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DEMOGRAPHIC STOCHASTICITY DOES NOT PREDICT PERSISTENCE OF GECKO POPULATIONS

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Abstract. We present a population viability model for an arboreal gecko (*Oedura reticulata*). This gecko needs a habitat of smooth-barked *Eucalyptus* woodlands. In Western Australia its distribution has declined dramatically, largely through clearance of woodlands, but populations persist within woodland remnants. Evidence from extensive field data suggests that the gecko was formerly distributed through much of the original eucalypt woodlands, and that geckos show little movement between patches. The populations in all woodland remnants seem to be isolated. We ask whether the present distribution of the gecko across remnants could have been produced solely by the extinction of populations through demographic stochasticity.

To test this possibility, we developed a stochastic, individual-based model including environmental stochasticity and estimated the percentage of extinct populations of different size from known field characteristics and the time span since the clearing of the woodland. The model predicted a relationship between remnant size and gecko persistence, driven by demographic stochasticity, that is qualitatively similar to the observed pattern. Despite extensive testing, however, we found that the model predicted an incidence function much too optimistic for the observed distribution of populations in small remnants. This discrepancy between field data and our model is due to a series of implicit assumptions. Thus, our modeling exercise sheds light on the procedures commonly applied to population viability analyses of single populations of endangered species. The implicit assumptions involved in such models make many predictions vague. We suggest that for the study of declining species like *O. reticulata* it is essential to adequately test extinction models and therefore population viability analyses.

Key words: extinction; gecko; incidence function; modeling; Oedura reticulata; *population viability analysis; Western Australian wheatbelt.*

INTRODUCTION

Population viability modeling has become an important tool in conservation biology (Lindenmayer and Possingham 1996). Such analyses have been performed for over 100 species, many of which are endangered, long-lived vertebrates (e.g., Reed et al. 1988, Red-cockaded Woodpecker; Noon and Biles 1990, Spotted Owl; Moehlman et al. 1996, black rhino; Wiegand et al. 1999, brown bear). Population viability analyses can provide helpful analytical tools and enable the exploration of the implications of many possible management strategies and scenarios (Lindenmayer and Possingham 1996). However, by concentrating on endangered species, population viability analyses are typically restricted to one or a few populations. As a consequence, the opportunities for model validation are extremely limited. This has two major impacts. First, except in some rare circumstances (e.g., Brook et al. 1997), the degree of realism of most population viability analyses remains untested. Thus, we have no way of knowing whether the predictions made by the model are realistic (Reed et al. 1988). Second, the lack of ability to test the realism of population viability models means that for any particular case we learn little about the extinction process itself. Thus, although there has been much work focusing on the prevention of population extinction, that research has told us little of an

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empirical or theoretical nature about extinction processes.

One way of using population viability analyses to investigate extinction processes is to model declining species that are yet to reach the point of endangerment. Such species provide case studies of species that are prone to extinction, yet permit empirical evaluations of the population viability models. By evaluating these models the extent to which a specific model reflects a natural situation can be determined. It therefore follows that any departures from nature in the predictions of the model will identify aspects of the extinction process not considered in the current model version.

Here, we present a population viability model of a species of arboreal gecko (*Oedura reticulata*) whose distribution has declined dramatically this century, largely through habitat destruction. Populations of this gecko persist within woodland remnants of the Western Australian wheatbelt despite the clearance of ~130 000 km^2 (>90%) of the original vegetation in the 20th century (Saunders et al. 1993). *O. reticulata* is highly dependent on smooth-barked eucalypt woodlands, mainly *Eucalyptus salubris, E. salmonophloia,* and *E. wandoo* that provide substantial amounts of dead wood for shelter (How and Kitchener 1983, Greer 1989). Well-documented changes in the vegetation (Arnold et al. 1991, Saunders et al. 1993) combined with a number of long- and medium-term population demographic studies (How and Kichener 1983, Kitchener et al. 1988, Sarre 1995*a*, 1996), presence/absence surveys (Kitchener et al. 1980, Sarre et al. 1995), and genetic studies (Sarre 1995*b*) make this species an ideal candidate for the development and evaluation of an extinction model.

As part of a study of the demography and genetics of *O. reticulata*, Sarre et al. (1995) conducted a survey of the distribution of *O. reticulata* in 32 smooth-barked *Eucalyptus* remnants. The considered area comprised >1500 km between Kellerberrin and Trayning in the Western Australian wheatbelt. Since 1900, ~90% of the original vegetation in the study area has been cleared for agriculture (Hobbs 1993), leaving over 450 vegetation remnants (size range <1–1190 ha). The peak of the vegetation clearing was around 1920. Of those 32 remnants surveyed, *O. reticulata* was present in 23 with a positive correlation between remnant size (number of trees) and the probability of occurrence (Sarre et al. 1995). This current pattern of distribution of *O. reticulata* among the woodland remnants depends on three factors: (1) the distribution of *O. reticulata* before the vegetation clearance, (2) the rate of extinction of local populations since the vegetation clearance, and (3) the rate of colonization of remnants following the extinction events. The nine remnants in which *O. reticulata* were not observed were part of larger regions of smooth-barked *Eucalyptus* woodland (suitable for *O. reticulata*) and are adjacent to formerly contiguous woodland that contain extant populations of *O. reticulata*. Thus, it is probable that *O. reticulata* were present in all 32 remnants before the vegetation clearance, and that the observed absences are the result of extinctions (Sarre et al. 1995). Genetic (Sarre 1995*b*), pitfall trapping (Sarre et al. 1995), and mark–recapture studies (Kitchener et al. 1988) indicate that if *O. reticulata* moves between remnants, then it is extremely rarely. Consequently, remnant populations separated by just a few hundred meters can be considered isolated. Thus, recolonization following extinction is unlikely. We therefore have a situation in which population extinction rates can be estimated from field data, uncomplicated by metapopulation dynamics (Hanski 1999).

