References and Notes

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Spider Populations: Extraordinarily High Densities on Islands Without Top Predators

Abstract. *Distributions and densities of orb spiders on small islands are extremely variable. Species occurrences are far more irregular for spiders than vertebrates on the same islands. Much variation in spider density is explainable by distance from the presumed source of colonists and presence or absence of vertebrate predators. As has been predicted for passive dispersers, densities decline exponentially with distance. For a given distance, spider densities are about ten times greater on islands without vertebrate predators than on those with such predators.*

Predators that occupy intermediate trophic levels are ecologically ambiguous; should they resemble top carnivores or should they be strongly influenced by predation upon themselves and thereby resemble many herbivores (*1*)? One way to resolve this ambiguity is to compare populations of such predators with and without top carnivores. For this purpose, the inhabitants of small islands provide an ideal natural experiment. Our test organisms were orb-weaving spiders (Araneae), an abundant intermediate-level predator on subtropical islands. Numerous such islands suitable for spiders exist both with and without top carnivores, in this case lizards and birds.

We censused diurnal vertebrates and spiders on 93 neighboring Bahamian islands, chosen such that a substantial number were both just above and just below the minimal island size having any resident vertebrate species (*2, 3*). We identified and counted spiders with webs on 80 of the islands; for the remaining 13, at least 60 percent of the island was censused and the total numbers of spiders were extrapolated. Four species—*Metepeira datona, Argiope argentata, Gasteracantha cancriformis, Eustala cazieri*—were common; a fifth—*Nephila clavipes*—occurred rarely. All resident vertebrates were lizards (*4*); in the general region, their densities are 10^{-1} to 10^{-2} per square meter.

Spiders occurred on smaller islands than did lizards. The smallest island with any spider species was 50 m^2 (vegetated area); other common species had only slightly larger minimal areas (55 to 112 m^2). The smallest island with a lizard population was 167 m^2; all larger islands also had lizards. All but two of the lizard-inhabited islands had the same species (*Anolis sagrei*), whereas any of the four spider species commonly occurred solitarily, a first indication of greater stochasticity in spiders. Below, we treat separately the 74 islands exceeding 50 m^2, the minimal area threshold for spiders [hereafter referred to as ST (spider threshold) islands], and the 55 islands exceeding the threshold (167 m^2) for lizards (hereafter referred to as LT islands).

We first made a number of simple analyses of covariance (ANCOVA's), using as the dependent variable either density or number of spiders of all species combined. When the effect of island area was taken into account, the number of spiders was smaller on islands with than without lizards (ST islands, $P = .02$; LT islands, $P = .02$; Fig. 1). Spider density was only slightly and negatively related to area; a negative relationship is to be expected given the statistical dependence of these two variables. When distance from a potential large source (*5*) was used as the continuous independent variable and spider density as the dependent variable, statistical significance was about the same as the previous analysis (ST islands, $P = .03$; LT islands, $P = .003$). Multiple ANCOVA's with spider number as the dependent variable and island area and distance as independent variables gave results no more significant than the simple

Table 1. Statistical analysis of factors affecting numbers of spiders on island. The *N* for ST was 74 and that for LT was 55. Abbreviations, *A*, area; *D*, distance; *M.d.*, *M. datona; G.c., G. cancriformis; A.a, A. argentata; E.c., E. cazieri; b* is a regression coefficient; S.E., standard error. Logs are to the base 10.

Dependent variable	Independent variables		Data set	Multiple ANCOVA P_F	Multiple regression									
					No-lizard islands					Lizard islands				
	X_1	X_2			b_1	S.E.$_1$	b_2*	S.E.$_2$*	r^2	b_1	S.E.$_1$	b_2*	S.E.$_2$*	r^2
Number spiders	*A*	*D*	ST	.010	0.03^{d}	0.006	−122.4	117.7	0.32	0.004^{c}	0.002	-155.1^{b}	69.8	0.27
	A	*D*	LT	.011	0.03^{b}	0.009	−140.2	173.3	0.28	0.004^{c}	0.002	-155.1^{b}	69.8	0.27
Log (number spiders + 1)†	log *A*	*D*	ST	$< 10^{-4}$	0.93^{d}	0.160	-4.87^{c}	1.55	0.45	0.73^{c}	0.229	-6.55^{c}	2.02	0.38
	log *A*	*D*	LT	$< 10^{-4}$	1.22^{d}	0.295	-5.90^{c}	1.91	0.45	0.73^{c}	0.229	-6.55^{c}	2.02	0.38
Log (all webs + 1)†	log *A*	*D*	ST	.020	1.06^{d}	0.157	−2.28	1.52	0.50	0.89^{d}	0.193	-2.92^{a}	1.71	0.48
Log (*M.d.* + 1)†	log *A*	*D*	ST	.001	0.76^{d}	0.174	-3.49^{b}	1.68	0.31	0.28	0.242	−2.47	2.15	0.07
Log (*G.c.* + 1)†	log *A*	*D*	ST	.298	0.13	0.070	−0.66	0.682	0.07	0.43^{b}	0.163	-3.29^{b}	1.45	0.27
Log (*A.a.* + 1)†	log *A*	*D*	ST	.001	0.23^{b}	0.108	−1.66	1.05	0.11	0.02	0.025	−0.22	0.224	0.05
Log (*E.c.* + 1)†	log *A*	*D*	ST	.511	0.15^{b}	0.075	−0.58	0.725	0.09	0.23^{a}	0.120	-2.20^{b}	1.07	0.19

