Extinction and Spatial Structure in Simulation Models

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Abstract: *Aspects of within-population spatial structure are often neglected in the modeling of population viability. To analyze the relevance of the spatial structure of single populations to population persistence, we compared the results of three models developed for the territorial, arboreal gecko* Oedura reticulata*: (1) a spatially structured model in which both low and high densities incur mortality costs due to increased movement, (2) a spatially structured model in which the Allee effect is removed, and (3) a spatially unstructured model in which there are no effects of density on mortality. Compared with nonspatial model populations, spatially structured populations exhibited reduced persistence. The Allee effect contributed only a small amount to the reduction in persistence. Increased mortality at high densities caused by difficulties in finding territories markedly reduced persistence in the spatially structured models compared with the density-independent nonspatial model. We argue that the inclusion of elements of spatial structure may considerably influence the estimation of extinction risk in population viability analyses.*

Extinción y Estructura Espacial en Modelos de Simulación

Resumen: *Los aspectos de la estructura espacial dentro de una población son frecuentemente ignorados en el modelado de viabilidad poblacional. Para analizar la importancia de la estructura espacial de poblaciones individuales en la persistencia de una población, comparamos los resultados de tres modelos desarrollados para un gecko arbóreo territorial,* Oedura reticulata*: (1) un modelo estructurado espacialmente en el cual tanto las densidades bajas como altas incurren en costos de mortalidad debido a un incremento en el movimiento, (2) un modelo estructurado espacialmente en el cual el efecto Allee es removido y (3) un modelo estructurado espacialmente en el cual no hay efectos de la densidad sobre la mortalidad. Comparados con modelos de poblaciones no espaciales, las poblaciones estructuradas espacialmente exhibieron una persistencia reducida. El efecto Allee contribuyó únicamente con una pequeña proporción de la reducción en la persistencia. El incremento en mortalidad a elevadas densidades debido a la dificultad en encontrar territorios, disminuyó marcadamente la persistencia en los modelos estructurados espacialmente en comparación con los modelos no espaciales, denso-independientes. Argumentamos que la inclusión de los elementos de la estructura espacial puede influenciar considerablemente la estimación de los riesgos de extinción en los análisis de viabilidad poblaciones.*

Introduction

All organisms are discrete entities that interact with neighboring individuals of their own or other species. This spatial confinement occurs not only for sessile organisms such as terrestrial plants but also for motile organisms. If organisms interact locally and their movement ranges are limited (e.g., due to movement costs), popula-

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tion densities do not change in response to average conditions across a large area but rather in response to the local conditions experienced by each individual (Tilman et al. 1997). It may be critical, from a conservation perspective, whether these differences cancel each other out or whether they have a noticeable effect on average population densities and thus on population persistence.

At low population densities, the spatial structuring of animal populations can lead to difficulties in finding mates. This may have a negative effect on the rate of increase of populations and therefore hasten the decline of small populations (Swart et al. 1993; McCarthy 1997; Kuussaari et al. 1998; Wells et al. 1998; Courchamp et al. 1999). Such negative effects of low density are generally known as Allee effects (Allee 1931). The spatial structuring of populations may also have negative effects at high population densities because of the difficulties individuals experience in finding empty territories. This is a special case of decreasing population growth at high densities (Verhulst 1838).

It is important to know whether density regulation at high or low densities due to the spatial structuring of territorial species has an influence on population persistence, because much of our conservation efforts concern territorial species such as birds or large mammals. Thus, it may be important to include the spatial structuring of territorial species in population viability analyses (PVA), typically by developing spatially explicit simulation models. Recent developments in spatially explicit population modeling emphasize the specific consideration of landscape features and spatial aspects of population dynamics (Pulliam et al. 1992; Kareiva & Wennergren 1995; Lima & Zollner 1996; Schippers et al. 1996; Letcher et al. 1998). But even though the rapid development of computer technology facilitates an increasing complexity in these models, the explicit consideration of space in population modeling requires large amounts of field data that may be difficult to obtain (Ruckelshaus et al. 1997, 1999; Beissinger & Westphal 1998; Mooij & DeAngelis 1999). Moreover, some of the most widely used generic PVA computer packages (e.g., VORTEX, Lacy 1993) do not permit explicit modeling of the spatial dynamics within populations (although they may allow for the inclusion of some density-dependent functions). Given these difficulties and the potential importance of spatial population structure, it is critical to determine whether the inclusion of spatial structuring in extinction models has an effect sufficient to warrant the use of spatial approaches in modeling.

We investigated the importance of territoriality for estimating time to extinction by modeling the arboreal, territorial gecko *Oedura reticulata.* We modified an existing extinction model for *O. reticulata* (Sarre et al. 1996; K. Wiegand et al. 1996, 2001) and compared model predictions with and without spatial structure for populations in different-sized forest remnants. We expected the cost of movement to be greater in large remnants and, consequently, differences among models to be greater for large remnants. Furthermore, we examined how density regulation due to spatial structure affects the mean time to extinction at high and low densities. Because of the increased predation risk that movement imposes on this species, we predicted a demographic Allee effect that notably reduced time to extinction. Furthermore, at high density, the combination of territoriality and high cost of movement leads to increased mortality. Therefore, we predicted that the removal of spatial structuring would increase persistence, although that increase would be moderate because it would occur at high density far from extinction.

