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The Interplay Between Life History and Environmental Stochasticity: Implications for the Management of Exploited Lizard Populations¹

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SYNOPSIS. The sustainable use of wild species by local people is emerging as an important conservation strategy. The premise is the economic value of species will justify their own preservation as well as the habitats they occupy. However, the lack of natural history and demographic information for the majority of species being exploited or with potential uses presents challenging problems for implementing sustainable use programs. Each year in Argentina and Paraguay, an average of 1.9 million tegu lizards of the genus *Tupinambis* are exploited for their skins. In spite of the importance of tegus as a resource, their biology is poorly known and their populations have never been managed. The life history of *Tupinambis*, like that of other exploited lizards, is characterized by a relatively long life span, a large clutch size, several years of growth before reproduction, and high mortality of hatchlings. Importantly, the mortality of young-of-the-year and the proportion of females reproducing each year are both probably strongly influenced by interannual environmental variation. When these parameters were randomized in life table projections to simulate the effects of environmental stochasticity, the population growth rate was highly sensitive to environmental fluctuations. Monte Carlo simulations of different harvest strategies showed that estimates of population growth rates were overwhelmingly influenced by environmental variation and the number of years included in the growth rate estimate, even in the face of seemingly large changes in adult mortality that would result from population management. These results are both encouraging and cautionary for *Tupinambis* conservation. On the one hand these patterns can help explain how *Tupinambis* populations may have persisted in spite of high and variable harvest levels during many years, but conversely, stochastic effects make it difficult to evaluate the effects of conservation measures. Size and sex can be determined from harvested skins, and pilot studies suggest that analyses of the annual harvest can provide valuable information for evaluating long-term population trends.

INTRODUCTION

Sustainable use as a tool for conservation

The sustainable use of wild species has been widely proclaimed as the most important conservation strategy for the 21st century. In order to escape the pervasive relationships among human poverty, population growth, and environmental degradation

conservationists have recognized the need to involve local people in conservation programs. Likewise, development specialists have recognized that in the face of environmental degradation, there is little chance of improving the quality of life of poor people (Lewis *et al.*, 1990; McNeely *et al.*, 1990; IUCN/UNEP/WWF, 1991; World Resources Institute, 1992). Resources should be managed, therefore, to guarantee not only persistence of the species themselves, but also continued benefits to the thousands of rural and indigenous people in developing regions of the world who depend on them. This approach to conservation implicitly

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requires that species be used, and that markets for their products be developed.

Although not stated as such in the conservation literature, the idea of sustainable use for conservation is based on the hypothesis that the economic value of wild resources can foster development in poor countries that is compatible with preserving biological diversity. The prediction is that if local people are allowed to value wild species, whether for tourism, subsistence use, or commercial trade, development can occur without sacrificing as much biological diversity as would be lost if the potential value of wild resources were not considered (Grigg, 1989; McNeely *et al.*, 1990; IUCN/UNEP/WWF, 1991). Obviously, the hypothesis can only be tested via the accumulation of case studies. One such study is presented here.

TUPINAMBIS LIZARDS: A CASE STUDY

Each year an average of 1,900,000 lizards of the genus *Tupinambis* (Sauria: Teiidae), commonly called tegus, are exported from Argentina and Paraguay to the U.S.A., Europe, and Asia (Hemley, 1984; Luxmoore *et al.*, 1988; Fitzgerald *et al.*, 1991). Two species are exploited: *T. rufescens* and *T. teguixin*. The skins are used for a variety of products, but the majority are destined to become cowboy boots in Texas (Fitzgerald, 1989; Rose, 1992). In spite of the importance of tegus as a resource, their populations have never been managed; they have only been exploited at a rate driven by market demand.

The exploitation of tegus has most of the ingredients to become a model for the sustainable use of wildlife in Latin America. The tegu skin trade is legal and relatively well monitored by the International Convention on Trade of Endangered Species (CITES). Although harvest levels have been high for more than a decade (Luxmoore *et al.*, 1988), there is no evidence that tegu populations are becoming endangered from over exploitation. Additionally, the resource is important to thousands of rural poor and indigenous people in northern Argentina and Paraguay who sell the skins and use the meat and fat (Donadio and Gallardo, 1984; Nor-

man, 1987; Fitzgerald *et al.*, 1991). Skin prices fluctuate between \$3.00 and \$7.00 depending on the size and year; thus, an annual harvest of 1.5 million skins would be worth \$4.5 million to \$10 million to the hunters themselves.

Although the concept of sustainable use for conservation is straightforward, applying it to the problem of tegu exploitation is a very tall order. Even if we disregard the difficulties of evaluating the benefits of sustainable use of tegus in terms of land use, economic development, and biological diversity, we are still faced with the challenging task of ensuring that *Tupinambis* harvests are sustainable. To evaluate the question of sustainability, long-term data on demographic parameters are required.

Monitoring *Tupinambis* populations

Tupinambis are difficult and costly to study in the wild, and population monitoring based on field census is not feasible. Still, demographic information is needed, and we suggested analyses of the annual harvest might provide valuable information for evaluating population trends (Fitzgerald *et al.*, 1991). The tanneries where *Tupinambis* are processed serve as giant collection points for skins. Snout-vent length and sex can be determined from raw and tanned skins; hence a great deal of information on population structure at large geographic scales is potentially obtainable from the harvest. The idea of harvest monitoring is not new; data collected from wildlife harvests have long been used by biologists to identify population trends. Elaborate examples can be found in the fisheries literature (Getz and Haight, 1989).

