Habitat and Landscape Distribution of *Calochortus greenei* S. Watson (Liliaceae) Across the Cascade-Siskiyou National Monument, Southwest Oregon

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ABSTRACT

The Cascade-Siskiyou National Monument includes a wide range of slope, elevation, soil types, and historic management activities. *Calochortus greenei* occupies a wide range of habitats primarily defined by topographic and edaphic factors. Several environmental factors are confounded with patterns of livestock use, making it difficult to separate the influence of individual factors. The inclusion of many environmental variables in multivariate models with little predictive power suggests that few generalizations about *C. greenei* abundance relative to environmental factors are valid across the larger landscape. Distance from vegetation edge was an important biotic variable incorporated in models of *C. greenei* population density across the landscape, suggesting that ecotones between soil types may play a role in defining suitable habitat. The varied localized influence of edaphic factors may indicate their indirect importance to *C. greenei* habitat by controlling the expression of mixed shrub and hardwood vegetation. Habitat analyses and examination of population size and change over time are similarly confounded by environmental and management factors. However, an examination within three areas of *C. greenei* aggregation with distinct soils and elevation indicate that the relative proportion of native perennial and non-native short-lived grasses are correlated with population size. These results suggest that invasive annual and short-lived perennial grasses may prevent the successful establishment and persistence of *C. greenei* seedlings, resulting in the long-term decline of populations in habitats and circumstances prone to invasion by ruderal species, including high livestock use areas.

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INTRODUCTION

The proclamation for the Cascade-Siskiyou National Monument (CSNM) requires a study of livestock impacts to Objects of Biological Interest before implementing changes in management that might affect livestock operation. This paper examines changes in *Calochortus greenei* populations size and habitat characteristics within a landscape context. The landscape context is provided by the analysis of spatial patterning of *C. greenei* populations density relative to topographic, edaphic, biotic, and management descriptors of the landscape. Habitat models are derived for *C. greenei* population sites and randomly located sampling sites across the landscape. Patterns of differential livestock use and recent non-use of individual grazing allotments and pastures provide a framework for potentially separating recent from historic livestock impacts on *C. greenei*.

Current knowledge about *C. greenei* distribution and impacts by management activities is largely derived from surveys and associated observations. Brock (1988) completed an extensive survey recording phenology, vigor, flowering rate, and impacts by wildlife. Knight (1990, 1992) examined similar variables at two populations in the Pilot Rock area of the CSNM over a six year period. Studies described in this paper include an analysis of landscape patterns of *C. greenei* , population trends, and seasonal changes to occupied *C. greenei* habitat in response to livestock grazing.

Biology and Habitat

Habitat plant community: C. greenei is associated with non-conifer plant communities including grasslands, shrublands and woodlands. A detailed description of plant communities that characterize *C. greenei* habitat is provided by Brock (1988). The grasslands vary in composition, including native grasses such as Roemer's fescue (*Festuca roemerii)*, and Lemmon's needlegrass (*Achnatherum lemmonii*). Non-native grasses such as bulbous bluegrass (*Poa bulbosa)*, medusahead (*Taeniatherum caput-medusae)*, cheatgrass (*Bromus tectorum*), and soft chess (*Bromus hordeaceous*) are also a common occurrence. Shrublands may be dominated by buckbrush (*Ceanothus cuneatus*), Klamath plum (*Prunus subcordata*), bitterbrush (*Purshia tridentata)*, or serviceberry (*Amelanchier alnifolia*), and often exhibit a variable mixture of species over distances of

a few hundred meters. Oregon white oak (*Quercus garryana* ssp. *garryana* at lower elevations, versus *Q. garryana* ssp. *breweri* at higher elevations) is often closely associated with *C. greenei* sites. Other trees include western juniper (*Juniperus occidentalis*), and ponderosa pine (*Pinus ponderosa*).

Other biotic, edaphic, and topographic variables: Several other vegetation attributes have been implicated in the distribution of *C. greenei* . At some sites, *C. greenei* appears to be located within, or close to the edge of shrub canopies (Brock 1988, 1996). This is postulated to be due to past livestock impacts. In areas of high vegetation cover, *C. greenei* occurs in open patches relative to the surrounding area, implicating minor soil types may confer *C. greenei* habitat within larger soil complexes. Brock (1988, 1996) provides a detailed analysis of soils underlying the *C. greenei* sites throughout the species range. In Oregon, soil depth at *C. greenei* sites ranges from shallow to moderately deep with an affinity for sites with more clay. Soils appear to vary in the amount of rock at the surface and within the soil profile. Some of the most prevalent soils are complexes, somewhat confounding the relationship of *C. greenei* to soil type. In terms of topography, *C. greenei* is predominantly found on south and west aspects, but may extend to east and northerly aspects where suitable habitat occurs as defined by plant community or soils (Brock 1996). Slopes tend to be gentle to moderate (10 to 30% slope; Brock 1996).

Growth characteristics: *C. greenei* is a long-lived perennial geophyte (> 50 years, Brock 1996) capable of reproducing both sexually and vegetatively. Seedlings show a high mortality rate. Plant emergence occurs in late March at lower elevations, and soon after snowmelt at higher elevations (late April/early May (Brock 1988 in Knight 1992). Flowering commences by July at low elevations (Brock 1988), but may extend to August at higher elevations (Brock 1996). Fruit maturation ranges from late July until early September.

Number of individuals, flowering, and seed set: The total number, the percent of individual plants found to be flowering, and seed set vary by site and by year (Menke and Kay 2006, Knight 1992, Brock 1988, 1996). Variability has been attributed to soil

conditions, elevation, forage utilization (by both native and non-native ungulates), die-back, staggered leaf emergence, and periodic dormancy (Brock 1996). This variability in *C. greenei* counts is likely accentuated by variable timing of site visits, and the limited number of visits per season on all surveys. Other factors that have been observed to influence plant counts or the percent of flowering plants include: herbivory by insects, jackrabbits, and other small mammals; successional changes resulting from increased fire return interval, and harvest (flowers or bulbs) by collectors. The influence of these factors appears to vary by location.

Historic and ongoing change of C. greenei habitat: Repeat photography and historic anecdotes suggest that *C. greenei* habitat has been strongly influenced by livestock and changes in the fire return interval. Heavy livestock use was initiated in *C. greenei* habitat soon after colonization by Euro-Americans. Large herds of sheep, cattle and horses roamed the area (Hosten et al. 2007a). Anecdotes and photos commonly reference the historic conversion of perennial bunchgrass to exotic annual grasses and weeds, and an increase in shrubs and trees (Hosten et al. 2007c). Recent studies have documented the patterning of broadleaved noxious weeds with livestock, distance from roads, the presence of shrink-swell clays, and other factors (Hosten 2007). While native grasses are increasing in abundance within the CSNM, historic livestock influences partly explain the current landscape patterning of exotic annual grasses. *Poa bulbosa* is the most common component of change in herbaceous communities in recent decades across a wide range of plant communities (Hosten et al. 2007b).

METHODS

I. Population Surveys / Habitat Analysis

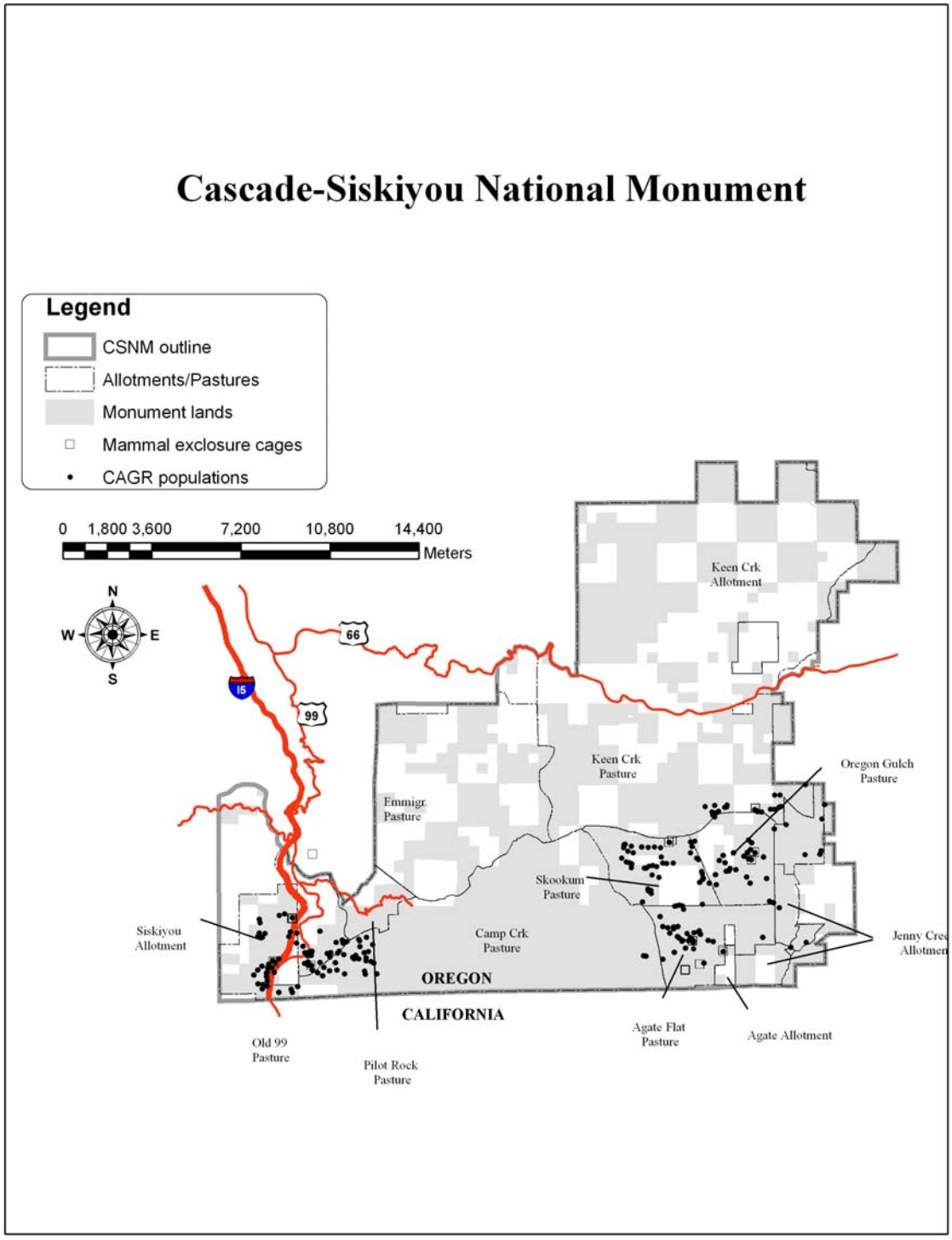
Field surveys for *Calochortus* and associated habitat analyses were conducted across three broad areas within the Cascade-Siskiyou National Monument, hereafter referred to as Agate Flat, Oregon Gulch / Skookum, and Siskiyou (see map, Figure 1). These three areas contain the large majority of *C. greenei* populations, are essentially coincident with defined grazing allotments, and span the range of livestock utilization levels present

within the monument. The Siskiyou area is ungrazed, Oregon Gulch / Skookum experiences moderate to low utilization, and Agate Flat receives the highest intensity of utilization (Hosten et al. in prep. b). Surveys for *C. greenei* were conducted in 2003, 2004 and 2005 between May 15 and July 1, coincident with the seasonal period of maximum visibility and most accurate identification for this species (Brock 1988, 1996).