Methods

Rules Common to All Model Variants

A detailed description and analysis of the original stochastic, individual-based spatial simulation model, here referred to as the "structured Allee model," is provided by Sarre et al. (1996) and K. Wiegand et al. (2001). To investigate the effect of spatial structuring on extinction, we developed two further model variants. In one variant, the Allee effect (i.e., cost of finding mates at low densities) was removed; in the second variant, space and thus movement costs were removed. Comparisons among these three models allowed us to test for the effect of spatial population structure on mean time to extinction in a territorial species.

The structured Allee model simulates the population dynamics of *O. reticulata* living in isolated forest remnants of 2–1000 *Eucalyptus* trees in the Western Australian wheatbelt. These forest remnants are leftovers of formerly contiguous woodlands dominated by *Eucalyptus salubris*, *E. salmonphloia*, and *E. wandoo* which were cleared early in the twentieth century (Sarre et al. 1995). The general aim of the model is to predict local extinctions of this gecko. We chose an individual-based approach (Judson 1994; Uchmanski & Grimm 1996) that enabled us to consider differences in sex, age, or the position of the territories of individuals. Within our basic time step of 1 year, each individual may change territory, die, or reproduce (if a partner is found). The destiny of each individual was determined by random numbers (uniformly distributed in [0,1]), which were compared to probabilities estimated from field data. Thus, our model included demographic stochasticity. Environmental stochasticity was incorporated through the occurrence of a random sequence of dry or hot years, which influenced reproduction and hatching.

Within our model, we assumed that all trees within a remnant had the same size and properties irrespective of remnant size. Thus, we assumed no correlation between remnant size and habitat quality from the standpoint of our gecko species. Based on the territoriality of *O. reticu-*

lata, we chose a spatial model that enabled us to relax the assumption of ideal mixing made by most approaches of modeling population viability (e.g., Shaffer 1983; Price & Kelly 1994; Forys & Humphrey 1999). Consequently, because of restricted movement of individuals, geckos were heterogeneously distributed within the simulated woodland remnant, although all trees were identical.

During each time step, first, the position of the territories of adults was updated; second, individuals might die; third, subadults (geckos in their first year of adulthood) chose territories; and fourth, adults reproduced. Trees were enumerated randomly at the beginning of a simulation. For each step, individuals were handled by the model according to this enumeration. Thus, the sequence of working through the territories was fixed during one simulation but differed among simulations. All parameters were chosen a priori according to published sources (How & Kitchener 1983; Kitchener et al. 1988; Sarre 1995) and the unpublished field notes of S.S. and K.H. No field data were available for a few parameters, so we were forced to supplement our information with data from an arboreal gecko that occurs on the same trees (*Gehyra variegata*). K. Wiegand et al. (2001) described a sensitivity analysis of the model.

We modeled the local dynamics of an isolated population within a single remnant. Each forest remnant could 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 was suitable for one tree. At the beginning of each simulation, we distributed trees randomly across cells and determined the nearest neighbor, the next neighbor, and so on. We considered only the rank of each neighborhood and not the actual distance.

Each tree could be used by several individuals. We fixed the maximum number of territories of adults on a single tree at five, the maximum carrying capacity of one tree. Besides these five adults, up to 10 juveniles could live on one tree. The observance of the adult carrying capacity was assured by the movement rules (see below). Whenever the juvenile carrying capacity was reached, supernumerary eggs were removed. We introduced these limits to avoid unrealistic densities. The initial density of all simulations presented here was four juveniles and four adults (sex ratio 1:1). This is well above equilibrium density (see below), but we chose this high density because it probably resembles the distribution of *O. reticulata* in the wheatbelt just after extensive clearing of the *Eucalyptus* woodlands (K. Wiegand et al. 2001).

We divided the model population according to age and sex: eggs, juvenile females and males, and adult females and males. Because juvenile females become adult at a mean age of 4.8 years and males at 2.8 years (Kitchener et al. 1988), juvenile females were subdivided into classes with an age of 1, 2, 3, or 4 years and juvenile males into classes with an age of 1 or 2 years. During the transition from the juvenile to the adult age class, individuals have to search for a territory (K. H. & B. Gruber, unpublished data). Our term "subadult" refers to individuals during this transition phase.

Every year, adult females may lay one clutch of two eggs (How & Kitchener 1983). In our model, environmental stochasticity influenced egg-laying probability and egg mortality. Once geckos hatched, their mortality was independent of weather but a function of age and sex (How & Kitchener 1983; see also K. Wiegand et al. 2001). To account for an increased predation risk due to a gecko leaving the territory, we implemented an additional mortality risk for each switch of territory to another tree. The movement mortality rates of adult males and females were fixed in such a way that the overall rate was similar to that of the field data. All simulations were run for several remnant sizes, which were selected to span the entire range (2–1000 trees) observed in the region.

