

Life-History Models of Extinction: A Test with Island Spiders

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ABSTRACT: This study analyzes extinction patterns for two species of orb spiders monitored annually on 77 islands over a continuous 20-yr period. One species, *Argiope argentata*, has large populations sometimes crashing quickly to extinction and a much weaker relation of extinction likelihood to population size than does the other species, *Metepeira datona*. Demographic models were built for both species and matched against observations. Differences between the species in life-history traits—estimated with measurements from the field—together with incorporation of demographic stochasticity, a population ceiling, and environmental stochasticity, were necessary to fit the observed extinction curves. As predicted from life-history patterns, long-term population growth rates (and hence predicted extinction probabilities) are relatively very sensitive to values of juvenile survivorship. Models are also sensitive to variation in the population ceiling and environmental noise, which tend to act in a complementary manner. A simple model with no age structure was able to fit the data on large initial population sizes but not on small initial population sizes, showing that life cycle characteristics interact with the various sources of stochasticity and hence have to be taken into account to produce a precise model of the extinction process.

Keywords: extinction models, spiders, islands, demographic stochasticity, environmental stochasticity, life histories.

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Along with the ever-increasing need for conservation, the study of population persistence and extinction is becoming the subject of much interest (Soulé 1987; Simberloff 1988; Caughley 1994; Belovsky et al. 1999; Holsinger 2000; Vucetich et al. 2000). The simplifications that understandably characterized early models of the extinction process may have resulted in failure to capture some of its essential features.

First, most extinction models ignored population structure, simply using as the dependent variable numbers of individuals (or females) in a population regardless of age or other factors. Recently, however, it has become clear that extinction models incorporating the essential features of a species life history (Caswell 1989; Ferrière et al. 1996; Mills et al. 1996; Legendre et al. 1999; Caswell 2000) have the potential to achieve a major advance. In particular, the number and nature of developmental stages and how stochastic and deterministic factors might vary with those stages may be crucial in unraveling interspecific differences in extinction patterns.

Second, many models excluded one or more fundamental properties of real populations. The first of these, demographic stochasticity, is inherent to the birth and death process itself: chance events might lead all members of a population to die before giving birth. The process is important for small population sizes (e.g., MacArthur 1972; Goel and Richter-Dyn 1974; Pimm et al. 1988), and a model including only demographic stochasticity demonstrated that persistence time increases roughly exponentially as a function of the carrying capacity (Lande 1993). The second property, environmental stochasticity, reflects the fact that the environment is changing over time and that individuals are not equally fitted to all environmental variations. This kind of stochasticity translates into vital rates changing over environments. Two subdivisions of environmental stochasticity are distinguished (Schaffer 1987): small-to-moderate perturbations that continuously arise and large perturbations (often called catastrophes) that are episodic and dramatically reduce population size. At moderate-to-large population sizes, both sorts of environmental stochasticity are more important than demographic stochasticity, since persistence time under environmental stochasticity increases only as a power function of the carrying capacity (Lande 1993). The effect of en-

environmental stochasticity depends on the magnitude of its variability (Pimm et al. 1988; Vucetich et al. 2000), on the shape of its variability (Ludwig 1996), on the temporal autocorrelation (Foley 1997), and, for catastrophes, on the magnitude and frequency of such events (Lande 1993). Finally, the necessity of a population ceiling or other form of density dependence has not often been assessed in the full context of population structure and kinds of stochastic extinction.

The respective importance of population ceilings, environmental stochasticity, and demographic stochasticity in determining extinction patterns in theory has been debated (Pimm et al. 1988; Schoener and Spiller 1992; Lande 1993; Mangel and Tier 1993, 1994; Vucetich et al. 2000). For example, environmental stochasticity is predicted to explain much population-size variation when populations are medium to large (Holsinger 2000), and extinction rates are predicted to be strongly and positively related to environmental variance (Vucetich et al. 2000; but see Belovsky et al. 1999). Without a ceiling, populations with a positive rate of increase might often be expected to reach huge sizes at which they are safe from all but catastrophic extinction (Goel and Richter-Dyn 1974). In the same way, just as demographic stochasticity alone cannot account for extinction of large populations, its action is required when environmental stochasticity and a population ceiling reduce numbers to small sizes (Foley 1997). Then, it is most likely that a combination of the three factors has to be involved. To determine to what extent this is true as well as to investigate the role of life-history structure, we analyzed appropriate population-size data for each of two spider species drawn from censuses of 108 islands with mostly 20-yr, continuous time series.

First, for the spider data we asked, can any one or pairwise combination of demographic stochasticity, environmental stochasticity, and a population ceiling satisfactorily explain the empirical extinction curves, or are all three factors necessary? These three elements may not be equally conspicuous in the spider system. While demographic stochasticity is an internal necessity, the others are in part properties of the environmental situation. Environmental stochasticity in the form of storms, drought, and other chronic variation is quite conspicuous (Spiller and Schoener 1988, 1995, 1996; Schoener and Spiller 1999). Extreme environmental catastrophes are not, however, reflected in our data; while devastating hurricanes impacted areas at or near our study site (Spiller et al. 1998; Schoener et al. 2001), no such event occurred during the 20-yr period over which the data used here were collected. A population ceiling may be produced by density-dependent factors such as competition and predation. Although we did not test for intraspecific competition, a field experiment failed to detect interspecific competition between the orb spiders

in this study (Spiller and Schoener 2001); this is consistent with most other field experiments on orb spiders (review in Wise 1993). The lack of competition in orb spiders may be partially explained by the foraging mode of the species (Wise 1993); spider densities need to be very high to cause competition for food. Cannibalism was found to be a density-dependent limiting factor in cursorial and burrowing wolf spiders (Wagner and Wise 1996; Moya-Laraño et al. 2002), and interference (including intraguild predation) may often be an important limiting factor for cursorial spider species in structurally simple ecosystems (review in Marshall and Rypstra 1999), but such interactions may be less important for sedentary orb spiders. However, predation by lizards was repeatedly shown to be a major limiting factor for the subject species (Schoener

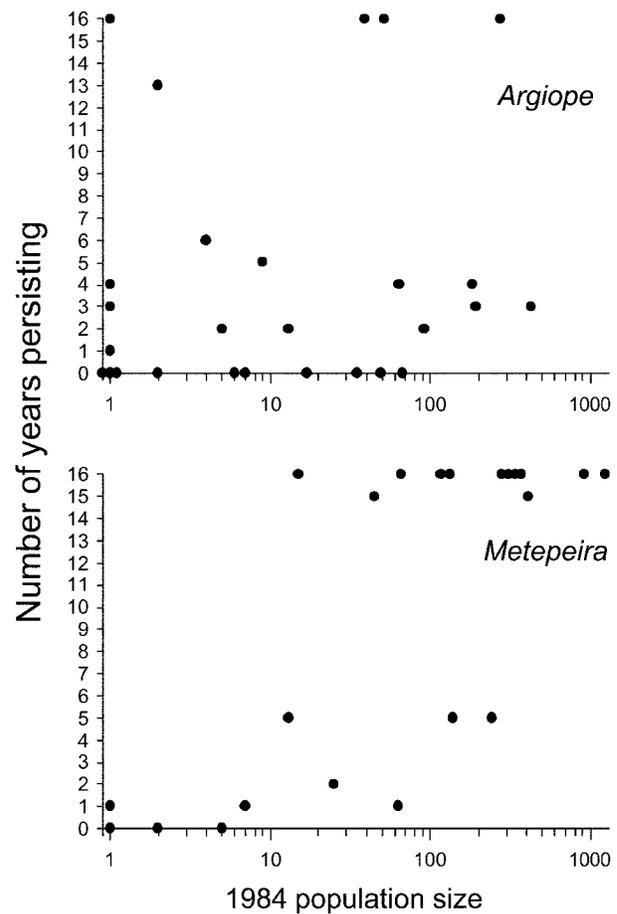


Figure 1: Extinction patterns in *Metepeira datona* and *Argiopo argentata*. The number of years of continuous persistence (censuses done annually each spring) are plotted against the initial population size, in this case, that recorded in 1984. Note that *Metepeira* has a more regular relationship and that large populations can rather frequently become extinct in *Argiopo*.

and Spiller 1999), and this interaction may be stronger in wet years, when spider densities are relatively high, than in dry years (Spiller and Schoener 1995, 1996). Although islands with lizards are not included in this study, the effect of other predators, such as birds, wasps, and other predatory arthropods, may also be density dependent. We have observed wasps attacking the subject species on small islands with high spider densities. Hence, when spiders become very dense, they may begin to attract wasps foraging in the general vicinity of the island; the higher the spider density, the more wasps they attract. This would produce a ceiling effect analogous to the one used in the present model. Indeed, our successful experimental introductions of *Metepeira* on large islands (Schoener and Spiller 1995) produced a rapid growth phase and then a (much fluctuating) leveling-off period.

