

The Effects of Daily and Seasonal Temperature Variation on a Model of Competing Lizard Species

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Abstract

Simulation models were used to study the effects of age-structured population growth and thermal amplitude variance on competitive interactions between hypothetical model lizard species. The competing species were identical in all aspects except their position along a resource axis. The lizards grew on a physiological time scale, with fecundity, survival, and position on the resource axis dependent on age. Competition was modeled by allowing the younger age classes of species B to overlap the older age classes of species A. The model included the simulation of natural variance in daily and yearly temperature regimes. The presence of thermal amplitude variance and size-structured population growth produced patterns that were dissimilar from typical Lotka-Volterra patterns. In competitive encounters, it was not usually possible to predict whether competitive exclusion would occur, nor which species would be excluded. Also, correlations between competing species showed no consistent trend with increasing levels of competition. Both size-structured population growth and thermal amplitude variance produced patterns of population growth that obscured the effects of interspecific competition.

INTRODUCTION

Much theoretical development in community ecology over the last 30 years has been based on logistic population growth models (Pianka, 1982). There are two basic problems associated with this fact. First, the assumptions associated with these models are usually violated and often ignored. For example, it seems clear that populations of poikilotherms in particular have size-dependent fecundity and survival, and may exhibit stage-structured population growth. The Lotka-Volterra models assume implicitly that all size/age classes grow at the same rate, and that populations exist in a stable size/age distribution. Similarly, the models assume that competitive effects are symmetrical. Violations of these assumptions are usually considered to be minimal or to have no significant impact on the qualitative results of the study. Whether this is true or not has yet to be determined. The second problem associated with the use of Lotka-Volterra type growth models is that, as demonstrated by the work of May (1973, 1974)

and Gonzales-Andujar and Perry (1993), even simple logistic population models can produce complex growth patterns. It is not clear what impact this behavior may have on our ability to discern patterns of competition in nature.

With respect to competition, field studies of community structure often produce equivocal results (Findley and Findley, 1985; Scheibe, 1987), and this is especially true in studies of lizards. The extensive work of Pacala and Roughgarden (1982), Pianka (1986), and Ricklefs et al. (1981) resulted in evidence for interspecific competition in lizards, while Dunham (1980, 1983), M'Closkey and Baia (1987), and Scheibe (1987) found weak or confusing patterns. This may be a consequence of epistemological problems (Conner and Simberloff, 1978, 1979; Strong et al., 1979; and Weins, 1977, 1984), but may also reflect the importance of climatic factors or phylogenetic history (Losos, 1990; but see also Losos, 1992; Roughgarden, 1992; Roughgarden and Pacala, 1989). Although reviews by Connell (1983), Schoener (1983), and Case and Bolger (1991)

have provided strong support for the competition hypothesis, and in fact few would deny the existence of competition, there is some argument about the magnitude of its effects relative to other factors (Abrams, 1986; Den Boer, 1986; Giller, 1986; Roughgarden, 1986).

The patterns observed in lizard communities may be a consequence of population dynamics that are influenced by ectothermy. Unlike birds and mammals, lizards tend to exhibit indeterminate growth. Lizards, just as insects, exist in physiological time in the sense that their behavior, performance, and ecology is directly related to the thermal environment. In fact, variation in the thermal environment may influence lizard population growth and result in fluctuating populations. Schoener (1985) concluded that lizard populations tend to be temporally constant, although his review was not based on long-term data. Recent work by Andrews (1991) has demonstrated considerable fluctuations in lizard population sizes. The potential for fluctuating populations and size-dependent fecundity and survival suggest that lizards may deviate from the assumptions of the Lotka-Volterra models sufficiently to make the predictions of the models meaningless for many lizard communities.

In this paper, I demonstrate that variation in the thermal environment, together with size- and density-dependent fecundity and survival and asymmetrical competitive effects, produce population growth patterns that display persistent and apparently random fluctuations. The resultant patterns mask the effects of interspecific competition to the extent that detection of interspecific competition is usually impossible, even when it is known to exist.

METHODS

The growth of coexisting lizard populations was studied using a computer simulation model. The model was comprised of three basic components: thermal environment routines, population growth routines, and interspecific competition routines. The thermal environment routines were designed to simulate daily and seasonal thermal variation, and to incorporate daily and yearly variance in temperature am-

plitudes. The population growth routines modeled coexisting lizard species with age-dependent fecundity and survival using renewal equations (Charlesworth, 1980). The competition routines were used to model density-dependent fecundity and survival schedules in a pattern consistent with the expectations of competitive effects.

The thermal environment model was based on that of Taylor (1981) and used a Fourier series of the form:

$$(1) \quad T(t) = \bar{T} - \frac{a_2}{2} \cos\left(\frac{2\pi}{365}t + \theta\right) - \frac{a_1}{2} \cos(2\pi t)$$

where temperature at time t is a function of the mean yearly temperature and both seasonal and daily temperature fluctuations. The parameter a_2 represents the yearly temperature amplitude, a_1 represents the daily temperature amplitude, and θ provides a lag time. The equation produces a curve in which temperatures rise and fall daily and yearly. Parameters a_1 and a_2 were treated as normal random variables with means μ_1 and μ_2 and variances σ_1 and σ_2 respectively. Thus, by specifying the means and variances of a_1 and a_2 , it was possible to produce daily and seasonal temperature curves that reflected accurately those found in nature.

The temperature-dependent development rate of the lizards was modeled using a normal curve:

$$(2) \quad R(T) = R_m \text{EXP}[-.5(T - T_m / T_\sigma)^2]$$

The parameters defining the development rate were the variance of the development curve and the mean of the curve, which represented the optimal development temperature. Thus, at low temperatures, the lizards grew very slowly, and as temperatures increased, growth increased up to the maximum development rate. Temperatures beyond the optimal temperature resulted in slower growth.

