Effect of Predators and Area on Invasion: An Experiment with Island Spiders

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To assay the effect of area and predators on invasion success, spiders were introduced onto islands that were large, with lizard predators; large, without lizard predators; or small, without lizard predators. Short-term survival was greater on islands without than with predators; area had no effect. Spiders initially increased substantially on both groups of islands without lizards, but after 5 years they nearly died off on small islands while persisting on most large islands; populations in the presence of predators never increased above initial sizes. Results show how predators as well as area are important in determining invasion success.

Factors determining a species' invasion success have become increasingly important to understand, given the increased mobility provided to organisms by human activities (*1*). Islands have often been used for such studies, but experiments have rarely been done (*2*, *3*). In this experiment, we systematically investigated two factors thought to affect substantially invasion success: island area and the occurrence of predators.

A system of orb spiders in the central Bahamas includes several common species widely distributed among more than 100 islands (with <9000 m^2 of vegetated area) spanning an ≈20-km chain. Occurrence and abundance of these spiders show a strong and negative relation to the occurrence of lizards, a predator, but a somewhat weaker (and positive) relation to island area (*4*, *5*). All smaller (<100 m^2) islands lack lizards. We designed an invasion experiment that varied island area and predator occurrence, using a range of island areas known to be large enough to have spiders at least sometimes. We selected five islands from each of the three available types (Table 1): small islands without lizards, large islands without lizards, and large islands with lizards [all have the widespread lizard *Anolis sagrei* (*6*)]. All islands initially lacked the spider species to be introduced.

The manipulated species was *Metepeira datona*, one of the three most common orb spiders in the island chain. Adult female body lengths average 2.5 to 4.5 mm, and adult males average 2 to 3 mm. The species is weakly colonial (*7*). Adult females and often immature individuals construct a conspicuous retreat of debris suspended in the barrier portion of the web; adult males are often found in a separate retreat or in the same retreat as the female.

The experiment consisted of two phases: introduction of small propagules (three females and two males) (Phase 1) and subsequent (*8*) introduction of large propagules (nine females and six males) (Phase 2). Individuals to be introduced were collected in separate vials 1 to 2 days before from Staniel Cay, an island ≈3 × 1 km in the same chain. Only individuals known from pedipalps to be mature males, or judged from their size to be mature or penultimate females, were used. Individuals were randomized before introduction, with the constraint that a range of female sizes be included in each propagule. During the small-propagule phase, survival of introduced females was noted after 4 days, and the number of all individuals was counted after 4 months and 1 year. During the second, large-propagule phase, female survival was noted after 4 days (*9*), and the number of all individuals was counted (*10*) after 4 months, 1 year, and then annually up to 4 years (immediately after which, one island was used for another experiment in which spiders were removed and others introduced from Staniel). Although this experiment thus formally lasted a total of 5 years, we continued to census all islands through 1994 (12 years since small-propagule introduction) to determine the long-term fate of successful invasions. Only one natural colonization was observed during the latter 7 years (represented by one individual in 1994); this implies that natural dispersal of the subject species to the study islands was probably low during the experiment (see also below and Table 1).

We tested two hypotheses: (i) that invasion is more successful on large islands without lizards than with lizards—the predator effect—and (ii) that given an absence of lizards, invasion is more successful on large than on small islands—the area effect. Invasion success was measured in the short term as survival of introduced spiders and in the long term as population persistence and size.

After 4 days, more spiders survived on islands without than with lizards. Survival percentages were similar in both phases of introduction (Fig. 1). Of the females introduced onto islands with lizards, 27 to 36% survived, whereas 67 to 80% survived on small islands without lizards, and 73 to 80% survived on large islands without lizards. The first hypothesis was statistically confirmed ($P = 0.0006$), but the second was not ($P = 0.400$) (*11*, *12*). The effect of lizards on spiders has been shown elsewhere (*13*) to involve both predation and competition for food. Our observation here that differences in survival between islands with and without lizards were apparent at 4 days implicates predation, as spiders are unlikely to starve to death in so short a time (*14*).