In addition to revisiting known *C. greenei* populations in these three areas, systematic surveys for new populations were completed across all other potentially suitable habitat within the monument. A handheld GPS unit was used to geo-reference the center of each new *C. greenei* occurrence. Where populations covered an area of an acre or greater, multiple GPS points were recorded along population boundaries so as to allow for the delineation of polygons. Individual *C. greenei* plants were defined and counted as single leaves or leaf clusters arising from an underground bulb. Counts of relatively large (e.g. > 500 individuals) and/or widely dispersed (> 1 acre) populations were repeated at least twice and the totals were averaged to arrive at a single population size estimate.

Across the area occupied by each *C. greenei* population, percent cover of canopy trees, shrubs < 2 m tall, forbs, graminoids and bare soil was estimated using the scale recommended as most accurate for ocular estimation of vegetation cover (Elzinga et al. 1998, Bonham 1989). Cover class scales were as follows: 1 (0 < % cover < 1), 2 (1 ≤ % cover < 5), 3 (5 ≤ % cover < 15), 4 (15 ≤ % cover < 25), 5 (25 ≤ % cover < 50), 6 (50 ≤ % cover < 75), 7 (75 ≤ % cover 95) and 8 (95 ≤ % cover < 100). Within the graminoid vegetation layer, an ocular estimate was also made of the relative proportion of native to exotic graminoids. To minimize potential errors, all estimates of vegetation cover were made by the primary author.

Figure 1. All *C. greenei* occurrences in the Cascade-Siskiyou National Monument distributed across livestock allotments / pastures.



II. Seasonal Changes in Occupied *C. greenei* Habitats

To investigate short-term seasonal changes to habitats in which *C. greenei* occurs across a range of livestock utilization levels, we established vegetation transects within 18 sites currently occupied by *C. greenei* across the monument. Six sites were located in Agate Flat (moderate-high livestock utilization), 7 sites in the Oregon Gulch/Skookum area (low-moderate utilization) and 5 sites were in Siskiyou (ungrazed). At each *C. greenei* site selected for sampling, we established two 40 m transects, with beginning points and azimuth bearings randomly selected and placed well away from fences, terrain breaks and other potentially confounding features. Point intercepts were collected at each 0.5 meter interval along transects and assigned into one of eight potential cover classes (shrub, native grass, exotic grass, forb, litter, bare ground, rock and cow dung). As an additional measure of livestock use, we counted cattle hoofprints and dung piles intercepting the entire length of each transect.

The initial "early season" sampling of vegetation along transects occurred between May 12-21, 2004, just before release of livestock, and the second "late season" sampling took place between June 16-July 7, 2004, towards the end of or immediately after the seasonal period of livestock use for these pastures. At the time of the late season sampling, we also categorized each site into one of seven qualitative browse utilization classes as defined in the Key Forage Plant Method (USDI BLM 1999).

III. GIS-based Landscape Analysis

Analysis of Key Variables: Actual number of *C. greenei* individuals in each population were counted by class for key categorical variables (Table 1) for comparison to calculated expected *C. greenei* population counts. We use the term population hereafter to refer to a relatively discrete and contiguous patch of individual plants. Expected *C. greenei* counts were calculated for each class as a the total number of counts multiplied by the proportion of area occupied by individual classes of the total analysis area (area occupied by all classes). Actual and expected *C. greenei* counts were compared graphically and subjected to chi-square analysis for statistical significance. Significance

was determined at a probability level of 0.1, using a Bon-Feroni adjustment for the number of variables examined.

Multivariate analysis: HYPERNICHE (MJM Software 2004), was used to explore the response of *C. greenei* to the range of predictor variables including topographic, edaphic, biotic, and management factors (Table 1). Nonparametric Multiplicative Regression (NPMR) was used to derive best-fit models describing the pattern of the above defined response variables relative to predictor variables. The Local Mean form of the NPMR regression enables the incorporation of binary or quantitative data. The modeling process includes an initial screening for variables of interest followed by an exhaustive modeling approach. As the number of predictor variables increases, a stepwise search is initiated. All predictor variables are assessed in one-variable models to determine the best one-variable model. Additional variables are added stepwise, assessing improvement at each step. This approach evaluates all possible combinations of predictors and tolerances.

In addition to identifying important variables, the modeling process provides several measures for assessing importance of individual variables and overall model quality. When a response variable is declared as quantitative, model quality is evaluated in terms of the size of the cross-validated residual sum of squares in relation to the total sum of squares. The HYPERNICHE manual calls this the "cross r^2" (xr^2) because the calculation incorporates a cross validation procedure. The xr^2 value is a measure of variability captured by the best fit model.

Sensitivity analysis provides a measure of the relative importance of individual quantitative predictors in NPMR models. The sensitivity measure used here refers to the mean absolute difference resulting from nudging the predictors, expressed as a proportion of the range of the response variable. The greater the sensitivity, the more influence that variable has in the model. With this sensitivity measure, a value of 1.0 implies a change in response variable equal to that of change in a predictor. A sensitivity of 0.5 implies that the change of response variable magnitude is half that of the predictor variable. A sensitivity of 0.0 implies that nudging the value of a predictor has no detectable effect on the response variable.

NPMR models can be applied in the same way that traditional regression models are used (McCune 2006). A major difference is that estimates from the model require reference to the original data. Three-dimensional plots of select predictor and response variables provide a visual assessment of how the relationship of predictor variables to response variables. The modeling approach as utilized by HYPERNICHE works well with variables defined in GIS as ASCII grids, allowing the formulation of probability estimate maps for response variables.

HYPERNICHE does not accommodate for spatial autocorrelation (MJM Software 2004), it remains for the user to ensure that results are not constrained by the pattern of observations. Since the C. greenei population locations were found to be spatially correlated, a method of analysis was adopted to enable a random sampling of response and predictor variables across the landscape within GIS using layers derived from a range of sources (Table 1). Four response variables (Table 1) representing C. greenei abundance (actual location, and population density at three search radii). Predictor variables (Table 1) include environmental descriptors (topographic, edaphic), biotic descriptors (canopy cover, plant community, distance from vegetation edge, etc), and indicators of past and present management (livestock utilization, distance from water, past management treatments, distance from roads, etc). All variables are represented as layers within GIS. The analysis of relationships between response and predictor variables is applied to the data derived by intercepting random locations and actual locations to the data layers in GIS.

The portion of the monument south of highway 66 was selected as the study area, since this area included all of the monument *C. greenei* locations and a wide range of ecological sites. 2,000 randomly generated points identified the random sampling sites in GIS. All sample sites (random and actual) falling within private lands or intercepting areas where critical environmental data was not available (e.g., the recently acquired Box O Ranch, and private lands) were excluded from the analysis, resulting in approximately 1,300 sample sites.

Several analyses were conducted to explore the influence of *C. greenei* auto-correlation and search radius employed in the creation of *C. greenei* density maps on associations with predictor variables. Several analyses using actual locations (presence

absence) together with intercepted population density (calculated at three search radii) as response variables were completed to assess the importance of predictor variables and the influence of spatial aggregation of *C. greenei* sites on results. Actual *C. greenei* locations were assessed on a presence/absence basis within datasets using random sample locations as context. In this first run, random samples falling within a 250 meter buffer of actual locations were removed, and replaced with the actual locations. In the second run of analyses, the above sample points (actual locations and random locations outside of the 250 meter buffer) were analyzed for potential relations between *C. greenei* density (calculated at 3 search radii) and the all of the predictor variables. In a third analysis, potential relations between *C. greenei* density and the all of the predictor variables was examined for the randomly located sample points intercepted with the response and predictor variables at random locations only.

Table 1. Description of the predictor variables

Variable	Source	Description
% clay	NRCS database	average percent clay (by soil horizon, then by soil component)
avg. soil depth	NRCS database	average soil depth (representative bottom depth for the deepest horizon, averaged by soil component)
% sand	NRCS database	average percent sand (by soil horizon, then by soil component)
% silt	NRCS database	average percent silt (by soil horizon, then by soil component)
% clayh1	NRCS database	percent clay of the first horizon of the most common soil component of a soil type
Deepest soil depth	NRCS database	deepest bottom representative soil depth of all soil components within a soil type
Heatload	NRCS database	heatload calculated from digital elevation data
Com. Depth	NRCS database	bottom depth of lowest soil horizon of most common soil component
elevation	digital elevation data	elevation derived from digital elevation data
slope	digital elevation data	slope derived from digital elevation data
years of rest	BLM grazing records	years of rest since most recent population assessment
distance from road	BLM road inventory	distance from road (100m increments)
% sandh1	NRCS database	percent sand of the first horizon of the most common soil component of a soil type
shallowest soil depth	NRCS database	shallowest bottom representative soil depth of all soil components within a soil type
% silth1	NRCS database	percent silt of the first horizon of the most common soil component of a soil type
average utilization	BLM grazing records	running average forage utilization for years when forage was mapped
maximum utilization	BLM grazing records	maximum recorded forage utilization for years when forage was mapped
vedge_15	LIDAR	vegetation edge within 15 m
vedge_5	LIDAR	vegetation edge within 5 m
vegetation height	LIDAR	maximum vegetation height check
% herbaceous	LIDAR	percent groundcover less than 1m high
Distance from water	BLM riparian inventory	distance from perennial and long-duration intermittent water (100m increments)
vegetation manipulation	BLM records	non-conifer management compiled from BLM records
coarse plant community	NRCS database	coarse plant communities derived from NRCS database
forest cover change	Conservation Biology Institute	forest change derived from TM satellite image differencing
Vertisol	NRCS database	vertisol soil derived from NRCS database
Ecological type	NRCS database	Ecological type

RESULTS

I. Population Trends and Habitat Relationships

Population Trends: A total of 172 *C. greenei* populations have been documented within the boundaries of the Cascade-Siskiyou National Monument, including 36 in Agate Flat, 80 in Oregon Gulch/Skookum and 44 in Siskiyou study areas, respectively. Of this total, 67 populations are resurveys of previously known occurrences and 93 were newly documented as part of this study. The remaining 12 *C. greenei* populations occur outside the focal study areas and were not revisited but were included in the landscape analysis. *C. greenei* population sizes vary from 1 to 2,500 plants (mean = 161), but most are < 100 plants (median = 61). Figure 2 portrays a wide range of intermingled population sizes distributed across the landscape. The drier portions of the monument, generally at lower elevations (e.g. Agate Flat, the Box O Ranch, and the eastern portion of Oregon Gulch) appear to have a greater proportion of smaller *C. greenei* populations (> 100 plants).