One way to understand the historical contingencies of the present biogeographical patterns is through the application of modern genetic methods (e.g., Sarre 1995*b*, Hänfling and Brandl 1998, Avise 2000). In the present paper, we point to an alternative approach to retrieve information about historical processes: the careful comparison of models that predict the dynamics of occurrence across remnants, and field data. Specifically, we address the question: Could extinction by stochastic demographic processes explain the observed occupancy patterns of *Oedura reticulata*? The distribution of this species has declined dramatically this century, largely through habitat destruction. We use the demographic characteristics of *O. reticulata* observed in field studies to construct a stochastic demographic population model and use this model to predict the expected occupancy pattern of *O. reticulata* across the 32 remnants. We hypothesize that the model will predict a positive correlation between remnant size and probability of occurrence, due to the higher extinction risk of smaller populations under demographic stochasticity (Lande 1993). Thus, we expect a qualitative agreement between model results and field observation. However, it is not possible to estimate a priori if the model results will be more optimistic, more pessimistic, or quantitatively similar to the field observations. We compare the observed and expected extinction data and use this comparison to discuss the possible mechanisms of extinction operating on *O. reticulata.*

THE MODEL

The general aim of our model is to predict the local extinctions in the gecko species *O. reticulata.* As we are concerned with extinction processes, it is important to be accurate at low population sizes. Consequently, we chose an individual-based approach (Judson 1994, Uchmanski and Grimm 1996), which enables us to consider differences in sex, age, or the position of the territories of individuals. Within our basic time step of one year, each individual may change territory, die, or reproduce. The destiny of each individual is determined by random numbers according to probabilities estimated from field data and thus our model includes demographic stochasticity. Environmental stochasticity is incorporated through the occurrence of a random sequence of dry or hot years, which influence reproduction and hatching.

Our model assumes that all trees within a remnant have the same size and properties irrespective of remnant size. Thus, our model assumes no correlation between remnant size and habitat quality from the standpoint of our gecko species. Based on the territoriality of *O. reticulata,* we chose a spatial model that enables us to relax the assumption of ideal mixing made by most approaches of modeling population viability (e.g., Shaffer 1983, Price and Kelly 1994, Forys and Humphrey 1999). Due to the restricted movement of individuals, geckos are heterogeneously distributed within the simulated woodland remnant, although all trees are identical.

During each time step (one year), the model performs four steps: first, the position of adults is updated; second, individuals may die; third, subadults (geckos in their first year of adulthood) choose their territories; and finally adults reproduce. Home trees are enumerated randomly at the beginning of a simulation. For each of the four steps, the individuals are handled by the model according to this numbering. Thus, the sequence of working through the territories is fixed during one simulation run but differs between simulations. All parameters (Table 1) were chosen a priori according to published reports (How and Kitchener 1983, Kitchener et al. 1988, Sarre 1995*a*) and unpublished field notes (S. Sarre, *unpublished notes*). For a few parameters, no field data were available and we were forced to supplement our information with data from an arboreal gecko occurring on the same trees (*Gehyra variegata*).

Trees

We view a woodland remnant as the number of trees suitable for *O. reticulata.* We regard all trees as identical and make the assumption that the remnants are perfectly isolated. Thus, we model the local dynamics of an isolated population within a single remnant. Each forest remnant may have a particular size and structure of nearest neighbor distances between trees. To generate ranks of neighbors, a remnant was modeled by a grid of the size (number of trees × number of trees). Each cell is suitable for one tree. At the beginning of each simulation, trees become randomly distributed across cells. This enables the determination of the nearest neighbor of each tree, the next neighbor, and so on. Note that we consider only the rank of neighborhood and not the actual distance.

As already noted, each tree may be used by several individuals. We fixed the maximum number of territories of adults on a single tree to five (maximum carrying capacity of one tree). Beside these five adults, up to 10 juveniles may live on one tree. We introduced these limits to avoid unrealistic densities. If not stated otherwise, the initial density of each simulation is four juveniles and four adults per tree (sex ratio 1:1). We chose this high density because *O. reticulata* was probably widely distributed throughout the woodlands of the wheatbelt at the beginning of the 20th century. The extensive clearing of the *Eucalyptus* woodlands was very rapid and probably forced this habitat specialist to move into the remnants, leading to high population densities. Simulations by Wiegand (1996) have shown that population persistence for 70 yr is insensitive to initial density as long as initial densities are not below one gecko per tree. Thus, our simulations start with conditions probably quite similar to the conditions just after the clearing of the forests and even if our estimate of initial density cannot be precise, this has minor effects only on estimated persistence.

Weather

During very hot years, eggs experience a high mortality rate. Environmental effects on survival are minimal for older individuals. However, during dry years, some females do not reproduce, probably because of their low nutritional status due to the low abundance of arthropods (see Henle 1990 for the sympatric species *Gehyra variegata*). Therefore, we incorporated the following simple weather regime using some rules of thumb guided by field experience: (1) the last one to three years of each decade are assumed to be dry; (2) 15% of the years are hot; and (3) hot and dry years are correlated (85% of hot years are also dry).

Age classes

We divided the model population according to age and sex: eggs, juvenile females and males, and adult females and males. Since juvenile females become adult at a mean age of 4.8 yr and males at 2.8 yr (Kitchener et al. 1988), juvenile females are subdivided into classes with an age of 1, 2, 3, or 4 yr and juvenile males into classes with an age of 1 or 2 yr. Twenty percent of the juveniles reach subadulthood one year early (females at age 4 instead of 5, males at age 2 instead of 3) and are being referred to as premature in Table 1. During the transition from the juvenile to the adult age class, individuals have to search for a territory.

Mortality

Mortality depends on age and sex (Table 1; How and Kitchener 1983). No data on age-dependent adult mortality are available, and we assume a constant mortality rate for adult geckos with no difference between sexes. For that reason, we did not adopt a sophisticated age structure for our model and instead, we used one age class for the adults. For changes in individual territories, we implemented an additional mortality risk for each switch to another tree (to account for an increased predation risk due to leaving the territory). Estimates of the movement mortality rates of adult males and females are not available. We selected them (Table 1) in such a way that the overall mortality rate is similar

TABLE 1. Overview of the parameter values used during most of the simulations and sensitivity analyses on remnant populations of the arboreal gecko *Oedura reticulata*.

