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September 2007
Ecology

The Ecological Role of the California Ground Squirrel (*Spermophilus beecheyi*)

Abstract

Burrowing, herbivorous mammals are remarkably similar in their effect on the structure of grassland communities and ecosystem processes worldwide. Ground squirrels influence the grassland ecosystem directly as prey, and indirectly through burrowing and foraging activities, suggesting a high level of interactivity. The California ground squirrel (*Spermophilus beecheyi*) is abundant in grasslands, yet little is known about the ecological role of this common species despite its' association with native species of conservation concern.

I investigated the effects of the California ground squirrel on grassland community structure and function by comparing the flora and fauna of paired colony and off-colony sites. Next I assessed the potential of this squirrel to act as a strongly interacting species. In chapter one, I examined avian assemblages using point counts and all-occurrences raptor sampling. Analyses revealed a pattern of higher avian species richness, diversity, and significantly higher abundance of birds on colony sites. The presence of raptors distinctly separated colony from off-colony sites, while a low abundance of ground gleaning and ground nesting passerines indicated off-colony sites. In chapter two, paired comparisons of grassland vegetation, invertebrates, mammals, and reptiles were examined. Colony sites exhibited lower plant diversity and richness, shorter vegetation, less residual dry matter and more open ground compared to off-colony sites. Small mammals demonstrated a pattern of lower abundance, richness and diversity on

colony sites. Colony sites attracted more terrestrial predators compared to off-colony sites with significantly more carnivore species and a higher frequency of snakes that prey on squirrels. In chapter three, the role of the squirrel as prey and ecosystem engineer is reviewed within the context of interactivity. The mosaic of vegetation structure, burrows and higher prey abundance on colony sites affected the composition of species on colonies. Because of the squirrel's unique dual role as prey and ecosystem engineer and its' association with an assemblage of increasingly rare and threatened species, I conclude that the California ground squirrel is a strongly interacting species. This common species is generally considered a rangeland pest, but I recommend that a more contemporary approach towards the management of this squirrel will benefit grassland conservation.

The Ecological Role of the California Ground Squirrel *(Spermophilus beecheyi)*

Juvenile California ground squirrel Photo credit: Scott Stender, Digit Video

Introduction

Burrowing, herbivorous mammals are remarkably similar in their effect on the structure of grassland communities and ecosystem processes world -wide (Davidson and Lightfoot 2006; Paine 2000; Whitford and Kay 1999). Some of these species, particularly rodents such as gophers (*Thomomys bottae, Geomys bursarius*), kangaroo rats (*Dipodomys spp*.), and black-tailed prairie dogs (*Cynomys ludovicianus*), are attracting attention as strong interactors because of their role in trophic interactions or as ecosystem engineers (Brown and Heske 1990; Davidson and Lightfoot 2006; Jones et al. 1994; Kotliar et al. 2006; Lawton and Jones 1995; Power et al. 1996). Ground dwelling squirrels, in particular, influence the structure and composition of the grassland ecosystem both, directly as prey and indirectly through burrowing and foraging activities, suggesting a high level of interactivity (Kotliar et al. 2006).

The California ground squirrel (*Spermophilus beecheyi*) is common in grassland communities extending from the coastal bluffs of the Pacific Ocean to the foothills of the Sierra Nevada. Previous work has focused on behavior (Boellstorff and Owings 1995; Owings et al. 1977) and conflicts with humans (Marsh 1994), yet surprisingly little is known about the ecological role of this species in the grassland community. In contrast, many studies have examined the functional importance of the black-tailed prairie dog (*Cynomys ludovicianus*), an analogous species in prairie grasslands (Kotliar et al. 1999; Kotliar et al. 2006). The burrowing and grazing activities of prairie dogs augment primary productivity, species densities and diversity, soil structure, and chemistry (Detling and Whicker 1988; Reading et al. 1989; Sieg 1988), creating a landscape mosaic that promotes a unique species composition and thus overall grassland diversity (Kotliar et al. 1999). Because of the functional similarities between prairie dogs and California ground squirrels, results from prairie dog studies may provide a model for predicting the effects of California ground squirrel activities on grassland communities.

Historically ground-dwelling squirrels have been considered pest species throughout western rangelands. Convinced that squirrels compete for forage, injure livestock, proliferate quickly and carry disease, landowners have attempted to eradicate them through shooting and poisoning. Since the turn of the century control programs have successfully decreased populations of the black-tailed prairie dog by 98% (Summers and Linder 1978), prompting the National Wildlife Federation to petition this once common species for listing under the Endangered Species Act (Graber et al. 1998). In California, ground squirrels are "considered the most serious pest on rangeland (Marsh 1998)." As a result, control programs keep most populations below carrying capacity

(Marsh 1987), with some local populations reduced by 90-95% (Hunt et al. 1995). Rangeland pest control not only reduces ground squirrel populations but also produces collateral damage through unintended poisoning of native wildlife associated with squirrel colonies (Hoover 2002; Smallwood et al. 2001). Like prairie dogs, California ground squirrel colonies are increasingly associated with many special-status species including the burrowing owl, the golden eagle, the San Joaquin kit fox, the California tiger salamander, and the California red-legged frog (Hunt et al. 1999; Loredo et al. 1996; Murray 1976; Thomsen 1971; USFWS 1998).

"Strongly interacting species" play key regulatory roles in community structure and ecosystem processes, contributing to the maintenance of ecological and species diversity (Jones et al. 1994; Paine 1969; Power et al. 1996; Soule et al. 2005; Whitford and Kay 1999). A strongly interactive species is operationally defined by the consequences that result from its absence or rarity leading to changes in features of the ecosystem such as structural or compositional modifications, decreases in species diversity, alterations in the import or export of nutrients, and loss of resilience to disturbance (Soule et al. 2003). Species with the highest interaction strength, such as the prairie dog, are usually considered keystone species (Soule et al. 2005). The overall objective for this dissertation is to investigate the influence of the California ground squirrel on grassland community structure and composition in order to assess the potential of this species to act as a strong interactor. Identification and restoration of strongly interacting species that have profound effects on ecosystem structure and function, rather than focus on single-species rescue efforts, can conserve entire systems (Rohlf 1991; Scott et al. 1987; Smith 1984).

A comparative approach was used to assess the interactive role of the California ground squirrel and make inferences about the strength and direction of interactions between squirrels and the flora and fauna of the grassland community. Five study locations were established within the Livermore Valley, California, 80 km east of San Francisco. Each of five ground squirrel colony sites was paired with a nearby off-colony site without squirrels. In chapter one (pp. 9-37), the community structure (species richness, diversity, and abundance) of avian assemblages was examined for differences between colony and off-colony sites. In chapter two (pp.38-68), paired comparisons of grassland vegetation and ground-dwelling invertebrates, mammals, and reptiles, were examined to determine the influence of California ground squirrels on community structure. In chapter three (pp. 69-107), the functional role of the California ground squirrel as prey and ecosystem engineer is examined within the context of interactivity with a view towards determining whether this squirrel qualifies as a “strongly interacting species”.

California ground squirrel colonies are spatially explicit patches of habitat that are structurally and functionally different from off-colony sites constituting the grassland matrix. Disturbance activities such as soil disturbance, mound building, nutrient input, and herbivory performed by ecosystem engineering rodents create a mosaic of habitat patches on the landscape across multiple scales (Davidson and Lightfoot 2006). Inside the colony patch habitat structure and function is altered providing resources that support a high abundance of grassland birds, ground dwelling invertebrates, and burrow dependent amphibians while the presence of California ground squirrels as prey draws a rich predator community including a higher frequency of raptors, carnivores and mammal eating snakes. These dual roles played by the California ground squirrel in trophic interactions and as an ecosystem engineer interact to create unique communities in time and space (Kotliar et al. 2006). Comparatively, off-colony sites offer refuge for a different composition of species that utilize the less disturbed grassland matrix where denser cover offers another set of resources for small mammals, more specialized birds and predators, among others. In combination, colony and off-colony sites increase overall beta diversity within grasslands.

While California ground squirrels are considered a nuisance in anthropogenic environments such as crop agriculture and urban parks, in rangelands and wildland parks, this interactive species maintains an assemblage of increasingly rare grassland species. The management of grasslands and thus, California ground squirrel populations, is largely in private hands; 86% of grasslands in the state are privately owned and managed for livestock grazing (Davis et al. 1998). Yet, livestock growers face increasing pressure to develop valuable rangeland, especially in rapidly urbanizing areas (Liffmann et al. 2000). In contrast, innovative research and management partnerships with private landowners and range managers that prioritize good stewardship can protect grasslands, conserve diversity, and educate landowners and the public about the ecological role of species such as California ground squirrel.

Interactive species function over a range of abundance levels but attain community importance only above a threshold density (Kotliar 2000). Below this threshold density communities of organisms maintained by interactive species decay through cascading effects and ecological simplification in structure and function (Paine 2000). Hence, it is imperative to maintain interactive species at an ecologically effective density and at the greatest spatial extent possible (Soule et al. 2005). The California Rangeland Resolution presents an integrative vision to manage grasslands as "working landscapes," viable for both livestock production and conservation by first, "keeping common species common" (http://carangeland.org). This type of shift in perception towards an ecological rather than pest view of the California ground squirrel will not only keep ground squirrels common but also interactive and ecologically effective.

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Chapter 1: The structure of grassland avian communities in association with the California ground squirrel (*Spermophilus beecheyi)*

1. Introduction

Through their foraging behavior and burrowing activity, California ground squirrels create patches of disturbance with more structural diversity than the surrounding grassland matrix without squirrels. This mosaic of disturbance and structural diversity may differentially attract certain groups or guilds of birds searching for food, shelter, or nesting opportunities. For grassland birds, the physical structure of a habitat can be a primary proximate factor for habitat selection, providing indirect cues to potential prey availability and diversity (Wiens 1969). California ground squirrels are themselves prey for larger raptors (Bell 2004; Cully 1991; Goodrich and Buskirk 1980; Hunt 1997; Kuenzi et al. 1998), and their burrows are used for nesting and shelter by burrowing owls (See Table 1.1 for scientific names) (Desmond et al. 2000; Loredo et al. 1996). Grazing and burrowing by California ground squirrels keeps vegetation low (Evans and Holdenreid 1943; Fitch and Bentley 1949; Howard et al. 1959) and in a patchy stage of early succession preferred by many grassland birds (Vickery 1996). Burrows and bare areas within the colony may be advantageous for insect breeding (Bangert and Slobodchikoff 2000; Koford 1958; Olson 1985) thereby attracting avian insectivores, and squirrel herbivory influences plant composition (Detling and Whicker 1988; Schitoskey and Woodmansee 1978) potentially creating a variety of resources for granivorous birds.

California ground squirrels are also associated with several grassland birds of conservation concern, such as the burrowing owl, ferruginous hawk, golden eagle, and prairie falcon (Bell 2004; Haug et al. 1993; Hunt 1997).

The California ground squirrel may perform an important ecological function within California grasslands, acting as an "ecosystem engineer" and possible keystone species, yet the species is still considered a pest on rangelands (Marsh 1998) and is largely overlooked in grassland conservation efforts. Pest management programs advocate control on over two million hectares within the state, keeping populations as low as 10-20% of carrying capacity (Marsh 1987), at abundance levels that may be inconsistent with the ecological role of ground squirrels in grasslands. An ecological keystone is a species that provides appropriate habitat conditions or prey for the continued existence of other species (Gilbert 1980; Terborgh 1986). The burrowing and grazing activity of ground-dwelling squirrels augments primary productivity, species densities and diversity, and soil structure and chemistry (Detling and Whicker 1988; Reading et al. 1989; Sieg 1988), creating a landscape mosaic that promotes a unique species composition and thus overall grassland diversity (Kotliar et al. 1999). Ecological similarities between the prairie dog (*Cynomys* spp.), which is widely recognized as a keystone species in Great Plains grasslands (Kotliar 2000; Kotliar et al. 2006; Miller and Cully 2001), and the California ground squirrel suggest that California grasslands may be strongly influenced by ground squirrel activity and abundance.

Despite extensive research on pest management practices (Marsh 1994) and squirrel behavior (Boellstorff and Owings 1995; Owings et al. 1977) surprisingly little has been published about the ecological importance of the California ground squirrel in grasslands. Additionally, little information exists on the distribution, abundance, and breeding requirements of the grassland bird community in California (Allen 2000), despite a disturbing trend showing steeper, more consistent, and more geographically wide-spread declines in North America's grassland birds than in any other behavioral or ecological guild (Knopf 1994). The objective of this study is to determine if California ground squirrels have a positive influence on the local grassland bird community. California ground squirrels create structural complexity on their colonies; hence we expect that avian species richness, diversity, and abundance will be higher on colony sites with ground squirrels as opposed to nearby paired off-colony sites without squirrels. We also expect that the composition of the bird community will differ between paired colony and off-colony sites; in particular, we expect a strong association between California ground squirrels and individual bird species that utilize ground squirrels as prey or use their burrows for shelter and nesting.

2. Materials and methods

Study area

The study area lies within the Livermore Valley area of the Central Coast Ranges, in eastern Alameda and Contra Costa counties, California, approximately 80 km east of San Francisco (37º41' N, 121º47' W) (Fig. 1.1). Within these two counties, 41% of the land area is covered by non-native annual grassland (Liffmann et al. 2000) dominated by introduced annual grasses and forbs (Sawyer and Keeler-Wolf 1995), species that are well adapted to the Mediterranean climate characterized by mild, wet winters and long, hot, dry summers. Plant growth begins with the onset of fall rains, beginning in

November or December, average annual precipitation ranges 38-63 cm, monthly temperatures range from a mean minimum of 3º C to a mean maximum of 30º C), and the mean freeze-free period is 200-250 days (Easterling et al. 1996). A detailed description of vegetation in the study area is available in Lenihan (2007b).

Site selection

We established five pairs of sites (each site 200 m x 200 m = 4 ha) within the Livermore Valley area, four in Alameda County and one in Contra Costa County (Fig. 1.1). Each of five ground squirrel colony sites was paired with a nearby off-colony site without ground squirrels to control for local variation in environmental conditions. Both sites within a pair were located on lands owned by the same property owner to further control for variation in land management and grazing regime. Three pairs were located in treeless grassland within the Altamont Hills region, and two pairs were located in oak savanna (2-4 oak trees / 4 ha site) around San Antonio Reservoir. We first designated colony sites where California ground squirrels were abundant then located comparable areas without ground squirrels 0.6-2.0 km distant. Colony sites supported 23-39 squirrels / ha, well within the average density for rangelands (Lenihan 2007c). California ground squirrel home ranges are <150 m in diameter (Van Vuren et al. 1997), and 300 m between sites is generally sufficient to preclude re-invasion by dispersing California ground squirrels (Stroud 1982), hence off-colony sites were beyond the dispersal range of the nearest known area of occupancy but close enough to preserve pair habitat similarity.

Survey methods

Birds were surveyed at all 10 sites using two methods, full census avian point counts and all-occurrences raptor sampling. In grassland habitats detection of individual birds can be as high as 99% at distances of 125 m (Nur et al. 1999), so we designed a three by three point count grid in which points were located 100 m apart. The observer stood at each point for one minute of quiet-time for acclimation followed by five minutes of survey time recording all bird species detected visually or aurally within 50 m of the point. Birds observed flying over the site greater than 50 m high were considered "fly-overs" and were excluded. Paired sites were surveyed together on the same morning between first light and 3 hours after sunrise. Survey order was reversed each time a pair of sites was re-visited to avoid bias. Point counts were conducted on paired sites three times during each season; winter (January to March), breeding (April to July), and fall (October to December) for two years, 2003 and 2004.

Raptors were included in point count data but were also surveyed separately using an "all occurrences" sampling method (Altmann 1974) for several reasons. First, raptor activity peaked later in the day when thermal conditions improved, after point counts occurred. Second, raptors were recorded less frequently on point counts than their actual occurrence because they often hunt from heights greater than 50 m. Third, for data analysis we edited the list of bird species recorded during point counts using decision rules (see below) that excluded rare but meaningful raptor species. We recorded only raptors that were actively hunting, those that traveled directionally across the site at heights greater than 50 m were considered "flyovers" and thus excluded. Common ravens were included in the raptor group because we observed them preying upon juvenile California ground squirrels. “All occurrences” raptor sampling occurred from June 2002 through March 2005. In addition, we searched for burrows occupied by burrowing owls. Burrows with evidence of burrowing owl use were monitored for confirmation of nesting activity and determination of reproductive success.

Statistical methodology

Differences in the bird assemblages between paired colony and off-colony sites were analyzed by comparing species richness, diversity, and abundance and by comparing the composition of the grassland bird community. Species richness, diversity, and abundance were determined using the entire data set of bird observations and all species recorded (n = 66) and were calculated separately for each site, during each season, and for both years. Species diversity was calculated using the Shannon-Weiner index (Krebs 1999). Total abundance was determined by combining the three point count survey results for each season, and repeated measures ANOVA was used to test for differences between colony and off-colony sites according to year and season. Total abundance by season was further tested for differences between paired sites using the non-parametric Wilcoxon Signed Rank Test (Sall et al. 2005). From the “all occurrences” sampling data, we calculated the number of raptors per hour of observation on each site by species and for all raptors combined, and we used the Wilcoxon Signed Rank test to compare raptors per hour between paired sites.

To compare bird community composition between colony and off-colony sites, we reduced the species list from 66 to 30 of the most commonly encountered grassland species by eliminating species only observed in trees, species seen at less than three of the five study locations, or species in which less than five total individuals were seen (Table 1.1). We first constructed an informational hierarchical clustering dendrogram to explore the pattern of similarity between sites in relation to grassland bird abundance. We then used repeated measures ANOVA to test for differences in species abundance between paired sites according to year and season. Sign rank z tests were used to compare differences between paired sites in abundance of individual species by season. We used Discriminant Function Analysis (DFA) to test the hypothesis that a distinct assemblage of bird species is associated with colony compared to off-colony sites. In all statistical tests we considered p-values of less than 0.05 to be significant.

3. Results

Species richness and diversity

Both species richness (colony $\bar{x}$= 14.86, off-colony $\bar{x}$= 12.03) and diversity (colony $\bar{x}$= 1.86, off-colony $\bar{x}$= 1.68) tended to be higher at colony sites, although neither richness (F-ratio = 0.67, p = 0.44) nor diversity (F-ratio = 0.55, p=0.48) showed a significant difference between paired sites. Species richness varied significantly with season (F ratio = 4.62, p= 0.026) but not ground squirrel presence. Mean richness however showed a trend of being higher at colony sites in all seasons (Figure 1.2).

Total Abundance

During all three seasons across two years of surveys we recorded 9,567 individual bird observations totaling 66 species. Colony sites contained 5,513 (57.6%) of the total observations while off-colony sites accounted for the remaining 4,054 (42.4%) observations. The highest number of birds was seen in winter (3791, 39.6%), followed by fall (3142, 32.8%), and then the breeding season (2634, 27.5%). In each season, more bird detections were recorded on colony (winter =23.8%, breeding=14.4%, fall =19.4%) than off-colony sites (winter =15.8%, breeding=13.2%, fall =13.4%).

Total abundance did not differ with year of the study so we were able to pool years using repeated measures ANOVA (F-ratio = 0.08, p = 0.791). Seasonal abundance was significantly different (F-ratio = 6.41, p = 0.024) so we could not pool seasons in subsequent analyses. Total abundance was higher on colony sites in all seasons (F-ratio = 7.71, p= 0.024). Higher abundance on colony sites was significant during winter (p=0.007) and fall (p=0.003) (Wilcoxon matched pairs test n=10 pairs, Figure 1.3).

Grassland species analyses

The reduced set of 30 grassland bird species used for the dendrogram and DFA accounted for 92.2% of 9567 total observations. Overall, the general pattern of the dendrogram revealed that off-colony sites were more clustered together in terms of their grassland bird community than were colony sites (Figure 1.4). Four of the off-colony sites clustered together with higher similarity (SRNO, BPNO, SA2NO, VCNO) compared to the cluster of four colony sites (SA2GS, BPGS, SA1GS, SRGS). Two sets of paired sites, Sweet Ranch and Vasco Caves, remained in close association with each other most likely because grazing management at these two locations kept vegetation height uniformly low reducing the structural differences created by squirrel herbivory. Ground squirrel colony sites were not only dissimilar from their paired sites but also formed a more site specific bird community when compared to the closer similarity of off-colony sites, suggesting that ground squirrel activity may create local patches of bird diversity within the more homogeneous matrix of grassland without squirrels. The most common grassland birds (western meadowlark, horned lark, savannah sparrow, Brewer's blackbird, and American pipit) made up 67.1% of all observations. In terms of total abundance, each of these five species was seen more often on colony sites (Fig. 1.5).