Rules Specific to the Models

STRUCTURED ALLEE MODEL

Our modeling of movement between trees in the structured Allee model simulated movement with respect to the establishment of new territories and the incurred risks of mortality. Sensitivity analyses show that this model behaves in a realistic manner (K. Wiegand 1996; K. Wiegand et al. 2001). In this model, a forest remnant consisted of n trees. Each tree had a maximum capacity of five (sub)adults and 10 juveniles. Subadults were forced to leave their native tree with a probability of 0.8 if there was an adult of the same sex on that tree. In all other cases they established a territory on that tree. Adults had a yearly probability (females, 30%; males, 45%) of changing their territory. Both subadults and adults searched up to 10 trees and underwent a mortality risk of 10% per tree searched. Adults that searched 10 trees without finding a territory returned to their initial tree, whereas subadults in this situation died. As a result of these rules, the total annual mortality increased with increasing population density and ranged from 10% to 40% (females) and 10-50% (males) (K. Wiegand 1996; K. Wiegand et al. 1996).

The Allee effect was modeled as follows. If a female gecko was without an adult male on the same tree, the nearest male moved to the female. A 10% mortality risk was associated with this movement. If that male died, the second nearest male attempted to move to the female, and so on. If there was no male within the neighboring 10 trees (or all remaining trees if $n \leq 11$) that could reach the female, that female did not reproduce. We kept the parameters constant because we were investigating the importance of spatial structure and were not interested specifically in the influence of single parameters on model predictions.

STRUCTURED NO-ALLEE MODEL

To create the "structured no-Allee model," we removed the Allee effect by allowing females to reproduce, provided that one male was present in the population of the forest remnant. Furthermore, mating did not cause males to change territories or to suffer additional mortality. All other rules remained the same as in the structured Allee model. Thus, the spatial structure still exerted a density effect on mortality at higher densities caused by movement due to territories being filled.

UNSTRUCTURED MODEL

In the unstructured model, territorial behavior, and thus the structural effect, was completely removed (as in most PVA models), and remnants were not subdivided into trees. In other words, this model was truly nonspatial. A remnant corresponding to *n* trees had a maximum capacity of 5**n* (sub)adult and 10**n* juvenile geckos. Mortality of adults was density independent and coincided with the mortality at "equilibrium" (most frequent) population density of the structured Allee model. Mortality of juveniles was the same as in the other two models.

In the unstructured model, all geckos could interact at any time. Therefore, there was no Allee effect (females reproduced, provided that one male was present in the population) and mortality did not increase with increasing densities (as long as the maximum capacity had not been reached).

Estimating Density and Mortality at Equilibrium

One consequence of removing spatial structure is that, in contrast to the structured Allee and structured no-Allee models, mortality rates in the unstructured model were density-independent. To standardize mortality between the structured Allee model and the unstructured model, and thus to ensure that mortality levels were equivalent between these two models, we generated estimates of the most frequent (or equilibrium) density in the structured Allee model and then measured the total mortality rates of adult females and males at that density. We used the frequency maximum located at a density greater than zero geckos per tree (Fig. 1a) as the equilibrium density. To estimate mortality rates at the equilibrium density for the structured Allee model in a range of remnant sizes, we recorded the mortality rates of adults in every tenth year for each run. These rates were averaged across all runs for each year. From these data, we selected the mean mortality rate for the year in which the mean density was closest to the equilibrium density (Fig. 1b). Those values were used to set the mortality rates for simulations under the unstructured model. For comparison between the structured Allee model and the unstructured model, we also determined the equilibrium density under the unstructured model.

Mean Time to Extinction

To calculate mean time to extinction, T_m, we used the method described by Frank et al. (2001), which is based on the negative exponential shape of the frequency distribution of persistence times. If $P_0(T)$ is the probability of extinction at time T, then plotting $-\ln(1\text{-}\ P_0(T))$ against T gives a straight line with slope $1/T_m$. The determination of the slope is possible even if not all simulated populations go extinct within the maximum simulated time period (in our case, 1000 years; in large remnants, 10,000 years).

In general, persistence times are distributed exponentially except for an initial phase, which can be determined with the plot proposed by Frank et al. (2001). Thus, the mean time to extinction fully describes this persistence time distribution. Given the underlying exponential distribution, T_m does not predict the central tendency but is closely related to the median time to extinction ($=\ln(2)^*\ T_m$). Furthermore, T_m can be used to calculate confidence limits for the mean time to extinction, and it can be converted to a statistic reflecting the extinction risk for any specified time frame (Wissel et al. 1994; Vucetich & Waite 1998).

