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# SCORPIONS AS MODEL VEHICLES TO ADVANCE THEORIES OF POPULATION AND COMMUNITY ECOLOGY: THE ROLE OF SCORPIONS IN DESERT COMMUNITIES

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The diversity (5-16 species) and abundance (0.2-1.0 individuals/$m^2$) of scorpions suggest that they may be quite ecologically important in desert communities. Ecological importance is considered in terms of population energetics (the quantity of energy and mass flowing through populations) and of regulation of community structure and dynamics (influence on the distribution and abundance of other species). The energetic analysis provided three conclusions: 1) Scorpions monopolise a relatively large share of animal biomass, particularly relative to vertebrates and other arthropods. 2) This relative success is due to a suite of autecological traits (very low metabolism and very high assimilation efficiency leading to low energy requirements; and great tolerances to water stress, heat and starvation) that allows scorpions to prosper under the unpredictable and low food availability conditions that characterise deserts. 3) However, these traits lessen their impact on energetics, prey and competitors. Thus the importance of scorpions relative to homeothermic vertebrates is less than an analysis of density and biomass suggest because scorpions require and process prey in quantities relatively low to their biomass. Nevertheless, as a group, scorpions are probably important conduits of energy flow in deserts.
Research on the interactions among scorpions and between scorpions and spiders strongly suggests that scorpions can play key roles in the structure and dynamics of their communities. Studies in the deserts of California, Baja California and Namibia show that intraguild predation by scorpions is a major force determining the (temporal and spatial) distribution, abundance and age structure of populations of their competitors/prey.□*Araneae, Scorpionida, age structure, distribution, intraguild predation, population and community ecology.*

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Ecology is a rapidly developing area with a great deal of internal argument and disagreement. As in other fields, theory has advanced far more rapidly than empirical work. Consequently, much theory is controversial and in need of empirical evaluation. Scorpions possess a number of characteristics that make them ideal models to test and advance ecological theory. Thus, it is relatively easy to collect rapidly great amounts of data and to manipulate experimentally individuals and entire populations. Research on scorpions has contributed to many areas of population, behavioral and community ecology: e.g., the evolution of life history theory (Polis and Farley, 1980), the evolution and ecology of age-structured populations (Polis, 1984a, 1988; McCormick and Polis, 1986a), the dynamics of cannibalism (Polis, 1980a, 1981, 1984b), the dynamics of intraguild predation (Polis and McCormick, 1986b, 1987; Polis *et al.*, 1989), the evolution and ecology of foraging strategies (Polis, 1980b; Bradley, 1988), patterns and processes in biogeography (Due and Polis, 1986) and the patterns and processes affecting community and food web structure (Bradley, 1983; Polis, 1991a).

In this paper I evaluate the 'ecological importance' of scorpions. Throughout, I indicate how research on scorpions has advanced our general understanding of ecology. Although scorpions occur in almost all non-boreal habitats, I focus on desert scorpions because much evidence suggests that they may be particularly important components of arid ecosystems and are a relatively 'successful' group. They are diverse, some taxa are extraordinarily abundant, and, as a group, they form a large proportion of the biomass of all desert arthropods and easily exceed the biomass of all desert vertebrates. Their success arises partially because they exhibit several physiological and ecological traits that pre-adapt them to the low and unpredictable food levels of deserts.

'Ecological importance' can be expressed in terms of either energetics and nutrient cycling

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(the quantity of matter and energy flowing through a population or functional group) or regulation of community structure and dynamics (the impact on diversity, distribution and abundance of other populations).

## ENERGETICS AND NUTRIENT CYCLING

The importance of desert scorpions on energy and nutrient cycling is a function of the quantity of prey biomass captured. The amount of captured biomass is a function of the density, population biomass, metabolism and efficiency of energy transfer. I now present a very rough approximation of the relative importance of scorpions to the flow of energy and nutrients in desert ecosystems. To approach this question, data were compiled from the literature reporting the diversity, density and biomass of various groups of desert taxa (see Polis, 1990, 1991b; Polis and Yamashita, 1991 for additional details). These data are not without bias and other problems. For example, studies are not usually conducted in areas where the focal taxon is absent or rare; nor are rare species studied as often as common ones. Consequently, the statistics presented here overestimate density and biomass and should be taken as a first approximation of actual parameters. However, the data are instructive and suggest that scorpions could be a major link in the flow of energy through desert communities.

| Group | Density (no./ha) | Diversity (no. species) | n |
|---|---|---|---|
| Mammals | 43 ± 130 | 28.5 ± 21.3 | 14 |
| Birds | 0.6 ± 1.1 | 46.7 ± 27.3 | 14 |
| Lizards | 36.8 ± 43 | 12 ± 4.6 | 12 |
| Insects | 35,100 ± 54,600 | 592 ± 796 | 10 |
| Termites | 4,025,000 ± 2,793,000 | 9.1 ± 15 | 7 |
| Isopods | 241,810 ± 336,850 | 1.3 ± 0.8 | 7 |
| Millipedes | 1150 ± 214 | 2.4 ± 2.1 | 7 |
| Spiders | 3220 ± 8800 | 54.4 ± 26.7 | 31 |
| Solpugids | | 9.9 ± 6.7 | 37 |
| Scorpions | 3210 ± 3500 | 7.1 ± 2.5 | 58 |