Avian community composition

Individual bird species did not exhibit significant differences in total abundance across years (repeated measures ANOVA), thus we were able to combine data within a season across the two years of the study. Most species were present in higher numbers on sites with ground squirrels than without squirrels, with the total abundance on colony sites exceeding that of off-colony sites for 73.5% of species. In addition, there were a significantly greater number of differences in abundance in favor of bird species at colony sites in all seasons (winter: $p = 0.004$; breeding: $p = 0.017$; fall: $p = 0.011$ Wilcoxon signed rank tests) (Fig. 1.6). Discriminant function analyses revealed that bird assemblages were distinct and significantly different between colony and off-colony sites (F-value=12.7, df = 8, 51, $p = 0.000$). Sites were identifiable and separated into colony or off-colony with an 87% classification success (Fig. 1.7). California ground squirrel colony sites were associated with high scores for raptors, specifically burrowing owl, golden eagle, and American kestrel, while off-colony sites without ground squirrels were associated with low scores for grassland passerines (Brewer's blackbird, horned lark, savannah sparrow).

Raptors

At every pair of sites, we observed a higher rate of total raptor utilization on colony compared to off-colony sites (mean raptors / hour on colony sites $\bar{x}$= 1.91, SD=0.93; off-colony sites $\bar{x}$= 0.42, SD=0.17). Of 16 raptor species recorded, 11 (69%) species were more frequently observed on colony sites (Fig. 1.8), (Wilcoxon Sign Rank p = 0.002). The white-tailed kite was the only common raptor species to show a preference for off-colony sites without California ground squirrels. The remaining four species were rarely observed because they were primarily species of forest or chaparral such as the Cooper's hawk (*Accipiter cooperii*) and the sharp-shinned hawk (*Accipiter striatus*), or generally rare within the study area such as the Swainson's hawk (*Buteo swainsoni*), and the peregrine falcon (*Falco peregrinus*). In all seasons, burrowing owls were recorded only at colony sites where ground squirrels were present; four of the five colony sites harbored nesting burrowing owls. During the 2002 and 2003 breeding seasons, eight active burrowing owl nests produced 3-6 fledglings per nest. Moreover, burrowing owls were present throughout the non-breeding seasons on the same four colony sites.

4. Discussion

Recent research on the prairie dog is prolific and focuses on this ground-dwelling squirrel's role as a keystone species (Kotliar et al. 1999; Kotliar et al. 2006; Smith and Lomolino 2004). There has been very little ecological research on the California ground squirrel and its' influence on ecosystems, although early (Fitch 1948; Grinnell and Dixon

1918; Linsdale 1946) and more recent work (Kuenzi et al. 1998; Loredo et al. 1996) both allude to numerous vertebrates found in positive association with California ground squirrels. The California ground squirrel is ecologically similar to the prairie dog. Both species are conspicuous members of grasslands that live in social colonies, serve as prey for predators, and engineer patches of disturbance in the landscape by burrowing and grazing. The activities of these squirrels increase habitat complexity and attract a wide variety of grassland species including birds that may rely on the presence of these large rodents for prey, shelter, and food resources (Smith and Lomolino 2004).

We found a trend towards higher avian species richness, diversity, and abundance at colony sites where California ground squirrels were present. This general pattern of higher avian utilization of colony sites was consistent with results from paired comparisons for prairie dogs (Smith and Lomolino 2004) and indicates that overall, ground squirrel colonies may offer more resources for birds. Seasonal differences drew attention to the pattern of grassland bird distribution on paired sites. Higher abundance of grassland birds on colony sites was consistent throughout all three seasons but more pronounced during the fall and winter seasons when grassland birds were not breeding. The arrival of migrant and wintering birds increases avian abundance throughout the study area. Yet, bird abundance (Fig. 1.3) and species utilization of paired sites (Fig. 1.6) were still greater at colony sites during the non-breeding season. Bird distribution during the non-breeding season reflects resource availability and thus may be a better indicator of biodiversity than distribution during the breeding season in which territoriality tends to stabilize bird abundance across the grassland landscape (Wiens 1969). The association between ground squirrels and non-breeding grassland birds suggests that habitat patches created by California ground squirrels may be important stopover and wintering sites. Wintering ecology of grassland birds, especially temperate passerines, is poorly known (Vickery et al. 1999), so differential use of grasslands based on California ground squirrel presence has potential implications for grassland conservation. Unlike many ground-dwelling squirrels that retire under-ground part of the year, some portion of this study's California ground squirrel population remains active and aboveground in all seasons (Fitch 1948, (Hunt 2002) influencing the avian community year-round.

We also found evidence to support our prediction that colony sites would contain different assemblages of bird species than off-colony sites without squirrels. Similar to avian communities on prairie dog colonies (Smith and Lomolino 2004), we found a distinct assemblage of birds utilizing ground squirrel colonies at different abundances than surrounding grassland without ground squirrels, as well as a strong distinction (87% classification success) between paired sites based on raptor presence and passerine species abundance. The presence of raptors (burrowing owl, golden eagle, and American kestrel) differentiated colony from off-colony sites, while a low abundance of ground gleaning and ground nesting passerines (Brewer's blackbird, horned lark, and savannah sparrow) indicated off-colony sites where ground squirrels were absent (Fig. 1.7). Species of conservation concern were also more abundant on colony sites (burrowing owl, golden eagle, Northern harrier, loggerhead shrike, prairie falcon, and California horned lark) with one exception, the grasshopper sparrow. Habitat requirements vary across the range of this species but in more arid grasslands grazing is considered detrimental (Saab et al. 1995), and closely cropped vegetation on ground squirrel colonies may deter the grasshopper sparrow, especially during the breeding season when 75% of individuals were located on off-colony sites. Mean differences in abundance (Fig. 1.6) revealed that some grassland birds that forage on aerial insects were more abundant at off-colony sites, including the cliff swallow and white-throated swift, as well as the western bluebird which hunts insects by aerial hawking and forage gleaning. Most other passerine species, particularly grassland species that forage and nest on the ground (Table 1.1), were more abundant on ground squirrel colonies throughout the year (Fig. 1.6).

Not only were paired sites different in terms of bird composition but, at the level of the landscape, bird assemblages within the grassland matrix without squirrels were more similar than those found on California ground squirrel colonies (Fig. 1.4). The burrowing and foraging activities of ground squirrels can alter the disturbance regime increasing non-equilibrium processes such as colonization (Chapin et al. 1997). This dynamic may result in a "shifting mosaic" model, in which fluctuations in the California ground squirrel population form different age patches occurring at various stages of succession, enhancing the dissimilarity in the bird assemblage between individual colony sites while increasing overall beta diversity across the landscape (Turner 1987). Hence, California ground squirrel colonies may act as islands of heterogeneity in a more homogeneous matrix. Historically, intermediate disturbance (Connell 1978) factors, exerted by fire and grazing by large herds of native ungulates and numerous rodents, may have created a "shifting mosaic" of habitat patches that California's grassland birds depended upon. Today, California ground squirrel colonies, dispersed as patches throughout the non-native annual grassland, may mimic the historic disturbance regime that once operated on the native bunchgrass prairie.

We found evidence of close associations between California ground squirrels and individual raptor species that utilize squirrels as prey or their burrows for shelter and nesting. Raptors were observed four times more frequently on colony sites. Grassland sites with California ground squirrels were in fact discriminated from paired sites without squirrels by the presence of three dissimilar raptors (Figure 1.8) that take advantage of California ground squirrels and their colonies in markedly different ways; the golden eagle hunts squirrels, the American kestrel hunts smaller prey by hovering over open ground, and the burrowing owl uses squirrel burrows for roosting and nesting. Indeed, all of the common grassland raptors within the study area were more often observed on colony sites with California ground squirrels, except for the white-tailed kite, which prefers California voles (*Microtus californicus*) that are more abundant in dense grasslands unaltered by squirrels (Ehrlich et al. 1988).

California ground squirrels and their young are vulnerable to many predators particularly raptors (Evans and Holdenreid 1943; Fitch 1948; Grinnell and Dixon 1918; Linsdale 1946). In our study area, California ground squirrels are an important diet staple for golden eagles (Hunt et al. 1995), prairie falcons (Bell pers.comm.), and red-tailed hawks (Kuenzi et al. 1998), and we observed common ravens preying upon juveniles. At every pair of sites, these four species were observed more often where squirrels were present. California ground squirrels are the most important prey for golden eagles in the interior coastal ranges of California (Estep and Sculley 1989), where nesting density is the highest recorded for the species (Hunt et al. 1995). We recorded over 20 times more golden eagles per hour on colony sites. Similarly, other studies found that golden eagle activity was focused on areas where California ground squirrels or their burrows were concentrated (Hoover 2002, Hunt 2002). Even the ferruginous hawk, an uncommon winter visitor, was recorded only at colony sites where individuals were observed hunting squirrels; ground-dwelling squirrels are the principle winter prey of ferruginous hawks (Bechard and Schmutz 1995; Plumpton and Andersen 1997; Plumpton and Andersen 1998; Schmutz and Fyfe 1987).

Raptor ecology and behavior is strongly influenced by prey availability (Newton 1979; Newton 1980), and grasslands support many potential prey species that exist at high density but may not be available when vegetation is dense (Olendorff and Stoddart 1974). California ground squirrel activities create areas of open ground and lower vegetation that may be conducive to prey capture by raptors (Janes 1985). In addition to the abundance of California ground squirrels as prey, colonies possess a higher abundance of passerine birds and ground dwelling invertebrates (Lenihan 2007b) that smaller raptors prey upon. Hence, a ground squirrel colony may become a focal point for a wide variety of hunting raptors. For example, neither the northern harrier nor the American kestrel hunts ground squirrels, but both were more common at ground squirrel colonies where they may prey upon associated birds and invertebrates. Like all raptors, the species discussed here forage where capture probabilities are highest and as a result, prey availability reliably predicts raptor density and habitat selection in all seasons (Baker and Brooks 1981; Bechard 1982; Wakeley 1978). Our results confirm that California ground squirrel colonies are highly attractive year-round to a wide variety of raptors that hunt both squirrels and smaller prey.

Finally, we found a strong association between burrowing owls and California ground squirrels; burrowing owls were found exclusively at squirrel colonies, where they successfully nested in ground squirrel burrows during the breeding season and roosted throughout the non-breeding season. The burrowing owl has declined throughout its range, in part because of reduced burrow availability due to rodent control (James and Espie 1997). These owls are closely associated with burrowing mammals (Haug et al. 1993) that act as ecosystem engineers, digging burrows and modifying the surrounding habitat in ways that facilitate burrowing owl reproduction (Machicote et al. 2004). Although the burrowing owl has been in continuous decline in California since the 1940s (Miller 2003), the state still supports one of the largest remaining breeding and wintering populations (DeSante and Ruhlen 1995; James and Espie 1997). Our findings highlight the importance of California ground squirrels in the conservation of burrowing owls.

Our results indicate that California ground squirrels are indeed exerting a positive influence on the biodiversity of grassland birds. Unlike many functionally important species that play one role as predators, prey, mutualists, or habitat modifiers, California ground squirrels fulfill a dual role acting as prey and modifying habitat structure and dynamics. California ground squirrels affect the physical structure of the grassland creating islands of disturbance that attract more grassland bird species at higher abundances, while the presence of squirrels as a concentrated prey resource attracts many raptor species. The California ground squirrel may be to California grasslands what the prairie dog is to the short-grass prairie, an ecosystem engineer and probable keystone species. Rather than being a rangeland pest, the California ground squirrel is an integral component playing a significant role in the ecological assembly of grassland communities.

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TABLE 1.1: Grassland species considered in the analysis, common name, scientific name, four letter code used to represent species in subsequent figures († Species not in list of 30 but discussed in raptor section), seasonal status (P = Permanent resident, Sb = Summer breeding species, W = Winter visitor), (*Species of conservation concern), foraging mode and ground nesting status.

Species Name	Species Code	Seasonal Status	Foraging mode	Ground nesters
American goldfinch (*Carduelis tristis*)	AMGO	P	foilage/ground gleaner	
American kestrel (*Falco sparverius*)	AMKE	P	hover/pounce	
American pipit (*Anthus rubescens*)	AMPI	W	ground gleaner	
Anna's hummingbird (*Calypte anna*)	ANHU	P	hover/glean/hawks	
barn swallow (*Hirundo rustica*)	BARS	Sb	aerial foraging	
black phoebe (*Sayornis nigricans*)	BLPH	P	hawks/hover/pounce	
Brewer's blackbird (*Euphagus cyanocephalus)*	BRBL	P	ground glean	X
Bullock's oriole (*Icterus bullockii*)	BUOR	Sb	foilage glean	
burrowing owl (*Athene cunicularia*)	BUOW	P*	hover/pounce/ground glean	X
cliff swallow (*Petrochelidon pyrrhonota*)	CLSW	Sb	aerial foraging	
common raven (*Corvus corax*)	CORA	P	ground gleaner	
European starling (*Sturnus vulgaris*)	EUST	P	ground gleaner	
ferruginous hawk (*Buteo regalis*)	FEHA†	W*	hover/pounce/swoop	
golden eagle (*Aquila chrysaetos)*	GOEA	P*	high patrol/swoop	
grasshopper sparrow (*Ammodramus savannarum*)	GRSP	Sb*	ground gleaner	X
house finch (*Caprodacus mexicanus*)	HOFI	P	ground gleaner	
horned lark (*Eremophila alpestris*)	HOLA	P*	ground gleaner	X
killdeer (*Charadrius vociferus*)	KILL	P	ground gleaner	X
lark sparrow (*Chondestes grammacus*)	LASP	P	ground gleaner	X
loggerhead shrike (*Lanius ludovicianus*)	LOSH	P*	hawks/aerial pursuit	
mourning dove (*Zenaida macroura*)	MODO	P	ground gleaner	
northern harrier (*Circus cyaneus*)	NOHA	P*	low patrol	
prairie falcon (*Falco mexicanus*)	PRFA	P*	aerial pursuit/low patrol	
red-tailed hawk (*Buteo jamaicencis*)	RTHA	P	high patrol/swoop	

Species Name	Species Code	Seasonal Status	Foraging mode	Ground nesters
red-winged blackbird (*Agelaius phoeniceus*)	RWBL	P	ground gleaner	X
Say's phoebe (*Sayornis saya*)	SAPH	P	hawks/hover/pounce	
savannah sparrow (*Passerculus sandwichensis*)	SAVS	W	ground gleaner	X
western bluebird (*Sialia mexicana*)	WEBL	P	hawk/foilage glean	
western kingbird (*Tyrannus verticalis*)	WEKI	Sb	hawks/hover/pounce	
western meadowlark (*Sturnella neglecta*)	WEME	P	ground gleaner	X
white-tailed kite (*Elanus leucurus*)	WTKI†	P*	hover/pounce	
white-throated swift (*Aeronautes saxatalis*)	WTSW	P	aerial foraging	

SEASONAL STATUS SOURCE LIVERMORE BIRDS 2005: http://fog.ccsf.cc.ca.us/%7Ejmorlan/livermore.htm

Conservation Priority: Species of Special Concern (SSC), Fully Protected (FP)
SOURCE: 1. CDFG CA bird SSC 2005: www.dfg.ca.gov/hcpb/info/bird_ssc.shtml
2. CDFG and PRBO. 2001. California Bird Species of Special Concern: Draft List and Solicitation of Input.

Diet, foraging and nesting SOURCE: Ehrlich, P. R., Dobkin, D. S. and D. Wheye. 1988. The Birder's handbook. Simon and Schuster Inc., New York, 785pp.

Figure 1.1: Study area map

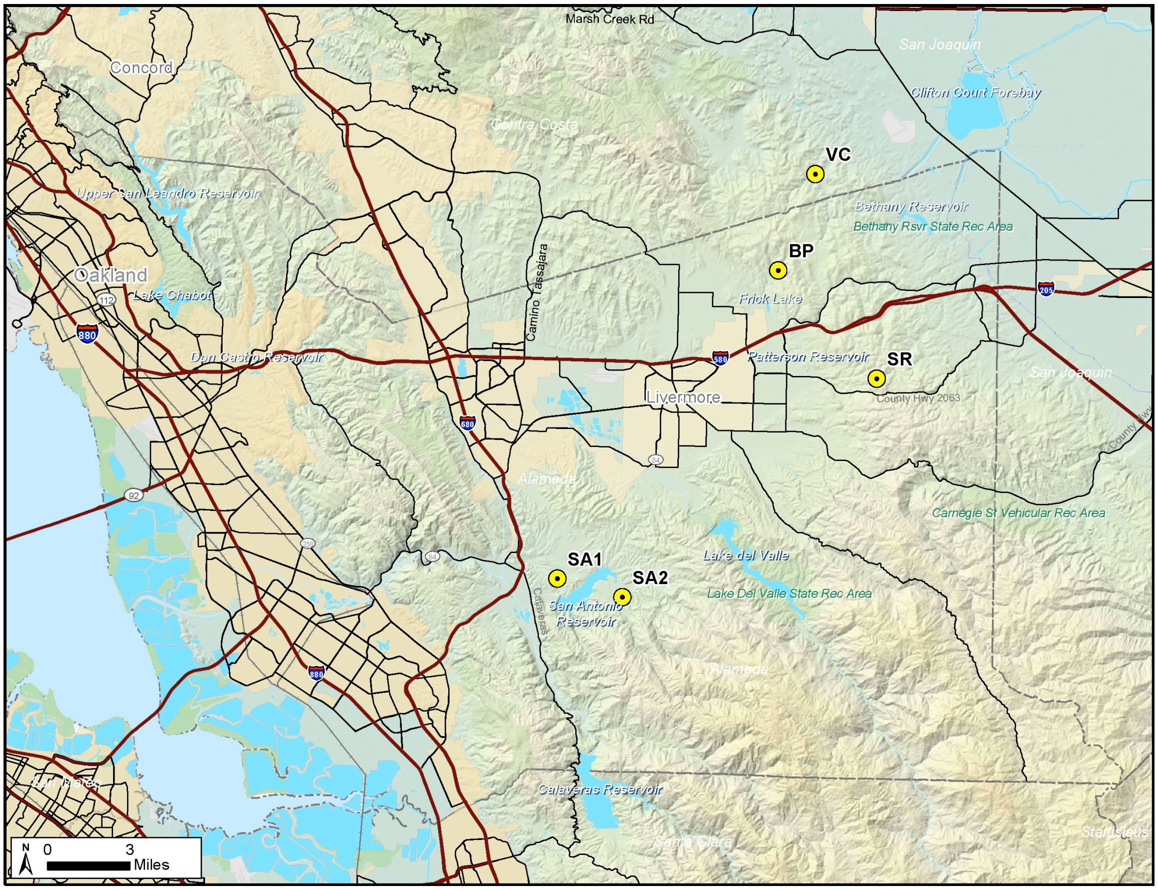

Figure 1.1: Vicinity of the study area east of San Francisco Bay, California indicating locations of paired sites surveyed in this study.
Site code designates the location of paired colony / off-colony sites (Vasco Caves = VC, Brushy Peak = BP, Sweet Ranch = SR, San Antonio 1 = SA1, and San Antonio 2 = SA2).

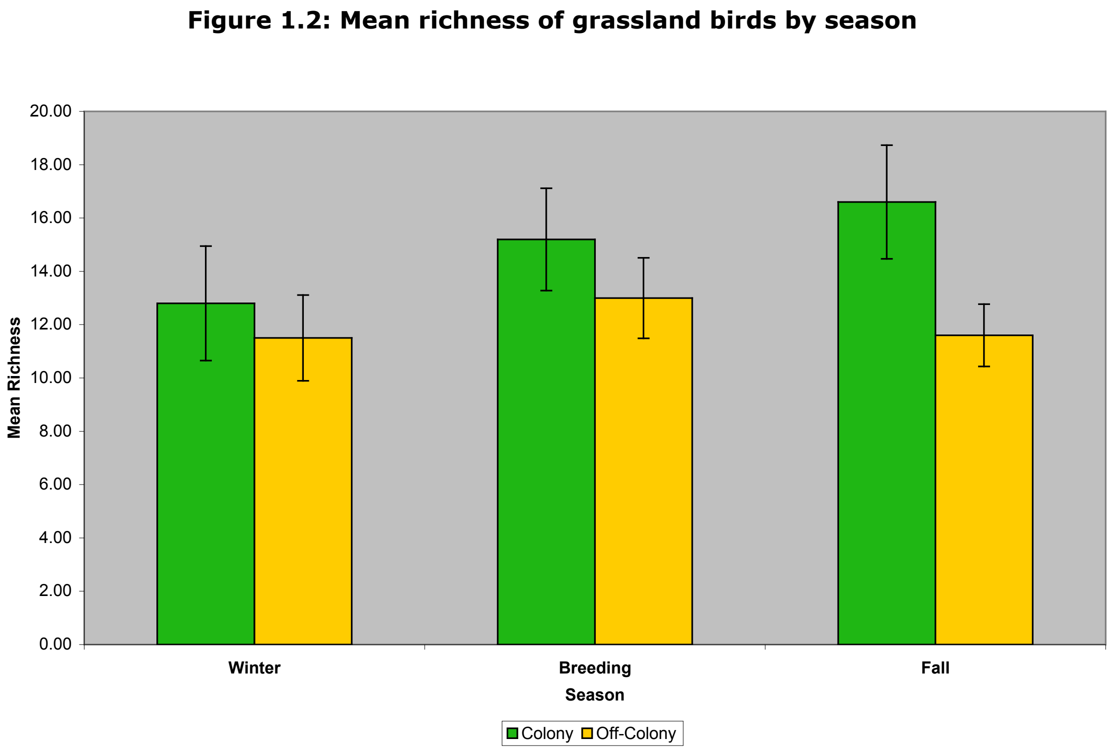

Figure 1.2: Mean richness of avian species during winter, breeding and fall (2003 and 2004 combined) on California ground squirrel colony and off-colony sites (for all species, n=10 sites for each treatment in each season). Bars represent mean (±) 1 SE.