Results

Population Density and Mortality Rates at Equilibrium

The density of geckos per tree at equilibrium in the structured Allee model decreased with remnant size from approximately five geckos per tree (two trees) to lower densities where the populations were dispersed among many (1000) trees (Fig. 2). For the unstructured model, the densities were systematically higher in remnants with <100 trees but, as in the structured Allee model, approached low densities at 1000 trees. Densities in the structured Allee model were lower because density-dependent mortality suppressed population size. In all cases, the equilibrium density was below the maximum capacity of 15 geckos per tree. This supports our intention to use the maximum capacity as a means to prevent unrealistically high population densities but not as a major regulatory mechanism. The decrease in equilibrium density with increasing remnant size was due to demographic stochasticity. Total population size at equilibrium, being a function of both density and remnant size, was larger for larger remnants. Thus, populations in large remnants could persist at low densities, whereas populations in small remnants face a high risk of extinction once they reach low density. The claim of concurrently increasing equilibrium density and extinction risk with decreasing remnant size was supported by field investigations showing a boundary effect (Fig. 3). The maximum observed population density decreased with

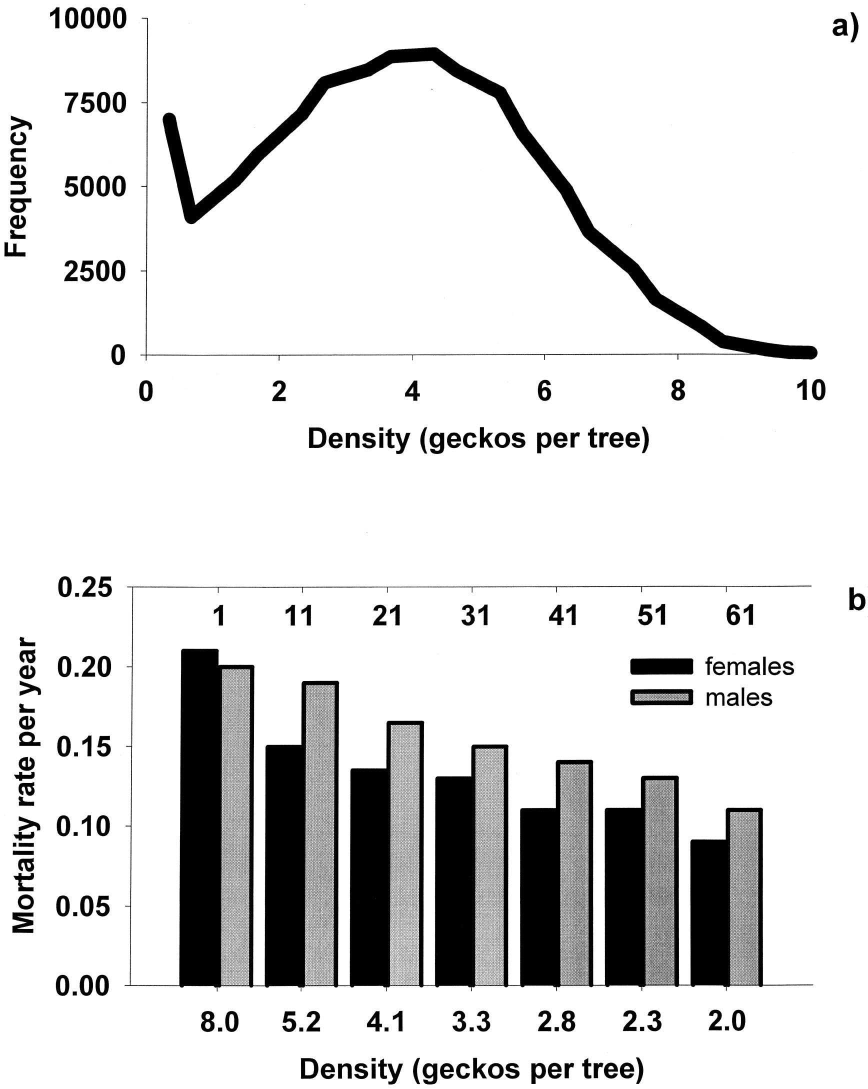

Figure 1. Estimation of density and mortality at equilibrium of a gecko, based on a remnant size of six trees as an example. (a) Frequency of population densities measured over 1600 simulation runs, each consisting of 70 years. In this case, there are two maxima: density of zero (extinction) and density of four geckos per tree. The equilibrium density as described in the text is four geckos per tree (cf. Fig. 2). (b) Average mortality of adult females and males as a function of average density measured every year across all 1600 simulation runs. The time steps at which mortality and density were measured are given at the upper edge of the graph. In year 21, density is at equilibrium density (four geckos/tree). The corresponding estimated mortality at equilibrium is about 0.14 per year for adult females and 0.17 per year for adult males (cf. Fig. 4).

increasing remnant size, indicating decreasing equilibrium densities, but small densities could occur in remnants of all sizes. Indeed, many small remnants had small populations, indicating that small populations drop frequently below equilibrium and thus undergo a high extinction risk (Fig. 3). In all models the risk of extinction was greater in small remnants.

In the structured Allee model, total mortality rates at equilibrium increased slightly as remnant size approached 11 trees (Fig. 4). This was because geckos may search more trees, causing a higher total mortality risk. As remnant size increased, however, the search radius of all geckos was limited to 10 trees. Thus, the increase of remnant size per se did not cause increased mortality risk in remnants with more than 11 trees. Total mortality decreased slightly when remnant size increased toward 1000 trees (Fig. 4). This effect was caused by the lower densities in larger remnants (Fig. 2). When densities are lower, it is easier for geckos to find empty territories, so mortality risk is lower. The effect of higher mortality due to increased searching for new territories was also present when female and male mortality rates were compared. Adult males had higher mortality rates than adult females because they were more likely to change territories (Fig. 4).