No attempt was made to model the effects of behavioral or physiological thermoregulation on the development rates. Thermoregulation by the lizards would result in more moderate body temperatures at high ambient temperatures, and higher body temperatures at low ambient temperatures. Thus, thermoregulation should result in a flatter curve. Preliminary trials revealed the

general results of the simulations to be robust with respect to the shape of the development rate curve.

The accumulation of developmental 'units' by the lizards was modeled by the equation:

$$(3) \quad D(t) = \int_0^t R(T(t)) dt$$

Thus, the development of the lizards was based on a physiological time scale, in which the animals developed rapidly (in clock time) during warm parts of the year and slowly (in clock time) during cold parts of the year.

Population growth was modeled using a renewal equation of the form:

$$(4) \quad B_f(t) = g(t) + \sum_{x=1}^t B_f(t-x) l(x,t) m(x,t)$$

$$(5) \quad g(t) = \sum_{x=t+1}^d n(x-t,0) l(x,t) m(x,t) \quad (t < d)$$

In these equations, time was measured as clock time while age was measured as developmental units using Equation (3) for the accumulation of development given above. $B_f(t)$ represents the births of females at time t . This equation expresses population growth as a function of the initial cohort $g(t)$ plus births of females at time $t-x$ times the age-specific survival $l(x,t)$ and age-specific fecundity $m(x,t)$ of female lizards aged x at time t . The contribution of the initial cohort to the female births at time t is simply the number of lizards in the initial cohort, $n(x-t,0)$, times the age-specific fecundity and survival of that cohort.

The age-specific survival function was a negative exponential of the form:

$$(6) \quad l_x = \text{EXP} [-kx(\ln(10+N_x))]$$

where k is a constant and N_x is the number of individuals of both species in the age (size) class. The shape of the survival curve under condi-

tions of increasing competition is shown in Fig. 1.

Age-specific fecundity was modeled as:

$$(7) \quad m_x = [(b_0 + b_1x) \ln x] \text{EXP}(-n_x/1000)$$

The form of the fecundity function was based on regressions of clutch sizes on female sizes for *Cnemidophorus* spp. and is shown in Fig. 2 as a function of increasing levels of competition. Thus, as lizards grew larger, they produced larger clutches. This phenomenon has been noted for many lizards (e.g., Abts, 1987; Vitt and Breitenbach, 1993). As the number of lizards within a specific age class approached the resource limit, fecundity declined as a consequence of the negative exponential term.

The life span of each species was chosen to be three years and was divided into 30 age/size classes. Initially, each size class contained an equal number of lizards. As a simulation progressed, animals accumulated 'developmental units' following Equation 3. The accumulation of 10 developmental units resulted in the transition of an animal from one age class to the next. Following the accumulation of 120 developmental units, animals could reproduce. If reproduction occurred, reproduction could occur again only after the accumulation of an additional 10 developmental units. Thus, the system models species that can potentially live three years, can begin reproduction in their second year, and can reproduce more than once each season. However, variance in the thermal regime, delayed onset of reproduction, and early seasonal cessation of reproduction limits the reproductive opportunities for the modeled organisms.

Since reproduction in lizards tends to be seasonal, reproduction was limited to warm months of the simulations. This was done by computing the maximum daily temperature every other day over a period of 10 days, then computing the regression coefficient of maximum temperature against day for that period. If the coefficient was positive, reproduction was possible 28 days later. Following the onset of reproduction, a similar regression coefficient was computed for the period 180 days later. Once the coefficients were negative, reproduction ceased

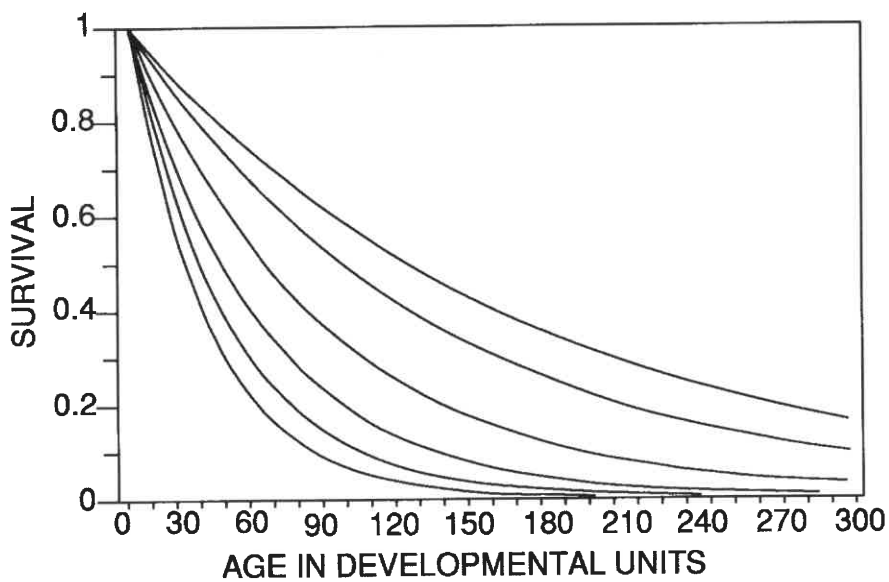


Fig. 1. Shape of the survival function in relation to increasing age (developmental units) and competition.

