TOP-DOWN IMPACTS ON CREOSOTEBUSH HERBIVORES IN A SPATIALLY AND TEMPORALLY COMPLEX ENVIRONMENT[1]

TED FLOYD[2]

Pesticide Research Laboratory, Pennsylvania State University, University Park, Pennsylvania 16802 USA

Abstract. I studied top-down effects on creosotebush (*Larrea tridentata*) insect herbivores by protecting them from bird and arthropod predation. The purpose of my study was to investigate experimentally the differential and/or interactive effects of two predator guilds on herbivore densities. I performed my experiments on 24 creosotebushes at each of three sites within the Jornada Long-Term Ecological Research Site in the Chihuahuan Desert of southwestern New Mexico, USA. At each site the experiment consisted of: six creosotebushes from which birds were excluded with nylon mesh cages; six creosotebushes from which arthropod predators were removed by hand or aspirator; six creosotebushes from which both birds and arthropod predators were removed; and six control creosotebushes from which neither birds nor arthropod predators were removed. I conducted nondestructive nocturnal visual censuses of herbivores on each creosotebush at the beginning of the experiments in mid-May, 6 wk after the start of the experiment in late June, and 12 wk after the start of the experiment in early August. I conducted these experiments and censuses in 1993 and again in 1994.

In both years the herbivore densities became significantly higher in experimental than in control creosotebushes. The effects of bird and arthropod predation on herbivore densities were additive in 1993, but they were compensatory in 1994. In 1994 arthropod predator densities became lower in creosotebushes from which birds had been removed than in creosotebushes from which birds had not been removed, but this result did not obtain in 1993. These results may be due to a combination of factors including: avian and arthropod predation on herbivores, "intraguild" predation of birds on arthropod predators, and competition within the herbivore community. The relative numerical impacts of the predator-removal experiments varied among seasons and among sites within either year, but temporal and spatial variation in predator impacts did not correlate strongly with known gradients of climatic or bottom-up heterogeneity in this system. The results of this study confirm the important direct and cumulative effects of multiple predator guilds, even against a complex background of temporal and spatial heterogeneity.

Key words: arthropod predation; avian predation; Chihuahuan Desert, New Mexico; creosotebush; field experiment; herbivorous insect populations; Larrea tridentata; *Long-Term Ecological Research (LTER) Site; predator-removal experiments; spatial and temporal heterogeneity; top-down forces.*

INTRODUCTION

Hairston et al. (1960) proposed that terrestrial herbivore populations are regulated primarily by predation. This view engendered considerable controversy and remains hotly contested (Strong 1988, Matson and Hunter 1992). The role of predation and other "top-down" forces has been investigated by theoreticians and empiricists alike, in many systems and from various conceptual perspectives. Recent interest has focused especially on the consequences of environmental heterogeneity for top-down forces (Hunter and Price 1992) and has emphasized the value of predator "exclosure" experiments (Price 1987).

The evidence for short-term impacts and potential long-term effects of terrestrial natural enemies on herbivorous insects is equivocal. Bird exclusion experiments have revealed short-term negative effects on herbivorous insects (Joern 1986), long-term effects (Bock et al. 1992), unclear effects (Wiens et al. 1991), or positive effects (Belovsky et al. 1990). Removals of arthropod natural-enemy populations have produced similarly ambiguous results. Removal of parasitoids may produce important effects (Gómez and Zamora 1994), as well as no effects (Price 1990), on herbivorous-insect densities. Likewise, arthropod predator removal experiments have documented weak (Spiller and Schoener 1994), modest (Warrington and Whittaker 1985), and drastic (Risch and Carroll 1982) top-down impacts on herbivorous-insect population densities.

The impacts of top-down forces in terrestrial ecosystems thus appear highly variable, and their ecological and evolutionary consequences are not fully understood. For example, the influences of predation on primary production (Strong 1992) or on the evolution of prey

[2] Present address: Department of Biology, Williams College, Williamstown, Massachusetts 01267 USA.

1544

diet breadth (Courtney 1988) are not well established. To understand and to predict variation in the strength of top-down forces, two premises must be accepted. First, the environments in which natural enemies and their prey populations occur are typically heterogeneous, and it is essential that environmental heterogeneity be incorporated into any consideration of top-down impacts specifically (Hunter and Price 1992, Karban et al. 1994, Kruess and Tscharntke 1994) or ecological processes generally (Levin 1992). A second, and related, complication is that herbivore populations are typically influenced by a variety of natural-enemy complexes (Holt 1984). In particular, competitive or predatory interactions within the natural-enemy community (Polis et al. 1989, Polis and Holt 1992) may in turn affect its impact on herbivores (Rosenheim et al. 1993, Spiller and Schoener 1994, Werner and McPeek 1994).

Herbivorous insects on creosotebush live in a heterogeneous environment, in which host plant quality can vary significantly both within and among stands of creosotebush (Lightfoot and Whitford 1987, 1989, 1991). Birds (Raitt and Pimm 1976) and arthropod predators (Chew 1961) are abundant and potentially important as top-down influences in this system. The creosotebush system is therefore suitable for examining the following questions: What are the direct influences of avian and arthropod predation on creosotebush herbivore densities? To what extent are predator effects mediated indirectly by intraguild interactions, such as predation within the predator community or competition within the herbivore community? In what ways do spatial and temporal heterogeneity modify the impacts of birds and arthropod predators on creosotebush herbivore populations?

METHODS

Study sites

I conducted all of my experiments and censuses at three sites scattered across a bajada–playa transition at the Jornada Long-Term Ecological Research (LTER) Site in Doña Ana County, New Mexico, USA. Each site was an approximately circular region ($\approx$2000 m^2) of Chihuahuan Desert scrub dominated by creosotebush (*Larrea tridentata* [DC] Cov.). Sites were chosen based on previous floral and faunal studies (Lightfoot and Whitford 1989, D. C. Lightfoot, *personal communication*, J. C. Schultz et al., *unpublished data*) and represented a range of environmental heterogeneity typical of the bajada–playa transition zone. Site A was centered at 32°28′42.36″ N, 106°44′15.36″ W and consisted primarily of creosotebush, tarbush (*Flourensia cernua* DC), and grasses in the genus *Bouteloua*. Site B, located at 32°30′58.09″ N, 106°47′36.60″ W, was a virtual monoculture of creosotebushes. Site C, centered at 32°30′31.78″ N, 106°47′12.51″ W, contained creosotebushes and a few honey mesquites (*Prosopis glandulosa* Torr.). Creosotebushes at Sites B and C have
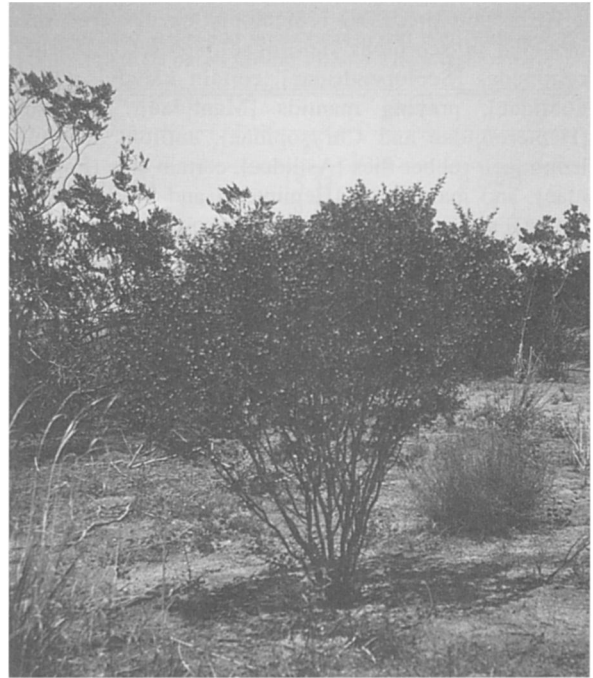

