

CENTRAL-PLACE FORAGER EFFECTS ON FOOD WEB DYNAMICS AND SPATIAL PATTERN IN NORTHERN CALIFORNIA MEADOWS

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Abstract. In this study, I examined the impacts of a presumed central-place forager on its prey and on the prey's resource. Western fence lizards, *Sceloporus occidentalis*, limit their activity and feeding in meadows to a variety of structures (e.g., stumps, logs, brush, and rock piles). The impact of lizards on their primary prey, grasshoppers, decreased at a decreasing rate with distance from structures that housed lizards; thus, grasshopper densities increased with distance. Consequently, the abundance of plants (grasshoppers' food) decreased with distance from these structures. However, the relative abundance of plants varied with distance. The proportion of herbaceous forbs (the grasshoppers' preferred resource) was greatest near lizard structures, whereas the proportion of less edible grasses was greater far from lizard structures. There were no such relationships between grasshoppers or plants and distance from similar structures that did not house lizards. Near the structure, an enclosure experiment showed a very strong impact of lizards on grasshopper populations. Plant biomass and the relative proportion of forbs were higher with lizards present than in lizard enclosures, suggesting a trophic cascade. An identical enclosure experiment far (15 m) from the structure, where lizard activity was greatly reduced, showed no such cascades. Thus, this study showed evidence for strong consumer effects in a grassland system. However, small-scale differences in foraging behaviors (possibly due to predation risk) may importantly affect the outcomes of these interactions.

Key words: central place; food chains; foraging; grasshoppers; meadows; *Sceloporus occidentalis*; trophic cascades; western fence lizard.

INTRODUCTION

A central-place forager is a consumer that has a place from which it forays, but to which it must return after a given foraging bout (Orians and Pearson 1979, Schoener 1979, Stephens and Krebs 1986). Consumers can be confined to a central place for a number of reasons. Animals that provide food for offspring on a nest, animals that hunt from a particular spot, and animals that defend their territories from a central area are all examples of central-place foragers. Another scenario in which consumers are restricted to a central place occurs when animals remain in or near refugia in order to reduce exposure to predators, but must emerge periodically to forage (e.g., Sih et al. 1988, Abramsky et al. 1990, 1992).

As a central-place forager ventures from its refuge, its costs increase with distance from the central place due to travel time (and predation risk if the forager is restricted to refuges from predation). By definition, a forager always returns to its central place after a given foraging bout. Thus, an optimal central-place forager should concentrate its efforts near refugia, and decrease its foraging effort with increasing distance from that refuge. Although not explicitly considered in foraging behavior models, the variability of foraging effort with distance from the central place necessarily affects the

population dynamics of the forager's prey. Thus, central-place foragers can have cascading effects on the rest of the food web, but those effects should vary spatially in relation to the proximity of the central place. The impacts of such foragers should be strongest directly adjacent to the central place, diminishing with distance. Regardless of the mechanisms that restrict a consumer to a central place (e.g., predation risk, territoriality, nests), patterns of food web dynamics and trophic abundances should vary in space relative to central places and refuges provided by the external environment (see also Power 1984, Power et al. 1989, Abramsky et al. 1990, 1992).

In this study, I examined the direct effects of a predator, the western fence lizard, *Sceloporus occidentalis* (Squamata: Iguanidae), on its insect prey (primarily herbivorous grasshoppers; Orthoptera: Acrididae and Tettigonidae), and the indirect effects extended to meadow plants. Western fence lizards, as their common name suggests, are generally found on or near various structures such as fences, rock and brush piles, and various other structures (Van Denburgh 1922, Smith 1946, Marcelini and Mackey 1970, Davis and Verbeek 1972, Leviton 1972, Stebbins 1985). I conducted observational studies to examine the extent and possible cause of the lizard's restriction to structures. In addition, I took advantage of a "natural experiment" in which lizards resided on most, but not all such structures, and tested for relationships between the abun-

dances of grasshoppers or plants and distance from structures with and without lizards. Finally, I conducted an enclosure experiment to test hypotheses about the causes of the observed patterns. I conclude that the impact of the western fence lizard on the meadow food chains varies considerably over small spatial scales, as a result of the lizard's restriction to a central place.

STUDY SYSTEM

Sceloporus occidentalis (hereafter, western fence lizards) are common and conspicuous diurnal insectivores that occur throughout much of western North America (Stebbins 1985). Western fence lizards are habitat generalists that occur in several different types of communities, including grasslands and meadows (e.g., Marcelini and Mackey 1970, Davis and Verbeek 1972, Rose 1976, Stebbins 1985). This study was conducted on the Angelo Coast Range Reserve in northern California (Mendocino County, California, United States; 39°44' N, 123°39' W), June–September 1995. Several small meadows (size range 0.5–8 ha) occur as islands within the old-growth Douglas fir (*Pseudotsuga menziesii*) and coastal redwood (*Sequoia sempervirens*) forest along the terrace of the South Fork of the Eel River. These meadows have been present at least as long as the earliest European settlements (Johnson 1979).