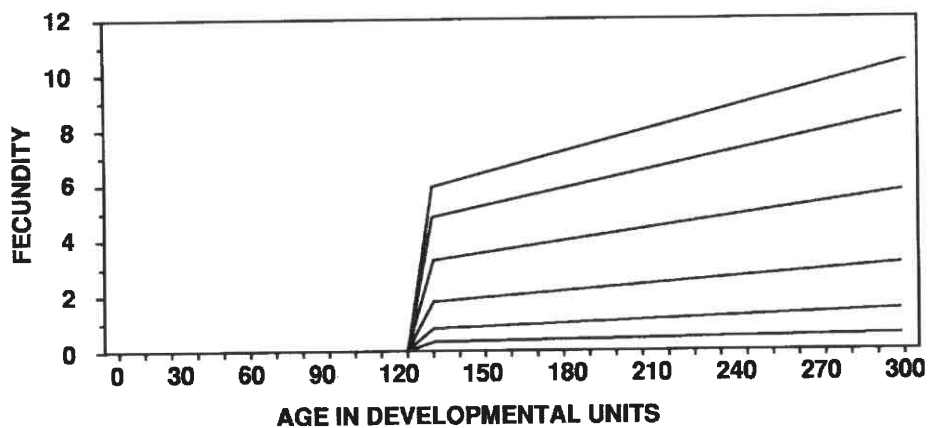


Fig. 2. Shape of the fecundity function in relation to increasing age (developmental units) and competition.

until the next season. This approach is not unrealistic, as indicated by the review of Duvall, Guillette, and Jones (1982). There is strong evidence that temperature plays a significant role in reproductive cycles of lizards. Although reproduction in lizards is more complex than a simple thermal relationship, the approach taken here provides a reasonable first step in the development of this modeling effort.

Each computer simulation modeled 100 years of population growth, one hour at a time. The simulations began with both species containing equal numbers of animals distributed evenly through all size classes. As the animals accumulated developmental units (determined by the thermal environment routines), they moved through the size classes of the population. For each hour, fecundity and survival were computed for each size class. Fecundity within reproductive size classes was dependent on the number of conspecific lizards in that size class and the number of lizards from the coexisting species that overlapped that size class. Survival in the first series of simulations was unaffected by competition. In the second series of simulations, survival of individuals in overlapping size classes decreased as per Equation (6). Thus, intraspecific competitive effects were manifested as fecundity effects. Interspecific competitive effects were manifested as fecundity effects for the first series of simulations and as both fecundity and survival effects for the second series of simulations. Interspecific overlap between species was modeled by allowing the older size classes of the first species to overlap with the younger size classes of the second species, under a uniform resource availability curve. That is, the carrying capacity for the overlapping size class was no larger than that for non-overlapping size classes. As population sizes of both species approached the carrying capacity for the overlapped size class, the fecundity and survival curves for both species were modified. Under these conditions, species B has a competitive advantage. Its most abundant size classes (newborns and young lizards) overlap initially with the least abundant and most fecund size classes of species A, thus significantly reducing the reproductive potential of species A.

The effects of interspecific competition were studied by performing independent replicates of

simulations at each level of competitive overlap. Overlap was increased at 10% intervals from the initial series of simulations with no overlap to the final series with complete overlap. A total of 181 simulations were performed for the trials in which fecundity was affected by competition, and 113 simulations were performed for the trials in which fecundity and survival were affected. The fate of each species and the product moment correlations between species for each simulation were compared graphically with those obtained from initial trials in which there was no thermal amplitude variance.

RESULTS

The results of the competition trials were dependent on the extent of overlap between the model species, the nature of the competitive effect (whether it affected fecundity alone, or fecundity and survival), and the thermal amplitude variances. When amplitude variances were zero and only fecundity was affected by competition, the results of the competition trials were similar to those expected from systems using the Lotka-Volterra models. As the extent of overlap between species increased, the population of one species tended to increase while the population of the second species tended to decrease (Fig. 3). Unlike the expected Lotka-Volterra results, neither species went extinct, even with complete overlap. This was a consequence of the magnitude of the competitive effect on fecundity. Increasing the magnitude of the effect would have resulted in the extinction of the rarer species.

When competition affected both fecundity and survival in the absence of thermal amplitude variance (Fig. 4), the results were fundamentally different. Here, there was a marked reversal of fortune when competitive overlaps exceeded 60%. When overlap was less than 60%, the population size of species B exceeded that of species A, as in the previous trial. However, overlaps between 60 and 65% resulted in the reduction of species B relative to A and the extinction of A at 67% overlap. The extinction of species A was caused by competitive effects on the fecundity of all reproductive size classes. Relaxation of the competitive effect on survival and the ensuing increased number of fecund

individuals tended to broaden this range. Even the extinction of species A, however, did not enable species B to grow significantly within the 100-yr simulation. Unlike a typical Lotka–Volterra system in which one species always has a competitive advantage, here that advantage was dependent on the extent of overlap.

The product moment correlations between yearly population sizes of the competing species in the absence of thermal amplitude variance are presented in Fig. 5. Typically, competition is expected to produce negative correlations between competing species, with the magnitude of the negative correlation an index of the intensity of competition. In this analysis, correlations were negative only when overlap was 67%. Furthermore, the correlations did not decrease monotonically with increasing competition. This suggests that correlations were a poor indicator of competition in this model. The fecundity and survival effects of competition resulted in changes in size structures of the populations, with subsequent changes in the intensity of competition between the species. Thus,

in spite of extensive overlap between the species, changes in size structure alleviated the intensity of competition.

