Spatiotemporal food web dynamics along a desert riparian–upland transition

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Increased awareness of spatiotemporal variation in species interactions has motivated the study of temporally-resolved food web dynamics at the landscape level. Empiricists have focused attention on cross-habitat flows of materials, nutrients, and prey, largely ignoring the movement of predators between habitats that differ in productivity (and how predators integrate pulses in resource availability over time). We set out to study seasonal variation in food web interactions between mammalian carnivores and their rodent prey along a riparian–upland gradient in semi-arid southeastern Arizona which features both spatial and temporal heterogeneity in resource availability. Specifically, we tested whether mammalian carnivores spill over from productive, near-river habitats into adjacent, desert-scrub habitats; and if they do, to document the effects of this spillover on rodent communities. Furthermore, we examined seasonal variation in top-down effects by measuring changes in carnivore diet and distribution patterns and rodent populations over time. The results indicate that carnivores track seasonally-abundant resources across the landscape, varying both their diet and movement patterns. In turn, desert-scrub rodent population dynamics track seasonal shifts in carnivore habitat use but not resource availability, suggesting that predation plays a role in structuring rodent communities along the San Pedro River. Further evidence comes from data on rodent community composition, which differs between desert-scrub habitats near and far from the river, despite similarities in resource availability. Our data also suggest that seasonal omnivory helps predators survive lean times, increasing their effects on prey populations. Taken together, these results underscore the importance of spatiotemporal variation in species interactions, highlighting the complexity of natural systems and the need for further detailed studies of food web dynamics.

Food webs provide a framework for understanding species interactions, with recent work drawing attention to the spatiotemporal context in which the interactions occur (Polis et al. 2004, Yang et al. 2008). Both landscape position and seasonal/annual variability in resource availability have been shown to influence the strength of species interactions and the structure of ecological communities (Ostfeld and Keesing 2000, Meserve et al. 2003, Anderson et al. 2008). However, integrating both spatial and temporal dimensions into a single study is difficult for empiricists and theoreticians alike (Polis 1994, Holt et al. 2003). From an empirical point of view, a consideration of landscape position and seasonal/annual variability imposes logistic and statistical challenges (i.e. increased study duration and spatial scale; spatial and temporal correlation of results). From a theoretical point of view, considering both space and time together imposes mathematical challenges. More factors result in greater complexity and make models less likely to yield analytical solutions, making interpretation difficult (Sabo et al. 2005).

We argue that, at present, theoretical development has outpaced empirical progress on food web studies in space and time. Redressing the situation will thus require temporally-resolved field studies of trophic interactions in a landscape context. Most recent empirical studies of food web interactions in space have focused on subsidies – allochthonous resource inputs from productive to less productive habitats (Polis et al. 1997). Subsidies elevate the abundance of consumers in the recipient habitats (Rose and Polis 1998, Sabo and Power 2002), thereby increasing (Sabo and Power 2002) or decreasing (Murakami and Nakano 2002) the abundance of “local” or “in-situ” prey. Thus, subsidy research has demonstrated how prey movement connects basal resources in one habitat to consumers in another habitat. Surprisingly, very little empirical work on food webs has addressed the complementary process of consumer movement. Yet, predator home ranges often cover large areas and couple food web dynamics in adjacent habitats that may differ in resource availability.

The notion that consumer movement across habitat boundaries can lead to novel interactions and dynamics has a sound theoretical foundation. Holt (1984) noted the potential for negative indirect effects between prey species living in different habitats, but sharing a common predator.
(i.e. apparent competition). Oksanen (1990) then considered the case where adjacent habitats differ in productivity, resulting in asymmetrical indirect interactions between prey species as a result of predator foraging across habitat boundaries. She dubbed this mechanism spillover predation, since predation appears to spill over from the productive habitat (where there are sufficient resources to support a predator) to the less productive habitat (where resources and prey are less abundant). Of particular interest is the potential for abundant predators from the resource-rich habitat to depress or eliminate prey populations in the resource-poor habitat (Cantrell et al. 2001, Schneider 2001).

Numerous studies report that, under certain conditions, in-situ predators can regulate in-situ prey populations (Erlinge et al. 1984, Power 1992, Oksanen and Oksanen 2000). Considerable empirical work also indicates that generalist predators forage widely across the landscape, varying their diet and movements based on season and resource availability (Willson and Halupka 1995, Valenzuela and Ceballos 2000, Rosalino et al. 2005; but see Jaksic et al. 1993). Taken together, these results suggest that spillover predation may occur where mobile predators consume prey species that occupy different habitats (Holt 1984). Nevertheless, only a few field studies have directly addressed the spillover predation hypothesis (Kristan and Boarman 2003, Storch et al. 2005, Rand and Louda 2006), in contrast with dozens of published articles on prey subsidies across habitat boundaries. A top-down mechanism for food web interactions at a landscape level, spillover predation, provides a logical complement to the bottom-up mechanism of cross-boundary subsidies.

Just as subsidies often vary over time (Nakano and Murakami 2001), so too spillover predation might be expected to differ from season to season in response to regional as well as habitat-specific variation in resource availability (Rand et al. 2006). Temporal variation in resource availability, including seasonality, year-to-year anomalies, and disturbance, alters food web interactions (Abrams et al. 1998, Polis et al. 1998, Nakano and Murakami 2001, Holt et al. 2003, Sears et al. 2004, Holt 2008). For example, Abrams et al. (1998) showed that temporal variation in resources can reverse the sign of species interactions, whereas Nakano and Murakami (2001) provided an empirical example of seasonal changes in the directional flow of resources between adjacent habitats. Since most ecosystems experience periodic or sporadic resource pulses (Ostfeld and Keesing 2000, Yang et al. 2008), the food web effects of prey or consumer movement must be qualified by the temporal frequency of these spatial links.

Theoreticians study predator-prey dynamics at two time scales: the behavioral, or functional response of predators to a short-term elevation of prey availability, and the population, or numerical response of predators to elevated prey availability over the course of one or more predator reproductive cycles. Both numerical (Holt 1984) and functional (Holt and Kotler 1987) responses by predators can lead to negative indirect interactions between prey species, possibly even resulting in habitat segregation in spatially-heterogeneous environments. However, exogenous environmental variation will modify predator-prey dynamics (Brasil 2006), potentially altering the strength and even the sign of indirect interactions between prey species. Since, the predicted effects of environmental variation depend upon a number of factors, empirical studies would contribute to the advancement of theory by directing attention to those factors most likely to be influenced by exogenous variation, and the range of outcomes that ensue.

