We used the VegCAMP data in California because our state agency partners suggested that it was more accurate compared to Landfire data, especially in open-country landscapes within that state. We chose a 10-km^2 grid to distribute surveys as we estimated that a maximum of 9 km of roadway could be surveyed in a single evening (Larson and Holt 2016).

We considered grassland, shrubland (ranging from chaparral, to scrub, and sagebrush), marshland/riparian, and agriculture land-cover types as potential Short-eared Owl habitat (Wiggins et al. 2020). Our sampling universe included grid cells with $\geq$70% of land cover ($\geq$60% in California to get enough

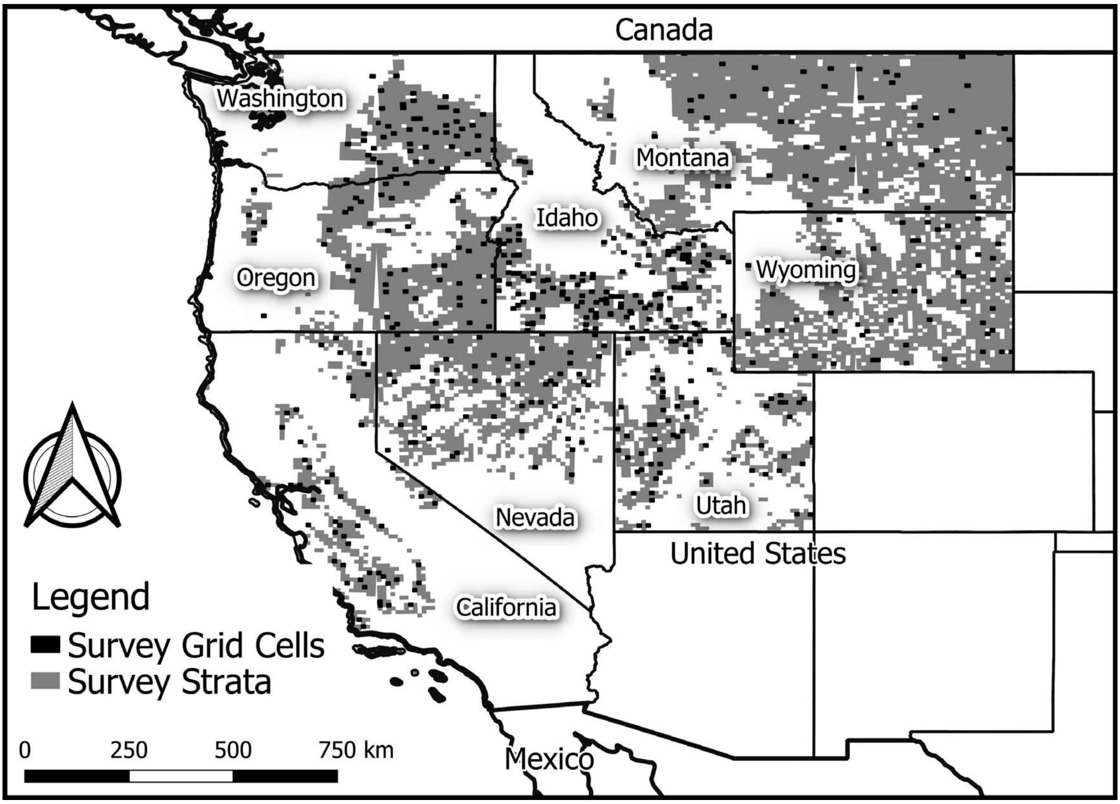

Figure 1. Study area where we conducted surveys for Short-eared Owls within eight western states of the USA, 2016–2020. The sampling universe is highlighted in gray and the sampled grid cells are highlighted in black.

coverage within the state) consisting of any combination of the four land-cover types, resulting in 8782 grid cells (87,820,000 ha) with possibly suitable land cover across our study area (Fig. 1). From this sampling universe, we selected 50 spatially balanced grid cells per state to sample using a generalized random-tessellation stratified process (Fig. 1; Stevens and Olsen 2004). We eliminated grid cells with no secondary roads, because they were a requirement of our road-based survey protocol.

Establishing Survey Routes. Our survey participants delineated a survey route within each sampled grid cell along one or more road segments that totaled approximately 9 km of secondary road. If multiple possible routes were available within a sampled grid cell, we encouraged participants to choose routes expected to have the least amount of traffic, routes on the edge of areas that were largely roadless, or routes where they expected the highest likelihood to detect Short-eared Owls. This selection of routes within the sampled grid cell may help decrease the bias from being restricted to roadways by surveying available areas that are least disturbed by traffic and roads. In limited cases, such as when participants could not find a 9-km section of road within a sampled grid cell, we allowed survey routes to extend outside of the sampled grid cell, but not for the purpose of accessing other areas with higher expectations of encountering Short-eared Owls.