Within the meadows, there are a variety of small structures on which western fence lizards appear to reside, including tree stumps, brush piles, and rock outcrops. These structures vary in size and location within the meadows, but appear to be central to the activity and residence of these lizards (Van Denburg 1922, Smith 1946, Davis and Verbeek 1972, Leviton 1972, Stebbins 1985). Grasshoppers (Orthoptera: Arididae and Tettigonidae), dominated by *Melanoplus devastator*, composed >85% (by biomass) of the grassland herbivores (invertebrate and vertebrate) at this site. Western fence lizards are generalist insectivore predators that readily catch and eat grasshoppers (Smith 1946, Rose 1976, Stebbins 1985). In these meadows, grasshoppers composed >80% of the lizard's diet (J. M. Chase, unpublished data), suggesting that this might be an important food web link.

The vegetation in these meadows consisted of perennial grasses, dominated by *Danthonia californica*, and several annual grasses including *Aira caryophyllea* and *Bromus* spp. Overall, grasses composed 60–95% of the total aboveground plant biomass. Several species of forbs occurred throughout the meadows, whereas others were more localized. Some of the more common forbs included: *Achillea borealis*, *Cirsium vulgare*, *Mardia* spp. (Asteraceae), *Plagiobothrys nothofulvus* (Boraginaceae), *Erodium* spp., *Geranium* spp. (Geraniaceae), *Lotus* spp., *Lupinus micranthus*, and *Trifolium* spp. (Leguminosae). For a complete description of these meadows and their associated plant communities, see Stebbins (1968) and Kotanen (1995). The most abundant grasshopper, *M. devastator*, and several rarer

members of the *Melanoplus* genus are generalist herbivores that readily consume most of these plant species at this site. These *Melanoplus* showed a specific preference for many of the forbs relative to the more silicaceous grasses (J. M. Chase, unpublished data); this diet preference is typical of the genus (e.g., Mulken et al. 1969, Joern 1983, Chapman 1990).

METHODS

Lizard, grasshopper, and plant abundances in relation to cover

I identified 12 meadows along the river terrace that were similar in abiotic conditions and plant composition. There was at least one structure (tree stump, brush pile, or rock outcrop) on which lizards resided in all 12 meadows; a subset of five of these meadows also had apparently similar structures on which lizards were never observed. In each of the 12 meadows, I identified rock or brush piles, referred to as "lizard structures," that were 0.5–1.5 m² in surface area, housed at least two lizards, and occurred away from the meadow–forest interface. In the five meadows with structures without lizards, referred to as "no-lizard structures," I identified those structures on which lizards were never observed (similar in size, location, and form to those structures with lizards). No-lizard structures were used as natural controls in comparison with patterns observed on lizard structures.

Lizard abundance near structures was estimated using visual surveys. During periods of high lizard activity (0900–1100) over a 3-d period (9–11 July), I systematically walked toward each structure in each meadow from a distance of >30 m. When I observed a lizard, I marked its approximate location relative to the structure to which it fled, and then measured the distance from the initial occurrence of each lizard to the structure. I used each lizard observed as a separate observation in examining the numbers of lizards at various distances from structures.

Taking advantage of the natural variation in the distribution of lizards on structures, I tested whether grasshopper densities differed between lizard and no-lizard structures. In each of 10 meadows, I established a transect for determining grasshopper densities from a lizard structure; in five meadows I selected an additional transect from no-lizard structures. I marked points at 0, 2, 4, 6, 8, 10, 12, 14, and 16 m from the structure along each of the 15 transects. These distances spanned the range of lizard activity in relation to cover. At each 2-m interval along a transect, I placed five wire rings (0.1 m²) 1 m from each other, equidistant from the structure. I censused grasshoppers by approaching each ring, gently disturbing the vegetation inside it with a long stick, and counting all grasshoppers flushed out. This technique appears to be accurate for censusing grasshopper abundances in grassland habitats (Onsager and Henry 1977). Thus, at each distance along the tran-

sect, I censused a total of 0.5 m² for grasshoppers. I censused grasshoppers once each month during the summer (July, August, and September), to test for seasonal variation.

To examine how plant abundance and diversity may have been indirectly influenced by lizard predation on grasshoppers, I established another set of transects from lizard structures (so that vegetation sampling did not influence grasshopper behavior) in each of eight meadows. In addition, I established transects from no-lizard structures in each of five meadows. These transects were also marked at 2-m intervals to 16 m. At each 2-m interval, I censused a 0.1 × 1 m (0.1-m²) strip of vegetation parallel to each structure along the transect. To do this, I clipped live plants at their base, separated grasses and forbs, dried them at 60°C for 48 h, and weighed them. To examine potential seasonal differences in vegetation biomass, I established separate transects from each structure once each month (July, August, and September) in order to avoid clipping plants in the same area clipped the previous month.