We tested the feasibility of monitoring *Tupinambis* demographics via the annual harvest by comparing large scale data sets from tanneries to data sets collected in the field. Although it was impossible to compare population size and growth between the data sets, we did test the idea that patterns observed in the field would be reflected in analyses of skins from tanneries (Fitzgerald, 1990; Fitzgerald *et al.*, 1991).

Differences in capture patterns by sex and size class play an important role in which sizes and sexes of tegus are most vulnerable

to hunters at a given time. Males are generally more active during spring breeding seasons and are more vulnerable to hunters in large areas. Females are more vulnerable to hunters in small areas. These observations were supported by data from capture-recapture studies of *T. rufescens* obtained over several consecutive seasons (Fitzgerald, 1990).

In November 1988, 19 tegus collected by hunters were sexed. Chi-square = 5.0, $P < 0.05$. The pattern was repeated in December 1988. Of 18 males (n = 33; Chi-square = 10.0, $P < 0.001$; Fig. 1). Small sample sizes precluded a more detailed analysis each year, but when data were pooled, there were no significant differences in the sex ratios between the two samples. Six of eight subadult males were males, however, and subadult males were more common than subadult females.

In 1988-89, 20,600 tegus were measured and sexed. In March 1989, the sex ratios of tegus hunted were comparable to those from 1988; sample sizes were large that trivially increased the statistical detectability of differences in proportions between samples and probably not biologically significant. In December 1988, 54% of the remaining tegus were subadult males. In the December sample, the proportion of adult males increased hunting and December, especially in the lag time between the capture and the processing of skins. The proportion of adult males in tanneries was near 50%. In the field, skins were sexed as males more difficult to sex

et al., 1991). Skin prices were \$3.00 and \$7.00 per skin per year; thus, an estimated \$10 million to the

potential of sustainable use. Straightforward, application of tegu exploitation is possible if we disregard the long-term benefits of sustainable terms of land use, economic, and biological factors faced with the challenge that *Tupinambis* pose. To evaluate the feasibility, long-term data and other parameters are required.

Tupinambis populations

Difficult and costly to monitor population monitoring is not feasible. Still, monitoring is needed, and we need the annual harvest data for information for trends (Fitzgerald et al., 1991). Where *Tupinambis* collection points, length and sex can be determined from raw and tanned skins; information on population geographic distribution is possible from the harvest. Monitoring is not new; wildlife harvests have allowed biologists to identify appropriate examples can be found in literature (Getz and

possibility of monitoring population dynamics via the annual large scale data sets collected in the field is impossible to compare and growth between field would be reflected from tanneries (Fitzgerald et al., 1991). Activity patterns by sex and important role in which tegus are most vulnerable

to hunters at a given time. Males are apparently more active than females during the spring breeding season and leave scent marks over large areas. Hunters' dogs track the lizards by scent; thus males are especially vulnerable to hunters during the breeding season. These observations were supported with data from carcass collections of *T. rufescens* obtained from hunters during two consecutive seasons, 1987-88 and 1988-89 (Fitzgerald, 1990).

In November 1987, 77.8% of the adult tegus collected by hunters were males ($n = 18$; Chi-square = 5.44; $P < 0.05$) and the pattern was repeated in 1988 when 78.8% of the adults sampled in November were males ($n = 33$; Chi-square = 10.88; $P < 0.001$; Fig. 1). Small sample sizes in some months precluded analyses of subadults for each year, but when the data from both years were lumped, there were no significant differences in the sex ratios of subadults in any sample. Six of eight subadults in November were males, however, so it seems likely that subadult males were also taken in disproportionate numbers during that month.

In 1988-89, 20,617 raw skins of *T. rufescens* and 8,507 raw skins of *T. teguixin* were measured and sexed between December and March. For the months available, the sex ratios of tegus hunted in the field were comparable to those from the tannery data (Fig. 1; sample sizes from the tannery were so large that trivially small differences were statistically detectable. The small differences in proportions of males between tannery samples and carcass collections were probably not biologically relevant.). Sixty percent of adult *T. teguixin* skins sampled in December were males, while adult and subadult males made up between 44% and 54% of the remaining samples. The high proportion of adult male *T. teguixin* in the December sample could have reflected increased hunting of males in November and December, especially considering the lag time between the capture of the lizards and the processing of their skins. The proportion of adult male *T. rufescens* from tanneries was near 50% throughout the study, while between 35% and 39% of the subadult skins were sexed as males. Small skins were more difficult to sex than large ones, so it is

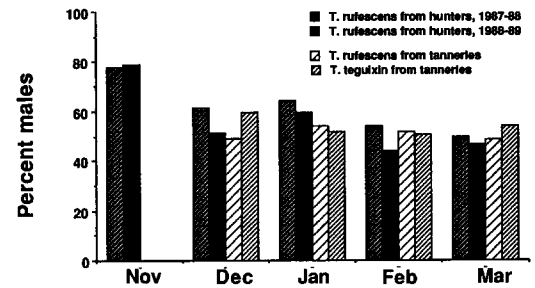


FIG. 1. Percent adult male *Tupinambis* (SVL > 325 mm) according to sample month in carcass collections from hunters and in samples from tanneries. For the months available, the sex ratios from tannery samples reflect well the sex ratios observed in the field.

likely errors in sexing biased the sample towards females (Fitzgerald, 1990). For future studies, it is crucial that samples from tanneries be made in November to test the prediction that more and larger males should appear in the tanneries at that time.