			Mean time to extinction			
Parameter	Standard value	Accuracy	T_{max} (yr)	T_{min} (yr)	+10% (yr)	−10% (yr)
A) General						
No. smooth-barked eucalypts in remnant	8–1000	1	⋯	⋯	⋯	⋯
Range of a gecko (unit, no. trees)	10	2	⋯	⋯	⋯	⋯
Maximum capacity per tree						
Juvenile	10	2	⋯	⋯	⋯	⋯
Adult	5	2	⋯	⋯	⋯	⋯
No. good years per decade	8	2	⋯	⋯	⋯	⋯
Probability of hot year	0.15	2	⋯	⋯	⋯	⋯
Probability that a hot year is also dry	0.85	2	⋯	⋯	⋯	⋯
B) Mortality						
Probability of not hatching						
Hot year	0.75	2	∞	192	⋯	⋯
Normal year	0.46	2	∞	24	−140	177
Mortality rate, females						
1st year	0.4	2	∞	35	−109	142
2nd year	0.3	2	∞	34	−79	90
3rd year	0.2	2	∞	45	−43	33
3rd year, premature	0.15	2	511	132	⋯	⋯
4th year	0.1	2	605	45	−29	13
Mortality rate, males						
1st year	0.4	2	534	42	−31	14
1st year, premature	0.2	2	386	196	⋯	⋯
2nd year	0.1	2	408	41	−17	3
Basic mortality, adult						
Females	0.1	2	∞	20	−112	152
Males	0.1	2	548	42	−32	7
Mortality per tree switch						
Adult females	0.1	3	∞	16	−69	78
Adult males	0.1	3	342	331	⋯	⋯
Adult females and males	0.1	3	∞	0	−121	166
Subadult females	0.1	3	550	112	⋯	⋯
Subadult males	0.1	3	360	234	⋯	⋯
Males looking for partners	0.1	3	475	25	−24	18
C) Miscellaneous						
Probability of prematurity	0.2	2	∞	250	⋯	⋯
Probability of a new territory search by adult						
Females	0.3	2	∞	71	−55	57
Males	0.45	2	553	239	⋯	⋯
Females and males	0.45† 0.3‡	2	∞	61	−72	68
Probability of establishment on a tree with a territory of an adult of the same sex						
Subadult female	0.2	2	290	589	⋯	⋯
Subadult male	0.2	2	345	331	⋯	⋯
Subadult female and male	0.2	2	617	96	−24	−1
Basic probability of rejecting a tail	0.1	2	330	293	⋯	⋯
Probability of rejecting a tail per tree switch	0.1	3	337	339	⋯	⋯
Probability of females with incomplete tail not laying an egg	1	3	342	341	⋯	⋯
Probability of females not laying an egg in dry year	0.1	2	357	180	⋯	⋯

Notes: Standard values were estimated a priori based on field data and educated guesses. The accuracy of each estimate was evaluated on a rank scale: well known, 1; approximately known, 2; not well known, 3. T_{max} and T_{min} are mean time to extinction in years under extreme values of the respective mortality parameters, 0 and 1. The infinity symbol (∞) indicates that all populations survived for 999 yr. The +10% and −10% columns report the changes in mean time to extinction when respective parameter values have been increased or decreased by 10% from the extreme parameter values, respectively. Remnant size is 50 trees, and all simulations consisted of 1600 runs. Mean time to extinction under the standard parameter set was 341 yr. For an indication of the significance of differences in T at the 5% level, we assumed that the mean time to extinction of repeated simulations under the standard parameter set (1600 runs) followed a normal distribution with the mean equal to the standard deviation. It follows that a deviation in any direction by more than ~17 yr is significantly different.

† Males.

‡ Females.

to the field data (about 25% under high density; Kitchener et al. 1988). Hot weather decreases the hatching rate. Therefore during hot years the hatching rate of eggs is reduced compared to normal years (Table 1).

Movement

O. reticulata is territorial. Aggressive behavior between males has been observed on a number of occasions (How and Kitchener 1983; S. Sarre, *personal observation*) and males and females form pairs. In our model, adults do not allow other adults of the same sex to establish a territory on the same tree. However, subadults may be accepted, which may lead to more than two adult geckos per trees, cf. below. To model the movement of individuals between trees within a patch, the following rules were formulated. Data to estimate the parameters associated with the movement between trees are not available for *O. reticulata.* However, field experience and data for the arboreal gecko *Gehyra variegata* (Henle 1990) suggest that the parameter values given below are in the correct order of magnitude. The rules for the movement of individuals are not meant to mimic the detailed behavior. Instead, we included those behavioral aspects that we believe to be relevant for the extinction process. (1) Juveniles remain on their tree of birth, but once they reach sexual maturity (that is in the first year of adulthood [subadults]) they become expelled with a probability of 80%. (2) Adults during their first year of adulthood may stay on trees that have no adults of the same sex. Additionally, they have a chance of 20% to establish a territory on a tree already occupied by an adult of the same sex, if the number of adults is below the carrying capacity. (3) Expelled subadults scout up to 10 trees in the neighborhood to find an available territory. This process starts with the nearest tree without taking into account the actual distance. As long as no adults of the same sex are living on that tree, subadults establish a territory. If adults of the same sex have occupied some territories on that tree, the subadult may establish a territory with a probability of 20% as long as the number of occupied territories is below the carrying capacity. For the case of not being able to establish a territory, the individual moves to another tree in the neighborhood and the process starts again. Subadults that fail to establish a territory after 10 attempts are assumed to be dead. However, model analyses showed that such long trips are rare. (4) Adults have a probability of 30% (females) and 45% (males) respectively, of leaving their territory. (5) Adults that decide to leave their territory have to scout up to 10 trees in the neighborhood to find a tree in which they can establish a new territory. In contrast to subadults, adults can only establish a new territory on trees without resident adults of the same sex. Adults that survive to search 10 trees without finding a territory return to their initial tree.

Tail

The tail of *O. reticulata* is quite fat and serves as an energy reserve (Greer 1989). When attacked by a predator, the gecko can autotomize the tail. Following such a loss, the tail regrows within a few months (K. Henle, *personal observation*). However the regrowth of the tail has some costs, which does not allow females of *G. variegata* to reproduce (Henle 1990). Therefore, we make the conservative assumption that this applies also to female *O. reticulata.* Hence, in the model, we have to follow the fate of the tail of female adults. At the beginning of each year we assume the tail to be complete, but, similar to the mortality rates, each adult female has a basic probability of 10% of losing the tail and an additional risk of 10% of losing the tail during movements between trees.

Reproduction

Every year adult females lay one clutch of two eggs (How and Kitchener 1983). For *G. variegata* field experience suggests that during dry years the resource situation allows only 90% of the females to reproduce (Henle 1990). Thus, in our model, during dry years, females have a probability of 90% (instead of 100%) of reproducing. If there is a female without a partner on the same tree, we look for an adult male that has a territory on one of the 10 nearest trees. This male moves to the female and undergoes a mortality risk of 10%. If that male dies or if there is no male in the neighborhood, the female does not reproduce in that year (Allee effect, Allee 1931, Stephens et al. 1999). Note that especially in the case of low population density, a male might have to move several times to mate.

MODEL PERFORMANCE

When modeling extinction, it is crucial to capture the most important dynamical features of the gecko population at low population numbers. To evaluate the performance of our model, we present six lines of evidence: (1) distribution of individuals across trees within a remnant; (2) distance traveled to establish territories; (3) longevity and mortality; (4) proportion of juveniles; (5) relationship between mortality and population density; and (6) population density and sex ratio across remnant sizes. After discussing these six points, we will present a more formal sensitivity analysis.

Distribution of the individuals across trees within the remnant

Our model incorporates a behavioral mechanism that controls the distribution of individuals within the habitat. Simulations of population trajectories over 70 yr show that the a priori chosen parameters lead to mean densities of about two individuals on each tree. This is a realistic value as it is within the range of densities observed among 11 remnant populations (0.00–2.17 individuals per tree; Sarre 1995*a*).