Populations for which historic count data exists and that were also resurveyed as part of this study are shown in Figure 3. Resurveyed populations exhibit a wide range of elapsed time between visits, varying between 2 and 25 years, respectively compared to areas rested from livestock grazing (median = 4 yrs.). Time between surveys is not uniformly distributed between study areas. A relatively high proportion of sites with longer periods between population counts (> 20 years) are located in Agate Flat, and those with short elapsed time (< 6 years) are in the Siskiyou study area at the western end of the monument (Figure 3).

Resurveyed *C. greenei* populations show increasing, no-change, and decreasing size trends across the monument (Figure 4). Areas that have been rested from livestock grazing exhibit relatively few population declines compared to areas under continued grazing (Table 2). The overall pattern of increasing, decreasing and no-change in population size is significantly different for grazed versus ungrazed areas using a chi-square analysis (p=0.0001).

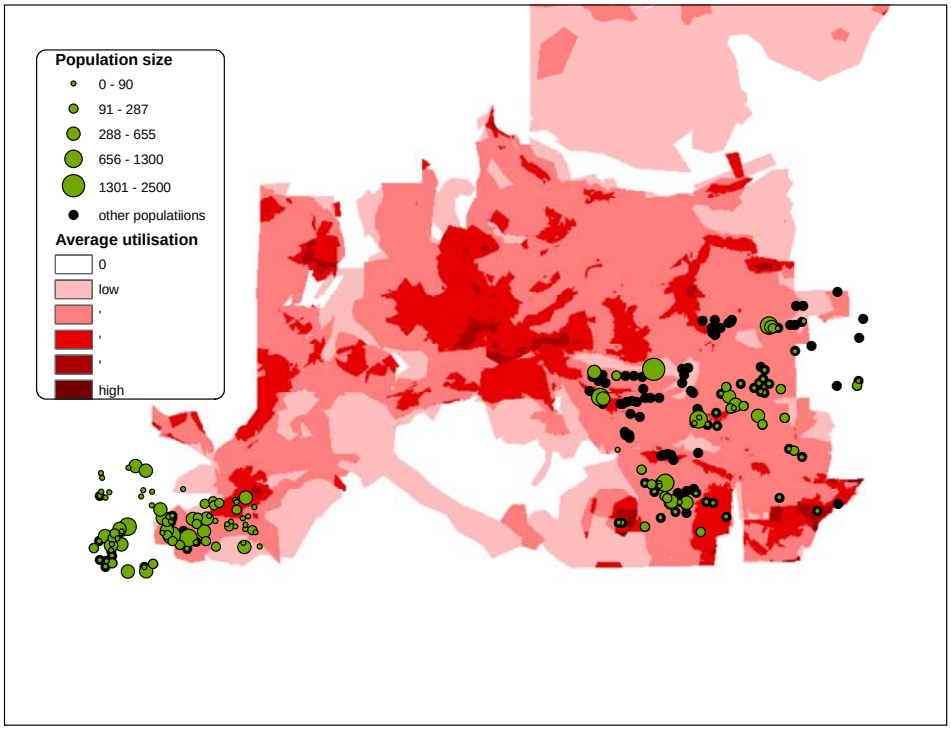


Figure 2. Distribution of *C. greenei* population sizes across the Cascade-Siskiyou National Monument in relation to patterns of livestock utilization.

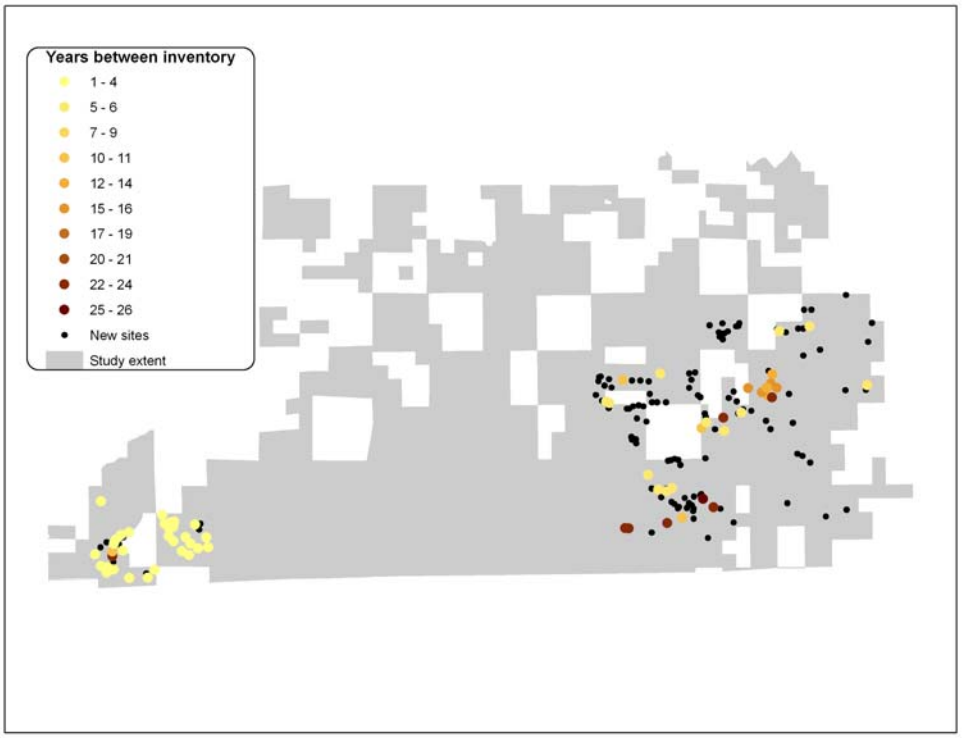


Figure 3. Number of years between historic and recent *C. greenei* population surveys.

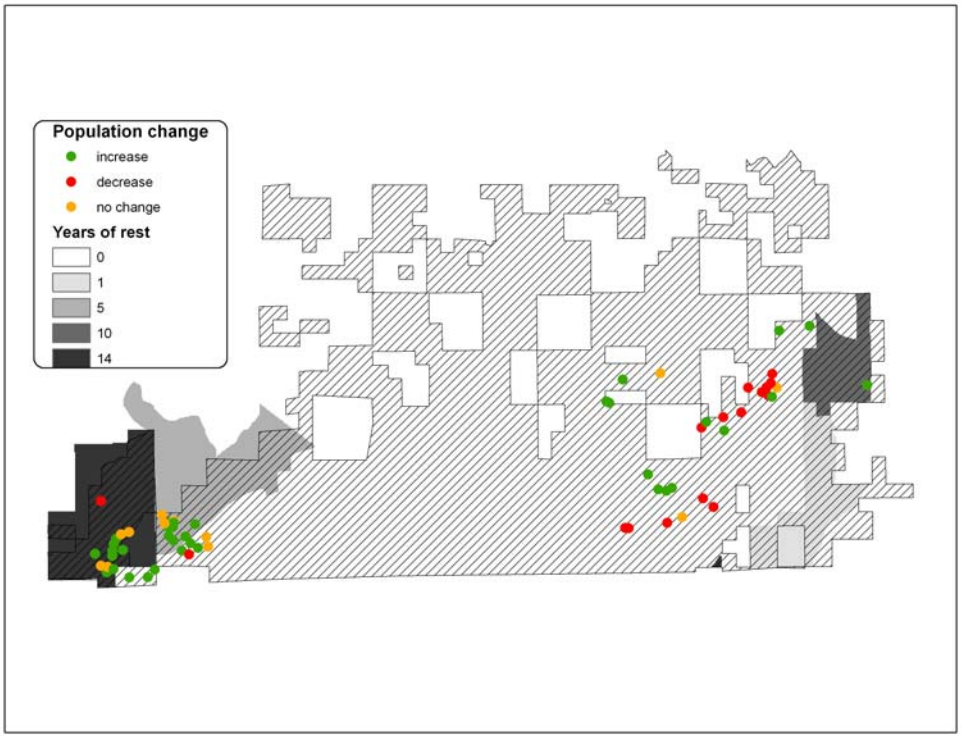


Figure 4. Identification of increasing, decreasing, and no-change *C. greenei* populations relative to areas rested from grazing.

Table 2. Number of *C. greenei* populations showing increase, decrease, or no change between surveys.

	increase	decrease	neutral
ungrazed	18	1	7
grazed	18	15	5

Habitat Relationships: Data on percent cover of vegetation functional groups for all surveyed *C. greenei* sites was inspected for normality using the Shapiro-Wilk test and normalized using a log transformation. A number of significant trends between *C. greenei* population size and vegetation cover are apparent in the data (Figure 5). Population size increases with increasing cover of bare soil, approaching maximum values at cover class 4 (15-25% cover) and remaining unchanged through cover class 6

(50-75%). Increasing population size also correlated with increasing shrub and forb cover, approaching largest measured values at cover class 5 (25-50%) and 4 (15-25%), respectively. Conversely, when total grass exceeds cover class 5 (25-50%), *C. greenei* population size declines. No apparent trend exists between *C. greenei* population size and tree cover (box plot not shown).