The incorporation of non-zero thermal amplitude variances in the model increased the variability in the results. Representative samples of population growth are shown in Fig. 6. Even in the absence of competition (Fig. 6a), there were considerable fluctuations in population size over the 100-yr interval. Since this sample trial models a population in the absence of interspecific competition, the fluctuations were a consequence of variable fecundity and survival, resulting from yearly and daily fluctuations in thermal amplitude. These fluctuations influenced the accumulation of developmental units and prevented the population from achieving a stable size distribution within the 100 yrs of the simulation. The sample trials for competing species, shown in Figs. 6b and 6c, illustrate the dynamic nature of the growth patterns and reveal that the competitive effects are not readily discernible from the underlying thermal, physiological, and size structure effects. These figures demonstrate that even careful multi-year field samples of compet-

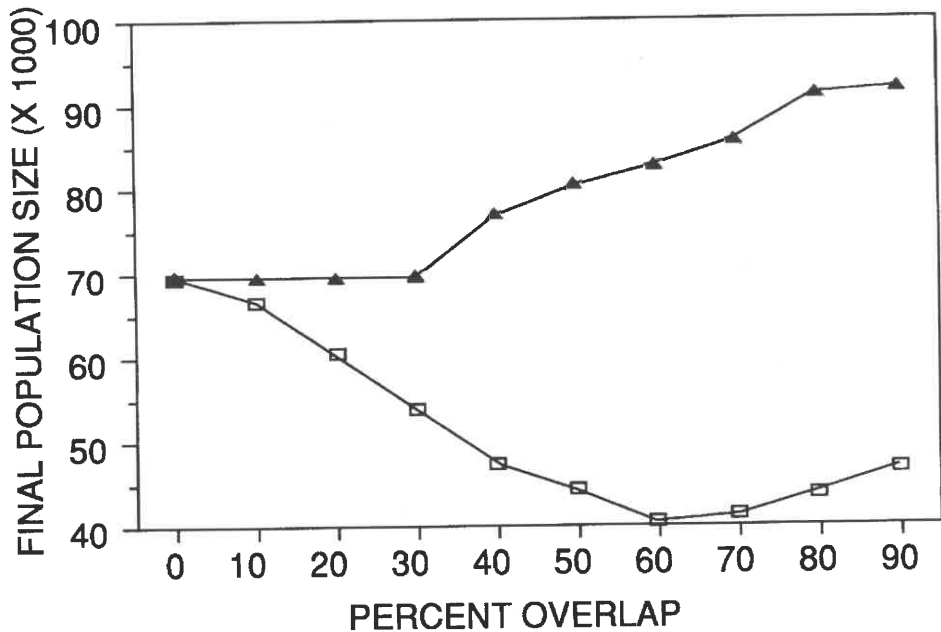


Fig. 3. Population sizes of species A (open rectangles) and species B (closed triangles) after 100 years of competition with no thermal amplitude variance. In these simulations, only fecundity was affected by competition.

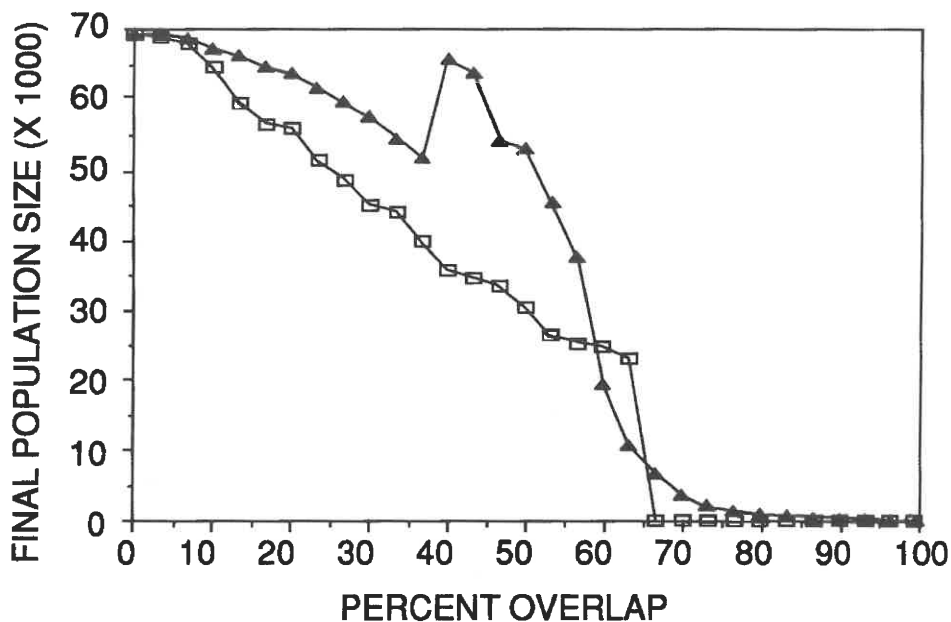


Fig. 4. Population sizes of species A (open rectangles) and species B (closed triangles) after 100 years of competition with no thermal amplitude variance. In these simulations, both the fecundity and survival functions were affected by competition.

