Extraordinarily high spider densities on islands: Flow of energy from the marine to terrestrial food webs and the absence of predation

GARY A. POLIS AND STEPHEN D. HURD

Department of Biology, Vanderbilt University, Nashville, TN 37235

ABSTRACT   Some islands in the Gulf of California support very high densities of spiders. Spider density is negatively correlated with island size; many small islands support 50–200 spiders per m^3 of cactus. Energy for these spiders comes primarily from the ocean and not from in situ productivity by land plants. We explicitly connect the marine and terrestrial systems to show that insular food webs represent one endpoint of the marine web. We describe two conduits for marine energy entering these islands: shore drift and seabird colonies. Both conduits are related to island area, having a much stronger effect on smaller islands. This asymmetric effect helps to explain the exceptionally high spider densities on small islands. Although productivity sets the maximal potential densities, predation (by scorpions) limits realized spider abundance. Thus, prey availability and predation act in concert to set insular spider abundance.

Some islands in the Midriff area of the Gulf of California support very high numbers of arthropodivorous consumers. Compared to adjacent islands and the mainland, the scorpion *Centruroides exilicauda* is 2 to >25 times more abundant; lizards (primarily *Uta* spp.) are 2 to >20 times more abundant (refs. 1–5; unpublished data). Here we focus on web-building spiders [primarily *Metepeira arizonica* Chamberlin and Ivie (Araneae: Araneidae)]. On many small islands, a single cactus often supports 100–1000 spiders, 1–3 orders of magnitude more than occurs on equivalent sized cacti on nearby (<10 km) larger islands and the mainland. Overall, populations during 1990 and 1991 on small islands were 2 to >100 times more dense (Table 1).

Small islands in the Bahamas and Caribbean support high densities of spiders; on these islands, the absence of *Anolis* lizards (significant predators of spiders) is the key variable determining spider numbers (6–9). In the Gulf of California, predators are also important (see below). However, the dynamics of a species in a food web is determined by two factors: its losses to enemies (predators, pathogens, parasites) and its supply of nutrients or food. Here we report the finding that productivity acts together with predation to set insular spider abundance.

MATERIALS AND METHODS

The research was conducted on islands in the Midriff region of the Gulf of California, Mexico, and the Baja California peninsula. Data primarily were collected from May through August in 1990 (11 weeks) and 1991 (9 weeks) during ≈4500 person-hours of field time.

Study Site. The principal study site comprises 17 islands between Bahia de los Angeles and Isla Angel de la Guarda, Angel and two satellite islands, and the adjacent coast along the Baja California peninsula (not all islands were surveyed both years). Bahia de los Angeles lies at lat. 28°55' N, long. 113°30' W. Mean annual precipitation is estimated to be <50 mm, and mean annual temperature is 20–22°C (10, 11). This amount of rainfall makes this area among the driest places in North America.

Perimeter/area (P/A) values for the islands are from Due (12). Topographical maps published by the Mexican government were enlarged 1.5 times and then digitized using a Hipad digitizing tablet (Houston Instruments) interfaced with Bioquant II (R & M Biometrics, Nashville) software. Images were digitized three separate times to ensure consistency, and the mean values for the three separate digitizations are presented here for perimeter and area values.

Insect Trapping. The abundance of aerial insects was estimated by using glue traps (Abepco, Orange, CA) tied to *Opuntia* cactus (cholla). Each trap is a piece of cardboard with an 8.5 × 12 cm glue area. The criterion for length of time trapped changed from 1990 to 1991. In 1990, traps were left on the islands for 15–19 days. By the end of this time, the traps were no longer sticky; this suggests that in any comparison of arthropod abundance from year to year, the 1990 data will be an underestimate of the true value. However, since all 1990 traps were left for a consistent length of time, comparisons between islands within that year are still valid. In 1991, the following time criteria were adopted: (*i*) traps left for <24 hr were excluded from comparisons since they do not encompass the full diel cycle; (*ii*) traps left for >120 hr were excluded since beyond 5 days the performance of the traps is compromised. In 1990, an average of 7.9 ± 3.4 traps were placed on 7 islands and the peninsula for an average of 120 ± 44 trap·days per site (total trap·days, 962). In 1991, an average of 13.1 ± 4.8 traps were placed on 13 islands and the peninsula with an average of 57 ± 19 trap·days per site (total trap·days, 801). Cacti used for insect trapping were chosen randomly from throughout the island (these cacti are not found in the supralittoral on any of the islands), so arthropod densities reported are the average density throughout the interior of the island.