The goals of this study were threefold. First we addressed the effects of predator movement across habitat boundaries. Specifically, we tested the notion that predators spill over from productive near-river habitats into more barren uplands, thereby depressing small mammal populations in desert-scrub habitats. Second, we examined variation in spillover predation over time. Productivity differences between riparian and scrub habitats vary depending upon temperature and rainfall patterns. We documented how predator responses to seasonal changes in the relative productivity of riparian and scrub habitats affect their prey by measuring shifts in predator diet and distribution patterns and small mammal populations over time. Third, we analyzed predator diet over time to explore how variation in resource availability may affect predator-prey dynamics. In so doing, our work explicitly addresses spatiotemporal coupling in food web dynamics across seasons and habitat boundaries.

**Study system**

We conducted this research in the San Pedro Riparian National Conservation Area (SPRNCA) along the upper San Pedro River in southeastern Arizona (Fig. 1). Located at ~1200 m elevation, the region is dominated by Chihuahuan Desert Scrub, but features high abiotic and biotic spatial heterogeneity due to the presence of the river and surrounding mountains. In the vicinity of the river, this heterogeneity includes distinctive habitat types such as cottonwood-willow forest, mesquite bosques, sacaton grasslands, and desert scrub (Fig. 2). It is important to note, however, that vegetation can vary considerably within a given habitat type (for the sake of simplicity, we use the term habitat to refer to these landscape features, regardless of whether we discuss them in a syn- or autecological context).

While numerous factors interact to determine habitat type, water table depth stands out as the most important, although other factors such as flood inundation, soil type, and elevation above sea level are important as well (Stromberg et al. 1996). Specifically, cottonwood-willow forest occurs within the river floodplain in areas where the water table is close to the ground surface, mesquite bosques and sacaton grasslands dominate river terraces with intermediate water table depth, and desert scrub occurs in upland areas where the water table is beyond the reach of plant roots. Water table depth increases with increasing distance from the river, but the relationship between the two factors is complex and depends on local topography.

Southeastern Arizona experiences pronounced annual variation in climate (Mock 1996). Temperatures vary from below-freezing lows in the winter to highs around 40°C during the summer, and the region receives 60% of its precipitation in the form of monsoon rains during July and
August. Nevertheless, inter-annual variation in climate can result in wet winters and/or relatively dry summers, complicating the seasonal variation described above. As with most dry systems, rainfall results in a pulse of primary and secondary production across the landscape, and flooding in the riparian habitats (Bagstad et al. 2005).

The San Pedro Watershed hosts a diverse and abundant group of small and medium-sized mammals, including 29 rodent and 16 carnivore species ([Supplementary material, Table S1] Soykan et al. 2009). Most rodents favor specific vegetation zones, with significant turnover between riparian and upland habitats (Soykan et al. unpubl.), while predators tend to forage widely across the landscape (Hass 2001, Soykan et al. unpubl.). Further detail on the San Pedro and its surroundings can be found in Stromberg et al. (1996) and Stromberg and Tellman (2008).

The landscape conditions described above match those required for spillover predation to occur (Rand et al. 2006): first, habitats that differ markedly in resource availability are juxtaposed; second, distinctive prey communities occupy each habitat type; and third, mobile, generalist consumers move between habitats, foraging on available food resources. Added to this spatial template is seasonal variation in rainfall – which, like groundwater, drives primary production. A study system that incorporates both spatial and temporal variation in resource availability provides a realistic, albeit complex setting for the empirical study of temporally-resolved food web interactions at the landscape level.

Research questions and hypotheses

Our overarching hypothesis was that mobile, wide-ranging consumers link food webs across spatial and temporal gradients in productivity via the process of spillover predation and a generalized diet. Testing this hypothesis required knowledge of seasonal variation in plant, herbivore, and predator communities across the landscape. For our study, we divided riparian habitats into two categories: floodplain (cottonwood-willow forest – CW); and river terrace (mesquite bosques and savannas – MQ). We also divided upland habitats into two categories: within 1 km of the river (near desert scrub – NS); and >1 km from the river (far desert scrub – FS). Our reasoning for the latter division was that most predators would be concentrated near the river and would focus their foraging in NS, rather than FS habitats.

The following specific hypotheses (see Table 1 for a summary) address a series of questions that, in combination, link spatial and temporal gradients in plant production to carnivore habitat use and diet, and thus to small mammal abundance.

How do plant resources vary across the landscape and over time?

Considerable work has addressed the physiological effects of water on arid-land plants. Dawson and Ehleringer (1991) demonstrated the importance of groundwater for streamside trees, while Goodrich et al. (2000) and Scott et al. (2000) provided evidence of the dual importance of both groundwater and precipitation for primary production by other types of riparian vegetation. Likewise, Huxman et al. (2004) demonstrated the link between precipitation pulses and primary production by shallow-rooted vegetation. Extending these physiological processes to the population and community level, Stromberg and colleagues (Stromberg et al. 1996, Bagstad et al. 2005, Lite et al. 2005, Stromberg
2007) have documented the importance of water availability and flood disturbance for plant community composition. Based on these studies, we hypothesize that: H1a – plant community structure changes and NPP declines with increasing distance from the river. Alternatively: H1b – flood disturbance drives differences in plant community structure and NPP among habitats. It is also possible that: H1c – plant community structure and NPP vary seasonally.

How does the distribution of predators vary across the landscape and over time?

The ideal free distribution (IFD) provides a framework for predicting the distribution of mobile predators across the desert landscape (Fretwell 1969, Fretwell and Lucas Jr 1969, Sutherland 1996). The IFD holds that if consumers have perfect (“ideal”) knowledge of the resource status in all patches (here “habitats”) and can move freely among them, then individual consumers will choose the habitat with the highest foraging reward and the density of consumers will closely track the production of resources in each habitat type (Fretwell and Lucas Jr 1969). By contrast, if consumers defend territories for feeding and/or breeding, then the individual consumer is not “free” to choose a foraging habitat, thus leading to the ideal despotic distribution (or ideal preemptive, etc.). Similarly, interspecific interactions can prevent the attainment of the IFD (Abrams et al. 2007). In this way we hypothesized that: H2a – predators will track the spatial and temporal availability of food resources distributing themselves in proportion to resource productivity. Alternately: H2b – consumers will not track gradients (in space or time) in resource productivity, reflecting the role of behavioral dynamics in affecting species distributions across the landscape.

How does predator diet vary over time?

Theoretical and empirical evidence exists in support of (Polis 1991, McCann and Hastings 1997) and against (Yodzis 1984, Jaksic et al. 1993) the notion that omnivory is common in ecological communities. Here we propose a pair of hypotheses to represent these opposing perspectives: H3a – predator diet reflects seasonal shifts in resource availability; H3b – predators have specialized diets that vary little over time.

How do small mammal communities respond to variation in resource productivity and predator abundance across the landscape?