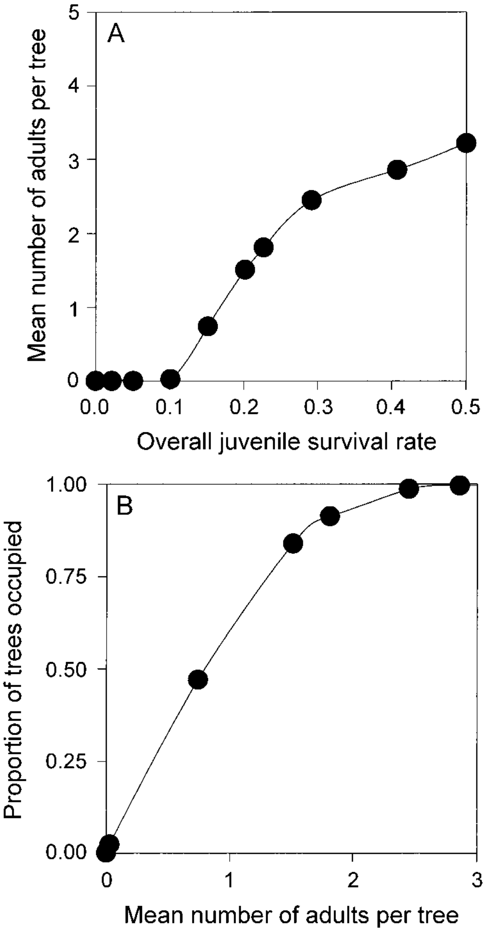

FIG. 1. (A) Mean number of adult geckos per tree after 70 yr vs. the overall juvenile survival rate and (B) proportion of trees occupied by at least one adult vs. the mean number of adult geckos per tree. The overall juvenile survival rate is the product of survival rates of females at ages 0 (egg), 1, 2, 3, and 4. For the set of parameter values given in Table 1 this survival rate is 0.15. Male survival rates are changed accordingly, but we fixed the ratio of overall male to overall female survival at 1.8. Initial density was four adults and four juveniles per tree; 1600 simulation runs; size of the forest remnant was 50 trees.

For a further investigation of the distribution of the model population, we looked at the average number of adults on each tree vs. the population density. Different adult population densities may become realized within our model by modifying mortality rates. We varied the juvenile mortalities in such a way that the probabilities of a female egg developing to adulthood were between 0% and 50% and changed male juvenile mortality rates accordingly (Fig. 1A). As expected, at low survival rates, most of the trees are empty. With increasing survival, the density increases but levels off at high survival rates. This is due to the fixed carrying capacity. One may view the distribution of geckos across trees in a different way by plotting mean adult density across trees vs. the occupancy of trees (Fig. 1B). With increasing population density the proportion of occupied trees increases. At a density of about 2.5 adults per tree almost all trees are occupied. Theoretically, a density of one adult per tree would be sufficient to occupy all trees. But, at this density, territories will be established on only 60% of the trees. At low densities, our simulated population tends to form male/female pairs. In this respect, the behavior of the model is realistic.

Distance traveled to establish a new territory

To determine whether the rules of our spatial model imitate the restricted movement patterns observed in *O. reticulata,* we counted the number of trees searched by adults and subadults in a large remnant with a high density (four adults and four juveniles on each tree; Fig. 2). We recorded all searches even if the individual died during this search for a new territory. Sixteen percent of those adults that left their territory traveled only to the nearest tree and either died or established a new territory. The frequency of individuals scouting more than one tree decreases monotonically. Only 10% of the males and 5% of the females found no territory after searching across 10 trees. Subadults established their territory on their tree of birth with a frequency of 28%. The number of subadults traveling to more remote trees declines almost exponentially with only 2.5% of subadults without a territory after searching across 10 trees. Note that we made these simulations at a situation of high density. Thus, at the more realistic density of two individuals on each tree, this number will be even less. In general, we conclude that our artificial rule to stop the traveling process after having searched 10 trees has no severe impact on the performance of the model.

Longevity

As model individuals undergo a certain mortality risk during each movement, our movement rules have a pronounced effect on overall mortality and, hence, on longevity. The comparison of longevity measured in the field and in the model gives some feeling about the realism of the chosen parameters.

In the model, we do not record the age of the adult individuals. Hence, we had to estimate their longevity by running the model with cohorts of adults of the same sex (in order to prevent reproduction, movement of males searching for [nonexistent] females was also prevented). The age can then be calculated by adding the duration of the juvenile phase to the year of death recorded for each individual of the cohort. Using the parameters of Table 1, we recorded a mean maximum longevity of 42 (males) and 47 (females) years (Table 2). R. A. How (*personal communication*) observed a field population and found a female surviving 19 yr and a male surviving 17 yr. At first glance, our model data seem to be high compared to the field data. However the field data on longevity are hampered by the low number of individuals followed and the fact that

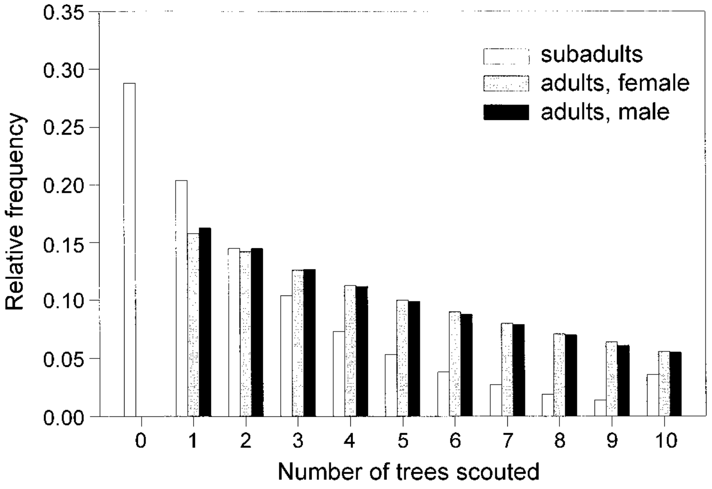

FIG. 2. Relative frequency of the number of trees scouted for territories by individual geckos (initial density: two female and two male adults and four juveniles per tree). The simulation (1600 runs) has been conducted for a large remnant of 1000 trees in order to minimize edge effects. Parameters are as given in Table 1.

the longevities are only minimum estimates. Nevertheless, longevities above 40 years are probably a bit too high and are caused by the fact that our model does not incorporate an increased mortality for old individuals. In contrast, the mean ages measured in our simulation experiment (Table 2) are realistic.

