

RIVER–WATERSHED EXCHANGE: EFFECTS OF RIVERINE SUBSIDIES ON RIPARIAN LIZARDS AND THEIR TERRESTRIAL PREY

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Abstract. Resource subsidies from external habitats can enhance the performance or population density of local consumers, altering their effects on in situ prey. Indirect effects of subsidies may be either positive or negative depending on the behavior of the shared consumer. Here we document strong links between riverine insects, riparian lizards (*Sceloporus occidentalis*), and terrestrial invertebrates. We hypothesized that aquatic insects subsidize riparian lizard populations leading to higher growth rates of these lizards in near-river habitats, and that subsidies exert short-term positive effects on terrestrial resources as a result of diet shifts by lizards to aquatic insects. To test these hypotheses, we used 2 m high fences, or “subsidy shields,” to experimentally reduce aquatic insect flux to large (91 m²) enclosures of lizards. Subsidy shields reduced aquatic insect flux by 55–65%. Growth rates of lizards were 7× higher in subsidized (no-shield) enclosures during the early summer but were not significantly different later in the summer, when ambient fluxes of aquatic insects dropped to 20% of their early season levels. Within the watershed, lizard growth rates (in mass) were positively correlated with the numerical abundance of aquatic insects. Thus, lizard growth rates tracked both seasonal and spatial availability of riverine insect subsidies during our experiment. Subsidies also had indirect effects on the ground-dwelling, terrestrial prey of lizards. Declines of diurnal terrestrial invertebrates were significantly higher in shield than no-shield enclosures, and the most common ground spider (*Arctosa* sp. [Lycosidae]) disappeared completely from shield enclosures by the end of the experiment. Declines in terrestrial invertebrate abundance did not differ between no-shield enclosures and lizard enclosures. These data suggest that riverine insects subsidize riparian *Sceloporus* and, in the short term, reduce their predation on terrestrial arthropods.

Key words: *Arctosa* sp.; functional response; ground spider; lizard; predation; riparian; river; river–watershed exchange; *Sceloporus occidentalis*; subsidy; watershed.

INTRODUCTION

Riparian habitats joining rivers and adjacent upland forests may harbor higher densities of consumers, or offer individuals better growth opportunities, as a result of resource exchange between aquatic and terrestrial habitats (Wiens 1992, Naiman et al. 1993, Polis and Hurd 1995, 1996a, b, Naiman and Decamps 1997, Fagan et al. 1999, Warkentin and Reed 1999). Allochthonous resources from more productive habitats subsidize consumers in adjacent, less productive habitats (Polis and Hurd 1995, Polis and Strong 1996). Subsidies occur in a wide variety of ecosystems (Polis and Winemiller 1996). For example, marine algal detritus and sea wrack have a strong influence on the food web dynamics of near-shore, terrestrial habitats (Polis and Hurd 1995, 1996a, b, Rose and Polis 1998, Anderson and Polis 1998, 1999). Other aquatic habitats coupled by spatial resource flow include the subtidal and intertidal (Duggins et al. 1989, Bustamante et al.

1995, Menge et al. 1997), coastal sea grass and deep sea habitats (Suchanek et al. 1985) and littoral and pelagic communities in freshwater lakes (Schindler et al. 1996, Blumenshine et al. 1997). These and similar studies challenge ecologists to redefine interaction webs to include strong links both within and across traditional habitat boundaries.

Identifying and understanding trophic links between aquatic and terrestrial habitats also is critical to understanding food web dynamics in watershed ecosystems (Jackson and Fisher 1986). To this end, stream ecologists have traditionally focused on fluxes from terrestrial to aquatic habitats (e.g., Hynes 1970, Cummins et al. 1973, Vannote et al. 1980). For example, leaf litter fuels detritus-based secondary production of stream invertebrates (Cummins et al. 1973, Vannote et al. 1980, Wallace et al. 1997, 1999), while terrestrial fruit (Goulding 1980) and invertebrates (Mason and MacDonald 1982, Nakano et al. 1999) feed stream fish. Resources also flow from rivers to terrestrial portions of watersheds (Jackson and Fisher 1986, Gray 1989, 1993), but less is known about the effects of these links on terrestrial consumer performance and fitness.

Subsidies also may exert indirect effects on local (or in situ) resources produced in the recipient habitat (Bustamante et al. 1995, Polis and Hurd 1996b, Nakano

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et al. 1999; Henschel, *in press*). Theoretical models of one predator/two prey communities suggest that these indirect effects may be either positive or negative depending on the level of resource limitation experienced by the consumer (Holt 1977), the consumer's resource-tracking behavior (Holt 1984, Holt and Kotler 1987), whether the predator experiences density dependence (Abrams and Matsuda 1996), and the time scale of the consumer's response (i.e., functional or numerical) to subsidies (Holt 1977, Abrams and Matsuda 1996, Abrams et al. 1999). Field experiments on the indirect effects of subsidies similarly demonstrate either strong negative effects via the consumer's numerical response (Bustamante et al. 1995; Henschel, *in press*) or positive effects via implicit consumer functional responses (Nakano et al. 1999).