TABLE 1. Estimated average density and diversity of major taxa of desert macrofauna reported from the literature. Diversity is the mean number of species per taxon from local sites in different deserts. Density statistics were standardized to a per hectare basis. Means are reported with their standard deviations; n = sample size. Note that these statistics should be viewed as very rough approximations rather than absolute values. Note that data on ants were insufficient to include here (see Polis and Yamashita, 1991 for further details).

How do desert scorpions measure against other groups of consumers for these parameters? First, scorpions are relatively speciose in deserts. On the average, 7.1 species co-occur in desert throughout the world (range: 2-16 sympatric species, typically, 5-9 species; Polis, 1990) (see Table 1 for comparison with other desert taxa). Furthermore, populations are often quite dense, averaging>3200 individuals/ha with several species maintaining populations 5000-10,000/ha (e.g., Shorthouse, 1971; Lamoral, 1978; Polis and Farley, 1980; Polis and McCormick, 1986a; Bradley, 1986; Polis, 1990). On the average, scorpions are reportedly more dense than all other macroscopic animal taxa in these deserts except 'insects', termites, and isopods (ants are undoubtedly also more dense) (Table 1). Since scorpions are among the largest of all terrestrial arthropods (adults of most desert species = 0.5-10g; Polis and Farley, 1980), these high densities produce rather large estimates of standing biomass (= density of individual species x mass of individual animal). Each species population of desert scorpion averaged 7.15 kg/ha. Only termites (and probably ants) support a greater population biomass per

| Taxon | Population per species | Biomass (kg/ha) per taxon | n |
|---|---|---|---|
| Mammals | 1.40 | 39.9 | 29 |
| Birds | 0.02 | 0.9 | 25 |
| Lizards | 0.57 | 6.8 | 46 |
| 'Insects' | 0.88 | 521.2 | 31 |
| Termites | 12.45 | 113.4 | 7 |
| Isopods | 9.91 | 12.8 | 2 |
| Millipedes | 1.15 | 2.8 | 2 |
| Spiders | 0.13 | 7.1 | 4 |
| Scorpions | 7.15 | 50.8 | 17 |
| All vertebrates | | 47.7 | |
| All arthropods | | 708.1 | |
| All macrofauna | | 755.8 | |

TABLE 2. Estimated population biomass for various taxa taken from literature. Population biomass per species is average wet weight of one species per hectare. This statistic was sometimes reported; however, it was often calculated by multiplying the average mass of an individual times the density. Population biomass per taxa is calculated as the product of population biomass per species and average diversity of that taxon. Note that data on ants were insufficient to include. Additional information is reported in Polis and Yamashita (1991). n refers to the number of species in a particular taxon for which biomass data exist. Note that these statistics are only gross approximations of reality.

species or per taxon (from the ordinal level down) than scorpions (Table 2).

When the biomass of all scorpions living sympatrically in desert areas is calculated (= mass of individual species x average number of sympatric species), scorpions as a group exhibit a greater biomass (= 50.8kg/ha) than all other taxa except termites (=113.4Kg/ha) and the sum of all other insects (= 521.2kg/ha; Table 2). Note also that the population biomass of scorpions is higher than any one group of vertebrates (e.g., mammals and lizards average 39.9 and 6.8Kg/ha) or all vertebrates combined (47.7kg/ha). Overall, scorpions form 6.7% of the biomass of all macrofauna species combined, 7.1% of the biomass of all macroarthropods and 106% of the biomass of all vertebrates.

Thus it would appear that they are important conduits for energy transfer in deserts. However, two characteristics lessen their importance. First, they exhibit the highest ecological (production) efficiencies (percent assimilated energy incorporated into new biomass) of all taxa that live in the desert (Table 3). Second, they exhibit metabolisms that are extremely low relative to other poikilotherms and endotherms (Table 4). Although these features are powerful adaptations that allow efficient use of food and partially explain the success of scorpions in deserts, they also function to decrease the amount of energy transferred. Thus a gram of scorpion does not process as much food as a gram of arthropodivorous vertebrate. Overall then, desert scorpions are less important in energy and nutrient cycling than their diversity, abundance and biomass suggest.

