



Original Article

Habitat Relationships of Great Gray Owl Prey in Meadows of the Sierra Nevada Mountains

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ABSTRACT Annual productivity of great gray owls (*Strix nebulosa*) in California, USA, is thought to be largely dependent on vole (*Microtus* spp.) and pocket gopher (*Thomomys* spp.; hereafter, gopher) abundance, yet factors influencing these prey populations have not been thoroughly investigated. The abundance of voles and gophers has been influenced by vegetation and cattle grazing in other regions; and many meadows are grazed within the breeding range of great gray owls in the Sierra Nevada Mountains of California. We evaluated the influence of vegetation and cattle grazing on great gray owl foraging habitat by quantifying vole abundance, gopher abundance, and vegetation features in grazed and ungrazed meadows in 2010 and 2011. We found that vole presence was positively associated with sward height and corn lily (*Veratrum californicum*) dominance; vole abundance was weakly negatively associated with cattle grazing. Gopher abundance was negatively associated with site wetness, and weakly positively associated with stem density, the frequency of forb presence, cattle grazing, and the dominance of corn lily. To efficiently manage vegetation and cattle grazing to benefit great gray owl prey, we suggest prioritizing habitat for voles in wet meadows because gophers were not likely to be abundant in wet sites. Particularly in areas with moist soils, we recommend maintaining sward height commensurate with the habitat relationships of voles found in this study; >290 mm where corn lily is not dominant and 125 mm where it is. Sustaining sward height for voles should benefit great gray owls and other meadow or forest edge carnivores. © 2014 The Wildlife Society.

KEY WORDS cattle grazing, gopher, great gray owl, habitat, *Microtus*, rodent, Sierra Nevada, *Strix nebulosa*, *Thomomys*, vole.

In the Sierra Nevada Mountains (hereafter, Sierra Nevada) of California, great gray owls (*Strix nebulosa*) are a State Endangered Species that receive special management consideration on U.S. Forest Service lands (U.S. Forest Service 2004, California Department of Fish and Game 2011). Great gray owls are of special concern in California because 1) estimates of population density and distribution are low (Winter 1986, Sears 2006, Hull et al. 2010); and 2) suitable nesting, roosting, and foraging habitats might be threatened because of forestry practices, development of campgrounds, and livestock grazing (Nero 1980, Bull and Duncan 1993). The U.S. Forest Service has established management standards to ensure that herbaceous vegetation in meadows is maintained at a height that is suitable for great gray owl prey (U.S. Forest Service 2004). However, conditions that make habitat suitable for great gray owl prey in the Sierra Nevada are not fully understood, and no specific vegetation height has been determined for management.

Great gray owls in the Sierra Nevada rely on montane meadow habitat with sufficient densities of voles (*Microtus* spp.) and pocket gophers (*Thomomys* spp.; hereafter, gopher) to achieve dietary needs (Winter 1986, Greene 1995, van Riper and van Wagtenonk 2006). Voles and gophers typically comprise >94% of owl-pellet biomass (Winter 1986, Reid 1989), and great gray owls have lower reproduction rates when vole and/or gopher populations are low (Winter 1986, Reid 1989, Greene 1995).

Several vole and gopher species that occur in the Sierra Nevada are strongly associated with meadows, yet within-meadow habitat associations of voles and gophers are different. Three vole species occur within great gray owl foraging habitat in the Sierra Nevada: montane vole (*M. montanus*), long-tailed vole (*M. longicaudus*), and California vole (*M. californicus*; Reid 1989, Moritz et al. 2008). These voles are positively associated with moist soils and herbaceous vegetation height, cover, and density (Smolen and Keller 1987, Sera and Early 2003, Getz et al. 2005). Mountain pocket gopher (*T. monticola*) and Botta's pocket gopher (*T. bottae*) occur within great gray owl foraging habitat and are generally found in drier soils with less vegetation cover relative to habitat used by voles (Ingles 1952, Greene 1995, Jones and Baxter 2004). In addition, diets of voles primarily consist of grasses rather than

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forbs (Verts and Carraway 1998), whereas gophers forage on all palatable plants within a body-length radius of feeding holes (Howard and Childs 1959). Despite these differences, voles and gophers regularly co-occur in the same meadows because of fine-scale heterogeneity of habitat conditions (Winter 1986, Greene 1995, Weixelman et al. 2011).

Cattle grazing is common in meadows of the Sierra Nevada and is suspected to be a key factor influencing prey abundance, and therefore great gray owl reproduction. However, specific relationships among cattle grazing and habitat conditions for voles and gophers have not been thoroughly evaluated. Previous studies on vole-habitat relationships in meadows of the Sierra Nevada were based on sign (e.g., Winter 1986, Reid 1989, Greene 1995), but results from sign indices may vary depending on vole species composition and abundance (Gervais 2010).

Several studies outside of the Sierra Nevada have found that cattle grazing diminished vole abundance, vegetation height, and cover (Jacob and Hempel 2003, Schmidt et al. 2005, Johnson and Horn 2008, Johnston and Anthony 2008). Rapid declines in vole abundance, female body weight, female survivorship, and recruitment have been associated with grazing and experimental reductions in standing biomass (Peles and Barrett 1996, Klaus et al. 1999, Jacob and Hempel 2003). For example, 8 months after initiation of grazing, Johnson and Horn (2008) observed drastic declines in vole abundance, vegetation height, and cover in a coastal grassland. Further, Birney et al. (1976) hypothesized that lack of vegetation cover may increase the amount of time between vole population peaks and reduce vole population density.