We examined the effect of river-derived insects on the growth rates of riparian *Sceloporus* lizards and the alternate, ground-dwelling prey of these terrestrial consumers. We experimentally manipulated the flux of riverine subsidies (aquatic insects) to large (91 m²) enclosures of *S. occidentalis* to evaluate the effects of subsidies on lizard growth and terrestrial insect abundance. We hypothesized that (1) aquatic resource subsidies would increase the growth rates of lizards in near-river habitats; and (2) subsidies would have short-term, positive indirect effects on in situ, terrestrial prey. We expected positive effects of subsidies on terrestrial invertebrates because lizards enclosed in reduced subsidy environments would not receive the abundant aquatic resources in unmanipulated plots, and therefore would consume a larger number of terrestrial prey.

STUDY SITE

Experiments took place along a 4-km reach of the South Fork (SF) Eel River (39°44' N, 123°39' W) in Mendocino County, California, USA. Cobble bars are lens-shaped, rocky habitats immediately adjacent to the river, averaging 0.54 ± 0.27 ha in area (range 0.28–1.04 ha) bordered by river on the downslope side and by forest or grassy meadows on the upslope side. Vegetation on the study cobble bars consists of sedges (*Carex nudata*) and riparian trees (e.g., *Fraxinus latifolia*, *Alnus glutinosa*) along the river boundary and sparse shrubs (*Ceanothus* spp. and *Baccharis* spp.) in drier microhabitats more distant from the river.

The climate in Mendocino County, California is Mediterranean, with rainy winters followed by a summer drought. Annual rainfall typically exceeds 150 cm with most precipitation falling between October and April. Because of winter rains and flooding, cobble bars serve only as temporary habitats to most animals. Western fence lizards, sagebrush lizards (*S. graciosus*), Western skinks (*Eumeces skiltonianus*) and Northern alligator lizards (*Elgaria coeruleus*) are common on cobble bars throughout the study reach.

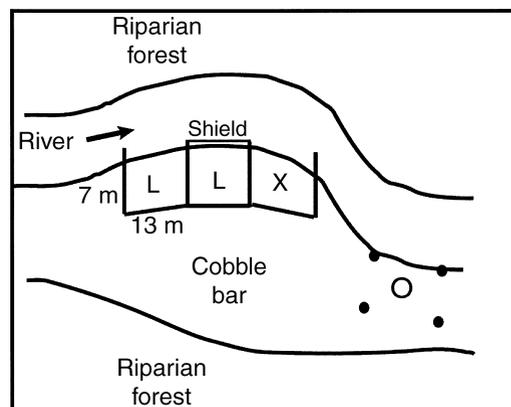


FIG. 1. Design of subsidy removal experiment involving lizard enclosures (L), with and without subsidy shields, a lizard enclosure (X) and open (O), unmanipulated plots. All treatments encompassed 91 m² of cobble bar habitat (7 × 13 m) and were randomized within each of four sites (blocks) along a 4-km reach of the SF Eel River. Open plots were randomized with respect to their position (upstream or downstream) relative to contiguous treatments.

METHODS

Experimental design and initial conditions

Our experiment included three treatments and an open control plot (Fig. 1) replicated once on each of the four sites (experimental blocks) within the 4-km study reach. The experimental treatments included two lizard enclosures and one lizard enclosure. *S. occidentalis* were enclosed or excluded with three cage walls, the river acting as a fourth barrier to emigration from and immigration into enclosures (*S. occidentalis* are extremely reluctant to swim). One enclosure had an additional fourth wall parallel to the river (Fig. 1), hereafter referred to as the subsidy shield. We used subsidy shields to reduce the flux of winged adults of aquatic insects from the river into shielded enclosures of *S. occidentalis*. Relative positions of treatments were randomized within sites. Open controls were randomly located upstream or downstream of experimental treatments. The experiment thus consisted of three treatments: shield and no-shield enclosures to test the effect of inputs of aquatic insects on *S. occidentalis* growth rates, and an unshielded enclosure to assess the impact of *S. occidentalis* on local, ground-dwelling terrestrial prey. Open plots provided data on ambient conditions (*S. occidentalis* growth rates and invertebrate abundance) throughout the experiment.

All plots were 91 m² (7 × 13 m). Enclosure and enclosure walls were 2 m high, made from 12.7-mm mesh bird netting (top 1 m) sewn to visqueen plastic (bottom 1 m). Back walls (facing the forest) had three flanges: bird netting (top 1 m), visqueen (middle 0.5 m) and 7-mm polypropylene netting (bottom 0.5 m). Visqueen was used to prevent lizards from climbing out of enclosures or into enclosures. A flange of finer

netting was attached to the back walls of cages (flush to the cobble substrate) to allow immigration and emigration by small invertebrates. This lower mesh flange was not included in side walls to maintain independence among treatments. Cage walls were attached by plastic cable ties to 2 m lengths of 3.5-cm diameter PVC pipe supported by rebar pounded into the cobble bar. We buried the lower flanges of cage walls in the cobble bar using sand secured by cobbles. Cobbles and sand were collected directly under the cage wall or from outside the plot to reduce disturbance in each of the experimental arenas. Subsidy shields were positioned 0.5 m into the river so that enclosed lizards in shield and no-shield enclosures had equal access to water.