Second, we wished to determine how the differing life histories of the common species might affect extinction patterns. *Metepeira datona* is a small-bodied species that has a relatively low extinction rate overall, with a high average standing population size over time and a relatively low coefficient of variation of population size over time (Schoener and Spiller 1992). In contrast, *Argiope argentata* is a large-bodied species that shows a relatively high extinction rate overall, with a moderate average population size and a relatively high temporal coefficient of variation. Most striking is the difference between the two species in persistence (= nonextinction) as a function of initial population size (fig. 1): while *Metepeira* shows a fairly strong such relation (Pearson's $r = 0.51$, $P = .015$), *Argiope* shows almost no relation ($r = 0.16$, $P = .43$); these differences are especially dramatic for large initial population sizes, which are much more likely to crash to extinction in *Argiope* than in *Metepeira*. The species were observed on the same set of islands and over the same time period, so the species differences just described cannot result from differences in habitat or weather conditions. The two spider species do, however, vary in life history: they differ substantially in fecundity (*Argiope's* is much higher) and developmental time (2 mo for *Metepeira* and 4 mo for *Argiope*), and they differ moderately in survivorship (*Metepeira* juvenile survival appears higher; *Argiope* adult survival is higher).

In short, our goals were to see whether we could predict the observed patterns of extinction reasonably closely and, if so, to determine what sources of stochasticity and levels of complexity in the life cycle needed to be incorporated to achieve this target. While thus emphasizing precision, which is especially important for conservation purposes, we do explore various ways to simplify such models in order to achieve greater understanding.

Methods

Sites, Species, and Census Procedures

Study islands were located in the central Bahamas, all within 20 km of Staniel Cay, Exumas. Islands ranged in vegetated area from 1 to 5,444 m² and were roughly log-uniformly distributed within this areal range (Schoener 1991). Individuals of the two species were located mainly in their webs but were counted wherever they occurred. While males in particular might not be in webs a substantial proportion of the time, most females and juveniles would be expected to be there, given that this is how they obtain food. Hence, our data are especially accurate for adult females and immatures (including females), making the female-based life cycle models approach particularly suitable. Recounts of the same islands a few days apart gave little difference (census details in Schoener and Spiller 1992).

Censuses were conducted at the same time of year (late April–May, the end of the dry season) annually from 1981 (or 1982) through 2000. Spiders censused frequently on a very large island had variation between years at this time less or no greater than between-year variation during other months (Schoener and Spiller 1992).

Metepeira datona adult females average 2.5–4.5 mm. *Argiope argentata* adult females average 20–25 mm. The larger size of *Argiope* than *Metepeira* is associated with at least two life-history features: the former has a much longer developmental time and a larger clutch size. The somewhat greater survivorship in adult *Argiope* may also be related to its larger size.

Simple Demographic Model

The main features of the age-structured models contained in the next section are first presented using a simple model with no age structure. This simple model was in fact built from the age-structured one and is used to see how deletion of age structure affects extinction likelihood. The simple model has a single equation describing change in population size n from one time step to the next:

$$n' = \lambda n. \quad (1)$$

In one of the species for which we have data, there is an approximately 2-wk period between clutches, and eggs hatch in a 2-wk period as well. Other developmental transitions occur in multiples of 14 d in both species. Hence, we selected a 14-d period as the time step: it is the largest time interval compatible with the estimated life cycle transitions in both species. The growth rate λ in equation (1) is computed from the life cycle of each species as embodied in the age-structured models. Indeed, λ cannot be esti-

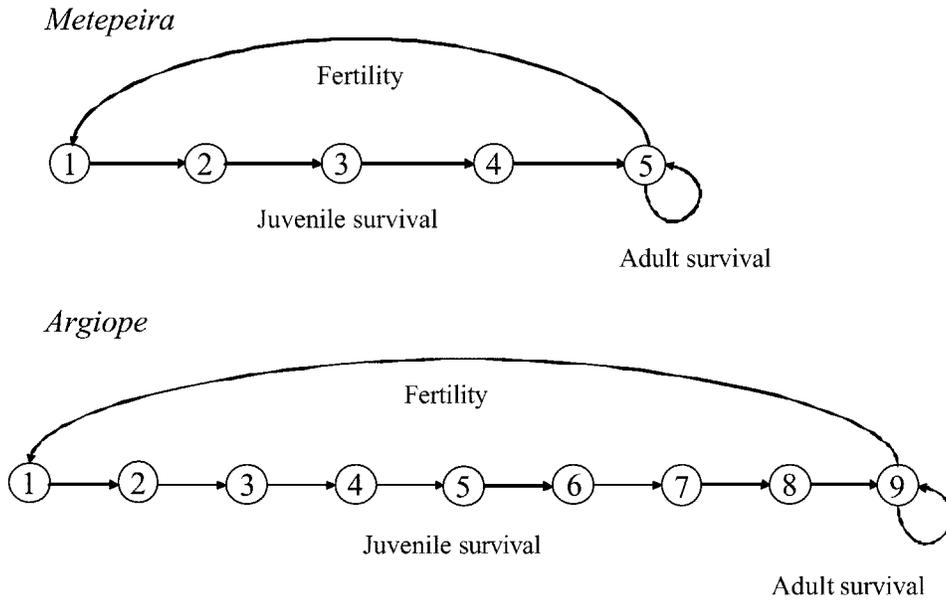


Figure 2: Life cycle graphs for *Metepeira* and *Argiope*

mated from the yearly population counts: such trajectories erratically fluctuate around some long-term value as determined by stochastic and other factors, rather than allowing potential growth rate to be measured as from an expanding population (see “Life Cycles” in “Results”).

To account for environmental stochasticity, relation (1) is modified:

$$n' = \lambda_c n, \tag{2}$$

with λ_c drawn from a normal distribution with mean λ and standard deviation θ (the distribution is truncated to ensure nonnegative values). To account for demographic stochasticity, the number of individuals at the next time step is computed by summing n samples of the Poisson distribution:

$$n' = \text{Poisson}(n, \lambda_c). \tag{3}$$

A population ceiling Ω is introduced as follows:

$$n' = \text{Poisson}(n_d, \lambda_c), \tag{4}$$

with

$$n_d = \text{if } n > \Omega \text{ then } \frac{\Omega^2}{n} \text{ else } n. \tag{5}$$

Equation (5) means that as soon as population size n goes above the ceiling Ω , it is set equal at the next time step to

Ω (the equilibrium value of n) times the proportional overshoot Ω/n .

Age-Structured Models

Life Cycles. Female-based life cycles (Caswell 1989, 2000) were constructed for *Metepeira* and *Argiope* on a 14-d time step basis. There were four juvenile age classes for *Metepeira* and eight juvenile age classes for *Argiope* as well as one adult class for each species (fig. 2). The number of juvenile age classes is determined by the estimated length of the developmental period (table 1; number = developmental time/14); it is not the actual number of juvenile instars. We mainly describe the model for *Metepeira*, with the model for *Argiope* being similar. Models were analyzed using the ULM software (Legendre and Clobert 1995; Ferrière et al. 1996).

Recursion relations from one time step to the next (time step = 14 d, n_i = number of individuals in the i th age class) were

$$n'_1 = s_0 \sigma \alpha f n_5, \tag{6}$$

$$n'_2 = s n_1, \tag{7}$$

$$n'_3 = s n_2, \tag{8}$$

$$n'_4 = s n_3, \tag{9}$$

$$n'_5 = s n_4 + v n_5. \tag{10}$$

Table 1: Life-history and demographic features on a 14-d basis

	<i>Metepeira</i>	<i>Argiope</i>
Population vector N	$[n_1, n_2, n_3, n_4, n_5]$	$[n_1, n_2, n_3, n_4, n_5, n_6, n_7, n_8, n_9]$
Egg survival s_0	.9 ^a	.9 ^a
Juvenile survival s	.59 ^a	.45
Adult survival v	.59	.78
Fecundity f	31	1,256
Probability of mating α	.8 ^a	.8 ^a
Primary sex ratio s	.5	.5
SD for environmental stochasticity δ	.26 ^b	.18 ^b
Population ceiling C	5–60 ^b	5–11 ^b
Growth rate λ^c	1.21	1.11
Generation time \bar{T}^c	5.9 (83 d)	11.4 (160 d)
Stable age distribution % ^c	[51 25 12 6 6]	[59 24 10 4 3 ^d]
Reproductive value % ^c	[3 6 12 26 53]	[3 ^e 4 10 24 59]

Note: Developmental time is 2 mo in *Metepeira* and 4 mo in *Argiope*.