Exclosure experiments

From 11–13 July 1995, I initiated an exclosure experiment to test potential causal mechanisms underlying patterns from the observational studies and natural experiment. Because my working hypothesis was that lizards might have different community impacts near and far from their structure, I established exclosures at these two extremes. In each of four meadows, I marked three 2-m² plots near (<1 m from) a lizard structure (different from those used in the previous censuses) and three 2-m² plots far (15 m) from the same structure. At both near and far distances, one plot was covered by a wooden-frame cage (2 × 1 × 1 m) covered with fiberglass window screening (1-mm mesh). This treatment, “plants only,” eliminated herbivore access to the plot (all resident insects were removed from the plot during treatment establishment), allowing an estimation of plant biomass and composition in the absence of herbivory. Similar screen-covered cages do not appear to directly affect plant abundance or quality at other grassland sites (J. M. Chase, *unpublished data*). A second plot at each distance was a “lizard exclosure.” Here, I cut a narrow slit into the ground around the entire plot with a shovel, and inserted a 20 cm wide strip of aluminum flashing vertically so that 16–18 cm were above ground. This aluminum wall was impenetrable to lizards, but did not appear to impede grasshopper movement in and out of the plots (J. M. Chase, *personal observation*). The last plot, referred to as “control,” was marked at the corners but was left open, allowing free access to all species. All treatments were identically cut around the boarder with a shovel as a sham control for the lizard exclosure treatment. In total, there were six treatments (three exclosure treatments × two distances) replicated in each of four meadows.

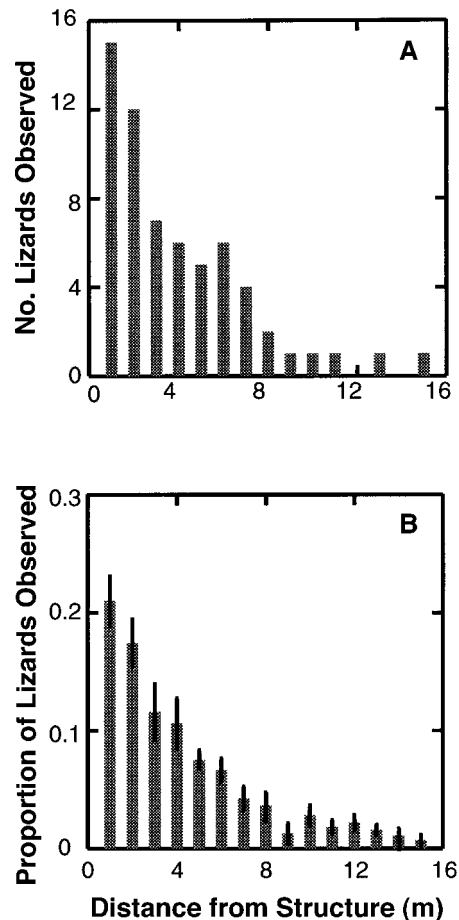


FIG. 1. (A) The number of lizards observed at different distances from the structures to which they fled. Each lizard was used as an independent observation. (B) The proportion of lizards (mean \pm 1 SD) in each meadow observed at various distances from structures.

After 60 d (10 September 1995), I terminated the experiment. I censused grasshoppers by stealthily approaching each plot and disturbing the vegetation with a stick to flush out all grasshoppers. Each grasshopper flushed from a plot was identified to species. No grasshoppers were present in the grasshopper exclosures. I censused vegetation by clipping a 0.1 m wide strip of vegetation along the long (2-m) axis of the plot (0.2 m² total area clipped). I then sorted the clipped vegetation into grasses and forbs, dried it, and weighed it as previously described.

RESULTS

Lizard, grasshopper, and plant abundance relative to distance from structure

The number of lizards observed decreased rapidly with increasing distance from a structure (Fig. 1). Each lizard was considered an independent observation to provide a histogram (Fig. 1A) of the number of lizards observed at each distance interval from a structure.

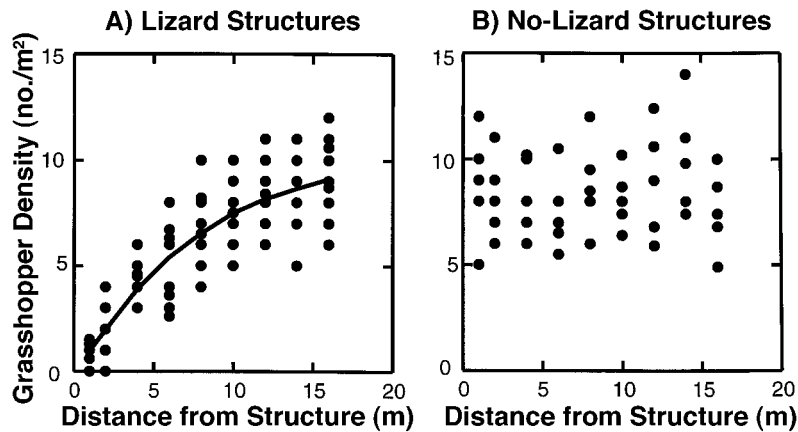


FIG. 2. The density of grasshoppers in relation to distance from lizard structures and no-lizard structures. Data for August censuses only are presented as representative (patterns were qualitatively similar in the other months). (A) Grasshopper density significantly increased with distance from lizard structures. (B) There were no relationships between grasshopper densities and distance from no-lizard structures.