Boxplots similar to those showing *C. greenei* population size and cover of vegetation functional groups are shown in Figure 6 for cover of native grass relative to exotic grass. In this case, each of the three study areas was analyzed separately in order to avoid potential biases associated with environmental/climatic differences and varying abundance of annual grasses (Hosten et al. 2007a). In all three study areas, *C. greenei* population size is correlated with increasing proportion of native grass (Figure 6). The largest *C. greenei* populations are associated with those sites having at least 50% of their grass cover recorded as native. At Agate Flat, most *C. greenei* sites were dominated by exotic grasses (e.g. proportion native grass less than 50%).

Polynomial regression analysis was used to statistically analyze the relationship between *C. greenei* population size and the ratio of native to exotic grass cover. In the three study areas, a quadratic model provided the best fit of the data (Figure 7), and all correlations were statistically significant ($p < 0.0001$). R^2 values for the three models vary from a high of 0.66 at Oregon Gulch/Skookum (n=80), to 0.64 at Siskiyou (n=44), and 0.37 at Agate Flat (n= 36).

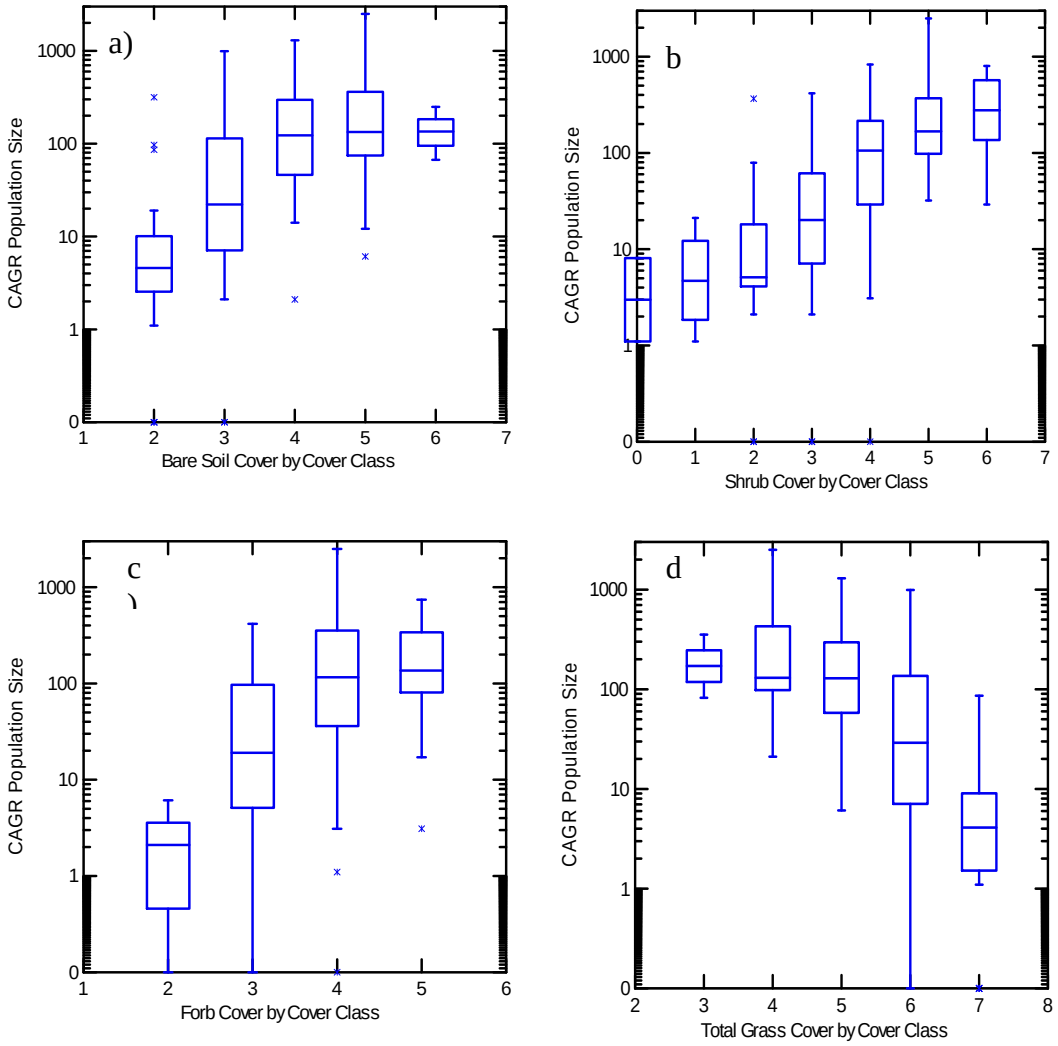


Figure 5. Box plots of log-normalized *C. greenei* population size as a function of the range in cover of vegetation functional groups a) bare soil, b) shrub, c) forb, and d) total grass cover by cover class (all study areas, n=160). Vegetation cover classes are as follows: 0 = absent, 1 = less than 1% ; 2 = 1-5% ; 3 = 5-15% ; 4 = 15-25% ; 5 = 25-50% ; 6 = 50-75% ; 7 = 75-95% ; 8 = 95-100%.

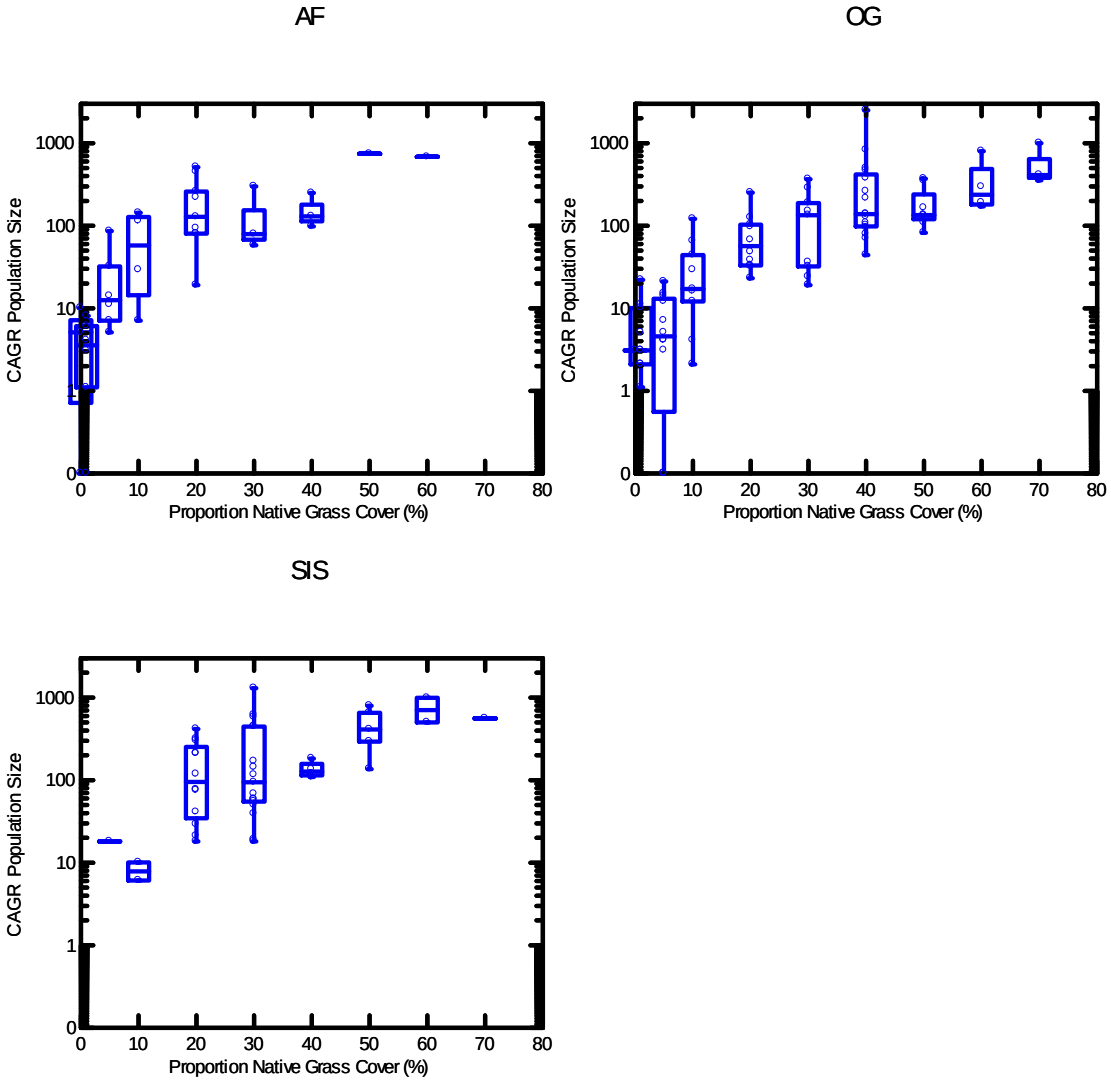


Figure 6. Box plots of log-normalized *C. greenei* population size as a function of the proportion of native grass cover (percent), for Agate Flat (AF; n=36) Oregon Gulch/Skookum (OG; n=80) and Siskiyou (SIS; n=44) study areas.