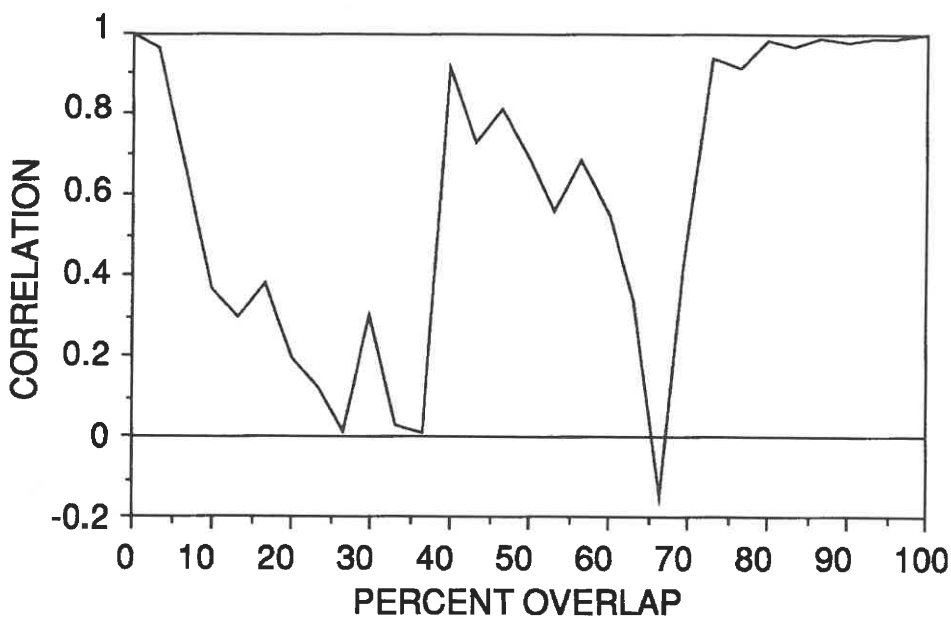


Fig. 5. Pearson product moment correlations between the population sizes of two competing species over 100 years, versus the level of overlap between competing species.

ing species may produce results that do not reveal interspecific competition.

The results of the correlation analyses for the trials with thermal amplitude variance are shown in Figs. 7a and 7b. In each figure, the upper, middle, and lower lines represent the upper quartile, median, and lower quartile of each distribution of correlation coefficients. It is clear that while there is some agreement between the expected and observed distributions, there is considerable variance in the correlation coefficients at most levels of overlap. The range of correlations for competing populations was smallest when overlaps were about 40 or 50%. It is within this range of overlaps that the youngest reproductive size classes of species B are first subjected to direct competitive effects. Below and above this range, variability in the correlations increased dramatically. Also, the median correlation coefficients were almost always positive, regardless of whether competition affected fecundity only, or survival and fecundity. There was no clear trend of increasingly negative correlations with increasing intensity of competition.

The fates of the two competing species in relation to their shared resource use are presented in Figs. 8 and 9. When fecundity was affected by competition, the abundance of species A relative to the final population of both species was usually greater than 50% at overlaps of less than 40% or greater than 70%. Between 40 and 70%, species A usually constituted less than 50% of the overall final population. The distribution of the quartiles over the range of overlaps indicates that species A generally dominated at low and high overlap values, but did poorly at intermediate overlaps. When both fecundity and survival were affected by competition, the abundance of species A relative to the overall final population was usually less than 50% at overlaps of 40 and 50% (Fig. 8b). At overlaps of 30 and 60%, species A generally predominated.

The extinction probabilities shown in Fig. 9a illustrate that species A is most likely to go extinct at intermediate levels of overlap, while species B is most likely to go extinct at low and high levels of overlap when competition affects fecundity. Species B almost always had a higher extinction rate than species A. The extinction

probabilities, however, were not monotonically increasing with increasing level of competition. When fecundity and survival were affected by competition, the extinction probabilities for both species were low at intermediate overlap values and higher elsewhere. Species B almost always had a higher probability of extinction than species A. Again, the extinction probabilities were not monotonically increasing with increasing level of competition.

DISCUSSION

In general, fecundity and survival are size-dependent in lizards and many species exhibit some degree of indeterminate growth (Abts, 1987; Shine and Charnov, 1992). These generalizations, together with the periodic and variable nature of the temperate thermal environment, suggest that populations of temperate zone lizards are unlikely to reach a stable size distribution. Thus, the implicit assumption of the Lotka-Volterra models that populations exist in a stable size distribution may be violated by lizards, and predictions about competition based on those models may be inaccurate.

Size-structured population growth is sufficient to cause fluctuating population densities. Although Schoener's (1985) review of the literature found population constancy in lizards, the reviewed work entailed relatively short time periods. Recent work by Andrews (1991) on tropical *Anolis* lizards revealed 5- to 8-fold changes in density over a 19-year period. The density fluctuations she observed were statistically related to seasonal rainfall. She hypothesized the dynamic nature of the fluctuations to result from random perturbations alleviated by density-dependent interactions. It has been demonstrated by Den Boer (1991) that in some empirical systems fluctuations in population density can be mimicked with sufficient closeness by random walk models. Similarly, even simple model systems are capable of chaotic growth (Allen, 1990; Batterman, 1993; May, 1973, 1974; Schaffer and Kot, 1986). Thus, there is good reason to doubt the universality of population constancy in lizards. The randomness and unpredictability observed in the model presented here suggest that temperate zone lizard communities may be so-called "non-equilibrium communities"