How much energy do desert scorpions process? We have two estimates. Polis (1988) calculated that average populations of *Paruroctonus mesaensis* used 9000 grams of prey/ha/year. The Australian *Urodacus yaschenkoi* requires 7900g/ha/year; this translates into 98,400 ants or 31,570 medium sized spiders eaten per hectare per year (Shorthouse, 1971; Marples and Shorthouse, 1982). It is uncertain exactly how such figures for individual scorpions or for the sum of all sympatric species of scorpions compare to those for vertebrates. This is an interesting question to pursue.

| Group | P/A% |
|---|---|
| Insectivorous mammals | 0.86 |
| Birds | 1.29 |
| Small mammals | 1.51 |
| 'Other' mammals | 3.14 |
| 'Homeotherms' | 3.1 |
| Fish | 9.77 |
| Social insects | 10.3 |
| Terrestrial invertebrates* | 25.0 |
| Solitary herbivorous insects | 38.8 |
| Solitary detritivorous insects | 47.0 |
| Solitary carnivorous insects | 55.6 |
| Spiders | 45-60 |
| Scorpions | 68.2 |

TABLE 3. Ecological (Production Efficiency) of various animal taxa. This efficiency is equal tothe proportion of assimilated energy that is incorporated into new biomass (=Production/Assimilation). Note that the highest efficiencies are found in carnivorous insects, spiders and scorpions. *Terrestrial invertebrates do not include insects or arachnids. (primarily from Humphreys, 1979; see Polis and Yamashita, 1991 for further details).

## INFLUENCE ON COMMUNITY STRUCTURE AND DYNAMICS

The second measure of ecological importance is to determine how a taxon influences the dynamics, distribution and abundance of other taxa. In theory, scorpions can influence desert communities in many ways: as predators affecting characteristics of their prey, as prey of other predators and as competitors of other arthropodivores.

One of the basic questions in ecology is: 'What factors determine the distribution and abundance of species?' To approach this question, researchers often focus on groups of similar species that use similar resources; especially those resources the supply of which may be limiting and in demand (e.g., food). Such species groups

| Taxon | Metabolic rate (ml/$O_2$/gm/hr) |
|---|---|
| **Homeotherms** (basal rates) | |
| Mammals | 0.07-7.4 |
| shrew | 7.4 |
| rodents | 1.80 |
| elephant | 0.07 |
| Birds | 2.3-4.7 |
| **Poikilotherms** (at 25°C) | |
| Insects | 1.665 ± 1.25 |
| Spiders | 0.92 ± 0.92 |
| Scorpions | 0.057 ± 0.048 |

TABLE 4. Metabolic rates of various animal taxa. The data are taken from many sources. The sample size for insects is 82 species; for spiders, 8 species; and for scorpions, 7 species. (see Polis and Yamashita, 1991 for further details).

are called guilds (= a group of species that use resources in a similar way and are thus potential competitors). For example, guilds of desert granivores (birds, ants, rodents) all eat seeds, regardless of specific differences in resource acquisition.

One approach to study guilds is to describe their patterns or structure. By guild structure, we mean the diversity and abundance of species members; spatial and temporal patterns and resource use (i.e., niche characteristics). However, such descriptive studies, although common, are not fully satisfying because they do not directly address the processes that produce the observed patterns.

An alternative approach is to determine if guild members interact, and if so, can such interactions significantly shape guild structure. There are several possible ways that guild members can interact. These range from cooperation and mutualism to competition and even predation. Such predation among guild members is called intraguild predation (Polis and McCormick, 1987; Polis *et al.*, 1989). Intraguild predation is an ubiquitous interaction among many assemblages of potential competitor but has received little formal attention from either theorists or empiricists (Polis *et al.*, 1989).

One major theme of my research with scorpions has been to analyze the characteristics and significance of intraguild predation. Many scorpion prey items (other scorpions, spiders and solpugids) are also potential competitors with scorpions (Polis, 1990; Polis, 1991a, b; Polis and Yamashita, 1991). I present information on three systems; in each, scorpions frequently eat species in the same guild of arthropodivorous predators and such intraguild predation significantly affects the distribution, abundance and population dynamics of these potential competitors. I used scorpions in these studies as models to delineate the characteristics and dynamics of intraguild predation. These studies illustrate how scorpions have proved to be extraordinarily amendable for ecological research: large amounts of data can be collected, interactions (e.g., feedings) observed and quantified relatively easily, and individuals or whole populations manipulated experimentally. For example, in the first study, field data were collected on 130,000 individuals, 2000 feedings and 6000 individual scorpions were manipulated in controlled field experiments.

## INTERACTIONS AMONG SCORPIONS IN THE COACHELLA VALLEY

Four species of desert scorpion co-occur in sandy habitats on the floor of the Coachella Valley (Riverside County, California). Three are in the family Vaejovidae (*Paruroctonus mesaensis* Stahnke, *P. luteolus* Gertsch and *Vaejovis confusus* Stahnke); one (*Hadrurus arizonensis* Ewing), the Iuridae (Polis and McCormick, 1986a, 1987). *Paruroctonus mesaensis* form >95% of all individuals and occur at densities in the range of 0.2-0.5 individuals/ha; the other three species are relatively rare. Each species requires 2-5 years to mature and is composed of several distinctly sized year classes. Size changes greatly, e.g., *P. mesaensis* increase 60-80 times in weight from 0.03g (instar 2) to 2.0-2.5g (non-gravid adults). The year classes and species overlap to various degrees in use of insect and arachnid prey; average overlap among all species is moderate to high (0.67 [prey size] and 0.43 [prey taxa]). Thus, the scorpions potentially compete for food.