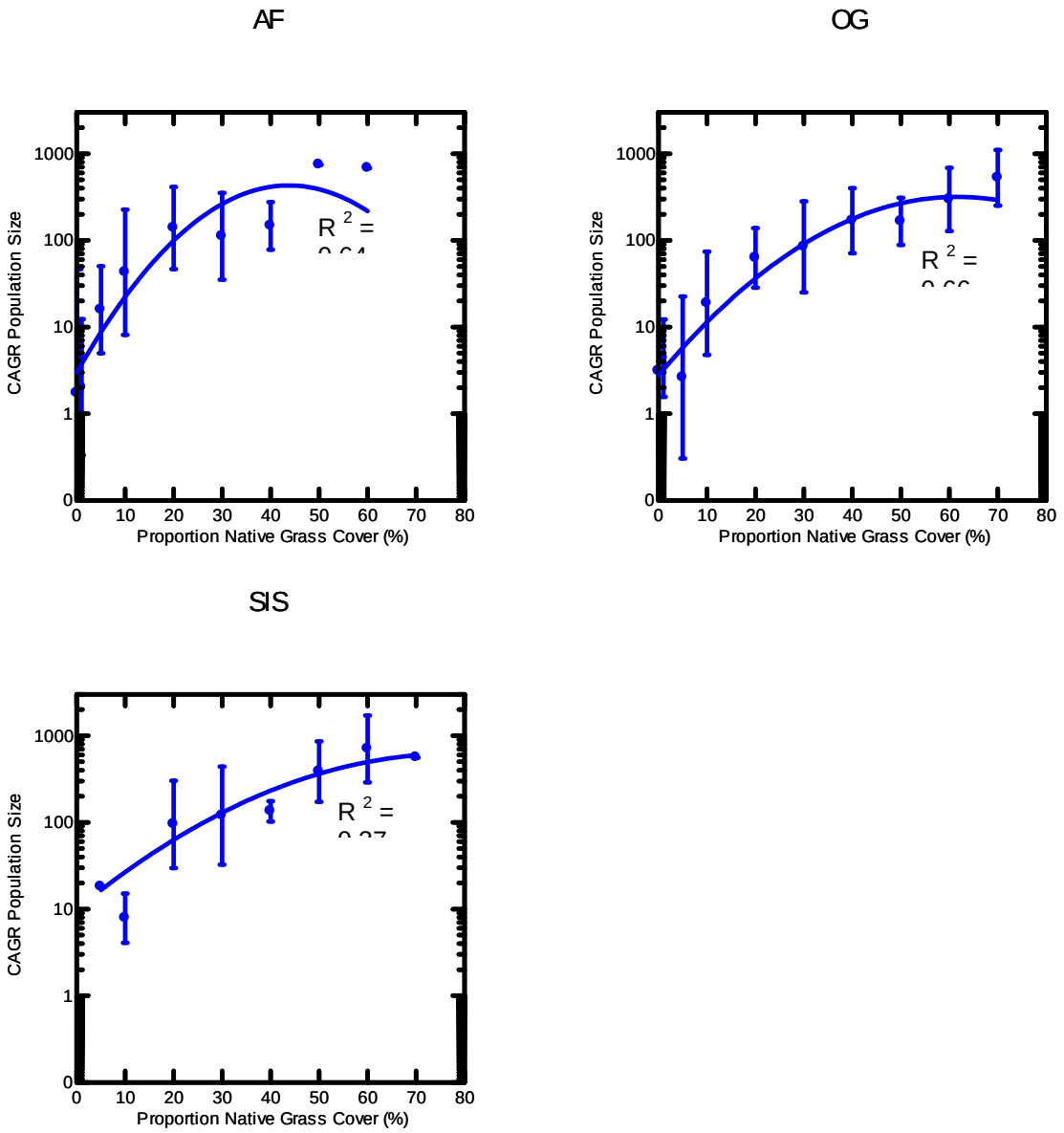


Figure 7. Quadratic regression models of log-normalized *C. greenei* population size as a function of the proportion of native grass relative to exotic grass cover, for Agate Flat (AF; n=36) Oregon Gulch/Skookum (OG; n=80) and Siskiyou (SIS; n=44) study areas

II. Seasonal Changes in Vegetation Cover and Indicators of Livestock Use

Changes in vegetation cover were first analyzed separately for each site, and then merged across all sites within each of the three study areas subject to different levels of livestock utilization (Figure 8). The total number of intercept points collected from transects varied between 1,620 (Siskiyou; 5 sites) and 2,592 (Oregon Gulch/Skookum; 7 sites). Figure 9 displays histograms showing the relative percent change in vegetation cover between early season (before livestock grazing) and late season (after grazing) measurements across the three study areas.

Significant differences exist between the percent of native and exotic grass cover along transects among the three study areas. Siskiyou exhibited the highest cover of native grass along transects (16-22%), followed by Oregon Gulch/Skookum (10-11%) and Agate Flat (0.8-1%), respectively. The inverse trend was found with respect to exotic grass – Agate Flat sites (39-40%) had significantly greater cover than either Oregon Gulch/Skookum (22-25%) or Siskiyou (25-31%) sites. No significant differences were found in terms of percent forb (21-34%) or litter cover (15-22%) between the three study areas.

Early to late season changes in vegetation cover varied for some vegetation cover types between study areas. For example, bare soil cover increased from 12% at the early season sampling to 22% late season along transects at Agate Flat, whereas bare soil remained mostly unchanged (13% and 15%) at Oregon Gulch/Skookum and significantly decreased from 11% to 3% at Siskiyou sites. Native grass cover did not change significantly between early and late season measurements at Agate Flat (0.8% to 1%) and Oregon Gulch/Skookum (10% to 11%), but significantly increased at Siskiyou sites (16% to 22%; Figure 8). No differences were apparent between study areas in seasonal trends for exotic grass, forb and litter cover.

The number of livestock dung piles and hoofprints counted along early and late season transects varied significantly among study areas (Figure 10; $p<.0001$, two-sample Kolmogorov-Smirnoff test). *C. greenei* populations at Agate Flat had the highest counts for both dung piles and hoofprints along transects, followed by Oregon Gulch/Skookum and Siskiyou sites. Total number of livestock dung piles increased from early season counts of 6 at Agate Flat and 3 along transects at Oregon Gulch/Skookum

sites, to late season counts of 35 and 13, respectively. Similarly, total counts of livestock hoofprints also increased, from 14 to 237 at Agate Flat and 32 to 166 at Oregon Gulch/Skookum sites. No livestock dung piles or hoofprints were counted along transects at ungrazed Siskiyou sites.

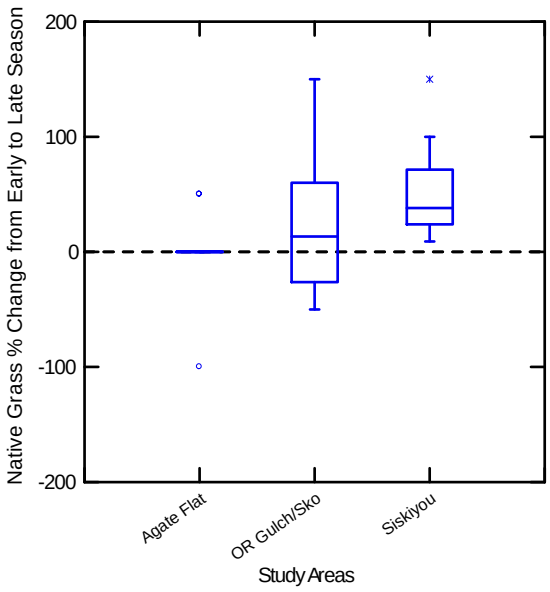


Figure 8. Percent change between early and late season native grass cover at sampled *C. greenei* sites grouped by study area (n=18).

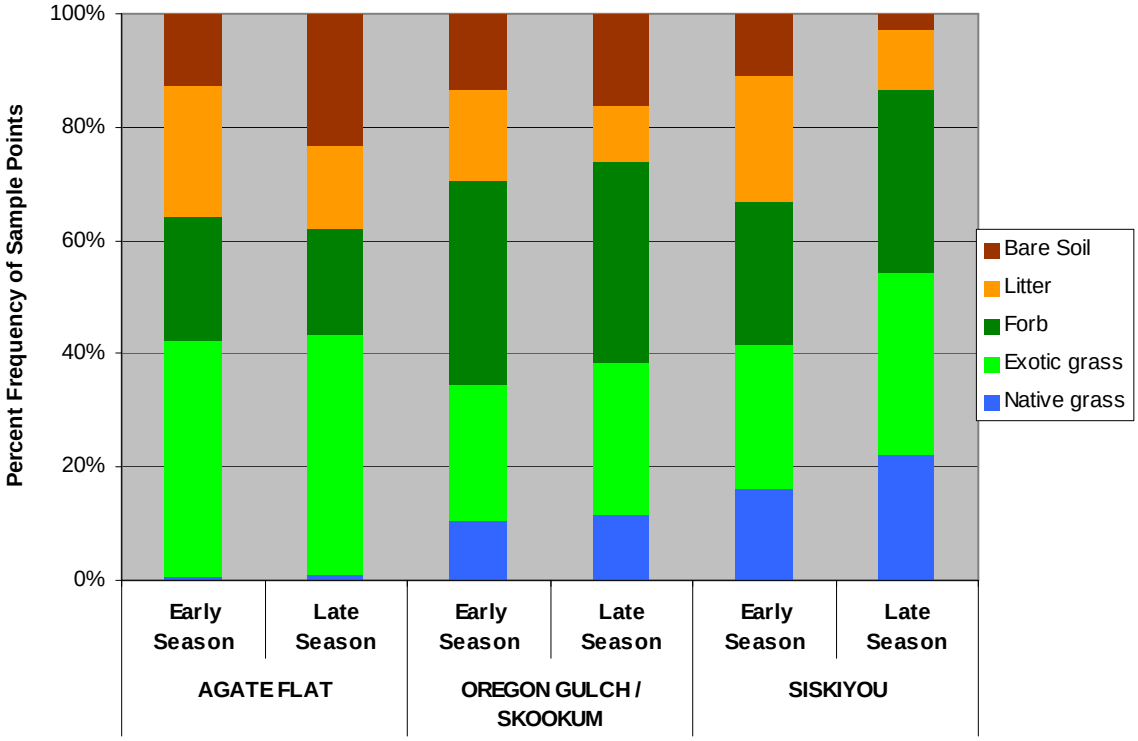


Figure 9. Relative percent change in vegetation cover between early and late season measurements within *C. greenei* populations across three study areas.