Field Methods. We accomplished our project largely with the participation of community-science volunteers who we recruited to conduct surveys for Short-eared Owls. We successfully recruited approximately 600 participants per year once our study area expanded to eight states and approximately 90% of participants were volunteers. We recruited state, federal, and nongovernmental organization biologists to conduct surveys in our sample of grid cells when we were unable to locate a volunteer. More than 1200 individuals conducted surveys and many

Table 1. Suggested timing for surveys of Short-eared Owls for each of two visits derived from mean elevation of the survey grid cell, latitude, and expected courtship period within states participating in standardized surveys in the western USA.

States[a]	Elevation Range, m	Visit 1	Visit 2
CA, ID, OR, WA	<1220	1 Mar–21 Mar	22 Mar–15 Apr
	1220–1829	16 Mar–7 Apr	8 Apr–30 Apr
	>1829	1 Apr–21 Apr	22 Apr–15 May
MT	<1220	16 Mar–7 Apr	8 Apr–30 Apr
	1220–1829	1 Apr–21 Apr	22 Apr–15 May
	>1829	15 Apr–6 May	7 May–28 May
NV, UT	<1524	1 Mar–21 Mar	22 Mar–15 Apr
	1524–1829	16 Mar–7 Apr	8 Apr–30 Apr
	>1829	1 Apr–21 Apr	22 Apr–15 May
WY	<1524	10 Mar–31 Mar	1 Apr–22 Apr
	1524–1829	24 Mar–14 Apr	15 Apr–6 May
	1830–2134	7 Apr–28 Apr	29 Apr–20 May
	>2134	14 Apr–5 May	6 May–27 May

[a] State abbreviations: CA = California; ID = Idaho; MT = Montana; NV = Nevada; OR = Oregon; UT = Utah; WA = Washington; and WY = Wyoming.

participants conducted surveys in one or two grid cells. Individual participants had a range of experience conducting surveys and identifying Short-eared Owls, but we were unable to account for variation in skill level in our survey design and analyses. Instead, we recruited the most knowledgeable participants possible, many of whom were committed birders and naturalists with skills exceeding those of some of the professional biologists, and we provided online and interactive training on all aspects of the program: route selection, survey protocol, owl identification, and data entry. We suspect that this variation in skill level would most likely dilute our ability to detect associations, thus increase our confidence in any Short-eared Owl–habitat associations we identified.

We asked participants to make two visits to each survey route during two specified 3-wk survey windows per year, timed to coincide with the expected 6-wk Short-eared Owl courtship-flight-behavior period (i.e., a period of maximum detectability; Larson and Holt 2016). Each of the two survey windows was 3 wk long. We established survey windows for each route based upon latitude and elevation to best align with the expected courtship period of Short-eared Owls within each state and elevation zone (Table 1). Participants could choose any day within the respective survey window to conduct each survey; however, we asked participants to separate the two visits by at least 1 wk.

We asked participants to survey points, separated by approximately 800 m along secondary roads, beginning 100 min prior to the end of local civil twilight, and to complete as many points as possible (8–11 points) during the 90-min survey period and complete the survey just before darkness (Larson and Holt 2016, Miller et al. 2016). We identified survey start times in advance for each survey route and each potential survey date. Participants surveyed the same points during the two visits, and we suggested, but did not require, that the same points be surveyed among years. At each survey point observers performed a 5-min point count, noting each individual owl observed minute-by-minute (i.e., with replacement). We instructed participants not to record observations of owls outside of the 5-min point count period and to survey 360° from each point. For each observation of a Short-eared Owl, participants recorded whether the bird was seen, heard, or both, and noted discernable behavior. Lastly, participants typically entered survey data in the project website portal, but we occasionally assisted them in this process.

Land-cover Data. For all analyses we used Landfire 2016 Remap Existing Vegetation Type data to categorize land-cover type (USGS 2019). For point-scale analyses we buffered each surveyed point by 1000 m. Larson and Holt (2016) reported that in favorable conditions Short-eared Owls could be correctly identified by sight at distances up to 1600 m, with high detectability up to 800 m. Calladine et al. (2010) measured a mean initial detection distance of 500–700 m, with a maximum recorded value of 2500 m. Based on these studies, we chose 1000 m as the distance we expected nearly all owl observations to fall within.

We quantified the Landfire data within each point buffer, aggregating similar cover types into broad categories largely based upon the Landfire Physiognomy (Table 2). We chose these broad categories of land-cover types (e.g., shrubland or grassland) to group similar land-cover types across our eight-state study area that at the next level of detail included divergent non-overlapping categories (e.g., combining Inter-Mountain Basins Big Sagebrush Shrubland and California Mesic Chaparral into "shrubland"). We split the agriculture physiognomy further to separate structured agriculture (e.g., cultivated cropland, alfalfa, wheat) from less structured agricultural land uses such as hay, pasture, and fallow or

Table 2. Land-cover type variables (mean proportion of land-cover type within 1000-m buffers around survey points; within buffers around transect [within 1000 m of all survey points on transect]; and mean for entire sampling universe) and source of land-cover data used in models of occupancy by Short-eared Owls in the western USA, 2016–2020.