Oksanen’s theory of spillover predation (1990) holds that productive habitats support more predators (via reproduction or a numerical response) that then spill over into less productive habitats and exert higher predation pressure on a meager food base. Here we hypothesize that behavioral resource tracking (a functional response to resources) leads to higher predator abundance in high-productivity areas. We then hypothesize that the activities of these mobile predators are likely to spill over into nearby habitats, whether productive or not. Spillover of predators leads to higher predation pressure, which can alter the abundance, survivorship, and species composition of prey communities (Sih et al. 1985). In this way we propose the following set of hypotheses: H4a – small mammal survivorship and abundance reflects spatial and temporal gradients in predation pressure (predator abundance) in the different habitat types, and species composition will be determined by resistance to predation and/or predator preference; H4b – the abundance, survivorship, and species composition of small mammals varies with resource productivity gradients in

Figure 2. Schematic map of the San Pedro River revealing the zonation patterns in vegetation due to differences in distance to groundwater.
Table 1. Summary of hypotheses and predictions.

<table>
<thead>
<tr>
<th>Hypotheses</th>
<th>Predictions</th>
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<tbody>
<tr>
<td>H1a – water availability affects plant community structure and NPP.</td>
<td>NPP and plant species composition should differ among CW, MQ, and desert-scrub habitats, but not between NS and FS habitats.</td>
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<tr>
<td>H1b – flood disturbance affects plant community structure and NPP.</td>
<td>NPP and plant species composition should differ between CW and MQ habitats.</td>
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<tr>
<td>H1c – temperature affects plant community structure and NPP.</td>
<td>NPP and plant species composition should vary across seasons.</td>
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<tr>
<td>H2a – resource availability will determine the distribution of predators across the landscape.</td>
<td>Predators will track the availability of resources along the riparian-upland gradient, leading to spatiotemporal variation in activity-abundance.</td>
</tr>
<tr>
<td>H2b – behavioral interactions will determine the distribution of predators across the landscape.</td>
<td>Predator activity-abundance will be similar along the riparian-upland gradient and will not change over time.</td>
</tr>
<tr>
<td>H3a – skunks, foxes, coyotes, and other common mammalian predators along the San Pedro River are generalists.</td>
<td>Predator diet will change over time in response to seasonal changes in resource availability.</td>
</tr>
<tr>
<td>H3b – skunks, foxes, coyotes, and other common mammalian predators along the San Pedro River are specialists.</td>
<td>Predator diet will change little over time.</td>
</tr>
<tr>
<td>H4a – small mammal abundance, survivorship, and species composition reflect spatiotemporal patterns in predation pressure.</td>
<td>Abundance and composition of rodent communities along the riparian-upland gradient will be affected by the distribution and abundance of predators along the gradient.</td>
</tr>
<tr>
<td>H4b – the abundance, survivorship, and species composition of small mammals reflect spatiotemporal patterns in primary and secondary productivity.</td>
<td>Abundance and composition of rodent communities along the riparian-upland gradient will reflect resource availability.</td>
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Field methods

Litter and vegetation sampling

We estimated NPP and plant community composition in different habitats by measuring litter production, plant diversity, and canopy coverage. We assumed that litter production provides an index of NPP (Whittaker and Marks 1975), which we used to compare resource availability among habitat types. To assess plant community structure, we measured canopy coverage and plant species composition, situating a total of thirty-two 25×25-m plots in four different habitat types (CW, MQ, NS, and FS) at four locations (each separated by >3 km from the others) along the upper San Pedro River (Fig. 2). We measured plant species composition in two 5×2-m sub-plots arranged in the same orientation for each of the 32 plots, and we measured canopy coverage in the center of each subplot using a spherical densitometer, recording values in each of four cardinal directions. We then averaged the canopy coverage values and combined the species composition data to give a mean estimate of canopy coverage and overall estimate of plant species composition for each plot. Finally, we collected and weighed all fine litter from two 0.5×0.5-m miniplots situated in opposite corners of each sub-plot (for a total of 4 litter samples per plot). This sampling design insured that our estimates were representative of the vegetation present in each of the study plots, while our selection of study plots, based on dominant vegetation type and landscape position insured that the plots were representative of the habitat types considered in this study.

Scent stations

We gathered information on the distribution and activity-abundance of mammalian carnivores in different habitat types using scent stations baited with a scent lure (1:1 ratio of Canine Call and Pro’s Choice [The Snare Shop, Carroll, IA]). Scent station visitation rates provide estimates of relative species abundance in different habitat types (Conner et al. 1983, Crooks 2002), and these two lures were selected because they have proven effective in attracting a similar assemblage of predators (Crooks 2002). We situated a total of 16 scent stations at four different sites, with each site containing a scent station in each of four habitat types (CW, MQ, NS, and FS). We baited and monitored the stations in June 2004 and monthly from October 2004 to October 2005 (see Supplementary material Appendix S1 for more-detailed methods).

Skunk radio-telemetry

Telemetry provides detailed spatiotemporal data on individual movement patterns that complement the spatially and taxonomically extensive data provided by scent stations. We selected striped skunks *Mephitis mephitis* for the telemetry study due to their abundance and ease of capture (gray foxes *Urocyon cinereoargenteus* would not enter the traps we set for them). Their generalist diet also makes striped skunks representative of the diverse group of small- and medium-sized carnivores that inhabit the region (most of which are omnivores). From June 2003 to July 2004 we tracked a total of seven striped skunks using radio-telemetry, recording habitat data and a GPS location each time a foraging individual was detected (see Supplementary material Appendix S1 for more-detailed methods).
Scat collection and analysis

The collection of scat at regular intervals allowed for a detailed, multi-year evaluation of temporal variation in predator diet. We collected predator scat along four transects monitored monthly from June 2003 to October 2005, accumulating a total of 1103 scats over 29 months (see Supplementary material Appendix S1 for more-detailed methods). The transects covered ca 12.5 km at two different sites, encompassing much of the variation among and within habitats along the upper San Pedro River.

Rodent trapping

We used three different approaches to trapping rodents: transects, quadrats, and robust design. The transects and quadrats were both spatially-extensive and included numerous different sites, but with limited trapping at each site. Conversely, the robust design was intensive in that it focused considerable trap effort at a single site. Live trapping rodents provides information on abundance, survivorship, and community composition in different habitat types along the river (see Supplementary material Appendix S1 for more-detailed methods).

Analytical methods

In the descriptions that follow, all data were checked for linearity (for linear regression), and for violations of the assumptions of normality and equal variance prior to analysis. The methods of data collection insured spatial and temporal independence. If necessary, data were log transformed to homogenize variances and normalize distributions of pooled residuals. An $\alpha$ level of 0.05 was used unless otherwise specified. For regression analyses, data points were checked for their influence using DFFITS, DFBETAS, and Cook’s D; influential points were removed both singly, and in pairs, and the analysis was rerun to see if the points altered the regression model.

