RESEARCH ARTICLE

Great Gray Owls (*Strix nebulosa*) in Yosemite National Park: on the Importance of Food, Forest Structure, and Human Disturbance

Charles van Riper III[1,4]

[1]US Geological Survey Southwest Biological Science Center
Sonoran Desert Research Station
University of Arizona
Tucson, Arizona 85721

Joseph J. Fontaine[2]
Jan W. van Wagtendonk[3]

[2]US Geological Survey Nebraska Cooperative Fish and Wildlife Research Unit
University of Nebraska – Lincoln
Lincoln, Nebraska 68583

[3]US Geological Survey Western Ecological Research Center
Yosemite Field Station
El Portal, California 95318

[4] Corresponding author: charles_van_riper@usgs.gov; 520-491-0721

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ABSTRACT: We studied great gray owls (*Strix nebulosa* Forster) in Yosemite National Park, California, measuring variables that could potentially influence patterns of occurrence and conservation of this state-endangered species. We found that owl presence was closely tied to habitat (red fir (*Abies magnifica* A. Murray) and the abundance of meadows), prey, and snags across the landscape. We also found that indicators of human recreational activities negatively influenced owl distribution and habitat use. Great gray owls appear to prefer mid-elevation red fir forest with meadows that are drier and more productive in terms of small mammal populations. That these areas also have the highest human activity presents a paradox, both for individual owls and for the future conservation and management of this California endangered species. The extent to which human recreation in natural areas affects animal behavior, species distribution, and productivity is a growing issue in natural area management. We present information that will allow land managers to better understand how existing natural resources, coupled with human recreation, influence the distribution and habitat use of the great gray owl.

Index terms: distribution, great gray owl, habitat selection, human disturbance, meadows, prey selection, Yosemite National Park

INTRODUCTION

Although great gray owls (*Strix nebulosa* Forster) are common throughout their Holarctic range (Mikkola 1983), North America's southern-most population is disjunct in the Sierra Nevada of California. This owl population is genetically different (Hull et al. 2010) and considered endangered by the state of California (Bull and Duncan 1993). Yosemite National Park, in the central Sierra Nevada of California, contains the core population for this southernmost population (Bull and Duncan 1993; van Riper and van Wagtendonk 2006). Yosemite National Park is renowned for its recreational opportunities and has one of the highest visitor use rates of any United States national park (Schwartz and Lin 2006). Great gray owls are generally considered reclusive in Yosemite, often avoiding human contact when possible (Wildman 1992), but the extent to which resource availability and human activities influence the distribution of owls across the landscape is unclear. These owls are, therefore, an ideal species for assessing potential influences of natural resources and human influences on population distribution and habitat use patterns. Whether owls simply respond to resource availability, or respond to human influences in their environment, has important implication as to how to best manage this endangered species within a changing natural landscape.

Mikkola (1983) in Europe, Bull and Henjum (1990) in eastern Oregon, and Franklin (1988) on the Idaho-Wyoming border in the United States, found that great gray owls hunt primarily in open forest areas. In Yosemite, open areas are almost exclusively meadows, and owl home ranges are centered within those meadow systems (van Riper and van Wagtendonk 2006). Therefore, we focused our survey efforts in areas surrounding meadows within Yosemite National Park. Within these sites, we surveyed for the presence of great gray owls and quantified potential behavioral, environmental, and anthropogenic influences on variations in owl distribution patterns. If major influences on owls are natural, we predicted that the availability of food and nest sites should be the primary predictor of owl distribution (Reid 1989; Bull and Henjum 1990; Bull and Duncan 1993). If owl distribution is influenced by anthropogenic factors, it was important that we determine whether humans affected owls by altering the landscape or through their presence. We predicted that if humans negatively affected owl distribution by modifying their habitats, then areas associated with more development (e.g., roads, buildings, and campgrounds) should have fewer owls. If human presence is a factor negatively affecting owl presence, then areas with the highest human use should have fewer owls, independent of human development, habitat type, food, or nest site availability.

STUDY AREA AND METHODS

Study area

Yosemite National Park is located in the central Sierra Nevada of California, USA (Figure 1). The park is over 300,000 ha