Figure 1.3: Mean abundance of grassland birds by season

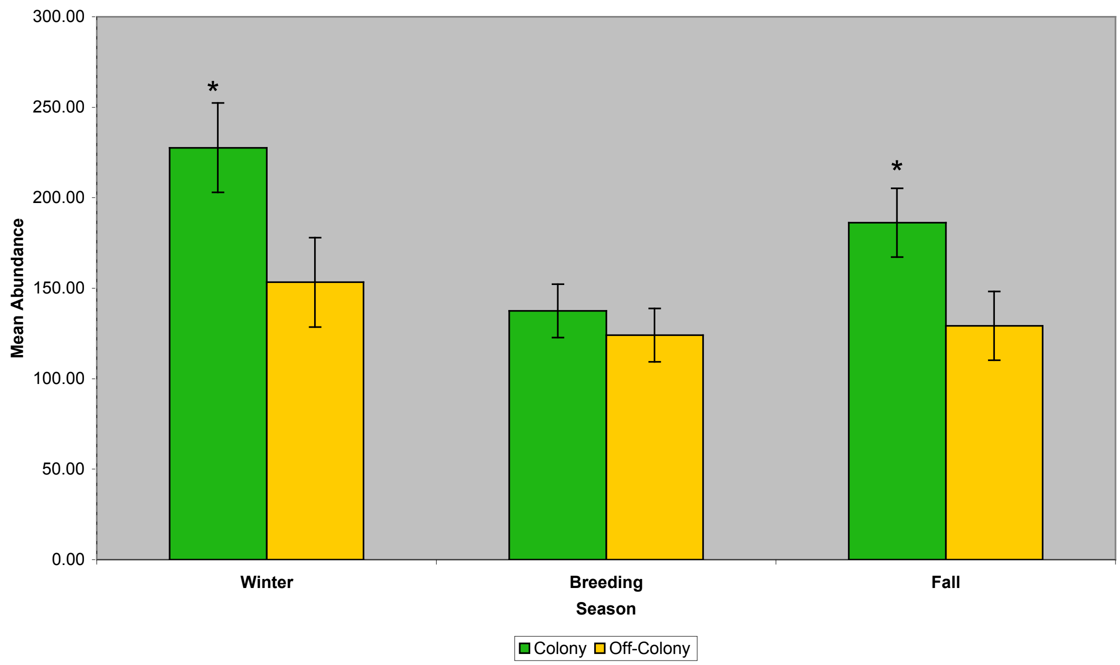

Figure 1.3: Mean total abundance of avian species during winter, breeding and fall (2003 and 2004 combined) on California ground squirrel colony and off-colony sites (for all species, n=10 sites for each treatment in each season). Bars represent mean (±) 1 SE (* $p<0.05$, based on Wilcoxon matched pairs t-test).

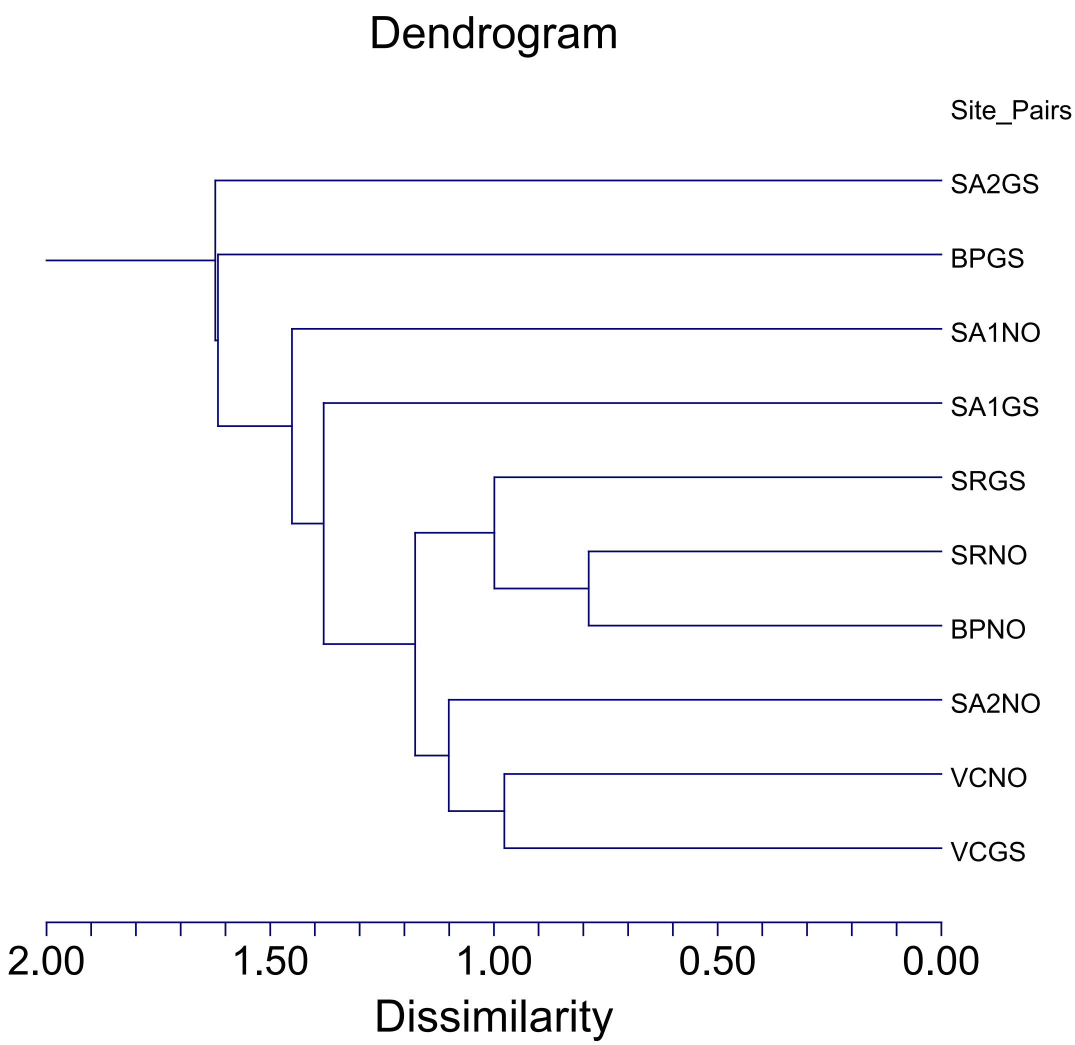

Figure 1.4
Using the reduced avian abundance data set (30 species) we constructed an informational hierarchical clustering dendrogram. This clustering technique groups study sites that share similar values across species composition and abundance. Each site constitutes an initial cluster. Site code designates the location of paired sites (Vasco Caves = VC, Brushy Peak = BP, Sweet Ranch = SR, San Antonio 1 = SA1, and San Antonio 2 = SA2), and site status (colony sites with squirrels = GS; off-colony sites without squirrels = NO). At each step the clustering process calculates the distance between each cluster, and combines the two clusters that are closest together continuing until all the points are in one final cluster.

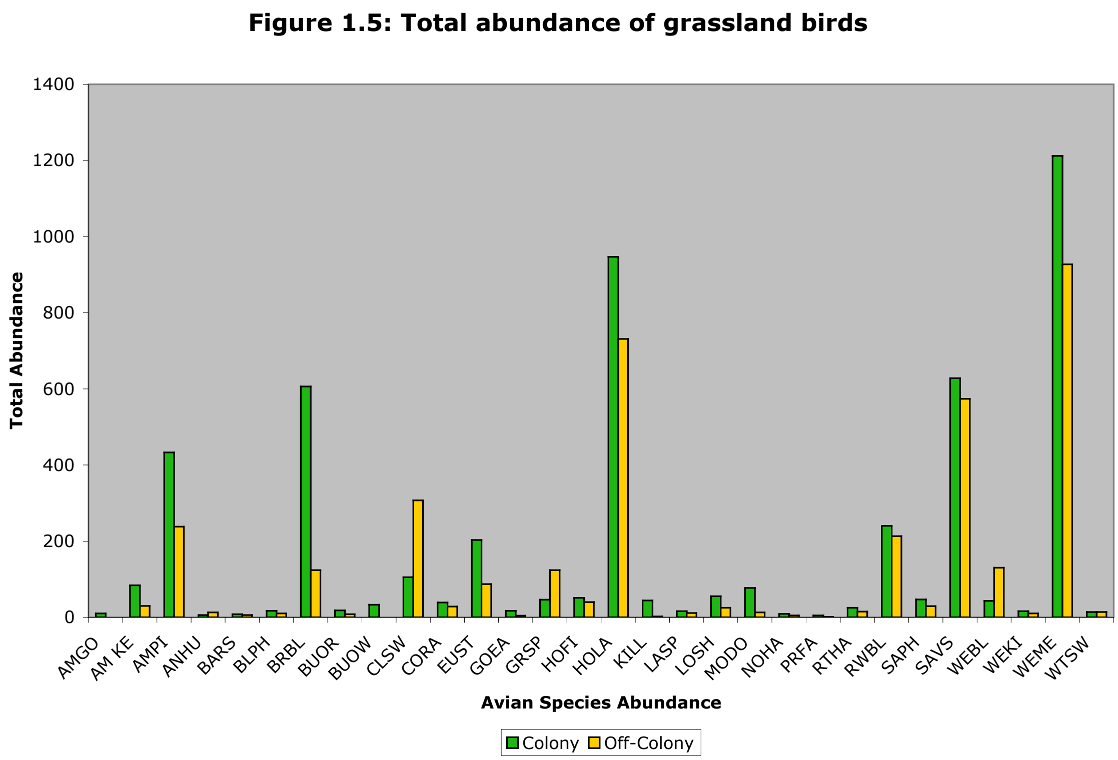

Figure 1.5: Total abundance of individual grassland avian species (seasons and years combined) on California ground squirrel colony and paired off-colony sites. See table 1 for common names corresponding to species code on X-axis.

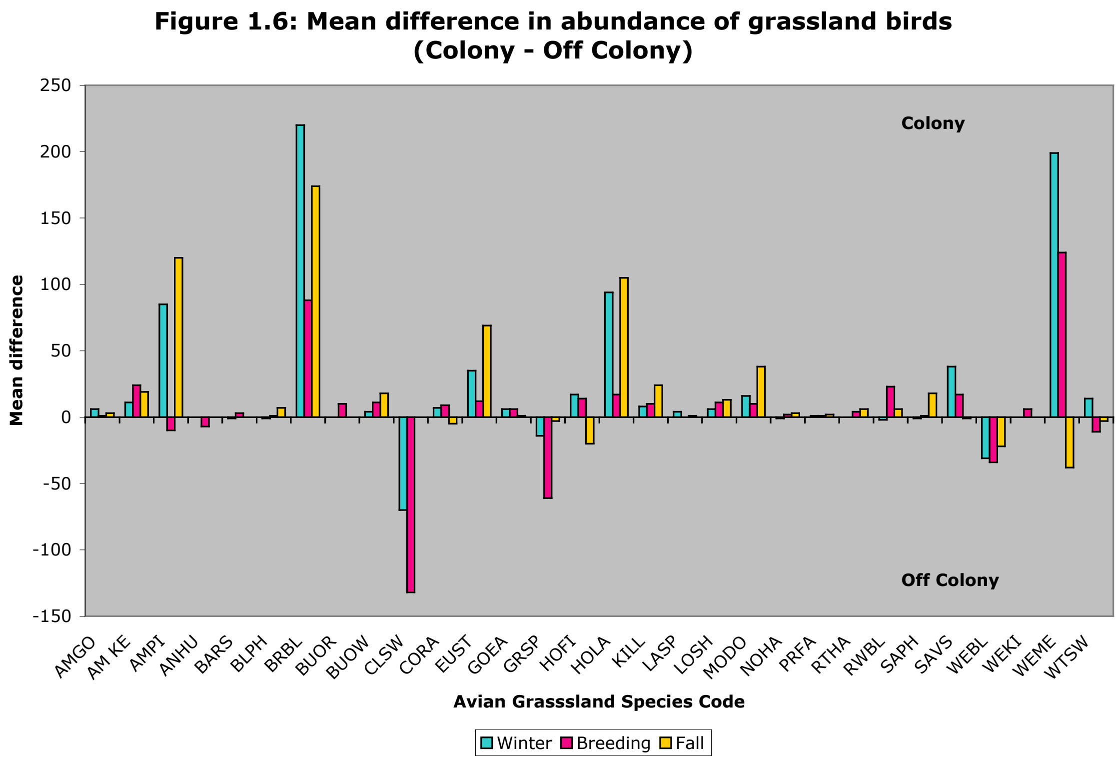

Figure 1.6: Mean difference in total seasonal abundance for individual grassland avian species (2003 and 2004 combined) between California ground squirrel colony and off-colony sites. Species with higher abundance on colony sites are positive on the y-axis while species with higher abundance on off-colony sites are negative on the y-axis. The number of species with greater abundance on colony sites is significant ($p<0.05$) for all seasons (Wilcoxon Sign Rank test). See table 1 for common names corresponding to species code on X-axis.

Figure 1.7

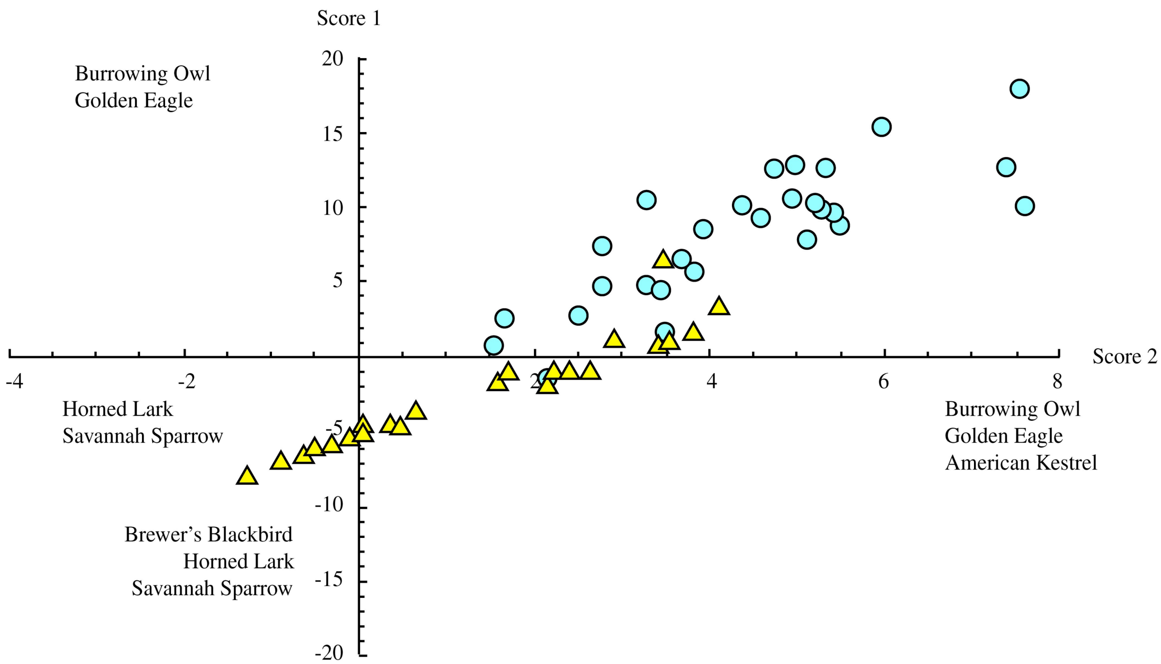

Figure 1.7: Plot of discriminant function factor scores for grassland avian communities on California ground squirrel colony and paired off-colony sites using the reduced data set of 30 species (seasons and years combined, n=60). Scores reflect total abundance of avian species at each of these sites (F-value=12.7, df=8,51, P=0.000). Blue O = California ground squirrel colony sites, yellow Δ= off-colony sites. Site status is identifiable as California ground squirrel colony or off-colony with an 87% classification success. Axes depict a gradient of abundance for specific species that uniquely discriminate site status. A low score represents fewer individuals of that species present, while a high score represents a relatively larger number of individuals in that species present. Species codes: *AMKE* American kestrel, *BRBL* Brewer's blackbird, *BUOW* burrowing owl, *GOEA* golden eagle, *HOLA* horned lark, *SAVS* savannah sparrow.

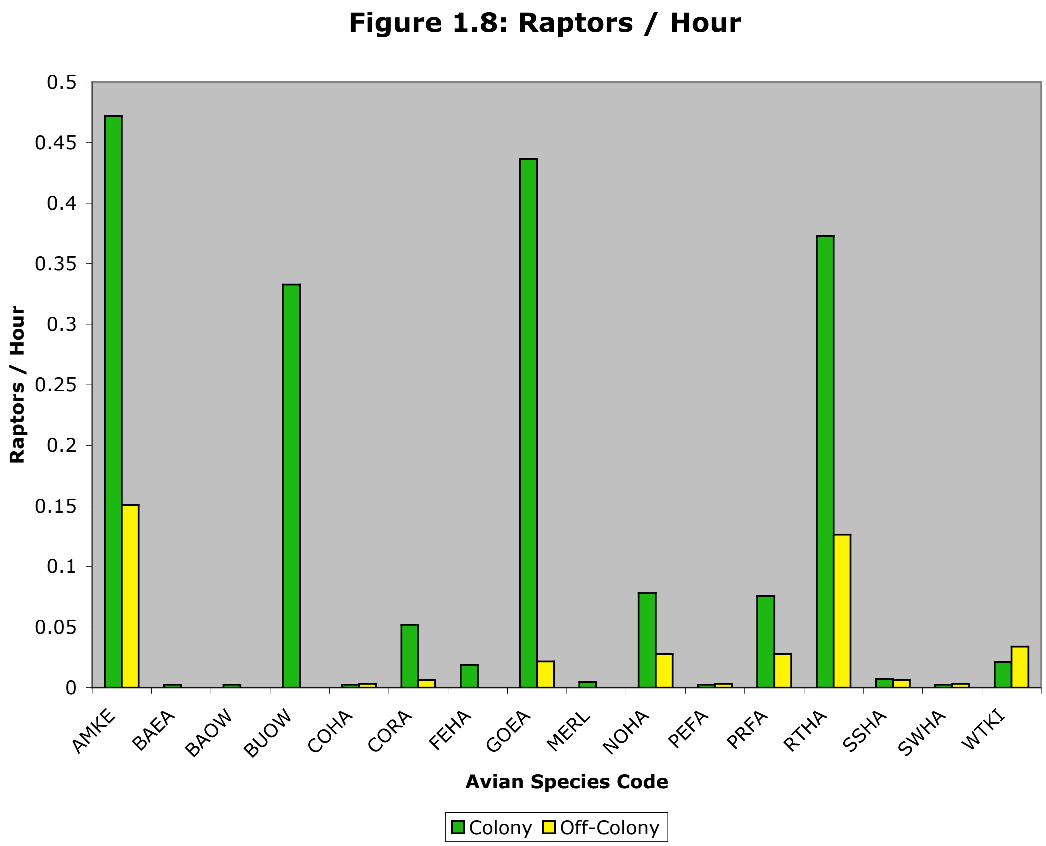

Figure 1.8: Comparison of recorded raptors / hour (years combined) on California ground squirrel colony and paired off-colony sites. Raptor frequency on colony sites is significantly greater (Wilcoxon signed rank test p=0.002).
Species codes: *AMKE* American kestrel, *BAEA* bald eagle, *BAOW* barn owl, *BUOW* burrowing owl, *COHA* Cooper's hawk, *CORA* common raven, *FEHA* Ferruginous hawk, *GOEA* golden eagle, *MERL* merlin, *NOHA* northern harrier, *PEFA* peregrine falcon, *PRFA* prairie falcon, *RTHA* red-tailed hawk, *SSHA* sharp-shinned hawk, *SWHA* Swainson's hawk, *WTKI* white-tailed kite.