Mean Time to Extinction

As expected, in all three models, persistence times increased with remnant size, but persistence times differed markedly across the models (Fig. 5). Compared with the structured Allee model, the structured no-Allee model resulted in higher mean time to extinction, especially in large remnants. The difference was caused by mates in the structured no-Allee model finding each other even at low population densities and by the lack of an additional mortality risk incurred from searching for partners. In the unstructured model, the total relaxation of spatial structure (and thus the introduction of density-

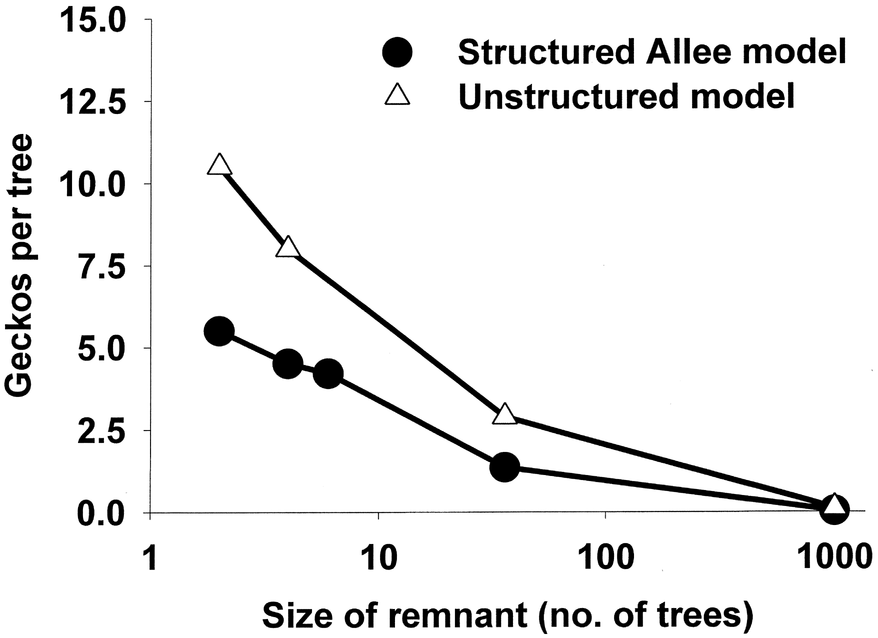

Figure 2. Mean density of geckos at equilibrium as a function of remnant size under the structured Allee model and the unstructured model. The mean was calculated across 1600 simulation runs (initial density of four adults and four juveniles on each tree).

independent mortality), led to a considerably increased mean time to extinction. The effect of removing density dependence was that populations could remain over long time periods at high densities without being pushed to lower densities. Also, the lower equilibrium density under the Allee model (Fig. 2) led to a higher risk of extinction because populations were more likely to drop to extremely low population sizes due to demographic stochasticity. Within one model type, mean time to extinction increased with increasing remnant size despite decreasing densities, because total population size at equilibrium increased with remnant size. To illustrate the meaning of the differences in mean time to extinction among the models (Fig. 5), in terms of the risk of extinction (P_0) within a given time horizon *t*, we used an approximation derived by Wissel et al. (1994):

$$P_0(t) = 1 - \exp(-t/T_m).$$

For example, the mean times to extinction, T_m, of the smallest remnant investigated (2 trees) were 50 years in the Allee and no-Allee models and 110 years in the unstructured model. Thus, within a time horizon of 50

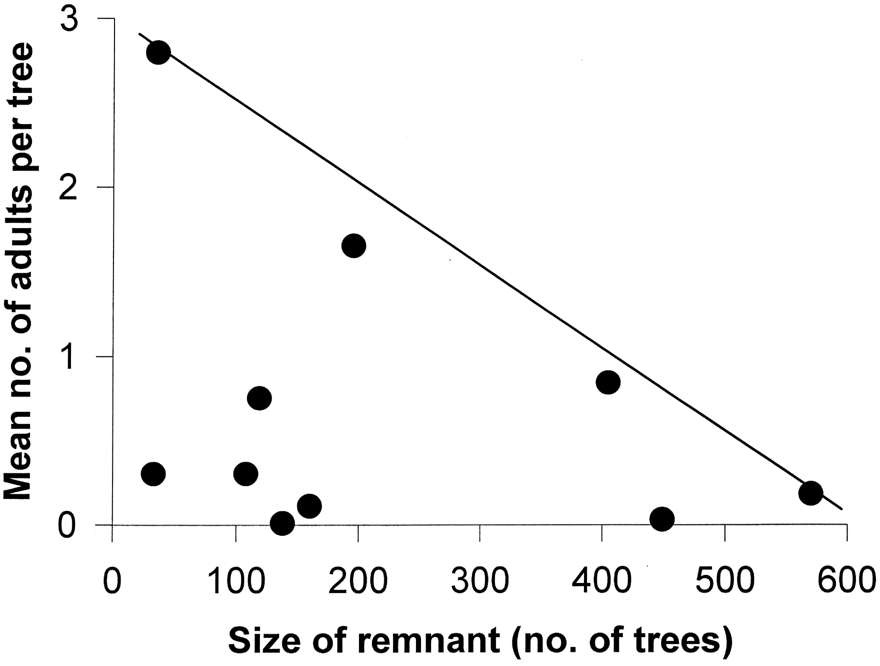

Figure 3. Number of adult geckos per tree versus remnant size. Line indicates an upper density limit as a function of remnant size. Data are from How and Kitchener (1983) and Sarre (1995).