Proportion of geckos less than one year old

Another characteristic largely determined by our mortality rates and rules is the proportion of geckos less than one year old. In the field, they constitute between 0% and 29% of the population. For three remnants of ~100 trees, the mean proportion was ~21% (Sarre 1995*a*). For comparison, we determined the proportion of one-year-old geckos in the model (100 trees, 1600 runs, the set of parameters is in Table 1). We found a range of 6–39% of juveniles less than one-year-old. In 22% of all runs, the proportion of one-year-old geckos was below the proportion measured in the field. Thus, compared to the field data, the proportion of juveniles is a bit high in our simulated populations, however, still in the right order of magnitude. In summary, we notice that the model is able to reproduce realistic values of mean age despite overestimating longevity because the proportion of juveniles (more precisely: proportion of geckos less than one year old) is somewhat overestimated as well.

TABLE 2. Life expectancy of geckos estimated from our model.

Geckos	Average age (yr)	Average maximum age (yr)	Individuals reaching 14 yr (%)
Males	8	42	25
Females	11	47	32

Note: Results are based on an average of 100 simulations and a remnant size of 200 trees; the initial number of males and females was 400 each.

Interaction of mortality and density

Our model incorporates a behavioral mechanism that generates density-dependent population regulation: the higher the density the higher the probability of movements between trees, which leads to an increased mortality. In Fig. 3, we plot average number of adults per tree as well as the mortality rates vs. time in remnants. Within the first 10 yr, the initial density of four geckos quickly drops to near one gecko per tree. The mortality rate of females and males is ~25% during the first year of the simulations. Again, mortality rapidly declines during the first decade. As expected, males have a higher actual mortality rate than females. This is a consequence of their greater probability of changing trees. From Fig. 3, it can be seen that mortality and density values are correlated. Thus, the high initial density leads to high mortality, which in turn causes the rapid decline of density.

Population size and sex ratio across remnant size

After 70 yr of simulation, absolute densities of geckos in different age classes are relatively unaffected by remnant size (approximate densities: 1.4 juveniles/tree, 0.8 adults per tree; cf. *Model performance: Distribution of the individuals*). Also, the fraction of adults that is female is roughly constant at ~50% across all remnant sizes. This lies within the range of observed field values (35–78%, Sarre 1995*a*). However, remnant size does have some influence on population structure via the distance individuals move in remnants of different sizes. This is because in small remnants (<10 trees) geckos may search only as many neighbor trees as there are in the remnant (<nine trees) instead of 10 trees in larger remnants. The number of males per female is able to capture these differences because it reflects changes in both females and males.

The number of males per female across remnant sizes in simulated populations surviving for 70 yr (Fig. 4) is a quantity with differences too subtle for comparison

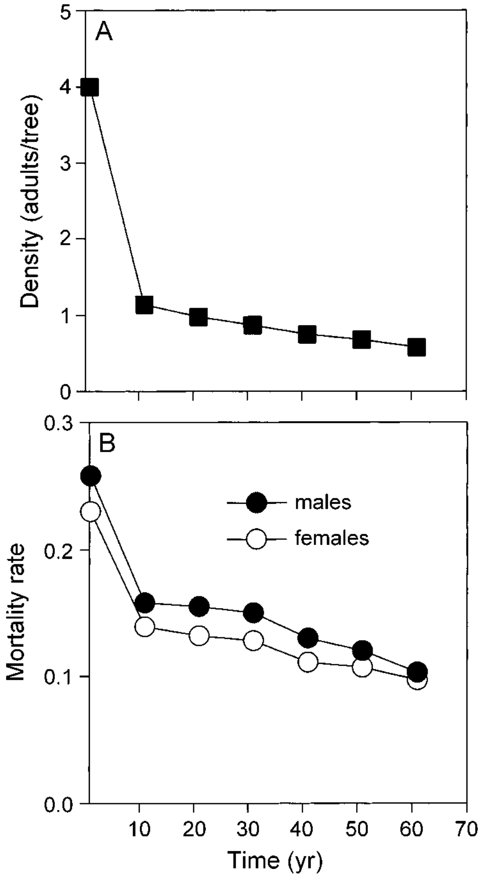

FIG. 3. (A) Mean density of adult geckos and (B) mean annual mortality rates of the two sexes vs. time. The mean was calculated across 1600 simulation runs; size of the forest remnant was 10 trees. Initial density was four adults and four juveniles on each tree; parameters are as given in Table 1. Note the correlation between mortality rates and densities.

with field data. However, from the relationship between male–female ratio and remnant size, we can gain a deeper understanding of the influence of remnant size on the behavior of our model. The number of males per female is a result of two factors. Juvenile males mature faster than females and thus (due to the similar mortality rates, Table 1), a higher proportion of males reaches adulthood. However, adult males are more likely to change territories than females (Table 1, the Allee effect is not important here because of the relatively high population densities) and therefore adult males suffer higher mortalities than adult females. In large remnants, this results in ~ 0.9 males per female (Fig. 4). However, in remnants smaller than 11 trees, the searching of geckos for new territories is restricted by the number of trees in their remnant. For example, in remnants five trees in size, they can search up to four (instead of 10) neighboring trees. Thus, the mortality risk of adults is reduced in smaller remnants. This is more pronounced for male adults because they are more likely to change their territory. Therefore, for small remnants, the numbers of males per female increases with decreasing remnant size (Fig. 4).

The main message from these considerations is that for sufficiently large remnants (>10 trees) and as long as populations are not in direct danger of extinction (low population size, where the Allee effect becomes important), remnant size does not influence survival of single geckos because of their limited range. However, this is not to say that extinction risk was independent of remnant size. Clearly, populations in smaller remnants tend to be smaller and therefore more prone to demographic stochasticity (Lande 1993).

Sensitivity analysis

Our central aim was to test the hypothesis that occupancy of remnants of different sizes could be predicted by stochastic processes. To determine those parameters that have the greatest influence on extinction, we conducted a sensitivity analysis. A remnant size of 50 trees and the a priori chosen parameters given in Table 1 (hereafter called standard parameters) are our point of reference for the analysis. The standard parameters result in a mean time to extinction of 341 yr. First, we investigated the overall influence of each parameter on the mean time to extinction by changing each single parameter to the minimum and then to the maximum possible value (e.g., 0.0 and 1.0 were the minimum and maximum values for all parameters measured as probabilities). We then included those parameters that had the power to reduce the mean time to extinction below 100 yr, that is within the time scale observed in the field, into a further sensitivity analysis. In Table 1 we give the mean time to extinction for the minimum and maximum value as well as values 10% below and above the standard value of each parameter. As a score for evaluating the influence of each parameter we used the range between the mean times to ex-

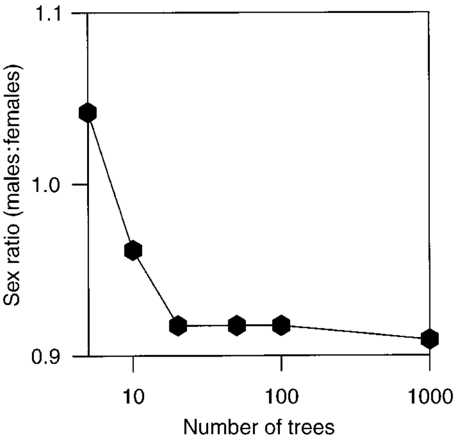

FIG. 4. Number of males per female as a function of remnant size (number of trees; note log scale) in the year 70 after simulation start (initial density: two female and two male adults and four juveniles per tree, 1600 runs per data point).

tinction with parameters 10% below and above the standard value (Caswell 1989).