Table 1. Number of individuals in populations of *M. datona*. Vegetated area of each island is shown in parentheses.

Islands	Phase 1		Phase 2*				
	4 months	1 year	4 months	1 year	2 years	3 years	4 years
Lizard islands (large)							
Ris Cay (3726 m^2)	0	0	0	0	0	0	0
Cran Cay (3224 m^2)	1	0	1	0	0	0	0
2nd Highest Cay (870 m^2)	0	0	3	0	0	0	0
Cay 313 (167 m^2)	0	0	4	0	0	0	0
Cay 315 (1189 m^2)	0	2	0	2	0	1	0
Large no-lizard islands							
Bul Cay (2016 m^2)	5	35	159	333	296	215	469
Yan Cay (344 m^2)	0	0	15	7	1	0	0
Longest Cay (301 m^2)	4	27	167	324	44	97	344
Cay 314 (197 m^2)	0	0	0	0	1	0	0
Dichotomous Cay (992 m^2)	1	0	14	243	138	100	251
Small no-lizard islands							
Cay 405 (44 m^2)	13	3	155	13	4	24	2
Cay 334 (51 m^2)	20	20	87	63	0	0	0
Cay 302 (11 m^2)	4	0	19	0	0	0	0
Cay 316 (17 m^2)	0	0	0	0	0	0	0
Cay 328 (27 m^2)	0	0	11	25	8	0	0

*Time designations for Phase 2 are since introduction of the second propagule. Total times since initiation of the whole experiment are obtained by adding 1 year to these times.

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Four months after the first introduction, with small propagules, population sizes had declined to zero on 4 of the 5 islands with lizards and on 4 of the 10 islands without lizards (Table 1). The most population expansion occurred on two of the small islands without lizards. By 1 year, one island with lizards (a different one than above) had spiders (probably this was a natural recolonization), and two large and two small islands without lizards had spiders. Population sizes of 20 or more existed on two large islands without lizards and on one small island. Four months after introduction of the second, larger propagule, populations existed on four of the five islands in each no-lizard class; two of each of these four were substantial (>50 individuals); in contrast, the three islands with lizards that had spiders after 4 months all had small populations (one to four individuals). Subsequent years saw populations on all islands with lizards decline to extinction. Temporal patterns on the two kinds of islands without lizards were different. Spiders on three large islands increased erratically to high numbers (251 to 469) of individuals at the experiment's end, whereas all small and two large islands failed to maintain substantial populations.

For each phase, we first evaluated long-term differences in population size (Fig. 2) statistically, using final numbers (*15*). No significant differences in final population size were found for Phase 1, but in Phase 2, large islands without lizards had larger final spider populations than did either large islands with lizards ($P = 0.006$, df = 1, 12) or small islands without lizards ($P = 0.008$). These values of P indicate significance at $\alpha = 0.05$ when a sequential Bonferroni test (*16*) is used to adjust for multiple comparisons. Secondly, the entire census series can be analyzed by repeated-measures procedures, but because only two census times are available for Phase 1, it is more important to concentrate on Phase 2, which has five available times. Although hypotheses about both area and predation effects had statistical support, the latter was more pronounced (means of the average number of individuals over the time series are: islands with lizards, 0.4; large islands without lizards, 128.8; and small islands without lizards, 16.4) and more statistically significant ($P = 0.005$ for comparison of the first and second island types, $P = 0.034$ for comparison of the second and third island types, df = 1, 12). Additionally, in univariate analysis, population sizes varied with time ($P = 0.003$, df = 4, 48), and the proportional difference between island types varied with time (island type–time interaction $P = 0.023$, df = 8, 48); a sequential Bonferroni test (*16*) with the above four P values gives significance for all at $\alpha = 0.05$ (*17*). When the latter result (island type–time interaction) is further analyzed with separate contrasts, the proportional difference between large and small islands without lizards varied notably with time ($P = 0.005$), but the proportional difference between large islands with and without lizards did not ($P = 0.523$). The former contrast gives some support to the observation that population size after 4 months tended to increase on large islands without lizards but tended to decrease on small islands without lizards. A similar analysis of the more restricted Phase 1 time series indicated no significant difference between island types nor significant overall time effect (*18*).