The influence of cattle grazing on gophers is not clear. Indices of gopher abundance have decreased with grazing in some studies (e.g., Hunter 1991) and increased with grazing in others (e.g., Powers et al. 2011). Gopher abundance may be positively associated with cattle grazing because grazing can lead to drier soil, lower water table, and quicker snow melt due to less vegetation cover (Gifford and Hawkins 1978, Armour et al. 1991). Conversely, cattle grazing may cause unfavorable alterations in plant species composition and decrease gopher burrowing ability because of soil compaction (Ingles 1952, Gifford and Hawkins 1978, Armour et al. 1991). A study in the Sierra Nevada found higher gopher abundance in grazed meadows (Powers et al. 2011).

We quantified vole abundance, gopher abundance, and vegetation features in grazed and ungrazed meadows within suitable great gray owl foraging habitat in the Sierra Nevada. Our objectives were to determine 1) vegetation conditions that correlate with vole and gopher abundance; and 2) the influence of cattle grazing on vole abundance, gopher abundance, and vegetation conditions. The goal of this research was to obtain information necessary to identify, enhance, and increase the amount of suitable great gray owl foraging habitat.

STUDY AREA

We conducted this study in meadows in Stanislaus National Forest (south of highway 4) and Yosemite National Park

(north of Glacier Point Road) on the western slopes of the central Sierra Nevada Mountains/Range in California, USA (Fig. 1). In Stanislaus National Forest, we surveyed meadows in cattle grazing allotments (hereafter, grazed) and meadows not in cattle grazing allotments (hereafter, ungrazed); all meadows in Yosemite National Park were ungrazed. Vegetation in these montane meadows included various species of grasses, sedges, rushes, forbs, and willows (Potter 2005). At 1,430 m elevation, average monthly temperature ranged from 0 °C to 10 °C in November–April and 10 °C to 25 °C in May–October. Average monthly precipitation was 136 cm in November 2009–October 2010 and 177 cm in November 2010–October 2011 (Western Regional Climate Center 2012). Precipitation occurred mainly in the form of snow in November through April.

MATERIALS AND METHODS

Site Selection

We identified meadows to include in this study based on great gray owl foraging habitat selection. All meadows selected were 1) on the western slope of the Sierra Nevada Mountain crest, 2) >4 ha in size or part of a complex >4 ha in size, and 3) between 1,100 m and 2,300 m elevation to correspond with great gray owl breeding elevation range (Winter 1986, Greene 1995, Beck and Winter 2000, van Riper and van Wagendonk 2006). In addition, all meadows were within 700 m of a road for accessibility. We confirmed great gray owl presence in some sites within the study area in 2010 and 2011 (Kalinowski 2012; J. Medley, U.S. Forest Service Pacific Southwest Research Station, personal communication).

Meadows were identified in ArcGIS (version 9.2) using meadow layers provided by the U.S. Forest Service (2010) and the National Park Service (2010). In 2010, we randomly selected 11 ungrazed sites in Stanislaus National Forest that met the study site criteria and matched them with 13 grazed sites that were nearest in elevation and location to the ungrazed sites. There were 2 more grazed sites than ungrazed sites because a meadow that was believed to be ungrazed was determined to be grazed upon further evaluation. From all suitable sites in Yosemite National Park, we randomly selected 4 ungrazed sites and paired them with 4 sites in Stanislaus that were most similar in elevation and location to the Yosemite sites. All sites surveyed in 2010 were surveyed in 2011, and we added 4 ungrazed sites in Yosemite and 2 grazed sites in Stanislaus in 2011. There was no significant difference in elevation between grazed and ungrazed sites ($t=0.43$, $df=37$, $P=0.670$).

Nine meadows (5 ungrazed and 4 grazed) were large enough to contain 2 sampling sites each. Sites within meadows were >200 m apart and were treated as independent because 1) home range movements of closely related vole species were <100 m (Getz et al. 1994); 2) gopher abundance sampling was completed within a 24-hr period and the average daily movements of Botta's pocket gophers were <38 m (Jones and Baxter 2004); 3) no marked animals (see "Vole and Gopher Abundance" section) were ever found