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Chapter 2: The influence of the California ground squirrel (*Spermophilus beecheyi*) on the flora and terrestrial fauna of grassland communities

INTRODUCTION

Ground-dwelling squirrels occupy a variety of habitats throughout much of North America. They have long been considered a threat to agriculture, but they are also important components of biotic communities, and their loss could have serious ecological consequences (Yensen and Sherman 2003). Ground-dwelling squirrels may have disproportionately large effects on habitat structure and community composition by acting as an ecosystem engineer causing physical disturbance within a localized area and through predator-prey, competitive, and mutualistic interactions with other species (Brown and Heske 1990; Dickman 1992; Jones et al. 1997; Mills et al. 1993). Within grassland communities many vertebrate species including some of conservation concern, have been found in association with ground-dwelling squirrels (Kotliar et al. 2006; Lenihan 2007a). California ground squirrels (*Spermophilus beecheyi*) are diurnal, medium sized rodents that live in loosely social aggregations called colonies. An important agent of disturbance in grasslands, ground squirrels and their activities such as grazing, trampling of trails, mound building, and tunneling underground create a mosaic of disturbance patches that stand out from the surrounding grassland matrix. Further, California ground squirrels are locally abundant, increasing the opportunity for interspecific interactions on colonies where ground squirrels may simultaneously play the role of mutualist, competitor, predator, or prey.

Another ground-dwelling squirrel, the black-tailed prairie dog (*Cynomys ludovicianus*), may provide a model for predicting the effects of California ground squirrels in grassland communities (Kotliar et al. 1999). Burrowing and grazing by prairie dogs augments primary productivity, species densities and diversity, and soil structure and chemistry (Detling and Whicker 1988; Reading et al. 1989; Sieg 1988), creating a landscape mosaic that promotes a unique species composition and overall grassland diversity (Kotliar et al. 1999; Lomolino and Smith 2003). In addition, prairie dogs have diverse interactions with other species in the grassland community (Hoogland 2003). Likewise California ground squirrels may influence the grassland community in two basic ways: as an ecosystem engineer that modifies habitat both above and below ground and through interspecific interactions with other grassland species. Patches of disturbance created by California ground squirrel activities are expected to differ from the surrounding grassland matrix by containing more bare ground due to burrowing and trampling, and less vegetative cover, less forbs, and more grass as a result of selective foraging (Fitch 1948; Fitch and Bentley 1949; Schitoskey and Woodmansee 1978). These habitat modifications combined with interspecific interactions should lead to differences in the composition of the terrestrial fauna occupying sites where squirrels are common compared to areas without squirrels. Differences have been shown for avian communities in the presence of prairie dogs and California ground squirrels compared to nearby sites without ground dwelling squirrels (Lenihan 2007; Smith and Lomolino 2004), and may occur in terrestrial species as well. Although many terrestrial grassland species, some of them imperiled, are thought to be positively associated with California ground squirrels (Hunt et al. 1995; Jennings and Hayes; Loredo et al.; Miller 2003), others may show no preference or even avoidance of squirrel colonies, making it necessary to determine the response of various taxa before recommending prescriptive management for grassland landscapes. Furthermore, because the activities of a particular species can be disproportionately significant for the survival of native communities, assessing interactivity while that species is relatively abundant is essential to determine the contribution of the interactor to the maintenance of ecological and species diversity (Soule et al. 2005).

We use a comparative approach to assess the interactive role of the California ground squirrel and make inferences about the strength and direction of interactions between ground squirrels and the flora and non-volant fauna of the grassland community. We compare the response of grassland vegetation and ground-dwelling invertebrates, small mammals, carnivores, ungulates, and reptiles, to determine whether the community structure (species richness, diversity, and abundance) differs with the presence or absence of the California ground squirrel. To our knowledge, this is the first comparative study to examine the association between California ground squirrels and the terrestrial grassland community.

MATERIALS AND METHODS

The study area lies within the Livermore Valley area of the Central Coast Ranges, in eastern Alameda and Contra Costa counties, California, approximately 80 km east of

San Francisco (37º41' N, 121º47' W) (Fig. 1.1). Within these two counties, 41% of the land area is covered by annual grassland (Liffmann et al. 2000). Prior to the arrival of the Spanish rancho culture which introduced domestic livestock to California in 1769, the grassland community was a prairie dominated by native perennial bunchgrasses and a multitude of colorful annual and perennial forbs (Burcham 1957). Today, it is a non-native annual grassland dominated by introduced annual grasses and forbs (Sawyer and Keeler-Wolf 1995), species that are well adapted to the Mediterranean climate characterized by mild, wet winters and long, hot, dry summers. Plant growth begins with the onset of fall rains, typically November or December. Annual precipitation ranges 38-63 cm and varies widely year-to-year, monthly temperatures range from a mean minimum of 3º C to a mean maximum of 30º C, and the mean freeze-free period is 200-250 days (Easterling et al. 1996). Growth ends with the cessation of precipitation, with temperature controlling growth rates within the growing season (George et al. 1988). The dominant species are mostly non-native grasses introduced from the Mediterranean basin such as soft chess (*Bromus hordeaceus*), red brome (*Bromus madritensis*), wild oats (*Avena spp*), ripgut brome (*Bromus diandrus*), and rat-tail fescue (*Vulpia myuros*). Common native forbs include lupine (*Lupinus spp*.), fiddleneck (*Amsinkia spp*.), popcornflower (*Plagiobothrys spp*.), California poppy (*Eschscholzia californica*), owl's clover (*Triphysaria spp*.), blue-eyed grass (*Sisyrinchium bellum*), and clarkia (*Clarkia spp*.). Non-native forbs such as filaree (*Erodium spp*.), clovers (*Trifolium spp.)*, yellow star thistle (*Centaurea solstitialus*), other thistles, mustard (*Brassica nigra* and *Hirschfeldia incana)*, vetch (*Vicia sativa)*, tarweeds (*Holocarpha virgata*), and turkey mullein (*Eremocarpus setigerus*) are also common components of these grasslands.

Site selection

We established five pairs of sites (each site 200 m x 200 m = 4 ha), four in Alameda County and one in Contra Costa County. Each of five ground squirrel colony sites was paired with a nearby off-colony site without ground squirrels to control for local variation in environmental conditions. Both sites within a pair were located on lands owned by the same property owner to further control for variation in land management and grazing regime. Three pairs were located in treeless grassland within the Altamont Hills region, and two pairs were located in oak savanna (2-4 oak trees / 4ha site) around San Antonio Reservoir. We first designated sites where California ground squirrels were abundant (23-39 squirrels / ha) then located comparable areas without ground squirrels 0.6-2.0 km distant. California ground squirrel home ranges are <150 m in diameter (Van Vuren et al. 1997), and 300 m between sites is generally sufficient to preclude re-invasion by dispersing California ground squirrels (Stroud 1982), hence during the study period sites without ground squirrels were beyond the dispersal range of the nearest known area of occupancy but close enough to preserve pair habitat similarity.

Survey Methods

We sampled vegetation along transects on all sites, coinciding with peak vegetation biomass in our study area during late spring (April and May) of 2003 and 2004. Vegetation transects originated from a permanently marked point in the center of each site and extended outward for 10 m in each of the four cardinal directions. Sampling occurred within a 25 x 40 cm quadrat placed on the left side of the transect line at 3, 6, and 9 m from the center point for a total of 12 quadrats per sampling point. Plants were identified to species by a trained botanist while an assistant recorded percent cover by individual plant species, average vegetation height, and percentage of bare ground and thatch. To determine the differential effect of ground squirrel foraging on vegetation biomass, we measured residual dry matter (RDM) at paired sites near the end of the dry season in 2003 and 2004 prior to the first effective fall rains (late September to early October). Residual dry matter is the amount of dry plant material left on the ground from the previous year's growth. Measures of RDM are commonly used as an index to evaluate the previous season's level of grazing use and to describe the health or condition of annual rangelands (Bartolome et al. 2002; George et al. 1996; Harris et al. 2002). We measured RDM at two locations per site by clipping and weighing all herbage within a circular plot (33.65cm diameter) to the nearest gram, which was then multiplied by 100 to obtain kg/ha of RDM (Guenther 1998).

We censused small mammal populations by trapping simultaneously on paired sites at the end of the dry season (mid-August through mid-October) during 2002, 2003, and 2004. Spring trapping was conducted once, in April- June 2003, and then discontinued because of trap disturbance by livestock. Data from spring 2003 are included in the summary data; all other analyses include only dry season data. Each trap grid was composed of 50 Sherman live traps (trap size: 8x9x23 cm) set 15 m apart in a seven by seven plus one square configuration (Johnson 2002) placed over a 100x100m (trap area=1 ha) area of grassland. The grid was positioned in the center of each 4-ha site to minimize capturing animals living beyond the site boundary. Trapping continued for four consecutive nights. Traps were set each evening with bait (bird seed) and cotton bedding then checked the following morning beginning at dawn. Small mammals were identified to species and hair clipped to distinguish different individuals. The number of unique individuals captured at each study site was used to determine abundance.

Carnivores, ungulates, and reptiles were recorded using an "all occurrences" sampling method (Altmann 1974) from June 2002 through March 2005. We calculated the time spent on each study site during daylight hours and recorded all terrestrial vertebrates observed.

We used cover-boards to census ground dwelling invertebrates. At each site, 10 plywood boards (0.61x0.61m= 0.37 m^2) were placed on the ground 20m apart along the diagonal across each site. Cover-boards were checked once a month from July 2004 to July 2005; invertebrates were identified at least to family, and counted.

Statistical Methodology

Species richness, diversity, and abundance were determined for each site within each year for both vegetation and small mammals. Species diversity was calculated using the Shannon-Weiner index (Krebs 1999). We combined vegetation data at each site within each year to calculate a mean value for species richness, vegetation height, RDM, and percentages of plant cover. Vegetation variables were tested for differences between paired sites and effect of year using the Wilcoxon Signed Rank Test (Sall et al. 2005). Differences in the small mammal community between paired sites (colony and off-colony) were analyzed first by comparing species richness, diversity, and abundance using repeated measures ANOVA. Next we used repeated measures ANOVA to test for differences in individual species abundance between colony and off-colony sites according to year. Because of the distribution of "0" terms in the cells of the analysis of the *Reithrodontomys megalotis* data, the ANOVA described above did not provide an estimate of the mean square term for geographical site nested within the status (colony / off-colony) term. Consequently, the nesting was removed and a two-way ANOVA was performed using status and year as the main effects term for this species. From the "all occurrences" sampling data, we calculated the number of terrestrial vertebrates / hour of observation on each site by individual species and by combining species within two important predatory guilds, carnivores and reptiles. We then used the Wilcoxon Signed Rank test to compare colony and off-colony sites. For invertebrates we compared total abundance and richness, as well as differences between taxonomic groups at colony and off-colony sites using a one-way ANOVA. For all statistical tests we considered a p-value of less than 0.05 to be significant.

RESULTS

Vegetation

There were no differences between years (2003, 2004) for plant species richness (z=-1.10, p=0.27) or diversity (z=-1.47, p=0.14). Comparisons between colony and off-colony sites differed, with lower plant species richness (colony $\bar{x}$ = 11.3, off-colony $\bar{x}$ = 15.0, z=1.90, p=0.057) and lower diversity (colony $\bar{x}$ =1.19, off-colony $\bar{x}$ =1.62, z=2.11, p=0.03 n=20) on colony sites. Annual precipitation varied between 2003 (42.5cm), and 2004 (32.5cm). Higher precipitation in 2003 produced taller vegetation (z=-1.93, p=0.05), heavier residual dry matter (z=-2.65, p=0.008), and a higher percentage of forbs (z=-1.89, p=0.05) but lower percentage of grass (z=2.00, p=0.045) compared with 2004.

Colony sites exhibited a pattern of shorter vegetation (colony $\bar{x}$= 17.55cm $\pm$1.92, off-colony $\bar{x}$=21.63cm $\pm$3.12) and lower residual dry matter (colony $\bar{x}$=994kg/ha$\pm$159, off-colony $\bar{x}$=1369kg/ha$\pm$252), with less forbs, more grass, and more bare ground during both years (Fig. 2.1). This pattern was more pronounced during 2004 when precipitation was lower.

Terrestrial Vertebrate Summary Statistics

We detected 20 species of mammals, nine species of reptiles, and four species of amphibians (Table 2.1). During four trapping sessions (Spring 2003, Fall 2002, 2003, and 2004) we captured a total of 595 small mammals representing six species in the following order of abundance: *Peromyscus maniculatus* (278), *Mus musculus* (119), *Perognathus inornatus* (91), *R. megalotis* (75), *Microtus californicus* (31), *Chaetodipus californicus* (1). The first five species were captured on colony sites and all six species were captured on off-colony sites. Colony sites contained 42% of the total individuals captured while off-colony sites contained 58%. Three species were predominantly encountered during the wettest year (2003), including 80% of captures for both *M. musculus* and *R. megalotis* and 88% of *M. californicus*. The most common species, *P. maniculatus,* was captured on all sites and accounted for approximately half of the total captures (47%). In the three years of fall trapping 549 small mammals were captured on all 10 sites. Fall capture rates at colony ($\bar{x}$= 0.0746) and off-colony sites ($\bar{x}$= 0.1083) were not significantly different (F-ratio=0.9884, p=0.3286). Capture rates tracked total precipitation during the three years of the study (2002=28.7cm, 2003=42.5cm, 2004=32.5cm) with the highest capture rate occurring during the wettest year in 2003 (58%), followed by the intermediate rainfall year in 2004 (35%), and the driest year in 2002 (7%).

Small mammal abundance and diversity

Using repeated measures ANOVA, we found no significant differences between colony and off-colony sites for small mammal abundance (F-ratio=0.76, p=0.45), species richness (F-ratio=0.85, p=0.42), or diversity (F-ratio=1.93, p=0.25). However, differences among years of the study were significant for abundance (F-ratio=10.52, p=0.0007), richness (F-ratio=21.06, p=0.00001), and diversity (F-ratio=5.10, p=0.015). Therefore, we were unable to pool the three years of trapping data, and yearly sample size was insufficient to conduct further statistical testing. However, a pattern of lower abundance, richness, and diversity was evident on colony compared to off-colony sites (Fig. 2.2, 2.3, 2.4), especially during 2003, the wettest year of the study.

Small mammal community / Site characteristics

The location of the study site pairs significantly influenced species richness (F-ratio= 7.51, p=0.001), and diversity (F-ratio= 3.60, p= 0.03), but not abundance (F-ratio=2.34, p=0.103). Only *R. megalotis* showed a significant difference in abundance between colony and off-colony sites (Fig. 2.5 and Table 2.2), while three species showed differences between years (*P. maniculatus, R. megalotis, and M. californicus*) and two species for paired study location (*P. inornatus and M. musculus*) (Table 2.2).

Large Mammals

Carnivore activity on colony sites ($\bar{x}$=0.071 $\pm$0.016 observations/hour) was significantly higher than off-colony sites ($\bar{x}$=0.022 $\pm$0.004 observations/hour) (z= -7.50, p=0.031). Carnivore activity was higher on colonies at every pair of sites, and individual carnivore species, with the exception of the striped skunk, were observed more often on colony over off-colony sites (Fig. 2.6). Deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) were also more common on colony sites while wild pigs (*Sus scrofa*) were encountered more often on off-colony sites. Although not included in our "all occurrences" sampling, cottontail rabbits (*Sylvilagus audubonni*) were frequently seen at burrows on colony sites but never seen at off-colony sites.

Reptiles

Reptiles were detected only from mid-March to November 1, so calculations of observation rates were limited to this time period. We encountered five species of reptiles on colony sites and seven species on off-colony sites (Fig. 2.7). Reptile activity was slightly higher on colony ($\bar{x}$=0.17 $\pm$0.06 observations/hr) compared to off-colony sites ($\bar{x}$=0.14 $\pm$0.06 observations/hr), but not significantly so (z=-0.5, p=0.5). Snake activity was higher on colony ($\bar{x}$=0.10 $\pm$0.03) compared to off-colony ($\bar{x}$=0.03 $\pm$0.02) sites but fell short of significance (z=-0.5, p=0.06). Rattlesnakes (*Crotalus viridis*) were 7 times and gopher snakes (*Pituophis catenifer*) 3 times more common on ground squirrel colonies (Fig. 2.7). Of 15 rattlesnakes detected, 13 were adults observed on colonies in close proximity to ground squirrel burrows (0.07 rattlesnakes observed/hr). The only rattlesnakes seen at off-colony sites (0.01 rattlesnakes observed/hr) were two small juveniles.

Ground dwelling invertebrates

Invertebrate abundance (colony $\bar{x}$=68.1, off-colony $\bar{x}$=49.75) and richness (colony $\bar{x}$=5.07, off-colony $\bar{x}$=4.95) were higher but not significantly different between colony and off-colony sites (abundance F-ratio= 1.55, p=0.22; richness F-ratio=0.04, p=0.84). Two groups of invertebrates showed significant differences in abundance between paired sites. Both centipedes (F-ratio=3.91, p=0.05) and ground beetles (F-ratio=4.93, p=0.03) were more abundant on colony sites (Fig. 2.8).

DISCUSSION

California ground squirrels may affect grassland communities directly through interspecific interactions with other grassland species and indirectly by physically modifying habitat structure and dynamics. Our results show that California ground squirrel activity lowers plant diversity and creates a pattern of more bare ground, shorter vegetation, lower residual dry matter/standing crop, less forbs, and more grass. Plant productivity responded more strongly to conditions of the year than to ground squirrel presence producing significantly taller, denser cover with more forbs during a wet year (2003) and a higher percentage of grass during a drier year (2004). High vegetative growth may have diluted the effect of foraging California ground squirrels on colony sites.

The interaction between vegetation modifications and burrow features may strongly influence the response of the terrestrial grassland fauna to ground squirrel colonies. Above ground, California ground squirrels reduce cover through herbivory and trampling while traveling around the burrow complex. Below ground, burrows offer critical refuge for terrestrial fauna by modulating the abiotic environment and creating a stable thermal microclimate (Hansell 1993; Meadows and Meadows 1991), especially in arid and semi-arid landscapes where conditions above ground can be severe (Whitford and Kay 1999; Wiens 1985). This combination of grazing and burrowing by ground squirrels within localized patches of disturbance can either create or destroy habitat for the terrestrial fauna residing within grasslands.

An increase in abundance of invertebrates on California ground squirrel colonies, particularly centipedes and ground beetles, may represent an important food resource that attracts other grassland species. Invertebrates are an important part of the diet for many grassland birds, including burrowing owls which are at times primarily insectivorous preying upon invertebrates that share the same burrow system (Columbe 1971; Earhart and Johnson 1970; Rich and Trentlage 1983). In fact, insectivorous birds were more abundant on colony than off-colony sites (Lenihan 2007a). Similarly invertebrates prefer prairie dog colonies due to characteristics of microhabitats, such as bare-ground and burrows (Koford 1958; Olson 1985). Movement of ground beetles were enhanced on prairie dog colonies, giving them increased access to resources and higher reproductive success there (Bangert and Slobodchikoff 2000).

Species that require vegetative cover such as many small mammals may be negatively affected by the activities of California ground squirrels. Accordingly, our results reveal a pattern of lower species richness, diversity, and abundance of small mammals on colonies. Small mammal populations varied significantly during the three years of our study. During wet years, vegetation grew higher and denser, increasing cover and producing more forbs as potential seed resources for small mammals, resulting in higher species richness, diversity, and abundance. Except for *P. maniculatus*, abundance of individual small mammal species was lower on colony than off-colony sites, perhaps due to each species' ecology in relation to habitat modifications made by California ground squirrels. *R. megalotis* prefers dense cover and builds grass nests above ground (Jameson and Peeters 1988) and was four times more common off-colony, where increased cover and seed likely provided food and protection. *M. californicus* was also more common at off-colony sites and was captured primarily during the wettest year when grass was densest. This species depends on adequate cover to move undetected along elaborate foraging runways, thus lack of cover and green vegetation for forage severely limits vole populations (Nowak 1991). The San Joaquin pocket mouse (*P. inornatus*) preferentially forages on forbs under the cover of shrubs (Jameson and Peeters 1988). Cover and forbs were both reduced on ground squirrel colonies, which could explain the higher abundance of pocket mice inhabiting off-colony sites. *M. musculus,* a non-native rodent uncommon in natural habitats (Brown 1985) was captured at only one study location where like most of the other small mammal species it was more common at the off-colony site.

