

## NUMERICAL RESPONSE OF LIZARDS TO AQUATIC INSECTS AND SHORT-TERM CONSEQUENCES FOR TERRESTRIAL PREY

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**Abstract.** Spatial subsidies, or inputs of resources from more productive donor habitats, can cause numerical responses in consumer populations via behavioral and demographic mechanisms. In addition, subsidies may have indirect effects on the in situ prey of these consumers. These indirect effects can be either negative (e.g., apparent competition) or positive (e.g., via diet shifts) depending on the relative strength of the predator's functional and numerical responses to prey subsidies. Here we report a numerical response by a lizard (Western fence lizard, *Sceloporus occidentalis*) to experimental reductions in the flux of river-derived insects. Initially, equal densities of lizards declined significantly faster in plots in which aquatic insect abundance was reduced by nearly 50% (season average) relative to controls. Abundance and biomass of terrestrial arthropods declined significantly between the start and end of the experiment across treatments. Despite consistently lower lizard abundance in plots with reduced subsidy levels, however, relative declines in the abundance and biomass of in situ terrestrial arthropods (all taxa combined) were not significantly different between reduced- and ambient-subsidy plots. Relative declines in spider biomass differed significantly between treatments and were higher in reduced-subsidy than ambient-subsidy plots, but only over one of three 3-wk sampling intervals. Thus, over the biologically active summer season, aquatic subsidies exerted brief positive or no significant indirect effects on the in situ prey of riparian lizards. These results suggest that, although aquatic insect prey may determine the spatial distribution and local abundance of riparian predators, the effects of increased predator density on in situ prey may be offset by higher per capita predation by these consumers on in situ prey in subsidy-poor relative to subsidy-rich habitats.

**Key words:** Carabidae; food web; indirect effects; insect; lizard; Lycosidae; numerical response; river-watershed exchange; riparian; *Sceloporus occidentalis*; subsidy; Western fence lizard.

### INTRODUCTION

Spatial subsidies are resource inputs from donor habitats that increase consumer density in recipient habitats (Polis et al. 1997). Subsidies have been empirically demonstrated between terrestrial and aquatic systems (Goulding 1980, Jackson and Fisher 1986, Gray 1989, Polis and Hurd 1995, 1996a, b, Nakano et al. 1999, Nakano and Murakami 2001), as well as between distinct aquatic habitats (Suchanek et al. 1985, Duggins et al. 1989, Bustamante et al. 1995, Blumenshine et al. 1997, Menge et al. 1997). Subsidies may elevate consumer density in recipient systems by increasing fecundity and survival of in situ consumers. Alternatively, subsidies may cause consumers to aggregate near the edges of more productive habitats. For example, both aquatic resource inputs and consumers of these resources decline with distance from the land-water interface of ocean and river habitats (Polis and Hurd 1995, 1996a, b, Sabo 2000, Henschel, *in press*,

Power et al., *in press*). Consumers may therefore respond numerically to subsidies via reproduction or habitat selection.

Aggregation of consumers in response to one resource may lead to higher encounter rates with a second resource (Schmitt 1987). In this way, subsidies may increase predation on local resources by apparent competition (Holt 1977, Holt and Kotler 1987). Several recent studies have documented subsidy-mediated effects of consumers on in situ prey (Bustamante et al. 1995, Nakano et al. 1999) or food chain dynamics (Henschel, *in press*). However, there have been few direct manipulations of subsidies that examine links between external resource supply, consumer density, and impacts on in situ resources.

We evaluated the response of a terrestrial consumer, the Western fence lizard (*Sceloporus occidentalis*), to inputs of river-derived aquatic prey. We also examined the effects of aquatic subsidies on the depletion by lizards of in situ prey (ground-dwelling terrestrial arthropods). Specifically, we predicted that (1) lizard density would be higher in areas with higher aquatic resource input and (2) that increased lizard density in these areas would lead to stronger depletion of in situ prey.

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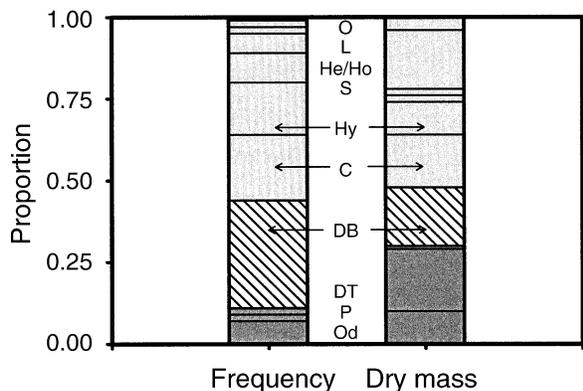


FIG. 1. Stomach contents of 12 adult *Sceloporus occidentalis*, captured on one of the four experimental sites (cobble bars) on 15 May 1996. We obtained samples by flushing the stomachs of live lizards to induce regurgitation. Samples were stored in EtOH until processing in the lab. Insects were categorized according to larval origin: terrestrial (light gray), aquatic (dark gray), or semi-aquatic (hatched lines). See *Methods* for details. Arthropod taxa sampled are as follows: C = Coleoptera; DB = Diptera, Brachycera; DT = Diptera, Tipulidae (Nematocera); He = Hemiptera; Ho = Homoptera; Hy = Hymenoptera; L = Lepidoptera (all larvae); O = Orthoptera; Od = Odonata; P = Plecoptera; S = spiders.

#### STUDY SITE

We conducted our experiments on four cobble bars along a 2.5-km reach of the South Fork Eel River (39°44' N, 123°39' W) in Mendocino County, California, USA. Cobble bars are open, sparsely vegetated fields of cobbles and boulders within the active river channel, which are dry during the summer drought under the regional Mediterranean climate regime. These habitats average 0.54 ha (range 0.28–1.04 ha) in area, and are bordered on one side by river and on the other by dense coniferous forest or grassy meadow habitat. Western fence lizards (*Sceloporus occidentalis*) occurred on cobble bars as well as in open, upland meadows 50–100 m from the river margin. Densities of *S. occidentalis* were more than seven times higher on cobble bars than on meadows (Sabo 2000). Moreover, these lizards aggregated along the edges of cobble bars, including microhabitats directly adjacent to the river, where densities exceeded 150 individuals/ha (J. Sabo and A. Amacher, *personal observation*).

Fence lizards are generalist predators of arthropods, including insects and spiders (Fig. 1; Fitch 1940, Rose 1976). Arthropod densities and biomass decline exponentially with distance from the river; so steeply that the flux is often reduced by ~50% within 10 m of the river margin (Power et al., *in press*). Thus, the spatial distributions of lizards and arthropod resources are congruent at two scales: within cobble bars (i.e., higher abundance of lizards and arthropods along the river edge), and between riparian cobble bars and upland meadow habitats (i.e., higher abundances in cobble bars than in more distant meadows). Lizards may occur at

higher density in cobble bar habitats than in meadows and along edges of cobble bars for a variety of reasons, including higher prey availability, increased cover from predators, or more favorable thermal environments. We experimentally manipulated inputs of aquatic prey from rivers to investigate the effect of these prey on the abundance of lizards in near-river habitats.