The tannery studies indicated that patterns observed from the carcass collections were reflected in large scale data sets. Carefully controlled harvest analyses should therefore provide long-term data for evaluating population dynamics. Moreover, harvest data will also reveal the effectiveness of management strategies aimed at selectively harvesting or avoiding specific segments of the population, such as adults and juveniles. Obviously, data on hunting effort is needed to help distinguish between natural and human-caused mortality, and they should be collected concurrently with harvest monitoring. Fortunately, the stage has been set for implementing monitoring programs for *Tupinambis* in Paraguay and Argentina, and steps are already being taken in these directions.

To evaluate the question of sustainability of the resource, one would hope to be able to monitor changes in population size, structure, and growth rate, then evaluate whether they were due to anthropogenic causes, such as management, or natural environmental fluctuations. All populations are subject to unpredictable periods of growth and decline (Dennis et al., 1991; Boyce, 1992), and the sensitivity of population growth to unpredictable variation in

the environment should be of concern to conservation biologists. In a recent paper, Pechmann *et al.* (1991) concluded that surprisingly large changes in population sizes of several amphibian species could be explained by fluctuations in recruitment between wet vs. dry years as opposed to anthropogenic causes. In the absence of long-term data, the observed declines could have been misconstrued as having been caused by pollution or habitat modification.

The aim of this paper is to model some of the difficulties in separating the effects of management from stochastic population fluctuations in species with life histories like *Tupinambis*. I pose two questions of interest: For species with life histories like *Tupinambis*, to what extent does environmental stochasticity nullify the effectiveness of management practices and our ability to predict their outcomes? Second, considering the likelihood that errors will be made in estimating demographic trends, what is the effect of stochastic variability on the time to collapse and recovery of *Tupinambis* populations?

ENVIRONMENTAL STOCHASTICITY AND LIFE HISTORY OF EXPLOITED LIZARDS

The sensitivity of a particular species to stochastic fluctuations depends in large part on its life history characteristics, such as age or size at first reproduction, clutch size, and reproductive life span (Crouse *et al.*, 1987; Caswell, 1989). We are slowly accumulating long-term studies of lizard species that provide an idea of the magnitude of variability in some important demographic parameters. In lizards, regardless of clutch size and life span, the survival of yearlings and the proportion of females that reproduce in a given year is highly variable, and can be largely explained by climate and resource abundance. Dunham (1982), for example, interpreted within and among population variance in demographic attributes of the short-lived, early maturing lizard, *Urosaurus ornatus*, in these terms. Environmental variability was also the primary factor responsible for within-population variation in demographic attributes for the long-lived chuckwalla, *Sauromalus obesus* (Abts,

1987). The apparent relationship between micro-climate and resource abundance affects the hatchling success of eggs (Snell and Tracy, 1985), the survival of hatchlings, and also limits the ability of females to garner sufficient energy for reproduction. The end result is good and bad years for recruitment into post-yearling age classes, stemming from variation in survivorship of young or the production of eggs, or both.

Lizards with long life spans tend to exhibit higher coefficients of variation (CV) in the survivorship of yearlings and the proportion of females breeding in a given year. In a classic study of two populations of the short-lived blotched lizard, *Uta stansburiana* (Tinkle, 1967) the CVs in yearling survival were 32% and 39%. The population of *Sauromalus obesus* studied by Abts (1987), exhibited CVs exceeding 70% for both yearling survival and the proportion of females producing clutches over a five year period (Abts, 1987). A population of the very long-lived and slow-growing Galápagos land iguana, *Conolophus subcristatus*, has experienced enormous variation in yearling survival (CV = 147%) and the proportion of females laying eggs (CV = 86%) over the last 15 yr (Snell and Snell, personal communication).

Exploited lizards are generally large species that have relatively long life spans, take several years to reach maturity, and produce a single large clutch annually (Dunham *et al.*, 1988). Lizards of the genus *Tupinambis* possess these attributes (Fitzgerald *et al.*, 1993), as do the large *Varanus* species (Sauria: Varanidae) (Auffenburg, 1988; Wikramanayake and Dryden, 1988), several species of which are exploited for their food, for pets, and the large iguanines such as *Iguana* and *Conolophus*, some species of which are exploited for their food, for pets, or for tourism (Luxmoore *et al.*, 1988).

Although there are no long-term data on *Tupinambis* species that would enable estimation of annual variation in population parameters, it is clear that such variation has potentially important effects on tegu demographics. Therefore, I developed a model to assess the potential effects of variation in yearling survival and total egg pro-

duction in *Tupinambis*. The model also offers insight into the accuracy of measures of population growth in the face of environmental stochasticity.