Extensive intraguild predation occurs among the four species; Table 5 presents a matrix of who eats whom. Several factors characterize this intraguild predation: 1) Each species was both an intraguild predator and prey. Such mutual predation occurs simply because the predator scorpion was always larger regardless of the species combination involved (n= 170 scorpion-scorpion predations). Thus scorpions of all species are vulnerable as they grow from small juveniles to full size adults and predatory reversals (mutual predations) are common. For example, young *P. mesaensis* scorpions are eaten by relatively larger adult *P. luteolus* and *Vaejovis confusus*; adult *P. mesaensis* prey on the (now) relatively smaller adults of these species. Thus age/size is a key

| | PREY | | | | |
|---|---|---|---|---|---|
| PREDATOR | *H.ari* | *P.lut* | *P.mes* | *V.con* | Total |
| *Hadrurus* | 0.0 | 6.3 | 12.5 | 3.1 | 21.9 |
| *P. luteolus* | 0.0 | 33.3 | 6.7 | 6.7 | 46.7 |
| *P. mesaensis* | 0.4 | 0.5 | 5.0 | 8.3 | 14.2 |
| *Vaejovis* | 0.0 | 0.0 | 8.0 | 4.0 | 12.0 |

TABLE 5. Scorpion-scorpion predation in the Coachella Valley. The entries represent the percent of the diet that each species forms as prey for each of the four scorpion species. The diagonal represents intraspecific predation (cannibalism) (from Polis & McCormick, 1987). *H.ari=Hadrurus arizonensis; P.lut = Paruroctonus luteolus; P.mes= Paruroctonus mesaensis; V.con =Vaejovis confusus.*

determinate of intraguild predation: adults are the predators and immature individuals are the prey significantly more frequently than expected by chance. 2) The most common species (*P. mesaensis*) was the predator in 91% of all intraguild predations observed. Its average overlap in prey use (= 0.44) with other scorpion species was second highest. 3) Intraguild predation, at least by *P. mesaensis*, is significantly more frequent when prey availability was low: when <1% of the population was feeding, heterospecifics formed 35% of all diet items. In contrast when the percent feeding was >5%, only 3.2% of all prey were other species of scorpion. 4) Mortality caused by intraguild predation was generally an inverse function of the density of both *P. luteolus* and *V. confusus*; this resulted because much of the surface activity of these two species occurred during (less productive) periods when *P. mesaensis* was absent from the surface. 5) Intraguild predation is important in scorpion population dynamics. When analyzed as percent mortality of small species (here = total number of individuals eaten by *P. mesaensis* divided by the total number ever observed), intraguild predation by *P. mesaensis* killed 8% and 6% of all *P. luteolus* and *V. confusus* ever observed.

Can such high rates of mortality cause the rarity of these species? It is only possible to approach this question using field experiments. Removal of >6000 *P. mesaensis* (=3.2Kg) from 300 (100m$^2$) quadrats over a 29 month period demonstrated that the rarity of these species is caused substantially by intraguild predation from *P. mesaensis*. 6) Both *P. luteolus* and *V. confusus* (but not *H. arizonensis*) increased significantly (600% and 135%) in removal as compared with 60 control quadrats. It was speculated that the rarity of the largest species (*H. arizonensis*) is a result of a bottleneck in adult recruitment; predation by *P. mesaensis* killed >10% of all newborn *H. arizonensis* observed during the study. 7) The age structure of these smaller species was significantly different in removal areas: first year juveniles were 1.75 to 2.85 more abundant in removals versus controls. This suggest that the numerical response by the rarer species would be even more dramatic if this experiment continued beyond its 29 month period. Note that a plausible alternative hypothesis exists: removal of *P. mesaensis* relaxed exploitation competition and thus allowed the observed increases in density. A robust test failed to detect competition in this system (Polis and McCormick, 1986b, 1987).

Thus, intraguild predation by *P. mesaensis* significantly depressed the abundance of the rarer species. Does intraguild predation likewise affect their distribution? Since predation is apparently a key factor in the population dynamics of these species, natural selection is expected to favor adaptations that reduce the probability that an individual will encounter its predator. Indeed prey often avoid places and times that their predators frequent or where the probability of predation is high (see Polis and McCormick, 1987). Typically, the large predatory entity (e.g., scorpion species and/or age class) occurs in productive periods and microhabitats whereas smaller entities coexist by spatial segregation in a heterogeneous habitat and by temporal displacement.