PLATE 1.   Creosotebush (*Larrea tridentata*). Photograph by J. C. Schultz.

been characterized as "poor" and "high" quality, respectively, by Lightfoot and Whitford (1989), based on chemical characterization of creosotebush leaf tissue. High-quality creosotebushes have higher foliar water and nitrogen contents and lower foliar resin contents than do low-quality creosotebushes (Lightfoot and Whitford 1989). Creosotebushes at Site A were not studied by Lightfoot and Whitford (1989), but have "high-quality" foliar chemical profiles, similar to the creosotebushes at Site C (J. C. Schultz and H. M. Appel, *unpublished data*).

Predator removals and herbivore censuses

Each of the three sites contained $\approx$100–200 creosotebushes that appeared to vary considerably in height, width, and apparent foliage "quality" (sensu Lightfoot and Whitford 1989). Within each site I selected 24 creosotebushes ($n = 72$ creosotebushes for the entire study) that were $\approx$1.5 m tall and 1.5 m wide, but whose foliage quality and other shrub chemical parameters were initially unknown. The standardization of creosotebush size was necessary to ensure statistically manageable sample sizes, to facilitate the construction and maintenance of whole-creosotebush predator removals, and to permit multiple and thorough whole-creosotebush arthropod censuses. Within each site I randomly assigned each of the 24 creosotebushes to one of the following four predator-removal treatments ($n = 6$ creosotebushes per treatment per site): controls; arthropod predator removals; bird removals; and bird and arthropod predator removals.

Arthropod predators (commonly encountered taxa included sunscorpions [Solifugae], spiders [Araneae], centipedes [Scolopendridae], certain katydids [Tettigoniidae], praying mantids [Mantidae], lacewings [Hemerobiidae and Chrysopidae], antlions [Myrmeleontidae], robber flies [Asilidae], certain ants [Formicidae], and many bugs [Hemiptera] and beetles [Coleoptera]) and parasitoids (mainly wasps [Hymenoptera]) were hand picked or aspirated from the six creosotebushes per site that were assigned to the arthropod predator-removal treatment. Known omnivores (e.g., certain katydids [Tettigoniidae] and stinkbugs [Pentatomidae]) also were removed. I visited each creosotebush in this treatment class 2–3 nights per week during every week of the 12-wk study period, and removed every predator or parasitoid that I encountered. The number of predators encountered decreased quickly after establishment of this treatment class (see *Results*), indicating the effectiveness of this technique. I did not perform a sham treatment for the arthropod predator removals, because my handling of the creosotebushes during the predator removals was nearly negligible. I inspected the creosotebushes by sight and removed almost all predators by an aspirator, which almost never came in contact with the foliage. Moreover, if there was a consistent bias, it would have been an error on the conservative side, as any disturbances would likely have reduced, not increased, herbivore densities. Birds had free access to creosotebushes in this treatment class.

Mesh cages were constructed around the six creosotebushes per site from which birds were to be excluded. Each bird exclosure was supported by a cube-shaped scaffold of four steel reinforcement rods ("rebar") whose tops were joined diagonally by polyvinyl chloride (PVC) piping and plastic connectors. The rebar uprights were 1 cm in diameter and 250 cm long. Each upright was driven 50 cm into the ground, so that each one was 200 cm tall. The PVC pipes were 2.5 cm in diameter and 300 cm long. Monofilament gill netting (1.25-cm mesh; stock number N103, Nylon Net Company, Memphis, Tennessee, USA) was draped fairly tightly around each exclosure and fastened to the rebar uprights and PVC crossbars with 4-kg test fishing line. The 1.25-cm mesh size was small enough to prevent access by the smallest insectivorous birds (hummingbirds [Trochilidae] and gnatcatchers [*Polioptila* sp.]) in the system but large enough to permit transit of even the largest arthropod predators (sunscorpions, mantids, and large ground beetles [Carabidae]). However, the possibility exists that transit of the largest arthropods could at least have been impeded by the 1.25-cm mesh size. The bird exclosure cages were probably completely effective at preventing avian access to creosotebushes. Bird exclosure cages similar to the type used in my study do not create microclimate alterations in rainfall, temperature in full sun, or temperature in shade (Bock et al. 1992).

The third treatment class, from which both birds and arthropod predators were removed, consisted of both the arthropod predator removals and the bird exclosure cages, described above. Lastly, the six controls at each site were unmanipulated and were completely accessible to birds and arthropod predators.

I established the study sites and predator removals in mid-May of 1993 and conducted whole-creosotebush non-destructive, nocturnal visual censuses of the arthropod fauna of each creosotebush at this time (Week 0). The census process was time consuming, so I could only census 8 of the 72 creosotebushes per night. The Week 0 arthropod census therefore required nine consecutive nights of work. Each night I censused two creosotebushes from each treatment or control class at one site. Commonly encountered herbivores on creosotebush at the Jornada LTER site are described in Lightfoot and Whitford (1987). Trophic levels of creosotebush arthropods (i.e., herbivores, predators, and a few omnivores) were determined by direct observation and discussion with G. S. Forbes and D. C. Lightfoot.

The order in which the censuses were conducted was rotated each night, preventing systematic time-of-night biases. I spent enough time at each creosotebush as was necessary for a thorough census of all arthropods. I censused each creosotebush again during a nine-night period in mid-June (Week 6) and a third time during a nine-night period in early August (Week 12). Week 0 occurred towards the end of the mild spring season and coincided with the onset of breeding by insectivorous birds. Week 6 marked the end of the typically hottest and driest period of the year. Week 12 occurred in the midst of the Chihuahuan Desert's marked rainy season. I repeated these censuses, on the same creosotebushes, during the same times of the year in 1994.