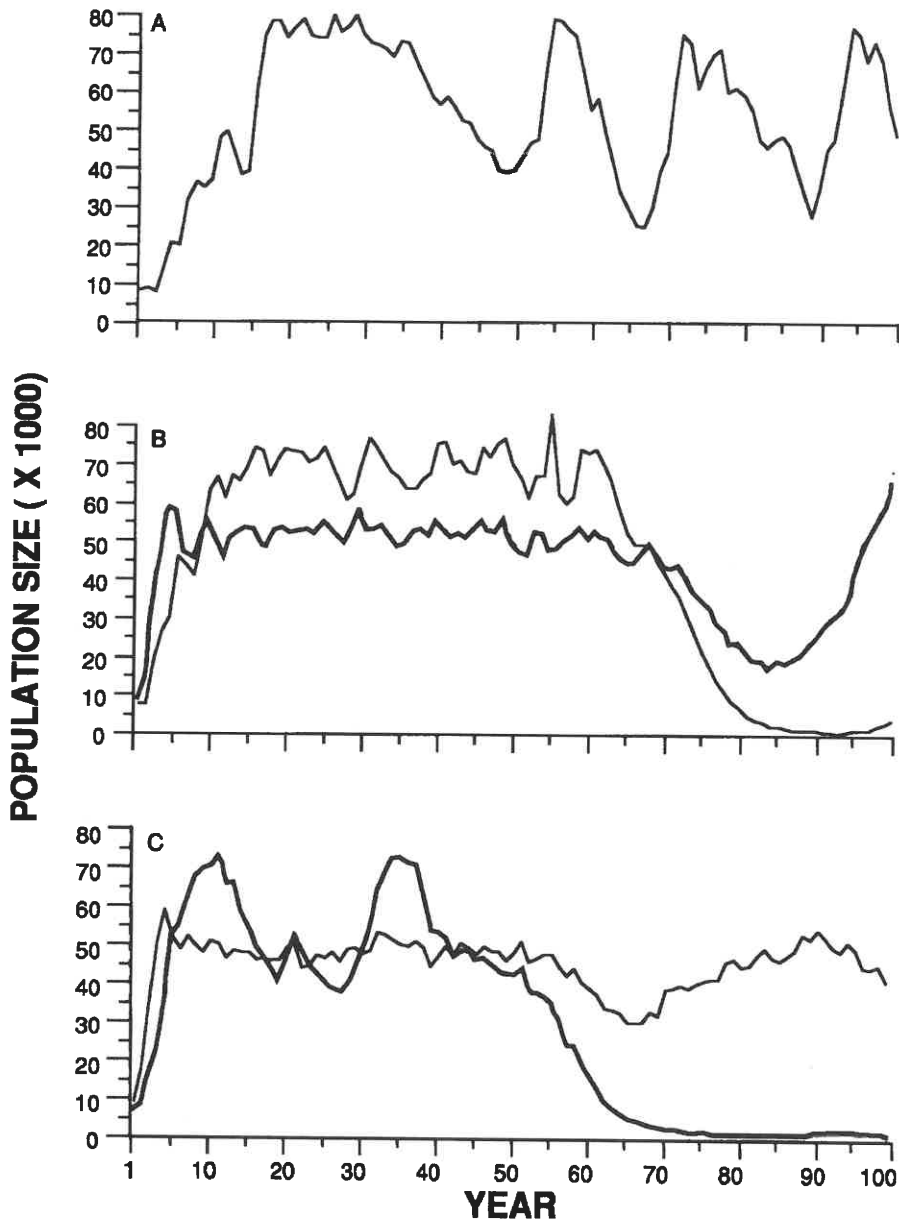


Fig. 6a-c. Representative growth curves for 1) a population without a competitor (6a), 2) a competitive system with 20 percent overlap (6b), and 3) a competitive system with 30 percent overlap (6c). In each simulation competition affected both fecundity and survival, and there was thermal amplitude variance.

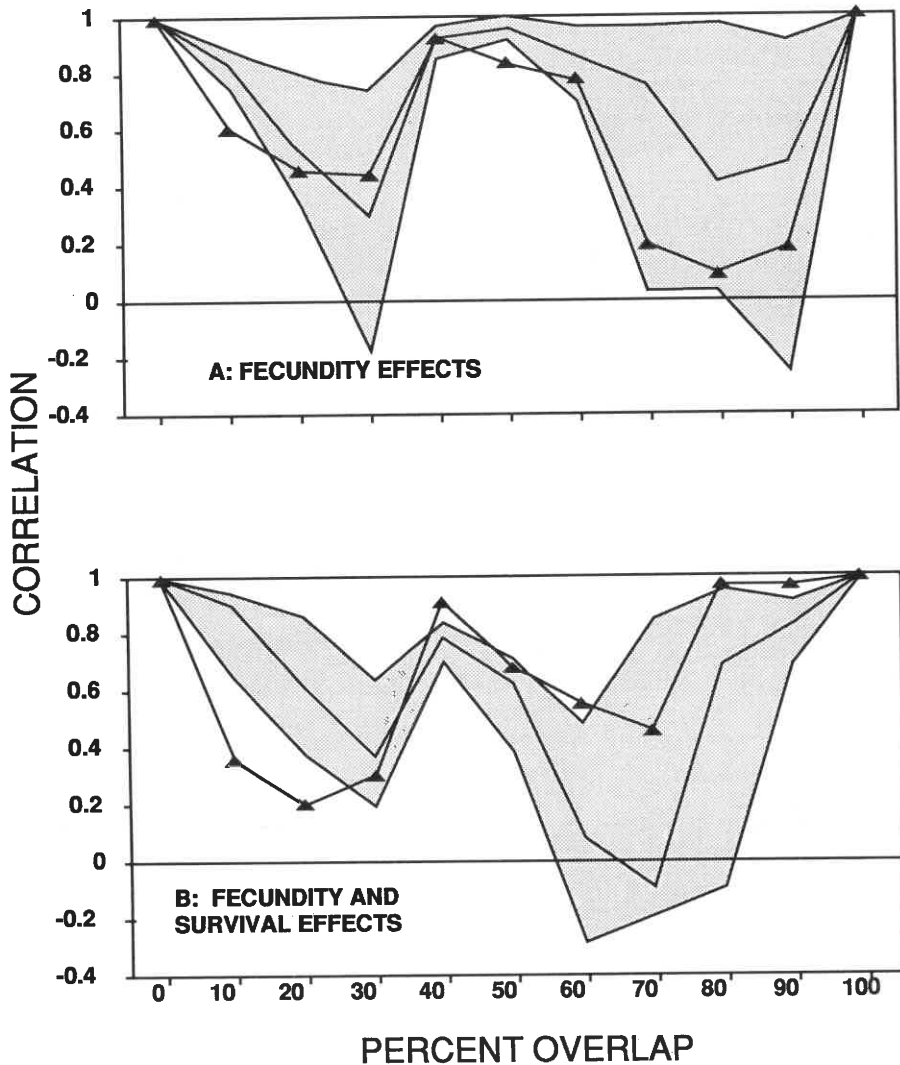


Fig. 7a-b. Correlation results for simulation trials in which competition affects fecundity (7a) and fecundity and survival (7b), relative to percent overlap. In each figure, the expected correlation (based on trials with no thermal amplitude variance) is indicated by closed triangles. The upper, middle, and lower lines in each figure represent the third quartile, median, and first quartile for each distribution of correlations.