Conversely, *P. maniculatus,* typically the most abundant small mammal in all areas they occupy (Nowak 1991), was the only species recorded at higher abundance on colonies. Prairie dog colonies were also inhabited by higher numbers of *P. maniculatus*

(Agnew et al. 1986; Johnson 2002; McCaffrey 2001; O'Meila et al. 1982). *P. maniculatus* may prefer disturbed areas on colonies in which vegetation is clipped and maintained by squirrels in a lower seral stage (Agnew et al. 1986) and where squirrel burrows can be used for shelter (Pers. Obs.).

Most grassland rodents in our study were less abundant on ground squirrel colonies, probably because they prefer dense vegetative cover and plentiful seed resources. Similarly, small mammal diversity, abundance, and richness were lower on prairie dog colonies, suggesting that prairie dogs reduce habitat quality for grassland rodents by decreasing cover and food resources, while increasing bare ground (Agnew et al. 1986; Brown and Heske 1990; Johnson 2002; McCaffrey 2001; O'Meila et al. 1982)

The number of carnivores observed per hour was over three times higher on colony sites compared to off-colony sites. Similarly, prairie dog colonies had 5.7 times the frequency of carnivores as off-colony areas (Krueger 1986). Moreover, carnivores were consistently observed at higher rates on colonies at every pair of sites. A wide variety of carnivores are known to prey on ground squirrels in our study area including American badger (*Taxidea taxus*), coyote (*Canis latrans*), the San Joaquin kit fox (*Vulpes macrotis mutica*), bobcat (*Lynx rufus*), mountain lion (*Felis concolor*), gray fox (*Urocyon cinereoargenteus*) and long-tailed weasel (*Mustela frenata*) (Evans and Holdenreid 1943; Fitch 1948; Kuenzi et al. 1998; Linsdale 1946; USFWS 1998). Every carnivore species we recorded, with the exception of the omnivorous striped skunk (*Mephitis mephitis*), are known California ground squirrel predators and were more frequently encountered on colonies compared to off-colony sites. The badger was detected only on colonies and never observed at off-colony sites. Badgers, like coyotes, were observed hunting on squirrel colonies where they frequently deposited scat on top of burrow mounds. Even the elusive bobcat was observed 1.5 times more often on colony sites. Coyotes were the most common carnivore observed and were recorded 2.8 times more often on squirrel colonies. California ground squirrels are an important component of coyote diets in our study area (Kuenzi et al. 1998) .

Snakes that predate upon ground squirrels, such as rattlesnakes and gopher snakes, were more abundant on colony sites. California ground squirrels comprise 69% of the diet for rattlesnakes and 44% for gopher snakes (Fitch 1948; Fitch and Bentley 1949). Conversely, common king snakes (*Lampropeltis getula*) that eat mostly lizards, other snakes, and eggs (Nussbaum et al. 1983; Stebbins 2003) were encountered equally at colony and off-colony sites. We often observed rattlesnakes hunting ground squirrels at burrow entrances, entering burrows, and digesting squirrel prey above-ground. We also observed multiple copulation events by rattlesnakes, suggesting that squirrel colonies may have been important as sites for reproduction. Further, rattlesnakes may depend on ground squirrel burrows for shelter, creating a complicated predator-prey relationship between the rattlesnake and California ground squirrel.

In addition to their importance as prey, ground squirrel colonies may attract predators and other mammals because of the availability of burrows. Carnivores such as the San Joaquin kit fox, coyote, and badger will commonly modify California ground squirrel burrows for their own dens (Morrell 1972; USFWS 1998). In addition, cottontail rabbits, a species not known to dig their own burrows (Lidicker 1989), were observed only on sites with squirrels where they were recorded at the burrow entrance and observed entering burrows. Above ground conditions in xeric grasslands can be severe and ground squirrel burrows provide a critical below ground microhabitat that serves as shelter for a variety of terrestrial fauna.

Prior to the introduction of domestic livestock by the Spanish in 1769, California's native perennial grasslands were grazed by abundant elk, pronghorn (*Antilocapra americana*), and deer, as well as ground squirrels (Heady et al. 1992). We found that ungulates were uncommon at all sites, but deer and elk were observed more often at colony sites, perhaps because of more nutritious forage. In the Great Plains, ungulates preferentially graze on prairie dog colonies because grazing by prairie dogs increases shoot nitrogen and digestibility of vegetation (Coppock et al. 1983; Detling and Whicker 1988; Krueger 1986) raising the possibility that ungulates would be associated with California ground squirrels. In contrast, wild pigs were observed only at one off-colony site.

Summary

California ground squirrels create patches of disturbance within the more uniform grassland matrix affecting the pattern of species diversity in grasslands. These patches feature less vegetative cover and more bare ground, with numerous mounds and burrows that attract a variety of terrestrial species including invertebrates, reptiles, carnivores, and ungulates, creating a complex web of opportunity for interactions between species. Comparatively, off-colony sites offer refuge for a different composition of species that utilize the less disturbed grassland matrix where denser cover offers another set of resources, particularly for small mammals, among others. In combination, colony and off-colony sites may increase overall beta diversity through patch dynamics.

The response of grassland organisms to ground squirrel presence varies. Habitat modifications result in positive benefits for species that prefer open habitats or require the refuge of a burrow system. On the other hand, species that prefer vegetative cover for protection from predators and ample plant food resources may avoid colonies. For example, ground-dwelling squirrels in general modify habitat patches to the detriment of more specialized grassland rodents. By reducing vegetation height and increasing bare ground, squirrels decrease the habitat value for most small mammal species. Alternatively, these modifications on colonies may increase habitat value for *P. maniculatus* and certain ground dwelling invertebrates, and these invertebrates may serve as prey that attracts grassland birds (Brown and Heske 1990; Lenihan 2007a). The concentration of California ground squirrels within colonies attracts a large suite of predators that consume as much as one-half of the annual production of ground squirrels (Fitch 1948). The California ground squirrel's role as prey for an array of terrestrial predators is a vitally important aspect of their ecological function in grasslands. In addition, many of the species that prey upon ground squirrels also utilize their burrows for shelter or nest sites, increasing the interactivity between squirrels and their terrestrial predators. Other terrestrial fauna such as ground-dwelling invertebrates, rabbits and deer mice may rely on burrows for shelter as well. Burrow complexes dug and maintained by California ground squirrels add a third dimension to grasslands offering refuge from above ground conditions. The multiple interactions between California ground squirrels and numerous other species indicates that ground squirrels, acting as both prey and an ecosystem engineer, are especially important members of the grassland community.

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Table 2.1: Non-volant terrestrial vertebrate species detected within the study area from July 2002- March 2005.

Common Name	*Scientific Name*	**Conservation Status**
Mammals		
San Joaquin kit fox *	*Vulpes macrotis mutica*	FE
Coyote	*Canis latrans*	
Striped Skunk	*Mephitis mephitis*	
American Badger *	*Taxidea taxus*	CSC
Mountain Lion	*Felis concolor*	
Bob cat	*Lynx rufus*	
Cattle	*Bos taurus*	
Feral Hog / Wild Boar	*Sus scrofa*	
Elk	*Cervus elaphus*	
Black-tailed Deer	*Odocoilius hemionus*	
California ground squirrel	*Spermophilus beecheyi*	
Pocket gopher	*Thomomys bottae*	
California pocket mouse	*Chaetodipus californicus*	
San Joaquin pocket mouse *	*Perognathus inornatus*	BLM-Sensitive
Deer mouse	*Peromyscus maniculatus*	
Western Harvest mouse	*Reithrodontomys megalotis*	
California meadow vole	*Microtus californicus*	
House mouse	*Mus musculus*	
Black-tailed Jackrabbit	*Lepus californicus*	
Desert cottontail	*Sylvilagus audubonii*	
Reptiles		
Western fence lizard	*Sceloperus occidentalis*	
Gilbert's skink	*Eumeces gilberti*	
California Legless lizard *	*Anniella pulchra pulchra*	CSC
Northern Alligator lizared	*Elgaria coerulea*	
Common Kingsnake	*Lampropeltis getula*	
Gopher snake	*Pituophis catenifer*	
Night snake	*Hysiglena torquata*	
Ring-necked snake	*Diadophis punctatus*	
Western Rattlesnake	*Crotalus viridis*	
Amphibians		
California Tiger Salamander *	*Ambystoma californiense*	FT, CSC
California Slender Salamander	*Batrachoseps attenuatus*	
Pacific Treefrog	*Hyla regilla*	
California red-legged frog *	*Rana draytonii*	FT, CSC

(*) Denotes species with federal or state designated conservation status.
(FE= federally endangered, FT= federally threatened, CSC= California species of concern, BLM/sensitive= Bureau of Land Management designated sensitive species)

Table 2.2: ANOVA values for comparison of small mammal species by status (colony vs. off-colony), geographical site, and year.

	STATUS	df=1, 3	**SITE**	df=3, 21	**YEAR**	df=2, 21
SPECIES	**F**	**p-value**	**F**	**p-value**	**F**	**p-value**
Peromyscus maniculatus	1.1	0.37	0.1	0.96	6.98	0.005*
Mus musculus	0.04	0.85	5.22	0.008*	2.62	0.09
Perognathus inornatus	0.42	0.56	6.94	0.002*	2.67	0.09
Microtus californicus	1.33	0.33	2.43	0.09	7.37	0.004*
		df=1, 24				df=2, 24
Reithrodontomys megalotis	5.92	0.023*	NA	NA	8.28	0.002*

(*) Denotes significant p-values less than 0.05. NA= no analysis available, see statistical methodology in text.

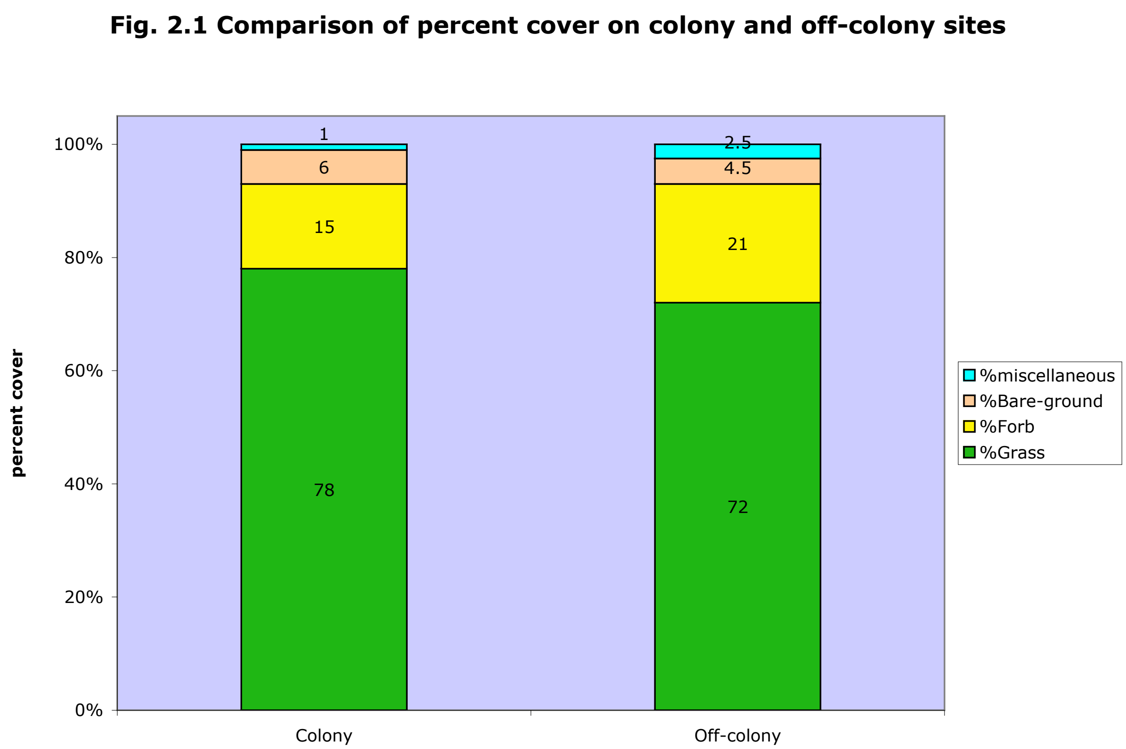

Figure 2.1: Comparison of percent cover on colony and off-colony site pairs by following characteristics: %forbs, %grass, %bare ground and %miscellaneous (includes moss, thatch, and cow manure); years combined.

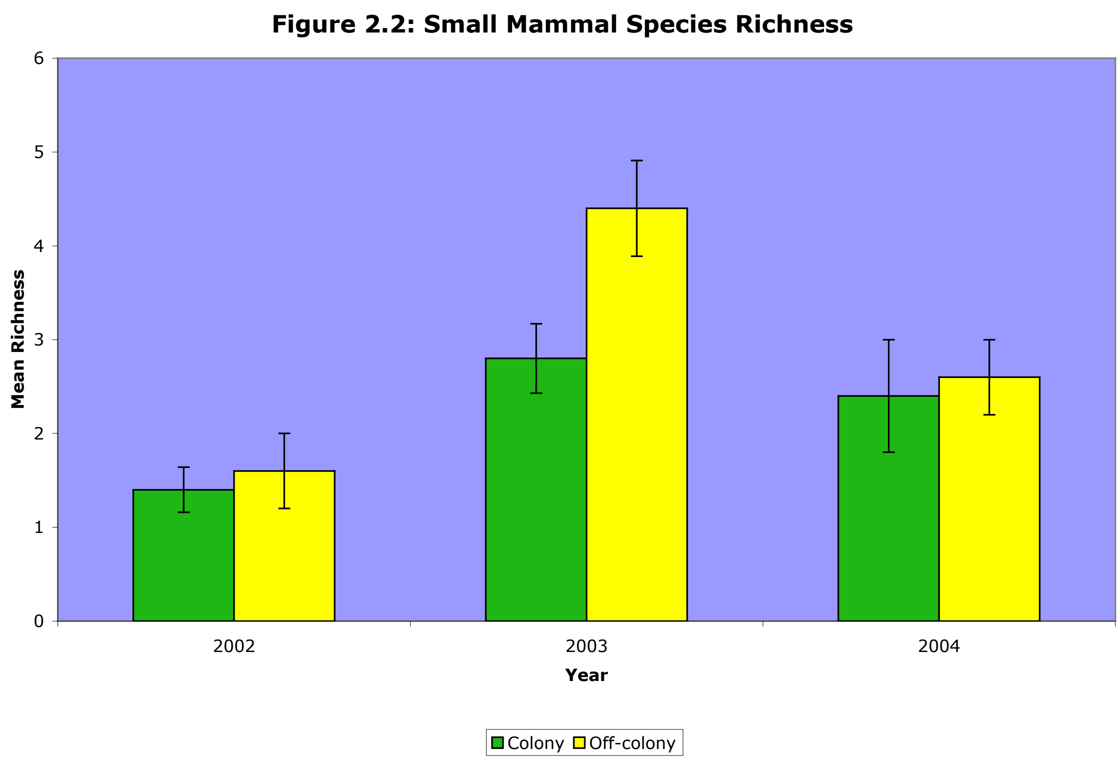

Figure 2.2: Small mammal species richness mean for each year of trapping on colony and off-colony sites (n=5 paired sites in each year). Bars represent mean (±) 1 SE.

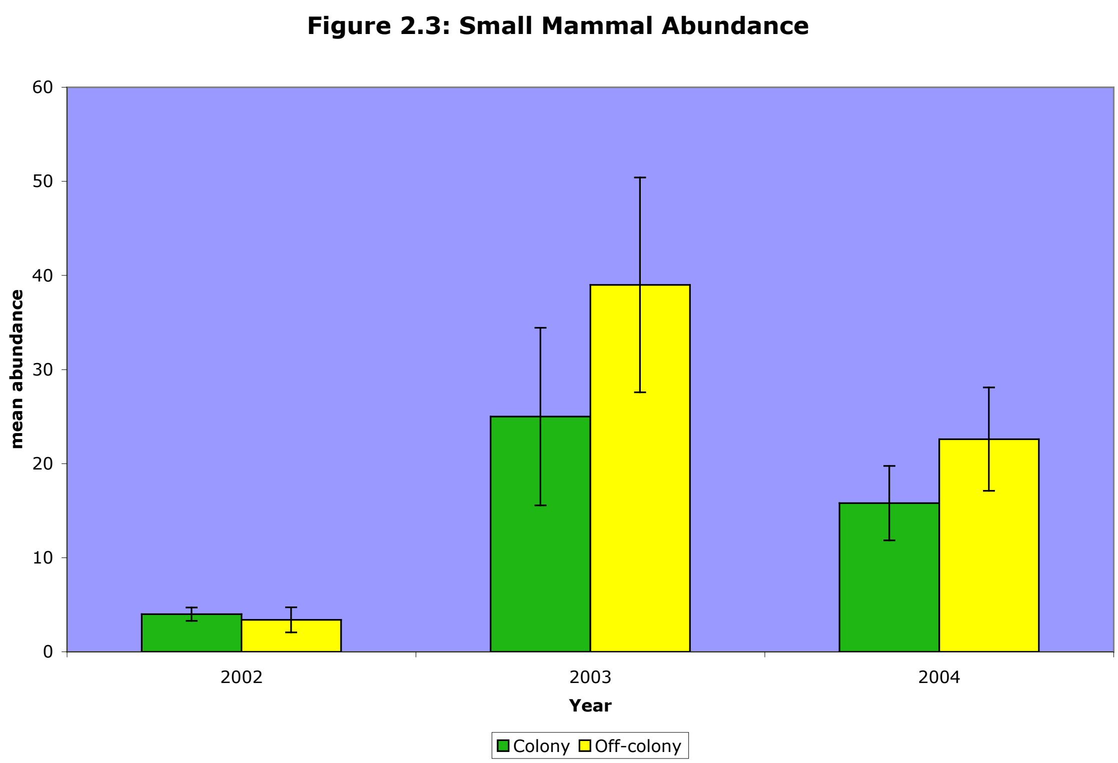

Figure 2.3: Small mammal mean abundance for each year of trapping on colony and off-colony sites (n=5 paired sites in each year). Bars represent mean (±) 1 SE.

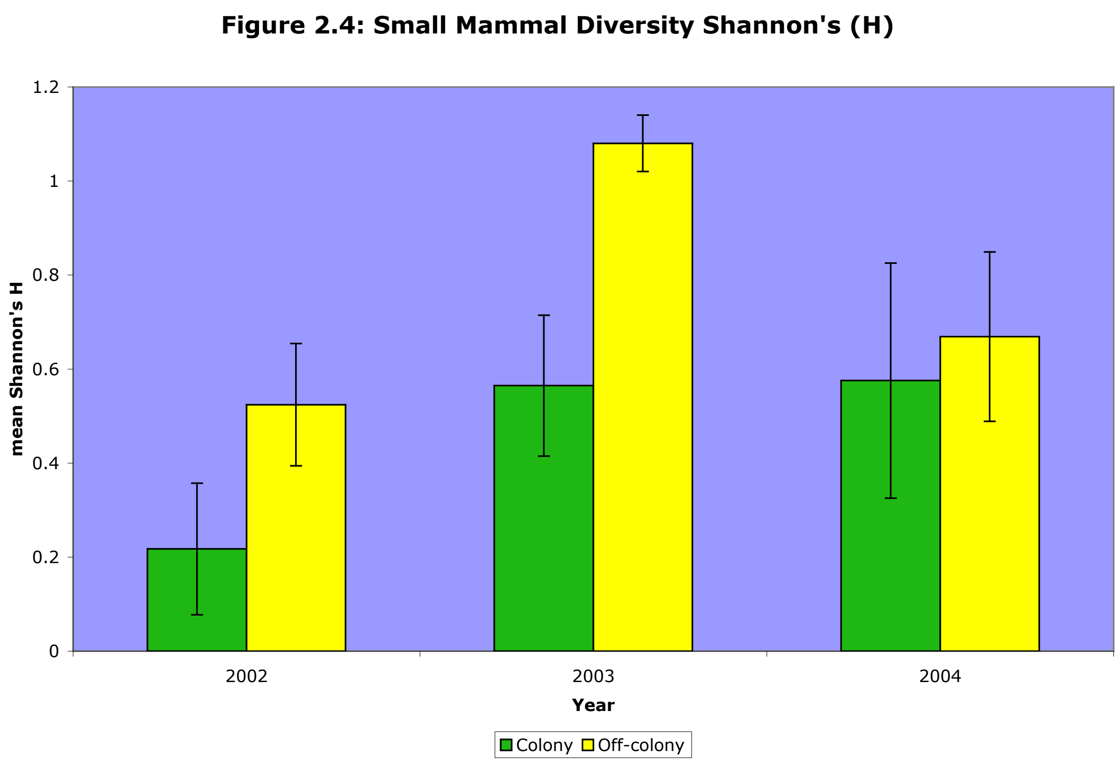

Figure 2.4: Small mammal species diversity (Shannon's H) means for each year of trapping on colony and off-colony sites (n=5 sites for each treatment in each year). Bars represent mean (±) 1 SE.