Statistical analyses

I used the repeated-measures multivariate analysis of variance (MANOVA) technique to test for effects of site, season, year, and predator-removal treatments on herbivore abundance. I excluded from analysis all adult moths [Lepidoptera], plus any herbivore that was not actually resting, eating, or interacting on a creosotebush. This adjustment reduced considerably my sample sizes, but it was required to eliminate from analysis any herbivores that may have been attracted to my head lamp. Data transformations, profile analyses, and experimentwise adjustments of critical α were based on the general treatment in Sokal and Rohlf (1981) and the specific recommendations in Warren (1986), Day and Quinn (1989), SAS Institute (1992), Scheiner (1993), von Ende (1993), and Bennington and Thayne (1994). I used the General Linear Models (GLM) procedure (version 6.07) in SAS (SAS Institute 1992) for all statistical analyses. I employed a critical α of 0.05 for rejections of null hypotheses. I used a repeated-measures approach, because multiple measurements were made of the basic sampling unit (i.e., a creosotebush). Herbivore counts were $\log_{10}$ trans-

TABLE 1. Repeated-measures MANOVA of the effects of site, bird exclosure (Bird), arthropod predator removal (Arth), and season (i.e., sampling week) on herbivore densities. Bird exclosure and arthropod predator removal constitute a 2 × 2 factorial design. Within-subject effects are analyzed using F approximations based on the Pillai's Trace test statistic.

Effect	df	1993		1994	
		F	P	F	P
Bird	1	30.12	<0.0001	15.52	0.0002
Arth	1	3.54	0.06	6.28	0.01
Bird × Arth	1	0.10	0.75	4.03	0.04
Site	2	18.60	<0.0001	15.52	<0.0001
Site × Bird	2	2.63	0.08	1.48	0.24
Site × Arth	2	1.42	0.25	0.47	0.63
Site × Bird × Arth	2	0.72	0.49	3.35	0.04
Residual 1	60				
Subtotal 1	71				
Week	2	23.73	<0.0001	7.16	0.002
Week × Bird	2	2.46	0.09	2.62	0.08
Week × Arth	2	4.19	0.02	0.94	0.40
Week × Bird × Arth	2	0.25	0.78	2.56	0.08
Week × Site	4	1.42	0.23	9.86	<0.0001
Week × Site × Bird	4	0.30	0.87	0.12	0.97
Week × Site × Arth	4	0.34	0.85	0.20	0.94
Week × Site × Bird × Arth	4	0.64	0.63	0.11	0.98
Residual 2	120				
Total	215				

formed, yielding data with standard deviations independent of means, producing equal variances, and reducing all coefficients of variation. To accommodate the logarithmic transformation of sampling zeros, 1 was added to each herbivore count. The covariance structure was not spherical (see von Ende 1993), so I analyzed time and time-by-treatment effects using the Pillai's Trace MANOVA test statistic (see Scheiner 1993).

Preliminary five-way repeated-measures MANOVA on herbivore counts indicated a complex interaction among year, sampling date, and site ($F = 4.84$; df = 4, 120; $P = 0.001$). In particular, no simple patterns of year-to-year variation were obvious. To simplify interpretation I analyzed the data for each year (1993 and 1994) separately in four-way repeated-measures MANOVAs, with bird removal, arthropod predator removal, and site as main effects and with sampling date (i.e., season) as a within-subject repeated measure (Table 1). I treated each among-subjects predictor variable as a fixed effect. Location (three levels: Site A, Site B, and Site C) was a fixed effect, because the three sites were nonrandomly selected to span the range of environmental heterogeneity typical of creosotebush-dominated bajada–playa transitions. Bird removal (two levels: birds excluded, birds present) and arthropod predator removal (two levels: arthropod predators removed, arthropod predators present) were treatment effects with fixed levels. Treating bird removals and arthropod predator removals as main effects in a 2 × 2 factorial design enabled me to test for additivity of predator effects. Because numerous main effects and interactions varied with sampling date, I also present ANOVAs of bird removal, arthropod predator removal, and site, for each level of season, in 1993 and in 1994 (Table 2). I used

profile analysis (see SAS Institute 1992, von Ende 1993) to analyze treatment-effect differences on adjacent sampling dates.

To test for differences among arthropod predator densities, I again relied on two separate four-way repeated-measures MANOVAs for the 2 yr, with bird removal, arthropod predator removal, and site (levels of each variable as in the analysis of herbivore densities, above) as main effects, repeated by sampling date (Table 3). Although I removed all arthropod predators that I encountered, I do not present data for flying predators or parasitoids that I judged to be highly mobile (e.g., lacewings, robber flies, and wasps), because it is unlikely that the hand-picking and aspirating techniques were effective at reducing densities of these arthropods. I interpreted the effects of predator removal as follows: (1) the effect of arthropod predator removal served to confirm the effectiveness of my removal technique; (2) the effect of bird removal tested whether birds depressed herbivore densities; (3) the interaction between bird and arthropod predator removal helped to explain how the effect of bird predation differed between creosotebushes with low vs. high arthropod predator density. As in the analysis of herbivore densities, I present profile analyses and ANOVAs of bird removal, arthropod predator removal, and site, for each level of season, in 1993 and in 1994 (Table 4).