LAND-COVER VARIABLE	MEAN POINT (RANGE)	MEAN TRANSECT (RANGE)	MEAN SAMPLING UNIVERSE	EVT PHYSIOGNOMY[a]	NATIVE/ ANTHROPOGENIC[b]	EXAMPLES
Shrubland	0.48 (0.00–1.00)	0.38 (0.00–0.99)	0.40	Shrubland	Native	sagebrush, shrub, scrub, chaparral
Grassland	0.05 (0.00–0.99)	0.10 (0.00–0.86)	0.17	Grassland	Native	grass, meadow, prairie
Marsh/ Riparian	0.03 (0.00–0.92)	0.04 (0.00–0.68)	0.03	Riparian, Wet Meadow, and Marsh	Native	riparian, pothole, marsh, wet meadow, floodplain
Development	0.09 (0.00–0.86)	0.04 (0.00–0.40)	0.02	Developed	Anthropogenic	developed, building, infrastructure
Cropland (cultivated)	0.17 (0.00–0.98)	0.17 (0.00–0.95)	0.10	Agriculture, subset[c]	Anthropogenic	row crop, close grown crop, alfalfa, wheat
Hay/Fallow	0.09 (0.00–1.00)	0.08 (0.00–0.75)	0.05	Agriculture, subset[d]	Anthropogenic	hay, pasture, fallow/ idle cropland
Exotic	0.08 (0.00–1.00)	0.09 (0.00–0.89)	0.05	Exotic Herbaceous	Mixed	ruderal grass and meadow, introduced forbs and grasses
Other	0.03 (0.00–1.00)	0.11 (0.00–0.72)	0.18	All types not previously included.	Mixed	

[a] Landfire Existing Vegetation Class (EVT) data (USGS 2019).

[b] Qualitative assignment that evaluates the extent of direct human alteration of the landscape. Native represents low human alteration, whereas Anthropogenic represents high human alteration. Exotic vegetation may invade either native or anthropogenic landscapes.

[c] Subset of agriculture including Western Cool Temperate Row Crop - Close Grown Crop, Western Cool Temperate Row Crop, Western Cool Temperate Close Grown Crop, Western Cool Temperate Wheat, Western Warm Temperate Row Crop - Close Grown Crop, Western Warm Temperate Row Crop, Western Warm Temperate Close Grown Crop, Western Warm Temperate Wheat (USGS 2019).

[d] Subset of agriculture including Western Cool Temperate Fallow/Idle Cropland, Western Cool Temperate Pasture and Hayland, Western Warm Temperate Fallow/Idle Cropland, and Western Warm Temperate Pasture and Hayland (USGS 2019).

idle cropland, as we expected owls may use these land-cover types differently (Table 2). These land-cover types roughly fell into native (shrubland, grassland, and marsh/riparian) and anthropogenic (hay/fallow, cultivated cropland, development) landscapes. Both native and anthropogenic landscape types could include exotic herbaceous vegetation, as invasive plants may spread into either landscape type. The result of this categorization process was eight land-cover types. We quantified the proportion of the buffer around each point for each of the eight land-cover types. We used the resulting eight variables in all point-scale analyses.

For transect-scale analyses, we performed a similar process, but dissolved all point buffers into a single transect buffer extending 1000 m around all points on the transect prior to extracting and quantifying the land-cover type data. The resulting mean transect buffer area was 2519 ± 1023 (SD) ha. Similar to the point buffer process, we quantified the proportion of the eight land-cover types within the transect buffer and used the resulting eight variables in all transect-scale analyses. We acknowledge potential inaccuracies in our broad-scale land-cover data and that aggregation of land-cover categories prevented identification of differences among shrubland land-cover types that we combined into a single category. Furthermore, due to our sampling approach and our limitation of surveys to secondary roads, cover-type composition along our sampled transects differed from that in the sampling universe as illustrated in Table 2.

Statistical Analyses. We analyzed data separately to address our two main goals: (1) quantify breeding season land-cover use by Short-eared Owls in the western USA, and (2) quantify how land-cover types are associated with annual site occupancy.