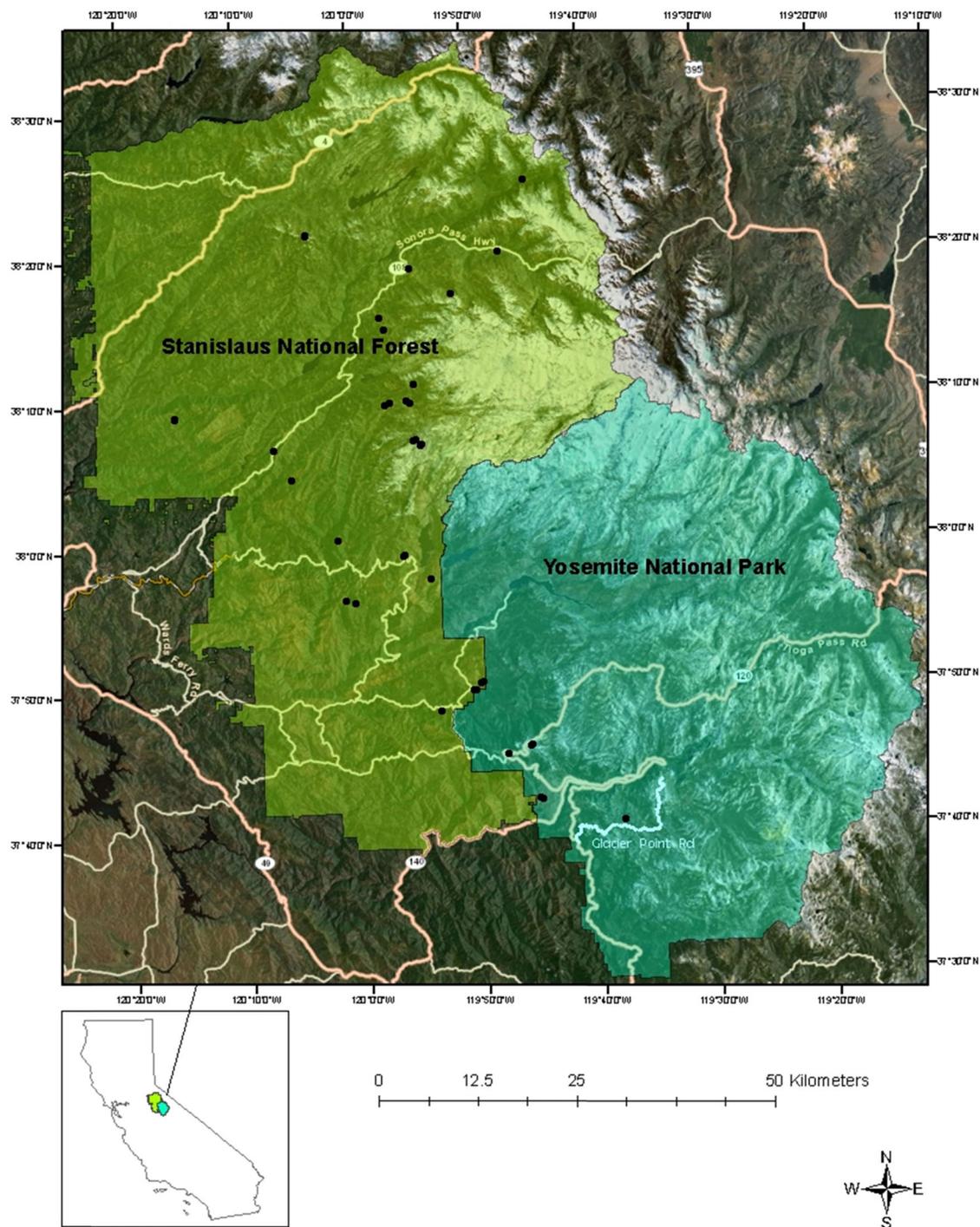


Figure 1. Map displaying sampling locations (black circles) where we evaluated the influence of vegetation and cattle grazing on great gray owl foraging habitat in Stanislaus National Forest and Yosemite National Park in the Sierra Nevada Mountains, California, USA, 2010 and 2011.

in more than one site; and 4) there were often detectable differences in vegetation, wetness, and small mammal abundances between sites within a meadow.

We surveyed for voles, gophers, and vegetation at 1 grazed and 1 ungrazed site or 2 grazed and 2 ungrazed sites simultaneously each week (1 week/site/yr) from mid-May to late July (2010) or early August (2011). We surveyed each site 6 days later in 2011 than in 2010 in an attempt to match

the timing after snowmelt (there was greater snow depth in 2011; Western Regional Climate Center 2012). Each year yielded 11 weeks of surveys that coincided with great gray owl nestling and fledgling stages (Bull and Henjum 1990). We were unable to survey during courtship and egg-laying/incubation stages (late Feb–early May; Verner and Boss 1980, Winter 1986) because of the logistical constraints of snow depth on roads and meadows.

Vole and Gopher Abundance

We used a trapping web at each site to estimate vole abundance (Parmenter et al. 2003, Buckland et al. 2004). We located the web center by walking from the center of the meadow along a randomly selected azimuth to a point 30 m from the forest edge. Starting 2 m from the web center, we established 12 radial lines of Sherman live-traps (8 cm × 8 or 9 cm × 23 or 25 cm; H.B. Sherman Traps, Inc., Tallahassee, FL) with 8 traps spaced 4 m apart/line totaling 96 traps/web. With this layout, traps were within 61 m of the meadow edge, which was found to be within the maximum distance (≤ 100 m) a great gray owl would fly from a meadow edge perch to hunt prey (Winter 1986, Bull and Duncan 1993).

Traps were always left open and were checked within 2 hr prior to sunset and again within 3 hr after sunrise. The first trap check took place on Sunday evening and the last on Friday morning, yielding 5 trap nights. We baited traps with rolled oats and peanut butter and added polyester batting for insulation (Sera and Early 2003). We marked small mammals that were captured with a uniquely numbered Monel ear-tag (Model 1005-1; National Band and Tag Company, Newport, KY). Immediately after processing, we released small mammals at the site of capture.

Gophers were not readily trappable, so we indexed gopher abundance by counting the number of fresh gopher mounds within three 10-m × 100-m belt transects/site (Powers et al. 2011). We centered the middle belt transect on the trapping web line that was most parallel to the meadow edge. The 2 other belt transects were parallel to the middle belt with 10-m spacing between belt edges. To obtain estimates, we walked the belt until fresh evidence was found, recorded the evidence as 1 gopher, and walked 11 m before counting any other evidence as another gopher. We chose this distance because Ingles (1952) found that the average female mountain pocket gopher territory size in summer was equivalent to an 11-m-diameter circle. Male territories were smaller and gophers were solitary except when mating, so 11-m spacing between observations allowed us to calculate a conservative index of gopher abundance (Powers et al. 2011). All procedures described for sampling small mammals were approved by the Institutional Animal Care and Use Committee at Humboldt State University (Study No. 08/09.W.65.A).