Litter and vegetation

We analyzed mean litter biomass and canopy coverage in the four habitat types using one-way ANOVAs with Tukey’s tests for post-hoc comparisons. With the species composition data, we calculated Sorensen’s similarity coefficients both within and between habitat types for the 32 plots using EstimateS (Colwell 2005). We also clustered the plots based on their species composition using average linkage cluster analysis. Cluster analysis groups plots with similar species compositions together into clusters; if there are systematic differences among habitats, then plots from the same habitat type should cluster together.

Scent stations

Rain and low sample sizes precluded a temporal analysis of predator visits to scent stations in different habitat types. Rather, we grouped data by habitat type and analyzed overall scent station visitation using a Kruskal-Wallis test; we did post-hoc nonparametric Tukey-type comparisons using the Nemenyi test to control for experiment-wide $\alpha$ levels (Zar 1999).

Skunk radio-telemetry

We entered the skunk UTM coordinates into ArcView and ArcGIS (ESRI, Redlands, CA) along with a map of the San Pedro River, calculating the minimum distance from each point to the river. To determine if skunks moved farther from the river as the monsoon rains progressed, we regressed distance to the river against ordinal day. To determine if skunks ranged more widely during the wet season, we compared the variance for dry- and wet-season distance-to-the-river estimates using an $F$ test for unequal variance. We also compared skunk habitat use during the two seasons with contingency tables in Systat (likelihood ratio chi-square). Since the rains began in early July, we assigned skunk positions before 7 July to the dry season category and those after 7 July to the wet season category.

Scat

We recorded the percentage of scats containing each of five diet items for each month of the study and analyzed the data using average linkage cluster analysis. The data were plotted over time to determine if diet composition varies seasonally. The diet items correspond to different prey types, including feathers (birds), scales (reptiles), fur (mammals), exoskeletons (arthropods), and seeds (plants). To determine if there were any relationships between prey items in the diet we calculated a Pearson’s correlation matrix with Bonferroni-adjusted $\alpha$ levels to assess significance. We also bootstrapped monthly mean and 95% confidence intervals for the percent of scats containing each diet item.

Finally, we compared tooth and skull remains in the scats with voucher specimens to identify rodent prey items to the genus level. To assess predator feeding preferences we used a Chi-square test to compare the time-averaged occurrence of rodent prey in scats with the time-averaged activity-abundance of rodents in the region (determined via the extensive live trapping described above).

As with the skunk radio-telemetry data, we assessed changes in predator habitat utilization by grouping scats into distance-from-river categories and comparing the distribution of scat (an indication of predator activity-abundance) before and after the onset of monsoon rains in early July. Changes in habitat utilization were compared using contingency table analysis. We also bootstrapped mean and 95% confidence intervals for the percent of scats containing each diet item.

The aforementioned analyses were run on all scats collected during this study. In order to compare patterns among different size-classes of predators (e.g. foxes and skunks versus coyotes and bobcats), we grouped the scats into size categories (≤10 ml, and >20 ml) and calculated mean and 95% confidence intervals via bootstrapping for both predator diet (percent of scat containing each diet item) and predator habitat utilization (percent of scats in...
each distance-from-river category. We also used contingency tables to test for changes in habitat utilization by each predator size category.

Rodent trapping

The spatially-extensive rodent trapping data were standardized to catch per trap-night, grouped into riparian (CW and MQ) and upland (NS and FS) categories, and analyzed using linear regression, with distance from the river as a predictor and activity-abundance as a response variable. These analyses were conducted on all rodents and on each of the most-abundant genera to determine if different species exhibited different patterns. We also paired rodent trapping data with the scent station data and ran a Pearson’s correlation between predator and rodent activity-abundance both before and after the onset of the monsoon rains.

Because low recapture rates precluded the use of more sophisticated methods, we used the minimum number (of individuals) known alive (MNKA), total number of individuals, and total number of captures as estimates of rodent abundance in the three habitat types. Although MNKA methods tend to underestimate population size (Krebs 1999), they are useful when other methods fail due to low recapture rates. Moreover, in our case we were interested in relative, rather than absolute, population sizes and the MNKA approach was therefore deemed reasonable. We estimated the MNKA for all rodents together, and for each of the genera separately to determine if different genera exhibited different patterns.

We derived two methods of survival estimation for our data. We estimated survival as the number of individuals that were recaptured in one, two, three, four, and five months; also we estimated the percentage of potential survival achieved by dividing the number of months that an individual is known to have survived by the maximum number of months that it could have been detected (e.g. if a rodent were caught in July, it could have been detected for three more months until the last sampling occasion in October. Its actual survival was compared against this maximum value to calculate the % potential survival achieved). Both of these methods are based on the Calendar of Catches approach developed by Petruszewicz and Andrzejewski (1962). Because these data were not normally distributed, we used nonparametric techniques to analyze them. We compared the survival distributions in the different habitats using a Kolmogorov-Smirnov test for goodness of fit, and we compared the % potential survival achieved using a Kruskal-Wallis test. Following the K-W test we did post-hoc multiple comparisons for data with unequal sample sizes and tied ranks (Zar 1999).

We used the data from both years of intensive trapping to estimate rodent community composition in riparian, NS, and FS habitats, and made comparisons among the three grids using EstimateS to calculate Sorensen’s index of community similarity (Colwell 2005). We calculated difference in species composition using the classic Sorensen index (for presence/absence), and differences in the abundance of species using a newly-developed abundance-based Sorensen index (Chao et al. 2005).

Finally, we compared capture rates for traps in the middle of the trapping grids with those on the edges of the grids to evaluate the possibility that increasing activity-abundance of rodents with increasing distance from the river may simply mean that rodents in dry areas have to use a larger home range and be more active to get the food they need, or that the bait in traps is more attractive in areas that have less high quality food.

Results

Plants

Previous research along the San Pedro suggests that distance to groundwater drives changes in plant species composition (Stromberg et al. 1996) and NPP (Goodrich et al. 2000, Scott et al. 2000, Huxman et al. 2004). Our data support these conclusions, indicating differences in plant structure, species composition, and litter biomass among habitat types (Supplementary material Fig. S1). Specifically, CW habitats have significantly more canopy coverage than do MQ habitats, and both CW and MQ habitats have significantly more canopy coverage than do NS and FS habitats. NS and FS habitats do not differ in canopy coverage or litter biomass. CW and MQ habitats also do not differ in litter biomass, but they both have significantly more litter biomass than do NS and FS habitats. Sorensen’s similarity index values suggest greater differences in plant communities between than within habitat types (within habitat SSI range = 0.54–0.69; between habitat SSI range = 0.12–0.55). However, the similarity values for the NS-FS comparison is high (0.55), suggesting that understory plant communities do not differ much between NS and FS habitats. Cluster analysis of desert-scrub habitats supports this result – NS and FS plots do not cluster separately. These data on NPP, canopy coverage, and community composition indicate fundamental differences in plant resources among CW, MQ, and desert-scrub habitats, but not between NS and FS.