Our experiment showed that certain islands without lizards can support the spider M. *datona* for moderately long periods even though it was absent naturally; after 7 years, three large islands had very large populations (up to 469 individuals) and a remnant population (2 individuals) still existed on one small island. One large-island population and the remnant were extinct at the 8-year census. Hence, at least some large islands initially without M. *datona* were not intrinsically unsuitable over the moderately long term.

The experiment can be contrasted to a similar one with lizards at the same general locality, in which the majority of introductions were successful, including those with the same propagule size and sex ratio (*3*). Corresponding to this is the observation that natural extinction rates in the same system are much higher for spiders than for lizards (*5*, *19*), so that spider populations naturally occurring on an island at any given time are on average less likely to persist into the future.

In our study, incidence of predators is more important overall in determining invasion success than is island area. Conservation-directed studies appear to have devoted more effort to area (*20*) than predation (*21*); however, our results suggest a more balanced research strategy for investigation of invasions.

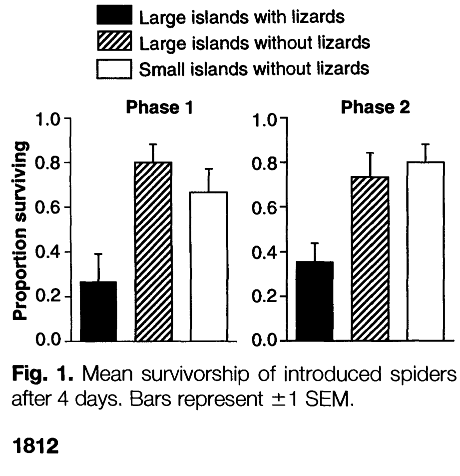

Fig. 1. Mean survivorship of introduced spiders after 4 days. Bars represent ±1 SEM.

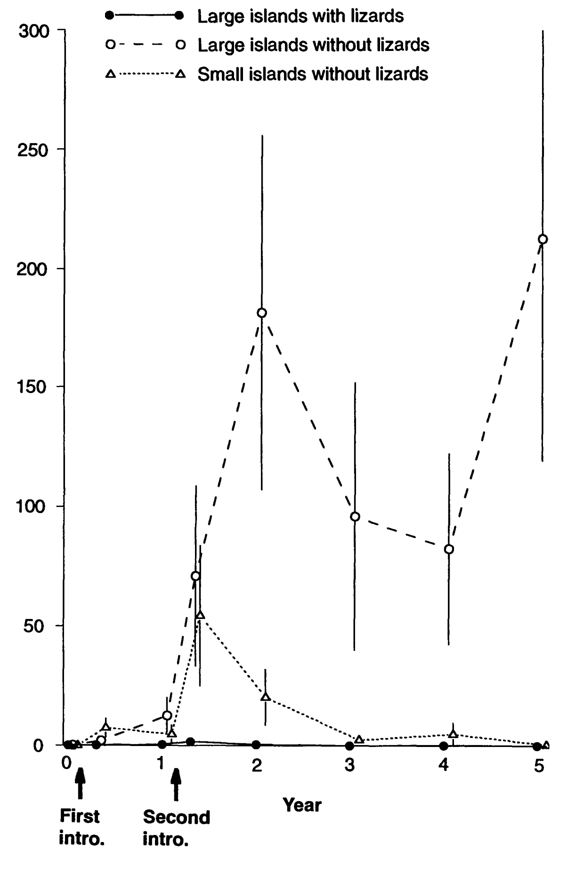

Fig. 2. Population size through time after experimental invasion. Symbols give means (n = five islands in each case); bars represent ±1 SEM.