To determine the effect of proximity to the ocean on insect abundance, eight traps were placed on fresh algae in the supralittoral and on plants 100–200 m inland. Also, to assess the temporal effects of nesting seabirds, 10 traps were placed on one island both during the seabird breeding season and several months after the nesting season had ended.

Trapped insects were counted and measured for length to the nearest millimeter under a microscope. Cursorial arthropods (ants and spiders) were excluded from counts to yield an estimate of aerial arthropod abundance. The total length of insects on each trap was divided by the period of time the trap was left on the island to determine the abundance of insects in $mm \cdot trap^{-1} \cdot day^{-1}$.

Surveys of Web-Building Spider Density. Web spiders were censused on two species of cholla cacti (*Opuntia*, subgenus *Cylindropuntia*: *Opuntia bigelovii* and *Opuntia acanthocarpa*); these species intergrade on the islands and the peninsula. Spiders were censused on 30–80 cacti on each island in each

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Table 1. Densities of spiders and aerial arthropods are much higher on small islands than on large islands or the peninsula

Island type	Spider density per m³ of cactus		Prey availability, mm·trap⁻¹·day⁻¹	
	1990 mean ± SD (range)	1991 mean ± SD (range)	1990 mean ± SD	1991 mean ± SD
Small (<0.5 km²)	28.9 ± 62.1 (0.7–225) (12 islands)	25.5 ± 16.5 (9.5–56.6) (13 islands)	6.1 ± 2.9 (4 islands)	13.4 ± 9.5 (9 islands)
Large (>0.5 km²)	5.0 ± 7.4 (0.2–15.8) (4 islands)	6.7 ± 8.5 (0.1–24.5) (7 islands)	3.7 ± 1.3 (3 islands)	7.9 ± 5.0 (4 islands)
Peninsula	1.3 ± 7.3 (30 cacti)	0.3 ± 1.5 (68 cacti)	0.9 ± 0.3 (6 traps)	4.0 ± 3.6 (11 traps)

year; if an island had <30 *Opuntia*, all cholla on the island were censused. Cacti were chosen randomly from throughout the island (these cacti are not found in the supralittoral on any of the islands), so spider densities reported are the average density throughout the interior of the island. Each cactus was measured for height, width, and length, and cactus volume was calculated as a box from these measures. All web spiders were counted; species present were *Metepeira arizonica*, *Argiope argentata*, *Cyclosa turbinata*, *Latrodectus hesperus*, *Theridion* sp., *Dictyna* sp., and *Uloborus* sp.

For spider density as a function of proximity to the coast, 100-m transect lines were laid immediately above the high tide line and 100 m inland. The two sites had similar topography (talus slopes). Spiders were surveyed for each linear meter to a height of 2 m, and values are presented as spiders per m² of surface area. For spider density as a function of seabird colonies, five cardon cacti (*Pachycereus pringlei*) of similar size and branching pattern were surveyed both within and away from seabird colonies on the same island. Spiders were censused to a height of 2 m, and values are presented as spiders per m³ of space available for web placement on the plant.

Algal Drift Measurement. Three supralittoral sites were chosen to collect and measure algal drift. Each site is on the mainland: one in Bahia de los Angeles, the second (Don Juan Cove) 10 km east, and the third (La Unica) 16 km east southeast of Bahia de los Angeles past Punta Pescador. Similar beach topography and algal species occur on and around the islands as well. At each site, 5–12 transects were permanently marked off in 10-m lengths (total, 27 transects). Each time the sites were visited, algal drift was collected, weighed, and disposed of inland so that it could not return to the transects. Plots were serially cleaned throughout the year to obtain yearly measures of algal drift. In total, these sites were surveyed 17 times. Algal drift was both dry and wet. If algae were wet, dry mass was determined by desiccating measured amounts until dry, reweighing it, and determining a factor to convert wet to dry mass. The data are presented as the average mass of algal detritus or carrion (see below) entering each meter of the supralittoral at each site.