^a Assumed values.

^b Adjusted values.

^c Computed from above parameters.

^d Total of last five age classes.

^e Total of first five age classes.

The first relation corresponded to hatchlings, with f the fecundity, σ the primary female sex ratio (proportion of females at birth), α the probability of a female being mated, and s_0 the egg survival. Relations (7)–(9) corresponded to juveniles, with s the juvenile survival rate, and relation (10) corresponded to adults, with v the adult survival rate. Demographic parameters are listed in table 1; their measurement is detailed below.

$$n'_1 = \text{Binom}[\text{Poisson}(m_5, f), s_0\sigma], \text{ with}$$

$$m_5 = \text{Binom}(n_5, \alpha), \tag{12}$$

$$n'_2 = \text{Binom}(n_1, s), \tag{13}$$

$$n'_3 = \text{Binom}(n_2, s), \tag{14}$$

$$n'_4 = \text{Binom}(n_3, s), \tag{15}$$

$$n'_5 = \text{Binom}(n_4, s) + \text{Binom}(n_5, v). \tag{16}$$

Environmental Stochasticity. Environmental stochasticity (Tuljapurkar 1990) was modeled by randomizing juvenile and adult survival rates around their mean values. We used (a variation of) the beta distribution with standard deviation δ , δ measuring the strength of environmental noise. The beta distribution has the advantage of being constrained between 0 and 1 and is therefore suitable for survival rates. For example, the stochastic juvenile survival rate was

$$s_e = \text{Beta}(s, \delta). \tag{11}$$

Demographic parameters α (probability of mating), f (fecundity), and s_0 (egg survival) were not randomized because they did not influence the dynamics significantly (see “Results”).

Demographic Stochasticity. Demographic stochasticity was modeled by building a branching process on the relations (6)–(10):

The notation $x = \text{Poisson}(n, f)$ means that the number of eggs x was computed as the sum of n samples of the Poisson distribution with mean the fecundity f , while $n' = \text{Binom}(n, s)$ means that the number n' of survivors was computed as the sum of n samples of the Bernoulli distribution with mean the survival rate s .

Population Ceiling. We used a population ceiling C acting on the last two age classes by elaborating equation (5). If the number $m = n_4 + n_5$ of individuals in those classes was above the ceiling at some time step, the reduction at the next time step was in proportion to C/m as follows. We distributed the number in age classes 4 and 5 proportionately to the number of individuals contributing to those classes. Since n_4 depends on the value n_3 at the previous time step while n_5 depends on n_4 and n_5 at the previous time step, we used the following formulas:

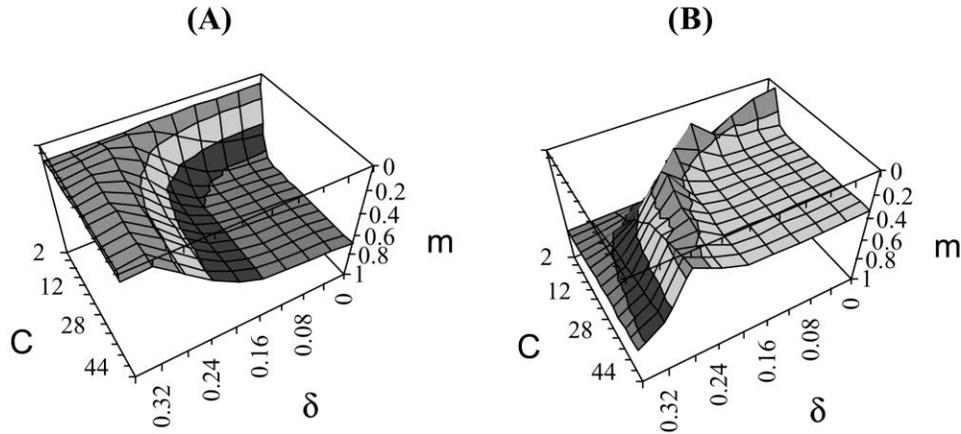


Figure 3: Fit m of simulated probability of extinction (P_e^{sim}) to observed probability of extinction (P_e^{obs}) for *Metepeira* as a function of population ceiling (C) and environmental stochasticity (standard deviation δ) under demographic stochasticity. The fit is computed as $m = \{(1/D) \sum_{i=1}^D [P_e^{\text{obs}}(i) - P_e^{\text{sim}}(i)]^2\}^{1/2}$ over D years of observation. A, Observation: one individual; initial population vector $N(0) = (0, 0, 0, 0, 1)$; $D = 13$ yr. B, Observation: 21–50 individuals; initial population vector $N(0) = (32, 16, 8, 4, 4)$; $D = 19$ yr.

$$n_{4d} = \frac{C}{m} \frac{n_3 C}{n_3 + m}, \tag{17}$$

$$n_{5d} = \frac{C}{m} \frac{mC}{n_3 + m}. \tag{18}$$

These numbers were rounded to their nearest integer values. Relations (12)–(16) become

$$n'_4 = \text{if } n_4 + n_5 > C \text{ then } n_{4d} \text{ else Binom}(n_3, s), \tag{19}$$

$$n'_5 = \text{if } n_4 + n_5 > C \text{ then } n_{5d} \text{ else Binom}(n_4, s) + \text{Binom}(n_5, v). \tag{20}$$

Immigration-Emigration. We assumed that most immigrants arrived via aerial dispersal (ballooning). The vast majority of ballooning spiders are between 0.2 and 1.0 mg (Greenstone et al. 1987), which is about the range of the first stage for both species in our study. Immigration with rate p was modeled by randomly adding one individual to age class 2 at each time step with probability p (Bernoulli sample with mean p). Emigration with rate q was modeled by reducing survival rate to age class 2 by $1 - q$. Thus, immigration was independent of population size, while emigration depended on the number of juveniles in age class 1. Relation (13) became

$$n'_2 = \text{Binom}[n_1, (1 - q)s] + \text{Ber}(p). \tag{21}$$

These parameters were only included in one set of simulations and, as we shall see, have the same effect as en-

vironmental stochasticity, so we did not explore them further.

Parameters Estimates and Fitting the Models

Age-structured models were constructed for both species by building recursion relations from the life cycle. Only two parameters were left free for each species: the population ceiling C and the environmental noise standard deviation δ (immigration-emigration was assimilated into environmental noise). To adjust C and δ , we computed the root mean squared difference between observed and predicted probability of extinction: figures 3 (for *Metepeira*) and 4 (for *Argiope*) present two cases with different initial population-size intervals. In those figures, the value of the fit is plotted as a surface that is a function of the adjusted parameters C and δ . A set of pairs (C, δ) —the ridges in figures 3 and 4—gives the best fit. The fit is such that C can be considered as an increasing function of δ . Therefore, C and δ were adjusted for each species in the following way. First, C was determined for the largest initial population-size interval so as to fit the corresponding extinction curve within the constraint that the corresponding simulated population size not exceed the approximate largest population size observed on the islands (note that by definition [see “Age-Structured Models”], C includes the last two age classes only). In this case ($C = 60$ for *Metepeira*, $C = 11$ for *Argiope*), fitted surfaces (figs. 3B, 4C) show that δ is constrained in a small range because the best fit ridge is almost parallel to the C -axis, the ridge having steep slopes. Then δ was fixed in a given species using the value for this largest population-size interval