Vegetation Sampling

We assessed herbaceous vegetation features that may influence vole and gopher abundance. To quantify vegetation, we measured the following at every third trap and at the beginning and end of each gopher belt (42 locations) during the first 2 days of trapping: 1) maximum vegetation height within the four outer corners of a 56-cm × 25-cm frame divided into twenty-five 10-cm squares; 2) proportion of vegetation cover by recording the number of times rooted vegetation or thatch was directly beneath each of the 16 intersections within the vegetation frame and dividing by 16; 3) vegetation stem density by counting the number of rooted plants within a 5 cm × 3.8 cm rectangle; 4) presence or

absence of grass, sedge, rush, and forb in the center square of the vegetation frame; 5) wetness, which was determined by touch with the following definitions: dry when no moisture other than morning dew was detected, moist when soil was wet enough to clump and stick to fingers, saturated when water bubbled up when soil was depressed with fingers, and flooded when water was present above the soil surface; and 6) sward height using a 170-g, 30-cm × 30-cm plate with a meter stick placed through a slit in the middle. We dropped the plate from 80 cm and recorded the height (in mm) where the plate rested (similar to the drop disc method; Holmes 1974, Stewart et al. 2001). For each variable, we averaged the values from the 42 locations at each site for analyses. We also measured soil temperature by inserting a soil thermometer 10 cm below the soil surface 3–5 hr after sunrise at 4 locations on the trapping web (the sixth trap from the center on every third trap-line). We averaged the 4 soil temperature measurements in each site. All vegetation measurements were 10 cm toward the web center from the associated trap location. In each site, we visually assessed whether corn lily (*Veratrum californicum*) was the spatially dominant plant for the site.

Analyses

We indexed vole abundance using Minimum Number Alive (Krebs 1966), which was the number of individuals captured in a trapping web (web area = 2,827 m²). Minimum Number Alive might represent population density better than distance-sampling theory when the number of animals captured is small (White et al. 1982, McKelvey and Pearson 2001). We indexed gopher abundance as the number of fresh gopher mounds tallied in the 3 sampling belts (total plot area = 3,000 m²) at each site.

We assessed the probability of detecting voles at a site with data grouped by year, grazing status, and corn lily dominance to determine whether occupancy modeling was necessary to account for imperfect detection. We used “occupancy estimation” analysis in Program MARK version 6.x (White 2012). Because the probability of detecting a vole at a site after 5 consecutive trapping nights was 0.99, we did not use occupancy modeling to examine effects of habitat. Instead, we used 26 logistic-regression models ranked with Akaike’s Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002) to evaluate whether vegetation variables (cover; sward ht; stem density; max. vegetation ht; corn lily dominance; and the probabilities of grass, sedge, rush, or forb presence), wetness, grazing status, year, or elevation influenced the presence or absence of voles at a site. The presence or absence of voles was used to determine vole–habitat relationships on all sites because abundance data were not normally distributed when all sites were included, even after transformations. We tested the top logistic-regression model (all other models had $\Delta AIC_c > 2$) *post hoc* using *k*-fold partitioning (*k* = 7) and a Receiver Operating Characteristic (ROC) curve (Fielding and Bell 1997). In addition to the logistic-regression models, we used 26 linear-regression models ranked with AIC_c to evaluate whether the variables (same

variables as the logistic-regression models) influenced vole abundance at sites where voles were present.

We used 21 linear-regression models ranked with AIC_c to determine which variables (same variables as the vole models, and soil temp) influenced gopher abundance. We model-averaged the coefficients, standard errors (SEs), and 95% confidence intervals (CIs) from competitive models ($\Delta AIC_c < 2$) for multi-model inference (Burnham and Anderson 2002).

We assessed normality and equal-variance assumptions for linear-regression analyses visually from a residual versus fitted values plot. To meet normality assumptions, we transformed sward height, stem density, maximum vegetation height, and the probability of rush presence using the natural $\log[x + (1/6)]$, and gopher abundance using the square root of the observed values.

We selected variable combinations for all modeled relationships prior to analyses using insights from the literature (e.g., Ingles 1952, Smolen and Keller 1987, Greene 1995, Sera and Early 2003, Jones and Baxter 2004) and our hypotheses as baseline information. We did not include maximum vegetation height in any models with vegetation cover and or sward height because the correlation coefficient (r) among these variables was >0.6 . We treated years as independent in all regression analyses because there were considerable differences in the abundance of both voles and gophers at the same site between years.

We compared vegetation cover, sward height, stem density, and wetness between grazed and ungrazed sites, and between years, using repeated-measures Multivariate Analysis of Covariance (MANCOVA). Elevation was a covariate in this analysis. We transformed sward height and stem density using the natural $\log[x + (1/6)]$ to meet normality assumptions. We did not include the probabilities of grass, sedge, rush, and forb presence because a multivariate normal distribution could not be achieved. We did not include maximum vegetation height because it was highly correlated ($r > 0.6$) with cover and sward height. Only repeated sites could be used, so we did not include the 6 sites that were new in 2011 in the repeated-measures MANCOVA. We tested for equal variance using Levene's Test and Box's Test of Equality of Covariance Matrices, and we assessed normality visually from a normal probability plot. We used a chi-squared test to determine whether the frequency of corn lily dominance differed between grazed and ungrazed meadows. We used a 2-tailed equal-variance Student's t -test to determine whether grazed and ungrazed meadows differed in elevation.