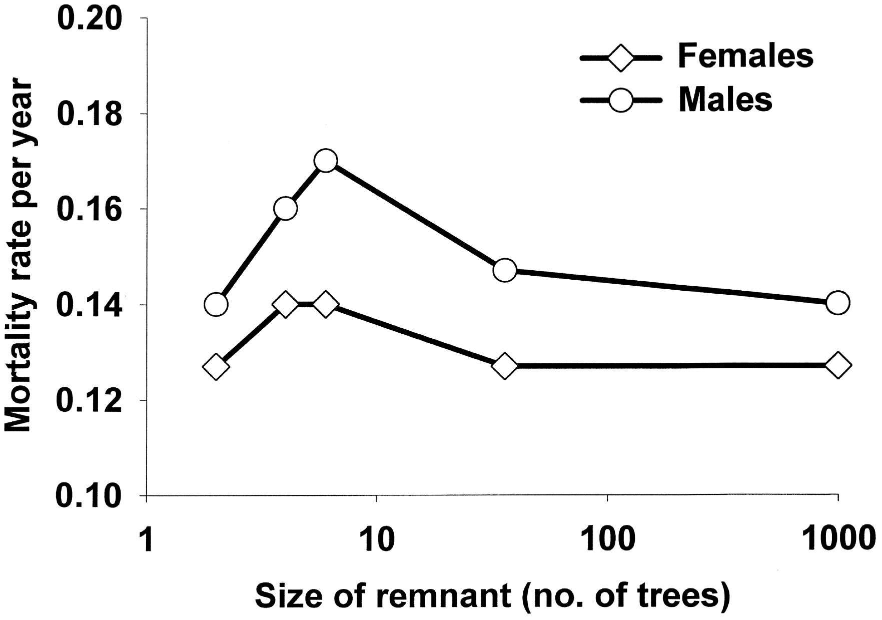

Figure 4. Mortality of adult geckos at equilibrium density as a function of remnant size under the structured Allee model for females and males. The mean was calculated across 1600 simulation runs (initial density of four adults and four juveniles on each tree). The measured mortality rates are mortality rates of the unstructured model.

years, the structured models predicted a risk of extinction of approximately 63%, whereas the unstructured model predicted extinction with a probability of about 37% only. In all cases, however, extinction was almost certain within the next 350 years ($P_0 \approx$ 100% and 96%, respectively). Differences between the models were most pronounced at intermediate remnant sizes. At 36 trees, for example the mean times to extinction (Fig. 5) were 375 years (Allee model), 500 years (no-Allee), and 3250 years (unstructured model). Thus, the estimated risks of extinction within, say, 200 years were 41%, 33%, and 6%, respectively.

Discussion

The Allee Effect

The potential importance of Allee effects on the dynamics of small populations has been shown in a number of theoretical studies (e.g., Lande 1987; Dennis 1989; Stephan & Wissel 1994). Numerous, but by no means all, observational field studies have reported evidence of Allee effects in many different species (references in McCarthy 1997; Kuussaari et al. 1998; Courchamp et al. 1999; Stephens & Sutherland 1999). In a spatially unstructured model for the

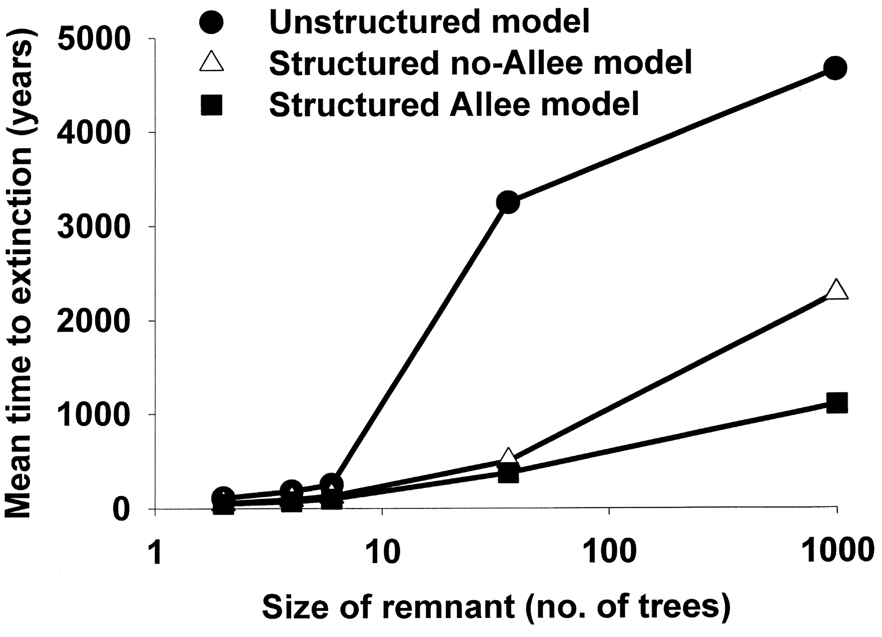

Figure 5. Mean time to extinction for geckos in remnants of different size under the structured Allee model, structured no-Allee model, and the unstructured model. The mean was calculated across 1600 simulation runs (initial density of four adults and four juveniles on each tree).