Alternatively, these data can be analyzed by taking each meadow as independent and calculating the proportion of lizards found at each distance (absolute numbers cannot be compared between meadows, because each meadow has a different lizard density). Figure 1B presents the per meadow mean (± 1 SD) proportion of lizards found at each distance from a structure.

Grasshopper densities increased at a decreasing rate with distance from lizard structures (Fig. 2A). Although both linear and asymptotic regressions were significant, I present asymptotic regressions since a likelihood ratio test comparing the residual sums of squares from the simple linear model with the more complex asymptotic model (see, e.g., Lebreton et al. 1992) showed that the latter provided a significantly better fit ($P < 0.05$). Asymptotic regression equations for grasshoppers vs. distance from lizard structures were qualitatively similar over the three months of censuses (July, $Y = 19.98[1 - e^{-0.10X}]$, $R^2 = 0.85$; August, $Y = 10.68[1 - e^{-0.12X}]$, $R^2 = 0.78$; and September, $Y = 12.15[1 - e^{-0.08X}]$, $R^2 = 0.86$). Slopes were not statistically different among months (ANOVA on jackknifed slope values between months: $N = 30$; $df = 2, 27$; F ratio = 0.95; $P > 0.40$), but the intercepts changed because of declining grasshopper abundance over the summer (ANOVA on jackknifed intercept values between months: $N = 30$; $df = 2, 27$; F ratio = 52.98; $P < 0.001$). There were no significant relationships between distance and grasshopper densities from no-lizard structures in any of the three months (Fig. 2B). Because the qualitative patterns of grasshopper abundances relative to distance from lizard structures were similar over the three months of censuses, I only present data from August, the middle month of censuses. There were no relationships between grasshopper densities and distance from no-lizard structures in any of the three months of censuses (Fig. 2B).

Plant biomass decreased at a decreasing rate with

distance from lizard structures (Fig. 3A). Here again, both linear and asymptotic regression were significant, and the likelihood ratio test showed that asymptotic regression provided a significantly better fit to the data ($P < 0.02$). Asymptotic regression equations of plant biomass vs. distance from lizard structures were again qualitatively similar over the three months of censuses (July, $Y = 165.32[e^{-0.04X}]$, $R^2 = 0.52$; August, $Y = 114.56[e^{-0.05X}]$, $R^2 = 0.73$; and September, $Y = 101.31[e^{-0.05X}]$, $R^2 = 0.79$). Slopes of the relationships between plant biomass and distance from lizard structures were not significantly different between months (ANOVA on jackknifed slope values between months: $N = 24$; $df = 2, 21$; F ratio = 0.93; $P > 0.41$), but the intercepts declined over the summer (ANOVA on jackknifed intercept values between months: $N = 24$; $df = 2, 9$; F ratio = 199.27; $P < 0.001$). No significant relationships were observed with distance from no-lizard structures (Fig. 3B).

In addition to changes in plant biomass with distance from lizard structures, the species composition of the plant assemblage changed: the proportion of forbs relative to grasses decreased with distance from lizard structures (Fig. 4A). As with overall plant biomass, both linear and asymptotic regression were significant, and the likelihood ratio test showed that the asymptotic regression fit the data best ($P < 0.04$). Asymptotic regression equations for each month (July, $Y = 0.49[e^{-0.08X}]$, $R^2 = 0.64$; August, $Y = 0.34[e^{-0.06X}]$, $R^2 = 0.48$; and September, $Y = 0.20[e^{-0.07X}]$, $R^2 = 0.42$) showed no difference in the slope of the relationships (ANOVA on jackknifed slope values between months: $N = 24$; $df = 2, 21$; F ratio = 2.26; $P > 0.13$), whereas the intercept significantly declined over the summer (ANOVA on jackknifed intercept values between months: $N = 24$; $df = 2, 9$; F ratio = 49.63; $P < 0.01$). No relationships were observed between plant relative abundances and distance from no-lizard structures (Fig. 4B).

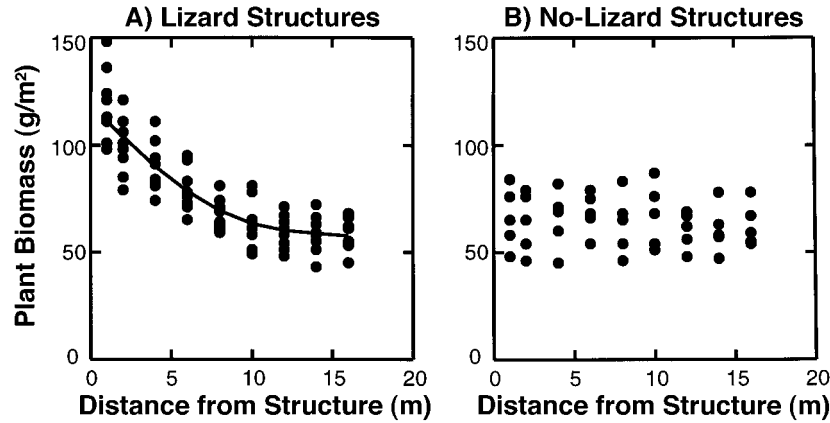


FIG. 3. The total biomass of plants in relation to distance from lizard and no-lizard structures. As in Fig. 2, only the data for August censuses are presented, because the qualitative patterns are similar in the other months. (A) Plant biomass declined significantly with distance from lizard structures. (B) There were no relationships between plant biomass and distance from no-lizard structures.