*To obtain true value, multiply by 10^{-4}. †We also added 0.1 and 0.01 to all log variables for most treatments. All *F*'s significant at the 5 percent level were still significant, and vice versa. In multiple regressions, two distance coefficients not significant with 1.0 were significant with 0.01, and one distance coefficient was the opposite; all involve single-species data. In all cases, the significance of area coefficients was unaffected. In all cases, the sign of the effect was unchanged. $^{a}.05 < P < .10$. $^{b}.01 < P < .05$. $^{c}.001 < P < .01$. $^{d}P < .001$.

ANCOVA's (Table 1). Nor did the partial regression coefficient for distance differ significantly from zero when all islands combined or ST islands were used (Table 1).

When spider density was plotted as a function of distance, however, the decline was exponential rather than linear, with the intercept about an order of magnitude higher for islands without lizards than those with lizards (Fig. 2). This relation is written

$$\text{Density} = \text{number/area} = ae^{-bD} \quad (1)$$

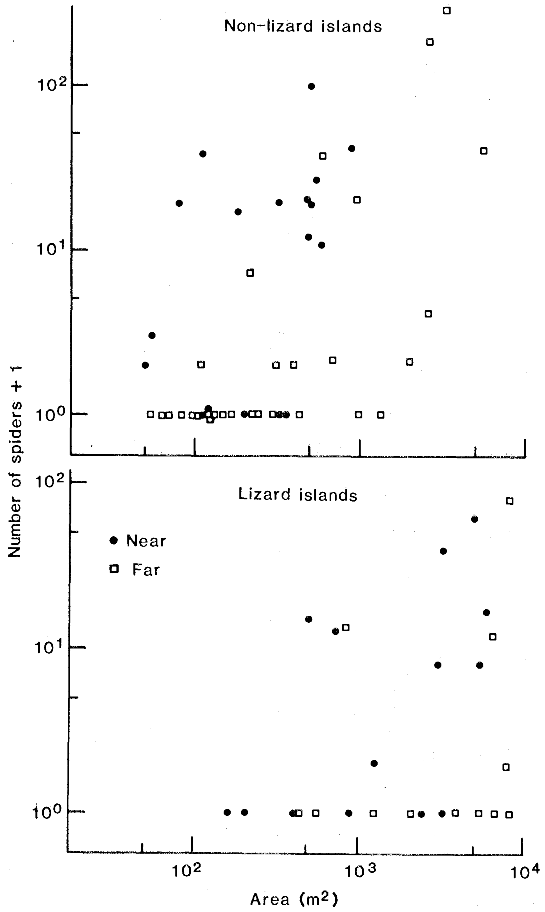
where D is distance and a and b are fitted parameters. Equation 1 is equivalent to

$$\ln(\text{number}) = \ln(\text{area}) + \ln(a) - bD \quad (2)$$

Equation 2 suggests that multiple ANCOVA and regression be tried with ln(number) as the dependent variable and ln(area) and distance as independent variables. Results were substantially more significant statistically than previous ones. The adjusted mean log number of spiders was 11 times greater on islands without than with lizards and distance was statistically highly significant and about as important as area. Adding a third variable reflecting vegetation complexity did not subtantially improve the ANCOVA's or regressions; area and distance showed a close correlation (the latter negative) to this variable (*6*).