#### METHODS

##### *Experimental design and initial conditions*

Our experiment consisted of reduced-subsidy (–subsidy) and ambient-subsidy (+subsidy) treatments, and an unmanipulated reference plot (open plots) replicated in a block design once on each of four cobble bars (Fig. 2). All plots were 91 m<sup>2</sup> in area (7 × 13 m). Paired treatments (+subsidy/–subsidy) were assigned randomly (upstream vs. downstream), and open plots were randomly assigned to either upstream or downstream positions relative to contiguous experimental treatments. Open control plots were monitored in order to assess ambient changes in the abundance of lizards and their resources.

In the year prior to this experiment (1997), we had conducted a pilot study in which we measured the effects of subsidy reduction on the colonization of near-river habitats by lizards following the recession of high water from winter rains. Results from this experiment showed that ambient lizard densities in riparian habitats were too variable (among similar 90-m<sup>2</sup> plots) to ensure equal numbers of lizards among treatments and replicates at the start of the experiment. By chance, lizards were initially twice as abundant in –subsidy vs. +subsidy treatments (mean ± 1 SEM: +subsidy, 0.6 ± 0.4; –subsidy, 1.2 ± 0.68; open control, 1.0 ± 1.0; four replicates per treatment). Nevertheless, lizards appeared to decline in –subsidy plots (from 1.2 to 0.6 lizards per plot), but not in +subsidy or open control plots (from 0.8 to 1 lizards per plot, respectively, in the early and late summer census). Though declines in reduced-subsidy treatments were not significant (repeated-measures ANOVA:  $F = 1.1$ ,  $df = 2, 8$ ,  $P = 0.35$ ), these qualitative patterns suggested that a design measuring emigration of lizards from manipulated resource environments would provide a more sensitive test of the effect of riverine subsidies on habitat use by lizards.

In the experiment reported here (June–September 1998), we enclosed ambient densities of lizards in designated treatment plots with three walls, with the river acting as a fourth wall because these lizards are incapable of locomotion in the cool river water (J. Sabo, *personal observation*). Enclosures were used in the initial phase of the experiment to standardize lizard densities in reduced- and ambient-subsidy enclosures at the start of the experiment. Lizards were enclosed for a period of 15–17 d, after which we removed temporary “back walls” (Fig. 2), thereby allowing lizards to col-

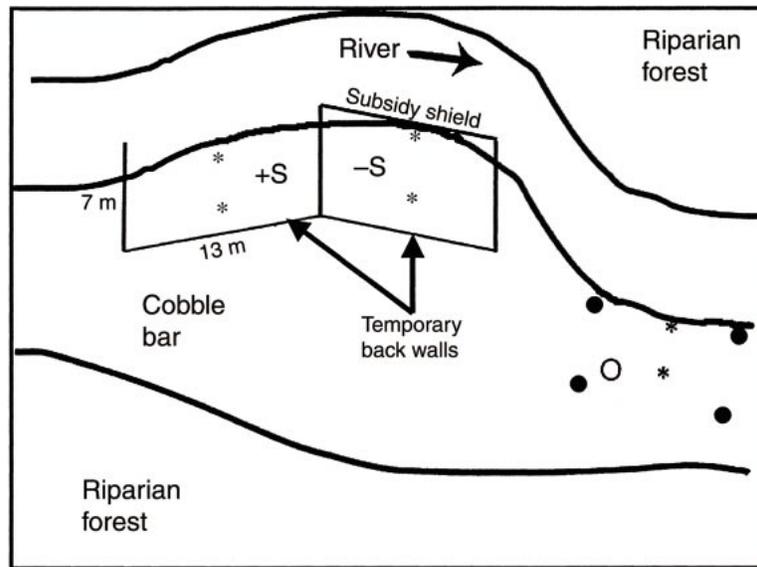


FIG. 2. (Top) Design of subsidy-reduction experiment involving a reduced-subsidy plot ( $-S$ ) and an ambient-subsidy plot ( $+S$ ), constructed as lizard enclosures ( $7 \times 13$  m) with and without a subsidy shield, and an open control plot (O). Five lizards were added to each temporary enclosure. Following a two-week acclimatization period, the temporary back walls were removed to evaluate the effect of subsidies on lizard abundance. All plots encompassed  $91 \text{ m}^2$  of cobble bar habitat ( $7 \times 13$  m) and were randomized within each of four sites (blocks) along a 2.5-km reach of the South Fork Eel River, California. Open plots were randomly placed either upstream or downstream of contiguous experimental treatments. Asterisks indicate insect-trapping stations at 0 and 6 m from the river margin. (Bottom) All enclosures consisted of 2 m high fences made from 12.7-mm mesh bird netting (upper material) and visqueen plastic (lower material) buried in the cobble substrate.

onize or emigrate from plots with these two resource treatments (see Table 1 for a timeline of experimental procedures). In this way, equal densities of enclosed lizards were initially exposed to controlled resource conditions (reduced- or ambient-subsidy treatments),

then allowed to move freely in and out of experimental treatments on subsequent sampling dates. We used emigration by lizards as a measure of the response of these consumers to initial experimental conditions, and changes in lizard abundance over the remainder of the

TABLE 1. Timeline showing dates of experimental procedures, insect trapping, and visual counts of lizards and odonates at the study site on the South Fork Eel River, California.

Date	Experimental protocol	Insect trapping	Lizard/odonate counts
June			
2–6		sample 1	
7–13	exclosure construction		
14–18		sample 2	
23–26	lizard additions		
July			
3–7		sample 3	
9–11			count 1
11	back wall removal		
23–27		sample 4	
28–31			count 2
August			
14–18		sample 5	
20–23			count 3
September			
6–10		sample 6	
7–9			count 4

Notes: All dates for insect samples are for sticky trapping intervals. Pitfall traps were collected three days earlier.

experiment as a measure of lizard responses to subsequent resource conditions, which changed seasonally.

In –subsidy treatments, we experimentally reduced aquatic insect subsidies using a fourth wall, the “subsidy shield,” placed along the river boundary. Side walls (perpendicular to the river) and subsidy shields were 2 m in height, composed of 1 m high 12.7-mm mesh bird netting on the top sewn to 1 m high 6 mil (0.15 mm) visqueen plastic on the bottom (Fig. 2b), which prevented lizards from climbing on enclosure walls and escaping. Temporary back walls were 1 m high visqueen. Enclosure walls were supported on PVC pipe anchored by rebar posts hammered into the cobble bar. We buried the visqueen portion of enclosure walls in the cobble bar with sand and cobbles. Sediment used to bury visqueen was collected from directly under the enclosure wall or from outside experimental arenas to minimize disturbance within enclosures. Subsidy shields were positioned 0.5 m into the river so that enclosed lizards in plots with and without shields both had access to river water for drinking.

Following construction of enclosure walls, we searched the temporary experimental enclosures on two consecutive days and removed all lizards. We identified all animals removed from treatment plots by individual toe clips, and used these toe clips to ensure that no animals used later in the experiment were introduced to their former home ranges. Half (6) of our experimental plots were devoid of lizards prior to enclosure construction, suggesting that colonization following winter floods was ongoing. All enclosures were then stocked with five subadult *Sceloporus occidentalis*. These lizards were each measured to the nearest mm and weighed to the nearest g using Pesola portable scales (Pesola, Kapuskasing, Ontario, Canada), and

given a unique toe clip and dorsal nail polish marking for individual identification throughout the experiment.