Breeding-season land-cover use. We used multi-scale occupancy modeling (Nichols et al. 2008) to evaluate Short-eared Owl land-cover use. Multi-scale occupancy models consist of three parameters: $p =$ the probability of detecting an owl at a point given that an owl is present, $\theta =$ the probability that a point is occupied given that the transect is occupied, and ψ $=$ the probability that the transect is occupied (Nichols et al. 2008). We implemented a minute-by-minute replacement design, allowing for simultaneous evaluation of probability of detection, point-scale occupancy, and transect-scale occupancy (Nichols et al. 2008). Following Pavlacky et al. (2012), we used a modified version of Nichols et al. (2008) where the point-scale occupancy analysis used spatial replicates, but unlike Pavlacky et al. (2012) we also included our temporal replicates (i.e., two visits), essentially producing a model where θ represents a combination of point-scale occupancy (i.e., the owl is within the point buffer) and point-scale availability (i.e., the owl is still alive and present on the transect to possibly be within the point buffer). We henceforth refer to this combination simply as point-scale occupancy, acknowledging the more complicated context (Pavlacky et al. 2017). To account for the integration of the two visits, we forced day-of-year into all models at the point-scale. As we were not specifically interested in the point-scale occupancy rate, this integration of occupancy and availability did not impair any aspects of our analysis.

We produced a model that included year, day of year, and minutes before the end of civil twilight as covariates influencing the probability of detecting an owl at a point given that an owl was present. Use of year in the model accounted for the possibility of varying probability of detection as our participant pool changed and we expanded from two states to eight states. Similarly, we included day of year to account for a change of owl behavior through the breeding season, and minutes before end of civil twilight because we expected owl behavior to change and owls to be more difficult to discern nearer darkness. Probability of detection is likely influenced by observer skill but we were unable to account for variation among observers or skill levels in our models due to the very large number of participants ($>$1200 individuals across years).

We created a multi-scale occupancy model including all eight transect-scale land-cover variables (proportion of each land-cover type within the transect buffer) plus year as predictors of occupancy at the transect scale; all eight point-scale land-cover variables (proportion of each land-cover type within the point buffer) plus day of year as predictors of occupancy at the point-scale; and year, day of year, and time predicting the probability of detecting owls. We evaluated all subsets of this model that included year at the transect scale and day of year at the point scale (see above). We ranked the resulting models using the Akaike information criterion adjusted for sample size (AIC_c; Burnham and Anderson 2002), choosing the best-supported model, and comparing it against the "null" model with just year and day of year as covariates. For each covariate appearing within our best-supported model, we produced a partial-dependency plot by varying the covariate over its measured range, while holding all other covariates at their median value. This process is used to illustrate the effect size of each covariate on the parameters of interest (i.e., p, θ, and ψ).

Land cover and annual site occupancy. To explore the association of land-cover types with annual site occupancy (site colonization, site re-occupancy, and site extinction) we utilized colonization/extinction modeling (MacKenzie et al. 2003). Modeling colonization/extinction augmented the multi-scale occupancy modeling we used to address our first objective by allowing us to separately analyze land-cover type influences on colonization and re-occupancy rates among years. We retained both multi-scale occupancy and colonization/extinction methods as each approach is more sensitive at addressing the core of each of our objectives, and neither was ideal to simultaneously address both objectives.

Colonization/extinction models consist of four parameters: p representing the probability of detection, γ representing the probability of colonization, ε representing the probability of extinction, and ψ representing the probability that the transect is occupied. As our study focused on detecting owls during conspicuous activities (i.e., foraging and courtship behavior) and not at nest locations, we conducted this modeling at the transect-scale instead of the point-scale (owls may forage across multiple survey points). We created a model that used the same transect-scale covariates from the multi-scale occupancy modeling plus year for both

Table 3. Best-supported models and corresponding null models from multi-scale occupancy and colonization/extinction models of Short-eared Owls as related to land-cover type in the western USA, 2016–2020. Greek letter ψ represents transect-scale occupancy and *p* represents the probability of detection in both modeling approaches, θ represents point-scale occupancy, γ represents the probability of colonization at the transect scale, and ε represents the probability of extinction at the transect scale.

ANALYSIS	MODEL[a]	K[b]	AIC_C[c]	ΔAIC_C[d]	DEVIANCE
Multi-scale Occupancy	ψ(~year + Grassland + Marsh/Riparian + Development + Cropland + Hay/Fallow) θ(~day of year + Marsh/Riparian + Shrubland) p(~day of year + year)	20	8545.1	0.0	8504.5
	Null: ψ(~year) θ(~day of year) p(~1)	8	8618.3	73.2	8602.2
Colonization/Extinction	ψ(~1) γ(~year + Shrubland + Hay/Fallow + Development) ε(~year + Shrubland + Grassland) p(~day of year)	16	977.6	0.0	945.6
	Null: ψ(~1) γ(~year) ε(~year) p(~day of year)	11	996.1	18.5	974.1

[a] Land-cover variables defined in Table 2.
[b] K = number of parameters in the model.
[c] AIC_c = Akaike information criterion adjusted for sample size.
[d] ΔAIC_c = difference in AIC_c values between individual model and model with lowest AIC_c.

the colonization parameter (γ) and the extinction parameter (ε), and day of year for the probability of detection parameter (*p*). As before, we evaluated all subsets of this model that included day of year using AIC_c, choosing the best-supported model and comparing against the null model (Burnham and Anderson 2002). We produced partial-dependency plots using the same methods as used for multi-scale occupancy.