Following cage construction, we removed all lizards from designated enclosures and exclosures. Each enclosure then was stocked with three subadult *S. occidentalis*, one male and two females, each marked with unique toe clips and dorsal nail polish sequences. Experimental densities (330 individuals/ha) matched those observed in similar unmanipulated habitats near the river edge (Sabo 2000). We used subadult lizards to maximize the potential for growth during the experiment. Lizards stocked in enclosures were size-matched to the nearest 1 mm between treatments (53.17 ± 3.86 mm; this and following data are reported as mean ± 1 SE) within the range of ambient subadult sizes in June (49.83 ± 7.43 mm; J. Sabo, unpublished data). Because male *S. occidentalis* are strongly territorial, we used subadults and a female-biased 2:1 sex ratio to eliminate potential confounding effects of male-male social interactions associated with mating on individual growth rates. All enclosures were monitored regularly for escaped animals. Over the course of the experiment ~20% of the lizards escaped, and the frequency of escapes was not significantly different in shield than no-shield enclosures ($\chi^2 = 0.5$, $df = 1$, $P > 0.25$). When animals were missing for more than three days, we replaced them with a lizard of the same sex, but size matched with a counterpart in the adjacent enclosure at that site.

Aquatic and terrestrial insect fluxes

We measured fluxes of aerial aquatic and terrestrial invertebrates in experimental and open plots using sticky traps (one per treatment) hung 1 m off the ground at the river margin at an equal distance from each side wall. Sticky traps were 612-cm² transparent acetate sheets covered with Tanglefoot insect trap coating (Tanglefoot, Grand Rapids, Michigan, USA) and rolled in a cylinder around rebar posts to capture insects flying from all directions. We set sticky traps for five-day intervals once prior to the experiment (4–8 June 1997) and four times following cage construction and lizard introduction (27 June–1 July, 16–20 July, 4–8 August, and 31 August–4 September 1997). After five days, traps were covered with cellophane and stored at 12°C until they could be processed in the lab.

We identified and measured lengths (± 1 mm) of specimens collected in sticky traps using a 10–35 \times dissecting scope. In total, we identified >3500 specimens collected during the five trapping intervals. We designated the larval origin of the specimens as either riverine (aquatic) or riparian (terrestrial) relying on identification to the ordinal level except for dipterans. In classifying dipterans, we identified five abundant dipteran families whose taxa were predominantly aquatic at our study site: Chironomidae, Tipulidae, Simuliidae, Stratiomyidae, and Tabanidae. All other dipterans (mostly Asilidae, Bombyliidae, Ephydriidae, Mycetophilidae, Muscidae, Rhagionidae, and Sciariidae) were considered terrestrial even if these families included taxa with semiaquatic life histories (e.g., Rhagionidae), or included a few, but not a majority of aquatic taxa. By combining terrestrial and semiaquatic dipteran families into a terrestrial category we potentially underestimate the true magnitude of the flux of riverine insects to riparian habitats. Our classification scheme is therefore conservative with respect to our hypothesis that river-derived insects enhance the growth of riparian lizards. We estimated the biomass of aquatic and terrestrial fractions of the samples using length-mass regressions generated from independently collected samples of invertebrates at the SF Eel River (Sabo et al. 2002).

Lizard growth rates

The experiment encompassed more than half of the active growing season (May–October) for subadult *S. occidentalis* at our study site. We measured all *S. occidentalis* stocked in experimental enclosures to the nearest 1 mm snout-vent length (SVL), and weighed them to the nearest 0.1 gram using Pesola spring scales (Pesola AG, Baar, Switzerland) three times: once prior to the onset of the experiment (23–26 June), at a midpoint (26–29 July), and at the end of the experiment (7–10 September). These three size measurements allowed us to assess growth rates for individually marked lizards in shield and no-shield enclosures during early and late summer, and across the entire experiment. For statistical analysis, we averaged growth rates of individuals within each enclosure excluding all animals used to replace escaped individuals.

Cage effects

Cage effects on resource availability were assessed by comparing invertebrate abundance in experimental enclosures to that in open controls. Cage effects on lizard growth rates were evaluated by comparing growth rates of lizards in no-shield enclosures to those of free-ranging lizards of the same initial size collected from the same experimental sites. Growth rates of free-ranging lizards were estimated from 34 individuals (8.5 ± 5.8 per site) captured in each of two routine mark-resight surveys in June and late August (J. Sabo, unpublished data). Due to the effort required to carry out

these surveys, we measured growth rates of free-ranging lizards only twice, but across a time period overlapping with the experiment. We used the mean values of these growth rates from each site as four replicates of ambient growth and compared these to growth rates over the entire experiment (26 June–1 September) in shield and no-shield enclosures.

Effects of lizards on ground-dwelling invertebrates

We used wet pitfall traps to quantify the abundance of ground-dwelling, terrestrial invertebrates in experimental treatments and open controls. Round plastic cups (8 cm in diameter) buried flush to the cobble surface, filled 2 cm deep with water and a few drops of dish soap, were placed at 0.25 and 6 m from the river (one per plot) along the midline of each plot. Pitfall traps were set during the five collecting periods for sticky traps, but for shorter, two-day periods to avoid desiccation of samples. After two days, we collected pitfall traps and preserved captured specimens in 70% EtOH. Eight traps were unearthed by animals during the experiment. Pitfall data are thus presented as plot means of samples from traps at the two specified distances.