Figure 2.5: Small mammal species abundance

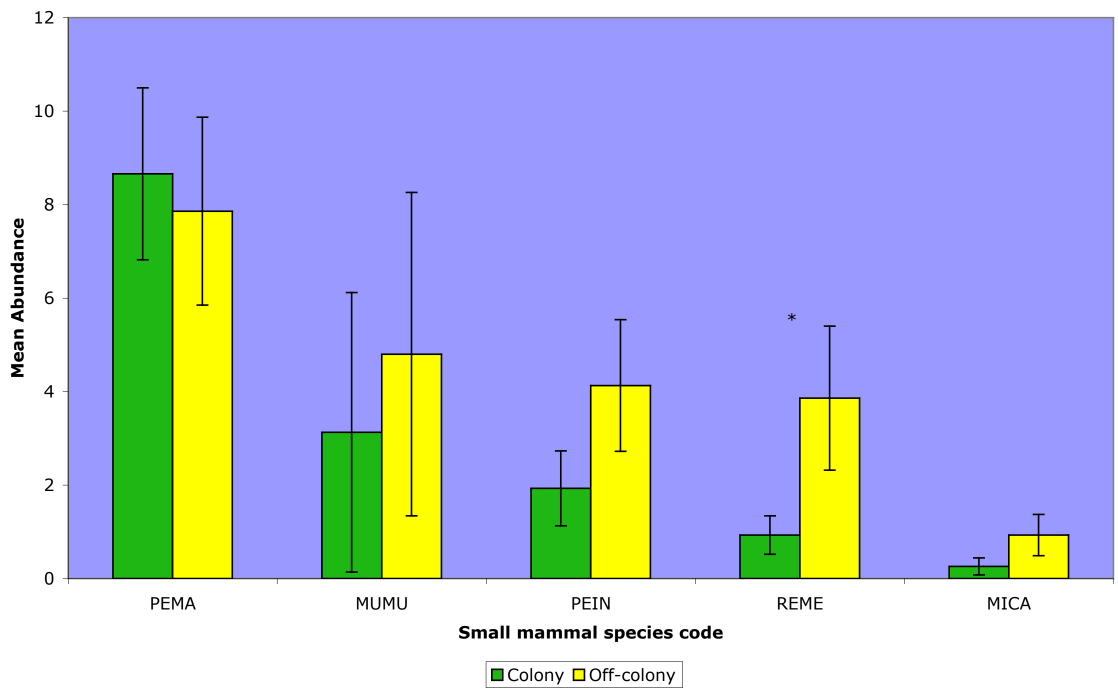

Figure 2.5: Mean abundance by small mammal species on colony and off colony sites (n=10 sites for each treatment with years combined). Bars represent mean (±) 1 SE. (species codes: *PEMA= Peromyscus maniculatus, MUMU=Mus musculus, PEIN=Perognathus inornatus, REME=Reithrodontomys megalotis, MICA=Microtus californicus).*

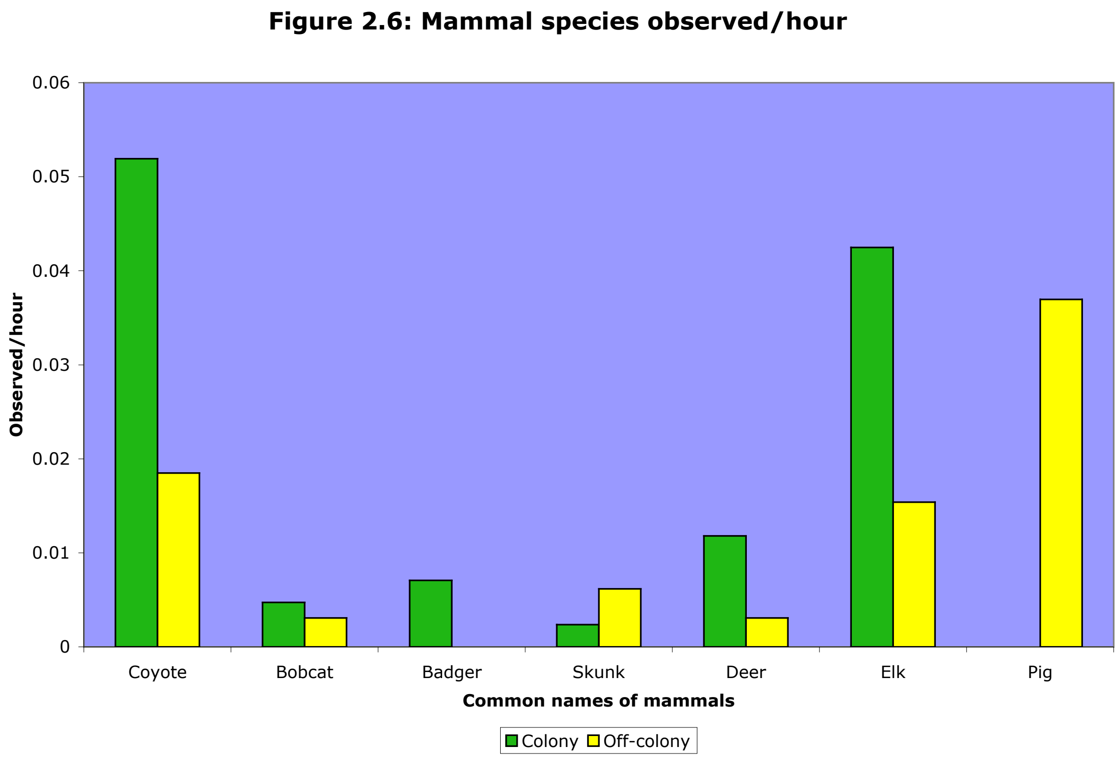

Figure 2.6: Comparison of recorded carnivore and ungulate species observed/ hour (years combined) on colony and off-colony sites.

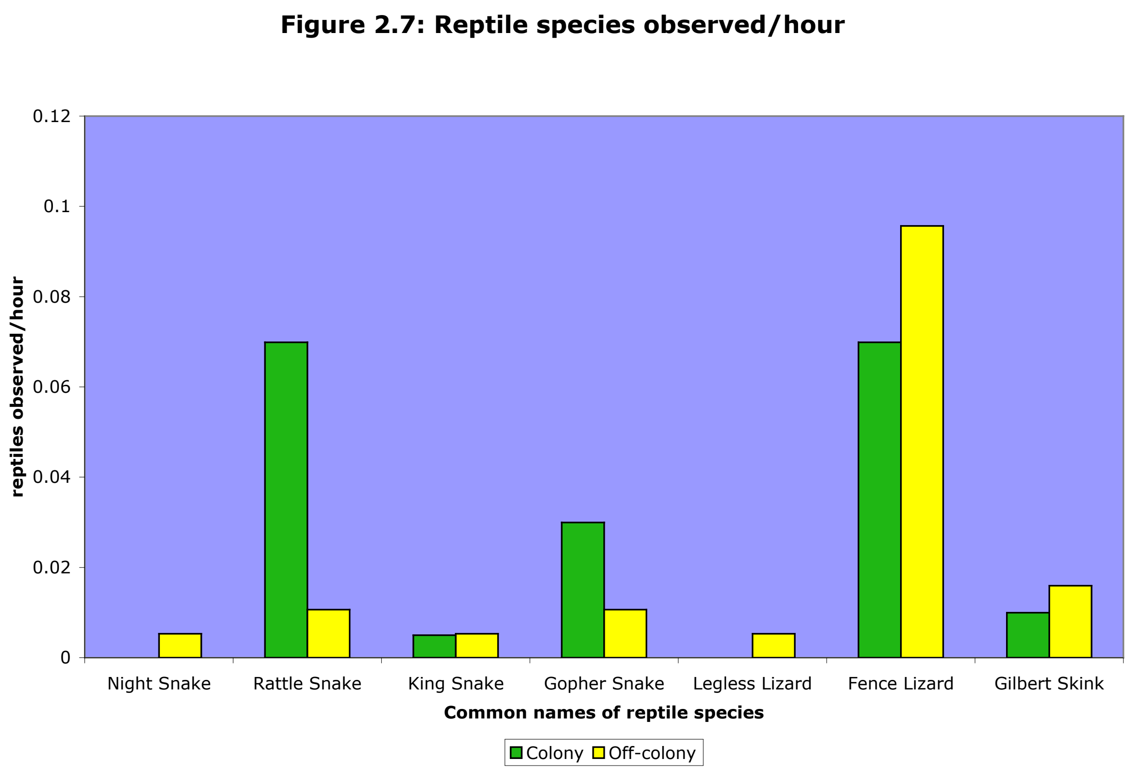

Figure 2.7: Comparison of recorded reptile species observed / hour (years combined) on colony and off-colony sites.

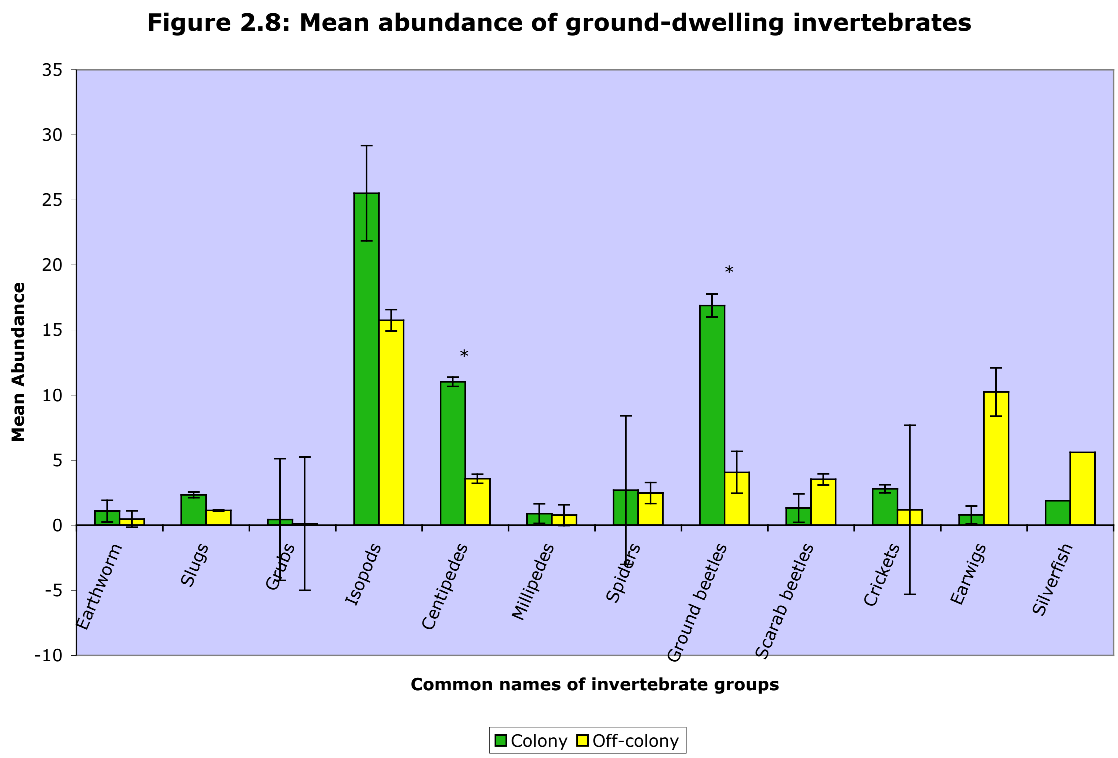

Figure 2.8: Mean invertebrate abundance by taxonomic group on colony and off colony sites Bars represent mean (±) 1 SE. Significant differences ($p<0.05$) are represented by an asterisk (*)

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Chapter 3: The Ecological Role of the California ground squirrel (*Spermophilus beecheyi*) in the grassland community: history, importance and suggestions for conservation

1. Introduction

Strongly interacting species play key regulatory roles in community structure and ecosystem processes, contributing to the maintenance of ecological and species diversity (Jones et al. 1994, Paine 1969, Power et al. 1996, Soule et al. 2005, Whitford and Kay 1999). Recognizing strong interactors can be problematic because functional roles for most species are unknown (Soule et al. 2003). For this reason a strongly interactive species is operationally defined by the consequences that result from its absence or rarity; structural or compositional modifications, decreases in species diversity, alterations in the import or export of nutrients, and loss of resilience to disturbance (Soule et al. 2003). Despite their capacity to significantly change system structure (Macarthur 1972, Paine 1980, Paine 2000), strongly interacting species are generally not the concern of environmental policy makers (Soule et al. 2003). Environmental laws, such as the Endangered Species Act, work to recover demographic viability of rare species, usually neglecting the complexity of species interactions that may be threatened well before species endangerment (Soule et al. 2003). By focusing on threatened species, the role of common species may go unnoticed until their population density falls below the threshold of ecological effectiveness, whereupon interactivity becomes functionally extinct (Soule et al. 2005). An ecological effective density is the population level that prevents undesired change in an ecological setting (Soule et al. 2005). Interactive species function over a range of abundance levels but attain community importance only above a threshold density (Kotliar 2000). Below this threshold or breakpoint density communities of organisms maintained by interactive species decay through cascading effects and ecological simplification in structure and function (Paine 2000). Identification and restoration of strongly interacting species rather than focus on single-species rescue efforts, can help conserve entire systems because of their profound effects on ecosystem structure and function (Rohlf 1991, Scott et al. 1987, Smith 1984). Recognizing the influence of strongly interacting species led to the suggestion that the primary mission of conservation should be to identify and restore the ecological effectiveness of strong interactors and that these species must not be permitted to fall below population density thresholds for ecological effectiveness, and their geographic ranges should be maintained as large as possible (Oksanen and Oksanen 2000, Schmitz et al. 2000, Soule et al. 2003, Soule et al. 2005, Soule and Terborgh 1999, Terborgh et al. 1999).

Grazing mammals are considered especially strong interactors within terrestrial ecosystems; particularly burrowing, herbivorous mammals that are remarkably similar in their effect on the structure of grassland communities and ecosystem processes world-wide (Davidson and Lightfoot 2006, Paine 2000, Whitford and Kay 1999). Some of these species, particularly rodents such as gophers (*Thomomys bottae, Geomys bursarius*), kangaroo rats (*Dipodomys spp*.), and black-tailed prairie dogs (*Cynomys ludovicianus*), are increasingly considered to be strong interactors because of their keystone effects, defined by their role in trophic interactions or as ecosystem engineers (Brown and Heske 1990, Davidson and Lightfoot 2006, Jones et al. 1994, Kotliar et al. 2006, Lawton and Jones 1995, Power et al. 1996). Keystone species exhibit disproportionately large control over the structure and functioning of ecosystems relative to their abundance (Power et al. 1996), and they are unique, performing roles not duplicated by other species or processes (Kotliar, 2000). Essentially, keystone species possess the highest interaction strength and are therefore the strongest interactors (Soule et al. 2005).

Ground dwelling squirrels influence the grassland ecosystem directly as prey, and indirectly through burrowing and foraging activities, suggesting a high level of interactivity (Kotliar et al. 2006, Lenihan 2007a, Lenihan 2007b). Squirrels of several species are locally abundant throughout the grasslands of western North America, where they are alternatively considered range-damaging pests or an important prey resource and ecosystem engineer (Davidson and Lightfoot 2006, Marsh 1998). The California ground squirrel (*Spermophilus beecheyi*) is common in grassland communities in low rolling hills and valleys extending from the coastal bluffs of the Pacific Ocean to the foothills of the Sierra Nevada. Previous work has focused on behavior (Boellstorff and Owings 1995, Owings et al. 1977) and conflicts with humans (Marsh 1994), and surprisingly little is known about the ecological role of this species in the grassland community. In contrast, many studies have examined the functional importance of the black-tailed prairie dog, an analogous species in prairie grasslands (*see* Kotliar, 1999). The burrowing and grazing activities of prairie dogs augment primary productivity, species densities and diversity, soil structure, and chemistry (Detling and Whicker 1988, Reading et al. 1989, Sieg 1988), creating a landscape mosaic that promotes a unique species composition and thus overall grassland diversity (Kotliar et al. 1999). Furthermore, prairie dogs serve as important prey for a variety of predators (Hoogland 2006). The decline of prairie dogs through shooting and poisoning has been linked to the near extinction of the black-footed ferret (*Mustela nigripes)* and the decline of several species recently proposed for listing under the federal Endangered Species Act including the swift fox (*Vulpes velox*), mountain plover (*Charadrius montanus*), burrowing owl (*Athene cunicularia*), and ferruginous hawk (*Buteo regalis*) (Miller et al., 2000; Kotliar, 2006). Prairie dogs are widely recognized as a strong interactor and even a "keystone species" throughout Great Plains grasslands (Miller et al., 2000; Kotliar, 1999, 2006). Because of the functional similarities between prairie dogs and California ground squirrels, results from prairie dog studies may provide a model for predicting the effects of California ground squirrel activities on grassland communities.

The California ground squirrel may similarly influence the structure, function, and species composition of Pacific coast grasslands. Previously, interest in the effect of California ground squirrels on grasslands was generally limited to concerns over range degradation, competition with domestic livestock, and burrowing damage (Berentsen and Salmon 2001, Fitch 1947, Howard et al. 1959, Marsh 1998). However, a small but growing body of information is available on trophic relations of California ground squirrels, as well as their possible role as an ecosystem engineer. Our objective is to review the available literature on California ground squirrels to determine if it is a “strongly interactive species” that plays a functionally important role for the conservation of wildlife in grassland landscapes. We begin by summarizing the historical ecology and natural history of the California ground squirrel. Next, we review the evidence for the California ground squirrel's capacity to influence the ecological structure, function, and composition of grasslands via trophic interactions and ecosystem engineering activity. Finally, using guidelines to determine interactivity, we assess the California ground squirrel's interactive role and its relationship to grassland diversity, species composition and conservation.

2. Background

The California ground squirrel (Fig. 3.1) is in the order Rodentia, subtribe Spermophilina (Hafner 1984), the same subtribe as the black-tailed prairie dog, which is similarly large-bodied and highly visible because of its diurnal habits and propensity to live at high concentrations within colonies in open habitat types. California ground squirrels were historically abundant throughout California's original prairie, an ecosystem that has largely disappeared, with less than 1% remaining today (Kreissman 1991 1995). Early accounts remarked on the abundance of California ground squirrels, "*We found the whole country to be a warren of a strange kind of conie* (ground squirrel)" (voyage of Sir Francis Drake, 1579), and their importance to native American Indians, "*the people eat their bodies and make great account of their skins, for their kings holidays coats are made of them*" (Jacobsen). Indeed, California ground squirrels were an important resource of skins and meat for Native Americans whose diet consisted mostly of small game and plant material (Wagner 1989).

By the late 1800's, a century after the introduction of livestock and exotic annual grasses by the Spanish in 1769, California's prairie vegetation dominated by native perennial bunchgrasses and a variety of forbs was essentially replaced by a non-native annual grassland (Heady et al. 1992). Much of the native grassland wildlife, particularly carnivores and ungulates, were decimated by the settlement of California (Pavlik et al. 1995, Storer and Tevis 1996, Wagner 1989). However, California ground squirrels persisted and perhaps flourished under anthropogenic land uses where novel food resources, heavily grazed grassland, and release from predation aided the ground squirrel population to a point where they were perceived as a nuisance (Jacobsen 1918, Kellogg 1931). As one observer commented, "*The swarming abundance of the California ground squirrel on foothill slopes and in fertile valley bottoms equals the congregations of prairie dogs in their most populous districts"* (Nelson 1918).

The outbreak of plague, confirmed in California ground squirrels by 1908, and shortly thereafter the war time demand for California crops and meat, crystallized public opinion against this species as "the most disliked mammal in California" (Dixon 1917). Consequently, control measures became a priority in the early 1900s to reduce crop damage, erosion of levees, risk of plague, and competition for cattle forage (Appendix 3.1). Methods of elimination became increasingly sophisticated with the advent of modern chemical poisons and innovative trap and delivery systems. Nearly 100 years later, eradication campaigns have poisoned California ground squirrels by foot, horse, vehicles, and aircraft using a variety of chemical toxicants (zinc phosphide, compound 1080, strychnine), anticoagulants (Warfarin, fumarin, Pival, diphacinone, chlordiphacinone), and burrow fumigants (aluminum phosphide, carbon disulphide, methylbromide, gas cartridges) (Clark 1986, Loredo-Prendeville et al. 1994, Marsh 1987).