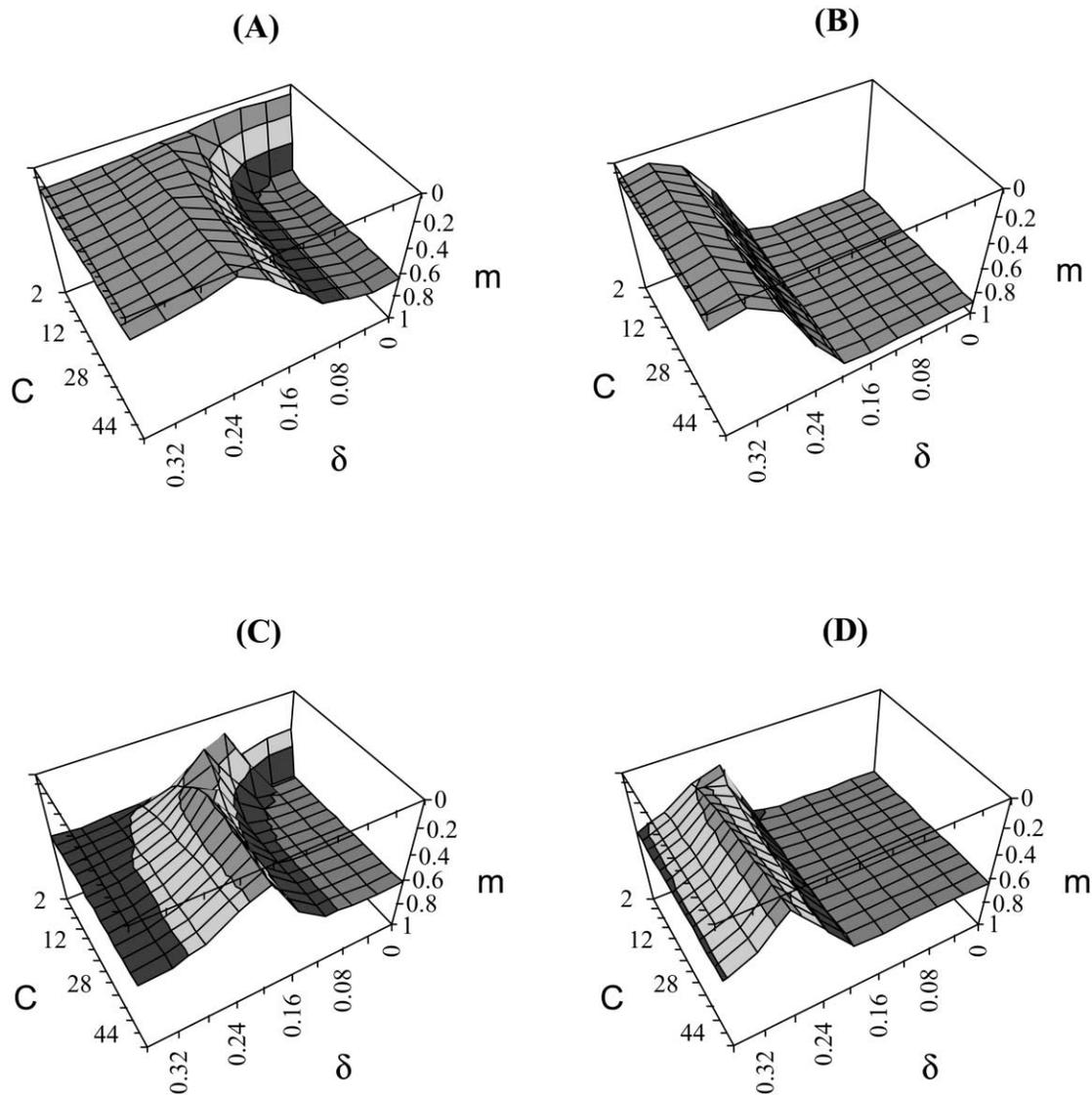


Figure 4: Fit of simulated probability of extinction to observed probability of extinction for *Argiope* as a function of the population ceiling (C) and environmental stochasticity (δ ; see legend of fig. 3). A, Observation: one individual; initial population vector $N(0) = (0, 0, 0, 0, 0, 0, 0, 0, 1)$; $D = 18$ yr. B, As in A but without demographic stochasticity. In this case, the fit requires a large δ and is almost independent of C . C, Observation: 21–50 individuals; initial population vector $N(0) = (0, 0, 0, 0, 16, 8, 4, 2, 2)$; $D = 18$ yr. D, As in C but without demographic stochasticity.

($\delta = 0.26$ for *Metepeira*, $\delta = 0.18$ for *Argiope*). Finally, the best C fitting the extinction curves was determined separately for each smaller initial population-size interval.

The simple model was fit using the same procedure as for the age-structured models; the growth rate λ was computed from the life cycle separately for each species (see “Results”). This resulted in environmental noise standard deviations of $\theta = 0.34$ and $\theta = 0.37$ for *Metepeira* and *Argiope*, respectively.

The values found for environmental noise standard de-

viations δ and θ are about 0.3 times the average parameter value, as commonly used when exploring environmental stochasticity (Mills et al. 1996).

The other parameters were not fitted in any way but were all estimated from biological considerations, including field data from the islands on which we measured extinction, as follows.

Survival and Developmental Time. For *Argiope*, we measured survival of cohorts of marked adults inhabiting

lizard-free islands. Four such cohorts (one to 22 individuals) were followed for periods spanning ~1.5 mo. Additionally, we followed two cohorts (four to 65 individuals) of hatchling *Argiope* deliberately introduced onto a single island for 1–1.5 mo. Developmental period was estimated as the length of time the average individual grew from hatchling to adult size.

We determined adult-female *Metepeira* survival using three sets of data from lizard-free islands. First, we followed introduced colonists (four to 10 individuals) on a single island for 15 d. Second, we used data from a previous introduction experiment on 10 islands at the same study site that were followed for 14 d (Schoener and Spiller 1995). Third, we measured survival over an 8-d period in enclosures on the main island of Staniel Cay from which lizards had been removed (Spiller and Schoener 1988). We combined those three sources of data by weighting estimates by the number of islands or plots used for the measurements. We assumed that survival in *Metepeira* juveniles, whose webs were often attached to those of adults, was the same as adult survival. Developmental period was estimated from a cohort deliberately introduced onto an island as the length of time the average individual grew from hatchling to adult size.

Table 1 gives the averages for both species.

Fecundity. The number of eggs per clutch were counted from nine clutches for *Metepeira* and two clutches for *Argiope* collected on Staniel Cay: these equal ($\bar{X} \pm 1$ SD) 30.7 ± 0.8 and $1,256.0 \pm 575.6$, respectively. During a previous study, daily observations revealed that adult female *Metepeira* under natural conditions produced one clutch about every 13 d (Spiller and Schoener 1990); we assumed a 2-wk interval between clutches for both species.

Parameters Determining Juvenile Numbers in the First Stage. The number of new juveniles produced at the first time step (eq. [1]) is equal to the product of five quantities: number of adult females, probability of mating, fecundity, egg survival, and primary sex ratio. Information on three of these quantities, which appear in the model only in equation (1), is nearly nonexistent for the species in question. From casual observation, we estimate egg survival as 0.9 and the probability of mating as 0.8. The primary sex ratio is estimated as 0.5 because the only data of which we are aware for spiders (Deevey 1949) have this value.

Determination of Extinction Probabilities as a Function of Initial Population Sizes

We included only populations from islands without lizards, since use of survival parameters from plots with lizards in the model for *Metepeira* gives a negative rate of deter-

ministic population growth. We had available to us 43 nonzero time series for *Metepeira* and 55 for *Argiope*, each lasting 19–20 yr and consisting of yearly counts.

Observed probabilities of extinction were classified according to similar initial population sizes. We used the following intervals: 1, 2–3, 3–5, 6–10, 11–20, 21–50, 51+ individuals. We computed extinction probabilities in two ways. In both ways, for each interval, the cumulative probability of extinction was computed from the number of observations falling within the interval that were followed by a zero: this corresponds to the number of populations going extinct whose initial number falls within the interval. In the first way, each population number was considered as an independent initial population size. In the second way, we used only population numbers preceded by zero as initial population sizes. Both ways appeared to give similar results, the reason most probably being that during a year at least three cohorts occur, rendering yearly counts basically independent. We used only the first way because of the much larger sample sizes it provided (table A1 in the online edition of the *American Naturalist*).

The ranges of initial population sizes were also corrected for the fact that males and females were actually counted in the field, while our model includes only females. Data from 1989, 1991, and 1997 showed that approximately 68% of *Argiope* and approximately 75% of *Metepeira* were females (note that very small individuals cannot be sexed). We therefore assumed 70% females in counts for both species. Thus, for example, the model range of 3–5 individuals corresponded to about 4–6 counted individuals (males and females) in the field.

To account for the fact that only a fraction of very young juveniles can actually be counted in the field and that we deliberately did not include hatchling numbers in our counts (see “Sites, Species, and Census Procedures”), the model number of observed individuals was counted as

$$n_{\text{obs}} = \left[\frac{n_1}{2} + n_2 + n_3 + n_4 \right] \sqrt{s} + n_5 \quad (22)$$

for *Metepeira* and

$$n_{\text{obs}} = \left[\frac{n_1}{4} + \frac{n_2}{2} + n_3 + n_4 + n_5 + n_6 + n_7 + n_8 \right] \times \sqrt{s} + n_9 \quad (23)$$

for *Argiope*. In these formulas, the number of juveniles is reduced, and the factor $s^{1/2}$ is introduced to correct for the fact that the model assumes mortality (or emigration) at the end of a time step, whereas observations occur at any time continuously throughout the time step.