All specimens were identified to at least the ordinal level. Nocturnal ground beetles (Carabidae), a common spider (*Arctosa* sp.), and an ant (*Pogonomyrmex* sp.) also were quantified. We assessed impacts of lizards on these terrestrial invertebrates by comparing relative changes in abundance over time and the final abundance of these taxa in pitfall traps in shield and no-shield enclosures and lizard exclosures. We assessed the overall impact of lizards on terrestrial arthropods under ambient aquatic resource conditions by comparing no-shield enclosures and exclosures and examined the effect of subsidy reduction on terrestrial arthropod abundance by comparing no-shield and shield enclosures.

All tests were performed on three categories of arthropods: (1) all diurnal taxa except *Pogonomyrmex* sp.; (2) *Arctosa*, which also were included in the total diurnal category; and (3) nocturnal carabids, which were not included in the diurnal category. We excluded *Pogonomyrmex* sp. from the total diurnal category because its numerical dominance (>50 individuals) in several traps suggested that we had disturbed nests of these ants while deploying the nearby pitfall trap. We analyzed *Arctosa* and carabid beetles separately because they are the numerically dominant taxa at our study site within the size range of prey chosen by these lizards, but differ in diel activity (Sabo 2000), and thus in their relative susceptibility to predation by lizards. Carabids are nocturnal, whereas many lycosid spiders, including *Arctosa*, have diurnal, crepuscular, or crepuscular/nocturnal activity patterns at our study site (J. Sabo, unpublished data). Because *Sceloporus* spp. rely on visual cues for prey detection (i.e., they do not dig or search actively for prey) and forage during daylight

and crepuscular (dusk) periods, *Arctosa* and other diurnal taxa should be relatively more vulnerable to predation by lizards. We predicted that (1) abundances of diurnal taxa and *Arctosa* would decline more rapidly in enclosures than in exclosures as a result of the presence of lizards in the former, (2) both terrestrial taxa would decline more rapidly in shield than in no-shield enclosures as a result of shifts in the diets of lizards, and (3) that carabid beetles would show no responses to lizard predation.

Data analysis

All statistical tests were performed in SYSTAT 9.0 (SPSS 1998). We analyzed differences between shield and no-shield treatments in aquatic and terrestrial invertebrate abundance from sticky traps using repeated measures ANOVA with time as the repeated measure ($t = 4$; 27 June–31 August 1997) and site as a blocking factor ($b = 4$). Similarly, we analyzed differences between these two treatments in growth rates with time as an explicit factor in our statistical model. However, because the two response variables, length and weight, may covary, we analyzed differences in growth rates using repeated measures MANOVA, with two repeated measures ($t = 2$), four experimental blocks, and length and weight as two dependent variables (Table 1). We used one-tailed critical values to test the a priori hypotheses that aquatic insect inputs and lizard growth rates would be lower in shield than in no-shield treatments.

To evaluate cage effects, we analyzed differences in time-averaged ($t = 4$) aquatic and terrestrial invertebrate fluxes and lizard growth rates among enclosures and open plots using ANOVA (insects) and MANOVA (lizard growth rates) both with randomized block designs. A repeated-measures model was not possible because we measured growth of free-ranging lizards over only a single time period. Finally, we used repeated measures ANOVA with a blocking factor to evaluate the effects of lizards on terrestrial invertebrates caught in pitfall traps. In this analysis “time” in our model had two levels: (1) “before” cage construction and lizard introduction; and (2) “after,” or the final sample at the end of the experiment. In these tests, our planned comparisons (no-shield enclosure vs. exclosure and no-shield vs. shield enclosure) were analyzed using Tukey’s hsd (when overall tests were significant) or Bonferroni multiple comparisons (when overall tests were nonsignificant; Miliken and Johnson 1992).

RESULTS

Effects of subsidy shields on relative resource availability

Aquatic insect abundance was reduced in shield enclosures relative to no-shield enclosures across all four sampling dates following cage construction (Fig. 2, Table 2). Shields reduced the abundance of aquatic insects

TABLE 1. Results from repeated-measures MANOVA on lizard growth rates during early and late summer 1997.

Source	SS	df	MS	F	P
Between subjects					
Treatment	0.020	1	0.020	6.799	0.04†
Block	0.012	3	0.004	1.391	0.396
Error	0.009	3	0.003		
Within subjects					
Time (W)	0.023	1	0.023	19.032	0.022
Time (W) × treatment	0.008	1	0.008	6.698	0.04†
Time (W) × block	0.002	3	0.001	0.608	0.654
Error	0.004	3	0.001		
Time (L)	0.019	1	0.019	5.323	0.104
Time (L) × treatment	0.032	1	0.032	9.261	0.028†
Time (L) × block	0.017	3	0.006	1.637	0.348
Error	0.010	3	0.003		

Notes: Abbreviations are: W, weight; L, length. The ANOVA model was: Repeat (Length 1, 2) + Repeat (Weight 1, 2) = constant + treatment + block + time (L) + time (W) + time (L) × time (W) + time (L) × treatment + time (W) × treatment + time (L) × block + time (W) × block + time (L) × time (W) × treatment + time (L) × time (W) × block for no-shield and shield treatments (Hotelling's *T* test). Higher order interactions (e.g., time × treatment × block) were not significant.

† One-tailed *P* values for test of no shield > shield.