Predators

Striped skunks and foxes (Urocyon cinereoargenteus and Vulpes macrotis) were the most frequent visitors to the scent stations, accounting for 24 and 54% of the tracks left behind respectively. A Kruskal-Wallis test suggests that predator visits to scent stations differed among habitat types (K-W test statistic = 8.05, p < 0.05). Predators visited scent stations in NS habitats most frequently, followed by MQ, FS, and CW habitats (Supplementary material Fig. S2). However, due to low power, post-hoc nonparametric Tukey-type multiple comparisons using the Nemenyi test could not distinguish among habitats, although differences between NS and CW and NS and FS were marginally significant (p ≈ 0.10).

Striped skunk habitat use differed significantly between dry and wet seasons (chi-square statistic = 14.02, p < 0.02 [Fig. 3]), with the skunks aggregating in near-river habitats during the dry season and using habitats more evenly during the wet season. These changes in habitat utilization are reflected by the mean distance of skunks from the river,
which increased over time, from dry to wet seasons (F = 17.33, p = 6.3 × 10^{-5}, DF = 111, R^2 = 0.14), and the variance in their distance from the river, which is significantly greater during the wet season than during the dry season (F = 4.71, p = 2.1 × 10^{-8}, DF = 56,53). Individual skunks that had greater than three observations per season (n = 5) all exhibited the same pattern as described above, with both mean and median distant-from-river estimates being greater during the wet season (Supplementary material Table S2).

The distribution of predators among habitat types (as measured by scat distance-from-river classes) follows the general pattern displayed by skunks, with predators occurring more frequently in near-river habitats during the dry season and using habitats more evenly during the wet season. This pattern is displayed by all (chi-square statistic = 27.85, DF = 5, p = 3.89 × 10^{-7}), small (chi-square statistic = 15.84, DF = 5, p = 7.32 × 10^{-3} [Fig. 4]), and large predators (chi-square statistic = 21.60, DF = 5, p = 6.23 × 10^{-4} [Fig. 4]). Together with the skunk telemetry data, these results indicate that mammal predator as a whole use near-river habitats during dry periods and forage more widely during the wet season.

Comparing the incidence of rodent teeth in predator scats with the activity-abundances of different species in the region reveals strong differences in what is consumed and what could be consumed by the predators (chi-square statistic = 143.01, p = 8.49 × 10^{-31}). Predators eat wood rats more often than expected by chance, whereas kangaroo rats and deer/grasshopper mice (*Peromyscus* and *Onychomys* tooth remains could not be distinguished so we lumped them for this analysis) were consumed less often than expected by chance. Pocket mice were consumed roughly in proportion to their activity-abundance (as determined via extensive live trapping).

Predator diet showed seasonal changes in resource utilization that were consistent from year to year (Fig. 5). Arthropods and reptiles were consumed primarily during the warmer months of the year when they were most abundant. Likewise, seeds were consumed from the late summer through the winter when mesquite pods were readily available. The consumption of mammals, on the other hand, appeared to complement the availability of seeds, with mammals being common in scats during seasons when mesquite seeds were not available (r = -0.76, p < 0.001, DF = 27). This pattern was displayed by all, small (Supplementary material Fig. S3), and large (Supplementary material Fig. S3) predators.
Rodents

The activity-abundance and biomass of all rodents in desert-scrub habitats (NS and FS) increased with increasing distance from the river ($F_{19} = 8.49$, $R^2 = 0.32$, $p < 0.01$, DF = 19) and $F_{19} = 8.50$, $R^2 = 0.32$, $p < 0.01$, DF = 19, respectively [Fig. 6]). There was no relationship between the activity-abundance or biomass of rodents in riparian habitats and distance from the river ($F_{19} = 0.99$, $R^2 = 0.05$, $p = 0.33$, DF = 19 and $F_{11} = 0.10$, $R^2 = 0.01$, $p = 0.75$, DF = 11, respectively). When the data are grouped by season, the abundance gradient in the desert scrub is strong, but only marginally significant during the dry season ($F = 4.79$, $R^2 = 0.44$, $p = 0.07$, DF = 7), and is non-significant at the onset of the monsoon rains ($F = 0.73$, $R^2 = 0.07$, $p = 0.41$, DF = 11) and after the rains in October ($F = 0.50$, $R^2 = 0.08$, $p = 0.51$, DF = 7). These extensive trapping data indicate an increase in rodent abundance with increasing distance from the river in desert-scrub habitats. Moreover, the pattern appears strongest during the driest part of the year, becoming less apparent over the course of the monsoon season. Rodent activity-abundance in riparian habitats, on the other hand, does not vary with distance from the river during the dry season ($F < 0.00$, $R^2 < 0.00$, $p = 0.98$, DF = 7), at the beginning of the monsoon rains ($F = 0.26$, $R^2 = 0.03$, $p = 0.62$, DF = 11), or following the monsoon season ($y = 0.000843x$, $R^2 = 0.36$, $p = 0.12$, DF = 7). The activity abundance and biomass patterns for individual rodent genera follow the same basic patterns described above, with a few exceptions. Specifically, pocket mice (genus *Chaetodipus*) increased with increasing distance-from-river in riparian habitats, while deer mice (genus *Peromyscus*) did not increase with increasing distance-from-river in desert scrub habitats.

A Pearson’s correlation between predator and rodent activity-abundance was non-significant in both the dry ($r = -0.37$, $p = 0.16$, DF = 15 [Supplementary material Fig. S4]) and wet seasons ($r = -0.09$, $p = 0.74$, DF = 15 [Supplementary material Fig. S4]). This non-significant pattern suggests that predator abundance does not track rodent abundance. If anything, the pattern suggests that rodent abundance may reflect predation pressure as indicated by the negative relationship (in the dry season).