Statistical software. We conducted all statistical analyses in Program R (R Core Team 2020) and used the *Rmark* package (Laake 2019) in Program R to interface with Program Mark (White and Burnham 1999) for multi-scale occupancy modeling. We fit colonization/extinction models using the R package *unmarked* in Program R (Fiske and Chandler 2011).

RESULTS

Over our five-year study period (2016–2020), participants completed surveys at 23,150 points during 1339 surveys on 534 transects. Of the 534 transects surveyed, 104 were surveyed in only one year, 157 were surveyed in two years, 156 were surveyed in three years, 66 were surveyed in four years, and 51 were surveyed in all five years of our study. Land cover along our sampled survey transects varied from that in the sampling universe (Table 2). Participants detected ≥1 Short-eared Owl at 599 points during 218 surveys on 152 transects. Of the 152 transects with owl detections, we detected owls on 102 transects in just a single year, on 38 transects in two years, on nine transects in three years, on two transects in four years, and on one transect in all five years of our study.

Breeding-season Land-cover Use. Shrubland dominated the buffers around our surveyed points, followed by cultivated cropland, hay/fallow agriculture, development, and exotic herbaceous land-cover types (Table 2). Compared to proportions of land-cover types across our sampling universe, buffers around points over-sampled shrubland, development, and cultivated cropland, and under-sampled grassland (Table 2). Our best-supported multi-scale occupancy model ranked significantly better than the null model (i.e., the model with just year and day of year as covariates; Table 3). We calculated the probability of detection of a Short-eared Owl at a point, given that there was an owl at the point (*p*), to be 0.52 ± 0.03 SE (95% CI: 0.46–0.59). The probability of detection decreased later in our survey seasons and varied among years (Fig. 2).

We estimated transect-scale occupancy (ψ) to be 0.17 ± 0.03 SE (95% CI: 0.12–0.23). Transect-scale occupancy by Short-eared Owls was most positively associated with higher levels of hay/fallow agriculture, followed by marsh/riparian, grassland, and cultivated cropland (Fig. 3). Transect-scale occupancy was negatively associated with development and varied among years.

We estimated point-scale occupancy (θ) to be 0.12 ± 0.01 SE (95% CI: 0.10–0.14). Given that at least one Short-eared Owl was present on the transect, point-scale occupancy was most positively

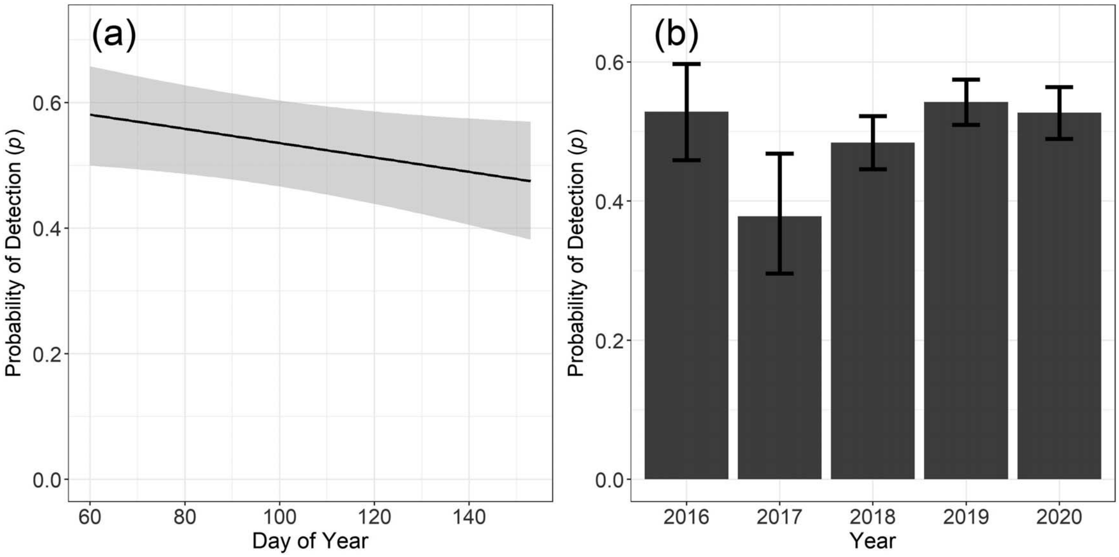

Figure 2. Probability of detecting a Short-eared Owl at a survey point, given that an owl was present at the point (p), estimated using multi-scale occupancy modeling, incorporating (a) day of year and (b) year, during the breeding season in the western USA, 2016–2020, shown with 95% confidence intervals.

associated with marsh/riparian land-cover type, and most negatively associated with shrubland (Fig. 4). Point-scale occupancy increased later in the year.