RESULTS

Herbivore densities

In 1993, bird predation significantly depressed herbivore densities (Table 1, Fig. 1). The season-wide effect of arthropod predation was not significant, but the impact of arthropod predator removal increased sig-
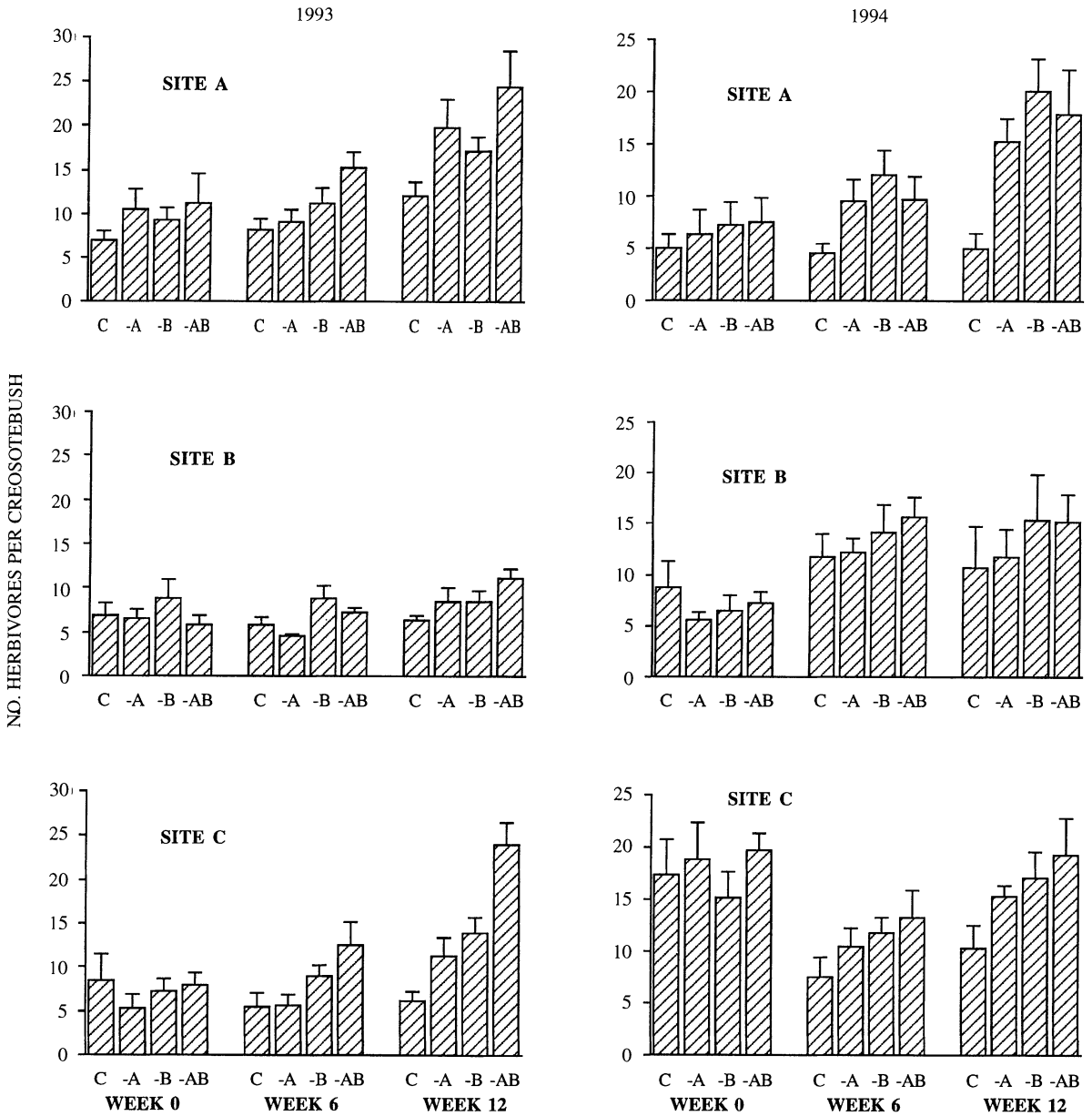
FIG. 1. Creosotebush herbivore densities (mean and 1 SE) at the Jornada Long-Term Ecological Research Site (New Mexico, USA). Herbivore densities are shown for each level of site (A, B, or C), season (Week 0, Week 6, or Week 12), and predator-removal treatment (C, controls; −A, arthropod predator removals; −B, bird removals; −AB, double removals).

nificantly during the year (Table 1, Fig. 1). In particular, the profile analysis (Table 2) indicated a significant change between Weeks 6 (no effect) and 12 (strong negative effect of arthropod predation). The combined impacts of bird and arthropod predation were additive (Table 1). Herbivore densities varied through time as follows: initial (Week 0) herbivore densities at each site were statistically indistinguishable with regard to any predator effect; by Week 6, herbivore densities were significantly higher in bird removals but not in arthropod predator removals; by Week 12 herbivore densities were significantly higher in both bird and ar-

thropod removals, and the combined effect of bird and arthropod predation was additive (Table 2, Fig. 1). Herbivore densities also varied significantly among sites, with higher densities at Site A than at Sites B or C (Table 1, Fig. 1). Site differences were consistent across weeks, and the overall effects of arthropod predator removal were independent of site (Table 1). In Week 12, however, the impact of bird predation was significantly stronger at Sites A and C than at Site B (Table 2, Fig. 1).

In 1994, both birds and arthropod predators significantly depressed herbivore densities, and an interac-

TABLE 2. ANOVAs of the effects of site, bird exclosure (Bird), and arthropod predator removal (Arth) on herbivore densities, at each sampling week. Bird exclosure and arthropod predator removal constitute a 2 × 2 factorial design. For each sampling week, residual df = 60 and total df = 71.

Sampling week	Effect	df	1993		1994	
			F	P	F	P
0	Bird	1	1.09	0.30	0.22	0.64
	Arth	1	0.20	0.66	0.22	0.64
	Bird × Arth	1	0.00	0.95	0.60	0.44
	Site	2	1.86	0.16	27.50	<0.0001
	Site × Bird	2	0.21	0.81	0.36	0.70
	Site × Arth	2	0.49	0.61	0.51	0.60
	Site × Bird × Arth	2	1.25	0.29	0.53	0.59
6	Bird	1	20.06	<0.0001	9.64	0.003
	Arth	1	0.19	0.67	2.47	0.12
	Bird × Arth	1	0.60	0.44	3.25	0.08
	Site	2	6.74	0.002	6.70	0.002†
	Site × Bird	2	0.60	0.55	0.37	0.69
	Site × Arth	2	1.04	0.36	0.04	0.96
	Site × Bird × Arth	2	0.09	0.92	1.54	0.22
12	Bird	1	28.90	<0.0001	11.92	0.001
	Arth	1	20.23	<0.0001†	5.56	0.02
	Bird × Arth	1	0.02	0.89	4.42	0.04
	Site	2	22.85	<0.0001	1.56	0.22†
	Site × Bird	2	4.18	0.02	0.93	0.40
	Site × Arth	2	0.87	0.42	0.27	0.77
	Site × Bird × Arth	2	0.19	0.83	1.69	0.19

† Indicates that the effect had changed significantly since the preceding sampling date (profile analysis critical α adjusted to account for experiment error rate).

tion between predator effects was significant (Table 1, Fig. 1). Herbivore densities varied through time as follows: initial (Week 0) densities at each site were statistically indistinguishable with regard to any predator effect; by Week 6, herbivore densities were significantly higher in bird removals but not in arthropod predator removals; by Week 12 herbivore densities were significantly higher in both bird and arthropod removals, and the combined effect of bird and arthropod predation was non-additive (Table 2, Fig. 1). Herbivore densities also varied significantly among sites, with lower densities at Site B than at Sites A or C (Table 1, Fig. 1). Moreover, this relationship was dependent on week (Table 1), due especially to high Week 0 densities at Site C and high Week 12 densities at Site A (Fig. 1). The effects of either removal treatment were independent of site (Table 1). However, the interaction between removal treatments varied among sites (Table 1), due primarily to stronger non-additivity of effects at Site A than at Site C (Fig. 1).