Lizards were size-matched to the nearest millimeter snout vent length (SVL) between treatments within each site. We used subadult lizards with a female-biased (3:2) sex ratio to reduce potentially confounding effects of mate choice and male–male social interactions on habitat choice by lizards. We selected non-resident lizards for enclosures to avoid the confounding effects of prior residence on habitat choice by lizards (Stamps and Krishnan 1994). Average ( $\pm 1$  SE) initial size of lizards in enclosures was  $45.3 \pm 0.53$  mm SVL (range 38–55 mm).

#### *Aerial aquatic and terrestrial arthropod fluxes*

We measured fluxes of aerial aquatic and terrestrial arthropods in –subsidy, +subsidy, and open plots using sticky traps hung on 1 m high rebar posts stationed at 0 and at 6 m from the river margin along the midline of each plot (Fig. 2a). Sticky traps were 612 cm<sup>2</sup> of Tanglefoot-coated (Tanglefoot, Grand Rapids, Michigan, USA), transparent acetate sheets rolled in a cylinder around each of the rebar posts. We set sticky traps during six 5-d sampling intervals between 2 June and 6 September 1998. These intervals included one sampling date prior to the experiment, one after enclosure construction but prior to lizard addition, one after lizard addition but prior to the removal of temporary back walls, and three sampling dates following removal of the temporary back walls (Table 1). Traps were covered with cellophane upon collection and stored at 12°C for processing in the laboratory.

We identified and measured lengths ( $\pm 1$  mm) of specimens on sticky traps under a dissecting scope (10–35 $\times$  magnification). Specimens were identified to the taxonomic level sufficient to establish their origin as

either riverine or terrestrial (order, or family for Diptera). We then estimated the biomass of all identified specimens using length–dry mass regressions generated from independently collected specimens at our field site (Sabo et al., 2002).

Our previous observations and stomach content analysis of *S. occidentalis* (Fig. 1) suggested that odonates made up a significant proportion of the diet of lizards, but that their abundance was underestimated by sticky traps. We counted conspicuous odonates along two 1 m wide transects (0 and 6 m) parallel to the river within each plot on four dates from 15 July–7 September 1998. We walked each transect (13 m) in ~1 min, counting all dragonflies (mostly *Ophiogomphus bicolor*) and damselflies (*Archilestes californica* and *Argia* spp.) flushed from cobble perches. Transects were paced quickly in order to minimize double counting of individual odonates. Data are presented as total plot-wide counts (sum of two transects) for all dates.

#### *Lizard abundance*

We counted lizards in +subsidy, –subsidy, and open plots on four dates between 9 July and 7 September 1998. These dates included one census before and three following the removal of the temporary back walls (Table 1). During a morning visit to each of these sites, we observed and systematically searched enclosures for lizards during four sequential observation periods spaced by 30–45 min. Individual lizards were identified by dorsal nail polish markings (when present), or by a combination of unique natural markings (unshed loose skin) and toe clip sequences (observed through binoculars) if nail polish marks had been lost during shedding. We recorded numbers of adults (and hatchlings, present only on last two dates) in each plot during each observation period. To eliminate double counting, we present plot-wide abundance as the sum of the total number of uniquely marked lizards seen in all four visits and the maximum number of unmarked lizards seen on any single visit.

#### *In situ resource abundance and biomass*

We measured the abundance and biomass of ground-dwelling terrestrial, or in situ arthropods in each plot using pitfall traps placed at 0.25 and 6 m from the river. Round plastic cups 8 cm in diameter were buried flush to the bar surface using fine gravel. Each cup was filled with ~2 cm of a dilute solution of clear dish soap to break the water surface tension and serve as a mild preservative. We set pitfall traps during all six sticky-trap sampling periods (Table 1), but for shorter two-day deployments to avoid sample desiccation. After two days, each sample was preserved in 70% EtOH. Pitfall data are presented as plot-wide averages in which the 0.25- and 6-m samples were averaged within each replicate for each sampling period.

Specimens were measured and biomass estimates obtained as for arthropods on sticky traps. We separated

two common taxa in our samples: ground beetles (Carabidae), which are largely nocturnal (Borror et al. 1997, Sabo 2000), and an abundant, but patchily distributed ant (*Pogonomyrmex* sp.) on our study site. In our analysis of the impacts of lizards on in situ arthropods, we examined effects on three classes of arthropods: (1) all taxa excluding *Pogonomyrmex* sp. (“All Taxa”), (2) carabid beetles, and (3) ground spiders (Lycosidae). We excluded *Pogonomyrmex* sp. from total arthropod abundance and biomass because high numbers of this ant (>25 individuals) in a few individual traps led us to believe that we had disturbed nests of this ant while deploying these pitfall traps. Thus, taxa included in “All Taxa” are, in decreasing order of abundance: carabids, spiders (mostly Lycosidae), non-carabid Coleoptera, Hymenoptera including ants (other than *Pogonomyrmex* sp.) and vespid wasps, mites, bristletails (Thysanura), Homoptera, Orthoptera (including tetrigid and acridid grasshoppers), Hemiptera, and larval Lepidoptera. We analyzed lizard effects on carabids and spiders separately because they are the two most abundant ground-dwelling taxa, but have contrasting patterns of diel activity at our study site (Sabo 2000). Many lycosids have either diurnal or crepuscular activity patterns overlapping, at least in part, with lizards. By contrast, carabids are entirely nocturnal and largely unavailable to diurnally foraging lizards.

#### *Data analysis*

All statistical tests were performed on SYSTAT 9.0 (SPSS 1998) using (ln + 1) transformed data. In all analyses, we used one-tailed probabilities in a planned comparison of +subsidy vs. –subsidy treatments to test our a priori hypotheses that +subsidy plots would have higher abundance and biomass of aquatic insects, higher numbers of lizards, and lower abundance and biomass of ground-dwelling terrestrial prey than –subsidy plots. Data from open controls are presented graphically for comparison. We used repeated-measures (rm) ANOVA with a blocking factor (four experimental sites) to analyze differences between –subsidy and +subsidy treatments in arthropod fluxes across the four sampling dates (3 July–10 September) when lizards were present in experimental plots. This test allowed us to assess overall seasonal trends, as well as differences in trends among treatments in arthropod abundance. We performed this test on the abundance and biomass of aquatic and terrestrial arthropods in 0-m traps and on the plot-wide averages of 0- and 6-m traps. Statistical analysis of 6-m traps (rm-ANOVA) was not possible because of two missing samples. Plot-wide data were based on a single 0-m sample in these two cases. Similarly, we analyzed differences in visual counts of odonates using rmANOVA.

We analyzed differences in lizard abundance between –subsidy and +subsidy treatments using two statistical tests. First, we used the Time × Treatment interaction in rmANOVA to assess differences in the

response of lizards to the removal of the temporary back wall between the first two census dates (9 July before removal, and 28 July 1998). Second, we used treatment effects in rmANOVA to analyze differences in lizard abundance between treatments across the three sampling dates after back wall removal (28 July–7 September 1998). In all analyses on lizard abundance, block effects were dropped from models (i.e., pooled block and error sums of squares; Winer et al. 1991) because they were not significant ( $P > 0.5$ ).