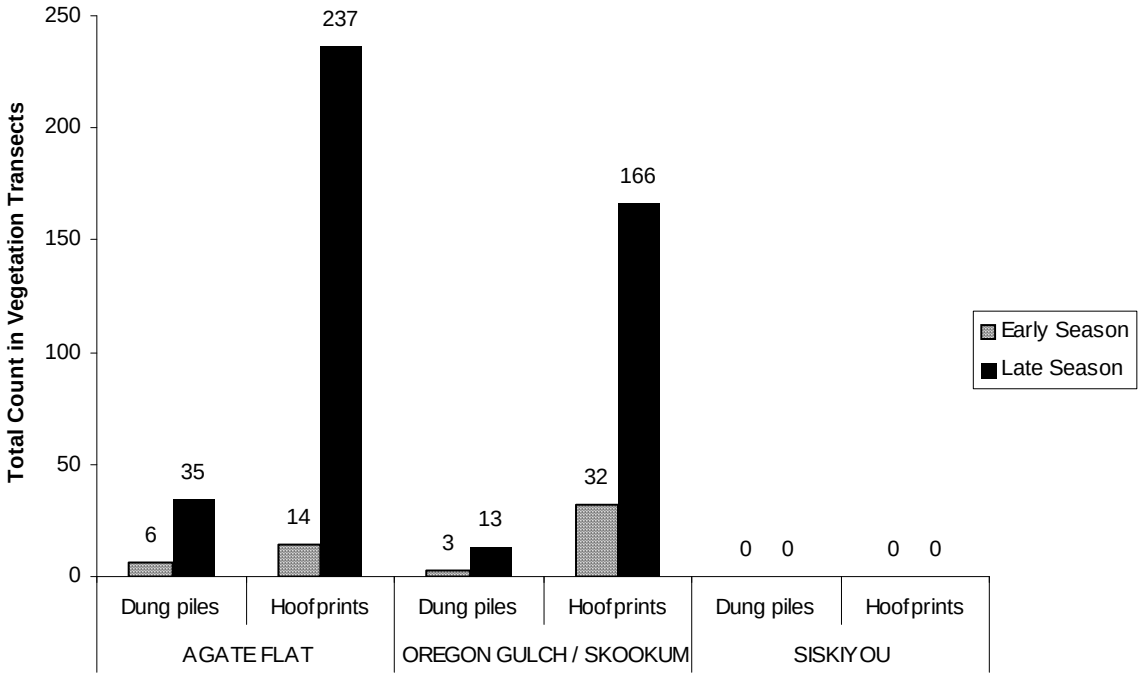


Figure 10. Seasonal changes in indicators of livestock use (number of livestock dung piles and hoofprints) within *C. greenei* population sites across three study areas.

III. Landscape-level Predictors of *C. greenei* Abundance and Distribution

Viewed as single, independent variables, coarse-scale plant communities (Figure 11), ecological type (Figure 12), average utilization (Figure 13), maximum utilization (Figure 14), time since last grazed (Figure 15), and distance from water (Figure 16) differed significantly from expected values ($p<0.001$). Non-conifer vegetation manipulation and distance from roads were not statistically significant ($p=0.98$ and 0.85 respectively).

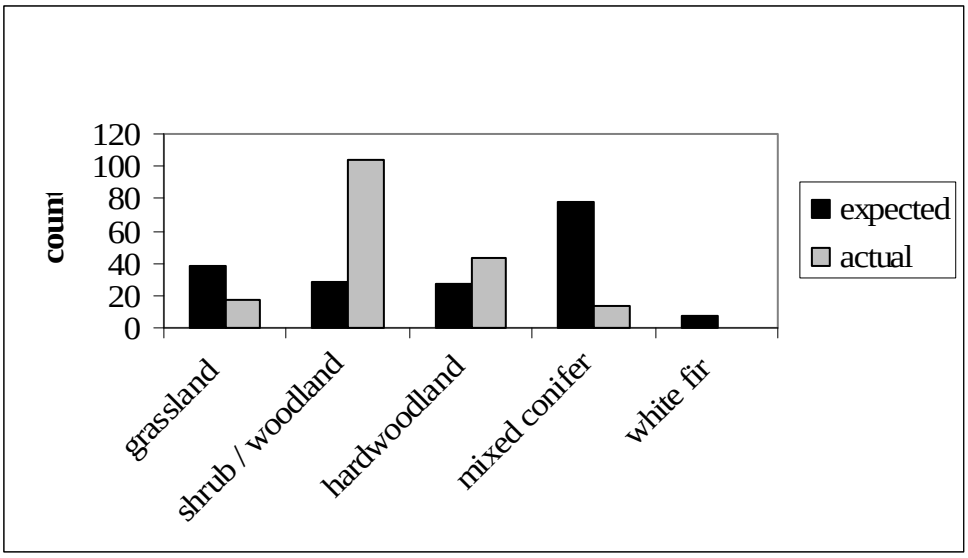


Figure 11. Actual and expected *C. greenei* population counts within coarse plant community classes.

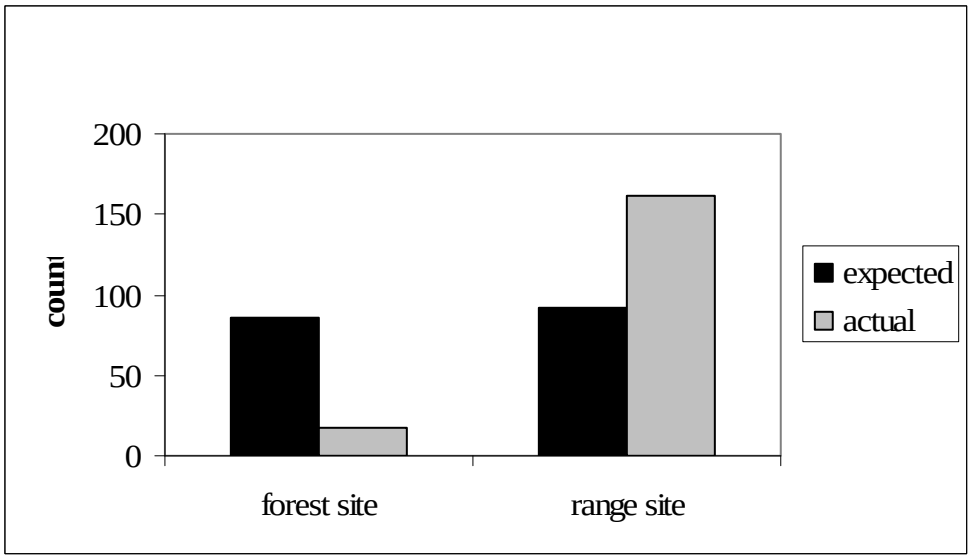


Figure 12. Actual and expected *C. greenei* population counts within NRCS defined ecological sites.

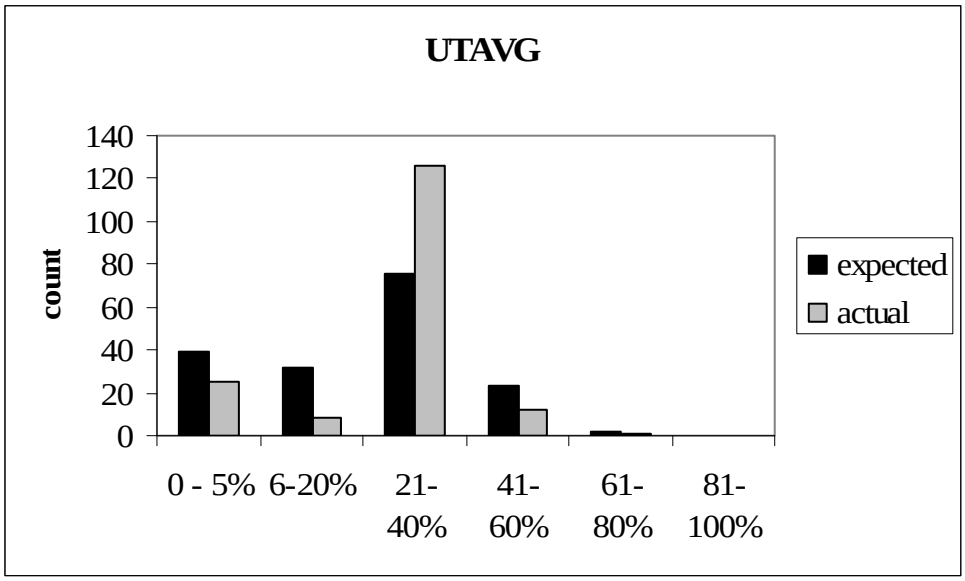


Figure 13. Actual and expected *C. greenei* population counts within average utilization classes.

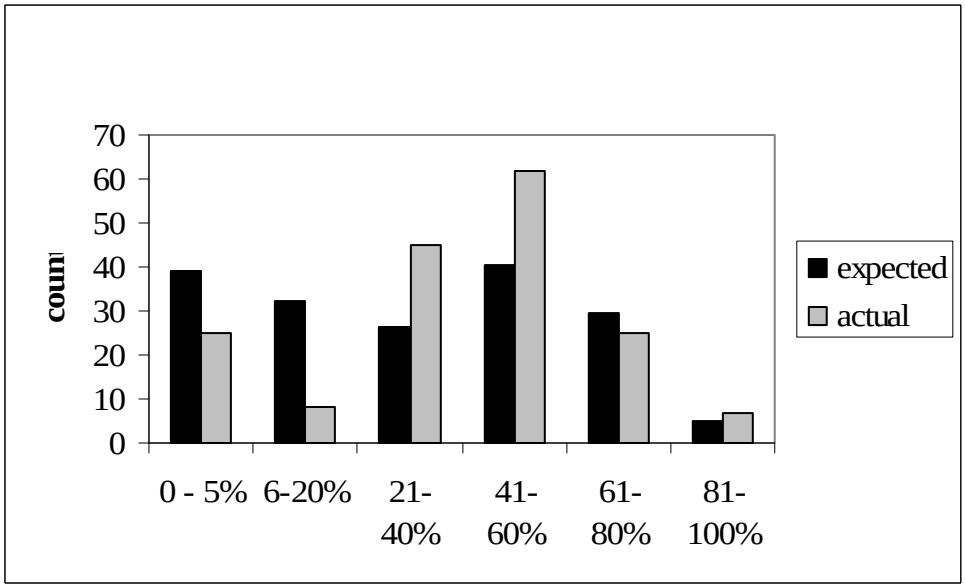


Figure 14. Actual and expected *C. greenei* population counts within maximum utilization classes.