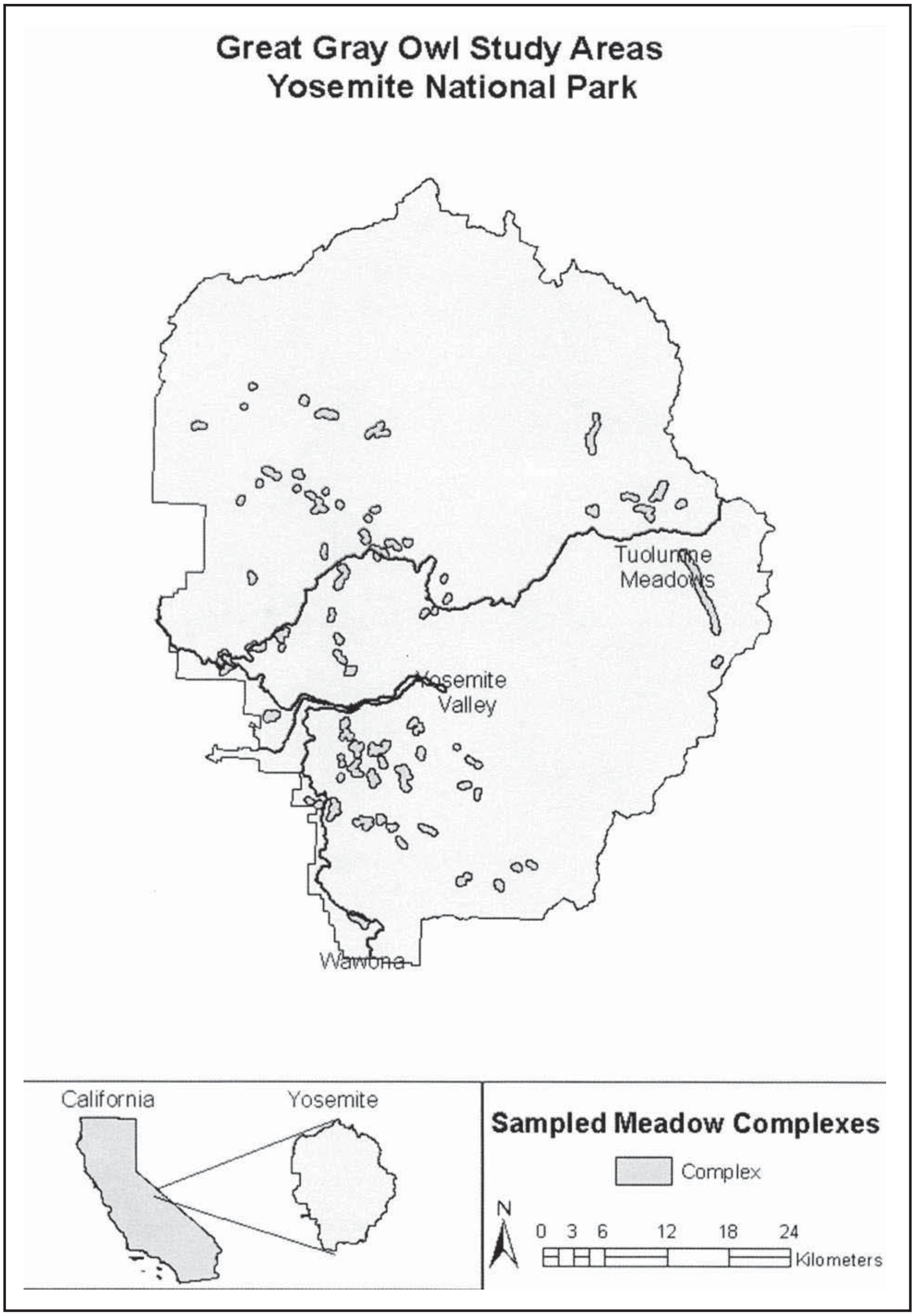

Figure 1. Great gray owl study areas in Yosemite National Park, CA. All core meadow complexes that were surveyed during 1987-1989 are identified, along with major roads and the Yosemite park boundary.

in size and varies in elevation from 600 m along the western boundary to more than 4000 m along the crest of the Sierra Nevada. The climate is predominately Mediterranean with temperatures ranging from a mean minimum of -1 °C in January at high elevations to 32 °C in July at low elevations (Elford 1970). Precipitation generally occurs from November to March and increases with elevation from 800 mm to a maximum of 1200 mm. Vegetation within the park also varies with elevation from shrub woodlands in the foothills, to montane forests at mid-elevations, and subalpine forests and alpine meadows at higher elevations (see Mayer and Laudenslayer 1988, for a detailed description). Yosemite National Park, because of its proximity to large California urban areas, experiences heavy recreational use, and to accommodate human recreation, the park has developed a series of trails, roads, and campgrounds, many near meadows.

Study species

The great gray owl is large, ranging in weight from 700 g to 1700 g and having a wingspan of 140 cm to 150 cm (Nero 1980). The species is widely distributed, occurring in conifer forests throughout much of northern Asia, North America, and Europe (Mikkola 1983). In Yosemite, great gray owls occur primarily in montane forests, and spend up to 80 % of their time in or near meadows that they require as foraging sites (Winter 1986; Reid 1989; van Riper and van Wagtendonk 2006). The availability of food resources can profoundly affect the distribution of a species (Fretwell 1972; Cody 1985; Morris 2003), including the great gray owl (Nero 1980; Mikkola 1983). The great gray owl hunts for food during crepuscular and nocturnal periods, employing a sit-and-wait strategy. The owl forages almost exclusively on small rodents, with the majority of their diet throughout their North American range consisting of pocket gophers (*Thomomys* spp.) and voles (*Microtus* spp.) (Reid 1989; Bull and Duncan 1993).