Table 2: Sensitivities (S_x) and elasticities (E_x) of growth rate λ to changes in values of demographic parameters (x) for *Metepeira* and *Argiope*

	<i>Metepeira</i>			<i>Argiope</i>		
	x	S_x	E_x	x	S_x	E_x
Egg survival s_0	.9	.23	.17	.9	.11	.09
Juvenile survival s	.59	<u>1.38</u>	<u>.67</u>	.45	<u>1.74</u>	<u>.70</u>
Adult survival v	.59	.33	.16	.78	.29	.21
Fecundity f	31	.007	.17	1,256	.00008	.09
Probability of mating α	.8	.26	.17	.8	.12	.09
Primary sex ratio σ	.5	.41	.17	.5	.20	.09

Note: Underlined values are the largest for a given species.

Results

Life Cycles

For *Metepeira*, the long-term growth rate λ was 1.21. Such a large growth rate (21% increase in 14 d) was observed on samples of expanding populations from small numbers of individuals experimentally introduced to small islands (Schoener and Spiller 1995). For *Argiope*, λ was 1.11 (11% increase in 14 d). These values of λ were used in the simple models (eq. [1]).

For both species, juvenile survival s was by far the most sensitive parameter, the one whose fluctuations impact the long-term growth rate the most. Table 2 illustrates this for demographic parameters using sensitivity and elasticity; the former measures arithmetic and the latter proportional (multiplicative) changes in λ as a function of changes in the parameter. Sensitivity to juvenile survival is typical of short-lived species (Lebreton and Clobert 1991).

For both species, the age structure included only a small proportion of adults, while reproductive value was concentrated in the last three age classes, with more than 50% in the adults (table 1).

Comparing Observed with Expected Extinction Probabilities

Figures 5–7 are plots of the fraction of populations becoming extinct as a function of time; they are thus cumulative probability distributions for extinction. Initial population distributions were chosen close to the stable age distribution, giving more weight to the later age classes (which are more likely to be observed). Each theoretical curve was computed from 1,000 Monte Carlo–simulated population trajectories. The number of observed individuals was computed from the number of simulated individuals using equations (22) and (23). For example, in figure 6D, the simulated initial population size is $32 + 16 + 8 + 4 + 4 = 64$, and by equation (22), this corresponds to 37 observed individuals, thereby falling within the range 21–50.

The complex models and data of figures 6 and 7 allow the following general conclusions.

1. The complex models fit the positions of the extinction curves for the two species quite well; that is, large *Argiope* populations have a higher extinction likelihood than do large *Metepeira* populations (cf. fig. 6D, 6E with fig. 7E, 7F), whereas small *Argiope* and *Metepeira* populations show less difference in extinction likelihood (cf. fig. 6A, 6B with fig. 7A, 7B). Differences between the species in the simulations come from differences in life-history traits, difference in adult carrying capacity range ($C = 5–60$ for *Metepeira* vs. $C = 5–11$ for *Argiope*), and difference in environmental noise intensity ($\delta = 0.26$ for *Metepeira* vs. $\delta = 0.18$ for *Argiope*).

2. For small initial population sizes, the probability of extinction is highly dependent on initial population age structure. For example, figure 7A shows for *Argiope* that populations consisting of one adult (*squares*) have a much lower extinction curve than populations consisting of one

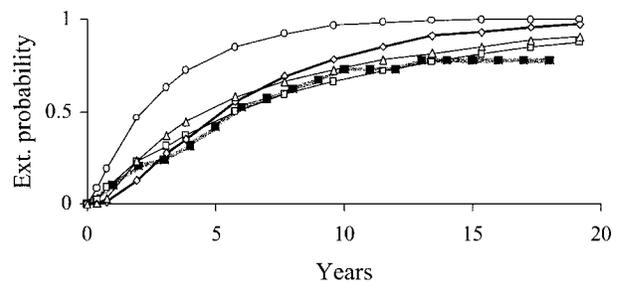


Figure 5: How variations in key parameters affect the probability of extinction for *Argiope*, models versus data. Observation: 21–50 individuals (*solid squares*). Simulation: initial condition $N(0) = (0, 0, 0, 0, 16, 8, 4, 2, 2)$. In each case, the best possible fit is shown. Demographic stochasticity + population ceiling ($C = 10$) + environmental stochasticity ($\delta = 0.18$; *open squares*). Population ceiling ($C = 40$) + environmental stochasticity ($\delta = 0.28$; *open diamonds*); demographic stochasticity + population ceiling ($C = 2$; *open circles*); demographic stochasticity + population ceiling ($C = 10$) + immigration-emigration ($p = q = 0.7$; *open triangles*). The last case shows that immigration-emigration acts similarly to environmental noise.

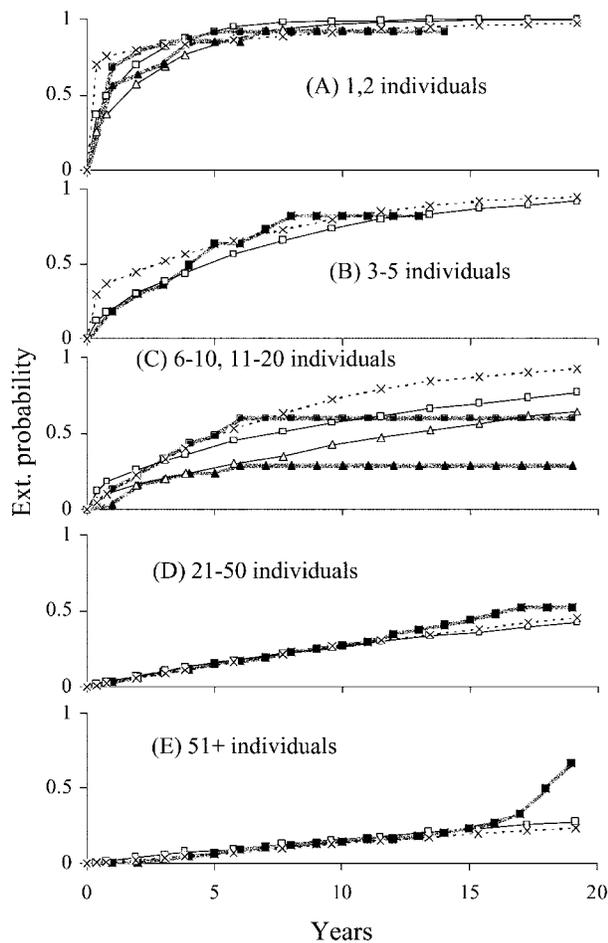


Figure 6: Probability of extinction as a function of time for *Metepeira*, with several initial population sizes: observed (solid symbols) and simulated (open symbols, age-structured model; crosses, simple model), with demographic stochasticity, population ceiling ($C = 5-60$; $\Omega = 50-1,500$), and environmental stochasticity ($\delta = 0.26$; $\theta = 0.37$). A, Observation: one individual (solid squares), two individuals (solid triangles). Squares, $N(0) = (0, 0, 0, 0, 1)$; $C = 5$. Triangles, $N(0) = (0, 0, 0, 1, 1)$; $C = 6$. Crosses, $n(0) = 1$; $\Omega = 50$. B, Observation: three to five. Squares, $N(0) = (0, 0, 4, 2, 1)$; $C = 12$. Crosses, $n(0) = 4$; $\Omega = 50$. C, Observation: six to 10 (solid squares), 11–20 (solid triangles). Squares, $N(0) = (8, 4, 2, 1, 1)$; $C = 20$. Triangles, $N(0) = (16, 8, 4, 2, 2)$; $C = 25$. Crosses, $n(0) = 15$; $\Omega = 50$. D, Observation: 21–50. Squares, $N(0) = (32, 16, 8, 4, 4)$; $C = 40$. Crosses, $n(0) = 64$; $\Omega = 200$. E, Observation: 51+. Squares, $N(0) = (64, 32, 16, 8, 8)$; $C = 60$. Crosses, $n(0) = 128$; $\Omega = 1,500$.

individual in the previous age class (triangles). This feature comes from demographic stochasticity.

3. The models are very sensitive to variation in the population ceiling C and to variation in environmental noise δ . This can be seen by looking at the fit surfaces (figs. 3, 4A, 4C). Unless the best fit ridge is followed, the fit drops abruptly as C or δ is varied. Note, however, that

within a given species, we use the same value for δ no matter what the initial population size (e.g., for all panels in fig. 6 or all panels in fig. 7) and that models fit well in all cases.