The model is most sensitive to egg and juvenile mortality rates (Table 1). A decrease in sensitivity of the juvenile mortality rates with increasing age is plausible for two reasons. First, the mortality rates lead to a monotonically decreasing age distribution. This means that the sensitivity of juvenile mortality decreases with the decreasing number of individuals in the respective age class. Second, since we changed all parameters by the relative rate of 10%, the change in overall mortality is greater for mortality parameters with higher values, that is for younger individuals.

Our model is also quite sensitive to the mortalities of the female adults (Table 1). Male mortalities are less important because we have not modeled *O. reticulata* as monogamous and hence, provided that population densities are not too low, the death of some males does not influence reproduction.

The remaining parameters are of minor importance. Their influence is buffered by the high longevity of *O. reticulata.* For example, the dropping of the tail in case of threat has basically no influence on the mean time to extinction (Table 1). Furthermore, environmental stochasticity, as included in the model, leads to a slight decrease of persistence time (Wiegand 1996). Thus, overall, our model is sensitive to the mortality rates only.

Predicting the distribution of populations across remnants

We compared the incidence function based on the actual absence/presence data (Sarre et al. 1995; statistical calculations to estimate the logistic regression were performed using STATISTICA version 5.5 with the module GLZ) to an incidence function derived from our model. In order to generate the incidence function we ran a series of simulations for a range of remnant sizes. For each simulation, we started at a high population density, corresponding to the situation shortly after clearing (see *The model: Trees*) and recorded if the population was able to persist more than 70 yr. Making a considerable number of simulation runs (1600) for each remnant size, we were able to estimate the probability of survival for at least 70 yr for each remnant size (Fig. 5).

Both the incidence function based on the field data, and the one predicted by our model, show that the probability of persistence increases with remnant size. However, in contrast to the observed absence/presence pattern, according to our model, gecko populations should have survived 70 yr and more even in quite small vegetation remnants. Except for extremely small remnants (≤5 trees), model predictions are above the confidence interval of the incidence function based on the actual absence/presence data.

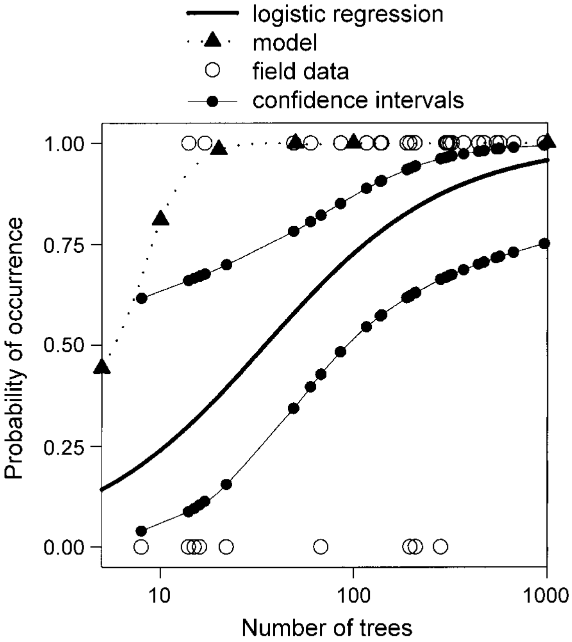

FIG. 5. Incidence functions derived from our model and derived from field data by logistic regression. Open circles represent the presence–absence data of the field survey across 32 remnants. The logistic regression was fitted to the field data using the log-transformed number of smooth-barked eucalypt trees as an independent variable (solid line). The regression line fits the data (-2 log likelihood $= 29.5$; df $= 30$; $P > 0.3$), and both intercept and slope are significant (Wald statistic, $P < 0.05$ in both cases). The confidence intervals of the prognosed occurrences are given for each of the 32 remnants (closed circles). Note that the model predictions are above the confidence interval of the prognosed occurrences in most cases. Regression equation: probability(occurrence) $= e^{-3.29+2.13\log(\text{trees})}/(1 + e^{-3.29+2.13\log(\text{trees})})$.

DISCUSSION

Sarre et al. (1995) observed a clear relationship between remnant size (number of trees) and the probability of occurrence of *O. reticulata.* Based on the history of the habitats and the biology of the gecko, we hypothesized that the present distribution pattern across habitat remnants could have been produced only by extinctions due to demographic stochasticity. Given that population structure in our model is fairly unaffected by remnant size, differences in persistence across remnants of different sizes can be attributed to population size alone. In other words, mortalities and reproductive rates as well as environmental stochasticity are largely the same across remnants, while the importance of demographic stochasticity increases with decreasing remnant size. However, for this to be true in nature as well, the simulated occurrence pattern of *O. reticulata* should fit the observed occurrence across remnants of different sizes. In small remnants, our model is clearly too optimistic, predicting a higher occurrence of *O. reticulata* than was observed, and implies that demographic stochasticity is not the only extinction process affecting the remnant populations of *O. reticulata.*

There are several possible explanations for the optimistic predictions made by our model. Field biologists may object that the structure and parameter values of our simulations are not a valid description of the gecko populations. However, we performed a very extensive analysis of the model to test its plausibility and agreement with field experience. The model passed our very stringent standards. Nevertheless, all models have parameters crucial for the results. The sensitivity analysis showed that the gecko model is sensitive to juvenile and female adult mortality rates. For example, the basic yearly mortality of females is 10%. An increase to 11% resulted in a decrease of the mean time to extinction from 341 to 220 yr (see Table 1). However, since the mortality rates used in the model were at the high end of possible values, the inclusion of more ''realistic'' mortality rates would increase the discrepancy between the model and the observed distributions. Furthermore, we have investigated alternative, simpler model formulations. Again, they lead to even higher persistence times (Wiegand et al. 2001). Modelers may object that the field data describing the absence of the gecko are inflated, because remnants with a very low gecko population density may have been erroneously scored as empty. However, the main difference between field data and model predictions is for small remnants (about 10–50 trees), where it is unlikely that individuals have been overlooked during the intensive field surveys. Statisticians may object that we did not provide statistical evidence of field observations and model predictions being significantly different and that Fig. 5 shows just one possible realization of alternative model realizations and parameterizations. However, Fig. 5 shows the empirical incidence function including confidence intervals along with a pessimistic model realization because, as just mentioned, the mortality rates used in the model were at the high end of possible values. We did not include a comparison of model and field equilibrium densities because we do not know field equilibrium densities. However, Wiegand et al. (2001) investigated equilibrium densities of the gecko model across remnant sizes. The case of the biggest remnant (1000 trees) is most interesting here, because it is safe to assume that living conditions in this large remnant have changed least in comparison to original, uncleared, vegetation. The resulting equilibrium density of 0.04 geckos per tree seems possible but rather low when considering that this species has survived in this habitat for many years.