We used rmANOVA to analyze differences in the relative change in abundance and biomass of crawling arthropods captured in pitfall traps across the four sampling periods in which lizards were present in the experiment. The Time  $\times$  Treatment interaction in this test evaluates differences between treatments in the *change* in terrestrial resource availability between experimental periods before and after the removal of temporary back walls. Univariate rmANOVA is an extension of a split-plot ANOVA design where Time is an explicit factor in the model. The validity of this extension and use of the resulting Time  $\times$  Treatment effect rests on the assumption that the variance in the difference between any two levels of the repeated-measure factor is equal (e.g., circularity, see Winer et al. 1991, von Ende 1993). For all rmANOVA results, we report  $P$  values based on Huynh-Feldt (H-F) corrected degrees of freedom that adjust significance levels according to deviations from this standard assumption (Winer et al. 1991).

## RESULTS

### *Effects of subsidy shields on aquatic and terrestrial arthropod fluxes*

Subsidy shields reduced aquatic insect fluxes more strongly than fluxes of terrestrial prey, and enclosure effects were minimal. Subsidy shields reduced plot-wide aquatic insect abundance and biomass by 49% and 38%, respectively, averaged over the experimental period in which lizards were present (Figs. 3 and 4, Table 2). More substantial reductions of aquatic insects occurred in 0-m traps (61% and 49%, abundance and biomass, respectively; Table 2). By contrast, shield reductions of terrestrial arthropod fluxes were relatively modest. Time-averaged, cage-wide terrestrial arthropod abundance and biomass were reduced by 24% and 17%, respectively, in  $-$ subsidy vs.  $+$ subsidy plots (Figs. 3 and 4), but neither difference was significant (Table 2). At the river interface (0-m traps), shields reduced the abundance of terrestrial arthropods by 38%, but differences in biomass were not significant. In summary, shields reduced the abundance of both aquatic and terrestrial arthropods in sticky traps at 0 m, but had significant effects on the biomass of only aquatic taxa. When averaged across entire plots, shields significantly reduced the abundance and biomass of aquatic but not terrestrial arthropods.

Aquatic insect abundance and biomass both declined sharply between 0- and 6-m traps (Figs. 3 and 4). In open plots, time-averaged aquatic insect abundance and biomass sampled on sticky traps declined away from the river, from 0 to 6 m, by 87% and 77%, respectively ( $t = 4.9$ ,  $df = 3$ ,  $P < 0.025$ , abundance;  $t = 4.97$ ,  $df = 3$ ,  $P < 0.025$ , biomass). In contrast, differences in the abundance and biomass of terrestrial arthropods on sticky traps were not significant ( $t = 1.6$ ,  $df = 3$ ,  $P > 0.2$ ;  $t = -0.8$ ,  $df = 3$ ,  $P > 0.5$ ; abundance and biomass, respectively).

Fluxes of aquatic and terrestrial arthropods varied seasonally as well (Figs. 3 and 4). Aquatic insect fluxes peaked in early July, increasing from near-zero levels in June by 47- and 28-fold in abundance and biomass, respectively. This peak coincided with the introduction of lizards to the temporarily walled enclosures. Plot-wide abundance and biomass of aquatic insects then declined by 91% and 96%, respectively, in open plots between the July peak and the final 6 September sample. Similar seasonal declines occurred in  $-$ subsidy and  $+$ subsidy plots both plot-wide and at 0 m (Time Effect, Table 2). By contrast, terrestrial arthropods sustained seasonal peaks in abundance for a longer period between 3 July and 23 July in abundance (Fig. 3), but exhibited no seasonal trends in biomass across all six sampling periods (Fig. 4). Abundance of terrestrial arthropods declined by 58% (Time Effect, Table 2), but changes in the biomass of terrestrial arthropods were not significant. The disparity in seasonal trends between abundance and biomass in terrestrial arthropods was due in part to late summer increases in large (late instar) grasshoppers. Finally, the abundance of both aquatic and terrestrial arthropods declined at different rates among sites across the final four sampling dates as indicated by significant Time  $\times$  Site interactions (Table 2).

Aquatic taxa were the numerically dominant prey species for lizards in river edge habitats. In unmanipulated control plots, aquatic insects made up 61% of the numbers and 49% of the biomass of total available aerial prey captured in sticky traps placed directly on the river margin, averaged across the four sampling periods (3 July–6 September 1998). Aquatic insects made up a smaller fraction of the total plot-wide arthropod abundance (49%) and biomass (38%) over the same sampling interval. Thus, the abundance and the relative dominance of riverine subsidies declined precipitously within  $<10$  m of the river margin (see also Power et al., *in press*).

### *Visual counts of odonates*

Odonates were more abundant in  $+$ subsidy than in  $-$ subsidy plots (Fig. 5). Abundance of odonates counted in visual surveys were on average 2.3 times higher in  $+$ subsidy plots over the interval when lizards were present (Treatment:  $F = 8.9$ ,  $df = 1, 3$ ,  $P < 0.05$ ). Treatment-wide odonate abundance declined by nearly