Intensive trapping grids revealed highest rodent abundances in riparian habitats, followed by FS, and then NS habitats (Table 2). In contrast, rodent biomass was highest in FS habitats, followed by riparian, and then NS habitats (Supplementary material Table S3). Thus, both rodent...
abundance and biomass are lowest in near-scrub habitats where predators are most abundant. The MNKA in FS habitats increased over the course of the dry season and declined with the onset of the monsoon rains, as did the MNKA in riparian habitats, while the MNKA in NS habitats increased after the onset of the monsoon rains (Fig. 7). Rodent biomass followed a pattern similar to the MNKA, although the changes were more attenuated in riparian and NS habitats (Fig. 7). The total number of captures and total number of individual rodents captured was highest in the riparian grid, followed by the FS, and then the NS grid (Table 2). A Kolmogorov-Smirnov test suggests a significant difference in months survived between the riparian and near-scrub grids \((p < 0.04)\), a non-significant difference between riparian and far-scrub grids \((p = 0.39)\), and a non-significant difference between near- and far-scrub grids \((p = 0.13)\). A Kruskal-Wallis test on percent potential survival achieved also suggests that survival differs between habitat types. Post-hoc comparisons show a significant difference between both riparian and NS \((p < 0.05)\) and NS and FS grids \((p < 0.05)\), complementing the results of the K-S test. These intensive trapping data indicate large differences in rodent abundance and survival among riparian, NS, and FS habitats.

The species composition of NS habitats, measured with Sorensen’s similarity index (SSI), is more like that of riparian habitats than FS habitats ([Table 3] riparian vs NS SSI = 0.92; riparian vs FS SSI = 0.73; NS vs FS SSI = 0.8). Likewise, the relative abundance of species in the NS habitats is more like that of riparian habitats than FS habitat (as measured with the abundance-based SSI: riparian vs NS AbSSI = 0.993; riparian vs FS AbSSI = 0.923; NS vs FS AbSSI = 0.971). Thus, habitats differ in both species composition and abundance, with certain taxa driving the patterns: both riparian and near-scrub grids are dominated by pocket mice *Chaetodipus penicillatus*, whereas the far-scrub grid contains more kangaroo rats *Dipodomys merriami* and grasshopper mice *Onychomys leucogaster*. The relative abundance of wood rats *Neotoma albigula* is highest in the far-scrub grid.

The ratios of interior to overall trap capture rates were higher in far-scrub than in near-scrub habitats for both years (Supplementary material Table S4). This suggests that rodents in far-scrub habitats do not have larger home ranges and/or are not more attracted to bait (due to resource limitation or a lack of high-quality food).

### Table 2. Rodent survival and abundance estimates.

<table>
<thead>
<tr>
<th>Months survived</th>
<th>Riparian</th>
<th>Near scrub</th>
<th>Far scrub</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>60%</td>
<td>83%</td>
<td>63%</td>
</tr>
<tr>
<td>1</td>
<td>23%</td>
<td>10%</td>
<td>11%</td>
</tr>
<tr>
<td>2</td>
<td>10%</td>
<td>6%</td>
<td>8%</td>
</tr>
<tr>
<td>3</td>
<td>3%</td>
<td>2%</td>
<td>10%</td>
</tr>
<tr>
<td>4</td>
<td>4%</td>
<td>0%</td>
<td>4%</td>
</tr>
<tr>
<td>5</td>
<td>1%</td>
<td>0%</td>
<td>4%</td>
</tr>
<tr>
<td>Mean % potential survival achieved</td>
<td>19.69</td>
<td>11.35</td>
<td>26.34</td>
</tr>
<tr>
<td>Total number of individuals</td>
<td>141</td>
<td>65</td>
<td>118</td>
</tr>
<tr>
<td>Total number of captures</td>
<td>317</td>
<td>119</td>
<td>298</td>
</tr>
</tbody>
</table>

Note: data are from the summer of 2005 for the riparian grid and the summer of 2004 for the near-scrub and far-scrub grids.

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### Discussion

Although food webs describe the flow of resources from producer and detrital pools to consumers, they are often conceived of as static and depicted as a single, unchanging figure (akin to a map). In this article we show how variable the influence of bottom-up and top-down forces can be across seasons and habitat boundaries, leading us to question the generality of static descriptions of species interactions. Instead, we favor a temporally-resolved landscape perspective that considers species interactions within the spatiotemporal context in which they occur. To us, food webs are more like a braided channel, varying in flow and often changing course, rather than a network of paths fixed in time and space.

Using a spatiotemporally-explicit approach, we gathered evidence supporting spillover predation by mammalian predators on rodents living in desert-scrub habitats. More specifically, we showed that the activity-abundance and biomass of rodents in the desert scrub increases with...
increasing distance from the river, that these patterns in abundance and biomass are not driven by differences in resource availability or plant species composition, and that the activity-abundance of mammalian carnivores is highest in riparian and near-river desert-scrub habitats. These lines of evidence support an important role for top-down structuring of rodent communities in near-scrub habitats. Our data also suggest a temporal aspect to the strength and distribution of top-down effects. Predation is concentrated in near-river habitats during the dry season, when primary and secondary productivity are very low in upland habitats. At that time, predators cluster near the river, focusing their foraging in riparian and near-scrub habitats. Following the monsoon rains primary and secondary productivity increase in upland habitats, changing the distribution of resources along the riparian–upland gradient. As a result, predators adjust their space-use patterns, spreading out across the landscape. This, in turn, results in increased predation pressure in far-scrub habitats and decreased predation pressure (relative to the dry season) in near-scrub habitats.

We further demonstrated that temporal variation in resource availability can increase predator effects on prey populations. The inverse correlation between mammal fur (most of which was from rodent prey) and seeds (most of which were from mesquite pods) in predator scat indicates that variation in diet (i.e. attack rates on prey items) allows predators to seasonally switch between different prey items, bolstering their survival and potentially reducing prey abundance in near-river habitats. This supports the theoretical assertion that exogenous variation does not always reduce the strength of indirect interactions via a shared predator (Brassil 2006). Indeed, when resources vary out of sync, mobile, generalist predators should benefit, increasing in abundance and exerting more pressure on their prey base (Anderson et al. 2008).

**Plant resources – a moving target**

Others have shown that primary production and community structure of plants vary in response to temperature, rainfall, and flood disturbance supporting H1a, H1b, and H1c. Temperature affects primary production in plants with access to groundwater (riparian trees and shrubs; Goodrich et al. 2000, Scott et al. 2000, Huxman et al. 2004), whereas temperature and rainfall combine to affect primary production of all other plants (Ogle and Reynolds 2004, Bagstad et al. 2005, Lite and Stromberg 2005). The species diversity of woody plants varies with distance to groundwater (Stromberg et al. 1996), while the species diversity of annual plants varies in response to rainfall, distance to groundwater, and flood events (Stromberg et al. 1996, Reynolds et al. 2004, Bagstad et al. 2005, Lite et al. 2005, Stromberg 2007).

Our results, combined with those described above, provide partial support for H1a, H1b, and H1c. Primary production differs between riparian and upland habitats, but not between habitats within these broader categories (i.e. primary production does not differ between CW and MQ habitats, nor does it differ between NS and FS habitats). We believe that it is not distance to groundwater, but rather access to the groundwater that drives differences in primary production in this system. Riparian trees with deep roots can access a different source of water than herbaceous plants and desert shrubs that tend to have shallow roots. Plant community structure, on the other hand, differs among habitat types, although differences between NS and FS habitats are minor and likely reflect differences in soils and other factors, rather than distance to groundwater. Cluster analysis further suggests that any differences are minor because NS and FS plots do not separate out. Collectively these data indicate complex spatiotemporal shifts in resources driven by landscape position, temperature, and rainfall.