A further possibility is that the poor fit of field data and simulations comes from implicit assumptions of the model. There are four implicit assumptions in the simulation model with some bearing on this issue: (1) all eucalypts were assumed to be the same; (2) catastrophes were assumed to be unimportant; (3) habitat quality was assumed to be unrelated to remnant size; and (4) inbreeding depression was assumed to be unrelated to remnant size.

1) We assumed that for *O. reticulata*, all eucalypts are of the same quality and that the habitat quality does not change with remnant size or time. Field experience shows that very few young trees exist in the remnants. Thus, during the history of each remnant since clearing, the mean age of trees has increased. Old trees are better for geckos than young trees since old trees provide hollows and other structures for small animals. The lack of regeneration of eucalypts, the implementation of management practices such as burning, and the application of fertilizers and insecticides, mean that the assumption that habitat quality has remained constant, is unlikely to hold true. Whether this means an increase or decrease in habitat quality is unknown.

2) Catastrophes such as droughts, floods, fire, and storms can play important roles in the survival of populations (Johst and Brandl 1997). Woodland remnants in the Western Australian wheatbelt are subject to such catastrophes (Yates et al. 1994). Similar catastrophes may occur also in undisturbed woodlands, but damage will be more serious for isolated remnants containing only a few trees. For example, recovery from small population sizes or extinctions caused by catastrophes will be less likely in isolated remnants than for contiguous populations because the probability of immigration from adjacent populations will decrease with increasing isolation. In addition, it is agricultural practice among farmers in the Western Australian wheatbelt to conduct control burns of the grass understory in woodland remnants (S. Sarre, *personal observation*), which may increase the frequency of fires. Catastrophes caused by fire can have severe impacts on gecko survival (R. How, *personal observation*)

Our simulations in which an environmental scenario with catastrophes was implemented, show that although catastrophes decreased the mean time to extinction, as would be expected, the probability of occurrence remained basically unchanged on the time scale of 70 years. Although the inclusion of catastrophes in our extinction model does not account for the discrepancy between modeled population incidence and that observed in the Kellerberrin region per se, our simulation experiments do indicate that the frequency of catastrophes is much less important than the power of the catastrophes (Fig. 6). Thus, rare but powerful catastrophes provide a plausible explanation for the discrepancy observed between the model predictions and field data.

3) Edge effects may play an important role in extinction processes, and will be most important in small remnants (Saunders et al. 1991), where a high proportion of trees stand near the borderline to the surrounding agricultural area. These trees may not be very attractive to geckos because of predators and other influences. The impact of harsh climatic conditions may increase mortality for individuals living on trees along

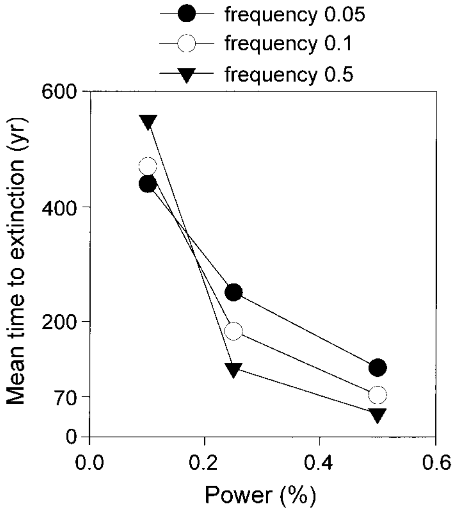

FIG. 6. Mean time to extinction vs. frequency and power of catastrophes. The power of a catastrophe is measured as percentage of individuals (irrespective of age or sex) that get killed during a catastrophic event. The frequency is measured as the annual probability that a remnant is affected by a catastrophic event. Note that the power of a catastrophe is much more important than the frequency. Parameters are as in Table 1; remnant size = 50 trees.

the border of the remnant. In general, this would increase the mean mortality rates with decreasing remnant size and cause the extinction rate in small remnants to be faster than predicted by our model.

4) The probability of mating between close relatives and the loss of genetic variation through genetic drift in isolated populations increases with decreasing population size. Thus, genetic malfunction may increase extinction rates in remnants with small populations beyond those predicted by our model. A survey of mitochondrial DNA variation within and among 12 populations indicated that the remnant populations had probably lost genetic variation since their isolation (Sarre 1995*b*). It is therefore conceivable, although untested, that genetic factors have influenced extinction probabilities in the remnant populations.

All of the four likely causes of the discrepancy between our model results and the observed presence/absence patterns are most likely in smaller remnants where model and field results deviate the most. Therefore all of them could contribute to this deviation. Two of these causes, catastrophes and genetics, are essentially stochastic processes and are typically considered in population viability analyses. The other two assumptions of the model that may be unrealistic, changing (declining) habitat quality and edge effects, are rarely modeled in population viability analyses (Caughley 1994), and yet may well be critical in landscapes such as the Western Australian wheatbelt. Irrespective of the influence of these ignored processes, it is clear that even a detailed specifically constructed stochastic demographic and environmental model such as the one described here, was inadequate in defining the extinction pressures on insular populations of *O. reticulata.* Such poor predictive abilities may have critical consequences when applied to the management of rare or endangered species.

In a very practical sense, being able to identify species that are vulnerable to extinction and then implementing conservation programs before those species came close to extinction would be a significant aid to conservation effort (MacNally and Bennett 1997). To identify extinction proneness a thorough understanding of the processes of extinction is required. Although the science of conservation biology is rich in theoretical explorations of stochastic extinction processes, clearly documented examples of such extinctions are rare (Caughley and Gunn 1996). This means that the importance of extinction through the various stochastic (demographic, genetic, environmental, and catastrophic) processes described by Shaffer (1983) remains untested. Many population viability analyses deal only with demographic and environmental stochasticity (e.g., Shaffer 1983, Armbruster and Lande 1993, Zhou and Pan 1997), which, in the case of *O. reticulata* described here, would provide an inadequate model of extinction. In order to advance our understanding of extinction, and to assess the role of stochastic processes in population extinction, we need to apply the tools of population viability analysis to situations where decline is in progress and can be measured, not at or close to its completion.