THE MODEL

I chose to model the dynamics of *Tupinambis* populations using a matrix model of expected population growth based on the lizard's life history. The stages of this method are: (1) parameterization and programming of the model to observe directly the effects of management parameterizations on population structure of the population. The life table projection method is a biological property of the population, and its quantitative characteristics are not dependent on the model (Dunham, 1989; Dennis, 1990). However, I was able to model the effects of management on the population by inserting random values into the model for varying lengths of time, and then using the model to predict the future population structure of *Tupinambis* populations. I chose to examine the effects of management rather than to examine the effects of natural population fluctuations.

The life table was constructed using a computerized matrix model in Excel 4.0 for Windows. The matrix model consists of columns corresponding to the age classes, and rows corresponding to the age classes, respectively. The number of individuals in each age class was calculated by multiplying the survivorship assigned to each age class by the number of individuals in the previous age class of the previous year.

The model was constructed to simulate the population history of *Tupinambis* species, but it is not limited to any large reptile species. The model was based solely on the life history of *Tupinambis* species, but it is not limited to any large reptile species. The model was based solely on the life history of *Tupinambis* species, but it is not limited to any large reptile species. The model was based solely on the life history of *Tupinambis* species, but it is not limited to any large reptile species.

relationship between resource abundance and success of eggs (Snell survival of hatchlings, ability of females to gather for reproduction. The bad years for recruiting age classes, stem in survivorship of eggs, or both. The spans tend to exhibit variation (CV) in the eggs and the proportion in a given year. In populations of the lizard, *Uta stansburiana*, the CVs in yearling survival were 39%. The population of *T. rufescens* studied by Abts had survival exceeding 70% for yearlings and the proportion of eggs over a five-year period (77%). A population of slow-growing *Galapagos* *Uta stansburiana* exhibited enormous variation in survival (147%) and the proportion of eggs (CV = 86%) (Snell and Snell, personal

communication). Generally large species with long life spans, take long to reach maturity, and produce few offspring annually (Dunham *et al.*, 1988). The genus *Tupinambis* (Fitzgerald *et al.*, 1988) includes several species (Saurians) (Saurians, 1988; Wikramanayake, 1988), several species of lizards such as *Iguana* and *Crotalus*, species of which are kept as pets, or for tour-

ism. Long-term data on population growth would enable estimation of the effects of variation in population growth that such variation has on tegu lizards. Therefore, I developed a model to estimate the effects of variation in population growth and total egg pro-

duction in *Tupinambis* populations. The model also offers insights into the likelihood of accurately measuring population trends in the face of environmental stochasticity.

THE MODEL

I chose to model hypothetical *T. rufescens* populations using simple numerical projections of expected future population sizes based on the lizard's life table. The advantages of this method were its computational and programming simplicity, and the ability to observe directly the effects of different parameterizations of the model on age structure of the population through time. The life table projections exhibited realistic biological properties and possessed mathematical characteristics of more elaborate quantitative models (Boyce, 1977; Tuljapurkar, 1989; Dennis *et al.*, 1991). Moreover, I was able to easily model unpredictable changes in the success of reproduction by inserting randomized life history values for varying lengths of time. The goal was not to predict the future size and structure of *Tupinambis* populations in nature, but rather to examine the dynamics of the hypothetical population under certain conditions.

The life table was constructed as an array on a computerized spreadsheet (Microsoft Excel 4.0 for Windows), with rows and columns corresponding to age classes and years, respectively. The number of individuals of each age was calculated by multiplying the survivorship assigned to that age class by the number of individuals in the previous age class of the preceding year. The number in age class 0 was determined by summing the reproductive output of each female in the previous year.

The model was designed to mimic what is known about *T. rufescens*, because its life history is better known than other *Tupinambis* species, but it is generally applicable to any large reptile species. The life table was based solely on females, because *Tupinambis* are polygynous and the availability of males in large populations is probably not limiting to females. The model made no allowance for density dependence, under the assumption that *Tupinambis* popula-

tions in nature are well below carrying capacity because of the continuous hunting pressures they have experienced over the last decade.

The age structure of the model was lumped into broad age categories (yearlings, subadults, adults) and was thereby analogous to a stage-classified model (Getz and Haight, 1989). Size and age are not well correlated in *T. rufescens* (Quintana, 1991), and it is probable that survivorship in these lizards is more dependent on size than age. Survival through year 1 was a stochastic parameter, modeled by randomly selecting variates between 0 and 1 from a beta distribution with a mean of 0.15 (Getz and Haight, 1989). The survivorship of subadults, age classes 2 and 3, was fixed at 0.65 for all the simulations. The survivorship of adults, age classes ≥ 4 yr, was manipulated from 0.50 to 0.70 by increments of 0.05 to simulate different levels of adult survivorship that would presumably result from management. Survivorship was fixed at 0.00 beyond year 13, because *T. rufescens* is known to live for 13 yr (Snider and Bowler, 1992).

Eighty-five percent of female *T. rufescens* from the Argentine chaco have laid eggs by their fourth spring, and the average clutch size of all females in one study was 21.4 ($n = 10$; $SD = 4.95$). All females do not breed every year, and there is evidence of a correlation between body size and clutch size (Vitt, 1986; Fitzgerald *et al.*, 1993). For the purposes of the model, I assumed 85% of the first-year reproductive females (four-year-olds) laid 10 female eggs each, and females older than 5 yr laid 12.5 female eggs each. The proportion of females ≥ 5 yr laying eggs was determined by randomly selecting variates between 0 and 1 from a beta distribution with a mean of 0.80.