Today distribution and density of squirrels is variable and may depend not only on habitat suitability, but also past history of pest management and current levels of control that vary with the tolerance of the landowner (Fitch 1947, Linsdale 1946, Marsh 1998). Density estimates range widely, from 11 to 39 squirrels/ha (Dobson 1981, Evans and Holdenreid 1943, Fitch 1947, Fitch 1948, Howard et al. 1959, Lenihan 2007b, Loredo-Prendeville et al. 1994), while historical estimates were higher, 50-190/ha (Grinnell and Dixon 1918). California ground squirrels typically live in colonies, defined as groups of individuals living in close association at aggregations of burrow entrances (Holekamp and Nunes 1989). In areas of high abundance contiguous colonies cover the grassland landscape and are recognizable at a distance by the large mounds which form as soil is deposited at the burrow entrance, and by the pattern of well-used foraging trails that connect the activities of colony residents (Grinnell and Dixon 1918, Merriam 1910). The California ground squirrel social system consists of a single-family female kin cluster with male breeding territoriality (Boellstorff et al. 1994). Although males defend breeding territories encompassing multiple females, females mate not only with adjacent males but will travel beyond their home range to mate with an average of 6.7 males in a promiscuous mating system termed “overlap promiscuity” (Boellstorff et al. 1994, Fitch 1948). Breeding occurs in January and February, and females wean one litter each year during April or May. Litters are large, compared to other sciurids, averaging 7.5 pups (Blumstein and Armitage 1998). Almost half of the juveniles disperse, primarily males (Dobson 1982), whereas most juvenile females are philopatric and settle on territories adjacent to their mothers (Boellstorff and Owings 1995).

Figure 3.2 provides a generalized schematic of above ground activity typical of California ground squirrel populations in the greater San Francisco Bay Region. The pattern of seasonal surface activity varies throughout the species' range, depending on differences in season with increasing latitude (Dobson and Davis 1986). Hibernation occurs during winter where heavy snowfall accumulates, but a proportion of the low elevation populations remain above ground throughout the year. Juveniles remain above ground during their first year of life (Fitch 1948). Adults estivate during the hot summer and fall, and may hibernate during a portion of the rainy season. Females remain above ground longer into the summer with the young of the year but emerge later than males in winter to mate (Holekamp and Nunes 1989). Annual mortality of adults is slightly higher for males than females, while adult survivorship from one breeding season to the next ranges 36-40% (Dobson 1982, Evans and Holdenreid 1943, Fitch 1948).

3. Evidence of Interactivity

Trophic interactions

Individual species can play key regulatory roles in community structure and ecosystem processes, interacting either directly through trophic level effects or indirectly at the level of the ecosystem (Jones et al. 1994, Paine 1969, Power et al. 1996, Whitford and Kay 1999). Predator-prey dynamics directly affect species distribution and abundance within a community of interacting animals (Connell and Slatyer, MacMahon et al. 1978). Ground dwelling squirrels often constitute an abundant food resource for a variety of aerial and terrestrial predators, and hence have the potential for playing a central trophic role. A well studied example is the black-tailed prairie dog, generally considered a keystone species, due in part to its highly interactive role as prey in trophic interactions with predators (Davidson and Lightfoot 2006, Kotliar et al. 2006, Miller et al. 2000). The precipitous decline of prairie dogs within the Great Plains ecosystem has contributed to the population reduction of several predators, including the near extinction of the black-footed ferret (Clark, Miller et al. 1996).

California ground squirrels serve as prey for a wide variety of predators, demonstrating the potential for a keystone role similar to that of the black-tailed prairie dog. California ground squirrels are the primary prey item for the golden eagle (*Aquila chrysaetos*), red-tailed hawk (*Buteo jamaicensis*), coyote (*Canis latrans*), and western rattlesnake (*Crotalus viridis*) (Biardi et al. 2006, Fitch 1948, Hunt et al. 1999, Kuenzi et al. 1998, Linsdale 1946). To a lesser degree ground squirrels are important prey for the prairie falcon (*Falco mexicanus*), San Joaquin kit fox (*Vulpes macrotis mutica*), gray fox (*Urocyon cinereoargenteus)*, gopher snake (*Pituophis catenifer*), American badger (*Taxidea taxus*), bobcat (*Lynx rufus*), and long-tailed weasel (*Mustela frenata)*(1998, Evans and Holdenreid 1943, Fitch 1948, Grinnell and Dixon 1918, Kuenzi et al. 1998). Certain characteristics of California ground squirrels expand their value and vulnerability as a prey resource; they are common, diurnal, and locally concentrated across the landscape within colonies, particularly on rangelands where cattle grazing increases habitat suitability for squirrels, which prefer more open vegetation (Evans and Holdenreid 1943, Fehmi et al. 2005, Fitch and Bentley 1949, Howard et al. 1959, Linsdale 1946, Marsh 1998). California ground squirrels are prolific and female fecundity is high (Blumstein and Armitage 1998). Juveniles are especially vulnerable to predators, with over half of the young of the year taken as prey annually (Fitch 1948).

Finally, California ground squirrels are large compared to other sympatric grassland rodents and hence compose a major portion of the biomass of predator diets (Fitch 1948, Hunt 2002, Kuenzi et al. 1998, Linsdale 1946).

The California ground squirrel and its predators share a long evolutionary history, with fossil evidence of sympatry between prey and predators dating back to at least the Pleistocene (Kurten and Anderson 1980, Lundelius et al. 1983, Miller 1912). As a result, the California ground squirrel has evolved complex behavioral and physiological tactics for avoiding predation. Colonial life in ground-dwelling squirrels may have evolved as a defense against predation (Hoogland 2006, King 1984). Highly vigilant, California ground squirrels vocalize in alarm to attract attention to predators and communicate that threat to kin, while also providing information to the larger colony (Hanson and Coss 1997, Owings 2002). This sentinel role may have an interactive effect warning other prey species (Schoenherr 1992) such as black-tailed jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*) that react to squirrel alarm calls by fleeing into squirrel burrows (Smallwood et al., 2001; Lenihan, pers.obs.). This interspecific warning may benefit burrowing owls (*Athene cunnicularia*) as well; the eradication of ground dwelling squirrels results in more predation mortality on owls at inactive colony sites versus active colony sites (Butts 1973, Desmond et al. 2000, Sidle et al. 2001).

The three types of predators that prey on California ground squirrels, raptors, carnivores, and snakes, differ in hunting techniques and hence in the response elicited from squirrels. Raptors attack swiftly, to which squirrels react immediately by emitting a single-note alarm vocalization while escaping into the nearest burrow (Leger et al. 1984, MacWhirter 1992, Owings and Hennessey 1984, Sherman 1985). Carnivores approach more slowly, giving squirrels time to retreat to the burrow entrance where they produce multi-note vocalizations, sometimes calling continuously, only retreating below-ground when threatened by the approach of the carnivore (Leger et al. 1984, Owings 2002). Snakes, especially rattlesnakes, elicit a different response. Snakes are approached and assessed by harassment as to their readiness to strike, especially by females with pups, which are vulnerable to snakes that may linger around burrows for days (Hersek and Owings 1994, Owings 2002). Squirrels use a complex set of behavioral and physiological traits to assess snake dangerousness by first slowly inspecting and then taunting the snake to induce rattling (Owings and Coss 1977), which provides information that squirrels use to auditorally discriminate the size and temperature of the snake revealing readiness to strike (Swaisgood et al. 1999). Adult squirrels can risk physical confrontations with snakes because they possess blood proteins that confer resistance to venom, but pups succumb to bites because they cannot neutralize as much venom as adults (Biardi et al. 2006, Poran and Coss 1990).

The importance of California ground squirrels to grassland predators is indicated by data on predator diet and distribution. Raptors responded to availability of California ground squirrels by focusing their hunting efforts on squirrel colonies; golden eagles hunted colony sites 20 times more frequently than nearby off-colony sites, and red-tailed hawks and prairie falcons hunted colony sites three times more frequently than off-colony sites (Lenihan 2007a). The world's highest nesting density of golden eagles is in the northern Diablo Range east of San Francisco Bay, and California ground squirrels are their primary prey resource, representing 69% of prey numbers and 64% of prey biomass (Estep and Sculley 1989, Hunt et al. 1995). Similarly, both red-tailed hawks and prairie falcons favor ground squirrels as prey, particularly during the breeding season when nutritional demands are greatest and juvenile squirrels are widely available (Fitch 1948, Kuenzi et al. 1998, Steenhof 1998). Prey fluctuations are known to influence reproductive success in raptors (Newton 1979) particularly that of golden eagles (Brown and Watson 1964, Tjenberg 1983, Watson et al. 1992). Like raptors, carnivore distribution is affected by ground squirrel availability, with significantly higher carnivore visitation rates on squirrel colonies compared to off-colony sites (Lenihan 2007a). The frequency of California ground squirrels in the diet of some carnivores is substantial, reported at 31-55% for coyotes, 25-38% for gray foxes (ranked second after voles), and 35% for San Joaquin kit fox (Fitch 1948, Kuenzi et al. 1998, Logan et al. 1992). A major portion of the western rattlesnake's diet, 69% by weight, consists of California ground squirrel prey (Fitch 1948, Fitch and Bentley).Considering the high level of interactivity between rattlesnakes and California ground squirrels, it is not surprising that western rattlesnakes were seven times more common on colony versus off-colony sites (Lenihan 2007b). Gopher snakes, whose diet can be as much as 44% ground squirrels, were three times more common on colony sites; in contrast the California king snake, not known to hunt squirrels, shows no preference for colony over off-colony sites (Fitch 1948, Fitch and Bentley, Lenihan 2007b).

Finally, within the grassland community California ground squirrels act not only as prey but also as predator. Although California ground squirrels primarily forage on vegetation, they are known to supplement their diet by feeding on bird and reptile eggs, as well as nestlings, gophers, moles, mice, lizards, juvenile rabbits, juvenile ground squirrels, arthropods, and carrion (Callahan 1993, Lidicker 1989, Schitoskey and Woodmansee 1978).

At the level of the community, the California ground squirrel influences predator-prey dynamics by interacting in multiple ways. They primarily serve as a prey resource that focuses the hunting effort of grassland predators resulting in a local increase in predator richness and abundance (Lenihan, 2007 a, b), and likely having an important influence on predator survival and reproduction. However, squirrels also may act as a sentinel species that warns other prey species, and even as a predator.

Ecosystem Engineer

In addition to their important trophic role as a prey resource, California ground squirrels may interact in a non-trophic manner by influencing grassland resources through their activities. An organism that physically changes the availability of resources that can then be utilized by other taxa is considered an "ecosystem engineer" (Jones et al.). Ground-dwelling squirrels forage above ground and tunnel below ground in a manner that restructures grassland resources (Davidson and Lightfoot 2006, Kotliar et al. 2006, Whitford and Kay 1999). A squirrel's mound and burrow system is an energetically expensive resource providing a complex structure in an otherwise simplified habitat. Burrows are maintained by resident squirrels, becoming relatively permanent structures inherited by subsequent generations and providing protection from the environment, defense from predators, places to store food, and nest sites for reproduction and rearing of young (Boellstorff and Owings 1995, King 1984).

The act of burrowing and the resultant burrow and entrance mound structure impacts grassland resources in remarkably similar ways across taxa and geographic locations by increasing soil fertility through turnover, increasing macroporosity of soil to allow deep penetration of precipitation, enhancing microbial activity, modifying local topography, and increasing the incorporation of organic materials into the soil (Hawkins, Meadows and Meadows 1991, Munn 1993, Whitford and Kay 1999). Moreover, selective grazing along with soil mixing, moisture, and the addition of fecal pellets and waste seed on burrow mounds can cultivate micro-plant communities that become favorable habitat for vertebrate, invertebrate and microbial symbionts (Hawkins 1996, Laundre 1998, Meadows and Meadows 1991, Schooley et al. 2000, Whitford and Kay 1999). Research on prairie dog and kangaroo rat mounds revealed differences in plant species composition, structure, and diversity that differentiate mounds as distinct patches of habitat (Davidson and Lightfoot 2006). Below ground, within the burrow network, tunnels provide a third dimension of available habitat structure in otherwise two-dimensional grassland. Especially in arid and semi-arid landscapes where conditions above ground can be severe (Wiens 1985 1999), burrows offer refuge for a variety of species, modulating the abiotic environment by creating a stable thermal microclimate (Meadows and Meadows 1991).

California ground squirrel colonies are patches of habitat that are structurally different from surrounding grassland without squirrels. While foraging, California ground squirrels create trails, trample vegetation, dig for buried seeds or roots, and decrease vegetative cover through herbivory (Evans and Holdenreid 1943, Howard et al. 1959). The effect of this foraging activity is to reduce plant diversity and distinguish colony sites as patches of grassland with more bare ground, shorter vegetation, lower standing crop, less forbs, and more grass than grasslands without ground squirrels (Lenihan 2007b). Burrowing rodents like the California ground squirrel are important generators of disturbance and pattern (Hansell 1993, Huntley and Inouye 1988, Meadows and Meadows 1991, Whicker and Detling 1988), especially when burrowing activities encompass large areas over longer time scales (Whitford and Kay 1999). California ground squirrel burrow systems can be elaborate, with 6-20 separate entrances and tunnels averaging 11m in length (maximum, 42 m), resulting in a burrow density of 105-237 entrances/ha (Fitch 1947, Grinnell and Dixon 1918, Lenihan 2007b, Murie and Michener 1984, Wilson and Ruff 1999). The mound effect is easily detected during spring when plant growth on California ground squirrel mounds is more vigorous and often contains species that differ from the surrounding matrix (Grinnell and Dixon, 1918; pers. obs.). California grasslands experience a long hot dry season, and California ground squirrel burrows may offer critical refuge from surface extremes (Davis 1976, Dobson and Davis 1986).

By modifying the grassland ecosystem both above and below ground, California ground squirrels may change the availability of resources to which co-occurring species respond, resulting in a different species composition on colony versus off-colony sites. By comparing sites with and without the key species, natural experiments can identify an ecosystem engineer through its' impact on ecosystem structure, function and biodiversity (Boogert et al. 2006). Comparison of the grassland fauna on California ground squirrel colonies and nearby off-colony sites revealed numerous differences (Appendix 3.2). Colonies support more ground dwelling invertebrates, particularly ground beetles and centipedes (Lenihan, 2007b); a similar difference was found on and off prairie dog colonies (Bangert and Slobodchikoff 2000, Koford 1958, Olson 1985). These invertebrates may provide food for two endangered amphibians, the California tiger salamander (*Ambystoma californiense*) and the California red-legged frog (*Rana draytonii*), that seek refuge within squirrel burrows during the dry season (Jennings and Hayes 1994, Stebbins 2003). Both species utilize burrows as important habitat initially during emigration from breeding ponds, while tiger salamanders continue to use burrows as permanent shelter, cohabitating in a commensal relationship with the California ground squirrel (Jennings and Hayes 1994, Loredo et al. 1996). Lagomorphs utilize California ground squirrel burrows as refuge sites (Lidicker 1989, Smallwood et al. 2001), and comparison of squirrel colonies with off-colony sites revealed desert cottontails using colonies but absent on off-colony sites (Lenihan 2007b). Carnivores such as the coyote, American badger, and San Joaquin kit fox commonly usurp and modify California ground squirrel burrows for their own dens (Schoenheff, 1992; USFWS, 1998), and rattlesnakes use squirrel burrows for shelter and reproduction (Hersek and Owings 1994, Stebbins 2003). Burrowing owls are a widely distributed species that is closely associated with burrowing mammals, which not only provide burrows but also modify habitat in ways that facilitate owl survival and reproduction (Haug et al. 1993, Machicote et al. 2004). Because these owls rarely dig their own burrows they depend on other burrowing mammals for nest sites, and burrow availability may limit owl abundance (Desmond et al. 2000, Thomsen 1971, Zarn 1974). Consistent with this pattern, research on California ground squirrels found that burrowing owls bred on squirrel colonies but were absent from off-colony sites (Lenihan 2007a).

Above ground activities of California ground squirrels alter habitat structure by creating patches characterized by more bare ground and shorter vegetation, as well as a shift from forbs to grasses (Lenihan 2007b), potentially affecting grassland birds. The physical structure of a habitat can provide birds with indirect cues to potential resource availability (Wiens, 1969); some grassland birds prefer early seral stage habitat (Vickery 1996) and respond positively to the habitat modifications of ecosystem engineers like the prairie dog and the kangaroo rat (Brown and Heske 1990, Smith and Lomolino 2004). Comparison of bird communities on California ground squirrel colonies and nearby off-colony sites revealed a greater species richness, diversity, and total abundance of birds on squirrel colonies, indicating that colony sites offer enhanced resources for birds (Lenihan 2007a). Open grassland habitat increases the availability of seed and invertebrate prey (Brown and Heske 1990, Janes). Compared to off-colony sites, ground squirrel colonies attracted a higher abundance of birds that forage by gleaning from the ground (Lenihan 2007a). Active squirrel colonies also attract smaller prey species that provide prey for raptors (Agnew et al. 1986, Lenihan 2007a, O'Meilia et al. 1982). Hence, increased raptor activity at squirrel colonies could result not only from availability of squirrels as prey, but also because of other prey that benefit from squirrel-modified habitat (Lenihan 2007a).

Alternatively, above ground activities by California ground squirrels could reduce habitat quality for those species that require dense grassland vegetation as foraging or cover. For example, grasshopper sparrows (Ammodramus savannarum), which prefer dense un-grazed grasslands for nesting (Saab et al. 1995), were more common at off-colony sites than colony sites during spring (Lenihan 2007a). Similarly, small mammal diversity, species richness, and abundance were lower on colony sites (Lenihan 2007b).

Only two predators were more common away from colonies; the white-tailed kite (Elanus leucurus), a raptor that forages in dense grasslands where California voles (Microtus californicus) are more abundant (Ehrlich et al. 1988), and the striped skunk(Mephitis mephitis), an omnivore that feeds on invertebrates, small vertebrates and plant material (Jameson and Peeters 1988).

4. Discussion

California ground squirrels play a central functional role within the grassland landscape in two basic ways (Fig. 3.3). First, ground squirrels perform an important trophic role in predator-prey dynamics by serving as prey for a wide variety of predators, they are predators themselves, and they may influence predation on other species through their alarm calls. Second, ground squirrels behave as ecosystem engineers, changing grassland resources through their activities that affect numerous other species. In combination these roles affect both grassland community structure and function, suggesting that this species warrants recognition as a strongly interactive species. Assessment of interactivity is based on changes to ecosystem structure, function, and composition that occur when a particular species is severely reduced or extirpated. Variation in interaction strength is measured by the removal of an interactive species and then comparing the response at sites with and without that organism (Menge et al. 1994), similar to the paired on and off colony comparisons performed in several studies of black-tailed prairie dogs (*see* Kotliar 1999, 2006), as well as one study of the California ground squirrel (Lenihan, 2007a,b). Guidelines for assessing interactivity stress the importance of dependency, species diversity, unique features, low functional redundancy and effects on ecosystem energy flow and disturbance (Soule et al. 2005) (Table 3.1). Increasing interaction strength increases dependency within a system (Menge et al. 1994, Soule et al. 2003). Fitness of a dependent species increases when a strongly interacting species is present (Kotliar et al. 1999). Four criteria determine dependence; meeting two or more of these criteria provides fairly convincing evidence for dependence on an interactive species (Table 3.2) (Kotliar et al. 1999). Strong interactors are associated with an assemblage of dependent species. Both the prairie dog and the California ground squirrel are associated with a distinct assemblage of species indicating the existence of dependency on these interactive squirrels (Table 3.2). Many of these dependent species are increasingly rare. The precipitous decline of prairie dogs has led to the near extinction of the black-footed ferret and the decline of the swift fox, mountain plover and ferruginous hawk, plus many more common species (Kotliar et al. 2006, Miller et al. 2000). Likewise, several species of conservation concern are associated with the California ground squirrel, the burrowing owl, golden eagle, prairie falcon, California tiger salamander, California red-legged frog, and San Joaquin kit fox (Thomsen 1971, Hunt 2002, Bell pers.comm. Loredo-Prendeville et al. 1994, Jennings and Hayes 1994, USFWS 1998). Further, the role of California ground squirrels as prey, as well as their role as ecosystem engineer, are functions performed only partly, if at all, by other species. This indicates a low functional redundancy, a key component for dependency (Kotliar 2000).

Guidelines used for assessing interactivity also describe the ecosystem consequences of losing a strongly interactive species (Table 3.1). For example, the loss of burrowing and foraging activities of California ground squirrels may influence productivity, nutrient cycling, and soil mixing (Meadows and Meadows 1991, Whicker and Detling 1988, Whitford and Kay 1999). California ground squirrel activities could increase resilience to abiotic disturbance. For example, squirrels reduce vegetation height and standing crop, potentially decreasing fire danger, and moisture content is higher in burrows, which may translate to crucial survival refuge for various species in time of drought (Kotliar et al. 2006, Meadows and Meadows 1991). Complex, long underground tunnels provide conduits for water acting as drains in floods (Reichman and Seabloom 2002, Whitford and Kay 1999). California ground squirrels may further add resilience to the ecosystem by mimicking aspects of the historic native prairie disturbance regime; California no longer supports large herds of free-ranging herbivorous ungulates, the extinct California grizzly bear no longer digs up large patches of prairie vegetation in search of bulbs, roots and larvae, and fire is largely suppressed throughout the non-native annual grasslands.