**Predator–prey dynamics along the riparian–upland gradient**

Predator diet and movement patterns support hypotheses H2a and H3a. Scat analyses indicate that both small (e.g. skunks, foxes) and medium-sized (e.g. coyotes Canis latrans) mammalian carnivores are opportunistic generalists that consume seasonally-available food resources. Although scent station data do not suffice to test the ideal free distribution, the telemetry and scat data indicate that predators vary their foraging locations based on the seasonal distribution of resources. Specifically, predator activity-abundance in different habitat types varies seasonally, likely in response to shifts in the distribution of resources.

We used rodents as an index of the strength of predation. Specifically, we hypothesized that predators would be relatively more abundant in near-scrub habitats as a result of proximity to the river, and that rodents would therefore have lower survival and abundance in the near scrub relative to the far scrub (see H4a above). We further expected that these differences would change over time with rain-driven changes in the relative productivity of terrestrial habitats along the riparian–upland gradient.

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Table 3. Species composition of the robust design trapping grids.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Riparian # Individuals</th>
<th>% of community</th>
<th>Near scrub # Individuals</th>
<th>% of community</th>
<th>Far scrub # Individuals</th>
<th>% of community</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chaetodipus</td>
<td>281</td>
<td>80.52</td>
<td>73</td>
<td>67.59</td>
<td>65</td>
<td>36.31</td>
</tr>
<tr>
<td>Dipodomys</td>
<td>7</td>
<td>2.01</td>
<td>23</td>
<td>21.30</td>
<td>71</td>
<td>39.66</td>
</tr>
<tr>
<td>Neotoma</td>
<td>10</td>
<td>2.87</td>
<td>2</td>
<td>1.85</td>
<td>9</td>
<td>5.03</td>
</tr>
<tr>
<td>Onychomys</td>
<td>1</td>
<td>0.29</td>
<td>4</td>
<td>3.70</td>
<td>26</td>
<td>14.53</td>
</tr>
<tr>
<td>Reithrodontomys</td>
<td>2</td>
<td>0.57</td>
<td>1</td>
<td>0.93</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>Sigmodon</td>
<td>1</td>
<td>0.29</td>
<td>0</td>
<td>0.00</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>Peromyscus</td>
<td>47</td>
<td>13.47</td>
<td>5</td>
<td>4.63</td>
<td>8</td>
<td>4.47</td>
</tr>
</tbody>
</table>

Note: includes capture data from both 2004 and 2005.
Rodent biomass is greatest in FS habitats that are low in productivity, contradicting the predictions of the bottom-up hypothesis (H4b). Moreover, the difference between near- and far-scrub habitats in rodent biomass and abundance suggests that predators depress rodent populations in NS habitats, supporting the top-down hypothesis (H4a). Data on survival in the different habitat types further supports H4a, as do differences in rodent community composition in riparian, near-scrub, and far-scrub habitats. Far-scrub habitats include a higher percentage of relatively long-lived, slow-reproducing species such as kangaroo rats, wood rats, and grasshopper mice (Smith and Jorgensen 1975, Eisenberg 1981, Nowak 1999). On the other hand, near-scrub habitats are dominated by the desert pocket mouse, a species with greater reproductive potential. Although one might expect kangaroo rats to be less susceptible to predation than pocket mice (lower predator attack rates), the dense physiognomy of the desert-scrub vegetation in this region reduces the advantage anti-predator specialists typically enjoy in more open habitats. This causes the ratio of reproductive potential to predator attack rate (r/a) to be greater for pocket mice than for kangaroo rats, wood rats, and grasshopper mice, giving pocket mice a survival advantage in near-scrub habitats (Holt 1984). In other words, if all species are about equally vulnerable to predators, it is those that can better withstand high predation pressure due to their reproductive potential that inhabit the riskiest habitats.

Temporal changes in rodent abundance also support H4a. Based on H4b, rodents living in all habitats would be expected to increase in abundance following the onset of monsoon rains. However, rodents in two of three habitats (riparian and far scrub) declined in abundance during the rainy season. The decline in far-scrub habitats can be explained by the dispersal of mammalian carnivores across the landscape, which also explains the increase in near-scrub habitats (due to a decrease in predation pressure relative to the dry season). The decline in riparian habitats, on the other hand, may reflect factors not considered in this study. In particular, snake activity increases dramatically during the rainy season and may result in increased predation pressure in areas where snakes are concentrated such as the riparian zone (Reynolds 1982, Soykan unpubl.). Alternatively, the decline may be due to flood events that sweep through low-lying areas and kill or displace resident rodents (Andersen et al. 2000).

**Community structure in perspective**

Even simple food webs can exhibit complex behavior (Hastings and Powell 1991). Thus, it would be simplistic to assume that spillover predation by mammalian carnivores is the only mechanism affecting rodent communities in this system. Other factors to consider include resource availability, alternate predators, annual variation in biotic and abiotic conditions, and behavioral interactions between predators and their prey.

We documented large differences in resource availability between riparian and desert scrub habitats, suggesting that increased productivity may explain the increased abundance (but not biomass) of rodents in riparian habitats. However, there are no differences in resource availability between near- and far-scrub habitats, even though there are large differences in rodent abundance and biomass. Furthermore, rodent community composition was similar in near-scrub and riparian grids (Table 3), even though riparian and near-scrub plant communities differed in their productivity and species composition. Predator activity-abundance, on the other hand, was similar in mesquite and near-scrub habitats. These results are inconsistent with a bottom-up hypothesis, but strongly support the predation hypothesis.

Grouping all mammalian carnivores together into a guild runs counter to our focus on detailed food web dynamics. Indeed, it is likely that not all mammals respond as described above, with some species acting as habitat and or diet specialists (Hass 2001). Nevertheless, those on which we focused – skunks, foxes, and coyotes – seem to be the most abundant regionally, and therefore are expected to have the strongest impacts on prey communities. According to a survey by Hass (2001), Mephitid skunks, coyotes, gray and kit foxes comprised 206/426 signs detected along the SP river (48.4%). If you include other generalist mammals (coatis, hognose and spotted skunks, ringtails, and raccoons), the numbers rise to 302/426 signs or 70.9%.

Our omission of non-mammalian predators can also be criticized; however, including other taxa (birds, snakes) would improve, but not alter our understanding of the system. Most birds of prey in the area are diurnal and do not interact with the nocturnal rodents that we studied. Snakes, on the other hand, are largely inactive during the dry season when spillover is most dramatic (Reynolds 1982, Soykan unpubl.).