The temporal and spatial distribution of smaller age classes and species of Coachella Valley scorpions reflect avoidance (in ecological and/or evolutionary time) of larger age classes and species. The overall distribution of *P. luteolus* and *V. confusus* tend to place these species on the surface during times (in winter, late fall) and in places (off sand) characterized by relatively low surface populations of adult *P. mesaensis*. These times and microhabitats support significantly less prey than those used by adult *P. mesaensis*; consequently *P. mesaensis* has a feeding rate (2.95%) significantly greater than all other species combined (1.70%). Further, the minority of *P. luteolus* and *V. confusus* that forage when and where *P. mesaensis* is active suffer a disproportionately greater chance of being eaten by *P. mesaensis*. Intraspecific predation (cannibalism) has produced similar patterns of temporal distribution, feeding and mortality patterns among age classes of *P. mesaensis* (Polis, 1980, 1984a).

Thus, intraguild predation is an important factor limiting the abundance and shaping the distribution of these scorpions. Many other assemblages of desert scorpions exhibit patterns that suggest that scorpion-scorpion predation is a major process shaping distribution and abundance (Polis and McCormick, 1987; Polis, 1990; but see Bradley, 1988).

## INTERACTIONS AMONG SCORPIONS, SPIDERS AND SOLPUGIDS IN THE COACHELLA VALLEY

Scorpions also frequently eat competitors other than other scorpions. For example, the diet of the scorpion *P. mesaensis* consisted of 8% spiders and 14% solpugids (Polis and McCormick, 1986b). Does such intraguild predation sig-

nificantly affect the distribution and abundance of these unrelated taxa? Spiders responded in the above experimental removal of >6000 *P. mesaensis* by doubling in removal quadrats as compared to controls. Surprisingly, neither solpugids nor all insects combined increased significantly (all p >.05) in removal plots. These taxa did not increase either because individuals dispersed from removal areas, because the increase of spiders and smaller scorpions compensated for the removal of *P. mesaensis* by eating surplus arthropods, or simply that scorpions exerted little impact on insect populations. The first explanation is likely true for widely foraging solpugids and is possible but unlikely for the more sessile insects. The second explanation is unlikely: the biomass increase of spiders and scorpions represented <10% of the removed *P. mesaensis* biomass. The third explanation, difficult to accept, is nonetheless a real possibility: *P. mesaensis* may take such a small proportion of all insects that its removal does not affect insect density.

## INTERACTIONS BETWEEN SCORPIONS AND SPIDERS IN THE NAMIB DESERT

Predation by scorpions on spiders also appears to be a key determinant of spider densities in the Namib Desert (Polis and Seely, unpublished research, 1988, 1989). Both the scorpion *Uroplectes otjimbinguensis* (Karsch) (Buthidae) and the spider *Gandanimeno echinatus* (Purcell) (Eresidae) live under loose bark on larger *Acacia* trees and are the major arboreal predators of insects on such trees. Populations of *G. echinatus* are severely reduced when they co-occur locally on *Acacia erioloba* trees with the scorpion *U. otjimbinguensis*. This system is a model example how predator-prey interactions are complicated greatly by patterns of local distribution. Not all suitable patches (*Acacia* trees) contain the full array of local species capable of existing within the patch. Trees grow along the banks of dry rivers (e.g., the Kuiseb) and become less dense and more sporadic with increasing distance from the river bed. The local abundance of scorpions and spiders on each tree is a function of differential dispersal, extinction and a predator-prey relationship with *U. otjimbinguensis* scorpions eating *G. echinatus* spiders. Although both species are found on river trees, *U. otjimbinguensis* is, with no exceptions, the numerically dominant species (10-50 scorpions/trees) and *G. echinatus* is relatively uncommon (5-20/tree). This occurs because scorpions are effective predators on these spiders.

However, this outcome is more variable on isolated trees further from the river and along smaller washes entering the river. On some trees close to the river, the abundance of scorpions and spiders is similar to that found in the river. However, some trees have no scorpions and great numbers of spiders (50-400/tree); some trees have neither scorpions nor spiders; and some, no scorpions and few (<20) spiders. Overall, trees without scorpions support significantly more spiders ($112.3 \pm 60.6$, n = 21) than trees with scorpions ($24.5 \pm 14.3$, n =20) (p <0.001; only experimental trees scored). This variation in abundance and these distributions exist because neither *U. otjimbinguensis* nor *G. echinatus* disperse far from the river, yet spiders disperse further than scorpions. Dense spider populations occur only in more isolated trees where scorpions are absent. In trees quite distant from the river, neither species occur.

Does intraguild predation by *U. otjimbinguensis* scorpions on *G. echinatus* spiders produce such patterns of distribution and abundance? Additions of *Uroplectes* over a one year period to scorpion-free trees (n = 11) highly significantly (p <.001) reduced *G. echinatus* populations to 42% of that on control trees (n = 12). Removal of scorpions from trees (n= 8) also produced a highly significant, 2.9 times increase in *G. echinatus* as compared to control trees (n= 12) with their full complement of scorpions.