We performed all analyses using R version 2.14.0 (GNU Operating System 2011) except the repeated-measures MANCOVA, which was conducted in PASW Statistics 18 (SPSS, Inc., 2009, Hong Kong). We reported means and coefficients ± 1 SE. We determined significance at α equals 0.05 except for univariate comparisons from the repeated-measures MANCOVA, where we used a Bonferroni adjustment. There were 4 response variables in the repeated-measures MANCOVA; therefore, we determined significance at $\alpha = 0.013$.

RESULTS

Estimates of vole abundance were similar between years, whereas estimates of gopher abundance varied considerably. From 17 May to 30 July 2010, we captured 51 individual voles and estimated 290 gophers from fresh mounds in 17 grazed and 15 ungrazed sites. Voles were present in 12 of 32 sites (38%), and vole abundance ranged from 0 to 13 voles/web and averaged $1.59 (\pm 0.57)$ voles/web. Gophers were present in 29 of 32 sites (91%), and gopher abundance ranged from 0 to 25 gophers/plot and averaged $9.06 (\pm 1.21)$ gophers/plot. From 23 May to 5 August 2011, we captured 66 individual voles and estimated 131 gophers from fresh mounds in 19 grazed and 19 ungrazed sites. Voles were present in 14 of 38 sites (37%), and vole abundance ranged from 0 to 11 voles/web and averaged $1.74 (\pm 0.52)$ voles/web. Gophers were present in 32 of 38 sites (84%), and gopher abundance ranged from 0 to 12 gophers/plot and averaged $3.45 (\pm 0.49)$ gophers/plot. Voles and gophers co-occurred in 9 of 32 sites (28%) where ≥ 1 vole or gopher was present in 2010 and in 13 of 33 sites (39%) in 2011.

Vole abundance varied slightly between grazed and ungrazed meadows; gopher abundance varied to a greater degree. Mean vole abundance for 2010 and 2011 combined was $1.50 (\pm 0.45)$ voles/web in grazed sites and $1.85 (\pm 0.63)$ voles/web in ungrazed sites. We displayed mean vole abundance separated by grazing status and year in Figure 2.

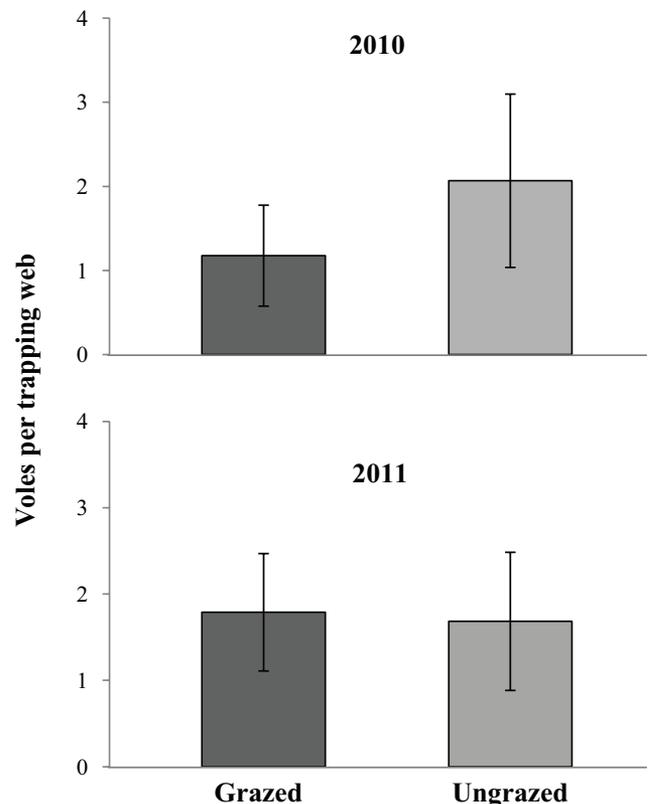


Figure 2. Mean number of individual voles captured per trapping web (± 1 SE) at meadows in the Sierra Nevada Mountains, California, USA. Abundance estimates displayed are from 17 grazed and 15 ungrazed sites in 2010 and 19 grazed and 19 ungrazed sites in 2011.

Mean gopher abundance for 2010 and 2011 combined was 7.31 (± 1.07) gophers/plot in grazed sites and 4.65 (± 0.83) gophers/plot in ungrazed sites. We displayed mean gopher abundance separated by grazing status and year in Figure 3. Of the voles captured, 51 of 117 (44%) were montane voles and 66 of 117 (56%) were long-tailed voles. These 2 vole species co-occurred in 5 of the 26 cases (19%) when ≥ 1 species was present. Though gopher abundance was estimated from fresh mounds, we also captured 4 gophers in traps; 3 were mountain pocket gophers and 1 could not be determined.

Vole-Habitat Relationships

Vole-habitat relationships were described best with presence-absence data. The top model explaining vole presence-absence included a positive association with the natural log of sward height and corn lily dominance (Table 1). The 95% CI for coefficients in the top model did not include 0. This model accounted for 0.41 of the total AIC_c weight and explained 29.28% of the null deviance. All other models were $>2 AIC_c$ from the top model so they were considered less competitive. The area under the ROC curve after k -fold partitioning was 0.84 (± 0.05). The model performed better at predicting absences than occurrences. Average sward height (actual sward ht, not transformed) in sites where voles were present was 143 (± 14) mm, while average sward height in sites where voles were absent was 84 (± 7) mm. Voles were present in 12 of the 17 cases (71%)