Land Cover and Annual Site Occupancy. Our best-supported colonization/extinction model with year, day of year, and multiple land-cover type covariates ranked significantly higher than the null model that included only year and day of year (Table 3). We estimated the overall colonization rate (γ) of transects among years to be 0.05 ± 0.02 SE (95% CI: 0.03–0.10), whereas the estimate of overall extinction rate (ε) on transects among years was 0.91 ± 0.06 SE (95% CI: 0.26–0.98). Colonization was positively associated with hay and fallow agriculture, and negatively associated with development and shrubland land-cover types (Fig. 5). Extinction was positively associated with shrubland and negatively associated with grassland land-cover types.

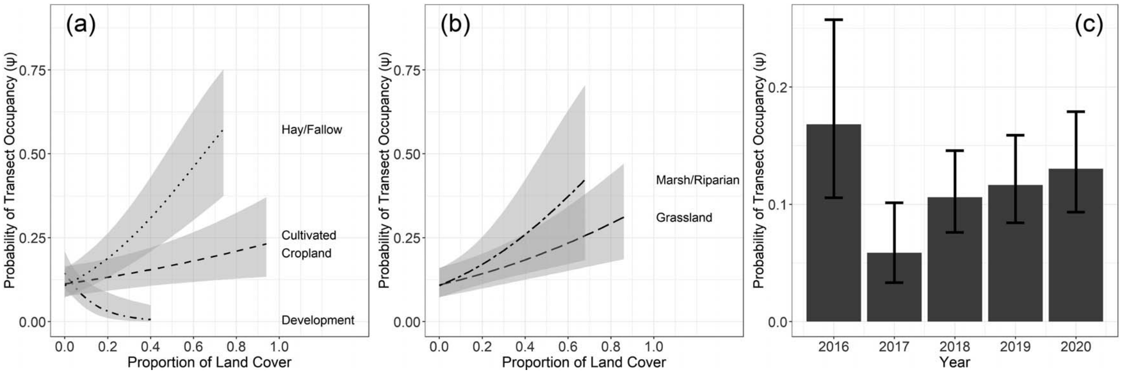

Figure 3. Transect-scale occupancy (ψ) by Short-eared Owls, estimated using multi-scale occupancy modeling, incorporating (a) anthropogenic land-cover types, (b) native land-cover types, and (c) year, during the breeding season in the western USA, 2016–2020, shown with 95% confidence intervals.

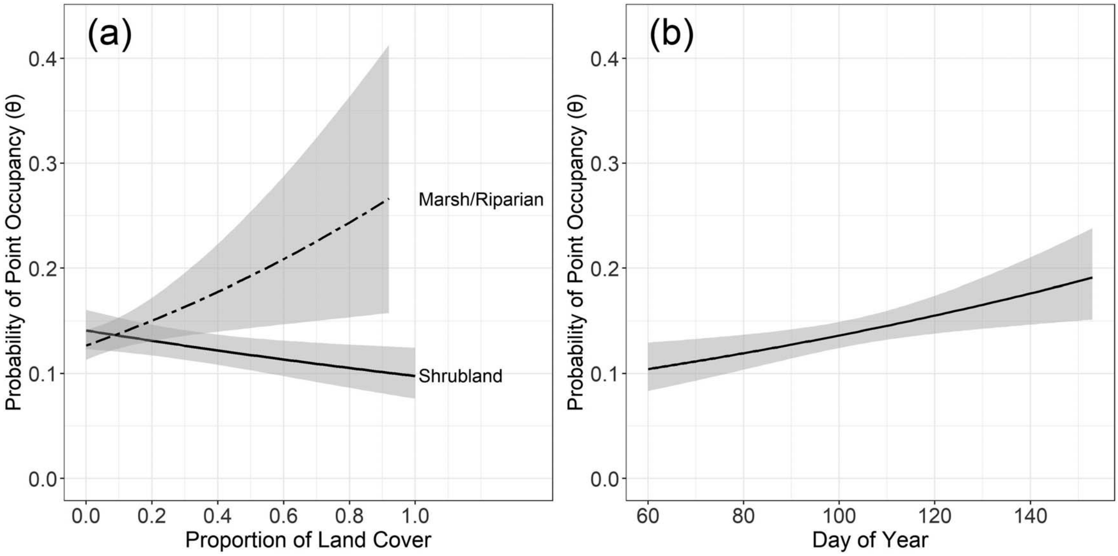

Figure 4. Point-scale occupancy (θ) by Short-eared Owls, estimated using multi-scale occupancy modeling, incorporating (a) land-cover types and (b) day of year, during the breeding season in the western USA, 2016–2020, shown with 95% confidence intervals.