5. Conservation Implications

The available evidence supports the designation of the California ground squirrel as a strongly interactive species. Anecdotal evidence suggests this role may be functionally significant over multiple scales and covering a range of habitat conditions (Davidson and Lightfoot 2006). Even small, isolated California ground squirrel colonies found within urban areas on ruderal fragments may provide viable habitat for breeding burrowing owls, foraging red tailed hawks, and on occasion a hunting golden eagle {Trulio & Ganns; Feeney, pers. obs.}, while colonies surrounding stock ponds provide refuge for California tiger salamander and California red-legged frog (Loredo-Prendeville et al., 1994; Jennings and Hayes, 1994; DiDonato, 2006; Bobzien, pers.comm.). Intact grasslands within parks or ranches support larger squirrel populations that are associated with the full complement of grassland species, including an assemblage of increasingly rare animals targeted for conservation (Lenihan, 2007a,b). We suggest that California ground squirrels are disproportionately significant for maintaining a unique community assemblage of native species within the larger grassland landscape (Fig. 3.3).

However, this perspective stands in contrast to the perceived role of the California ground squirrel as a pest; the species is "considered the most serious pest on rangeland, competing directly with livestock for forage" (Marsh 1998). As a result of control programs employing toxicants, most populations of ground squirrels are held at densities well below carrying capacity (Marsh 1987), with some local populations reduced by 90-95% (Hunt et al. 1995). Continued poisoning threatens the ecological role of California ground squirrels in grassland communities, and the ecological loss may be out of proportion to the percentage reduction in density. Interactive species function over a range of abundance levels but attain community importance only above a threshold density (Kotliar 2000). Below this threshold density communities of organisms maintained by interactive species decay through cascading effects and ecological simplification in structure and function (Paine 2000). Hence, it is imperative to maintain interactive species above the threshold density and at the greatest spatial extent possible (Soule et al. 2005).

California grasslands are experiencing ongoing habitat loss, fragmentation and encroachment from rapidly urbanizing areas, resulting in the degradation of habitat, the decline of native species, the loss of species interactivity, and potentially the unraveling of community assemblages. Disregarding the ecological role of the California ground squirrel as a strongly interactive species will only hasten the degradation of diversity and resilience of the California grassland ecosystem. Community persistence depends on strong interactivity, and “functional extinction of species interactions can occur well before the species themselves have completely disappeared (Soule et al. 2005).”

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Table 3.1: Assessing Interactivity

Guidelines for assessing Interactivity
1. Does the absence or decrease in abundance of the species lead directly or indirectly to a change in habitat structure or composition of the ecosystem?
2. Does the absence or decrease in abundance, or range contraction of the species directly or indirectly reduce reproduction or recruitment of other species?
3. Does the absence or decrease in abundance of the species lead directly or indirectly to a reduction in local species diversity?
4. Does the absence or decrease in abundance of the species lead directly or indirectly to a change in productivity or nutrient dynamics in or between ecosystems?
5. Does the absence or decrease in abundance of the species change an important ecological process in the system?
6. Does the absence or decrease in abundance of the species reduce the resilience of the system to disturbances such as fire, drought, flood or exotic species?

(adapted from Soule 2005)

Table 3.2. Criteria for dependency

1. Abundance of dependent species is higher on California ground squirrel colony sites than comparable areas without colonies.
2. Dependent species use features of colonies, which are a direct consequence of ground squirrel activities (burrows) or presence (prey), at greater frequencies than similar features off colonies
3. Survivorship or reproductive success of the dependent species is lower off colonies than on colonies.
4. Populations of dependent species decline if the ground squirrel populations decline.
The following vertebrate species satisfy at least ONE of the above criteria for dependence on California ground squirrels.
Amphibians California tiger salamander (*Ambystoma californiense*), California red-legged frog (*Rana draytonii*)
Reptiles western rattlesnake (*Crotalus viridis*), gopher snake (*Pituophis catenifer*)
Birds killdeer (*Charadrius vociferus*), golden eagle (*Aquila chrysaetos*), northern harrier (*Circus cyaneus*), red-tailed hawk (*Buteo jamaicensis*), ferruginous hawk (*Buteo regalis*), American kestrel (*Falco sparverius*), prairie falcon (*Falco mexicanus*), mourning dove (*Zenaida macroura*), burrowing owl (*Athene cunicularia*), western kingbird (*Tyrannus verticalis*), black phoebe (*Sayornis nigricans*), Say's phoebe (*Sayornis saya*), horned lark (*Eremophila alpestris*), common raven (*Corvus corax*), loggerhead shrike (*Lanius ludovicianus*), American pipit (*Anthus rubescens*), European starling (*Sturnus vulgaris*), savannah sparrow (*Passerculus sandwichensis*), lark sparrow (*Chondestes grammacus*), western meadowlark (*Sturnella neglecta*)
Mammals American badger (*Taxidea taxus*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), San Joaquin kit fox (*Vulpes macrotis mutica*), deer mouse (*Peromyscus maniculatus*), Audubon's cottontail (*Sylvilagus audubonii*), mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*)
References: Lenihan 2007a,b, Loredo et al. 1996, Kuenzi et al. 1998, Hunt 1995, 2002, Jennings and Hayes 1994, Fitch 1948, Owings 2002, DiDonato 2001, Bobzien and Bell, Pers. Comm.

(Adapted from Kotliar 1999, 2006)

Figure 3.1: California ground squirrel (*Spermophilus beecheyi*)
Order: Rodentia, Family: Sciuridae, sub-family: Sciurinae,
sub-tribe: Spermophilina (includes two genuses: *Spermophilus* & *Cynomys*)

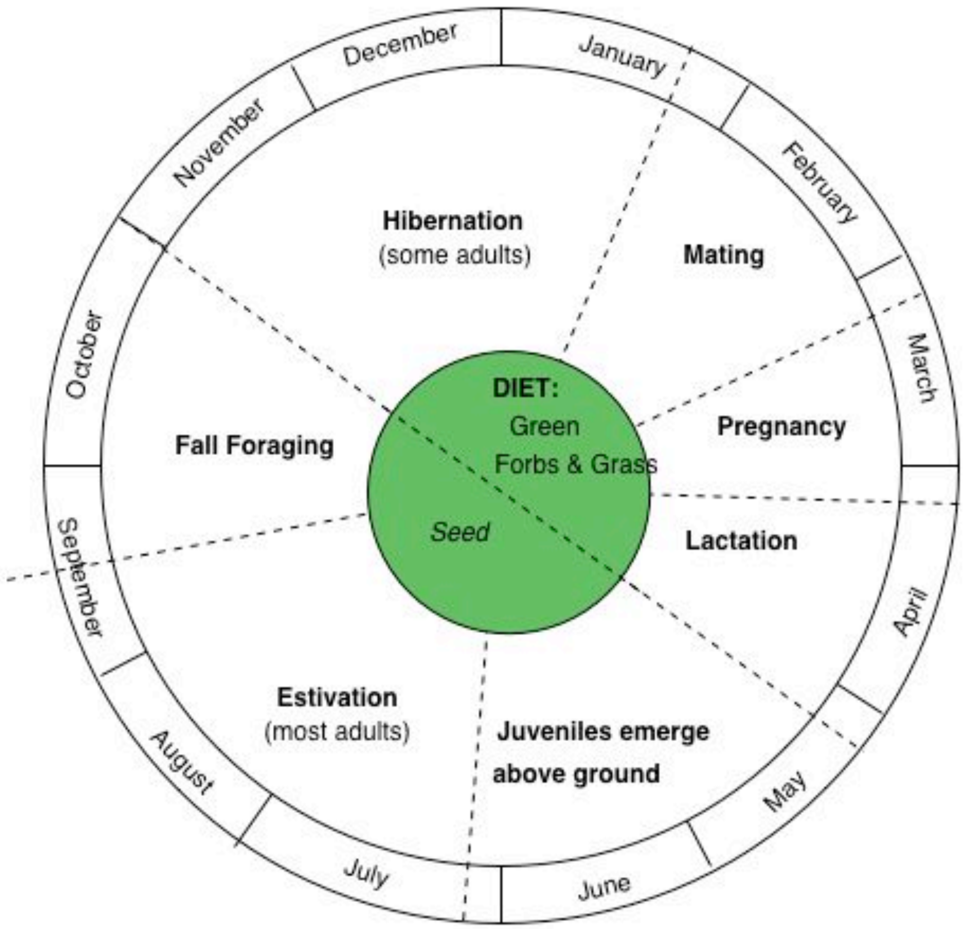
Photo credit: Joe DiDonato, EBRP

Description

A large ground squirrel the California ground squirrel weights range from 350-885g, it is about 383-500mm long, including the moderately bushy tail. The tail is longer (140-233mm) than half the head and body length.

The California ground squirrel has a general gray-brown coloration mottled or dappled with lighter flecks on its back. A mantle or darker gray band of color extends from the ears back onto the shoulders (inconspicuous or lacking in some sub-species). The shoulders and sides of the head are light gray and under parts are light buff. The large size, dark mantle, and usual lack of stripes distinguish this species from other ground squirrels in California (Jameson and Peeters, 1988).

Figure 3.2. Generalized annual schedule of California ground squirrels surface activity, dormancy, reproduction, and diet in the San Francisco Bay Area. (see text for details)



Adapted from: Dixon 1917, Marsh 1994, Dobson & Davis 1986, Holekamp & Nunes 1989, Whisson

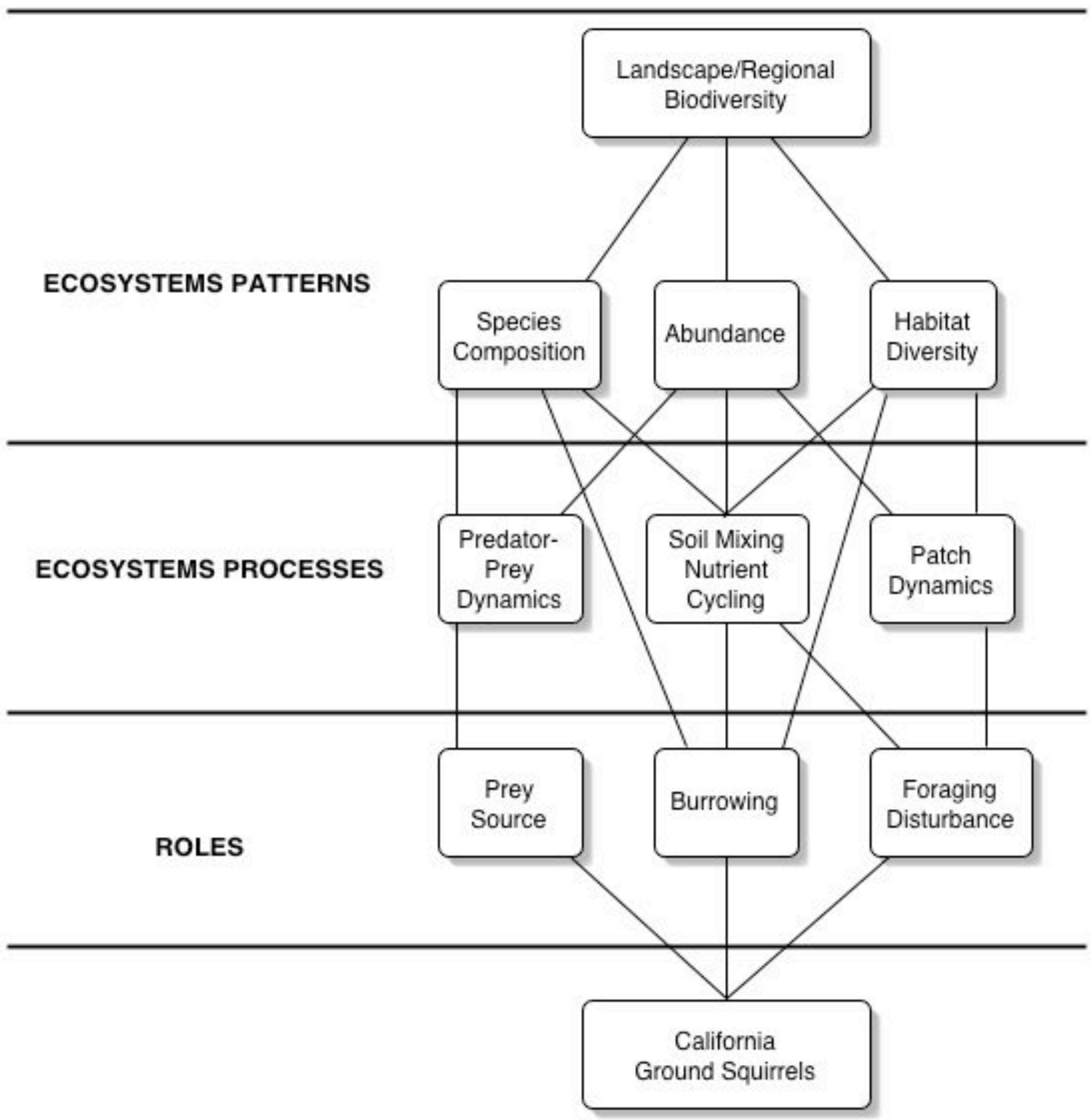


Figure 3.3: Dominant Pathways by which CAGS affect ecosystem structure and function. (adapted from Kotliar, Ceballos)

Appendix 3.1: History of California ground squirrel control measures
❖ 1808: First collective effort by a community to control the California ground squirrel from raiding gardens in the Santa Barbara area using strychnine bait (Jacobsen, 1931).
❖ 1850: Control measures were instituted as bounties (5cents/ground squirrel), millions of squirrels were killed but the bounty system was deemed a failure due to fraud (Jacobsen 1918, Dixon 1918).
❖ 1876: a legislative act created ground squirrel inspection districts requiring landowners to eliminate squirrels on their property or face fines/liens (Jacobsen 1918).
❖ 1908: Plague was confirmed in the California ground squirrel and eradication became a priority, especially in Alameda and Contra Costa counties where squirrel populations were large. A plan for the creation of a "squirrel free zone" was created within these counties to prevent plague fleas from infecting rats in the highly populated Oakland/Berkeley area (Jacobsen 1918).
❖ 1917: California Legislature authorizes County Agriculture Commissioners to take charge of rodent control and designate the California ground squirrel as a "pest of agriculture and public nuisance" (Kellog 1931).
❖ 1918: The "California ground squirrel WARS" begin.
MEMO: Geo. H. Hecke, Commissioner of Horticulture, Sacramento, CA *"Understand you are undertaking campaign for the eradication of ground squirrels in California. This has my hearty approval as these squirrels destroy vast quantities of food which might otherwise be used for support of our armies abroad and the allies. The school children should be of great assistance in this campaign and the knowledge that they are doing a patriotic duty should stimulate them to their utmost efforts." -Herbert Hoover, United States Food Administrator-*
❖ 1915: The federal government allocated money for rodent control.
❖ 1920's: Millions of ground-dwelling squirrels (prairie dogs and ground squirrel species) were poisoned annually under the Federal program.
❖ 1929: the United States Biological Survey created the Division of Predatory animal and rodent control.
❖ 1931: "Following a decade of relatively effective squirrel control there was a 75% reduction in the squirrel population (Marsh 1997).
❖ 1931: Animal Damage Control Act passed providing statutory authorization for poisoning, trapping, shooting both on and off Federal lands. This act remains in effect today (Miller and Reading 2002).
❖ 1940-1975: The rodenticide 1080 (sodium fluoroacetate) was used, baiting 4-6 million acres of rangeland annually for ground squirrel control (Marsh 1998)
❖ 1975: The rodenticide 1080 is taken off the market. Alternative rodenticides are less effective, range forage losses increase (Marsh 1998).
❖ Current control measures: California ground squirrel is considered the "most serious rangeland pest." Increased restrictions and regulation on chemical control agents has decreased the level of control. Integrated Pest Management offers fair to moderate control on rangelands (Marsh 1998).

Appendix 3.2: Comparison of vertebrate species abundance at colony and off-colony sites. Features used by vertebrate species at sites are designated as: CAGS= California ground squirrel taken as prey, OP= other prey found, BU= burrows used for nesting or shelter, BG= open vegetation or bare ground used for nesting or foraging VEG= grassland vegetation unmodified by CAGS used for nesting or foraging

Vertebrate species	Features	Reference
Abundance higher on colony sites		
California tiger salamander (*Ambystoma californiense*)	BU	2, 4
California red-legged frog (*Rana draytonii*)	BU	4, 10
western rattlesnake (*Crotalus viridis*)	CAGS, BU	1, 9
gopher snake (*Pituophis catenifer*)	CAGS, BU	1, 9
American badger (*Taxidea taxus*)	CAGS, BU	9
coyote (*Canis latrans*)	CAGS, BU, OP	6, 9
bobcat (*Lynx rufus)*	CAGS, OP	9
deer mouse (*Peromyscus maniculatus*)	BU, BG	9
Audubon's cottontail (*Sylvilagus audubonni*)	BU	2, 9
killdeer (*Charadrius vociferus*)	BG, OP	8
golden eagle (*Aquila chrysaetos*)	CAGS, OP	3, 8
northern harrier (*Circus cyaneus*)	OP	8
red-tailed hawk (*Buteo jamaicensis*)	CAGS, OP	6,8
ferruginous hawk (*Buteo regalis*)	CAGS, OP	8
American kestrel (*Falco sparverius*)	OP, BG	8
prairie falcon (*Falco mexicanus*)	CAGS, OP	8, 11
mourning dove (*Zenaida macroura*)	BG	8
burrowing owl (*Athene cunicularia*)	BU, BG, OP	8

Abundance higher (cont)		
western kingbird (*Tyrannus verticalis*)	BG, OP	8
black phoebe (*Sayornis nigricans*)	BG, OP	8
Say's phoebe (*Sayornis saya*)	BG, OP	8
horned lark (*Eremophila alpestris*)	BG	8
common raven (*Corvus corax*)	CAGS, OP	8
loggerhead shrike (*Lanius ludovicianus*)	OP, BG	8
American pipit (*Anthus rubescens*)	BG	8
European starling (*Sturnus vulgaris*)	BG	8
savannah sparrow (*Passerculus sandwichensis*)	BG	8
lark sparrow (*Chondestes grammacus*)	BG	8
western meadowlark (*Sturnella neglecta*)	BG	8
Abundance equivalent		
California king snake (*Lampropeltis getula*)	OP	9
sharp-shinned hawk (*Accipiter striatus*)	OP	8
Cooper's hawk (*Accipiter cooperii*)	OP	8
Swainson's hawk (*Buteo swainsoni*)	OP	8
Merlin (*Falco columbarius*)	OP	8
peregrine falcon (*Falco peregrinus*)	OP	8
white-throated swift (*Aeronautes saxatalis*)	OP, BG	8
barn swallow (*Hirundo rustica*)	OP, BG	8
house finch (*Carpodacus mexicanus*)	BG, VEG	8

Abundance lower on colony sites		
western fence lizard (*Sceloperus occidentalis*)	VEG	9
Gilbert's skink (*Eumeces gilberti*)	VEG	9
striped skunk (*Mephites mephitis*)	VEG, OP	9
San Joaquin pocket mouse (*Perognathus inornatus*)	VEG	9
western harvest mouse (*Reithrodontomy megalotis*)	VEG	9
California vole (*Microtus californicus*)	VEG	9
house mouse (*Mus musculus*)	VEG	9
white-tailed kite (*Elanus leucurus*)	OP	8
Anna's hummingbird (*Calypte anna*)	VEG	8
grasshopper sparrow (*Ammodramus savannarum)*	VEG	8
cliff swallow (*Petrochelidon pyrrhonota*)	VEG, OP	8
western bluebird (*Sialia mexicana*)	VEG, OP	8
American goldfinch (*Carduelis tristis*)	VEG	8
Unkown: insufficient sightings		
black-tailed jackrabbit (*Lepus californicus*)	VEG, BU	2, 12
wild pig (*Sus scrofa*)	VEG	9

Reference Citations: 1. Fitch 1948, 2. Lidicker 1989, 3. Hunt 1995, 2002, 4. Jennings and Hayes 1994, 5. Loredo et al. 1996, 6. Kuenzi et al. 1998, 7. Didonato 2001, 8. Lenihan 2007a, 9. Lenihan 2007b, 10. Bobzien Pers.Comm., 11. Bell, Pers.Comm., 12. Pers.Obs.