Experimental results

Grasshopper densities were analyzed using a two-way factorial ANOVA including enclosure treatment (lizard enclosure and control), distance from lizard structure, and their interaction. There was a significant treatment effect and a significant treatment by distance interaction (Table 1). Tukey's hsd for pairwise comparisons ($P < 0.05$) showed that grasshoppers were significantly more abundant in the lizard enclosures near lizard structures, whereas there was no effect of lizard enclosure far from lizard structures (Fig. 5).

Plant biomass was analyzed using two-way ANOVA including enclosure treatment (plants only, lizard enclosure, and control), distance from lizard structure (near, far), and their interaction. As with grasshopper abundances, there was a significant treatment effect and a significant treatment by distance effect on plant biomass (Table 2). Near lizard structure (Fig. 6), plant biomass was lower in the lizard enclosure than in the

plants only or control treatments (Tukey's hsd: $P < 0.05$), which, in turn, did not differ significantly (Tukey's hsd: $P > 0.05$), indicating a trophic cascade from lizards. Far from lizard structure plant biomass was again greatest in the plants only treatment (Tukey's hsd: $P < 0.05$), but there was no difference between lizard enclosures and controls (Tukey's hsd: $P > 0.1$) (Fig. 6), indicating no trophic cascade from lizards. In addition, a similar two-way ANOVA on the relative abundance of forbs (arcsine square-root transformed) showed similar relationships (Table 2). Near lizard structures, the proportion of forbs was greater in the plants only and control treatments than in the lizard enclosure treatment (Tukey's hsd: $P < 0.05$; Fig. 7).

DISCUSSION

Three approaches to ecological research were used in this study: observation, natural experiments, and field manipulation experiments (sensu Diamond 1986).

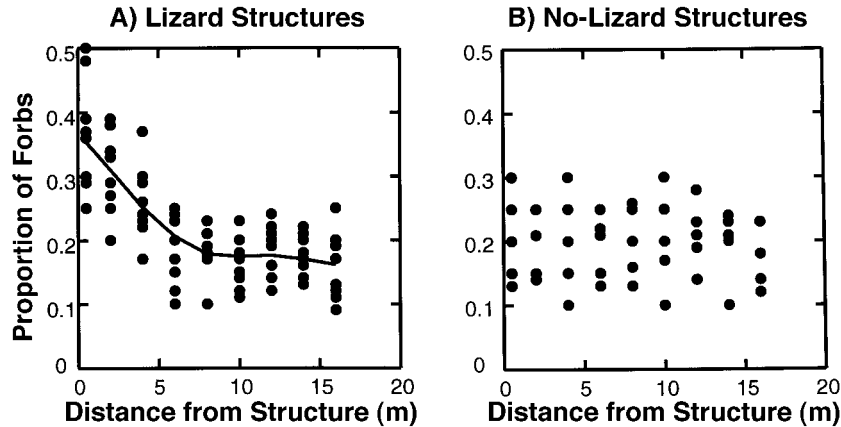


FIG. 4. The relative proportion of forbs in relation to distance from (A) lizard structures and (B) no-lizard structures. Data are presented as in Fig. 3.

TABLE 1. Two-way ANOVA results on grasshopper densities from the experiment. Factors are treatment (lizard enclosure, control) by distance (near, far) from a lizard structure.

Source	df	MS	F	P
Distance	1	10.56	3.57	0.09
Enclosure treatment	1	39.06	12.93	0.004
Distance \times treatment	1	39.06	12.93	0.004
Error	12	3.02		

I used observation to explore the extent and possible cause of the apparent restriction in western fence lizard activity to the vicinity of various structural elements in the habitat. I used natural experiments to examine patterns of grasshopper and plant abundances in relation to structures that naturally housed lizards and those that had none. Finally, I employed a field manipulation experiment to test possible causal mechanisms for the observed patterns.

The observational study showed that western fence lizards appear to restrict their activity within these meadows to structures such as stumps, rock piles, and brush piles (Fig. 1), as well as fences and other human-constructed structures. Natural historians have recognized this association for years (hence, the species' common name), and the following hypotheses for this affiliation have been proposed. (1) Structures may act as refugia reducing exposure to predators, particularly birds; (2) structures may aid in thermoregulation, providing sun-basking sites when the air temperature is cool and shaded cover when it is too hot; (3) elevation provided by the structures may assist hunting by enabling lizards to view a larger area and to detect prey more readily; (4) structures may simply provide a central place from which to defend a territory; and (5) structures may be used as arenas for courtship and substrates for egg-laying. All of these factors could explain the association of western fence lizards with structures

(Van Denburg 1922, Smith 1946, Marcelini and Mackey 1970, Davis and Verbeek 1972, Leviton 1972, Rose 1976, Stebbins 1985).