Survey locations

Within Yosemite National Park, we focused our efforts on montane and subalpine meadows, which are the center of owl abundance (van Riper and van Wagtendonk 2006). By limiting our study to open meadow areas, we enhanced our ability of detecting the presence of owls because of increased aural and visual detection distances associated with meadow systems. We used digital orthophoto quadrangles to identify 211 non-contiguous meadows within the park, based on accessibility and elevation. In order to consolidate the 211 meadows into complexes that were more biologically meaningful than single meadows, we used a geographic information system (GIS) to delineate a 275-m buffer around each meadow. We chose a 275-m buffer because that distance would circumscribe the 95% adaptive kernel estimate of great gray owl home range size in Yosemite, as determined by van Riper and van Wagtendonk (2006). All meadows within the buffer were included in the same complex, and meadows that were greater than 550 m apart were considered to be in different complexes. The end result was 81 meadow complexes within the park, for which we calculated the area, perimeter, and average elevation, and collected owl survey data (Figure 1).

Habitat types

Great gray owls are known to nest in red fir (*Abies magnifica* A. Murray), white fir (*A. concolor* [Gord. & Glend.] Lindl. ex Hildebr.), lodgepole pine (*Pinus contorta* Douglas ex Louden), or incense-cedar (*Calocedrus decurrnens* [Torr.] Florin) (Winter 1986; Franklin 1988; Reid 1989; Bull and Duncan 1993). We calculated the area of vegetation types containing those species within the buffers of each meadow complex using the California Wildlife Habitat Relationships types (Mayer and Laudenslayer 1988).

Owl occurrence

We determined owl presence by conducting nocturnal surveys in each of the 81 meadow complexes during July–August of 1987 – 1989. Because surveys were separated by years, we considered each sampling period as independent. During the late evening and early night, when owls are most active, one observer crossed the meadow complex stopping every 50 m to play a tape of a great gray owl primary call, while a second observer stationed at the meadow edge recorded all owl responses. Great gray owls are territorial and generally respond to the presence of another owl by calling or approaching (Bull and Duncan 1993). In addition to conducting nocturnal call surveys, we also undertook two systematic daylight searches of each meadow complex for owls. If during any visit we detected an owl or found great gray owl feathers, we considered the meadow complex occupied. We also utilized locations (n = 5338) of 12 radio-tagged birds (see van Riper and van Wagtendonk 2006), and conducted repeat surveys of meadows suspected of having owls, to more thoroughly assess occupancy in the park.

Food availability

In the Yosemite region, great gray owls subsist primarily on pocket gophers and voles (Reid 1989), both of which can vary in abundance temporally and spatially (Andersen and MacMahon 1981; Hanski et al. 2001), thus potentially influencing habitat use by owls. Both rodent species leave obvious visual evidence of their presence in the form of fresh mounds (gopher) and lanes (voles) that are easily differentiated from older mounds and lanes, thus allowing us to estimate their relative abundance (see Ingles 1952). Gophers dig holes in the ground and pile soil up at the burrow entrance, and the fresh mounded soil is easy to differentiate from the older burrow soil-mounds. Voles create runways through the grass, and active runways do not have grass falling into the runway opening, like those that have been abandoned. Starting at the head of each surveyed meadow complex, we walked 45-degree diagonal transects back and forth to the meadow edge until reaching the meadow bottom, recording the number of active gopher mounds and vole lanes within 10 m of the transect line. Because meadows differ in size, we corrected our sampling effort by dividing the number of detections by the total transect length. We surveyed transects during July – August each year. However, because all meadows were not visited every year, and because preliminary models suggested that food resources acted additively, we used the additive mean detections of both mammal species as an index of food availability within the meadow system.

Snag availability

Because great gray owls often rely on large snags for nest sites (Mikkola 1983; Franklin 1988; Bull and Henjum 1990; Bull and Duncan 1993), we felt that the local availability of snags may limit owl distribution. To assess snag availability, where each diagonal transect reached a meadow edge, we chose a random azimuth and walked 50 m and established a 10-m diameter circular plot. Within that plot we counted all trees > 25 cm diameter-at-breast-height (dbh). A suitable owl nesting location was considered to be any snag > 25 cm dbh tree that was broken off horizontally or at a slight angle, thus providing a suitable nesting substrate (Bull and Henjum 1990).

Human development and recreational use

For each surveyed meadow complex (including a buffer), we determined the amount of human development by recording roads, buildings, and campgrounds within the complex. Roads were recorded in linear meters (m) where they intersected any meadow complex. We placed 100-m buffers around buildings and campgrounds and recorded the area in m^2 of the intersection of the campground with the meadow complexes. As an index of recreational activity, we documented the presence of fire rings and linear meters of hiking trails at each of the 81 meadow complexes, based on Yosemite National Park field surveys (Holmes 1973). We felt that we could use this index because data from van Wagtendonk (1981) and Boyers et al. (2000) showed the number did not appreciably change in the 12 years following our study. However, between the 1970s and 1996, the number of recreational visitors to Yosemite increased to a peak of over 4 million visitors. Since that time, the number has fluctuated between 3.3 and 3.9 million visitors (Figure 2).