Carcass Drift Measurement. Carrion washed into the supralittoral was measured at the same three sites as algal drift. Transects were longer, ranging in length from 630 to 1800 m for a total of 4230 m. Permanent transect areas were established, and all carcasses were collected, identified, and permanently removed from each site. Carcasses removed in the first survey are not included, since we cannot determine in what length of time these carcasses had washed ashore (this exclusion eliminated from consideration a fresh 16.8-m fin whale carcass with estimated mass of at least 25,000 kg). Average mass for adults and juveniles for each species of dead bird and marine mammal was determined from the literature (13–17).

Data Analysis. Data were tabulated and means and standard deviations were extracted. Data were checked for homoscedasticity and normality. If necessary, data were log-transformed to achieve normality and homoscedasticity; if data

were still heteroscedastic, t tests sensitive to unequal variances were used. ANOVAs, t tests, and regressions were conducted using SYSTAT. If data were log-transformed for statistical tests, means and standard deviations presented in tables are reverse-transformed.

RESULTS AND DISCUSSION

Spider density and island area are significantly correlated (Fig. 1*a*), with spiders at higher densities on smaller islands. Insect abundance is also negatively correlated with island area (Fig. 1*b*)—i.e., higher densities of insects occur on small islands than larger islands and the mainland. These observations suggest that smaller islands are more productive, at the level of both predators and their resources, than are larger islands within the
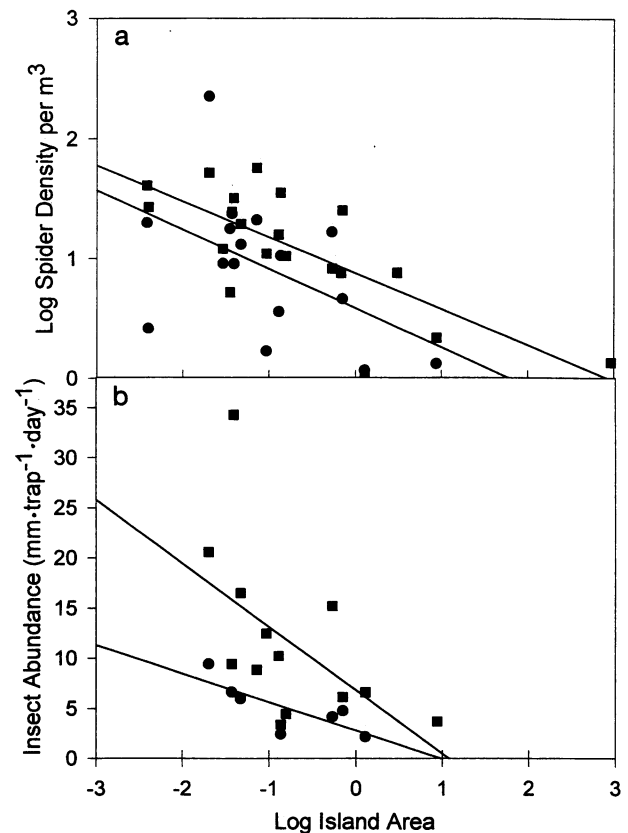

FIG. 1. (*a*) Spider density on cactus is negatively related to island area. ●, 1990: log spider density = 0.59 − 0.33 (log island area); $n = 16$; $R^2 = 0.25$; $P = 0.05$. ■, 1991: log spider density = 0.88 − 0.30 (log island area); $n = 20$; $R^2 = 0.55$; $P < 0.0005$. (*b*) Abundance of aerial arthropods decreases with increasing island area. ●, 1990: mm·trap⁻¹·day⁻¹ = 2.79 − 2.84 (log island area); $n = 7$; $R^2 = 0.62$; $P = 0.03$. ■, 1991: mm·trap⁻¹·day⁻¹ = 6.82 − 6.33 (log island area); $n = 13$; $R^2 = 0.30$; $P = 0.05$.