I believe that refugia from predators may be the primary reason for the lizards' association with structures (see Van Denburgh 1922, Smith 1946, Leviton 1972, Stebbins 1985). Over the course of the summer, I observed Common Ravens (*Corvus corax*) stalking and eating lizards on several occasions. When a raven captured a lizard, I estimated the location of the predation event in relation to the nearest structure suitable for lizard cover. Of the 15 successful predation events that I observed, only one was within 5 m of a given structure; all others were >10 m from a structure, suggesting that lizards may be more susceptible to predators as they venture farther from structures. Regardless of the mechanism restricting the lizards to structures, the influence of lizards on the rest of the food web should vary with distance from the structure in similar ways.

Taking advantage of the variation in lizard distribution as a natural experiment, I examined how central-place utilization by western fence lizards (i.e., restriction to the vicinity of structures) might affect the spatial pattern of food web dynamics. Transects from lizard structures showed an asymptotic increase in grasshopper densities (Fig. 2A), a decrease in plant abundance (Fig. 3A), and a decrease in relative proportion of forbs (Fig. 4A) with distance from the structure. Transects from no-lizard structures showed no such relationships of grasshopper or plant abundances with distance (Figs. 2B, 3B, 4B). These patterns lead to a complex spatial mosaic of species abundances within the meadows. Near lizard structures, grasshoppers are rare and plants (particularly highly edible forbs) flourish. Far from those structures, grasshoppers flourish and plants (especially forbs) are depauperate. The strong relationships of grasshoppers and plants with distance from structures with, but not those without, lizards suggest

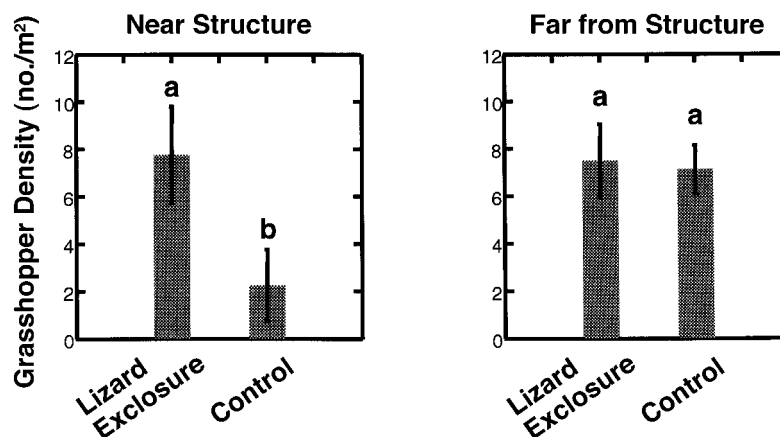


FIG. 5. Densities (mean \pm 1 SD) of grasshoppers in lizard enclosures and control plots near vs. far from lizard structures at the end of the experiment. Different letters denote significant differences among treatments (Tukey's hsd for pairwise comparisons, $P < 0.05$).

TABLE 2. Two-way ANOVA results on plant biomass and the relative proportion of forbs (arcsine-transformed) in the experiment. Factors are treatment (plants only, lizard enclosure, control) by distance (near, far) from the lizard structure.

Source	Total plant biomass				Proportion of forbs		
	df	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Distance	1	539.60	2.63	0.12	0.01	2.89	0.10
Exclosure treatment	2	4940.77	24.11	0.001	0.11	30.22	0.001
Distance × treatment	2	870.62	4.24	0.03	0.02	5.1	0.02
Error	18	240.34			0.006		

that lizards are likely to play a key role in determining these patterns.

Despite the strong relationships revealed by the observational studies and natural experiments, results from nonmanipulative studies were equivocal. Thus, I conducted the field experiment to test more explicitly the hypothesis that the impact of lizards on these meadow food chains varies as a function of distance from central-place structures. Several lines of evidence from the experiment support this hypothesis. First, herbivory by grasshoppers and other insects significantly reduced plant biomass, which was highest in the grasshopper exclosure cages both near and far from lizard structures (Fig. 6). In addition, the relative proportion of forbs was highest in grasshopper exclosures (Fig. 7), suggesting a possible disproportionate effect of grasshoppers on forbs relative to grasses. An alternative explanation for the change in plant abundances with distance from structure may be different environmental conditions near and far from the structures. However, plant biomass (Tukey's hsd: $P > 0.6$) and the relative proportion of forbs (Tukey's hsd: $P > 0.3$) did not differ from one another in the plants only treatments near and far from lizard structures, indicating that plant biomass in the absence of higher trophic levels did not appear to be affected by any environmental differences related

to distance from structure. Instead, any variation in plant abundance in the remaining treatments was probably due to differences in biotic food web interactions among lizards, grasshoppers, and plants.

Near lizard structures, these lizards reduced grasshopper densities by nearly 75% of their density in the absence of lizards (Fig. 5). In addition, plant biomass (Fig. 6) and the relative proportion of forbs (Fig. 7) were much higher with lizards than without. Thus, near structures, lizards appeared to be important food web interactors, strongly reducing grasshopper abundances and causing a trophic cascade in plant abundance and composition. These results accord with those of the natural experiment, in which lizard structures had fewer grasshoppers, more plants, and a higher proportion of forbs than did nearby no-lizard structures.