STATISTICAL ANALYSIS

We used the program *Presence* (MacKenzie et al. 2002; Hines 2006) in a series of models to assess the likelihood of a great gray owl being present in a given meadow complex. By using *Presence,* we are able to account for incomplete detection of owls during repeated surveys. For the purposes of this analysis, we identified a survey by year, as few meadows were surveyed multiple times within a year. Because we surveyed meadows using two different approaches, call surveys and physical evidence surveys, we made use of the multiple method approach in *Presence* allowing us to include all possible oppor-

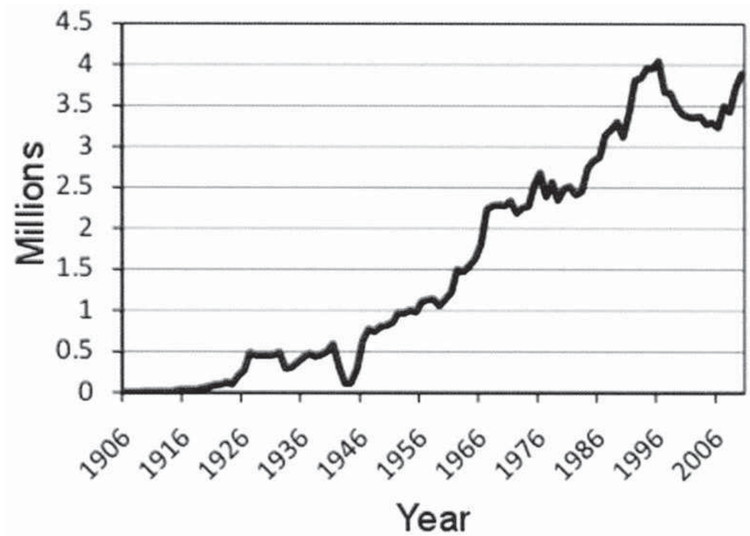

Figure 2. Visitor use levels, between 1996 and 2010, in Yosemite National Park, CA.

tunities for detecting an owl in a meadow while controlling for possible confounding effects of different sampling approaches by incorporating method into the model (Θ) (Nichols et al. 2008). Sampling effort was not consistent between techniques, among meadows, or across years; therefore, we performed an initial assessment to determine whether detectability (p) varied with sampling efforts (following Frost and Powell 2011). We compared three models: (1) ψ(.)Θ(.)p(.), constant detectability; (2) ψ(.)Θ(.)p(call surveys + physical surveys), detectability varies with the number of surveys specific to each type within a meadow; (3) ψ(.)Θ(.)p(total surveys), detectability varies with the total number of surveys independent of type. We used Akaike's Information Criterion (AIC) scores (Burnham and Anderson 1998) to select the model that best described detectability. We then modified the best detectability model in order to assess the effect of natural and anthropogenic factors on the likelihood of a great gray owl being present in a meadow complex (ψ). We used a biologically relevant hierarchical approach that considered occupancy within a habitat selection framework based on stepwise decisions made at increasingly smaller spatial scales as suggested by Arnold (2010). First we developed a series of models that identified occupancy within a forest type (e.g., red fir, white fir, lodgepole, Sierra mixed conifer). For the top models (ΔAIC < 2), we then added meadow specific descriptors (elevation, complex area, meadow area) to develop another set of competing models. We followed this protocol adding next breeding requirements (food availability, snag availability) and finally anthropogenic factors (trail coverage, road coverage, building coverage, campground coverage, number of fire rings) to produce final lists of competing averaged models, aimed at explaining the natural and anthropogenic factors determining levels of great gray owl occupancy in Yosemite National Park. Following the suggestions of Arnold (2010) regarding model selection utilizing AIC: (1) we tested models based on working hypotheses that were based on the best information known on the ecological parameters influencing owl populations; (2) as our primary objective was to identify the most parsimonious model, analyses were conducted in a hierarchical sequential modeling approach that allowed use to isolate the most informative parameter in a biologically meaningful framework, and that allowed unsupported variables to be eliminated without further reporting; and (3) we present the outcomes of the model averages in a table format which will allow readers to discern the relative importance of each of the parameters in predicting owl occupancy. All analyses were conducted on non-transformed data; but, where appropriate, figures show estimated marginal means based on a binary logistic regression analysis.

RESULTS

From 1987 through 1989, we conducted research on great gray owls in Yosemite, with nocturnal surveys undertaken in 1988 and 1989 within 81 meadow complexes (Figure 1). During our nocturnal play-back surveys, 23 males in 17 complexes and 16 females within 11 of the meadow complexes vocally responded to broadcast calls. Visual detections occurred in 20 meadow complexes, while we found great gray owl feathers in 29 of the complexes. Combining all survey methods, owls occupied 37 (45.6%) of the 81 surveyed meadow complexes. Human development in the form of campgrounds and fire rings occurred on 28 (34.5%) of the meadow complexes. Meadows with these developments included 8.99 (±1.68) hectares of campgrounds and 16 (±3) fire rings, respectively. In addition, 49 (60.5%) of the meadows had roads, while 46 (56.8%) included trails, which transected 1.31 km (±0.11) and 1.40 km (±0.11) of the affected meadows, respectively. Active gopher mounds were present in 64 (79%) meadows while vole lanes were recorded in 46 (57%), with an average of 0.24 (±0.03) and 0.05 (±0.01) detections per linear meter of transect respectively. In 148 snag plots, we recorded a total of 16,384 trees, of which 30.7% (*n* = 5036) were identified as snags. Of all snags, 265 (5.3%) were deemed as possible suitable owl nesting locations.