Unfortunately, we could not include both years of data for the trapping grids. The excluded data resemble what we report here, albeit they are less reliable due to the difficulties mentioned in Supplementary material Appendix S1. More generally, it would be interesting to track variation in rodent community dynamics over a longer period of time to determine the effects of yearly variation in precipitation, predator abundance, etc.

Although the aforementioned mechanisms involve direct trophic interactions, the distribution and abundance of mammalian carnivores and rodents along the riparian–upland gradient can also be interpreted from a behavioral perspective. For example, Hugie and Dill (1994) modeled the distribution of predators and prey using a game-theoretic approach that assumes ideal free habitat selection. They asked, “what will happen if predators are able to adjust their distribution in response to the habitat choice decisions of their prey?” The model predicts that prey will respond little to differences in productivity, counter to the prediction of traditional ideal free theory. Rather it is habitat riskiness (i.e. risk of predation) that is the dominant factor driving the distribution and abundance of prey. Likewise, predators will not necessarily be distributed according to the distribution of their prey (as predicted by the ideal free distribution), but rather they will respond to habitat riskiness and habitat productivity (as measured two trophic levels below them).

Morris (2005) developed a similar theory, but based it on the assumption that the predators are omnivores instead of carnivores. His results, described as a “behavioral paradox of enrichment”, suggest that prey will avoid areas...
of enhanced resource availability if they are susceptible to predation by omnivorous predators that are also drawn to such areas. More generally, in ideal free distribution models that include risk of predation, the competitor type with the higher risk of predation (lower value of \( r/a \)) tends to avoid the riskier habitat (Grand and Dill 1999). In the context of our system, certain species of rodents may choose to avoid near-river desert scrub habitats due to the elevated abundance of predators near the river.

These mechanisms for explaining the distribution of predators and their prey are not mutually exclusive. It is quite possible that they combine to produce the patterns observed in this study. However, the results of our analyses (rodent survival, abundance, and species composition; predator diet and habitat use) suggest that top-down trophic interactions are the primary mechanism driving the observed pattern. Thus, we conclude that predation by mammalian carnivores during the dry season is the dominant process affecting small mammal abundance and community composition in near-scrub habitats.

**Apparent competition in space and time**

Temporal changes in food resources force mammalian carnivores (which neither migrate nor undergo torpor) to adjust their diet and foraging patterns, which, in turn, appear to drive changes in rodent community structure along a gradient from near- to far-scrub habitats. Hence, seasonal changes in resource availability result in changes in the relative strength of top-down and bottom-up control of prey communities. These results parallel recent work documenting spatial (Denno et al. 2005), seasonal (Gratton and Denno 2003), annual (Meserve et al. 2003), and spatiotemporal (Polis et al. 1998, Anderson et al. 2008) variation in top-down effects on ecological communities.

A change in focus from bottom-up (subsidies) to top-down (predator movement) processes broadens the study of species interactions across habitat boundaries. Unlike subsidies, which occur primarily due to the life history strategies of prey organisms (Naiman et al. 2002, Sanzone et al. 2003) or passive transport (Polis and Hurd 1996), predator movement is a behavioral mechanism. As such, its study requires different approaches, theory, and often a larger spatial perspective (Storch et al. 2005). Nevertheless, we argue that passive transport of resources and life-history shifts in habitat utilization are less common than predator movement among habitat types, giving top-down forces an important role in shaping food webs interactions across habitat boundaries.

We believe that the lack of empirical examples documenting spillover predation stems from the difficulty of conducting research at the appropriate scale rather than a lack ecological importance. Additionally, a lack of awareness on the part of researchers likely contributes to its absence from the literature. Many examples of spillover predation can be gleaned from studies of other food webs. For example, Estes et al. (1998) suggest that declines in pinniped abundance in the open waters of the North Pacific led killer whales to seek out alternate food items – nearshore sea otters – leading to dramatic sea otter declines and community change in the kelp forest. Likewise, Micheli and Peterson (1999) demonstrate that blue crabs – subsidized by resources in vegetated estuarine habitats – traverse sea grass corridors to intertidal oyster reefs where they affect the abundance and species richness of benthic macroinvertebrates. Finally, Crooks and Soule (1999) showed that domesticated cats – subsidized by food from their owners – exert strong negative impacts on native prey in habitat fragments surrounded by human development.

Just as apparent competition in space (i.e. spillover predation) may play an important role in structuring ecological assemblages, so too may apparent competition over time. Our results provide evidence that seasonal shifts in diet may increase consumer impacts on their prey. Generalists that shift their diet to feed on what is most available will often incorporate food items from multiple trophic levels. Thus, whereas omnivory is usually thought to dampen the strength of top-down effects in ecological communities (Finke and Denno 2004), seasonal omnivory may enable predators to survive periods of resource scarcity, bolstering their numbers and allowing them to exert stronger top-down control on their prey (McCann and Hastings 1997, Anderson et al. 2008). This appears to be the case in our system, where mesquite seeds provide an important seasonal food resource for mammalian carnivores (Mares et al. 1977), increasing their chances of survival during the winter months. This temporal subsidy resembles the alternate prey concept in biological control (Murdoch et al. 1985), in that it reduces oscillations in predator numbers and allows for more effective top-down control of prey populations.

**Theoretical implications**

Our work reinforces the common-sense notion that predators respond to gradients in resource availability. Since these gradients vary over space and time, they result in seasonal variation in attack rates on prey species in different habitat types. Although variation in attack rates may reduce apparent competition (Brassil 2006), it did not in our case. We suspect that the reason was that resources varied asynchronously, allowing the predators to exploit different prey over the course of the year. We contend that asynchronous variation in resources is a common feature of empirical food webs, and that theoreticians should focus more effort on incorporating it into their models. Theory should also incorporate spatiotemporal variation in predator diet and habitat use because both are associated with asynchronous variation in resources in heterogeneous landscapes. For example, models used to gauge the effects of spillover predation on endangered prey (Schneider 2001) should include temporal variation in predator movement and diet, as this variation may alter the strength of the interaction. Additionally, models that explore temporal variation in species interactions across habitats or in open populations (Holt and Barfield 2003, Holt et al. 2003), should incorporate omnivory and adaptive behavior, since both are common and can have significant effects on predator persistence and prey population dynamics.

Although important from a dynamic modeling perspective, these results also apply to the study of food web properties. Specifically, our work suggests that the number of species, the number of connections among those species,
and the strength of effects associated with those connections all vary seasonally as a result of cross-habitat predator movements and a changing network of indirect interactions. Thus, numerical analyses of food webs must quantify and embrace this very real variation in network architecture in order to achieve generality.

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