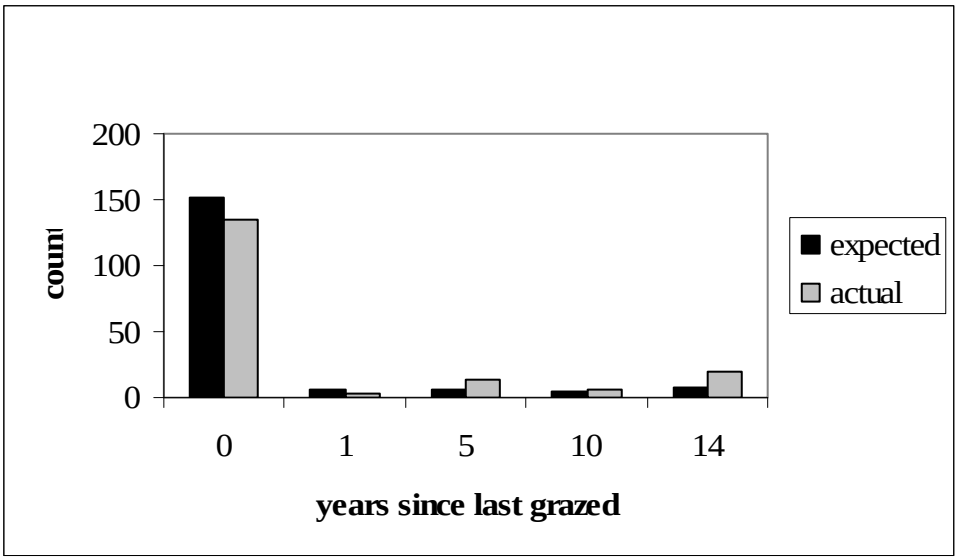


Figure 15. Actual and expected *C. greenei* population counts by the number of years since last grazed.

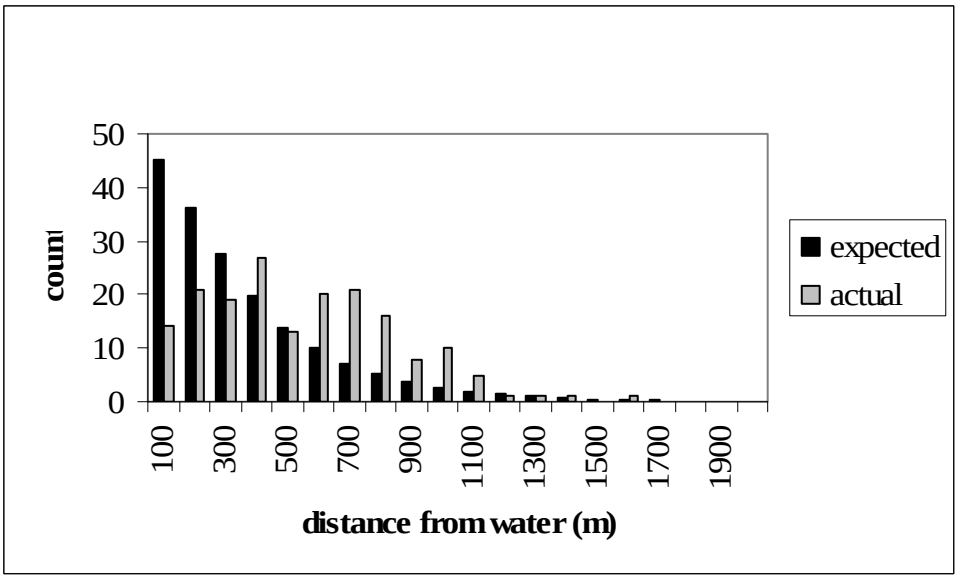


Figure 16. Actual and expected *C. greenei* population counts within 100 meter distance classes from water.

Results of the nonparametric multiplicative regression exercise are summarized in several tables. First, the cross R^2 value of single variable models are provided as a measure of relative importance of individual predictor variables (Table 3). Second, the best fit models based on a free choice of predictor variables, associated cross R^2 value, and variables incorporated in the models are provided for easy comparison between measures of *C. greenei* response (presence absence in the context of random locations, and *C. greenei* density at three search radii with and without actual locations) (Table 4). Additional tables depict tolerance (to identify local versus global significance of predictor variables - Table 5) and sensitivity (relates change in variable to change in response – Table 6) allow an assessment of the importance of individual predictor variables within best fit models.

Cross R^2 values derived from single variable models: The cross R^2 value for variables derived from the NRCS soil database are considerably higher than cross R^2 values for variables describing topography or management activities (Table 3). The cross R^2 values for variables derived at random and actual *C. greenei* sites are higher than the cross R^2 values derived for random locations only. Based on the magnitude of cross R^2 values for individual predictor variable models, soil composition and depth are the most important variables for describing *C. greenei* locations and density. The inclusion of the spatially aggregated actual site locations greatly contributes to the cross R^2 value for individual predictor variables in the above single variable models.

Table 3. Individual variable cross R^2 values for models of response variables (*C. greenei* counts at actual locations and *C. greenei* density at random locations only, as well as at random and actual locations) to individual predictor variables (only cross R^2 values higher than 0.1 are provided).

	Cross R^2 values						
Predictor Variable	Actual locations	Random locations and actual locations			Random locations only		
		R=125	R=250	R=500	R=125	R=250	R=500
% clay	0.2369	0.2387	0.2365	0.2455	0.0489	0.1063	0.1539
% silt	0.2327	0.2356	0.2349	0.2423	0.0466	0.1	0.1496
% sand	0.2354	0.2374	0.2347	0.2429	0.0501	0.1059	0.1459
Deepest soil depth	0.1745	0.1771	0.1818	0.1766	0.0327	0.0569	0.0813
Com. Depth	0.1677	0.1705	0.1766	0.1707	0.0314	0.0568	0.0761

Model significance, number, and identification of predictor variables: The number of variables included in the best fit models examining patterns in *C. greenei* presence/absence or *C. greenei* density vary by response variable (presence absence/search radius used in calculating *C. greenei* density (Table 4). The cross R^2 values increase with search radius used for calculating *C. greenei* density. The optimal model in terms of spatial resolution of the data and use of randomized data only (shaded column of Table 4) shows a relatively low cross R^2 value compared to other models.

Table 4. Overall model significance (cross R^2) and variables retained by models describing the pattern of predicator variables to response variables (actual *C. greenei* locations, *C. greenei* density at 3 search radii for datasets incorporating actual locations, and without actual locations). Optimal model identified by shading.

	Actual locations	**Random locations only**		
		R=125	R=250	R=500
xR^2	0.3954	0.1409	0.209	0.2753
No. Predict.	17	13	16	8
Predictor variables	shallowest soil depth	Deepest	Shallowest soil depth	% sandh11
	Com. Depth	Shallowest soil depth	Com. Depth	vedge_5
	% sand1	vedge_5	% clayh1	vedge_1
	% silth11	vedge_1	vegetation height	elevation
	vegetation height	slope	vedge_1	avg. soil depth
	vedge_1	elevation	elevation	apti_sc
	Slope	avg. soil depth	Heatload	maximum utili.
	elevation	apti_ss	avg. soil depth	years of rest
	% silt	% sand	vertisol	
	% sand	maximum utilization	% herbaceous	
	fchgonl	distance from water	Fchgonl	
	maximum utili	distance from road	maximum utilization	
	average utili	vegetation manipulation	average utilization	
	years of rest		years of rest	
	distance from water		distance from water	
	distance from road		distance from road	

Description of the optimal model: The optimal model describing *C. greenei* population density across the monument landscape includes topographic, edaphic, biotic, and management factors. Soil depth is the most sensitive variable, showing the largest change in response to small change in depth. The low low tolerance by soil depth indicates this relationship is only valid for a small portion of the dataset. Distance from water showed the second highest sensitivity, also with a relatively tolerance, implying importance over a small portion of the dataset. Elevation and measures of utilization show relatively low sensitivity over a moderate portion of the dataset. Distance from woody vegetation edge appears to be a variable of importance across much of the extent of *C. greenei*, but with a relatively low sensitivity, indicating that a change in distance form vegetation edge elicits a relatively small change in predicted population density.

Table 5. Sensitivity and tolerance of variables retained within optimal model (search radius = 125m) predicting CAGR density. Values are ranked by size.

Predictor	Sensitivity1	Predictor	Tolerance
deepest	0.8207	vedge_5	75
distance from water	0.1253	vedge_1	75
elevation	0.0652	avg. soil depth	65
maximum utilization	0.0488	maximum utilization	65
distance from road	0.0485	Shallowest soil depth	60
apti_ss	0.0204	slope	60
vedge_1	0.0078	% sand	50
vedge_5	0.0066	apti_ss	40
avg.soil depth	0.0008	elevation	35
Shallowest soil depth	0.0007	distance from road	35
% sand	0.0003	distance from water	15
Slope	0.0002	deepest	5
vegetation manipulation	n/a	vegetation manipulation	n/a

Graphic output from optimal model: Predicted population density declines with elevation and increases with slope (Figure 17a). *C. greenei* is found in soils of moderate depth, likely excluding soils with the ability to support conifer communities, and grassland sites maintained by shallow soils (Figure 17b), and a minimum of sand (Figure 17c). Predicted *C. greenei* density declines only slightly with recent maximum utilization, but shows a stronger relation with distance from water (Figure 17d). The low population density closer to water suggests slow attrition of plant populations under severe livestock utilization. Measures of *C. greenei* density are highest at the shortest distance from vegetation edge (Figure 17e).