Each run of the model began with 100,000 female hatchlings. The population size in a given year ($n_{(t)}$) was the sum of all individuals in that year. The true population growth rate, μ , was calculated as the average ratio of the log-transformed population sizes between years:

$$\mu = 1/q \left(\sum_{i=1}^q [\ln n_{(t)} / \ln n_{(t-1)}] \right)$$

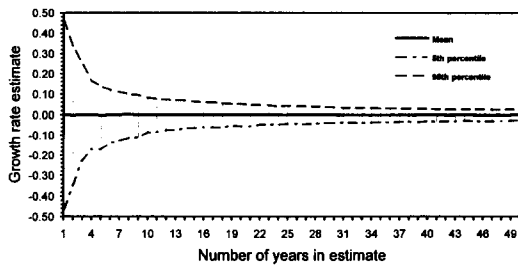


FIG. 2. Convergence to the long-run estimate of population growth, μ , with 90% confidence limits calculated from 500 independent runs of the model with 50% CV in recruitment of yearlings and proportion of females breeding in a given year.

where q = the number of years included in the growth rate. This estimate is the numerical analog of the infinitesimal mean of the diffusion process of population growth in an analytical model (*sensu* Tuljapurkar and Orzack, 1980; Caswell, 1989; Dennis *et al.*, 1991). As μ is the average of the growth rate process, longer time series allow more accurate estimates of the population trajectory. True long-term, or parametric, values of μ presented below were those calculated over 100 yr intervals. To investigate the sensitivity of the length of time series available for demographic analysis on conservation problems, estimates of μ , denoted g , were computed from shorter time series: 3, 6, 9, 18, 36, and 72 yr. Shorter estimates of g were taken from comparable points along the time series.

Stochastic population processes have been studied extensively (Tuljapurkar, 1989; Dennis *et al.*, 1991) and it is well known that, all else being equal, increased variance in population processes results in a decrease in the true growth rate, μ (Boyce, 1977, 1992). I assumed constant levels of stochasticity for each simulation. Therefore, where appropriate, I accounted for the non-linearity in μ by adjusting slightly the level of adult survivorship to retain zero population growth (ZPG) as a base line.

Simulations were done to investigate the interplay between variable recruitment (resulting from environmental stochasticity) and different levels of adult survivorship (resulting from management). I manipulated the variance of the stochastic parameters according to five CVs within the

range of variability known for lizard populations: 10%, 25%, 50%, 75%, and 100%. The same CV was used for both stochastic parameters, yearling survival and proportion of breeding females, in a given simulation. For each CV, simulations were run for each of the five levels of adult survivorship. Each simulation consisted of 500 independent runs of the model. To diminish the effect of initial conditions, the first 20 yr were not included in the analyses.

RESULTS AND DISCUSSION

Stochasticity and convergence to the long-term population growth rate

The population growth rate was extremely sensitive to stochastic recruitment. Even a CV as low as 10% caused year-to-year population growth rates ($\ln n_{[t]}/\ln n_{[t-1]}$) to fluctuate between 0.50 and -0.50 , even though the long-term μ was actually 0.00. An increase in the CV to 25%, still low for lizards, resulted in unpredictable fluctuations in population growth from 1.50 to -1.50 between years.

Fluctuations in population growth resulted in very long convergence times to a precise estimate growth representative of the real population trajectory. With 5 yr included in the estimate, and 50% CV in recruitment, for example, 90% limits of μ ranged between 0.16 and -0.16 for a population at ZPG (Fig. 2). As more years were included in the time series, the confidence limits of μ converged toward the mean, but remained broad for long periods. With 15 yr included in the estimate, which in practice is a very long-term data set for sustainable use programs aimed at justifying biological diversity, there was a 90% chance that μ would fall between 0.06 and -0.06 . These ranges of growth rate estimates are far from trivial; a *Tupinambis* population as modeled here declining at 10–15%/yr would be $<10\%$ its original size in 10–15 yr. So these differences in μ are important, but there is a high probability of getting an incorrect estimate.

Type II errors in growth rate estimates

Each 5% change in adult survivorship caused a 3.0–3.5% change in the long-term value of μ , thus changes of this magnitude

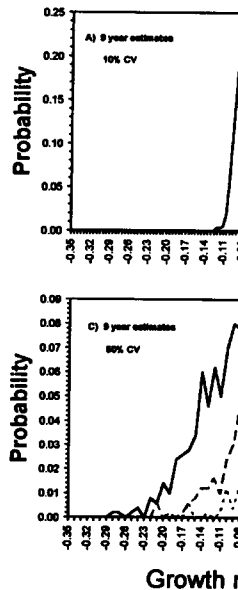


FIG. 3. Probability distributions of interannual yearling growth rates.

are important in a population management context. How does increased variance in estimates of the long-term growth rate affect our ability to distinguish between population management options?

I calculated probability distributions of μ from 500 independent simulations at each level of adult survivorship and level of variation. The distributions responded to population growth rates in very different ways, with considerable overlap between populations (Fig. 3). The overlap depended on the level of variability, the number of years, g , and the difference in growth rate trajectories resulting from different adult survivorship levels. Simulations from populations with declining adult survivorship, for example, had little overlap with simulations with high CV and high adult survivorship by 10%.