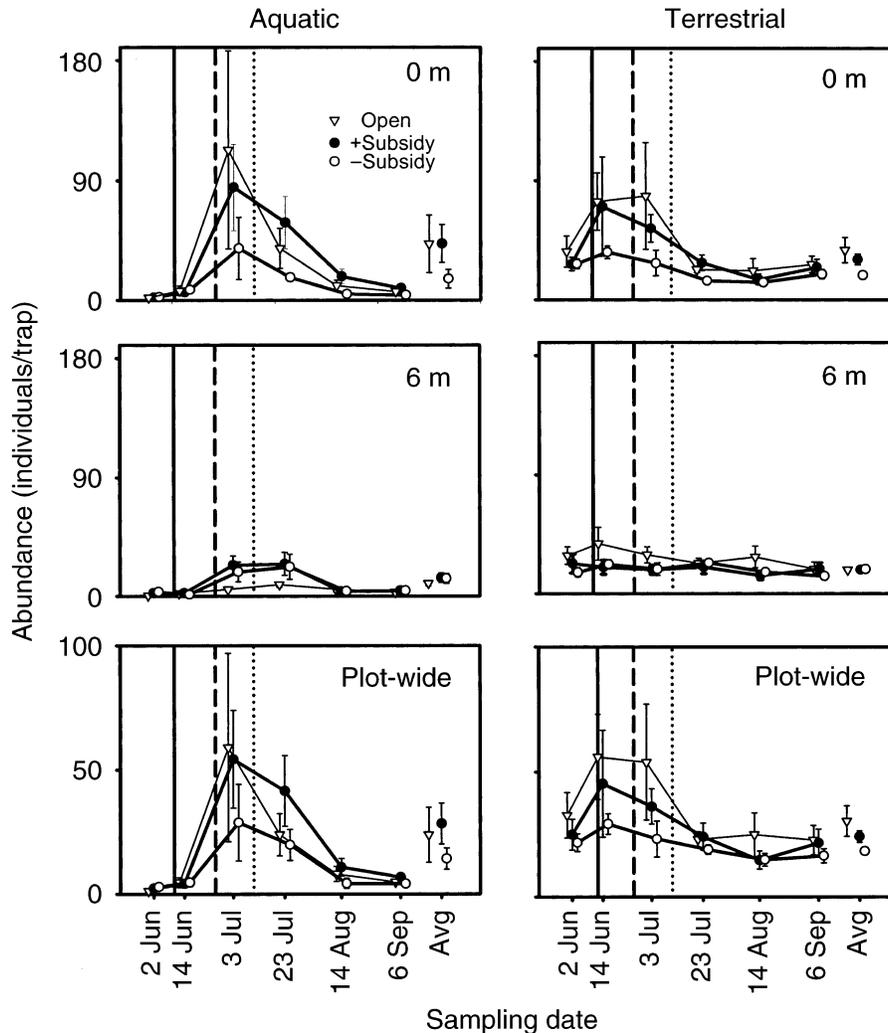


FIG. 3. Effects of subsidy shields on resource abundance. Mean ( $\pm 1$  SE) abundance of (left panels) aquatic and (right panels) terrestrial arthropods caught on sticky traps placed at (top panels) 0 m from the river, (middle panels) 6 m from the river, and (bottom panels) averaged across 0- and 6-m traps (plot-wide) within each plot. Sticky traps were set during 5-d sampling periods at ~3-wk intervals between 2 June and 10 September 1998. Vertical reference lines correspond to enclosure construction (solid lines), lizard addition (dashed lines), and removal of temporary back walls (dotted lines). Average resource abundance (Avg) experienced by lizards (3 July–10 September) is also presented for comparison in each panel.

60% between the seasonal peak in late July (30 July) and the end of the experiment in September (Time:  $F = 11.03$ ,  $df = 3, 9$ ,  $P < 0.05$ ).

#### Effects of subsidy shields on lizard abundance

Lizard abundance declined significantly faster in -subsidy plots than in +subsidy plots and in open controls following the removal of the temporary back walls, and remained consistently higher in +subsidy plots and open controls throughout the remaining six weeks of the experiment (Fig. 6). Lizard abundance declined 2.5 times faster in -subsidy vs. +subsidy plots (Time  $\times$  Treatment:  $F = 6.2$ ,  $df = 1, 6$ ,  $P < 0.05$ ), leading to 2.75 times higher numbers of lizards in +subsidy plots during the first open plot sample.

The emergence of hatchlings in early August led to late season (20 August) increases in lizard abundance (J. Sabo, *personal observation*). Despite these changes in abundance over time, total lizard abundance was 1.6 times higher in +subsidy relative to -subsidy plots when averaged across the three censuses following back wall removal (Treatment:  $F = 4.29$ ,  $df = 1, 6$ ,  $P < 0.04$ ). Finally, lizard abundance in open plots closely paralleled that in +subsidy plots on all but the last sampling date, suggesting that densities in +subsidy plots were in fact ambient (Fig. 6).

#### Effects of subsidy shields on ground-dwelling terrestrial arthropods

Ground-dwelling terrestrial arthropods peaked in mid-June, several weeks earlier than aerial aquatic in-

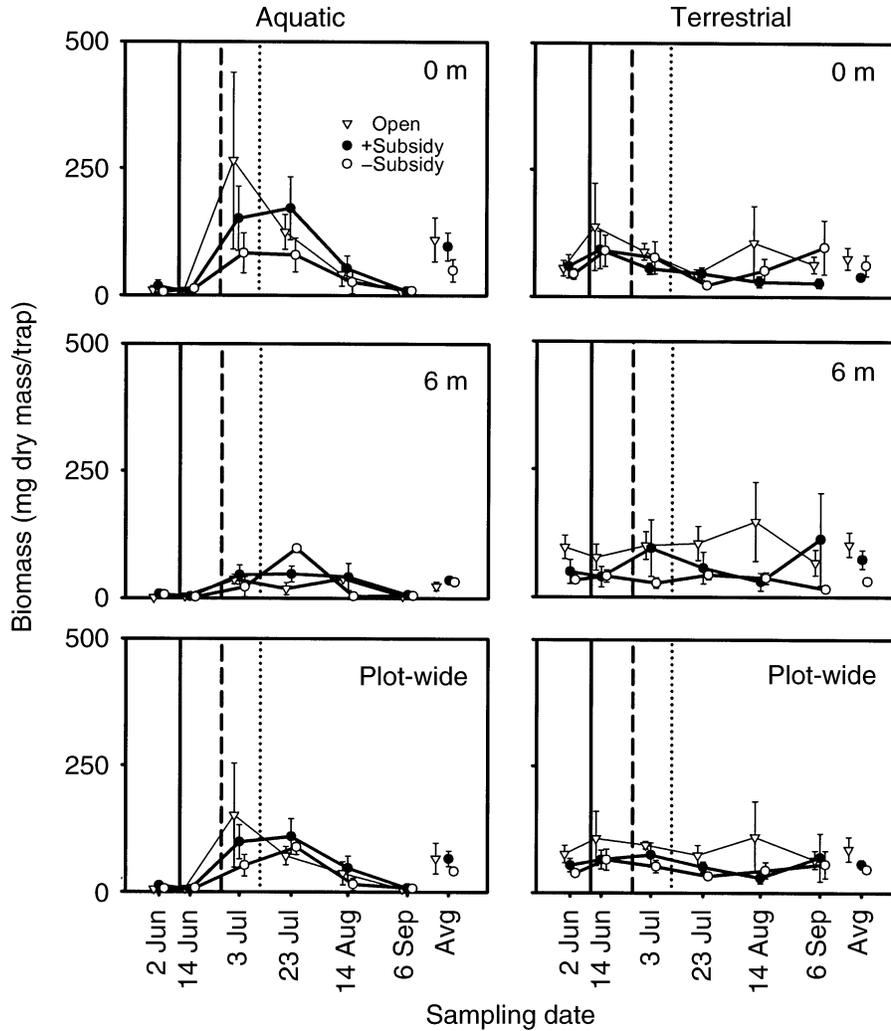


FIG. 4. Effects of subsidy shields on resource biomass, estimated as dry mass from length–dry mass regression. Mean ( $\pm 1$  SE) dry mass of (left panels) aquatic and (right panels) terrestrial arthropods caught on sticky traps placed at (top panels) 0 m from the river, (middle panels) 6 m from the river, and (bottom panels) averaged across 0- and 6-m traps (plot-wide) within each plot. Vertical reference lines correspond to enclosure construction (solid lines), lizard addition (dashed lines), and removal of temporary back walls (dotted lines). Average resource biomass (Avg) experienced by lizards (3 July–10 September) is also presented for comparison in each panel.

TABLE 2. Values of *F* from repeated-measures ANOVAs on plot-wide averages (0- and 6-m traps) and in 0-m traps for abundance and dry mass of aerial aquatic and terrestrial resources in –subsidy and +subsidy plots between 3 July and 10 September, 1998.