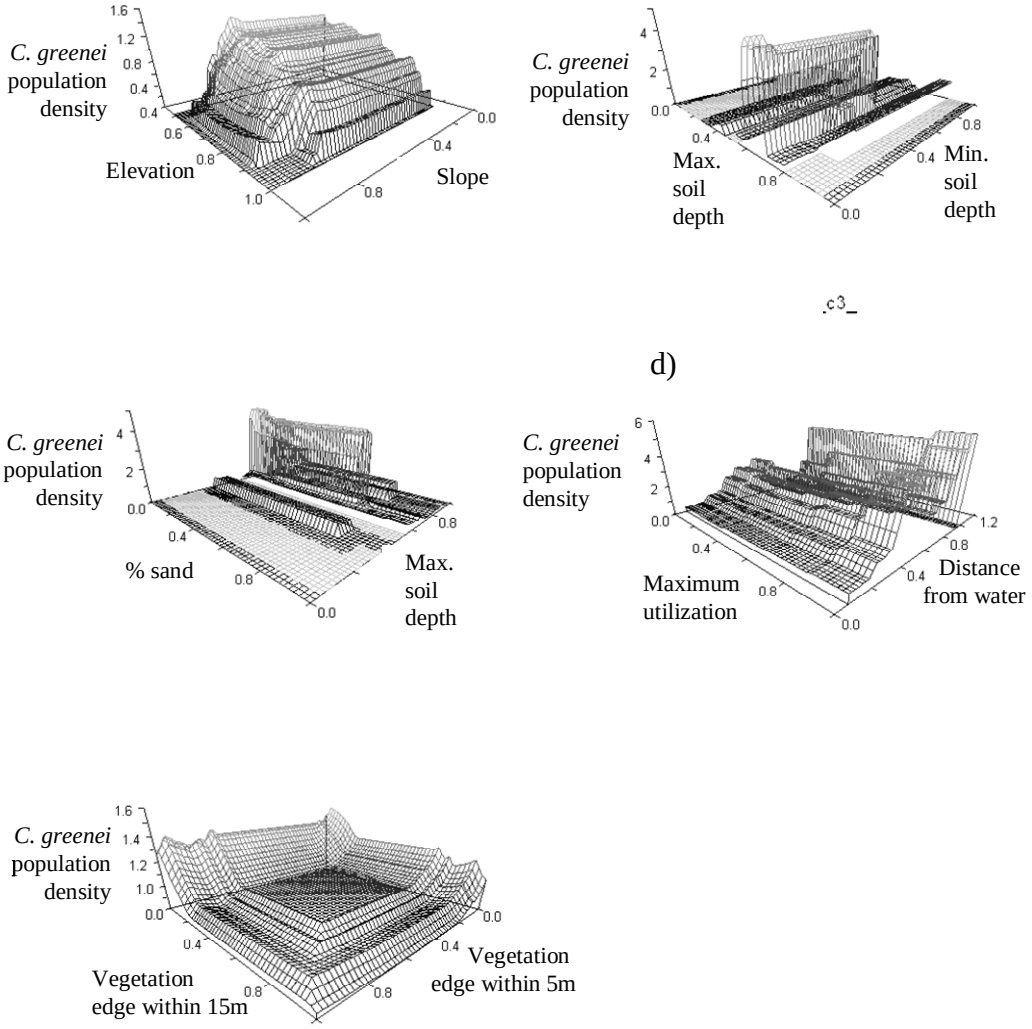


Figure17. Graphic output from the optimal model predicting *C. greenei* population density within a 125 m search radius. Note that all predictor variables are relativised.

DISCUSSION

Population Trends and Habitat Relationships

Of those *C. greenei* populations that were resurveyed in this study, significantly more declines were found at grazed versus ungrazed sites. While this pattern is suggestive of a grazing-related effect, we note that it may be biased by the fact that a disproportionate number of *C. greenei* sites with three or less years between surveys (e.g. those in the Siskiyou study area) are also ungrazed and generally located at higher elevations. Another confounding factor is that many *Calochortus* species, including *C. greenei* , are known to exhibit bulb dormancy and may not produce above-ground structures every year. As a result, annual population counts at any given site vary widely (Menk and Kaye 2006, Brock 1996, Fiedler 1987, Fiedler et al. 1998). Future revisits at surveyed sites are needed in order to increase confidence that population changes identified here reflect real trends.

Our analysis of plant community attributes associated with three major *C. greenei* sites reveals that more robust populations tend to be associated with spatially complex, fine-grained patchiness in vegetation structure, characterized by relatively high cover of shrubs, forbs and bare soil, and low to intermediate grass cover. *C. greenei* population size increases with a higher ratio of native perennial to exotic grasses. Similar findings have been reported by other authors working on this species.

Seasonal Changes in Vegetation and Livestock Use

One of the major differences between study areas is that sampled *C. greenei* habitats at Agate Flat had much lower native grass and bare soil cover, but much higher exotic grass cover than other areas. Native grass abundance is low at many *C. greenei* sites within the Agate Flat area, and most are strongly dominated by medusahead (*Taeniatherum caput-medusae)*, bulbous bluegrass (*Poa bulbosa)*, cheatgrass (*Bromus tectorum*), and foxtail fescue (*Vulpia myuros*). Other studies have also reported significantly greater cover and abundance of exotic grasses at Agate Flat relative to other portions of the monument (Menke and Kaye 2006, Hosten et al. 2007 a). This pattern is

likely the result of differing histories of human disturbance (Hosten et al. 2007 b) and the presence of other environmental factors, such as “shrink-swell” clay soils, that favor ruderal species (Hosten 2007).

Our data from seasonal transects found that levels of livestock use in 2004 were sufficient to result in measurable changes to vegetation and soil surface attributes in areas occupied by *C. greenei*. Specifically, moderate to high livestock utilization at Agate Flat sites was associated with an increase in bare soil and a decrease in native grass cover from early to late season measurements. Other indicators of livestock use – number of hoofprints and manure piles – were also correlated with livestock utilization level among study areas. These changes in habitat are not likely to adversely affect individual *C. greenei* plants directly, but may reduce habitat quality over time by changing competitive relations between native bunchgrasses and ruderal species, including annual grasses.

A number of studies conducted in grassland and woodland ecosystems in California have found that a principal effect of livestock grazing is to promote exotic annuals over native perennial grasses (Mack 1989, D’Antonio and Haubensak 1998, Hayes and Holl 2003, Gelbard and Harrison 2003, Kimball and Schiffman 2003), and heavy thatch layers produced by exotics tend to reduce the diversity of native grasses and forbs (Gerlach et al. 1998, Meyer and Schiffman 1999, Carlsen et al. 2000, Seabloom et al. 2003, Corbin et al. 2004). However, the likelihood that livestock will cause the above impacts depends on numerous factors including site conditions, plant community type, dominant species and the grazing regime involved (Hobbs and Huenneke 1992, Meyer and Schiffman 1999, DiTomaso 2000, Kie and Lehmkuhl. 2001, Harrison et al. 2003).

With particular reference to *Calochortus*, grazing by livestock in northeastern California has been observed to adversely impact a congeneric species, *Calochortus longebarbatus* var. *longebarbatus* (Jokerst 1983). The author suggests that decline of grazed populations is due to “upsetting of competitive interactions” and “damage to *C. longebarbatus* microhabitat” (Jokerst 1983). An ongoing demographic study of *C. greenei* in the monument using exclosure cages has found that fencing showed a significant increase in *C. greenei* size and reproduction for the last five years of monitoring (Menke and Kaye 2006). The exclusion of all ungulates (native and non-

native) and smaller mammals implies that the combined influence of all these wildlife may also affect persistence and reproductive output of *C. greenei* over the long term.

Given our findings regarding habitat attributes at known *C. greenei* sites and seasonal changes in occupied habitats, we suspect that high cover of exotic grass has an adverse impact on *C. greenei* populations. This effect may be expressed either through direct competition with mature plants, or more likely, by reducing *C. greenei* seedling survivorship.

Predicting Landscape-Scale Patterns of *C. greenei* Distribution

Analysis of individual variables using chi-square analysis indicates *C. greenei* has an affinity for non-conifer communities with a mix of shrubs and hardwoods found within NRCS range sites. While measures of utilization are significant in their apparent influence on *C. greenei* presence/absence, the lack of a piospheric pattern over the range of utilization levels suggests that spatial aggregation of populations may bias the interpretation of individual variable analyses of measures of utilization level. The persistence of *C. greenei* sites adjacent to water-points indicates that populations can survive years of intense livestock use.

Differences in cross R^2 values for free search models of *C. greenei* presence/absence versus *C. greenei* density at random locations with and without actual locations are a consequence of the spatially auto-correlated *C. greenei* population sites. The optimal models examining *C. greenei* density at random locations across the landscape include a range of topographic, edaphic, biotic, and management predictor variables. However, the overall cross R^2 values remain small, indicating a weak association between response and predictor variables.

Considering the optimal free-search model of population density across the landscape it is apparent that topographic (slope and elevation), edaphic (soil composition and depth), biotic (patterning of vegetation), and management (native and non-native ungulate utilization) factors play a role in explaining the overall patterning of *C. greenei* across the landscape. Historic livestock mediated vegetation change (Hosten et al. 2007 a, 2007c) and reduced population densities close to water implicate a direct and indirect historic influence by livestock on the persistence of *C. greenei* populations. Measures of

recent utilization (by native and non-native ungulates) are also included in models. These utilization values show moderate tolerance and low sensitivity, implying that large herbivore grazing is an important influence in portions of the landscape, but is not the primary determinant of predicted *C. greenei* distribution or abundance. Model output depicting population density in response to maximum utilization provides a graphic depiction of this observation.

The high tolerance value for distance to woody vegetation edge indicates the importance of this variable across the dataset relative to other factors. This suggests that the influence of elevation and soil may be indirect through the expression of woody and herbaceous vegetation characteristics.

The variability of predictors included with models and lack of predictive power compared to similar analyses suggest that *C. greenei* is tolerant of a wide range of conditions, and that few generalizations can be drawn about patterns of change across the monument landscape. This observation was also made by Fiedler (1987) for other *Calochortus* species. Results from similar analyses for other organisms within the monument indicate that predictor variables may act synergistically in their influence on *C. greenei* population density (Hosten 2007). High livestock use on soils with shrink-swell characteristics may thus exacerbate annual grass and forb invasion in these areas, perhaps influencing the persistence of *C. greenei* persistence on these sites.

CONCLUSIONS

The optimal free search model of *C. greenei* population density includes topographic, edaphic, biotic, and management factors. Only edapic factors (soil depth and composition) show a cross R^2 greater than 0.1. Of the biotic variables, plant communities including a shrub component and woody vegetation edges are important variables for describing *C. greenei* abundance. While models include current grazing regime as measured by utilization levels, the influence of these variables cannot be isolated from other environmental factors. The lack of predictive power of models suggests variables are mostly of local importance, perhaps through their influence on vegetation composition and patterning. The location of *C. greenei* sites adjacent to new water-points

indicates that populations can be persistent in areas of heavy livestock use in the shorter term, though the lower density of populations close to water-points also suggests a slow attrition over time. The decline in population size of this long-lived plant in grazed areas may indicate a lack of successful recruitment in the longer term. The larger relative abundance of annual grasses in areas of declining *C. greenei* populations size suggests that early growing season competition of *C. greenei* seedlings with annual grasses may be an important factor preventing the establishment and persistence of new *C. greenei* individuals.

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