4. The best-fitting population ceiling C increased with initial population size within each species. This is in agreement with the fact that larger initial population sizes in the data should on average come from islands having larger areas and hence larger carrying capacities.

5. Demographic stochasticity could not be excluded. This is shown in figure 4B and 4D for *Argiope*: when demographic stochasticity is ignored, a large (unrealistic) δ is required, and the fit is almost independent of the population ceiling C . Moreover, when demographic stochasticity is excluded, the shape of the extinction curve with time can differ qualitatively from the shape of the observed curve (fig. 5, open diamonds).

6. Environmental stochasticity could not be excluded. Figure 5 (open circles) shows that omitting environmental stochasticity necessitates a very small C , and the shape of the simulated curve deviates greatly from the observed one, quickly reaching a plateau with time.

7. A population ceiling was necessary. The largest observed population size was 1,920 individuals for *Metepeira* and 671 individuals for *Argiope*. For *Metepeira*, the ceiling was hit about 20% of the time; for *Argiope*, the ceiling was hit about 15% of the time. When there is no ceiling, simulated population trajectories blow up to very large numbers. For example, in the case of figure 6A with one individual introduced, in 2 yr about half of 1,000 Monte Carlo simulations gave extinction, while population size of the others attained an average size of about 100,000 individuals.

8. The immigration-emigration process acts nearly equivalently to environmental noise in these models. Figure 5 illustrates that large immigration-emigration rates and no environmental noise (triangles) produce nearly the same fit as environmental noise and no immigration-emigration (squares).

The Fit of the Simple Model with No Age Structure

As in the complex model, the best-fitting population ceiling Ω increased with initial population size, less steeply for *Argiope* ($\Omega = 200-300$) but more steeply for *Metepeira* ($\Omega = 50-1,500$) than in the complex model (note that population ceilings represent all individuals, in contrast to those for age-structured models: see “Age-Structured Models”). The best-fitting environmental noise intensities were about equal for the two species ($\theta = 0.37$ for *Metepeira* vs. $\theta = 0.34$ for *Argiope*) and larger than for the complex model.

The simple models sometimes fit the extinction curves

as well as the age-structured ones (crosses in figs. 6C, 6D, 6E, 7D, 7E, 7F). The fit is less good for small initial population intervals (crosses in figs. 6A, 6B, 7A, 7B, 7C), with the lack of fit being more pronounced in *Argiope*, which has a longer immature period than *Metepeira*.

Discussion

Sensitivity of the Model Predictions to Variation in Parameter Values

If sensitivities or elasticities of the long-term growth rate λ to a given parameter (table 2) are relatively high, then extinction probabilities are also expected to be strongly affected by variation in that parameter (Caswell 2000). The deterministic long-term growth rate λ was especially sensitive to small variations in juvenile survivorship: an x percent decrease in this value translated into a $(2/3)x$ percent decrease in λ . This is expected where juvenile survivorship rate is operating, since for both species length of the immature phase was relatively great (four to eight transitions). In contrast, models were relatively insensitive to variation in fecundity (clutch size; see table 2). Finally, the probability of extinction was very much dependent on values of both δ and C .

Limitations of the Estimated Parameter Values

The life-history data have various weaknesses. Three of the four parameters in table 1 are assumed values, although the model is not very sensitive to them (see "Results"). Data on fecundity are rather sparse for *Argiope*, although model sensitivity to this parameter was also low. Model predictions were most sensitive to survival, especially juvenile survival. Although cohort sizes were often small (unfortunately necessarily so) for *Argiope*, here we had on-site data, some experimentally obtained. For *Metepeira*, data on adult survival were especially good, but juvenile survival was assumed. Developmental period was measured by observing how long individuals took to mature, again on site, but it was only measured for one or two cohorts for each species. However, even though some of the estimated parameter values were based on small sample sizes or just assumed values, predicted extinction rates of the full model were close to observed values. This suggests that the life-history data were obtained on typical islands during typical times and that our assumed values were fairly accurate.

Precision of the Model Fits

Although the models have either invariant parameters or (in two cases) parameters that are varied within limits,

they fit the data on island-spider extinction overall rather well, not just in terms of the qualitative shape of the curves but even in terms of their quantitative position. However, in some cases, we might wonder whether a good observed fit is obtained for the wrong reason. For example, the model generates good predictions of extinction rates even for small population sizes without considering potential Allee effects (Courchamp et al. 1999; Legendre et al. 1999). Yet, some of our populations might consist of only a single female so that no male could have been available to allow reproduction. Even though we explicitly ignored these extreme situations, we may have inadvertently reproduced an Allee effect on female mating by fitting an artificially low ceiling, thereby enhancing extinction probability. To examine an Allee effect explicitly, we generated for small population sizes extinction probabilities using a two-sex model (Caswell and Weeks 1986; Legendre et al. 1999) and compared them with those given by the female-based model used above. The two models produced only marginally different extinction probabilities (results not shown). Indeed, note that the elasticity for mating probability is much smaller than that for juvenile survival (table 2).

Deviations between the observed and predicted curves occur for both species in the tail of the curves (fig. 6 for *Metepeira*; fig. 7 for *Argiope*). The way the probabilities of extinction are estimated cumulatively introduces a systematic bias that can be considered a sampling-error effect: as time elapses, a smaller number of observations contribute to the estimation (table A1). Hence, a relatively small number of extinctions at the end of the time series can give a large apparent deviation. This occurred for *Metepeira* in figure 6E, where the observed curve jumps above the predicted one at the end. Most of the observed curves, however, have a tendency to level off while the predicted ones still increase, mainly because of environmental stochasticity. The reason for this slight discrepancy might be related to the fact that islands are not, even accounting for differences in area, identical replicates as in a laboratory experiment. For example, some have shorter vegetation and/or are more exposed (Toft and Schoener 1983). These differences will translate into environmental fluctuations of different magnitudes. Among a group of similar initial population sizes, those on islands expressing high environmental fluctuations will have short persistence times. Those on islands having low environmental fluctuations will have long persistence times and eventually will dominate in the cumulative curve of extinction probability. Hence, islands with low environmental fluctuations (therefore low probability of extinction) will accumulate as time elapses, causing a flattening of the cumulative extinction curve. This probable selection effect is comparable to the one observed when trying to detect senescence in natural

Necessary Components of an Extinction Model

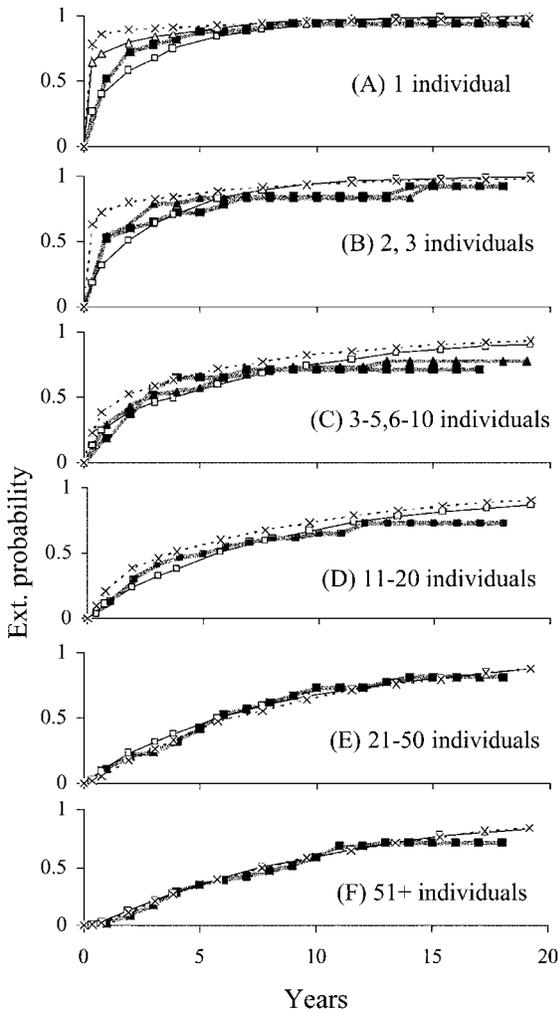


Figure 7: Probability of extinction as a function of time for *Argiope*, with several initial population sizes: observed (solid symbols) and simulated (open symbols, age-structured model; crosses, simple model), with demographic stochasticity, population ceiling ($C = 5-11$; $\Omega = 200-300$), and environmental stochasticity ($\delta = 0.18$; $\theta = 0.34$). A, Observation: one individual. Squares, $N(0) = (0, 0, 0, 0, 0, 0, 0, 0, 1)$; $C = 5$. Triangles, $N(0) = (0, 0, 0, 0, 0, 0, 0, 1, 0)$; $C = 5$. Crosses, $n(0) = 1$; $\Omega = 200$. B, Observation: two (solid squares), three (solid triangles). Squares, $N(0) = (0, 0, 0, 0, 0, 0, 0, 1, 1)$; $C = 5$. Crosses, $n(0) = 2$; $\Omega = 200$. C, Observation: three to five (solid squares), six to 10 (solid triangles). Squares, $N(0) = (0, 0, 0, 0, 0, 4, 2, 1, 1)$; $C = 8$. Crosses, $n(0) = 12$; $\Omega = 200$. D, Observation: 11–20. Squares, $N(0) = (0, 0, 0, 0, 0, 8, 4, 2, 2)$; $C = 10$. Crosses, $n(0) = 20$; $\Omega = 250$. E, Observation: 21–50. Squares, $N(0) = (0, 0, 0, 0, 16, 8, 4, 2, 2)$; $C = 10$. Crosses, $n(0) = 64$; $\Omega = 250$. F, Observation: 51+. Squares, $N(0) = (0, 0, 0, 64, 32, 16, 8, 4, 4)$; $C = 11$. Crosses, $n(0) = 128$; $\Omega = 300$.