In summary, the number of spiders from all species combined was strongly related to island area and distance; when these relations were taken into account, numbers were substantially less on islands with than without lizards. A negative interaction between lizards and spiders may reflect predation. Lizards on Bahamian islands eat spiders (*7*) and will snatch them from webs. However, two spider species are brightly, possibly aposematically, colored; one of these bears thornlike projections which may deter predation. A third spends most of its time in a shelter fashioned of debris. Competition may also account for low spider densities on islands with lizards. Experimental attempts to detect interspecific competition among spiders themselves have been uniformly unsuccessful; only strong intraspecific competition has been found (*8*) despite the fact that spider species may often partition resources in a nonrandom manner (*9*). However, in that lizards reach high densities and are much larger than spiders, competition for food from lizards could be much stronger than from other spider species; indeed, competition between numbers of distant taxa is not uncommon (*10*). To evaluate these hypotheses, we further analyzed our data in two ways.

First, we repeated the most significant multiple ANCOVA and regressions using all webs, whether occupied or not, as the dependent variable. Several nocturnally active species of orb weavers are common in the central Bahamas, and most empty webs are probably theirs (*11*). For ST islands, the F value was still significant, but the ratio of adjusted means (ratio of number without lizards to number with lizards) was merely 1.5 as compared to 11 in the analysis when only occupied webs were used. Multiple r^2's were comparatively high because of a strong effect of area, but distance coefficients were not significant (Table 1). Because nocturnal species would seldom



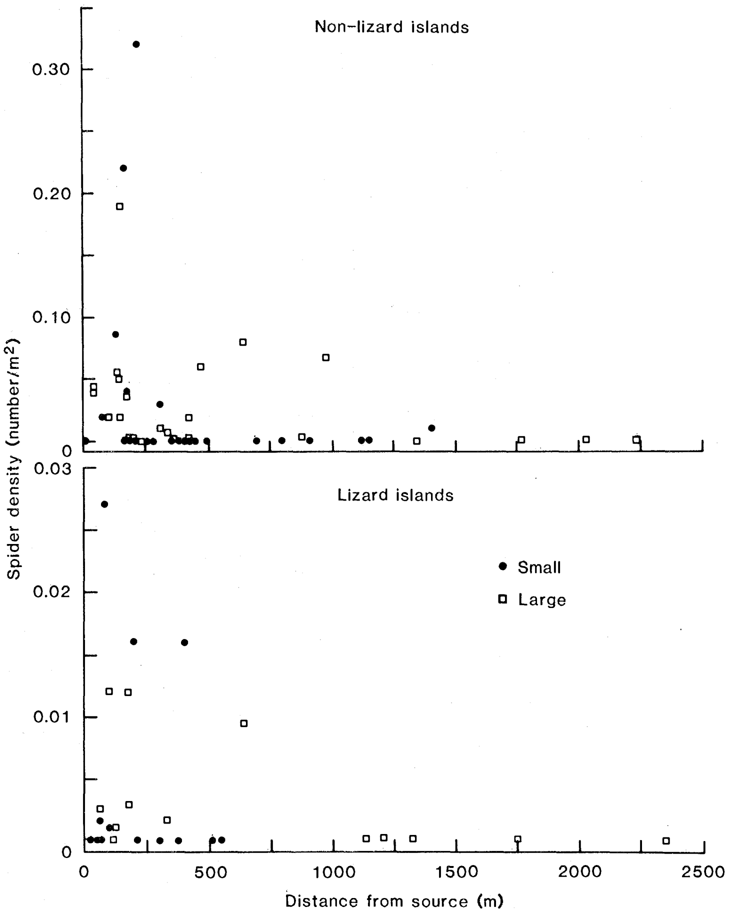


Fig. 1. Relation of number of spiders to area for no-lizard and lizard islands, log-log scale. Far islands (< 230 m) tend to have fewer individuals than near ones of the same area; however, there are some near islands that are apparently suitable for spiders but without them. Fig. 2. Spider density decreases exponentially with distance for both lizard and no-lizard islands, but density is about an order of magnitude greater on islands without lizards (note change of scale on vertical axis). There is little relation of density to island area. (For each plot, islands were divided into two groups of equal size on the basis of island area: no-lizard islands—small ≤ 282 m^2; lizard islands—small ≤ 2512 m^2.)

be subjected to predation from diurnal lizards [they feed almost entirely on active prey (*7*)], these results support the predation hypothesis. Because diurnal lizards are more likely to eat the same foods as diurnal rather than nocturnal spiders, an argument could also be made for competition. However, unoccupied webs, if fresh enough, can catch prey, so this argument is less convincing.