Far from structures (15 m), the outcome of the exclosure experiment was very different. Here, as with the near-structure treatment, plant biomass and relative abundance of forbs were highest in the herbivore exclosure. However, the lizard exclosure treatment at this distance had no effect on the rest of the food web. Grasshopper density was the same in control and lizard exclosure plots (Fig. 5), and plant biomass (Fig. 6) and composition (Fig. 7) were unchanged. The observational study showed that lizard activity was extremely

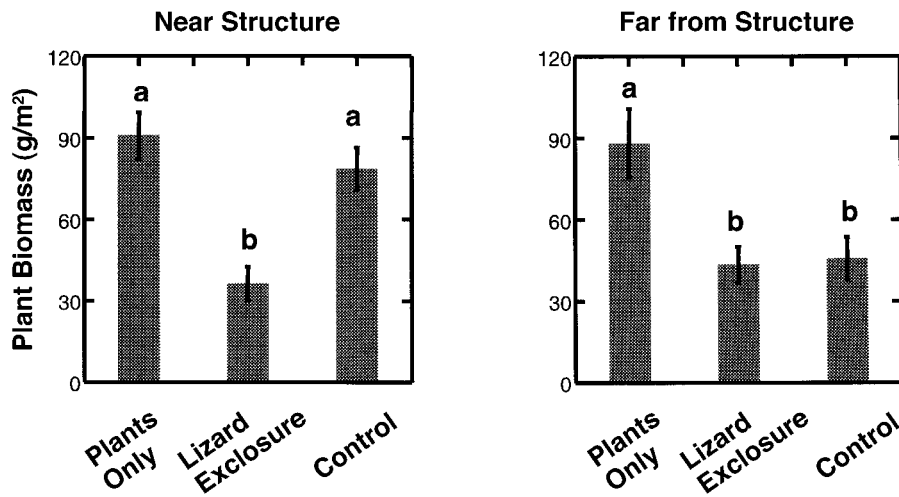


FIG. 6. Plant biomass (mean \pm 1 SD) in the plants only, lizard exclosure, and control plots near vs. far from lizard structures at the end of the experiment. Different letters denote significant differences between treatments (Tukey's hsd for pairwise comparisons $P < 0.05$).

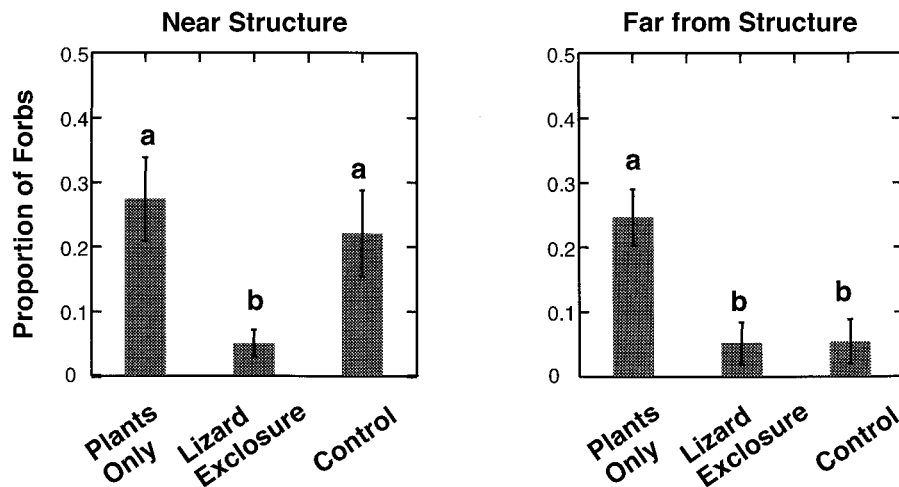


FIG. 7. The proportion (mean \pm 1 SD) of forbs from the different experimental treatments, as in Fig. 6. Different letters denote significant differences between treatments (Tukey's hsd for pairwise comparisons $P < 0.05$).

rare at distances >10 m from a structure (Fig. 1); it is not surprising that lizard impact on the food web is negligible at such distances. The natural experiment also indicated that, far from structures, there were no differences in grasshopper densities or plant biomass and composition between lizard and no-lizard structures.

Western fence lizards are common and conspicuous in a variety of community types throughout the warmer climates of the western United States (Stebbins 1985). These often-abundant insectivores might be expected to have large effects on the food web under certain circumstances. However, strong evidence for such top-down food web effects has been rare in terrestrial systems, particularly in grasslands. The relative dearth of evidence for top-down control in terrestrial systems has led some ecologists to suggest that such interactions may be largely restricted to aquatic habitats (e.g., Strong 1992, Polis and Strong 1996), despite the fact that many conceptual underpinnings of the top-down view were based on terrestrial patterns (Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981). Indeed, reviews of the evidence for trophic cascades in limnetic systems show their frequent importance (Leibold 1989, Carpenter and Kitchell 1993, Brett and Goldman 1996, 1997, Leibold et al. 1997). Nevertheless, some studies have experimentally shown top-down trophic cascades from insectivorous spiders, lizards, and birds to herbivorous insects and plants in terrestrial systems (Kajak et al. 1968, Schoener and Spiller 1987, Spiller and Schoener 1990, 1994, Marquis and Whelan 1994, Schmitz 1994, Dial and Roughgarden 1995, Chase 1996). These studies have only examined a subset of the community (e.g., insects on a single species of plant), and may not have allowed for compensation among other members of the community. Here, I explored the food web effects of a terrestrial predator on

a broader scale, allowing for species compensation, as well as for variation in predator effects through space.