Effectiveness of the predator removals

In 1993, arthropod predator densities were significantly higher in controls and bird removals than in arthropod predator removals and double removals, and this difference increased significantly through the year (Table 3, Fig. 2). Arthropod predator densities varied through time as follows: initial (Week 0) arthropod predator densities at each site were not statistically different among predator removal treatments; by Week 6 densities were significantly higher in controls and bird removals than in arthropod pred-

ator removals and double removals, and in Week 12 this difference was again significant (Table 4, Fig. 2). Arthropod predator densities also varied significantly among sites (Table 3), with generally higher densities at Site C than at Sites A or B (Fig. 2). The main effect of arthropod predator removal did not vary with site, and the effect of site was independent of the effect of week (Table 3).

In 1994, the season-wide effect of arthropod predator removal on arthropod predator densities was not significant (Table 3). However, the effect of arthropod predator removal showed complex and significant variation through the year, as follows: Week 0 densities at each site were statistically indistinguishable among removal treatments; in Week 6 densities did not differ significantly among treatments, but relative to Week 0 densities they were significantly higher in controls and bird removals than in arthropod predator removals and double removals; in Week 12, densities were significantly higher in controls and bird removals than in arthropod predator removals and double removals (Table 4, Fig. 2). Arthropod predator densities differed significantly among sites (Table 3), with densities generally lower at Site B than at Sites A or C (Fig. 2). The effect of site was independent of sampling date, and the effect of arthropod predator removal was independent of site (Table 3).

Avian depression of arthropod predator densities

In 1993 there was no season-wide depression of arthropod predator densities in the controls and arthropod
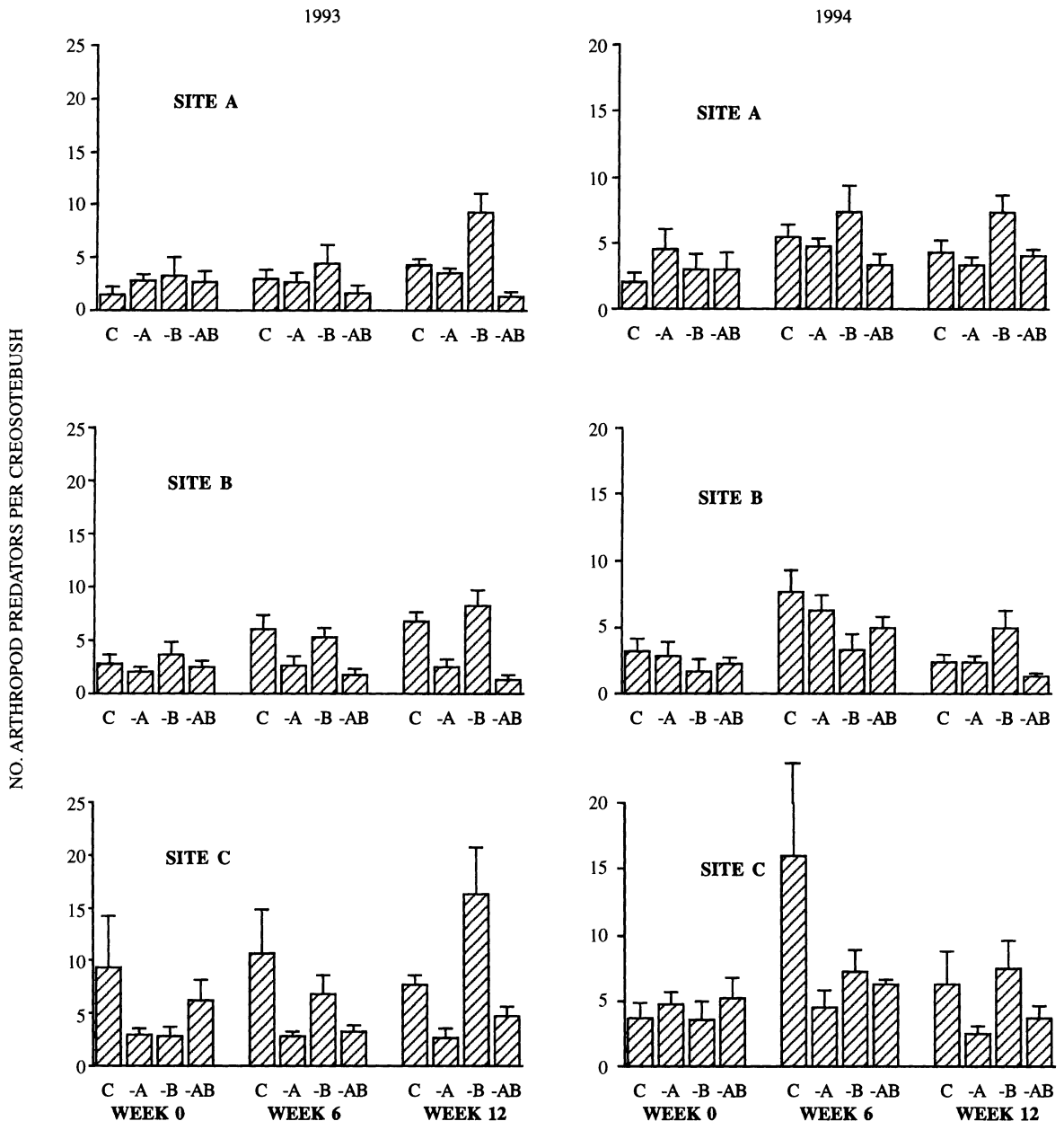
FIG. 2. Arthropod predator densities (mean and 1 SE) at the Jornada Long-Term Ecological Research Site (New Mexico, USA). Arthropod predator densities are shown for each level of site (A, B, or C), season (Week 0, Week 6, or Week 12), and predator removal treatment (C, controls; −A, arthropod predator removals; −B, bird removals; −AB, double removals).

predator removals relative to the bird removals and double removals, and this relationship showed no pattern of significant variation through the year (Table 3). However, the effects of birds on arthropod predator densities may have been masked by an interaction with the effect of arthropod predator removal (Table 3). In particular, birds tended to depress arthropod predator densities in creosotebushes from which arthropod predators had not been removed, but not in creosotebushes from which arthropod predators had been removed (Table 3, Fig. 2). Moreover, the effect of bird removal on

arthropod predator removal varied with site (Table 3), due to a stronger influence of arthropod predator removal on bird removal effects at Sites A and B than at Site C (Fig. 2).

In 1994 there was again no season-wide depression of arthropod predator densities in the controls and arthropod predator removals relative to the bird removals and double removals, but this relationship varied significantly throughout the year (Table 3, Fig. 2). Effects of bird removal on arthropod predator densities varied through time as follows: in Weeks 0 and 6 densities in

TABLE 3. Repeated-measures MANOVA of the effects of site, bird exclosure (Bird), arthropod predator removal (Arth), and season (i.e., sampling week) on arthropod predator densities. Bird exclosure and arthropod predator removal constitute a 2 × 2 factorial design. Within-subject effects are analyzed using F approximations based on the Pillai's Trace test statistic.