Effect	Response							
	0 + 6-m Average				0-m Traps			
	Abundance		Biomass		Abundance		Biomass	
	Aquatic	Terrestrial	Aquatic	Terrestrial	Aquatic	Terrestrial	Aquatic	Terrestrial
Treatment (1,3)	1348.4***	3.17	12.65*	0.55	43.27**	98.59***	4.99*	1.19
Site (3,3)	873.5***	3	10.85*	23.08*	11.47*	43.57**	6.3	6.34
Time (3,9)	104.52***	16.01**	22.14***	2.05	64.6***	9.49**	15.89***	2.55
Time $\times$ treatment (3,9)	0.895	1.87	1.69	0.86	1.23	1.6	1.1	3.7
Time $\times$ site (9,9)	3.69*	3.74*	1.57	1.97	2.4	1.5	1.2	2.02

Notes: Degrees of freedom for each effect and the corresponding error term are given in parentheses. Each column summarizes results from a single ANOVA.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

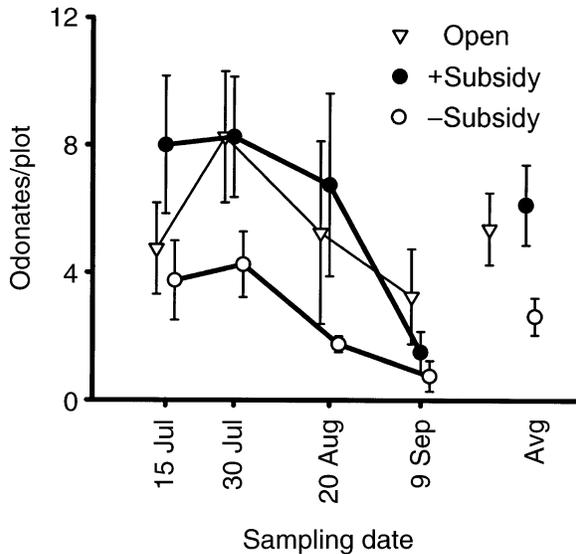


FIG. 5. Effect of subsidy shields on the abundance of odonates, a large and conspicuous aquatic resource. Mean ( $\pm 1$  SE) number of dragonflies (e.g., *Opheogomphus* spp.) and damselflies (e.g., *Archilestes californicus*) counted in two transects spanning the plot width at 0 and 6 m from the river margin. All censuses were conducted after enclosure construction and experimental lizard addition. Average abundance (Avg) is also presented for comparison.

sects, and then declined in abundance and biomass later in the season (Fig. 7, Table 3). Despite consistently higher lizard abundance in +subsidy plots, relative changes in the abundance and biomass of ground-dwelling terrestrial arthropods ("All Taxa") were not significantly different between +subsidy and -subsidy treatments (Fig. 7, Table 3). Only the relative change in the biomass of lycosid spiders differed significantly between these two treatments (Table 3); however, these differences were significant for the cubic ( $F = 33.4$ ,  $df = 1, 3$ ,  $P < 0.01$ ), but not quadratic ( $F = 0.04$ ,  $df = 1, 3$ ,  $P > 0.8$ ) or linear ( $F = 0.42$ ,  $df = 1, 3$ ,  $P > 0.05$ ) components of response curves of +subsidy and -subsidy treatments. This result suggests that, although relative changes in spider biomass differed significantly between +subsidy and -subsidy treatments across the four dates analyzed, the linear decline in biomass (Figs. 7 and 8), per se, was not significantly different between treatments. Further analysis of changes in spider biomass between consecutive time periods using multiple univariate tests ("Profile Analysis," O'Brien and Kaiser 1985) revealed a significantly higher decline in -subsidy than in +subsidy plots across the midseason sampling interval (23 July, 14 August;  $F = 18.8$ ,  $df = 1, 3$ ,  $P = 0.012$ ; Bonferroni-adjusted  $P = 0.0167$ ), but not across other sampling intervals during the time lizards were present in the experiment. Declines in the abundance and biomass of carabid beetles were not significantly different between +subsidy and -subsidy treatments (Table 3).

## DISCUSSION

Subsidies are a prevalent feature of many aquatic and terrestrial food webs (Polis and Strong 1996, Polis and Winemiller 1996, Polis et al. 1997; Polis et al., *in press*). In watershed systems, reciprocal subsidies link aquatic and terrestrial food webs (Wallace et al. 1997, 1999, Nakano et al. 1999, Sabo 2000, Nakano and Murokami 2001; Henschel, *in press*, Power et al., *in press*). Subsidies that increase the local density of consumers in recipient habitats may alter the impact of these consumers on local resources (Bustamante et al. 1995, Polis et al. 1997). To date, however, few experiments have demonstrated the mechanisms by which consumers respond numerically to external resource fluxes (but see Bustamante et al. 1995, Sanchez-Piñero and Polis, 2000). Our experiment suggests that consumers that respond numerically to external resource inputs through habitat selection may not exert observable effects on abundances of their in situ resources.

### Numerical responses of riparian lizards to riverine subsidies

Western fence lizards responded behaviorally to variation in aquatic prey fluxes on cobble bar habitats. Emigration rates of lizards were 2.5 times faster in -subsidy plots where aquatic insect biomass flux at the river margin was reduced to about half the input of +subsidy and ambient control plots (Figs. 4 and 6). By contrast, 0-m and plot-wide biomass of aerial terrestrial arthropods was not significantly different among treatments over this same period, suggesting

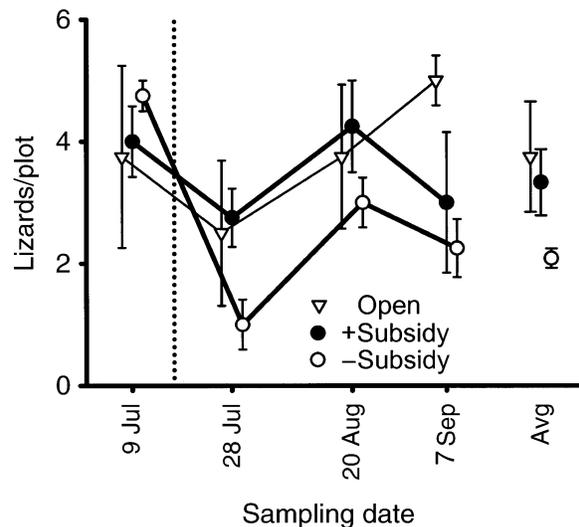


FIG. 6. Numerical response of lizards (*Sceloporus occidentalis*) to experimental subsidy reduction. Mean ( $\pm 1$  SE) numbers of lizards (adult and hatchling) counted in 10-min observations on four sampling dates. The dotted vertical reference line indicates the removal of temporary back walls initially enclosing lizards in -subsidy and +subsidy treatments. Average lizard abundance (Avg) over the final three census dates is presented for comparison.