The problem of overlapping distributions of g is a common one that describes the probability of getting a growth rate estimate that differs from the real population

variability known for lizard populations, 10%, 25%, 50%, 75%, and 100%. CV was used for both stochastic recruitment, yearling survival and proportion of breeding females, in a given simulation. For each CV, simulations were run at the five levels of adult survivorship. Each simulation consisted of 500 independent runs of the model. To diminish the effect of initial conditions, the first 20 years were not included in the analyses.

RESULTS AND DISCUSSION

Stochasticity and convergence to the long-run population growth rate

Population growth rate was extremely variable with stochastic recruitment. Even a 10% CV caused year-to-year population growth rates ($\ln n_{[t]}/\ln n_{[t-1]}$) to fluctuate between 0.50 and -0.50 , even though the true μ was actually 0.00. An increase in the CV to 25%, still low for lizards, led to unpredictable fluctuations in growth from 1.50 to -1.50 over 10 years.

Large variations in population growth rates led to very long convergence times to a stable growth rate representative of the true population trajectory. With 5 yr of data for the estimate and 50% CV in recruitment, for example, 90% limits of μ were between 0.16 and -0.16 for a population with $\mu = 0$ (Fig. 2). As more years were included in the time series, the confidence intervals converged toward the mean, but they were still broad for long periods. With 15 yr of data for the estimate, which in practice is a long-term data set for sustainability programs aimed at justifying biological conservation, there was a 90% chance that the estimate would fall between 0.06 and -0.06 . The large range of growth rate estimates are not surprising; a *Tupinambis* population was declining at 10–15%/yr for 100 years, 10% of its original size in 10–15 years. Thus, differences in μ are important, and a high probability of getting an accurate estimate.

Effect of variability in growth rate estimates

A 10% change in adult survivorship or a 5% change in the long-term growth rate leads to changes of this magnitude

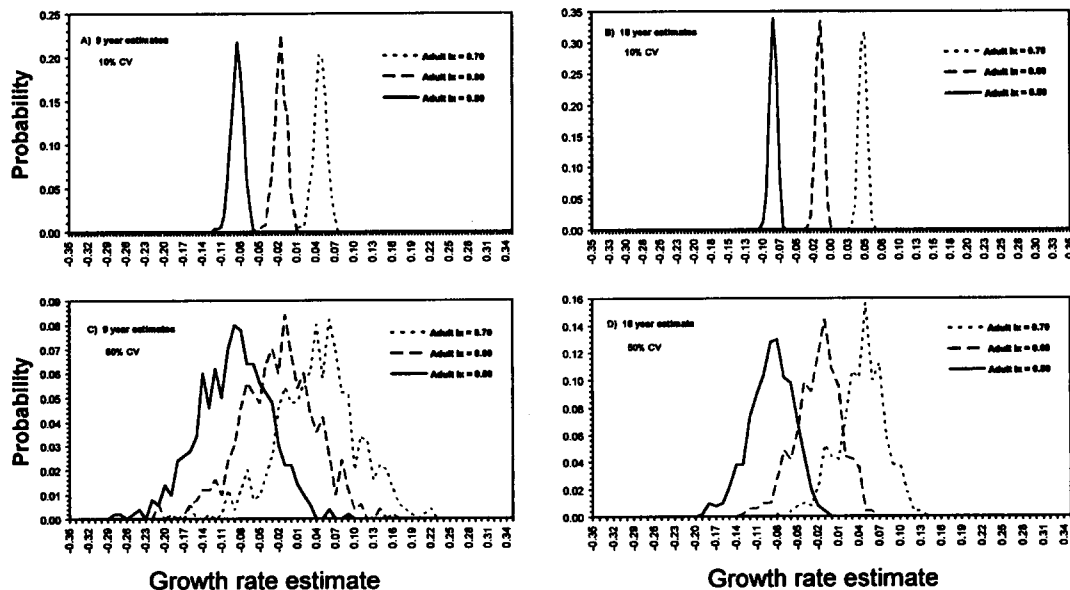


FIG. 3. Probability distributions of g resulting from different levels of adult survivorship (lx), and different CVs in interannual yearling survival and the proportion of breeding females.

are important in a population management context. How does the inherent variability in estimates of the long-run growth rate affect our ability to distinguish the outcome of population management from stochastic fluctuations?

I calculated probability distributions of g from 500 independent runs of the model for each level of adult survivorship and for each level of variation. These distributions corresponded to populations growing or declining at very different rates, but there was considerable overlap between the g s of different populations (Fig. 3C, D). The degree of overlap depended upon the magnitude of variability, the number of years included in g , and the difference in the true population trajectories resulting from modifications in adult survivorship. The distributions of g from populations with 10% CV and differing in adult survivorship by 20%, for example, had little overlap compared to populations with high CV and differing in adult survivorship by 10% (Fig. 3).

The problem of overlap between two distributions of g is important because it describes the probability of obtaining a growth rate estimate that does not indicate the real population trajectory. Discounting

5% of the area of overlap to account for the usual alpha level in a one-tailed test (Type I rate of error), this error amounts to a statistical Type II error, or the likelihood of accepting the null hypothesis when it is in fact, false (Sokal and Rohlf, 1981). The null hypothesis in this case being that the true population trajectory, g , indicates the true population trajectory.