populations (Keyfitz 1985). Although being general, the effect will show up only when the mean probability of extinction is not that great, that is, for medium-to-large population sizes.

Three basic ingredients of an extinction model—demographic stochasticity, environmental stochasticity, and a population ceiling—were all found necessary to match the spider extinction data both qualitatively and quantitatively. Although one or more of these ingredients are sometimes left out of theoretical treatments of extinction, the reasons here for their necessary inclusion suggest that this omission may be inappropriate (Caughley 1994; Foley 1997).

When demographic stochasticity is omitted, small populations persist too long and larger populations almost never become extinct, unless δ is unrealistically large (see fig. 4B, 4D). Demographic stochasticity is always present, of course, so ignoring it simply means that one is hoping that large-number behavior will be overriding. But populations become small on their way to extinction, so demographic accident can act as a terminal push for extinction driven by environmental noise. Thus, ignoring demographic stochasticity would act to overemphasize the role of environmental stochasticity.

For growing populations, once a population is no longer small, it is effectively safe from demographic-stochastic extinction (e.g., MacArthur 1972; Goel and Richter-Dyn 1974). However, environmental stochasticity allows moderately large populations to become extinct (Lande 1993). A ceiling prevents such populations from becoming so large as to be effectively safe from all but catastrophic extinction; when sufficiently small, C can interact with demographic stochasticity to determine extinction probability (MacArthur 1972; Goel and Richter-Dyn 1974; Lande 1993). In our study, without a ceiling, populations having the demographic characteristics of the spider species used would achieve numbers vastly greater than observed. Moreover, our modeling of density-dependence was rather loose because of stochasticity: population size could go well above the ceiling before being set below it at the next time step. On our small study islands, this type of ceiling may be produced by wasps or other transient predators (e.g., birds) that are attracted to islands with high spider densities (see the first section of this article). Experimental introduction of *Metepeira* onto small islands suggests that a fluctuating ceiling does exist (Schoener and Spiller 1995). This loose density dependence is reflected in figures 3 and 4: the best fit ridge is almost parallel to the C -axis, leaving room for a range of C values compatible with environmental noise δ . This might also come from a hidden correlation in the data between noise and the carrying capacity, since environmental stochasticity is potentially affecting both the mean value of the demographic parameters as well as the value of the ceiling. Indeed, it is known (Boudjema and Cazelles 2001) that long time series

(more than 200 entries) are needed to factor out the roles of environmental stochasticity and density dependence.

Complex population dynamical behavior is known to be another source of population variation (Metz et al. 1992), and the addition of environmental stochasticity might enhance this complexity further. As advocated by Ludwig (1996) and supported experimentally by Belovsky et al. (1999), complex dynamical behavior might commonly be responsible for extinctions, especially in species with a high potential growth rate or with a life cycle prone to show this type of behavior. This was indeed the case for our two species. Once more, were density dependence and its interaction with the life cycle (which partly determines the incidence of complex dynamical behavior) ignored, variation due to a ceiling would be ascribed to variation in the environment, leading again to an overemphasis of the role of the latter source of stochasticity and potentially to inappropriate conservation strategies.

However, although being all-important in explaining the observed patterns of extinction, the exact magnitudes of the effects of environmental stochasticity, population ceilings, and demographic properties of the species are difficult to measure, since several combinations of environmental noise δ and the population ceiling C yield approximately the same fit to the observed patterns (figs. 3, 4). For example, in figures 3 and 4, the best fits are obtained either for small values of δ and C or for high values of δ and C . This might result from the impossibility, with data on counts, to discriminate between the effect of environmental stochasticity and the effect of complex population dynamics when C is small (Leirs et al. 1997; Belovsky et al. 1999). To be able to measure more precisely the respective intensity of these effects (not their operational effect, which was clearly demonstrated above), longitudinal data on rates or even on some environmental variables might prove necessary.

Life Cycle Complexity and Population Behavior

Our study contrasts two types of life histories. In *Metepeira*, developmental time is relatively short and clutch size relatively low. In *Argiope*, developmental time is relatively long and clutch size relatively high. Additionally, the species vary in survivorship—*Argiope* adults survive better and its juveniles apparently less well than do *Metepeira* (recall also that *Argiope* is much larger than *Metepeira*)—and in growth rate λ , with that of *Metepeira* being larger (table 1). This latter difference might explain why *Metepeira* has a lower extinction risk overall (fig. 1). Relative effects of fecundity versus survival can be assessed for the two species using elasticities of their demographic parameters (table 2), which is appropriate when parameters have different dimensions. Although some large dif-

ferences in fecundity exist, the contribution of fecundity to variation in λ is quite small in both species as compared with that of juvenile survival. *Argiope* is more dominated by variation in juvenile survival than *Metepeira*: juvenile survival per stage is lower and drives eight transitions as compared with four in *Metepeira* (fig. 2). In short, the population dynamics of *Argiope* are dominated by the length of the immature period (the juvenile survival) and secondarily by the adult survival rate, while those of *Metepeira* are also dominated by the juvenile survival, but fecundity plays as important a role as adult survival rate (table 2). The longer immature period of *Argiope* makes it more sensitive to perturbation (perturbation effects last longer) and indeed closer to semelparity, a trait known to promote cycling (Caswell 2000). Greater fluctuations in *Argiope* bring its populations closer to small values where demographic stochasticity can push the population to zero, thereby giving *Argiope* greater extinction rates.

The fact that the simple model was able to fit data for moderate-to-large populations fairly well could be explained by environmental stochasticity increasing in importance and thereby compensating in part for the lack of age structure. For both species, the fitting procedure gave a large (and similar) environmental noise in the simple model ($\theta = 0.37$, *Metepeira*; $\theta = 0.34$, *Argiope*), whereas the fitted environmental noise values were smaller in the age-structured model, especially for *Argiope* ($\delta = 0.26$, *Metepeira*; $\delta = 0.18$, *Argiope*). Because perturbations in age structure also produce transient oscillations (Tuljapurkar 1990), noise in population trajectories results from the combined effect of environmental stochasticity and age structure; in the simple model, only the former is available. Because *Argiope* has a longer immature period, the contribution of age structure is more marked than in *Metepeira*; this might explain why the simple model has more difficulties compensating for age-structure variation with environmental stochasticity in *Argiope* than in *Metepeira*.

Although environmental noise can partly mimic the effect of age structure for larger population sizes, this is not true for the smallest sizes. While evident for both species, this failure is more pronounced in *Argiope*. Transient oscillations resulting from a deviation from the stable age distribution not only are caused by the structure of the life cycle in interaction with environmental stochasticity; they will also be more pronounced at small than at medium-to-large population sizes, in part because demographic stochasticity causes greater deviations at small sizes. In our case, the transient phase would be more important for *Argiope* than for *Metepeira* because of the former's longer immature period.

In short, inadequacies of the simple model probably mainly come from its inability to incorporate the inter-

actions between the structure of the life cycle and the various sources of stochasticity, particularly glaring when initial populations are small. This is especially important to realize for applications, since it is typically small populations that are the focus of conservation efforts. Just as for the population ceiling, ignoring an inherent property of a process—in this case, the life cycle of the species—will overemphasize the role of environmental stochasticity to the detriment of other factors, potentially leading to inappropriate conservation strategies.