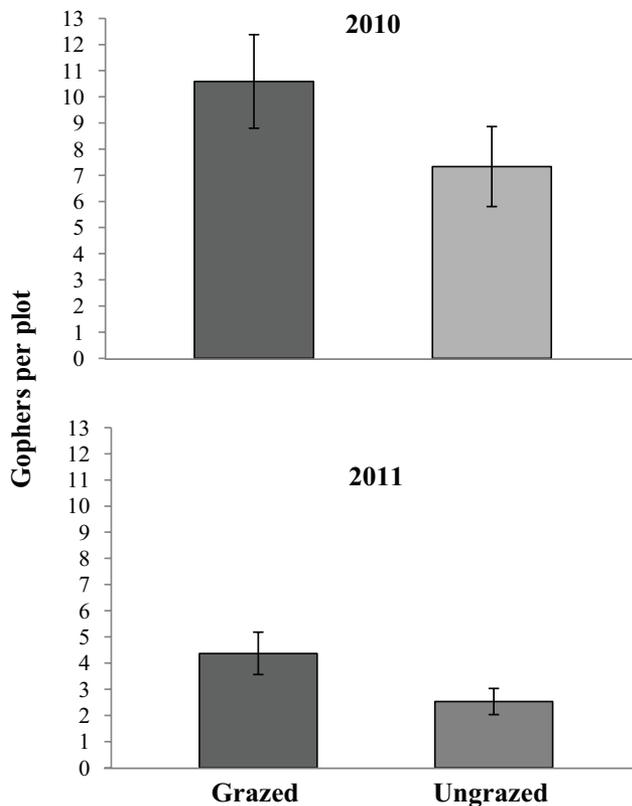


Figure 3. Mean number of gophers per plot (± 1 SE) estimated from fresh mounds at meadows in the Sierra Nevada Mountains, California. Abundance estimates displayed are from 17 grazed and 15 ungrazed sites in 2010 and 19 grazed and 19 ungrazed sites in 2011.

Table 1. Top logistic-regression model for predicting vole presence-absence at meadows in the Sierra Nevada Mountains, California, USA, in 2010 and 2011. All 25 other candidate models had $\Delta AIC_c > 2$. % deviance explained = 29.28. $K = 3$ (no. of parameters). $\Delta AIC_c = 0.00$ (difference between AIC_c of the model specified and the model with the lowest AIC_c). $w_i = 0.41$ (Akaike wt; indicates the probability that the model specified is the best predictive model within the set of candidates).

Variables	β -coeff.	SE	95% CI	
			Lower	Upper
Intercept	-13.62	3.96	-21.39	-5.85
Natural log of sward ht	2.75	0.84	1.10	4.40
Corn lily dominance	1.69	0.70	0.31	3.07

where corn lily was dominant and 14 of the 53 cases (26%) where corn lily was not dominant.

Vole-habitat models did not perform well using abundance data. The top model explaining vole abundance in sites with voles present included a negative association with grazing ($\beta = -2.13 \pm 1.49$) and accounted for 0.28 of the total AIC_c weight. However, this model only explained 7.79% of the null deviance and the 95% CI for the coefficient of grazing included 0. All other models were $>2 AIC_c$ from the top model.

Gopher Habitat Relationships

Habitat relationships of gophers were described well using abundance data. Four candidate models explaining gopher abundance had $\Delta AIC_c < 2$, so coefficients, SEs, and the 95% CIs were model-averaged. Gopher abundance was negatively associated with site wetness, and it was positively associated with stem density, frequency of forb presence, grazing, and the dominance of corn lily (Table 2). The model-averaged 95% CI for the coefficient of wetness did not include 0; the model-averaged 95% CI for all other variables included 0. The top 4 models accounted for 0.63 cumulative AIC_c weight and the model-averaged percent null deviance explained was 52.35.

Vegetation Relationships

There was some spatial and temporal variation in meadow vegetation and wetness. Vegetation variables (cover, sward ht, and stem density) and wetness were significantly different between years ($F = 10.83$; $df = 4, 26$; $P = 0.000$) and by elevation ($F = 2.82$; $df = 4, 26$; $P = 0.045$), but were not significantly different between grazed and ungrazed sites

Table 2. Model-averaged linear-regression model for predicting gopher abundance at meadows in the Sierra Nevada Mountains, California, USA, in 2010 and 2011. Four candidate models that had $\Delta AIC_c < 2$ were included in the model average. Model-averaged % deviance explained = 52.35.

Variables	β -coeff.	SE	95% CI	
			Lower	Upper
Intercept	2.15	0.70	0.77	3.53
Wetness	-1.38	0.17	-1.81	-0.95
Stem density	0.39	0.29	-0.17	0.96
Grazing	0.25	0.22	-0.09	0.58
Frequency of forbs	2.10	1.24	-0.33	4.53
Corn lily dominance	0.41	0.25	-0.08	0.91

($F = 1.60$; $df = 4, 26$; $P = 0.204$; means and SEs in Table 3). The year effect was driven mainly by stem density (significantly greater in 2011; $F = 9.65$; $df = 1$; $P = 0.004$) and site wetness (marginally wetter in 2011; $F = 6.80$; $df = 1$; $P = 0.014$), and the elevation effect was driven primarily by site wetness (not significant, but suggesting more wetness at higher elevations; $F = 3.99$; $df = 1$; $P = 0.055$). There was no significant difference in the frequency of corn lily dominance between grazed and ungrazed sites ($\chi^2 = 0.18$, $df = 1$, $P = 0.673$).