Second, we repeated the statistical analyses separately for each common spider species (Table 1). Although lizards had a negative effect on all four species, two did not show a significant difference between lizard and nonlizard islands. One of these, *G. cancriformis*, is both brightly colored and has spines. This seems to support the predation hypothesis. The other, *E. cazieri*, is both nocturnal and diurnal. With few exceptions, only juveniles are active during day, and these have no obvious predator defense. Moreover, juveniles probably eat smaller prey than do larger spiders (because their webs are flimsier) so juveniles would overlap in food size with lizards least. Hence *E. cazieri* seems to support the competition hypothesis. Finally, *A. argentata*, a species highly affected by lizards, had a higher proportion of juveniles on islands without lizards. Because juveniles build webs close to the ground and are thereby especially vulnerable to lizard predation, this species supports the predation hypothesis.

In conclusion, somewhat more support now exists for the predation than competition hypothesis, but both may be important.

Like plots for all species combined, within-species plots of density as a function of distance show exponential decline. MacArthur and Wilson (*12*) proposed that, for arthropods, numbers of individuals dispersing passively (for example, by wind) should decline exponentially. This relation would result if the probability that an aerial disperser survived a given small distance, rather than dropped to the ground, were constant regardless of the disperser's distance from the source. Possibly our plots reflect such a process, implying that favorableness of islands did not influence population size, apart from the presence of lizards. Alternatively, distant islands may be less favorable to spiders; indeed they tend to have scrubbier vegetation in most of the Bahamas, including our study site (see above) (*3*). Whatever the etiology, we know of no other study showing a decline in density with distance for any species, although many studies have already shown such a decline (*3, 12, 13*).

Table 2. Probabilities that individual species occurrences are random with respect to island area (Mann-Whitney U test). For all near (< 152 m) islands, $N = 29$; for all far (> 152 m) islands, $N = 64$.

Species	Island group	P
	Spiders	
Metepeira datona	Near	.04
	Far	.01
Gasteracantha cancriformis	Near	.04
	Far	.03
Argiope argentata	Near	.14
	Far	.18
Eustala cazieri	Near	.01
	Far	$< 10^{-3}$
Nephila clavipes	Near	.15
	Far	.02
	Lizards	
Anolis sagrei	Near	$< 10^{-4}$
	Far	$< 10^{-4}$

Spider populations can explode very quickly. On one island *A. argentata* increased from 0 to 115 individuals in less than a year; most occupied a tenth of the island's 352-m^2 area. Explosive growth to similar densities was observed for this species on five other islands in the same period. In another species, the colonial *M. datona*, numbers typically changed more slowly, but it reached even higher densities than *A. argentata*.

We showed that lizard occurrence, island area, and distance from source were all important in predicting spider numbers. However, a number of near islands apparently suitable for spiders were without them (Fig. 1). Moreover, spider species were substantially more haphazard in their occurrences on islands than were lizard species. To show this for island area, we used the occurrence-sequence technique (*3*), in which islands were ranked by their area and the presence or absence of a given species was noted. A Mann-Whitney U test can be used to determine whether the sequence of presences and absences is significantly nonrandom. We treated near (< 152 m) and far islands separately. Lizard occurrences were more regular than all spiders and substantially more regular than all but *E. cazieri* (Table 2). Highly regular occurrence sequences for lizards characterize those species elsewhere in the Bahamas, and occurrence sequences are almost as regular for birds (*3*). While other features of islands may give more regular sequences for spiders than area, many habitat variables show a high correlation to area (*3, 6*), so that they will give similar results. The lizard-spider comparison, especially as it was done for the same set of islands, strongly supports a growing consensus that arthropod distributions and abundances are on average less simply patterned than those of vertebrates (*14*). For arthropods that are also intermediate-level predators, our report suggests that the nature of higher trophic levels, as well as physical factors such as dispersal by wind, contribute to this greater apparent stochasticity.

THOMAS W. SCHOENER
CATHERINE A. TOFT
Department of Zoology,
University of California, Davis 95616

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5. Chosen as the nearest island exceeding 4658 m^2 (5×10^5 square feet). This somewhat arbitrary choice represents to the nearest half-order of magnitude a natural discontinuity in the sizes of large islands in the region.
6. The variable was maximum vegetation height; the Pearson correlation with log area for all ST islands is 0.55. Distance was not as well correlated with the vegetation variable, and it was sometimes negatively so. The vegetation variable, log-transformed or arithmetic, never had a partial regression coefficient significant at $P < .10$, with one exception (islands without lizards, arithmetic height, $P = .082$). The best ANCOVA run that included the vegetation variable gave an F value of 24.32, as compared to $F = 21.01$ without it (see Table 1).
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