These experiments showed that intraguild predation was concentrated on young spiders and could significantly alter age distributions (p <.001 for each of the following comparisons): The smallest size class of spiders on experimental trees represented 49% of the population (n = 728 spiders) one year after scorpions were removed compared to only 31% (n = 221) on control trees where scorpions remained; similarly, the smallest size class formed 48% of all spiders (n = 903) on trees where scorpions were not present compared to 34% (n = 820) on those trees to which scorpions were added.

Thus differential dispersal and semi-deterministic biotic interactions combined with differing isolation of patches are major determinants of the distribution, abundance and age structure of these species. In general, historical and stochastic dispersal events in patchy environments are a paramount factor explaining the distribution and abundance of predators and their prey and species of competitors (Polis, 1991b; Polis and

Yamashita, 1991). Such conditions can produce local extinctions or great variance in abundances via deterministic biotic interactions, but promote global coexistence. I suspect that such situations are normal among many species living in the notoriously heterogeneous desert. Many such assemblages occur in patches; differential dispersal, local extinctions and 'hide-and-seek' dynamics are undoubtedly extremely important in determining the exact structure of local assemblages. Unfortunately, little research has focused on these processes. The system with scorpions and spiders on *Acacia* trees is ideally suited to analyze such processes and represent another example of the use of scorpions to advance our comprehension of ecological processes.

## INTERACTIONS BETWEEN SCORPIONS AND SPIDERS ON ISLANDS IN THE GULF OF CALIFORNIA

This system shows several of the same general processes as the one on *Acacia* trees in the Namib and illustrates the importance of predator-prey interactions occurring between spatially structured populations. Spider, scorpion and/or lizard populations on small islands (approximately $<1km^2$) are 1-3 orders of magnitude more dense than on larger islands (approximately 1-$1000km^2$) and the mainland; significant negative relationships occur between island size and density for each of these taxa. For example, the scorpion *Centruroides exilicauda* is 2-25 times more abundant on small islands. Three major variables likely explain the great variance in spider abundance: 1) the presence of scorpion predators (often absent from small islands); 2) the dispersal and colonizing ability of spiders relative to scorpions (better colonizers of small islands as compared to scorpions); and 3) differential energy flow from marine to terrestrial systems (much greater to small islands).

This research has been in progress for four years (1989-1992) in the Midrift area of the Gulf on 41 island and 6 mainland sites between Bahia de Los Angeles (Baja California del Norte, Mexico) and Guaymas (Sonora, Mexico) (Polis unpublished). Scorpion and spider abundance were quantified at each site; spiders were counted on >4000 cacti (one sample unit) and $>8000m^2$ of supralittoral shoreline (another sample unit). Insect abundance was estimated at these sites for >1000 trap days.

Small islands ($<1km^2$) exhibit highly significantly greater secondary production of arthropods than larger islands and mainland areas. However, high productivity is not from autochthonous primary production by terrestrial plants. Evidence strongly suggests that allochthonous production from the ocean is the prime source of productivity. Many islands are 'desert islands' with limited primary productivity from terrestrial plants. Several of the most productive small islands support 2-28 plants (individuals, not species) yet 200-1000 spiders can occur on a single cactus!

Small islands are more productive than large islands and mainland areas for two reasons. First, the Perimeter : Area ratio of an island decreases with size (perimeter is a linear function; area, a square function). Thus small islands have relatively more shoreline per unit area of land and consequently, receive relatively more nutrient and energetic input from marine drift (shore wrack–algal and animal detritus). Second, species-area relations are such that small islands lack predators of nesting marine birds; thus small islands support large colonies of pelicans, gulls, petrels and terns.

Marine detritus and material from nesting birds are eaten by many (semi-) terrestrial arthropods. Some arthropods eat dead bird tissue (eggs, chicks, adults) and fish scraps. However, dipteran parasites are dense consumers of nesting birds and form an important conduit of energy from the sea to spiders. Trapping shows that insect abundance is highly significantly ($p<0.001$, all comparisons) greater in both supralittoral zones and around nests than other areas on these islands and on islands with colonies of marine birds compared to those without colonies (also see Due and Polis, 1985). Dietary analysis shows that detritivorous and parasitic arthropods act as conduits of energy from the sea when converted to large populations of terrestrial spiders, scorpions and/or lizards. For example, spiders are 2-5 times more dense on islands with colonies of marine birds versus those without colonies.

Predation is also an extremely important variable determining the abundance of these taxa. On Gulf Midrift islands, spider abundance is significantly lower in the presence of scorpions and lizards (particularly, *Centruroides exilicauda* and *Uta stansburiana*; 1990: $0.19/m^3$ cactus; 1991: $2.5/m^3$) versus their absence ($63.4/m^3$; $28.2/m^3$; both $p<.005$). The importance of scorpions but not lizards on spider abundance is suggested by the analysis of 10 islands near Guaymas in Sonora. Here, spider density is 38 times less

($0.41/m^3$ cactus) on all islands with *C. exilicauda* (n=8) compared to those with lizards ($15.3/m^3$ cactus; n=2).