Table 2.   Primary and secondary productivity from allochthonous (marine) and autochthonous (terrestrial) sources

Taxon measured	Allochthonous source	Autochthonous source	t	P
	Algal drift	Terrestrial productivity		
Plant productivity, dry mass	$1.3{-}46$ kg·m^{-1}·yr^{-1}	Estimated 0.098 kg·m^{-2}·yr^{-1}*	NA	NA
	Supralittoral	Inland		
Arthropod prey, mm·trap^{-1}·hr^{-1}	175.8 ± 2.0	1.6 ± 2.5	11.84	<0.0005
Spiders, per m^2 of area	0.155 ± 0.040	0.025 ± 0.017	3.00	0.003
	Seabird colony islands	Noncolony islands		
Arthropod prey, mm·trap^{-1}·day^{-1}	17.6 ± 4.1	6.2 ± 1.2	2.9	0.014
Spiders (1990), per m^3	18.1 ± 4.0	3.2 ± 3.4	2.40	0.0175
Spiders (1991), per m^3	25.1 ± 2.1	6.2 ± 3.9	2.30	0.0185
	Bird breeding season	Postbreeding season		
Arthropod prey, mm·trap^{-1}·day^{-1} (on a seabird colony island)	455.0 ± 1.1	17.1 ± 1.2	15.33	<0.0005
	Within seabird colonies	Away from colonies		
Arthropod prey, number/day†	12.3 ± 1.0	4.5 ± 1.8	4.01	<0.02
Spiders, per m^3	14.3 ± 1.5	1.8 ± 1.5	7.97	<0.0005

*Estimate of terrestrial productivity from Lieth's precipitation model (20), using 50 mm for mean annual precipitation.
†Data on prey abundance within and away from seabird colonies are from Hews (2).

same system (Table 1). However, such high secondary productivity does not arise from *in situ* production by land plants, which is very limited. The Midriff islands are one of the driest places in North America, receiving <50–100 mm of precipitation annually (10). Primary productivity on land is a direct function of precipitation (18–20) and these desert islands are among the least productive habitats on the continent. The plant cover on each of the 23 islands surveyed was always <10%; on several small islands, 0–30 individual plants (not species) were present in 1990/1991, yet spiders, lizards, scorpions, and/or centipedes were abundant.

Allochthonous marine input, rather than *in situ* terrestrial productivity, is the source of most prey of these consumers. The unproductive Midriff islands are surrounded by very productive waters that support high densities of plankton, fish, seabirds, and marine mammals (21–23). In general, primary productivity in the central Gulf is estimated to be at least 5 times greater than that on Midriff islands (20, 21) (Table 2); when the strong upwelling in the Midriff waters is included, marine productivity may be up to 50 times greater (24). Energy flows directly and indirectly from the ocean to consumers on land via marine detritus and large colonies of marine birds. Such material overwhelms *in situ* productivity. Annual input of detrital algae to each meter of shore perimeter is 1.3–46 kg/yr; this represents an immense source of imported biomass in energy into a terrestrial system where primary productivity by desert plants is estimated to be 0.098 kg·m^{-2}·yr^{-20} (based on 50 mm of precipitation per yr).

This organic material is eaten by and converted into terrestrial detritivores and scavengers in the supralittoral [species eating marine drift that are eaten by spiders, scorpions, and lizards (Diptera: Ephydridae, Coelopidae, Canaceidae, Ceratopogonidae, Sphaeroceridae, and Anthomyiidae; Hemiptera: Saldidae; Coleoptera: Tenebrionidae and Histeridae; Crustacea: *Ligia* isopods and *Hyale* amphipods) (refs. 5 and 25–27; unpublished data)]. Inland during seabird breeding months, a superabundance of parasites and carcass-scavenging insects convert marine bird tissue to potential prey {species on birds that are eaten by spiders, scorpions, and lizards [Diptera: Calliphoridae, Chamaemyiidae (*Paraleucopis mexicanus*), and Ceratopogonidae (*Dasyhelea* spp.); Coleoptera: Dermestidae and Tenebrionidae (*Argoporis* sp.); ticks (Argasidae, *Ornithodoros denmarki*)] (refs. 1–3 and 28; unpublished data)}. These conduits of marine productivity make the abundance of potential prey of spiders significantly greater in the supralittoral zone, on islands with seabird colonies, and during the

breeding season than other areas and times (Table 2; see also refs. 1–3, 5, and 28). These arthropods are extensions of the marine web: in the supralittoral, >99% of trapped prey are detritivores; inland during the seabird breeding season, >99% of potential prey trapped and 98% of prey actually recovered from spider webs are seabird ectoparasites.