DISCUSSION

We successfully recruited a corps of community-science participants to implement a multi-year survey of Short-eared Owls at a geographic scale large enough to produce meaningful results for this often nomadic species. Our approach of using both multi-scale occupancy and colonization/extinction modeling provided insights that would be difficult to acquire through one approach alone, especially for a

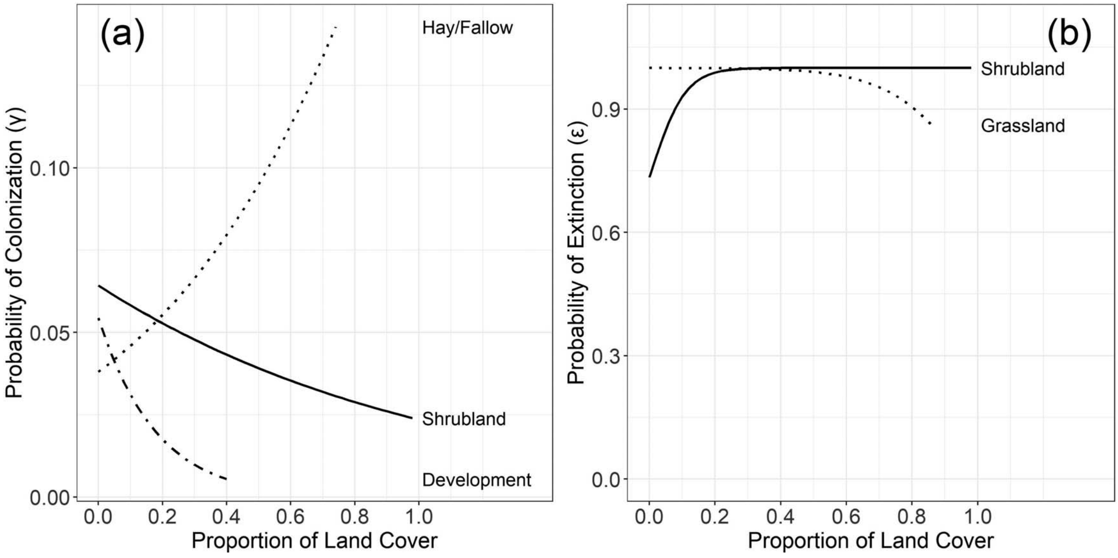

Figure 5. Land-cover type associations of Short-eared Owls with (a) colonization rates (γ) and (b) extinction rates (ε) at the transect scale during the breeding season in the western USA, 2016–2020. Note: The y-axes are at different scales.

species that uses a variety of landscapes in different ways.

Short-eared Owl transect occupancy was associated with both natural (e.g., marsh/riparian and grasslands) and anthropogenic (e.g., hay/fallow and cultivated cropland agriculture) landscapes, but annual transect occupancy varied among these landscapes. Hay and fallow agriculture land-cover types were the most positively associated with transect occupancy and transect colonization but neither was associated with point-scale occupancy nor associated with transect extinction. This suggests that hay and fallow agriculture land-cover types might provide important resources for Short-eared Owls, such as higher prey density or more easily acquired prey, but may not be land-cover types where owls spend most of their time, at least during our evening survey period. Calladine and Morrison (2013) provided evidence that Short-eared Owls use different landscapes for different activities and at different times of the day and season.

Hay and fallow agricultural land-cover types may be the land-cover types in the western USA most similar to those available in the prairie grasslands in the central USA where historical Short-eared Owl breeding density has been high (Swengel and Swengel 2014). Hay fields in the western USA are often irrigated, which may result in higher prey abundance than in non-irrigated fields (Moulton et al. 2006) and may possibly stabilize prey abundance, reducing the amplitude of cycles (Myers 2018); this could explain the importance of these land-cover types to Short-eared Owls. Fallow fields often provide grain remnants that can promote higher prey abundance, and small mammals (the primary prey of Short-eared Owls) often reproduce in fallow agriculture during early spring, the time of our surveys and of the beginning of the Short-eared Owl breeding season (Heroldová et al. 2007). Because our surveys were conducted during periods most likely to coincide with courtship flights, the lack of Short-eared Owl association with hay/fallow agriculture for point-scale occupancy suggests that Short-eared Owls may not be courting within these land-cover types. Clark (1975) reported use of hayland for nesting, but at a much lower density than in grasslands. Wiggins et al. (2020) reported hay and fallow land-cover types composed up to 38% of nesting sites. The lack of association with hay/fallow agriculture at the point-scale in our study may imply that courtship does not take place near the nesting location (Calladine and Morrison 2013). This pattern may also be influenced by other factors we were unable to measure such as the effects of predators or competition, which have been shown to influence raptor land use and nesting distributions (Rebollo et al. 2017).

Following hay and fallow land-cover types, the anthropogenic land-cover type most strongly associated with occupancy at the transect-level was cultivated cropland. Short-eared Owls may be attracted to cropland because areas under cultivation can support relatively high prey abundance, especially in alfalfa (Moulton et al. 2006, Heroldová et al. 2007), make it easier to capture prey (Schlaich et al. 2015), or both. However, cultivated cropland had a smaller estimated effect than hay/fallow agriculture (Fig. 3), and was not included in the best-supported model of occupancy at the point-scale. Across much of our study area, cultivated cropland crops were just sprouting during our survey windows and thus provided little cover as protection from predators and competitors. Not surprisingly, development had a strong negative association with transect occupancy even though we only sampled areas with a lower intensity of development (maximum of 30% at the grid cell level).