(Weins, 1984). Attributes of such assemblages include biotic decoupling, abiotic limitation, and large stochastic effects.

Competition between the modeled lizard species was not symmetrical. Resource use was assumed to be size-dependent and the species existed on a size continuum. The larger, older, most fecund, and least abundant size classes of the smaller species overlapped the smaller, younger, and most abundant classes

of the larger species. Although some work has been done on coexisting teiid lizards (Casas-Andreu and Gurrola-Hidalgo, 1993; Medica, 1967; Milstead, 1957a, 1957b, 1965; Mitchell, 1979), the life history and diet data necessary to validate assumptions of symmetrical competition are not available for lizards. The assumptions are not unreasonable, however, and certainly asymmetric interactions between species are not uncommon and may have im-

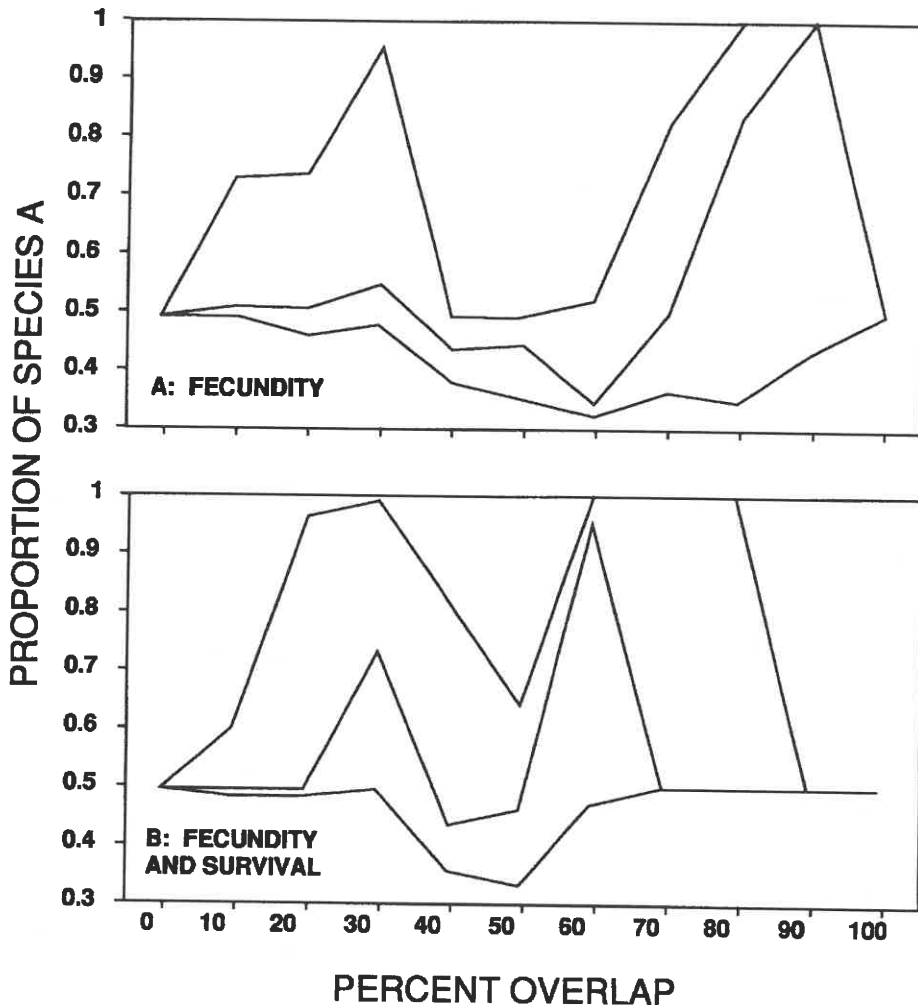


Fig. 8a-b. Proportion of species A in the two species population following 100 years of competition, for trials in which competition affected fecundity only (8a) and fecundity and survival (8b). In each figure, the upper, middle, and lower lines represent the first quartile, median, and third quartiles of the distributions respectively.

portant consequences for the behavior of the system, especially if the competitor populations are size structured.

Overlapping size structured species may experience variable intensities of competition as a consequence of fluctuating densities and size structures. Thus, it is not surprising that in this model increased levels of competition did not result in obvious density-dependent effects. As the intensity of competition increased, the expected interspecific correlations did not become increasingly negative, nor did they decrease monotonically. Furthermore, even when thermal

amplitude variance was zero, increased competition did not produce monotonically decreasing correlations between species. Thus fluctuating size-structured populations with asymmetric overlaps did not respond to interspecific competition in the expected way. With the inclusion of non-zero thermal amplitude variance, interspecific correlations were generally positive and were not monotonically decreasing. This suggests that the size structure of the populations and fluctuating densities, both driven by the physiologically based development routines and influenced by the variable thermal environment,