Effect	df	1993		1994	
		F	P	F	P
Bird	1	0.05	0.82	0.32	0.57
Arth	1	29.49	<0.0001	2.16	0.15
Bird × Arth	1	0.76	0.39	0.02	0.88
Site	2	9.03	0.0004	4.19	0.02
Site × Bird	2	0.17	0.84	0.48	0.62
Site × Arth	2	1.52	0.23	0.37	0.69
Site × Bird × Arth	2	4.03	0.02	1.45	0.24
Residual 1	60				
Subtotal 1	71				
Week	2	10.04	0.0002	24.40	<0.0001
Week × Bird	2	0.73	0.49	4.52	0.01
Week × Arth	2	16.14	<0.0001	5.63	0.005
Week × Bird × Arth	2	3.63	0.03	2.78	0.07
Week × Site	4	0.53	0.72	2.06	0.09
Week × Site × Bird	4	1.51	0.20	0.21	0.93
Week × Site × Arth	4	0.15	0.96	1.20	0.32
Week × Site × Bird × Arth	4	0.25	0.91	1.50	0.20
Residual 2	120				
Total	215				

creosotebushes from which birds had been removed did not differ significantly from densities in creosotebushes from which birds had not been removed; in Week 12 densities were significantly higher in creosotebushes from which birds had been removed than in creosotebushes from which birds had not been removed (Table 4, Fig. 2).

DISCUSSION

Natural enemies frequently have modest effects (Holmes et al. 1979, Joern and Rudd 1982, Gómez and Zamora 1994), but may sometimes produce severe effects (Beddington et al. 1978, Risch and Carroll 1982, Terborgh 1992), on terrestrial herbivore populations.

TABLE 4. ANOVAs of the effects of site, bird exclosure (Bird), and arthropod predator removal (Arth) on arthropod predator densities, at each sampling week. Bird exclosure and arthropod predator removal constitute a 2 × 2 factorial design. For each sampling week, residual df = 60 and total df = 71.

Sampling week	Effect	df	1993		1994	
			F	P	F	P
0	Bird	1	0.16	0.69	0.65	0.42
	Arth	1	0.10	0.75	1.12	0.29
	Bird × Arth	1	0.61	0.44	0.01	0.94
	Site	2	2.99	0.06	1.81	0.17
	Site × Bird	2	0.30	0.74	0.06	0.94
	Site × Arth	2	0.78	0.46	0.08	0.92
	Site × Bird × Arth	2	2.41	0.10	0.97	0.38
6	Bird	1	0.45	0.50	3.31	0.07
	Arth	1	18.76	<0.0001†	2.48	0.12†
	Bird × Arth	1	0.11	0.74	2.35	0.13
	Site	2	5.22	0.008	2.44	0.10
	Site × Bird	2	0.01	0.99	0.85	0.43
	Site × Arth	2	0.87	0.42	2.11	0.13
	Site × Bird × Arth	2	0.90	0.41	2.40	0.10
12	Bird	1	0.76	0.38	4.05	0.04†
	Arth	1	76.95	<0.0001	16.19	0.0002
	Bird × Arth	1	8.76	0.004	2.57	0.11†
	Site	2	5.69	0.005	7.84	0.0009†
	Site × Bird	2	3.31	0.04	0.29	0.75
	Site × Arth	2	0.51	0.60	0.42	0.66
	Site × Bird × Arth	2	2.84	0.06	1.52	0.23

† Indicates that the effect had changed significantly since the preceding sampling date (profile analysis critical α adjusted to account for experimentwise error rate).

In my study, overall herbivorous insect density was >50% lower on controls than on creosotebushes from which birds and arthropod predators had been removed. The creosotebush system is obviously heterogeneous, however, even within the narrow spatial and temporal windows in which I worked. Overall herbivore densities varied greatly with site, season, year, and a complex interaction among all three. Plant chemistry, precipitation, and temperature vary considerably in this system (Lightfoot and Whitford 1989, New Mexico State University Climate Network, *unpublished meteorological data*). Bird and arthropod predators therefore encountered a heterogeneous resource base in a complex chemical and physical environment. Against this backdrop of environmental heterogeneity, the relative roles of, and interactions between, bird and arthropod predation were complex and variable.

Effects of predators

In 1993 the effects of bird and arthropod predation on herbivore densities were additive. Therefore, competition for food (i.e., herbivores) did not appear to limit the joint impacts of bird and arthropod predators. Herbivore populations had begun to respond to predator removals by Week 6. There was no effect of arthropod predator removals at this time, but herbivore densities were higher in bird removals. Densities were 1.5 times higher in bird exclosures than in controls and 1.6 times higher in double removals than in controls, and there was no interaction between the effects of bird and arthropod predation. Thus, there appeared to be a direct negative effect of bird predation and no effect of arthropod predation by Week 6. By Week 12 there were significant effects of both bird predation and arthropod predation, and there was no interaction between the effects. Herbivore densities were 1.6 times higher in bird exclosures than in controls, 1.5 times higher in arthropod predator removals than in controls, and 2.3 times higher in double removals than in controls. Thus, either predator class removed approximately the same number of herbivores in single removals as in double removals, suggesting little if any competition between the two predator classes. Although the overall effects of bird and arthropod predation were strongly additive in 1993, my study was not designed to test the possibility of non-additive interactions within a predator guild.

In 1994, however, the effects of bird and arthropod predation on herbivore densities were not additive. Instead, densities in the double removals were approximately equivalent to densities in the single removals. A possible explanation is that birds and arthropod predators were in competition for herbivore food resources in 1994. When one predator class was removed, the other predator class consumed food resources whose availability may have been limited by competition. By Week 6, birds had a significant negative effect on herbivore populations but arthropod predators did not, as

in 1993. There was a nonsignificant trend toward non-additivity of predator effects by this time, with herbivore densities 1.4 times higher in arthropod predator removals than in controls, 1.7 times higher in bird exclosures, and 1.6 times higher in double removals. By Week 12, there were significant negative effects of both bird and arthropod predators, and there was a significant interaction between the effects of the two predator classes. Herbivore densities were 1.8 times higher in arthropod removals than in controls, 2.1 times higher in bird removals, and also 2.1 times higher in double removals. Birds and arthropod predators may have competed for food resources, since their combined presence did not depress herbivore densities below densities in the presence of a single predator class. However, my study was not designed to detect the consequences of competition, such as emigration or reduced feeding or growth rates, in the presence of presumed competitors. Moreover, it is possible that non-additivity of predator effects was caused, in part, by intraguild predation (see below).