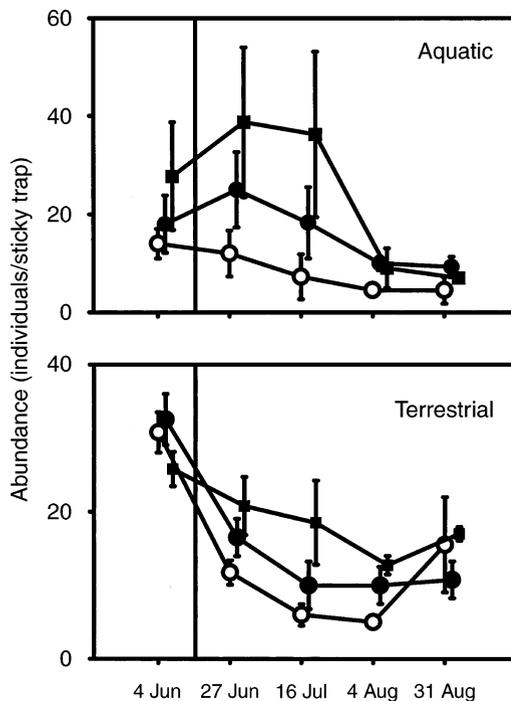


FIG. 2. Treatment effects on resource abundance. The histograms show mean (± 1 SE) abundances of aquatic (top) and terrestrial (bottom) invertebrates caught on sticky traps in shield enclosures (open circles) and no-shield enclosures (closed circles) during 5-d sampling periods at ~ 3 -wk intervals between 4 June and 31 August 1997. Dates indicate start dates for each sampling period. The vertical reference line indicates cage construction and lizard addition such that 4 June samples are unmanipulated abundances on experimental sites prior to the start of the experiment. Abundance in open plots (squares) of each class of invertebrates is presented for comparison.

by 55% when averaged over these four sampling dates. Biomass of aquatic insects also was $2.9\times$ higher in no-shield than in shield enclosures. Aquatic insect abundance declined significantly between June and August and also varied significantly among experimental sites (see time and block effects, Table 2). By contrast, the abundance of aerial terrestrial invertebrates did not differ significantly between no-shield and shield enclosures over the four sampling periods following cage construction (Fig. 2, Table 2). Abundance of aerial terrestrial invertebrates declined by twofold over the entire summer (4 June–31 August), and local fluxes of terrestrial arthropods did not differ significantly among sites (Table 2).

Effects of shields on lizard growth rates

Lizards in no-shield enclosures grew $2.6\times$ and $1.9\times$ faster in length and weight, respectively, over the entire experiment (Fig. 3, Table 1). Early-season growth rates were as much as $7\times$ higher in no-shield enclosures relative to shield enclosures. Despite significant differences in the early summer, growth rates later in the summer showed no response to the shield treatment (Fig. 3). Effects of the shields on growth rates varied between early and late experimental periods for both weight and length (time × treatment effect, Table 1) but the seasonal decline in growth rate was significant only for weight (time effect, Table 1). Significant among-site variation in aquatic insect abundance (block effect, Table 2) suggested that lizard growth rates also may have varied spatially as a function of these invertebrate fluxes. To quantify the effect of aquatic insect abundance on lizard growth rates across the study site we used linear regression of aquatic insect abundance on growth rates averaged across the entire experiment (26 June–10 September). Lizard growth in

TABLE 2. Results from repeated-measures ANOVA on abundance (individuals/trap) of aerial aquatic and terrestrial invertebrates caught in sticky traps on four dates (27 June–31 August 1997; Fig. 2).

Source	ss	df	MS	F	P
Aquatic taxa					
Between subjects					
Treatment	294.031	1	294.031	29.619	0.006†
Block	381.906	3	128.302	12.924	0.032
Error	29.781	3	9.927		
Within subjects					
Time	659.031	3	219.677	6.503	0.012
Time × treatment	140.906	3	46.969	1.390	0.154†
Time × block	766.781	9	85.198	2.522	0.092
Error	304.031	9	33.781		
Terrestrial taxa					
Between subjects					
Treatment	87.781	1	87.781	0.946	0.402†
Block	85.844	3	28.615	0.308	0.820
Error	278.344	3	92.781		
Within subjects					
Time	205.031	3	68.344	6.546	0.012
Time × treatment	80.656	3	26.885	2.575	0.119†
Time × block	151.594	9	16.844	1.613	0.244
Error	93.969	9	10.441		

Note: The ANOVA model was: Repeat (Abundance 1, 2, 3, 4) = constant + treatment + block + time + time × treatment + time × block for shield and no-shield treatments.

† P values are one tailed for no shield > shield.

weight varied positively with aquatic insect abundance ($F = 5.7$, $df = 1, 11$, $P < 0.05$, $R^2 = 0.38$). This relationship was not significant for growth in length ($P > 0.05$).

Cage effects

Cage effects on aquatic resource abundance and lizard growth rates were small compared to shield effects. Fluxes of aquatic insects and terrestrial insects were slightly higher in both abundance and biomass in open plots than in no-shield enclosures (Fig. 3), but differences were not significant (all P values > 0.2). Cages did not affect lizard growth in length but free-ranging lizards grew 1.6× faster in weight ($F = 16.03$, $df = 2, 6$, $P < 0.01$) than lizards enclosed in no-shield treatments (Fig. 3).