DISCUSSION

Trapping data indicated that vole abundance has been low in the central Sierra Nevada for 3 consecutive years (LaManna 2009, this study). In addition, vole runways were very scarce and we observed only 3 voles while walking through our study sites. For comparison, an anecdotal report from Yosemite National Park stated that during high vole abundance, vole runways were very numerous and voles were seen regularly by people walking through meadows (Dunmire 1957). The best available information on vole population cycling and density is from meadows of the northern Sierra Nevada where voles underwent 2–6-year population cycles (Hoffman 1958, Fitzgerald 1977). Abundance ranged from 5 to 16 voles/ha (Jenkins 1948) and from 0 to 359 voles/ha (Fitzgerald 1977). The lack of contemporary research on the length, predictability, and magnitude of vole population cycles makes determining trends difficult, but we believe the low number of voles observed during our study warrants management attention. Voles are critical ecosystem components that constitute the prey base for many species of predatory birds and mammals in the Sierra Nevada. Low vole abundance across multiple years may adversely affect reproduction and survival of many species (Sera and Early 2003).

During this study, when we found low vole abundance, great gray owl reproductive success was also low (J. Medley, U.S. Forest Service, personal communication). This relationship was consistent with other studies that suggested voles are critical prey for great gray owl

reproductive success (Hilden and Helo 1981, Winter 1986, Bull and Henjum 1990, Duncan and Hayward 1994, Hipkiss et al. 2008) and highlights the importance of considering vole habitat in meadow management.

Estimating vole–habitat relationships and vole abundance is difficult without live-trapping. Several studies have examined vole habitat and abundance in meadows of the Sierra Nevada based on sign (e.g., Winter 1986, Reid 1989, Greene 1995), but most vole–sign is inconspicuous (Gervais 2010). In addition, long-tailed voles do not usually construct runways—the most detectable form of sign created by montane voles (Ingles 1965, Johnson and Johnson 1982, Smolen and Keller 1987). In our study, long-tailed voles comprised 56% of the total vole captures, and the 2 vole species co-occurred 19% of the time when ≥ 1 species was present. Therefore, estimating vole abundance and habitat relationships based on the presence of runways might have been inaccurate in our study area. Trapping appeared to provide a better estimate of abundance because we captured voles in many sites where we observed no vole sign. Also, small mammal species were identified in-hand with very high confidence compared with sign-based procedures.

We found a weak negative correlation between grazing and vole abundance in sites where voles were present in this study. Other studies have also found a negative correlation between grazing and vole abundance, or vegetation features used by voles (e.g., Greene 1995, Jacob and Hempel 2003, Schmidt et al. 2005, Johnson and Horn 2008, Johnston and Anthony 2008). The negative correlation we found between grazing and vole abundance explained little deviance, but may indicate a pattern that would be more evident with greater vole abundance, heavier grazing, or a different study design. Because we were interested in the influence of current cattle grazing regimes on owl prey and vegetation during the owl nesting season, we surveyed meadows based on elevation and vegetation phenology rather than before and after grazing. We were also interested in assessing regional patterns by maximizing spatial coverage rather than monitoring the response of small mammals to grazing on

Table 3. Means and standard errors for vegetation, wetness, and soil temperature at grazed and ungrazed meadows in the Sierra Nevada Mountains, California, USA, in 2010 and 2011.

Variables	2010				2011			
	Grazed ($n = 17$)		Ungrazed ($n = 15$)		Grazed ($n = 19$)		Ungrazed ($n = 19$)	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Max. veg. ht. (mm)	198	22	220	29	195	25	264	29
Cover (%)	60	5	65	4	57	4	65	4
Stem density ^a	6	1	6	1	8	1	7	0
Sward ht (mm)	108	17	91	11	108	20	112	11
Frequency of grass ^b	0.33	0.07	0.38	0.07	0.50	0.07	0.49	0.07
Frequency of forb ^b	0.92	0.02	0.92	0.03	0.93	0.02	0.91	0.02
Frequency of sedge ^b	0.45	0.08	0.44	0.07	0.29	0.06	0.37	0.07
Frequency of rush ^b	0.02	0.01	0.14	0.06	0.11	0.04	0.16	0.05
Wetness ^c	0.85	0.18	0.92	0.18	1.17	0.13	1.43	0.16
Soil temp. (°C)	14	1	15	1	14	1	14	1

^a Stem density was the no. of rooted plants within a 5-cm \times 3.8-cm rectangle.

^b Frequency was the no. of presences divided by the total no. of samples at a site (42).

^c Wetness was 0, 1, 2, or 3 for dry, moist, saturated, or flooded, respectively.

fewer sites with a before–after control–impact design. Our sampling scheme led to several cases where grazed meadows were surveyed prior to the onset of grazing for that year, which may have explained the lack of vegetation differences between grazed and ungrazed sites. Other studies that monitored voles and grazing over longer periods of time found that voles were positively associated with greater physical vegetation features (e.g., cover and ht) and negatively associated with grazing (Peles and Barrett 1996, Jacob and Hempel 2003, Johnson and Horn 2008). There may be a lag time to detect this response depending on grazing intensity, time of year, vole abundance, and preexisting meadow conditions (Johnson and Horn 2008).

We found a positive association between vole presence and sward height. Because cattle grazing should inherently reduce sward height in areas with palatable plant species, we infer that sward height and vole prevalence may be increased by reducing and/or managing cattle movements. This may be especially important in National Forests where there is a high proportion of grazed meadows. We recommend maintaining sward height throughout the grazing season at values that resulted in the highest probabilities of vole presence. In sites not dominated by corn lily, our analyses suggest that mean sward height of 290 mm yielded a 90% predicted probability of vole presence. In sites dominated by corn lily, mean sward height of 125 mm yielded a 90% predicted probability of presence (Fig. 4).