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LITERATURE CITED

Allee, W. C. 1931. Animal aggregations. A study in general sociobiology. University of Chicago Press, Chicago, Illinois, USA.

Armbruster, P., and R. Lande. 1993. A population viability analysis for African elephant (*Loxodonta africana*): how big should reserves be? Conservation Biology **7**:602–610.

Arnold, G. W., J. R. Weeldenburg, and D. E. Steven. 1991. Distribution and abundance of two species of kangaroo in remnants of native vegetation in the central wheatbelt of Western Australia and the role of native vegetation along road verges and fencelines as linkages. Pages 273–280 *in* D. A. Saunders and R. J. Hobbs, editors. Nature conservation 2: the role of corridors. Surrey Beatty and Sons, Melbourne, Australia.

Avise, J. C. 2000. Phylogeography: the history and formation of species. Harvard University Press, Cambridge, Massachusetts, USA.

Brook, B. W., L. Lim, R. Harden, and R. Frankham. 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island woodhen *Tricholimnas sylvestris* (Sclater). Biological Conservation **82**:119–128.

Caswell, H. 1989. Matrix population models:construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology **63**:215–244.

Caughley, G., and A. Gunn. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, Massachusetts, USA.

Forys, E. A., and S. R. Humphrey. 1999. Use of population viability analysis to evaluate mangement options for the endangered lower keys marsh rabbit. Journal of Wildlife Management **63**:251–260.

Greer, A. E. 1989. Gekkonidae—geckos. Pages 51–96 *in* A. E. Greer, editor. The biology and evolution of Australian lizards. Surrey Beatty & Sons PTY Limited, Chipping Norton, Australia.

Hänfling, B., and R. Brandl. 1998. Genetic variability, population size and isolation of distinct populations in the freshwater fish *Cottus gobio* L. Molecular Ecology **7**:1625–1632.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.

Henle, K. 1990. Population ecology and life history of three terrestrial geckos in arid Australia. Copeia 1990(3):761–781.

Hobbs, R. J. 1993. Fragmented landscapes in Western Australia: introduction. Biological Conservation **64**:183–184.

How, R. A., and D. J. Kitchener. 1983. The biology of the gecko *Oedura reticulata* Bustard, in a small habitat isolate in the Western Australian wheatbelt. Australian Wildlife Research **10**:543–556.

Johst, K., and R. Brandl. 1997. Body size and extinction risk in a stochastic environment. Oikos **78**:612–617.

Judson, O. P. 1994. The rise of the individual-based model in ecology. Trends in Ecology and Evolution **9**:9–14.

Kitchener, D. J., A. Chapman, J. Dell, and B. G. Muir. 1980. Lizard assemblage and reserve size and structure in the Western Australian wheatbelt—some implications for conservation. Biological Conservation **17**:25–62.

Kitchener, D. J., R. A. How, and J. Dell. 1988. Biology of *Oedura reticulata* and *Gehyra variegata* (Gekkonidae) in an isolated woodland of Western Australia. Journal of Herpetology **22**:401–412.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist **142**:911–927.

Lindenmayer, D. B., and H. P. Possingham. 1996. Applications of population viability analysis in conservation biology in Australia. Pages 102–110 *in* J. Settele, C. Margules, P. Poschlod, and K. Henle, editors. Species survival in fragmented landscapes: from the local to the landscape level. Kluwer Academic Publishers, Dordrecht, The Netherlands.

MacNally, R., and A. F. Bennett. 1997. Species-specific predictions of the impact of habitat fragmentation—local extinction of birds in the box-ironbark forests of Central Victoria, Australia. Biological Conservation **82**:147–155.

Moehlman, P. D., G. Amato, and V. Runyoro. 1996. Genetic and demographic threats to the black rhinoceros population in the Ngorongoro Crater. Conservation Biology **10**:1107–1111.

Noon, B. R., and C. M. Biles. 1990. Mathematical demography of spotted owls in the Pacific Northwest. Journal of Wildlife Management **54**:18–27.

Price, M. V., and P. A. Kelly. 1994. An age-structured demographic model for the endangered Stephens' Kangaroo rat. Conservation Biology **8**:810–821.

Reed, J. M., P. D. Doerr, and J. R. Walters. 1988. Minimum viable population size of the red-cockaded woodpecker. Journal of Wildlife Management. **52**:385–391.

Sarre, S. 1995*a*. Size and structure of populations of *Oedura reticulata* (Reptilia: Gekkonidae) in woodland remnants: implications for the future regional distribution of a currently common species. Australian Journal of Ecology **20**: 288–298.

Sarre, S. 1995*b*. Mitochondrial DNA variation among populations of *O. reticulata* (Gekkonidae) in remnant vegetation: implications for metapopulation structure and population decline. Molecular Ecology **4**:395–405.

Sarre, S. 1996. Habitat fragmentation promotes fluctuating asymmetry but not morphological divergence in two geckos. Researches on Population Ecology **38**:57–64.

Sarre, S., G. T. Smith, and J. A. Meyers. 1995. Persistence of two species of gecko (*Oedura reticulata* and *Gehyra variegata*) in remnant habitat. Biological Conservation **71**: 25–33.

Saunders, D. A., R. J. Hobbs, and G. W. Arnold. 1993. The Kellerberrin project on fragmented landscapes: a review of current information. Biological Conservation. **64**:185–192.

Saunders, D. A., N. T. Hobbs, and C. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology **5**:18–32.

Shaffer, M. L. 1983. Determining minimum viable population sizes for the grizzly bear. International Conference on Bear Research and Management **5**:133–139.

Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? Oikos **87**:185–190.

Uchmanski, J., and V. Grimm. 1996. Individual-based modelling in ecology: what makes the difference? Trends in Ecology and Evolution **11**:437–441.

Wiegand, K. 1996. Extinktionswahrscheinlichkeiten kleiner Reptilienpopulationen—Der Gecko *Oedura reticulata*. Diploma thesis. University of Marburg, Marburg, Germany.

Wiegand, K., K. Henle, and S. Sarre. 2001. Extinction and spatial structure in simulation models. Conservation Biology, *in press*.

Wiegand, T., J. Naves, T. Stephan, and A. Fernandez. 1999. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. Ecological Monographs **68**:539–570.

Yates, C. J., R. J. Hobbs, and R. W. Bell. 1994. Landscape-scale disturbances and regeneration in semi-arid woodlands of southwestern Australia. Pacific Conservation Biology **1**: 214–221.

Zhou, Z. H., and W. S. Pan. 1997. Analysis of the viability of a giant panda population. Journal of Applied Ecology **34**:363–374.