Model comparison with program *Presence* indicated that the null model of a constant detection probability was the best model (for the other models ΔAIC > 4). Geophysical, habitat, resource, and anthropogenic factors all contributed to the selected models of owl occupancy. Overall great gray owls showed limited preference for forest type based on availability in the landscape (Figure 3), but the presence of red fir was an important, although weak, predictor in our landscape analysis (Table 1; $\beta_{red\ fir}$ = 2.00 x 10^{-6}, SE = 1.29 x 10^{-4}) and in all further model sets. Within red fir forests, occupied meadow complexes tended to be found at lower mean elevations than unoc-

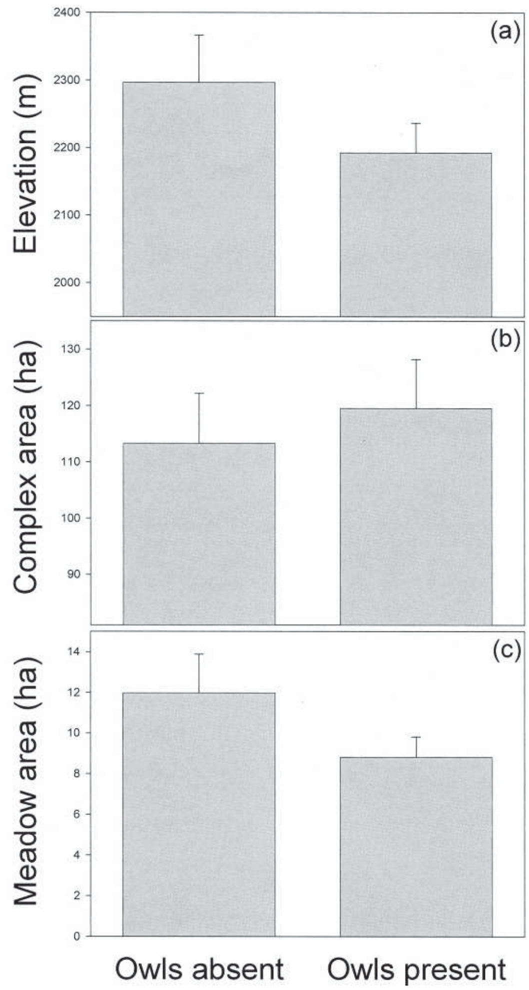

Figure 3. Geophysical characters tended to differ between occupied and unoccupied meadows, and while elevation was a regular component of the top models, only meadow size (c) showed an independent significant relationship with meadow occupancy. Columns indicate means ± SE.

cupied complexes ($\bar{x}$ = 2180 m vs. 2300 m), were larger ($\bar{x}$ = 120 ha vs. 115 ha), and had less meadow area ($\bar{x}$ = 9 ha vs. 12 ha) (Figure 4); however, only elevation was included in the top model of our meadow analysis and the overall influence was weak (Table 2; $\beta_{elevation}$= -1.30 x 10^{-3}, SE = 2.22 x 10^{-4}). Owl occupancy was positively related to both snag abundance and food availability (Figure 5), but only the availability of food was included in the top models and its influence on occupancy was strong (Table 3; β_{rodent}= 2.90, SE = 1.04). Anthropogenic changes to Yosemite Park meadows showed both positive and negative effects on great gray owl occupancy (Figure 6); but, overall, the influences were weak and did not lead to an improvement in the top model (Table 4). Ultimately, the top model occupancy estimate (47.4%) was only a slight improvement over the naïve estimate (45.6%), but this is likely largely due to the relatively high detection probability (59.6%) associated with the incorporation of multiple sampling methods. Based on model averaging, it is clear that food is the predominate predictor of owl occupancy in this system (Table 5); however, of the parameters included in the top models, only one, white fir, had estimates that encompassed zero, indicating that each parameter is potentially important in predicting owl habitat decisions.

DISCUSSION

Understanding the factors determining the distribution of animals is imperative to effective management. Bull and Henjum (1990) and Franklin (1988) both found that pocket gophers had a strong influence on habitat use by great gray owls. Winter (1986), along with van Riper and van Wagtendonk (2006), suggested that the availability of food had important implications on the distribution of the great gray owl in California. In this study, we found that the presence of food resources was the most important variable in determining the presence of the great gray owl in Yosemite National Park. Indeed, the inclusion of food dramatically improved the model sets (Tables 3, 4) and was by far the strongest factor influencing great grey owl occupancy (Table 5). Pocket gophers occurred in 79% of the meadows that we surveyed, but there was a great deal of variation in abundance, and all mid-elevation meadows in the park were found to have high numbers of active gopher mounds. Unfortunately, it is also these same meadows where a large degree of campgrounds and roads occur in Yosemite. The abundant food resources of these mid-elevation meadows may be the underlying reason why we found that owls appear to prefer meadows that presently have extensive human development (e.g., campgrounds; Figure 6).