The final variables in this system are spatial structure and colonization ability. Incidence functions (percent occurrence on islands classified by area) describe the ability of taxa to disperse to and successfully remain on islands of different sizes. The incidence curves suggest that relative ability to colonize small islands roughly can be ranked: Spiders> *Uta* lizards> Scorpions> Nest predators >Songbirds. Colonization would be deterministic if a particular taxon were always present or absent for all islands of a particular size class. In fact, incidence values for smaller island size classes are neither 0 nor 100%, suggesting that presence or absence of a particular taxon is somewhat stochastic. Thus some small islands exhibit high densities of spiders because scorpions are absent whereas other similar sized islands exhibit low densities of spiders because scorpions are present.

An integration of colonizing abilities, productivity and predation is required to understand the distribution and abundance of these taxa. Each factor varies more or less regularly with island size: generally, as size increases, secondary productivity decreases, predation increases and the importance of differential colonizing ability diminishes. Multivariate analysis allows statistical dissection to determine the relative contribution of each of these factors to the observed variance in spider density. This analysis (Table 6) shows that spider density is a significant positive function of prey availability and significantly depressed in the presence of scorpions. Arthropodivorous lizards are a seemingly unimportant factor, explaining almost none of the variance in spider abundance on Midrift islands.

| **1990 data with lizards** | df | SS | MS | F | p>F |
|---|---|---|---|---|---|
| Regression | 4 | 3.25 | 0.81 | 8.67 | 0.0008 |
| Error | 15 | 1.42 | 0.09 | | |
| Total | 19 | 4.65 | | | |
| Perimeter: Area | | | | 10.3 | 0.0058 |
| Scorpion presence | | | | 4.29 | 0.0559 |
| Lizard presence | | | | 0.32 | 0.5827 |
| Cactus volume | | | | 1.20 | 0.2902 |
| Total $R^2$ this model =0.70 | | | | | |
| **1991 data with lizards** | df | SS | MS | F | p>F |
| Regression | 3 | 3.13 | 1.04 | 11.01 | 0.0004 |
| Error | 16 | 1.51 | 0.09 | | |
| Total | 19 | 4.65 | | | |
| Perimeter: Area | | | | 9.06 | 0.0083 |
| Scorpion presence | | | | 5.80 | 0.0285 |
| Lizard presence | | | | 3.76 | 0.9687 |
| Total $R^2$ this model =0.674 | | | | | |

TABLE 6. Multivariate regression of factors that may influence spider abundance on islands in the Gulf of California in 1990 and 1991. The maximum R improvement technique is used; this produces the best model given all the independent variables. Independent variables include lizard presence, scorpion presence, perimeter: area ratio of island, mean cactus volume/island and prey availability/island. The best two variable model includes perimeter: area ratio and scorpion presence. Three variable models are presented with lizards. The effect of lizards is always non-significantly weak, regardless of what higher order model is used.

In summary: Productivity sets potential maximal population size. Small islands are much more productive than larger islands because of the relative greater input of marine allochthonous productivity from drift and marine birds. Colonizing ability establishes the insular species combinations; species-area relations show that larger islands are more diverse and support more types of predators. The realized abundance of terrestrial taxa is limited by (intraguild) predation. For example, if scorpion predators are absent, spiders are dense on small, high productivity islands. When scorpions are present, spider density is lower (but still higher than on large islands and the mainland) and the density of scorpions is relatively high. As island size increases, productivity decreases because nest predators are present (thus bird colonies disappear) and allochthonous detrital input decreases as a function of island Perimeter : Area ratio. Eventually, as island size increases (with decreases in productivity and increases in predation), the abundance of spiders, lizards and scorpions decreases until abundance on very large islands approaches that of the mainland. Strong predation from many sources occurs on the relatively low productivity mainland; consequently, populations of spiders, scorpions and lizards are quite low.

## CONCLUSIONS

This paper presents various types of data to evaluate the 'ecological importance' of scorpions in deserts. Ecological importance was first considered in terms of population energetics (the quantity of energy and mass flowing through scorpion populations) and second, in terms of the regulation of community structure and dynamics (how intraguild predation by scorpions influen-

ces the distribution and abundance of their competitors/prey). The energetic analysis provided three conclusions: 1) Scorpions are quite diverse and abundant in deserts. They monopolize a relatively large share of animal biomass in desert communities, particularly relative to vertebrates and other arthropods. 2) Their relative success is due to a suite of autecological traits that are particularly suited to the harsh and variable climatic conditions of deserts. These traits (very low metabolism and very high assimilation efficiency leading to low energy requirements; and great tolerances to water stress, heat and starvation) preadapt them to prosper successfully under the unpredictable and low productivity food availability that characterize deserts. 3) However, these traits (low metabolism and high assimilation efficiencies) lessen their impact on energetics, prey and competitors. Thus the importance of scorpions relative to homeothermic vertebrates is less than an analysis of density and biomass suggest because scorpions require and process prey in quantities relatively low to their biomass. Nevertheless, as a group, scorpions are probably important conduits of energy flow in deserts.