Effects of lizards on in situ terrestrial resources

Ground-dwelling arthropods declined more in shield than in no-shield enclosures (Fig. 4). On average, these taxa declined 3.4-fold between initial and final samples across all treatments. Declines did not differ significantly among treatments in the full model (time × treatment effect, Table 3). Declines were significantly higher in shield vs. no-shield enclosures (planned comparison, Bonferroni $P < 0.05$, Table 3) but did not differ significantly between no-shield enclosures and enclosures (planned comparison, Bonferroni $P > 0.75$, Table 3).

Arctosa also declined more strongly in shield than in no-shield enclosures and these spiders appeared to be completely absent from all shield cages by the end

of the experiment (Fig. 4). Although *Arctosa* persisted in no-shield enclosures, enclosures, and open plots, declines in *Arctosa* abundance were not significantly different either in full tests (repeated measures ANOVA, $F = 2.17$, $df = 3, 9$, $P > 0.15$) or planned comparisons (no shield vs. shield, $P > 0.60$; no shield vs. enclosure, $P > 0.90$). Final densities of *Arctosa* were only marginally higher in no-shield enclosures despite their complete disappearance from all replicates of the shield treatment ($F = 4.77$, $df = 1, 3$, one-tailed $P < 0.065$). Differences between enclosure and no-shield enclosure treatments were not significant ($F = 0.33$, $df = 1, 3$, one-tailed $P > 0.30$).

Nocturnal carabid beetles did not differ significantly in initial abundance among treatments ($F = 0.78$, $df = 3, 9$, $P > 0.50$). These beetles declined 3.8-fold across all treatments between the initial pitfall sample and the end of the experiment. Seasonal declines in carabid abundance appear to result from estivation during the dry months of July and August at our study site. However, in contrast to diurnal taxa, declines of carabids did not differ significantly among treatments ($F = 0.57$, $df = 3, 9$, $P > 0.6$) or in planned contrasts (no shield vs. shield: $F = 0.24$, $df = 1, 3$, $P > 0.65$; no shield vs. open: $F = 0.96$, $df = 1, 3$, $P > 0.4$).

DISCUSSION

Our results suggest that “rivers can feed the forest.” Previous studies have shown that the export of aquatic insects is an important pathway of energy flow between rivers and terrestrial portions of desert and grassland ecosystems (Jackson and Fisher 1986, Gray 1989). The

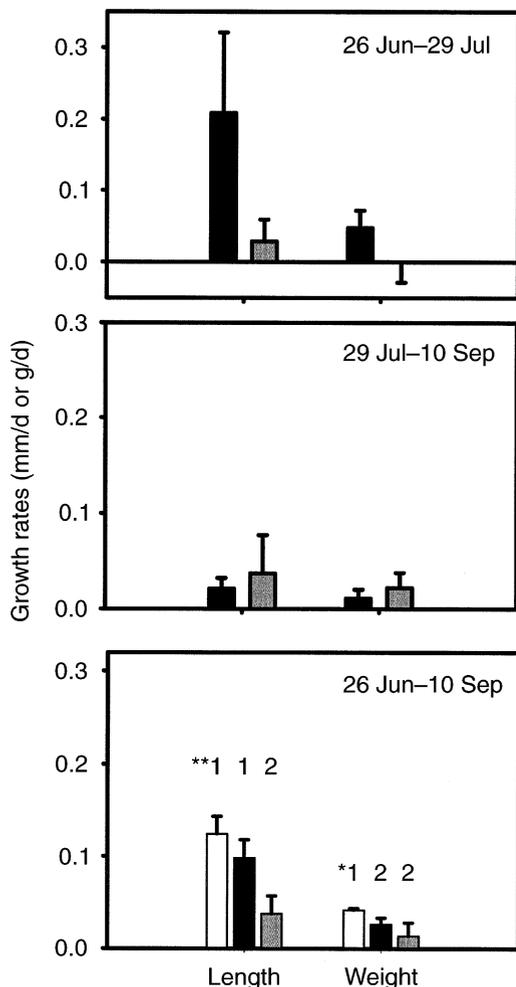


FIG. 3. Effects of subsidy reduction on lizard growth rates. The graphs show mean (+1 SE) growth rates in terms of length (mm/d) and weight (g/d) in no-shield enclosures (black bars) and shield enclosures (gray bars) during the first half (top panel) and second half (middle panel) of the experiment. Means and variance estimates were derived from cage means for replicates of each treatment. Growth rates in no-shield enclosures were significantly higher over the entire experiment (repeated-measures MANOVA, $P < 0.05$) and declined significantly faster between the first and second half of the experiment (see Table 1). The bottom panel shows mean growth rates over the entire experiment for free ranging lizards (white bars), no-shield enclosures (black bars), and shield enclosures (gray bars). For free ranging lizards, means and standard errors were derived from site means of 8.5 ± 5.8 individuals. Data for enclosures are based on cage means of animals in individual replicates averaged between early and late growing seasons. In the bottom panel, nonmatching numbers within groups indicate significant differences between individual treatments (Tukey's hsd $P < 0.05$). Asterisks indicate significance levels for overall tests: * $P < 0.05$, ** $P < 0.01$.