The impact of human development on animal habitat use has been studied extensively and has led to important changes in how we manage wildlife and their habitat (Mills et al. 1989; Blair 1996; Bolger et al. 1997; Ries et al. 2004; Aguilar et al. 2006). Although understanding the impact of human development is obviously important, human recreational activities seem also to have a negative influence on great gray owl distribution, particularly in remote natural areas of the park. Indeed, numerous studies (Boyle and Samson 1985; Hockin et al. 1992; Reijnen et al. 1995; Rogers et al. 1999; Reed and Merenlender 2008), including one on great gray owls (Wildman 1992), show that human recreation can profoundly influence animal behavior. But, how individual human behaviors alter animal distribution patterns is less clear (Gill et al. 2001). Here we found such an effect; the level of human recreational activities as denoted by the presence of trails and fire rings appears to negatively influence great gray owl distribution in

Table 1. Top occupancy models based on Akaike's Information Criteria (ΔAIC < 2; Null = 6.62) for forest types (Red Fir, White Fir, Lodgepole Pine, Sierra Mixed Conifer) within Yosemite National Park after accounting for multiple survey methods.*

Variables	AIC	ΔAIC	w_i	K	-2*ln (Likelihood)
Red Fir	326.64	0	0.4592	6	314.64
Red Fir + White Fir	327.5	0.86	0.2987	7	313.5
Red Fir + Lodgepole	327.92	1.28	0.2421	7	313.92

* In Tables 1-5, where (AIC) reflects the overall fit of the model after dis-counting for overfitting, (ΔAIC) is the difference in fit of the model from the top model; (wi) is the weight of evidence that the model is best given the candidate models; and, (K) is the number of variables in the model.

$$\text{AIC} = 2\ln(\text{likelihood}) + 2 * \text{K} + \frac{2*K*(K+1)}{(n-K-1)}$$

$$\Delta\ \text{AIC} = \text{AIC}_i - \min - \text{AIC}$$

$$W_i = \frac{\exp(-0.5*\Delta_i)}{\sum \exp(-0.5*\Delta_i)}$$

Yosemite (Figure 6; Table 5). In the park, owls primarily use meadows with lower levels of human activity.

Although human activity was undoubtedly greatest in areas that had roads, buildings, and campgrounds, the presence of these structures alone did not influence occupancy (Figure 6; Table 5). This apparent paradox highlights both the resiliency and the fragility of this owl species. Great gray owls are able to cope with human development, some even occurring and breeding in areas with campgrounds (Reid 1989). However, our data on radio-marked owls show that even though great gray owls occur near campgrounds, they largely avoid those areas when people are present, only returning to the vicinity of the campgrounds when they are closed or people absent (Wildman 1992; van Riper, pers. observation). Additionally, although Yosemite Valley and Big Meadow have extensive meadow habitat, none of our radio tagged owls were ever found to utilize these heavily visited areas of the park, even though owls did fly over Yosemite Valley to reach their lower elevation wintering grounds (van Riper and van Wagtendonk 2006). We found that throughout Yosemite National Park, great gray owls can use meadows within developed areas, but the presence of people makes these habitats less than ideal habitat for the owl.

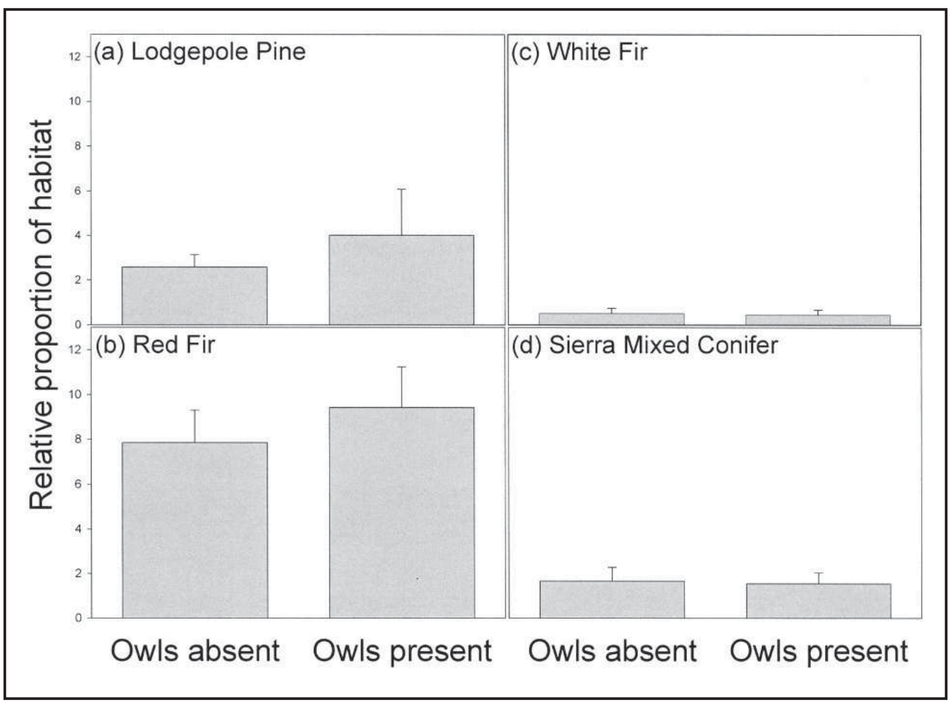

Figure 4. Although red fir was included in the majority of top models, none of the forest habitat types showed a significant relationship independently. Columns indicate means ± SE.