Intriguingly, the time course of extinction varied in our study, depending on whether the agent was predator- or area-related. Spider populations on islands with predators never increased above initial (introduction) sizes. In contrast, among predator-free islands, spiders on small islands frequently showed rapid population growth initially, even sometimes outstripping growth on large islands (*22*). Nonetheless, all those populations eventually became extinct, in contrast to some on large islands which have now persisted for 12 years since the initial introduction. Given possible variation in both natural and human-induced immigration rates, such differences allow insight into the temporal dynamics of species preservation.

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2. K. L. Crowell, *Am. Nat.* **107**, 535 (1973); M. V. Lomolino, *ibid.* **123**, 468 (1984); T. Ebenhard, *J. Biogeogr.* **14**, 213 (1987).
3. T. W. Schoener and A. Schoener, *Nature* **302**, 332 (1983).
4. T. W. Schoener and C. A. Toft, *Science* **219**, 1353 (1983).
5. C. A. Toft and T. W. Schoener, *Oikos* **41**, 411 (1983); T. W. Schoener, in *Community Ecology*, J. Diamond and T. J. Case, Eds. (Harper and Row, New York, 1986), pp. 556–586.
6. Birds and other predators of spiders may be more common on islands with lizards, but removals (*13*) and introductions (*23*) of lizards implicate the latter as causal.
7. T. W. Schoener and C. A. Toft, *Behav. Ecol. Sociobiol.* **12**, 121 (1983); D. A. Spiller and T. W. Schoener, *J. Anim. Ecol.* **58**, 509 (1989).
8. In the second introduction, individuals were released at three closely adjacent sites in groups of five, one of which sites was the same as in the first introduction.
9. To assay survival, we first identified each resident female on the five islands still having them by tagging her web and noting her body size. After 4 days, when censusing for survival of introduced spiders, we did not include individuals in or near tagged webs that were the same size as the appropriate residents.
10. Introductions and yearly censuses were done in May or very late April, 1982 through 1987. Census methods were as described (*4, 5*).
11. P values are from contrasts (df = 1, 12) in repeated-measures analysis of variance (ANOVA), one-tailed tests. Frequencies were arcsine–square root transformed before analysis. Sequential Bonferroni tests (*16*) at $\alpha = 0.05$ were used to adjust for multiple comparisons; all P values given in the paper are raw (that is, uncorrected for multiple comparisons). Because propagule size and certain other conditions (*12*) were different for the two phases, separate analyses of survival were also done (contrast $P = 0.003$, 0.215 for the first and second hypothesis, respectively, for Phase 1; $P = 0.016$, >0.5, respectively, for Phase 2); the first hypothesis in each phase is significant with a sequential Bonferroni test. Nonetheless, in repeated measures, neither the phase ($P = 0.507$) nor phase-treatment ($P = 0.548$) source of variation was significant, causing rejection of hypotheses of survival differences associated with the two phases. All analyses in this paper were done with SAS software.
12. Although other explanations are possible, weak evidence exists that spiders apparently remaining from the first introduction had a positive effect: Islands with a large number (20 to 35) of already-established spiders had greater survivorship than did the other islands without lizards (mean survival frequencies 0.93 versus 0.70; equal variances $t = 1.92$, two-tailed test, $P = 0.091$).
13. T. W. Schoener and D. A. Spiller, *Science* **236**, 949 (1987); D. A. Spiller and T. W. Schoener, *Ecol. Monogr.* **58**, 57 (1988); *Oecologia* **83**, 150 (1990); *Ecology* **75**, 182 (1994).
14. A. L. Turnbull, *Annu. Rev. Entomol.* **18**, 305 (1973).
15. All population sizes were log(x + 1)-transformed before analysis. Contrasts used one-tailed tests.
16. W. R. Rice, *Evolution* **43**, 223 (1989).
17. Mauchly's Sphericity Test is not significant ($P = 0.137$), allowing acceptance of sphericity, so we report unadjusted P values [as recommended in R. J. Freund, R. C. Littell, P. C. Spector, *SAS system for Linear Models* (SAS Institute, Cary, NC, 1986); our design, in which time is the repeated factor, follows the example in this source (see chapter 6)]. The Huynh-Feldt (H-F) Epsilon is very high (0.961), and the H-F adjusted probabilities are very close to those we report. Multivariate repeated-measures evaluations (Wilks') are not significant [in the order given in text, $P = 0.230$ (df = 4, 9), $P = 0.376$ (df = 8, 18), $P = 0.158$ (df = 4, 9) and $P = 0.600$ (df = 4, 9)], but for our design the multivariate procedure has statistical power below that recommended, and assuming sphericity allows one to use the univariate results [J. Stevens, *Applied Multivariate Statistics for the Social Sciences* (Erlbaum, Hillsdale, NJ, ed. 2, 1992)]. Unequal variances of the treatments implies that these ANOVAs should be interpreted cautiously. With the use of the means of the five census times, separate F-tests lead to the conclusion that variances of the two large-island types are unequal, whereas those of the two no-lizard types are not. The appropriate separate t tests give $P = 0.025$ and $P = 0.071$, respectively, for the two contrasts.
18. However, the interaction between time and the contrast of large versus small islands without lizards has raw $P = 0.063$. Univariate and multivariate repeated-measures analyses are identical here.
19. T. W. Schoener, *Oikos* **41**, 372 (1983); T. W. Schoener and D. A. Spiller, *Nature* **330**, 474 (1987).
20. T. E. Lovejoy and D. C. Oren, in *Forest Dynamics in Man-Dominated Landscapes*, R. L. Burgess and D. M. Sharp, Eds. (Springer-Verlag, New York, 1981), pp. 8–12; G. R. Robinson and J. F. Quinn, in *Applied Population Biology*, S. K. Jain and L. W. Botsford, Eds. (Kluwer Academic, Norwell, MA, 1992), pp. 223–248.
21. However, a moderate number of nonexperimental studies of the effect of predators on invasion success exist [for example, R. D. Goeden and S. M. Louda, *Annu. Rev. Entomol.* **21**, 325 (1976); D. Simberloff, in *Ecology of Biological Invasions of North America and Hawaii*, H. A. Mooney and J. A. Drake, Eds. (Springer-Verlag, New York, 1986)]. The first reference underscores the paucity of experimental studies and calls for the sort of investigation done here.
22. This could be positive density dependence, given the smaller potential area for mate location on smaller islands. Possible factors causing small-island populations eventually to become extinct include severe storms, drought, depletion by spiders of their own prey organisms, and emigration, as well as demographic stochasticity characterizing small populations.
23. T. W. Schoener and D. A. Spiller, in preparation.