Predation also appears to have occurred within the predator guild. In 1994, arthropod predator densities became significantly higher in creosotebushes from which birds had been removed than in creosotebushes from which birds had not been removed. In 1993, overall arthropod predator densities did not differ between creosotebushes from which birds had been removed and creosotebushes from which birds had not been removed. In both years, however, the effects of bird removal were modified by arthropod predator removal in a manner that helps to highlight the possibility of intraguild predation in the creosotebush system. In particular, the negative impact of birds on arthropod predator densities was stronger where arthropod predator densities were high (i.e., in a comparison of controls and bird removals) than where they were low (i.e., in a comparison of arthropod predator removals and double removals). In 1993, Week 12 arthropod predator densities were 1.6 times higher in bird removals than in controls, and in 1994 densities were 1.5 times higher in bird removals than in controls. By Week 12 of both years, then, intraguild predation of birds on arthropod predators was strongly suggested. In a similar study, predatory scorpions preyed upon and depressed the densities of predatory spiders (Polis and McCormick 1986) or each other (Polis and McCormick 1987). The weaker effect of bird predation in the arthropod predator removals and double removals was probably due to the fact that my removal technique simply reduced densities to equally low levels in both treatment classes.

Because birds depressed arthropod predator densities, and because arthropod predators in turn depressed herbivore densities, there was the possibility that birds may have indirectly enhanced herbivore populations by depressing arthropod predator densities. However, herbivore densities at the end of the study period were

consistently lower in controls than in bird removals, so it seems especially unlikely, although not disproved, that bird predation on arthropod predators resulted in increased herbivore densities. These results contrast with those of Pacala and Roughgarden (1984), in which exclusion of top predators (lizards) caused increases of intermediate predators (spiders) and subsequent decreases of foliage insects. My results do, however, accord with Diehl's (1993) prediction that predators that consume resources from more than one trophic level (as do birds in this system) should not show indirect positive effects on basal prey densities.

The results of this study support the view that interactions within a natural enemy community can be complex (Polis et al. 1989, Polis and Holt 1992), and they support the growing body of evidence that direct and indirect interactions among predators can have significant consequences for the overall expression of top-down forces in a system (e.g., Rosenheim et al. 1993, Karban et al. 1994, Spiller and Schoener 1994, Werner and McPeek 1994). In the creosotebush system, I present evidence for additive effects of predation (Rosenheim et al. 1993), compensatory effects of predation (Campbell et al. 1983), intraguild competition (Belovsky et al. 1990), and intraguild predation of birds on other predators (Adolph and Roughgarden 1983). A cascading effect (Bock et al. 1992) either did not occur or was obscured due to bird predation on both arthropod predators and herbivores. The results of this study are consistent with Holt's (1984) conclusion that predator effects on prey populations must be considered in terms of complex interactions within the predator community.

Consequences of environmental heterogeneity

Studies of top-down effects on terrestrial herbivore populations have tended to focus on situations that are either inherently homogeneous (Fowler et al. 1991) or whose heterogeneity was intentionally minimized (Bock et al. 1992). In contrast, the creosotebush system is highly heterogeneous, especially for "bottom-up" phenomena such as host plant quality (Lightfoot and Whitford 1989), or abiotic phenomena such as nutrient and soil characteristics (Lajtha and Schlesinger 1986) and climatic patterns (Cable 1975). Heterogeneity in the creosotebush system therefore enables a consideration of the conditions under which top-down forces may be expected to be important (Hunter and Price 1992). Although the variability per se of top-down forces among systems (Price 1987), and to a lesser extent within systems (Karban et al. 1994), has been well established, there is comparatively little theory predicting when and where top-down forces should most likely be important (Hairston et al. 1960, Oksanen et al. 1981, Liebold 1989). Even rarer is empirical evidence that the strengths of top-down forces vary systematically along gradients of one or more heterogeneous environmental parameters (Kruess and Tscharntke 1994).

In my study, environmental conditions were known to vary as follows. First, creosotebush leaf chemical quality was poorer at Site B than at either Sites A or C (Lightfoot and Whitford 1989; J. C. Schultz and H. M. Appel, *unpublished data*). Second, in both years Week 6 coincided with the end of the hottest and driest conditions of the year, whereas Week 12 occurred well into the milder rainy season. Third, precipitation and temperature were normal during the 12-wk study period in 1993, whereas record-high temperatures and below-average precipitation occurred during the 1994 study period (New Mexico State University Climate Network, *unpublished meteorological data*).

Do predator impacts, then, vary spatially and temporally in the creosotebush system? In particular, are predator effects strongest where bottom-up resources are most abundant, as suggested by Arruda (1979) and further developed theoretically by Oksanen et al. (1981)? The evidence from the creosotebush system is equivocal. First, predator removal treatments had a greater numerical impact on herbivore densities at Sites A and C than at Site B in both years, but site × treatment interactions were not significant for most comparisons. Second, the effects of birds on herbivore densities were approximately equivalent in Weeks 6 and 12 of either year, but effects of arthropod predators on herbivore densities were absent in Week 6 but present in Week 12 of both years. Third, the effects of bird and arthropod predation were additive in 1993 but not in 1994, indicating possible increased competition among predators in 1994. Predator impacts were variable in this system, but it is not clear that predator impacts varied systematically along gradients of bottom-up heterogeneity.

Overall variation in herbivore densities was significantly attributable to the main effects of top-down forces and site-to-site heterogeneity, but considerable variation remained unexplained at the end of each year (Week 12 $r^2 = 0.64$ in 1993; Week 12 $r^2 = 0.34$ in 1994). Moreover, the mechanistic link between environmental heterogeneity and variation in predator effects remains to be elucidated. Large-scale (site-level) and especially small-scale (plant-level) leaf chemical differences may play a role, by influencing the behavior and densities of herbivores (Lightfoot and Whitford 1987). Heterogeneity in plant architecture, which is an important determinant of avian breeding biology (Tomoff 1974) and foraging biology (Robinson and Holmes 1984), could influence the effectiveness of birds as predators in this system. Weather may produce important direct or indirect effects, too. As a direct effect, weather is likely to affect the foraging behavior of birds and arthropod predators. As an indirect effect, weather is likely to affect plant phenology, chemistry, and architecture, which could, in turn, influence herbivore behaviors and densities.

Predation is clearly important in this system, and its impact varies within the predator community and in

space and in time. A general model incorporating the effects of predation, site, and season left unaccounted for one third of the variation in herbivore densities in 1993 and two thirds of the variation in herbivore densities in 1994. The results of this study imply that the remaining one third to two thirds could be accounted for by further investigating the competitive and predatory interactions among natural enemies, by considering the direct and indirect impacts of weather on predator behavior and densities, and by focusing on the local (i.e., within-site) effects of plant quality or other bottom-up influences on herbivore populations.