We posit that corn lily may benefit voles primarily by providing cover from predators. Corn lily is not typically consumed by herbivores and may be one of the few species providing cover in meadows grazed extensively by cattle (Potter 2005). However, corn lily is not eaten by voles (Cervantes 1992) and may reduce food availability by shading-out nutritious plants. During our study, we observed anecdotally that plants were less abundant under corn lily compared with areas where corn lily was absent. Additionally, it is unclear whether corn lily height and robustness reduces owl foraging success beyond a certain threshold.

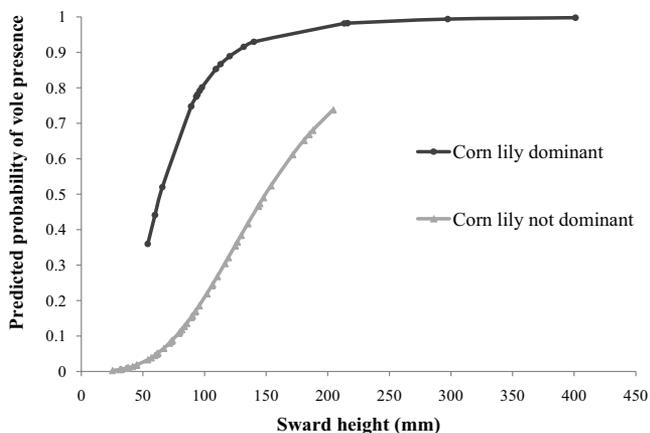


Figure 4. The influence of sward height on predicted probability of vole presence at corn lily–dominated and non-corn lily–dominated meadows in the Sierra Nevada Mountains, California, USA, 2010 and 2011. Model-averaged coefficients from *k*-fold validation procedures and observed sward heights were used to obtain predicted values.

Greene (1995) found that owls foraged most often in sites that correlated with vole habitat (taller vegetation, higher vegetation cover, and wetter soil) but that owl presence decreased when vegetation was very tall (500–750 mm). Corn lily can grow 1–2 m tall (McNeal 2012).

Gophers are important prey species that may increase great gray owl survival when vole density is low (Winter 1986, Reid 1989). However, results from other studies suggest that owl reproduction is linked to a diet abundant in voles (e.g., Winter 1986) and meadow conditions associated with vole habitat and abundance (e.g., Greene 1995). In our study, gopher abundance was positively correlated with grazed meadows (though the 95% CI for the coefficient of grazing included 0, which indicated a weak relationship). Gopher abundance was also associated with dryness and the frequency of forb presence (though the 95% CI for forb presence included 0), which have been correlated with grazing (Gifford and Hawkins 1978). Similar to our study, Powers et al. (2011) found that gophers were denser in grazed, rather than ungrazed meadows of the Sierra Nevada.

When interpreting the relationship we found between gopher abundance and grazing, it is important to consider the potential influence of grazing intensity. Grazing intensity was not incorporated into this study because grazing intensity was difficult to quantify given the high degree of variation in cattle numbers, grazing duration, and onset of cattle from year to year (Gillen et al. 1984, McIlroy et al. 2011). But, grazing allotments in our study area permit between 50 and 440 cow–calf pairs. Other researchers have found lower gopher abundance in grazed sites and suggested that high intensity grazing may have reduced forage quality and burrowing capability because of soil compaction (Phillips 1936, Hunter 1991). There may be a positive relationship between gopher abundance and grazing intensity to a certain threshold, at which point the relationship may become negative. In our study, gophers were positively associated with grazed sites, but also with stem density (though the 95% CI for stem density included 0). Stem density did not differ significantly between grazed and ungrazed sites in this study, but has decreased with high intensity grazing in other studies (Blydenstein et al. 1957, Vankat and Major 1978).

We observed a 62% decrease in the number of gophers per plot from 2010 to 2011. This may have been caused by the increase in wetness from 2010 to 2011, and the negative correlation we found between gopher abundance and wetness. This negative association with wetness was consistent with several other studies of gopher habitat relationships (Ingles 1952, Greene 1995, Jones and Baxter 2004). Because gopher abundance in this study was indexed from fresh mounds, it was possible that gopher activity, not gopher density, changed over the 2 years. However, gopher mound surveys have successfully represented gopher abundance in other studies (e.g., Reid et al. 1966), and Ingles (1952) found that radiomarked gophers sometimes shifted their home ranges from wet areas to drier areas prior to snowmelt.

MANAGEMENT IMPLICATIONS

The habitat relationships of both voles and gophers should be considered when managing meadows for great gray owls. We suggest that management of meadows for great gray owl prey may be optimized by focusing on the spatial arrangement of grazed sites; an ungrazed meadow in close proximity to a grazed meadow could provide a pair of owls with foraging opportunities for both voles and gophers, depending on their respective availability in a given year. In our study, habitat that supported voles was much less common than habitat for gophers, so we suggest enhancing vole habitat to improve prey variety needed for owl survival and reproduction. Management may be most efficient by prioritizing wet meadows for voles because gophers were not likely to be abundant in wet sites, and vole abundance has been correlated with moist soils. Therefore, particularly in areas with moist soils, we recommend maintaining sward height commensurate with the habitat relationships of voles found in this study. If cattle grazing takes place in meadows managed for vole habitat, we recommend maintaining sward heights of at least 290 mm on sites that are not dominated by corn lily and 125 mm on sites that are.

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