Human impacts on natural systems can be both profound and subtle; in either case, understanding the causal mechanism leading to changes in ecosystem structure and function is imperative for successful restoration and management. This may be particularly important in natural areas like national parks that have been established "to conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such manner and by such means as will

Table 2. Top occupancy models based on Akaike's Information Criteria (ΔAIC < 2; Null = 9.93) for meadow habitat attributes (elevation, complex area, meadow area) within the top forest models after accounting for multiple survey methods.

Variables	AIC	ΔAIC	w_i	K	-2*ln (Likelihood)
Red Fir + Elevation	323.33	0.00	0.552	7	309.33
Red Fir + White Fir + Elevation	325.07	1.74	0.2313	8	309.07
Red Fir + Lodgepole + Elevation	325.20	1.87	0.2167	8	309.20

leave them unimpaired for the enjoyment of future generations" (National Park Service 1916). Although great gray owl populations in Yosemite presently appear stable (van Riper and van Wagtendonk 2006), it is apparent from this study that human recreation does influence owl presence. It is unlikely that human use of the park is going to decrease in coming years, and 85% of meadows that we surveyed are already experiencing some human activity. In fact, visitation to Yosemite National Park has continued to increase in the years following our study (see Figure 2). Many of the core mid-elevation meadows that owls occupied during our study are developed, and have experienced increases in human activity over the past 50 years. This suggests the importance of further study into how great gray owl behavior is being changed by human recreation, if habituation to human presence is occurring, and if this will ultimately lead to changes in owl productivity and distribution. By understanding the relationship between food resources, human disturbance, and great gray owl distribution patterns we can further our understanding of the management and conservation of this state-endangered species, and possibly other reclusive owl species (e.g., Mikkola 1983; Willey and van Riper 2007).

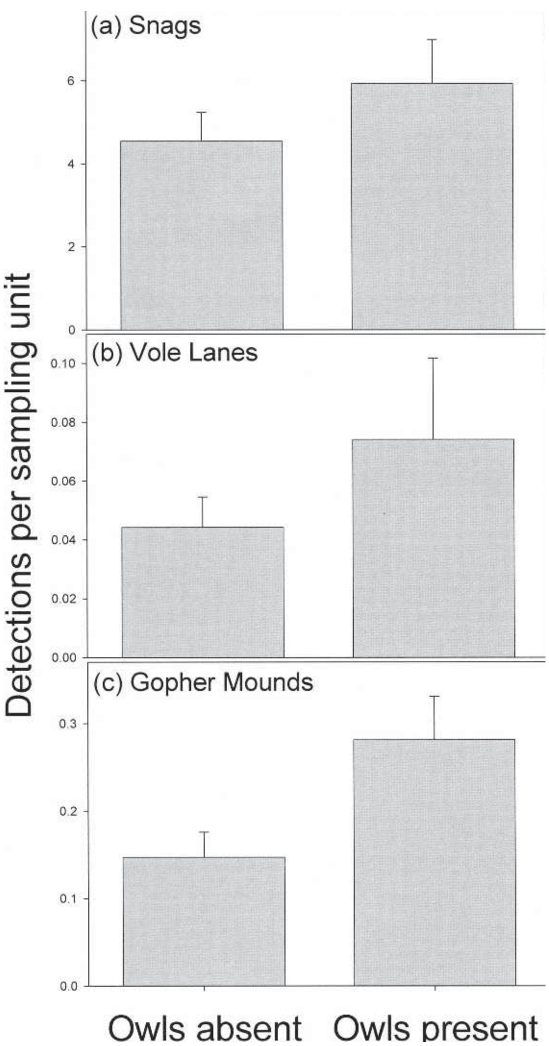

Figure 5. Snag and food resources clearly differed between occupied and unoccupied meadows and were an important component of the top model sets, but only gopher abundance (c) showed a significant relationship with owl distribution independently. Columns indicate means ± SE.

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Table 3. Top occupancy models based on Akaike's Information Criteria (ΔAIC < 2; Null = 20.56) for owl breeding requirements (rodents, snags) within the top forest and meadow habitat models after accounting for multiple survey methods.