abundance of common terrestrial insectivores (e.g., bats, birds, and spiders) increases along natural gradients of aquatic resource availability within watersheds in a variety of biomes (Gray 1993; Henschel, *in*

press; Power et al., *in press*). Our study provides experimental support for the value of these resources for terrestrial consumers and may explain the high densities of lizards in near-river habitats. Moreover, our results suggest that aquatic resources in riparian habitats may affect lower terrestrial trophic levels indi-

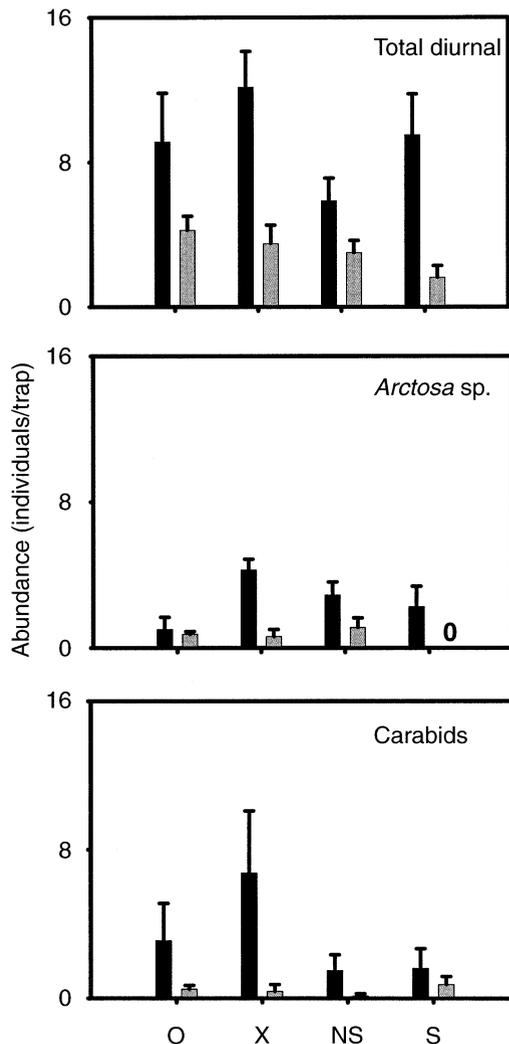


FIG. 4. Indirect effects of subsidy reduction treatment on abundance of ground-dwelling terrestrial invertebrates. The histograms show mean (+1 SE) abundances of total diurnal taxa, the most abundant ground-dwelling spider, *Arctosa* sp. (Lycosidae), and nocturnal ground beetles (Carabidae) caught in pitfall traps before enclosures were built (1 June; black bars), and at the end of the experiment (1 September; gray bars) in open plots (O), lizard enclosures (X), and no-shield (NS) and shield (S) enclosures. Ground-dwelling terrestrial invertebrate and spider abundances were not significantly different among treatments before the start of the experiment. Declines in total diurnal taxa were significantly greater in shield than in no-shield enclosures. Declines in spider abundance were not significantly different between these two treatments, despite extinction of spiders in shield enclosures and marginally significant differences in final spider abundance (one-way ANOVA, $P < 0.065$).

TABLE 3. Results from repeated-measures ANOVA on abundance (individuals/trap) of ground-dwelling, diurnal terrestrial invertebrates.

Source	SS	df	MS	F	P
Full model					
Between subjects					
Treatment	1.063	3	0.354	2.189	0.159
Block	1.625	3	0.542	3.345	0.069
Error	1.458	9	0.162		
Within subjects					
Time	6.300	1	6.300	41.871	0.000
Time × treatment	1.039	3	0.346	2.298	0.146
Time × block	0.831	3	0.277	1.839	0.210
Error	1.356	9	0.151		
Contrast of shield and no-shield treatments					
Between subjects					
Treatment	0.006	1	0.006	0.020	0.898
Block	0.772	3	0.257	0.853	0.550
Error	0.905	3	0.302		
Within subjects					
Time	3.672	1	3.672	96.458	0.002†
Time × treatment	0.671	1	0.671	17.626	0.025†
Time × block	0.840	3	0.280	7.353	0.068†
Error	0.114	3	0.038		
Contrast of no-shield and enclosure treatments					
Between subjects					
Treatment	0.016	1	0.016	0.140	0.733†
Block	0.861	3	0.287	2.514	0.234†
Error	0.342	3	0.114		
Within subjects					
Time	1.507	1	1.507	14.790	0.031†
Time × treatment	0.009	1	0.009	0.088	0.786†
Time × block	0.656	3	0.219	2.146	0.273†
Error	0.306	3	0.102		

Notes: ANOVA excludes nocturnal beetles (Carabidae) and *Pogonomyrmex* sp. All counts were $(\ln + 1)$ -transformed prior to analysis to control for heteroscedacity.

† Bonferroni critical α levels = 0.025.

rectly via lizards. Abundant aquatic resources appear to swamp the functional response of lizards, reducing predation pressure on terrestrial invertebrates by these common predators over short time scales.