Terrestrial consumers (spiders, scorpions, and lizards) eat these prey derived from the marine food web. In the supralittoral, detritivorous and algivorous insects and crustacea form >99% of their diet (5, 25–27). On many islands, these consumers thrive, although land plants are absent or occur 25 to >100 m away. Around the nests of marine birds during breeding months, >90% of the diet of various arthropodivores

Table 3.   Multiple linear regression of 1991 spider density (log of total density per m^3) as a function of bottom-up productivity (indicated by island P/A ratios) and top-down predation (indicated by presence or absence of scorpions and lizards)

	DF	SS	MS	F	P
Regression	3	3.313	1.104	12.749	<0.0005
Error	16	1.386	0.087		
Total	19	4.699			

	Coefficient	Standardized coefficient	T	P
Intercept	1.180		6.34	<0.0005
P/A	0.015	0.504	2.85	0.011
Scorpion (+/−)	−0.597	−0.613	4.50	<0.0005
Lizard (+/−)	−0.140	−0.144	0.82	0.426 (NS)

Model: log density/m^3 = 1.180 + 0.015 (P/A) − 0.597 (scorpion) − 0.140 (lizard); $n = 20$; $R^2 = 0.705$. Both productivity and scorpion predation significantly influence insular spider abundance; lizard presence does not significantly affect spider density on cholla cactus. P/A values represent increasing input of marine productivity per unit area as island size increases. In both 1990 and 1991, secondary productivity of arthropod prey (as measured by trapping) was significantly and directly correlated with P/A values (1990: $R = 0.872$, $n = 7$, $0.01 < P < 0.05$; 1991: $R = 0.529$, $n = 15$, $0.01 < P < 0.05$). P/A values are used here to extend the analysis to islands for which we do not have insect trap data. A two-way ANOVA of spider density, with the independent variables high or low states of productivity and presence or absence of *C. exilicauda* predators, is also highly significant ($P < 0.0003$) with $R^2 = 0.66$. Both predation ($P < 0.0004$) and productivity ($P < 0.0034$) were significant but did not interact significantly ($P = 0.1135$). DF, degrees of freedom; SS, sum of squares; MS, mean square; F, sample variance ratio; T, sample statistic of t distribution; NS, not significant.

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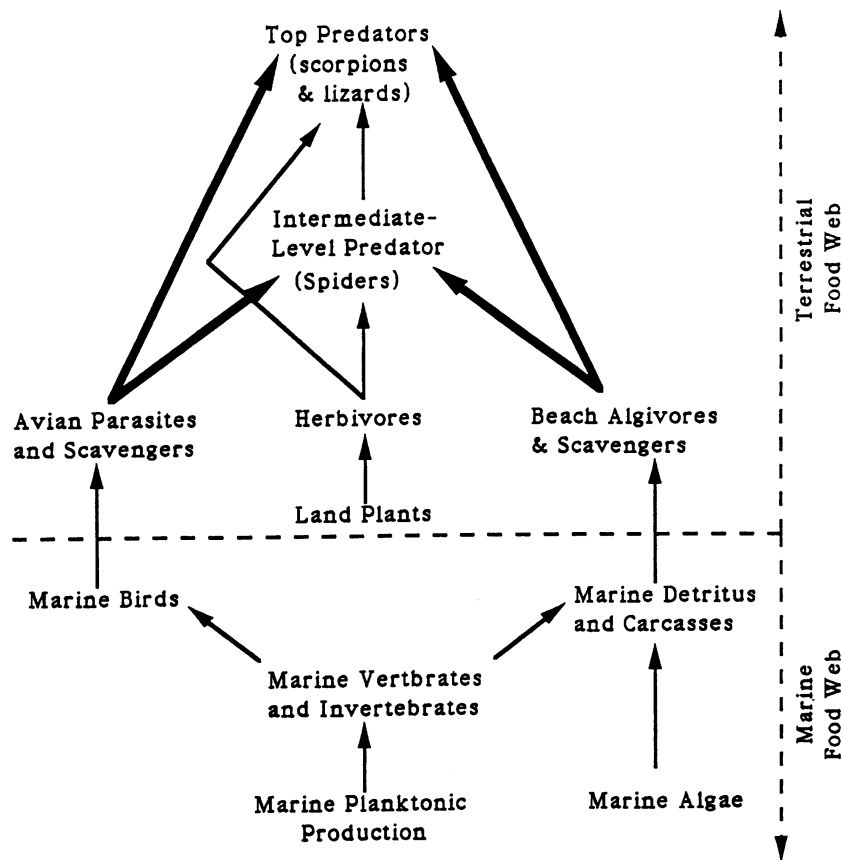
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FIG. 2. Schematic food web of small islands in the Gulf of California.