Conclusion

Our investigation can be considered a variant of population viability analysis (PVA), which attempts to characterize population persistence under various conditions. Some of the above pitfalls—together with a claimed lack of biological realism, ambiguity in the variable to be considered (quasi extinction vs. extinction, expected time to extinction vs. extinction probability), difficulty in estimating parameters describing the different types of environmental variations, and poor precision of predicted extinction rates (Ludwig 1996; Foley 1997; Holsinger 2000; Vucetich et al. 2000)—have led to some skepticism about the use of PVA models (Caughley 1994; Beissinger and Westphal 1998). However, part of this skepticism is related to the fact that PVA models have often been tested against inappropriate data (Ralls and Taylor 1997; Beissinger and Westphal 1998). Here we have documented patterns of extinction for two spider species over a set of islands continuously monitored for 20 yr. The extinction curves we documented are best explained by the interaction of three factors: a population ceiling, demographic stochasticity, and environmental stochasticity. Moreover, life-historical features are necessary to simulate extinction. A good fit to the observed curves could be obtained in some cases with models of lower complexity, excluding demographic stochasticity or age-structure, by ascribing to environmental stochasticity variation due to an excluded factor. However, the use of models simplified in such a way might lead to false conclusions about respective contributions of the various factors to the extinction process, in turn possibly misleading conservation policies.

What then is the role for simple models, if any, in the studies of extinction? Simple, analytically transparent models have explanatory power: they allow us to understand in a qualitative way how natural processes should work. This may be sufficient for a general overview of the ecological world in its structure and dynamics. Applied areas of ecology, particularly conservation, may have a different objective, however. In the case of preserving species, precision is at a premium; a small mistake in a quantitative prediction about extinction can lead to permanent

loss, so we wish our models to contain everything we know that is likely to make a difference. The study reported here supports strong interactions between the structure of the life cycle and the various sources of stochasticity, especially at small population sizes. Therefore, we advocate as an initial step in such modeling inclusion rather than simplification. Sensitivity analysis of inclusive models can then point to how reductions in complexity might best be achieved, in turn guiding the most efficient data-gathering strategy in further studies and perhaps eventually allowing better analytical understanding.

Acknowledgments

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Literature Cited

- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.
- Belovsky, G. E., C. Mellison, C. Larson, and P. A. Van Zandt. 1999. Experimental studies of extinction dynamics. *Science* 286:1175–1177.
- Boudjema, G., and B. Cazelles. 2001. Extraction of nonlinear dynamics from short and noisy time series. *Chaos Solitons and Fractals* 12:2051–2069.
- Caswell, H. 1989. *Matrix population models*. Sinauer, Sunderland, Mass.
- . 2000. *Matrix population models*. 2d ed. Sinauer, Sunderland, Mass.
- Caswell, H., and D. E. Weeks. 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. *American Naturalist* 128:707–735.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell 1999. Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* 14:405–410.
- Deevey, G. B. 1949. The developmental history of *Latrodectus mactans* (Fabr.) at different rates of feeding. *American Midland Naturalist* 42:189–219.
- Ferrière, R., F. Sarrazin, S. Legendre, and J. P. Baron. 1996. Matrix population models applied to viability analysis and conservation: theory and practice using the ULM software. *Acta Oecologica* 17:629–656.
- Foley, P. 1997. Extinction models for local populations. Pages 215–246 in I. A. Hanski and M. E. Gilpin, eds. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego, Calif.

- Goel, N. S., and N. Richter-Dyn. 1974. Stochastic models in biology. Academic Press, New York.
- Greenstone, M. H., C. E. Morgan, A. Hultsch, R. A. Farrow, and J. E. Dowse. 1987. Ballooning spiders in Missouri, USA, and New South Wales, Australia: family and mass distributions. *Journal of Arachnology* 15:163–170.
- Holsinger, K. E. 2000. Demography and extinction in small populations. Pages 55–72 in A. G. Young and G. M. Clarke, eds. *Genetics, demography and viability of fragmented populations*. Cambridge University Press, Cambridge.
- Keyfitz, N. 1985. *Applied mathematical demography*. Springer, New York.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- Lebreton, J. D., and J. Clobert. 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling. Pages 105–125 in C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, eds. *Bird population studies*. Oxford University Press, Oxford.
- Legendre, S., and J. Clobert. 1995. ULM, a software for conservation and evolutionary biologists. *Journal of Applied Statistics* 22:817–834.
- Legendre, S., J. Clobert, A. P. Møller, and G. Sorci. 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. *American Naturalist* 153:449–463.
- Leirs, H., N. Chr. Stenseth, J. D. Nichols, J. E. Hines, R. Verhagen, and W. Verheyen. 1997. Stochastic seasonality and non-linear density-dependence factors regulate population size in an African rodent. *Nature* 389:176–180.
- Ludwig, D. 1996. The distribution of population survival times. *American Naturalist* 147:506–526.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York.
- Mangel, M., and C. Tier. 1993. Dynamics of metapopulation with demographic stochasticity and environmental catastrophes. *Theoretical Population Biology* 44:1–31.
- . 1994. Four facts that every conservation biologist should know about persistence. *Ecology* 75:607–614.
- Marshall, S. D., and A. L. Rypstra. 1999. Spider competition in structurally simple ecosystems. *Journal of Arachnology* 27:343–350.
- Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define fitness for general ecological scenarios? *Trends in Ecology & Evolution* 7:198–202.
- Mills, L. S., S. G. Hyes, C. Baldwin, M. J. Wisdom, J. Citta, D. J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* 10:863–873.
- Moya-Laraño, J., J. M. Orta-Ocana, J. A. Barrientos, C. Bach, and D. H. Wise. 2002. Territoriality in a cannibalistic burrowing wolf spider. *Ecology* 83:356–361.
- Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. *American Naturalist* 132:757–785.
- Ralls, K., and B. L. Taylor. 1997. How viable is population viability analysis? Pages 228–235 in S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, eds. *The ecological basis of conservation*. Chapman & Hall, New York.
- Schaffer, M. L. 1987. Minimum viable populations: coping with uncertainty. Pages 69–86 in M. E. Soulé, ed. *Viable populations for conservation*. Cambridge University Press, Cambridge.
- Schoener, T. W. 1991. Extinction and the nature of the metapopulation: a case system. *Acta Oecologica* 12:53–75.
- Schoener, T. W., and D. A. Spiller. 1992. Is extinction rate related to temporal variability in population size? an empirical answer for orb spiders. *American Naturalist* 139:1176–1207.
- . 1995. Effect of island predators and area on invasion success: a field experiment with spiders. *Science* 267:1811–1813.
- . 1999. Indirect effects in an experimentally staged invasion by a major predator. *American Naturalist* 153:347–358.
- Schoener, T. W., D. A. Spiller, and J. B. Losos. 2001. Natural restoration of the species-area relation for a lizard after a hurricane. *Science* 294:1525–1528.
- Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* 19:473–511.
- Soulé, M. E., ed. 1987. *Viable populations for conservation*. Cambridge University Press, Cambridge.
- Spiller, D. A., and T. W. Schoener. 1988. An experimental study of the effect of lizards on web-spider communities. *Ecological Monographs* 58:57–77.
- . 1990. Lizards reduce food consumption by spiders: mechanisms and consequences. *Oecologia (Berlin)* 83:150–161.
- . 1995. Long-term variation in the effect of lizards on spider density is linked to rainfall. *Oecologia (Berlin)* 103:133–139.
- . 1996. Food-web dynamics on some small subtropical islands: effects of top and intermediate predators. Pages 160–169 in G. A. Polis and C. Winemiller, eds. *Food webs: interaction of pattern and dynamics*. Chapman & Hall, London.
- . 2001. An experimental test for predator-mediated

- interactions among spider species. *Ecology* 82:1560–1570.
- Spiller, D. A., J. B. Losos, and T. W. Schoener. 1998. Impact of a catastrophic hurricane on island populations. *Science* 281:695–697.
- Toft, C. A., and T. W. Schoener. 1983. Abundance and diversity of orb spiders on 106 Bahamian islands: biogeography at an intermediate trophic level. *Oikos* 41: 411–426.
- Tuljapurkar, S. 1990. Population dynamics in variable environments. *Lecture notes in biomathematics*. Springer, Berlin.
- Vucetich, J. A., T. A. Waite, L. Qvarnemark, and S. Ibargüen. 2000. Population variability and extinction risk. *Conservation Biology* 14:1704–1714.
- Wagner, J. D., and D. H. Wise. 1996. Cannibalism regulated densities of young wolf spiders: evidence from field and laboratory experiments. *Ecology* 77:639–652.
- Wise, D. H. 1993. *Spiders in ecological webs*. Cambridge University Press, Cambridge.

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