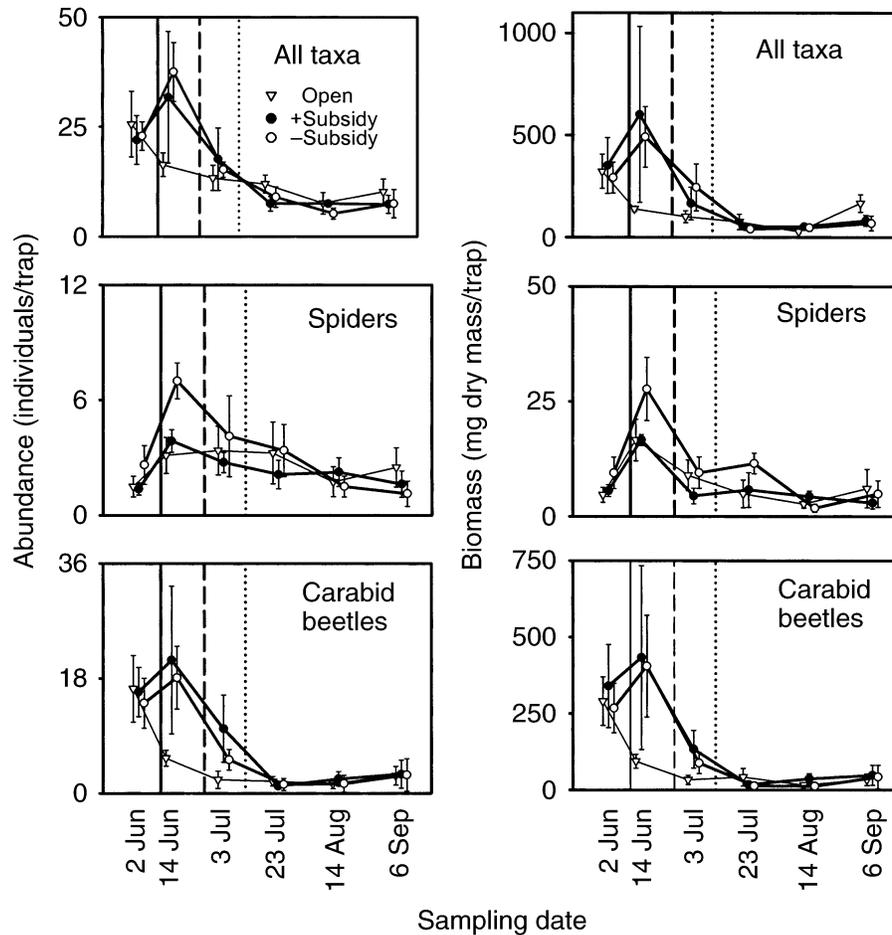


FIG. 7. Indirect effects of subsidy reduction on ground-dwelling terrestrial arthropods. Mean ( $\pm 1$  SE) (left panels) abundance and (right panels) biomass of all (top panels) ground-dwelling arthropods (excluding *Pogonomyrmex* sp., see *Methods*), (middle panels) lycosid spiders, and (bottom panels) carabid beetles captured in pitfall traps. Vertical reference lines correspond to enclosure construction (solid lines), lizard addition (dashed lines), and removal of temporary back walls (dotted lines).

that lizards were responding to aquatic prey reductions. Though our experiment was not explicitly designed to quantify the relationship between aquatic insect inputs and lizard abundance, or “input matching” (e.g., Fret-

well and Lucas 1970, Power 1984, Kennedy and Gray 1993), our results support the hypothesis that fluxes of prey from rivers have a strong positive effect on the local abundance of these lizards in river boundary hab-

TABLE 3. Values of  $F$  from repeated-measures ANOVAs on plot-wide averages of abundance and dry mass of in situ terrestrial resources in  $-$ subsidy and  $+$ subsidy plots between 3 July and 10 September, 1998.

Effect	Response					
	Abundance			Biomass		
	All taxa†	Spider	Carabid	All taxa†	Spider	Carabid
Treatment (1,3)	0.39	0.048	6.31	0.21	0.2	3.36
Site (3,3)	11.25*	2.05	51.84***	3.13	1.7	3.37
Time (3,9)	6.65**	1.82	8.78***	3.87*	2.5	5.45*
Time $\times$ treatment (3,9)	0.74	0.39	0.144	0.7	3.12*	0.54
Time $\times$ site (9,9)	2.13	1.3	2.83	1.07	1.47	1.65

*Notes:* Degrees of freedom for each effect the corresponding error term are given in parentheses. Each column summarizes results from a single ANOVA.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

† Excluding *Pogonomyrmex* sp., (see *Methods*).

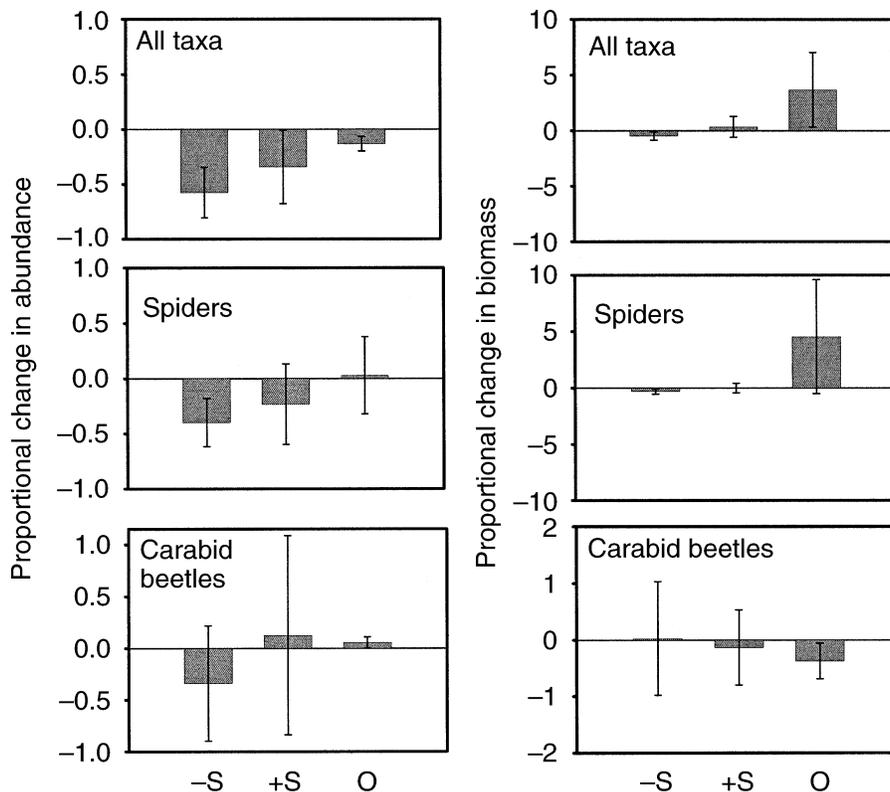


FIG. 8. Proportional change in (left panels) abundance and (right panels) biomass of all (top panels) ground-dwelling arthropods (excluding *Pogonomyrmex* sp., see *Methods*), (middle panels) lycosid spiders, and (bottom panels) carabid beetles between the start (3 July 1998) and end (10 September 1998) of the experiment. Each panel shows changes for +subsidy (+S) and -subsidy (-S) treatments, and for open plots (O). Only relative changes in the biomass of spiders were significantly different between -subsidy and +subsidy treatments (see Table 3 and *Results*).

itats. When averaged over the entire experiment, lizard densities and aquatic insect biomass inputs were both 1.6-fold higher in +subsidy than in -subsidy plots.