consists of avian parasites and scavengers (1–3, 28). Thus, prey exploiting these two conduits of the marine web form the energy base for the large populations of spiders, scorpions, and lizards. Spider densities are 6 times greater in the supralittoral than inland, 4–5 times greater on islands with colonies of marine birds compared to those without, and 12 times greater within versus away from colonies on the same island (Table 2). Overall, the flow of marine material to land, its ingestion by primary consumers (detritivores, scavengers, and parasites), and predation on these consumers by arthropodivores operationally connect the marine and terrestrial food webs on small islands.

Compared to larger islands and the mainland, small islands receive more marine energy for two reasons. (*i*) Island P/A ratio decreases with island area. Perimeter increases as a linear function, while area increases as a squared function. While the specific shape of each island's coastline affects this relationship, small islands will as a group exhibit more shoreline per unit area (greater P/A) and consequently receive relatively more detrital input. (*ii*) Species–area relations are such that small islands often lack predators of nesting marine birds; thus, some islands support large colonies of pelicans, gulls, petrels, and terns (29). This observed scaling effect is counterintuitive to the general notion that larger islands are more productive; large islands are thought to catch more rain and show higher primary productivity than smaller ones (30, 31).

Multiple linear regression (Table 3) of the 1991 data shows that 70% of the variance of insular spider abundance is explained by productivity (represented by island P/A ratios) and predation (the presence of scorpions). It is not surprising that spider density is partially determined by the joint forces of predation and prey availability. Spiders are known to respond numerically to increased prey (32–36) and decreased predation (6–9, 37, 38). The scorpion *C. exilicauda* appears to depress significantly spider density here; scorpion predation is a key

factor limiting spiders elsewhere (38). It is possible that the effect attributed to scorpions here is in part due to arthropodivorous land birds (e.g., rock wrens, cactus wrens), which in some years have a distribution on these islands co-occurrent with *C. exilicauda*. Unexpectedly and in contrast to previous work (6–9), lizards explain practically none of the variance in spider density. These observations are consistent with the fact that *C. exilicauda* climb in cholla cactus, whereas *Uta* spp. cannot negotiate these spiny plants. Predation clarifies why islands of similar size (Fig. 1*a*) may support different numbers of spiders; scorpions are usually present on most islands below the regression line (in 1990, four of five islands with scorpions were below the line; in 1991, six of nine scorpion islands were below the line). Nevertheless, spider density significantly correlates to P/A even in the presence of scorpions ($R^2 = 0.670$; $n = 9$; $P = 0.007$) or lizards ($R^2 = 0.421$; $n = 11$; $P = 0.03$).

In general, such top-down (predatory) and bottom-up (productivity) factors are key determinants of consumer abundance (39–43). A simplified web (Fig. 2) illustrates their interaction; material from the ocean provides energy for growth of spider populations, whereas mortality due to scorpion predation lowers spider numbers. Such factors integrate to explain the patterns of spider abundance as a function of island size. Secondary productivity sets the potential maximal population size; realized abundance at any site is limited by predation. Compared to large islands or the mainland, smaller islands receive relatively more marine energy, are relatively more productive per unit area, generally contain fewer predators, and thus support more spiders.

It is likely that similar phenomena (energy input from the sea; the joint importance of productivity and predation) determine the abundance of terrestrial consumers on other island systems. Although the importance of allochthonous flow and/or predation is most clearly evident on small islands (28, 44–46), they are undoubtedly important to most islands

and even mainland coastal areas throughout the world. One future challenge is to understand food web interactions at the water and land interface.

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