black-footed ferret (*Mustela nigripes*), Harris et al. (1989) found a slight decrease in population survival when mortality was increased in a step-wise fashion at low density introducing an Allee effect. Our model provided similar results: a slight decrease in mean time to extinction due to an Allee effect on mortality at low densities. This result can be explained as follows. At population densities low enough to exert a negative effect on population dynamics, extinction risk was high because of demographic stochasticity (cf. Goodman 1987). In our model, therefore, the relative contribution of the Allee effect to the probability of extinction was small, but it nevertheless noticeably decreased population persistence, at least in large remnants.

Spatial Structuring at High Densities

The spatial structuring inherent in our spatially structured Allee model resulted in a clear decrease in mean time to extinction when compared to that of the unstructured model. This result is in contrast to a frequently cited paper by Ginzburg et al. (1990), who argue that density dependence should have a positive effect on population persistence because density effects act as restoring forces (i.e., push populations into equilibrium). In their model of the cod *Gadus morhua*, weak to realistic levels of density-dependent recruitment favor stabilization of populations around equilibrium via maximum recruitment near equilibrium density. In contrast, the comparison of our structured Allee and structured no-Allee models to the unstructured model assumed no difference in population regulation (survival) at equilibrium among the compared models and a strong negative effect of density dependence at high densities in the two structured models. In our unstructured model, populations did better because they could increase well beyond equilibrium density without any disadvantages, whereas populations were stabilized around equilibrium in the density-dependent scenarios of Ginzburg et al. (1990).

Stacey and Taper (1992) investigated different scenarios of density regulation in the population growth rate of the territorial Acorn Woodpecker (*Melanerpes formicivorous*). Based on the ideas that territories are not all of the same quality and are compressible, and that there is a cost to territory defense, they fitted their field data on population growth as a function of population size to a θ-logistic model, because the θ-logistic gives a marked decrease in population growth at high densities. Median time to extinction under the θ-logistic model is substantially lower than under a logistic population growth model. Even though Stacey and Taper (1992) focused on different aspects of territoriality than we did (decreasing quality vs. movement costs), our study is in agreement with their results that territoriality suppresses populations at high densities. This ultimately leads to shorter persistence times because populations are more often at intermediate densities from which they can drop more easily to extinction.

Lima et al. (1998) had a different motivation for including density dependence in extinction models of three small mammal species (two rodents and a marsupial). These species tend to cycle, partly because of delayed density dependence (Lima & Jaksic 1999). A comparison among density-dependent and density-independent models showed that, in the former, lower persistence is observed for all three species (Lima et al. 1998). This is in agreement with the results of Ginzburg et al. (1990) under strong density dependence. In the model of Lima et al. (1998), strong density dependence no longer acts as a restoring force but overcompensates for changes in population density. This causes damped cycles from which stochasticity allows populations to reach even lower levels, resulting in lower persistence time than without density dependence (Ginzburg et al. 1990). But Ginzburg et al. (1990) consider this scenario unrealistic for the fish they investigated.

Several studies indicate that density dependence influences the estimation of persistence times, but the direction in which population regulation acts depends on the form and strength of density dependence investigated. All the modeling approaches were influenced by the species under study (bird, cod, gecko, and small mammals), and a transfer of these results to other species must take into account specific population traits.

Population Viability Analyses and Spatial Structuring

Our model comparisons demonstrate that the decrease in mean time to extinction caused by an Allee effect on mortality at low densities is small when compared with the effect of density-dependent mortality caused by spatial structure at high densities. The major effects of density dependence on the population growth of species with low reproductive rates and long life spans, and on populations that are more limited by resources, occur near carrying capacity (Fowler 1981). Consequently, the consideration of density dependence at high densities is extremely important for analyses of the population viability of most territorial species, but the way in which density dependence is incorporated into models dramatically influences the results of PVAs (Mills et al. 1996). We agree with Mills et al. (1996) that the importance of density regulation in specific modeling studies should always be tested by including a scenario without density dependence.

One critical assumption of our study was the parameterization of the unstructured model. It could be argued that differences between the structured Allee and unstructured models depended on the choice of mortality rates in the unstructured model. An alternative approach would be to determine mortality rates directly from field data. Unfortunately, predictions from our model were sensitive to mortality rates (K. Wiegand 1996; K. Wiegand et al. 2001). More extensive data than those currently available are required to determine mortality rates with the necessary precision to avoid confounding by problems of measurement accuracy, but having a model enables us to circumvent this problem. Taking the model as the real system, we assumed it was most likely that a researcher would measure mortality at the most frequent density, the equilibrium density. Thus, it is most likely that a nonspatial, density-independent model would have been parameterized the way we did. This virtual ecology approach (Grimm et al. 1999) enables us to make realistic comparisons between models with and without spatial structure.