Relative changes in lizard abundance in -subsidy and +subsidy treatments were also consistent with the relative abundance of odonates, one of this lizard's most common prey types (~20% by biomass, Fig. 1). These large and highly mobile prey were 2.3 times more abundant in +subsidy relative to -subsidy plots (experiment average, Fig. 5), close to observed differences in lizard abundance between these two treatments (Fig. 6). While several studies have demonstrated strong inverse relationships between prey abundance and the size of a habitat (territory) occupied by an individual lizard (Simon 1975, Kreckorian 1976), our results suggest that prey inputs may also determine the number of lizards in a local habitat, perhaps as a result of this inverse relationship (e.g., Fretwell and Lucas 1970, but see Guyer 1988a, b). Finally, rapid (two- to three-week) changes in lizard abundance in response to reductions in aquatic prey suggest that subsidies may increase the density of consumers in recipient habitats not only by increasing demographic rates (e.g., higher growth rates [Sabo and Power 2002], leading to in-

creased size-dependent survival, fecundity), but by habitat selection as well.

#### *Aquatic resource inputs and lizard density at larger spatial scales*

Despite numerical responses of lizards to subsidies on cobble bars, experimental reduction of aquatic insects did not produce density differences as extreme as natural gradients in lizard abundance between cobble bars and meadows. These lizards occur at seven times higher density on cobble bars than in grassy meadow habitats located >50 m from the river channel (Sabo 2000). This density gradient is more than twice that observed between -subsidy and +subsidy treatments on cobble bars (2.75-fold). We offer three potential explanations for this. First, aquatic resources were reduced, but not eliminated by shields. Complete elimination of aquatic resources may have led to a stronger numerical response by lizards, more closely approximating the natural density gradient between riparian and upland habitats.

Second, *Sceloporus occidentalis* rarely move between cobble bars and upland meadows within or between growing seasons, despite seasonal evacuation of

bars by lizards in response to winter rains and flooding. Over a five-year period, we observed very few (<10) individual movements between cobble bar and meadow habitats (among >600 lizards marked and resighted at least once). The lack of movement between near-river and upland habitats suggests that higher density in cobble bars than meadows may reflect demographic differences between these two habitats, rather than habitat selection at the watershed scale. For example, growth rates of *S. occidentalis* decline up to sevenfold when lizards' access to ambient subsidy inputs were experimentally reduced (Sabo and Power 2002). Higher growth in response to aquatic subsidies may allow cobble bar females to reproduce earlier and allocate more energy to reproduction than females in poorer habitats more distant from the river.

Finally, resource availability may be only one of several factors contributing to high near-river density of *S. occidentalis*. Thermal differences between these two habitats may interact with resource availability to augment clutch production by females in cobble bar habitats (Sabo 2000). Nevertheless, the strong response of lizards to experimental reductions of aquatic prey supply supports the hypothesis that these resources are, at least in part, responsible for the observed gradient in lizard abundance between cobble bars and meadows.

#### *Patterns of in situ arthropod abundance and biomass*

The seasonal patterns of in situ resource abundance (e.g., ground-dwelling, terrestrial arthropods) paralleled those of aerial terrestrial arthropods captured in sticky traps. Peak abundance occurred during the second sampling interval (14 June) for terrestrial taxa in the air (Fig. 3) and on the ground (Fig. 7). Peak levels of terrestrial arthropods (air and ground) occurred earlier than those for aquatic insects, most likely as a result of more rapidly rising spring temperatures in air than in water (M. E. Power, *personal observation*). This suggests that lizards may derive benefits from river-edge habitats not only because aquatic resources are more available in these areas, but also because peak abundance of aquatic and terrestrial resource bases are asynchronous (Nakano and Murakami 2001). Patterns of in situ resource abundance were more consistent among groups of taxa and less variable than patterns of biomass. Higher variability in the biomass of ground-dwelling taxa most likely resulted from the chance event of trapping a single individual of a relatively large taxon (e.g., grasshopper or lepidopteran larva). These chance events most likely explain the disparate trends in abundance and biomass of non-carabid taxa during the second and third sampling intervals (Fig. 7).

#### *Short-term indirect effects of subsidies*

In this experiment, lizards responded numerically to alternate, aquatic resources, but higher lizard abundance (in +subsidy plots) did not lead to increased

predation on ground-dwelling terrestrial arthropods. Instead, we observed statistically indistinguishable declines between +subsidy and -subsidy treatments in both the numerical abundance and biomass of carabid beetles and all in situ taxa combined (Figs. 7 and 8). Similarly, declines in lycosid spider abundance did not differ between treatments. Only changes in spider biomass differed significantly between treatments. Spider biomass declined significantly faster in -subsidy treatments, but only over a single midseason sampling interval. Although this suggests a short-term positive indirect effect of aquatic insects on spiders via a shared lizard predator, our overall results indicate that aquatic prey subsidies do not alter *total* predation by lizards on terrestrial arthropod prey. We offer two possible explanations for this finding.

First, theoretical models of one predator-two prey systems suggest that the indirect effects experienced by alternate prey species through a shared predator can vary in sign (negative or positive) and magnitude (strong to nonexistent) depending on the relative strength of the functional and numerical responses of a predator to alternate resources. Negative indirect effects (i.e., apparent competition) occur when an alternate prey species increases the reproductive or behavioral numerical response of a shared predator, and higher numbers of these predators consume more local resources (Holt 1977, Holt and Kotler 1987). By contrast, positive indirect effects prevail when predators prefer one resource, or when alternate resources are abundant enough to saturate the functional response of the predator (Abrams and Matsuda 1996). Our results suggest that the numerical response of lizards (lower predator density in -subsidy plots) may have been offset by an equally strong functional response (higher per capita predation on in situ prey in -subsidy plots).

Alternatively, many terrestrial arthropods themselves rely on aquatic insects as prey. Predatory arthropods may have emigrated, like lizards, in response to reductions in aquatic insects in -subsidy treatments. Emigration of these predatory arthropods from -subsidy treatments, and increased predation on these arthropods by lizards in +subsidy treatments could have produced statistically indistinguishable effects of the different treatments on abundances of these predatory arthropod taxa. The response of nocturnal carabid beetles (Figs. 7 and 8), however, suggests that emigration was not a likely response of terrestrial arthropod predators to subsidy reduction. Carabids are known predators of aquatic insects (Hering and Platcher 1997), and are most likely not susceptible to predation by *S. occidentalis* because these lizards rely on visual cues for prey detection not provided by diurnally inactive carabids. If shields had caused resource-related emigration by arthropods, we would have expected carabids to decline faster in -subsidy treatments. Instead, these beetles declined at similar rates in -subsidy and +subsidy treatments. This comparison lends tentative sup-

port to the first hypothesis that the numerical response of lizards to aquatic subsidies (increased predator abundance in +subsidy treatments), combined with an equally strong functional response (increased per capita consumption by lizards of in situ resources in -subsidy treatments), led to similar net effects of lizards on terrestrial arthropod prey between subsidy treatments.

In summary, lizards responded numerically to riverine insect subsidies. Over the spatial (tens of meters) and temporal (months) scales of our experiment, this numerical response did not result in increased depletion of in situ prey by lizards. Short-term negative effects of aquatic insects on in situ prey were most likely offset by a countervailing changes in functional response of lizards. Thus, our data suggest that the strength and sign of indirect effects of subsidies to predators on their in situ prey will depend on the balance struck between the predator's functional and numerical responses over the time scales observed.

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