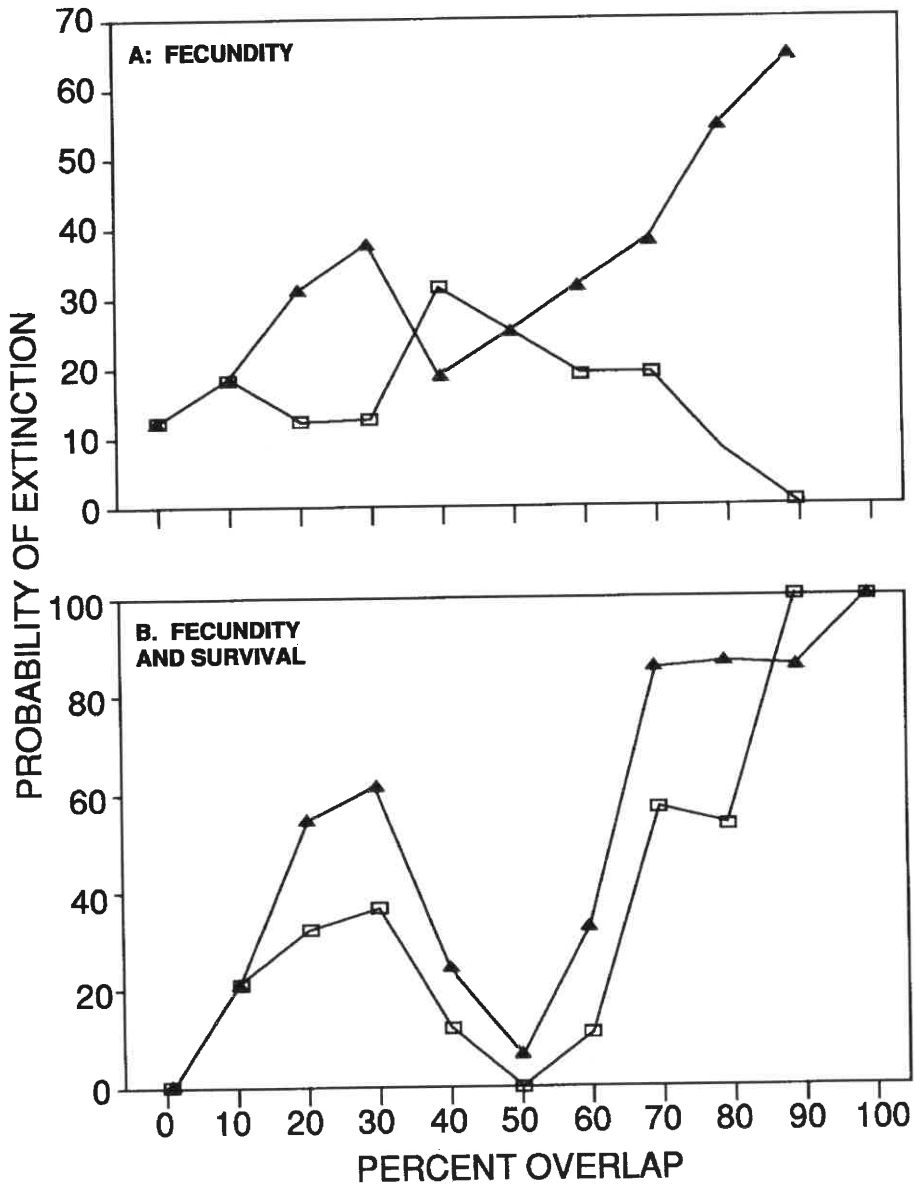


Fig. 9a-b. Probability of extinction versus level of competitive overlap for species A (open rectangles) and species B (closed triangles). In 9a, only fecundity is affected by competition while in 9b both fecundity and survival are affected.

may have ameliorated the effects of competition on the overall densities of the species.

The simulation results were dependent on competitive mechanisms and the presence of thermal amplitude variance. That is, when competition affected fecundity and survival, the results were different than when competition affected fecundity alone. Even though the re-

sults shown in Fig. 3 (no thermal amplitude variance; competition affects fecundity, but not survival) tend to be consistent with patterns expected from a Lotka-Volterra model, the introduction of competitive effects on survival produced an entirely different result. Here, increasing levels of competition did not result in a consistent increase in the probability that the larger

species B would displace species A. In fact, species displacement was dependent on the amount of overlap. Even in a simple world (no thermal amplitude variance) it is difficult to predict if competitive exclusion will occur and which species will be excluded.

Numerous studies have demonstrated the effects of resource limitation or environmental uncertainty on lizard reproduction (Abts, 1987; Patterson, 1991; see also Shine and Harlow, 1993; and Shine and Schwarzkopf, 1992). Although survival effects are more difficult to demonstrate, they are also an expected consequence of resource limitation (Shine and Charnov, 1992). Detailed knowledge of how multiple species systems respond to resource limits and environmental fluctuations seems essential if we are to understand how competitive effects are manifested. As shown here, the presence of thermal amplitude variance produced results inconsistent with the predictions of competition theory. Repeated trials exhibited a great deal of variance with respect to long-term persistence in competitive encounters (Fig. 6). Although species B had a competitive advantage, with low levels of overlap species A usually did better than species B. Only when overlap was about 40 or 50% did species A follow the predicted trend. As overlap increased beyond 70%, species B again exhibited a competitive advantage most of the time. But, the variation from one trial to the next (Figs. 7 and 8) illustrates clearly how the system is unpredictable. This suggests that even a comprehensive knowledge of the competitive mechanism may be insufficient if the populations are size structured and responsive to environmental variance.

I used a model based on physiological time and size-structured population growth to observe the effects of interspecific competition when it did in fact exist. If the results reflect natural processes, then our difficulty in demonstrating competition in the field is understandable. The environmental and demographic forces impinging upon population size may overwhelm or mask the effects of competition.

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