A common feature of most natural food webs is that trophic levels are not internally homogeneous; instead, heterogeneity (i.e., more than one species per trophic level) and compensation within trophic levels can dilute the effects of top-down trophic cascades (e.g., Leibold 1989, 1996, Hunter and Price 1992, Strong 1992). There is considerable evidence for such compensation within trophic levels in both aquatic (e.g., Leibold 1989, Leibold et al. 1997) and terrestrial (e.g., Schmitz 1994) systems. In this study, I showed that even though consumers caused significant trophic cascades from the top down, there was also a significant change in plant species composition as a result of differential food web effects (Figs. 4 and 7). In the natural experiment, the relative abundance of forbs decreased with increasing distance from cover, presumably as a result of the increasing density of grasshoppers with distance. In addition, the manipulation experiment indicated that the relative proportion of forbs was highest with low levels of herbivory and lowest with high levels of herbivory. I suggest that this pattern may have arisen from one or a combination of two processes. First, the two most common species of grasshoppers in this study are of the genus *Melanoplus*, members of which typically prefer to consume forbs (Mulhern et al. 1969, Joern 1983, Chapman 1990; J. M. Chase, *unpublished data*). Because the majority of grasshoppers (by abundance) at this site prefer forbs, they should disproportionately consume them relative to grasses. This alone could lead to the observed pattern of forb abundances, because herbivory was highest far from lizard structures. The different levels of herbivory, combined with the grasshoppers' preference for forbs, may also have altered the competitive relationships among the plant species (e.g., Louda et al. 1990, Ritchie and Tilman 1993,

Schmitz 1994), causing a change in the relative abundances of grasses vs. forbs with changing levels of herbivory.

Results from the natural and manipulative experiments show that the presence of lizards on structures in meadows is important to local-scale food web processes. That is, the qualitative structure of the food web varies with distance from the structures, and the variation is a result of differential effects of lizard predation. However, the importance of the western fence lizard's restriction to structure in affecting food web interactions on a larger scale, such as whole meadows, remains to be tested. It is possible that the presence of lizard refugia may allow some degree of limitation of total grasshopper populations. Thus, meadows with more lizard structures may have fewer grasshoppers and more plants than meadows with fewer lizard structures, but this hypothesis remains to be tested. Another factor to be tested is the long-term impact of these trophic cascades on the community. This study was conducted during the summer, after the majority of plant growth had ceased. Grasshoppers may eat vegetation during summer drought conditions, but heavy winter and spring rains, with reduced herbivory due to grasshopper inactivity, may dilute this effect over the long term. Nonetheless, there was considerable live-plant biomass throughout the summer. Because many of these plant species are long-lived, it is likely that significant biomass impacts over the summer may lead to long-term effects. In addition, the gradients of plant abundance and composition with distance from the natural experiment have probably been formed over much longer time periods than the duration of this study.

In this study, the effects of lizards as predators in meadow food webs varied predictably with distance from their central-place structures. Use of a central place for foraging and other behaviors is common among a variety of animals, particularly those that use refugia from predators, feed young on a nest, or guard territories. Models of optimal foraging predict that a central-place forager should forage for shorter periods of time at increasing distance from its central place (Orians and Pearson 1979, Schoener 1979, Stephens and Krebs 1986). Although not explicitly considered in these foraging models, it follows that the impact of the central-place forager on its prey populations should decrease with distance from the central place, as was observed with the western fence lizards in this study. Models of optimal foraging were initially developed to gain insights into community dynamics (e.g., MacArthur and Pianka 1966), yet the degree to which knowledge of consumers' behaviors is necessary for understanding and predicting community outcomes is rarely studied.

There has been an increasing emphasis on exploring the relative strength or importance of species interactions within food webs (e.g., Paine 1988, 1992, Polis and Winnemiller 1996, Wootton 1997) and the relative

importance of top-down (consumer effects) vs. bottom-up (resource effects) food web regulation (Hunter and Price 1992, Power 1992a, Polis 1994, Leibold et al. 1997). This study showed that the top-down importance of lizards varied substantially through space. Other studies have shown similar spatial variation in predator effects (e.g., Power 1984, 1992b, Power et al. 1989, Abramsky et al. 1990, 1992), suggesting that this may be a common phenomenon. Such spatial variation in predator effects can be important for understanding how species distributions and abundances vary through space, but are rarely accounted for in conceptual analyses of food web structure and dynamics

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