Direct effects of aquatic subsidies on lizard growth

Riparian corridors may offer lizards high quality habitat for a number of reasons. First, rivers provide water, which can limit the growth of other iguanid lizards during the dry season in tropical climates (Stamps and Tanaka 1981). Second, river cobble bars provide overnight retreat and nesting sites for ectotherms (Huey et al. 1989). These substrates are much less abundant in upland habitats and may increase seasonal clutch production of riparian lizards (Sabo 2000). Third, emerging riverine insects also offer an abundant resource supply to riparian lizard populations. Our results demonstrate that inputs of aquatic insects from rivers increase growth rates of *S. occidentalis* in riparian habitats, supporting the third hypothesis.

The value of aquatic prey for lizards was demonstrated in three ways by our experiment. First, experimental reduction of aquatic insect subsidies depressed lizard growth rates. Lizards grew more slowly in enclosures in which an experimental subsidy shield re-

duced aquatic insect inputs by 55–65% relative to unshielded enclosures. Second, lizard growth rates in both treatments declined with decreasing seasonal abundance of aquatic resources. Inputs of aquatic insects dropped fivefold between the first and second half of the experiment, while terrestrial aerial invertebrate fluxes decreased by only 18% over this same period. Lizard growth slowed or stopped, and was not significantly different between treatments. Finally, the coupling of variation in the abundance of aquatic insects and lizard growth rates within and among cobble bars suggested that lizard growth may track spatial variation in aquatic insect availability at a variety of spatial scales within the watershed.

For several reasons, our experiment may underestimate the influence of aquatic insect subsidies on lizard growth. Subsidies were reduced but not completely removed in shield relative to no-shield enclosures. Even with a 55% reduction, aquatic insects still outnumbered terrestrial resources in the first half of the experiment in shield plots (see Fig. 2). The three walls common to both shield and no-shield enclosures also reduced aquatic insect abundance in no-shield cages by as much as 32% relative to open plots over the entire experiment (Fig. 2). Thus, lizards in shield enclosures still had

access to some sources of aquatic prey, and lizards in no-shield treatments may not have had full access to these resource because of cage effects. Differences in weight gain between lizards in no-shield enclosures and free-ranging lizards support this latter interpretation. Nevertheless, experimental reduction of aquatic insect fluxes to lizards significantly diminished the growth rates of these insectivores in riparian habitats.

Higher growth rates of lizards in high subsidy environments may provide one explanation for higher densities of these lizards in riparian habitats. Increased growth rates of lizards may result in increases in reproductive output or survivorship. For example, faster growing juvenile females may attain threshold sizes for reproduction at an earlier age. Higher growth rates of hatchlings in riparian habitats also may lead to greater fat reserves at the onset of winter resulting in increased over-winter survivorship.

Effects of aquatic insects on terrestrial invertebrates: direct or indirect?

Terrestrial invertebrates may respond to emerging aquatic insects directly (e.g., as predators aggregating to prey) or indirectly as a result of changes in the foraging behavior or density of a shared predator. Greater declines of terrestrial arthropods in low subsidy enclosures thus could have been brought on by either emigration in response to resource reduction or by lizard predation. The different responses of diurnal (including crepuscular) and nocturnal prey to the shield treatment in our experiment support the latter hypothesis. Carabid beetles are largely nocturnal, whereas *Arctosa* are both crepuscular and nocturnal (Sabo 2000). Both carabid beetles and ground spiders consume aquatic insects (Hering and Platcher 1997; M. Parker and M. Power, unpublished data). If greater declines in terrestrial invertebrate abundance in shield enclosures were brought on by resource limitation, both carabids and *Arctosa* should have declined to similar late-season levels. However, declines in diurnal taxa, including *Arctosa*, were significantly higher in shield vs. no-shield treatments whereas declines in nocturnal carabids were not significantly different. Hence, reductions of diurnal taxa were likely due to predation by lizards or emigration in response to a higher threat of predation in subsidy-poor environments.

Our data also suggest that *Sceloporus* are not food limited during periods of high aquatic resource abundance, and that these lizards may prefer or be satiated by aquatic prey when this alternate resource is highly available. We hypothesized that lizards would deplete terrestrial arthropod prey more rapidly when denied access to subsidies (shield > no shield) but also would depress terrestrial prey abundance even with inputs of aquatic insects because of food limitation and nonselective foraging behavior (no shield > enclosure). Greater declines of terrestrial prey in shield vs. no-shield enclosures supported the first hypothesis; how-

ever, declines of these taxa in enclosures did not differ significantly from those in no-shield enclosures. Combined, these results suggest that *Sceloporus* shift to terrestrial prey only when denied access to adequate supplies of aquatic prey. These effects, however, may only be seasonal. The net indirect effect of aquatic subsidies on terrestrial invertebrates may depend on a more long-term balance between behavioral and numerical responses of lizards (Holt 1977, Holt and Kotler 1987, Abrams and Matsuda 1996).

In summary, our study suggests that energy flow from rivers to their watersheds may be important in forests, supporting the generality of similar findings in grasslands (Gray 1989, 1993) and deserts (Jackson and Fisher 1986). Aquatic insect subsidies enhanced the growth rates of riparian lizards in our system, and altered their impacts on terrestrial prey. Demonstration of strong links between rivers and surrounding watersheds has implications for resource management. Land use (e.g., river impoundment) that alters downstream productivity and diversity (e.g., Dahm et al. 1995) may influence not only downstream river biota (Power et al. 1996), but adjacent terrestrial biota as well.

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