The probability of making Type II errors was always large with CVs $> 10\%$ when few years were included in g (Fig. 4a). With CV = 50% in the model and 9 yr used to compute g , the probability was more than 0.40 of committing a Type II error when trying to detect a 6% change in population trajectory (from a 10% change in adult survivorship). The probability remained substantial, but dropped to 0.27 when g was based on an 18 yr time series. Eighteen years were sufficient, however, to detect a 6% difference in population trajectory with a CV of 25% in the model, or to detect a 13% difference with CV of 50% (Fig. 4b). Larger CVs resulted in maintaining high probabilities of committing Type II errors for exceedingly long periods when trying to detect $\leq 6\%$ changes in population trajectory.

Summarizing, because of the sensitivity

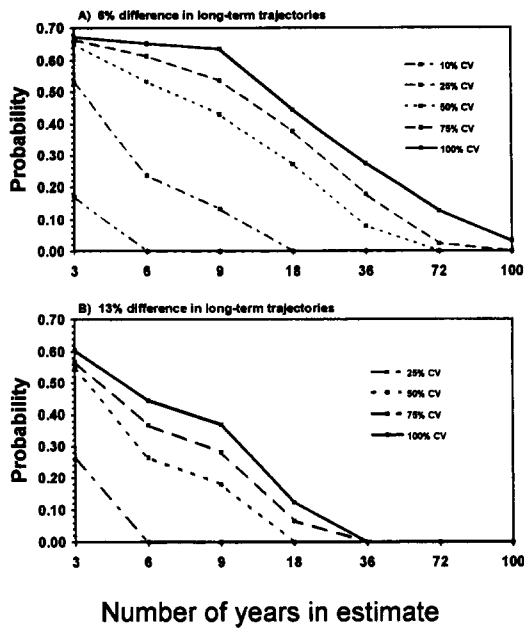


FIG. 4. Probabilities of obtaining estimates of population growth that do not correspond to the true, or long-run, trajectory (Type II errors). The upper graph (A) shows the probabilities of failing to detect a 6% change in trajectory, which could arise from a 10% change in adult survivorship. The lower graph (B) shows the probabilities of committing Type II errors when trying to detect a 13% change in trajectory.

of *Tupinambis* populations to recruitment of yearlings, stochastic effects had dramatic effects on the population growth rate, which resulted in broad confidence limits around the true, or long-term, population trajectory. Based on the probability of committing Type II errors, it appears that long-term data sets spanning decades would be required to estimate population trends with much precision. If variability in vital rates of *Tupinambis* is as high as in other lizard species, there will always be a significant probability that the short or middle-term growth rate estimates do not reflect the true population trajectory.

It is important to note that the stochastic parameters in the model were independent from each other, thus autocorrelation in the time series was limited to that resulting from the age structure of the population. Increasing autocorrelation in the model would result in even longer convergence times by keep-

ing g away from the long-term mean for extended periods (Taylor, 1986). Additionally, management practices in the real world will change and these changes will be superimposed, adding to the difficulties of evaluating the effectiveness of those same practices.

Effect of variation on time to collapse and recovery

To examine the effects of environmental variation on the time for hypothetical populations to reach one-half their original size ($n_0/2$) and recover from the lowest size reached after a period of decline, I simulated decline and recovery phases for populations under different levels of stochastic variation. Each simulation began with adult levels of mortality fixed at 10% higher than that needed to maintain a ZPG trajectory, and was projected for 15 yr. At year 16, adult mortality was decreased to 10% lower than the ZPG level to stimulate recovery, and the population was monitored for an additional 25 yr. The time periods were chosen arbitrarily to approximate feasible planning horizons. The criterion of half-size was chosen as an indicator of poor stock condition on the basis that changes in policy would be needed if a population had fallen to half-size (Getz and Haight, 1989).

As annual variation in reproductive output increased, the probabilities of the population declining to half-size were dampened. With CV = 10%, the probability was 0.00 for 5 years, but increased to 0.50 within 8 yr. The probability of being below half-size was 1.00 within 12 yr. With CV = 50%, however, the chances of the population falling below half-size were 0.18 by year 5, but remained <0.50 by year 8 (Fig. 5). As variation increased, the maximum probability of reaching half-size decreased substantially. With CV = 100%, for example, there was a 0.50 probability of reaching half-size after 10 yr, and the maximum probability the population would be below half-size was 0.70 after 16 yr (Fig. 5).

Increasing stochasticity had important effects on the potential for recovery of populations. With CV = 100%, the mean population size grew to 3.50 times its initial size (before decline) in 25 years, compared to

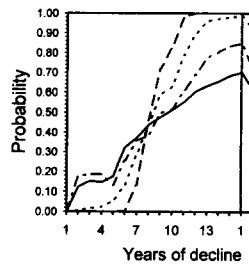


FIG. 5. The probability of reaching half-size in a given year according to the model. The left half of the decline period of 15 yr, followed by a recovery period of 25 yr.

only about 2.00 for the 10% CV. Interestingly, populations with 100% CV stood a greater chance of reaching half-size following the decline phase. The population with 50% CV had a 0.50 probability of recovering to initial size after 10 yr, to a 3% chance for the 100% CV. With 100% CV, there was a 45% chance of reaching half-size within 10 yr, a 45% chance of recovering to initial size within 10 yr, and a 45% chance of recovering to initial size within 10 yr.