24. We thank E. Temeles and C. Toft for field assistance and NSF for support.

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Demonstration of Positionally Disordered Water Within a Protein Hydrophobic Cavity by NMR

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The presence and location of water of hydration (that is, bound water) in the solution structure of human interleukin-1β (hIL-1β) was investigated with water-selective two-dimensional heteronuclear magnetic resonance spectroscopy. It is shown here that in addition to water at the surface of the protein and ordered internal water molecules involved in bridging hydrogen bonds, positionally disordered water is present within a large, naturally occurring hydrophobic cavity located at the center of the molecule. These water molecules of hydration have residency times in the range of 1 to 2 nanoseconds to 100 to 200 microseconds and can be readily detected by nuclear magnetic resonance (NMR). Thus, large hydrophobic cavities in proteins may not be truly empty, as analysis of crystal structures appears to show, but may contain mobile water molecules that are crystallographically invisible but detectable by NMR.

Water of hydration (that is, bound water) has long been known to play an important structural and functional role in proteins (*1*). In particular, buried water molecules may stabilize protein structure by acting as bridges between protein hydrogen bond donors and acceptors, whereas surface water molecules located at the active site participate in catalysis and ligand recognition. Experimentally, bound water can be detected either in the crystal state by x-ray and neutron diffraction or in solution by NMR spectroscopy. Only positionally ordered water molecules can be detected in crystal structures, as the observed electron density represents a linear superposition of all the atomic positions during the course of the experiment (which typically lasts many hours). Thus, the detection of a water molecule at a given location in the crystal structure, although independent of its residency time, requires that the potential of mean force at this point has a well-defined

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