The research on the interactions among scorpions and that between scorpions and spiders strongly suggests that scorpions can play key roles in the structure and dynamics of the communities in which they live. These studies showed that intraguild predation by scorpions was a major force determining the (temporal and spatial) distribution, abundance and age structure of populations of their competitors/prey. However, as an important caveat, these interactions must be viewed in the context of the environment in which they occur. Dispersal ability, spatial structure and productivity are just some of the possible important factors that moderate the predator-prey interaction between scorpions and their intraguild prey.

The role of all ecologists is to integrate these factors to produce a synthetic understanding of the processes and dynamics that structure natural communities. I suggest that scorpions are particularly suited for this task and will continue to be a productive vehicle to advance the theoretical and empirical body of ecology.

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## LITERATURE CITED

BRADLEY, R.A. 1983. Complex food webs and manipulative experiments in ecology. Oikos 41: 150-152.

1986. The relationship between population density of *Paruroctonus utahensis* (Scorpionida: Vaejovidae) and characteristics of its habitat. Journal of Arid Environments 11: 165-171.

1988. The influence of weather and biotic factors on the behaviour of the scorpion (*Paruroctonus utahensis*). Journal of Animal Ecology 57: 533-551.

DUE, A.D. & POLIS, G.A. 1985. Biology of the intertidal scorpion, *Vaejovis littoralis*. Journal of Zoology 207: 563-580.

1986. Trends in scorpion diversity along the Baja California peninsula. American Naturalist 128: 460-468.

HUMPHREYS, W.F. 1979. Production and respiration in animal populations. Journal of Animal Ecology 48: 427-454.

LAMORAL, B. 1978. Soil hardness, an important and limiting factor in burrowing scorpions of the genus *Opisthophthalmus* C.L. Koch, 1837 (Scorpionidae, Scorpionida). Symposium of the Zoological Society of London 42: 171-181.

MARPLES, T.G. & SHORTHOUSE, D.J. 1982. An energy and water budget for a population of arid zone scorpion *Urodacus yaschenkoi* (Birula 1903). Australian Journal of Ecology 7: 119-127.

MCCORMICK, S.J. & POLIS, G.A. 1990. Prey, predators and parasites. 294-320. In Polis, G.A. (ed.) 'Biology of Scorpions'. (Stanford University Press: Stanford, California).

POLIS, G.A. 1980a. The significance of cannibalism on the population dynamics and surface activity of a natural population of desert scorpions. Behavioral Ecology and Sociobiology 7: 25-35.

1980b. Seasonal and age specific variation in the surface activity of a population of desert scorpions in relation to environmental factors. Journal of Animal Ecology 49: 1-18

1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics 12: 225-251.

1984a. Age structure component of niche width and intraspecific resource partitioning: can age

groups function as ecological species? American Naturalist 123: 541-564.

1984b. Intraspecific predation and "infant killing" among invertebrates. Pp. 87-104. In Hausfater, G. and Hardy, S. (eds). 'Infanticide: Comparative and Evolutionary Perspectives'. (Aldine Publ. Co.: New York).

1988. Exploitation competition and the evolution of interference, cannibalism and intraguild predation in age/size structured populations. 185-202. In Persson, L. and Ebenmann, B. (eds), 'Size Structured Populations: Ecology and Evolution'. (Springer-Verlag: Heidelberg).

1990. Ecology. Pp. 247-293. In Polis, G.A. (ed.), 'Biology of Scorpions'. (Stanford University Press: Stanford).

1991a. Complex trophic interactions in deserts: An empirical critique of food web theory. American Naturalist 138: 123-155.

1991b. Desert communities: an overview of patterns and processes. Pp. 1-26. In, Polis, G.A. (Ed), 'The Ecology of Desert Communities'. (University of Arizona Press: Tucson).

POLIS, G.A. & FARLEY, R.D. 1980. Population biology of a desert scorpion: survivorship, microhabitat, and the evolution of life history strategy. Ecology 61: 620-629.

POLIS, G.A. & MCCORMICK, S.J. 1986a. Patterns of resource use and age structure among species of desert scorpions. Journal of Animal Ecology 55: 59-73.

1986b. Scorpions, spiders and solpugids: predation and competition among distantly related taxa. Oecologia 71:111-116.

1987. Intraguild predation and competition among desert scorpions. Ecology 68: 332-343.

POLIS, G.A., MYERS, C.A. & HOLT, R. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20: 297-330.

POLIS, G.A. & YAMASHITA, T. 1991. The ecology and importance of predaceous arthropods in desert communities. Pp. 180-222. In Polis, G.A. (ed.), 'The Ecology of Desert Communities'. (University of Arizona Press: Tucson).

SHORTHOUSE, D. 1971. Studies on the biology and energetics of the scorpion, *Urodacus yaschenkoi* (Birula, 1904). (Ph.D. dissertation, Australian National University: Canberra).