Apparently during the runs, increasing stochasticity in the sequences of high and low recruitment increased the chance of reaching half-size. The increase in variability in recruitment in some runs with very high variability of reaching half-size during the runs and persisted through the recovery phase.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Results from the model converged on the conclusion that populations with life histories like that of *Tupinambis* and other species of high stochasticity were highly vulnerable to years of low recruitment. The long life span of *Tupinambis* enabled the population to persist through sequences of bad years, but not with sustained periods of low recruitment. High variability in years of recruitment

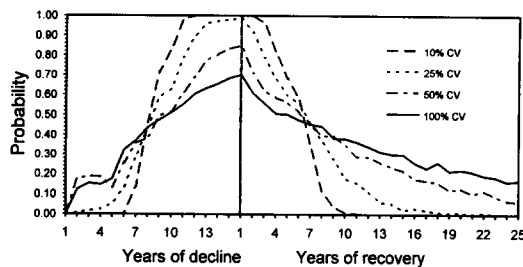


FIG. 5. The probability of the population being $<n_{00}/2$ in a given year according to 4 levels of variance in the model. The left half of the graph corresponds to the decline period of 15 yr, followed by a recovery period of 25 yr.

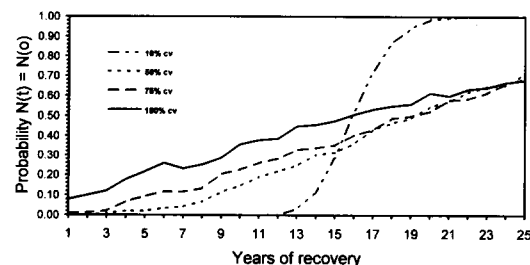


FIG. 6. The probability of the population recovering to its original size before decline (n_{00}) according to 4 levels of variation in the model. The x-axis is years of recovery following a decline of 15 yr.

only about 2.00 for smaller CVs. Surprisingly, populations with higher variability stood a greater chance of recovering sooner following the decline (Fig. 6). The population with 50% CV had a 25% chance of recovering to initial size in 13 yr compared to a 3% chance for the population with 10% CV. With 100% CV in the model, there was a 45% chance of recovery in the same amount of time.

Apparently during the decline phase of the runs, increasing variation permitted sequences of high recruitment, which increased the chances that some runs would maintain a relatively high population size. The increase in variation also resulted in some runs with less than average recruitment, which explains why the probability of reaching half-size was higher earlier in the runs and persisted throughout the recovery phase.

CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

Results from the life table simulations converged on the conclusion that for species with life histories like *Tupinambis*, the risks of stochasticity were far outweighed by the chances for years of exceptional recruitment. The long life span of the lizards enabled the populations to withstand sequences of bad years for recruitment even with sustained periods of high adult mortality. High variability allowed for boom years of recruitment that accumulated to

achieve more rapid recovery rates than when variability was low.

Although managers may be forced to accept limited precision when evaluating the demographic patterns of many exploited populations, management strategies aimed at causing large differences in population trajectory should be much easier to detect. Thus to learn quicker how populations respond to harvesting, and what levels of exploitation are sustainable in the real world, it may be productive to experiment with deliberately alternative management policies. This is the basic concept of "adaptive management" (Walters, 1986). The apparent resilience of *Tupinambis* to high and variable harvests, their Fitzgerald *et al.*, 1991) reduce the likelihood of catastrophe, and may make the *Tupinambis* exploitation system well suited for "management experiments."

Unfortunately there are no easy solutions, and there are risks associated with adaptive management when we have little data, limited experience, and fledgling monitoring programs. By manipulating populations dramatically, we may disrupt biotic interactions that may not be restorable if unforeseen population collapses occur. From the perspective of the sustainable use strategy, the risk is that unstable supplies of the target population could reduce the short-term economic benefits of exploitation, increasing the incentives to shift to alternative, more destructive land uses.

Alternately, seemingly "conservative" management strategies may be misleading,

in that maintenance of the status quo may not be conservative. In the case of *Tupinambis* exploitation, it remains uncertain whether basing management on traditional levels is over or under exploiting the populations. Additionally, the probability of evaluating the effects of small changes in policy with accuracy is low. Nowhere have problems of this sort become more evident than in fisheries management, where elaborate and conservative management has been attempted with unforeseen collapses occurring anyway (Walters, 1986).

In summary, the results are both encouraging and foreboding for conservation. On the one hand the modeling results can help explain how *Tupinambis* have endured high and variable harvest rates for many years. On the other hand, stochastic effects and the Type II error problem mean that it will be difficult to assign causes to population trends even when equipped with long-term data sets. As more sustainable use programs are initiated, we are faced with the dilemma of managing resources with limited data, and perhaps being unable to determine if management is affecting the population in ways we predict. Clearly, institutionalized monitoring programs are required, but establishing informative ones is yet another challenge to developing the sustainable use for conservative strategy. Of great importance is that monitoring programs incorporate estimates of variance in key population parameters.

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