Variables	AIC	ΔAIC	w_i	K	-2*ln (Likelihood)
Red Fir + Elevation + Rodents	312.70	0.00	0.7301	8	296.70
Red Fir + White Fir + Elevation + Rodents	314.69	1.99	0.2699	9	296.69

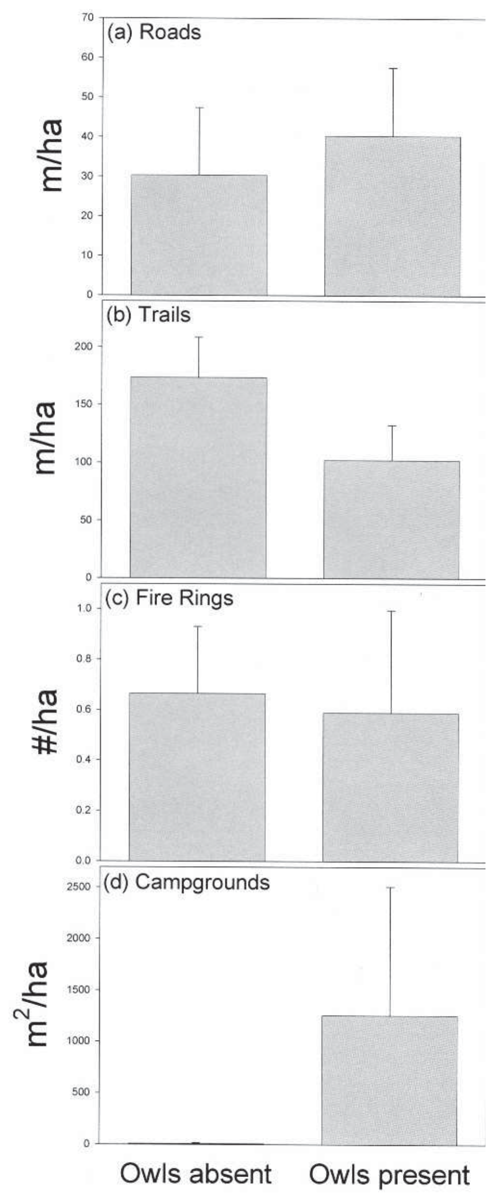

Figure 6. Anthropogenic change to Yosemite meadows showed both positive and negative effects on owl distribution with indices of both activity and development being found in the top model set. Development, including roads (a) and campgrounds (d) was generally positively associated with owl occupancy, while activity including trails (b) and fire rings (c) were negatively associated with owl occupancy. Columns indicate means ± SE.

Charles van Riper III is an ST Research Ecologist with the US Geological Survey, Southwest Biological Science Center, and Professor in the School of Natural Resources and the Environment at the University of Arizona, Tucson. His research interests focus on avian migration, disease, breeding, and conservation in ecosystems of North and South America.

Joseph Fontaine is a research ecologist with the US Geological Survey, Nebraska Cooperative Fish and Wildlife Research Unit, stationed at the University of Nebraska, Lincoln. His research focuses on understanding variation in avian life history strategies.

Jan van Wagtendonk is an emeritus research forester with the US Geological Survey, Western Ecological Research Center, stationed at Yosemite National Park. For the past 40 years, he has studied the ecology and role of fire in Sierra Nevada ecosystems.

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Table 4. Top occupancy models based on Akaike's Information Criteria (ΔAIC < 2) for human development (road, trail, campground, fire ring) within the top forest, meadow, and breeding requirement models after accounting for multiple survey methods.

Variables	AIC	ΔAIC	w_i	K	-2*ln (Likelihood)
Red Fir + Elevation + Rodents	312.70	0.00	0.2035	8	296.70
Red Fir + Elevation + Rodents + Trails	312.97	0.27	0.1778	9	294.97
Red Fir + Elevation + Rodents + Camps	313.01	0.31	0.1743	9	295.01
Red Fir + Elevation + Rodents + Trails + Camps	313.56	0.86	0.1324	10	293.56
Red Fir + Elevation + Rodents + Fire Rings	314.55	1.85	0.0807	9	296.55
Red Fir + Elevation + Rodents + Trails + Fire Rings	314.58	1.88	0.0795	10	294.58
Red Fir + Elevation + Rodents + Roads	314.66	1.96	0.0764	9	296.66
Red Fir + White Fir + Elevation + Rodents	314.69	1.99	0.0753	9	296.69

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Table 5. Average model parameter estimates based off of the top eight great grey owl occupancy models (ΔAIC < 2). Variables denoted by (*) do not overlap zero based on 95% confidence intervals.

Variables	Estimate	SE	Upper 95% CI	Lower 95% CI
Red Fir*	2.00×10^{-6}	2.00×10^{-8}	2.03×10^{-6}	1.97×10^{-6}
White Fir	0	1.00×10^{-8}	1.00×10^{-8}	-1.00×10^{-8}
Elevation*	-1.17×10^{-3}	5.00×10^{-8}	-1.17×10^{-3}	-1.17×10^{-3}
Rodents*	2.97	1.09	5.15	0.79
Trails*	-8.08×10^{-5}	2.02×10^{-5}	-4.07×10^{-5}	-1.21×10^{-4}
Campgrounds*	5.56×10^{-6}	1.20×10^{-7}	5.80×10^{-6}	5.32×10^{-6}
Fire Rings*	-1.16×10^{-3}	4.26×10^{-5}	-1.24×10^{-3}	-1.07×10^{-3}
Roads*	5.12×10^{-6}	2.00×10^{-8}	5.08×10^{-6}	5.16×10^{-6}

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