LITERATURE CITED

Adolph, S. C., and J. Roughgarden. 1983. Foraging by passerine birds and *Anolis* lizards on St. Eustatius (Neth. Antilles): implications for interclass competition, and predation. Oecologia **56**:313–317.

Arruda, J. A. 1979. A consideration of trophic dynamics in some tallgrass prairie farm ponds. American Midland Naturalist **102**:254–262.

Beddington, J. R., C. A. Free, and J. H. Lawton. 1978. Characteristics of successful natural enemies in models of biological control of insect pests. Nature **273**:513–519.

Belovsky, G. E., J. B. Slade, and B. A. Stockhoff. 1990. Susceptibility to predation for different grasshoppers: an experimental study. Ecology **71**:624–634.

Bennington, C. C., and W. V. Thayne. 1994. Use and misuse of mixed model analysis of variance in ecological studies. Ecology **75**:717–722.

Bock, C. E., J. H. Bock, and M. C. Grant. 1992. Effects of bird predation on grasshopper densities in an Arizona grassland. Ecology **73**:1706–1717.

Cable, D. R. 1975. Influence of precipitation on perennial grass production in the semidesert Southwest. Ecology **56**: 981–986.

Campbell, R. W., T. R. Torgersen, and N. Srivastava. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. Forest Science **29**:779–790.

Chew, R. M. 1961. Ecology of the spiders of a desert community. Journal of the New York Entomological Society **69**:5–41.

Courtney, S. 1988. If it's not coevolution, it must be predation? Ecology **69**:910–911.

Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs **59**:433–463.

Diehl, S. 1993. Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. Oikos **68**:151–157.

Fowler, A. C., R. L. Knight, T. L. George, and L. C. McEwen. 1991. Effects of avian predation on grasshopper populations in North Dakota grasslands. Ecology **72**:1775–1781.

Gómez, J. M., and R. Zamora. 1994. Top-down effects in a tritrophic system: parasitoids enhance plant fitness. Ecology **75**:1023–1030.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**:421–424.

Holmes, R. T., J. C. Schultz, and P. Nothnagle. 1979. Bird predation on forest insects: an exclosure experiment. Science **206**:462–463.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist **124**:377–406.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73**: 724–732.

Joern, A. 1986. Experimental study of avian predation on coexisting grasshopper populations (Orthoptera: Acrididae) in a sandhills grassland. Oikos **46**:243–249.

Joern, A., and N. T. Rudd. 1982. Impact of predation by the robber fly *Proctacanthus milbertii* (Diptera: Asilidae) on grasshopper (Orthoptera: Acrididae) populations. Oecologia **55**:42–46.

Karban, R., D. Hougen-Eitzmann, and G. English-Loeb. 1994. Predator-mediated apparent competition between two herbivores that feed on grapevines. Oecologia **97**:508–511.

Kruess, A., and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. Science **264**:1581–1584.

Lajtha, K., and W. H. Schlesinger. 1986. Plant responses to variations in nitrogen availability in a desert shrubland community. Biogeochemistry **2**:29–37.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943–1967.

Liebold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. American Naturalist **134**:922–949.

Lightfoot, D. C., and W. G. Whitford. 1987. Variation in insect densities on desert creosotebush: is nitrogen a factor? Ecology **68**:547–557.

Lightfoot, D. C., and W. G. Whitford. 1989. Interplant variation in creosotebush foliage characteristics and canopy arthropods. Oecologia **81**:166–175.

Lightfoot, D. C., and W. G. Whitford. 1991. Productivity of creosotebush foliage and associated canopy arthropods along a desert roadside. American Midland Naturalist **125**: 310–322.

Matson, P. A., and M. D. Hunter. 1992. The relative contributions of top-down and bottom-up forces in population and community ecology. Ecology **73**:723.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemala. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118**:240–261.

Pacala, S., and J. Roughgarden. 1984. Control of arthropod abundance by *Anolis* lizards on St. Eustatius (Neth. Antilles). Oecologia **64**:160–162.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology and Evolution **7**:151–154.

Polis, G. A., and S. J. McCormick. 1986. Scorpions, spiders and solpugids: predation and competition among distantly related taxa. Oecologia **71**:111–116.

Polis, G. A., and S. J. McCormick. 1987. Intraguild predation

and competition among desert scorpions. Ecology **68**:332–343.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics **20**:297–330.

Price, P. W. 1987. The role of natural enemies in insect populations. Pages 287–312 *in* P. Barbosa and J. C. Schultz, editors. Insect outbreaks. Academic Press, San Diego, California, USA.

———. 1990. Evaluating the role of natural enemies in latent and eruptive species: new approaches in life table construction. Pages 221–232 *in* A. D. Watt, S. R. Leather, M. D. Hunter, and N. A. C. Kidd, editors. Population dynamics of forest insects. Intercept, Andover, England.

Raitt, R. J., and S. L. Pimm. 1976. Dynamics of the bird communities in the Chihuahuan Desert, New Mexico. Condor **78**:427–442.

Risch, S. J., and C. R. Carroll. 1982. Effect of a keystone predaceous ant, *Solenopsis geminata,* on arthropods in a tropical agroecosystem. Ecology **63**:1979–1982.

Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk **101**:672–684.

Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia **96**:439–449.

SAS Institute. 1992. SAS/STAT user's guide. SAS Institute, Inc., Cary, North Carolina, USA.

Scheiner, S. M. 1993. MANOVA: multiple response variables and multispecies interactions. Pages 94–112 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman & Hall, New York, New York, USA.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York, New York, USA.

Spiller, D. A., and T. W. Schoener. 1994. Effects of top and intermediate predators in a terrestrial food web. Ecology **75**:182–196.

Strong, D. R. 1988. Insect host range. Ecology **69**:885.

———. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology **73**:747–754.

Terborgh, J. W. 1992. Maintenance of diversity in tropical forests. Biotropica **24**:283–292.

Tomoff, C. S. 1974. Avian species diversity in desert scrub. Ecology **55**:396–403.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113–137 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman & Hall, New York, New York, USA.

Warren, W. G. 1986. On the presentation of statistical analysis: reason or ritual. Canadian Journal of Forest Resources **16**:1185–1191.

Warrington, S., and J. B. Whittaker. 1985. An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*) I. Lepidoptera larvae. Journal of Applied Ecology **22**:775–785.

Werner, E. E., and M. A. McPeek. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology **75**:1368–1382.

Wiens, J. A., R. G. Cates, J. T. Rotenberry, N. Cobb, B. Van Horne, and R. A. Redak. 1991. Arthropod dynamics on sagebrush (*Artemesia tridentata*): effects of plant chemistry and avian predation. Ecological Monographs **61**:299–321.