Short-eared Owls in our surveys had a positive association with the presence of cultivated cropland; however, agricultural intensification may negatively influence use of this land-cover type by Short-eared Owls (Fernández-Bellon et al. 2021), even with the expected higher prey abundance in cultivated cropland cover types. Several possible factors could negatively influence owl use of intensive agricultural landscapes including anthropogenic disturbance, lack of nesting habitat, and increased mortality or nest destruction risks due to agricultural practices (N. Paprocki pers. comm.).

In native landscapes, marsh/riparian land-cover types were positively associated with occupancy during the courtship period at both the transect and point scales, suggesting that they provide an important resource, and that owls tend to occupy these areas during courtship. Marsh land-cover types may provide Short-eared Owl nesting habitat in our study area, in contrast to other areas where grasslands tended to be used for nesting (Clark 1975, Wiggins et al. 2020).

In our study, Short-eared Owl occupancy at the transect scale was positively associated and extinction was negatively associated with grassland land-cover type. Short-eared Owls may select transects with a higher proportion of native grassland but were not associated positively or negatively with the proportion of grassland at the point scale. Assuming that we were surveying these owls in their courtship areas, these grassland observations support the hypothesis that courtship and nesting may not occur at the same location.

Native shrubland, the dominant land-cover type in our study, was not associated positively or negatively with occupancy at the transect-scale, suggesting that it was used in proportion to its availability, but was negatively associated with occupancy at the point scale, had a negative association with transect colonization, and had a positive association with transect extinction. These conclusions came as a surprise as several successful and repeat nesting attempts have been observed in native shrubland (R. Miller unpubl. data).

Overall, our estimated transect extinction rate was relatively high. This may not be a surprise for a species that exhibits low site fidelity and nomadism (Village 1987, Korpimäki and Norrdahl 1991, Johnson et al. 2017). From a conservation perspective this presents a challenge. To provide landscapes that support Short-eared Owls, it may be necessary to conserve areas that may not currently be occupied, but support owls in the future, such as hay and fallow agricultural fields, marshland, and grasslands. As grasslands had a negative association with extinction, they may represent more stable landscapes for Short-eared Owls, possibly because they support higher prey abundance, diversity, and availability (Casagrande et al. 2008).

Conversion of native landscapes to exotic herbaceous landscapes (e.g., cheatgrass [*Bromus tectorum*] invading native shrubland or grassland) continues across the western USA (Bradley et al. 2018). Replacement of native grassland with exotic herbaceous land-cover may lower prey abundance in these areas (Hall 2012). Our results suggest this conversion would decrease Short-eared Owl occupancy rates across the region, which were positively associated with native grassland but had no association (positive or negative) with exotic herbaceous land cover. We suspect that exotic herbaceous land-cover type is underrepresented in our land-cover data as this conversion is happening quickly and at broad spatial scales. Bradley et al. (2018) estimated that 31% of all landscapes in the Intermountain West (a significant portion of our study area) have been invaded with cheatgrass at a level of $\geq$15% cover. This invasion is expected to accelerate because cheatgrass alters the fire regime, further amplifying its foothold (Bradley et al. 2018). Conservation actions to slow this conversion and restore native land-cover types associated with higher occupancy by Short-eared Owls (grassland and marsh wetlands) are likely to benefit Short-eared Owls. State and federal refuge systems in the western USA often work to preserve this habitat, but maintaining Short-eared Owl populations may require more habitat than is available in refuges alone as nearly all of our observations occurred outside of refuge systems (Margules and Pressey 2000). Other conservation measures receiving support from our results include implementing practices that create conditions where Short-eared Owls can exist within agricultural landscapes (both hay and cultivated cropland) and promoting the presence of fallow agriculture fields that remain fallow through the breeding season.

Through the combination of our survey protocol and timing, we were able make statistical inference regarding Short-eared Owl habitat relationships across a large region of the western USA that augments previous broad-scale survey programs such as the Breeding Bird Survey and Christmas Bird Count. Our results have provided a level of detail to state conservation organizations not available in previous work as evidenced by the current integration of our results into the state wildlife action planning process of all eight participating states (e.g., Idaho Department of Fish and Game 2017). We encourage the continued implementation of this program for Short-eared Owl monitoring and for concepts from the program (e.g., deliberately stratified sampling scheme, careful recruitment and training of skilled volunteers, and a protocol to ensure that surveys occurred during courtship) to be used for other at-risk species not well sampled by existing programs.

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The project-specific data used in this analysis are hosted on Avian Knowledge Northwest, a regional node of the Avian Knowledge Network, where access to data may be requested (https://avianknowledgenorthwest.net/projects/short-eared-owls/).

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