We recommend that the modeling of density-dependent parameters be based on structural knowledge of the species under consideration instead of the general application of approaches provided by simulation packages. Unfortunately, the analysis of density dependence of population parameters requires long-term data and complicated analysis based on specific statistical models (Pollock et al. 1990; Barker & Sauer 1992; Dennis & Taper 1994). In the absence of hard data, a realistic representation of density dependence is difficult to achieve in spatially unstructured models. Thus, in many cases the most natural way to model the density dependence of territorial species will be by imitating the effects of the inherent causes of density dependence, the spatial structure of populations (cf. the structured Allee model; Hildenbrandt et al. 1995; Letcher et al. 1998; K. Wiegand et al. 2001). The explicit consideration of spatial population structure has the following advantages. If data are scarce, it is important to make use of structural knowledge that cannot be easily incorporated into more abstract models. This requires the matching of the model scale to the scale of population structure. In the case of the structured Allee model, this has been done by explicitly considering the spatial distribution of territories. With a similar model and observational scale, one can use secondary model predictions to test whether the model rules are sensible. For example, one might look at patterns such as the number of occupied territories as a function of population size (density). In the case of the Allee model, this and other relationships were used to test the validity of the rules of the model (K. Wiegand et al. 2001). This approach is closely related to the pattern-oriented modeling approach (Grimm et al. 1996).

The results of our study demonstrate that spatial structure can be a critical means of determining extinction times in territorial species. Both Lamberson et al. (1994) (Northern Spotted Owl [*Strix occidentalis caurina*]) and Letcher et al. (1998) (Red-cockaded Woodpecker [*Picoides borealis*]) found that dispersed territories result in lower population growth rates for their respective species than do clumped territories. This emphasizes the importance of space even at intermediate population densities. These, and our results, indicate that at least for territorial species the construction of spatial PVA models is worth the effort, but species-specific models will often have to be developed to ensure adequate realism.

Costs and Benefits of Spatially Explicit Simulation Models

A problem raised by Wennergren et al. (1995) and Ruckelshaus et al. (1997) is that simulation models can become data hungry as one adds a spatial component and thus more assumptions. Even though the scenarios chosen by Ruckelshaus et al. (1997) were of moderate biological realism (South 1999) and the error propagation in their dispersal model turned out to be less dramatic than previously thought (Mooij & DeAngelis 1999), most scientists would agree that the collection of data for parameterization of spatially explicit models may be cost-intensive, and errors in estimating parameters may add up to shaky model predictions. On the other hand, our results show that developing spatially explicit simulation models may enhance the predictive ability of PVA. Thus, ecologists and conservation biologists are confronted with a dilemma: how to take advantage of the opportunities of spatially explicit models without being overwhelmed by their disadvantages.

Grimm et al. (1996) point out that ecological modeling presents a dilemma between too much detail and too much free abstraction. As a way out they propose to guide model development by patterns observed in nature in an iterative fashion, for example, adding more detail step by step (see also Thulke et al. 1999). We suggest using such an iterative, pattern-oriented modeling approach for the development of spatially explicit models. Initially, the exploration of different hypothetical yet realistic (given available biological knowledge) scenarios of parameters presumed to be important (e.g., movement) should be conducted before intensive data collection is attempted. "Scenarios" refers to both structural assumptions and parameter values. Simulation of many different scenarios will identify those aspects of space that may have a significant effect on persistence time. If not, space can be dropped at this point.

If some scenarios indicate that spatial effect may be important, however, it will be necessary to decrease the number of potential scenarios. This can be done by comparing one or several patterns produced by the model to the corresponding patterns observed in the field, hereafter called "pattern analysis." Only those scenarios that lead to realistic patterns are potential representatives of the processes acting in the field. Examples illustrating this idea of pattern-oriented modeling have been given by Drechsler (2000) (decision analysis for management of a parrot under uncertainty), Jeltsch et al. (1997) (model of the spread of rabies), T. Wiegand et al. (1999) (a nonspatial PVA model of a bear), and K. Wiegand et al. (2000*a*, 2000*b*). Patterns used in these studies range from trend and variation of population size (Drechsler

2000) to the exact size and spatial distribution of trees (K. Wiegand et al. 2000*a*, 2000*b*). Field information on the pattern selected should be easier to obtain than information on the underlying processes. This is the case in all the examples we provide.

Once the number of possible scenarios has been reduced through pattern analysis, the influence of the remaining scenarios on persistence should be revisited. If all scenarios exhibiting significant influence on persistence are unrealistic, based on the pattern analysis, space may be eliminated from the simulation model. If not, biologists should take field measurements and/or conduct experiments to test the hypothesis underlying the remaining scenarios and thus further limit the number of possible processes acting in the field (Lepš 1990; Levin 1992). The next step is to measure model parameters in the field. The effort geared toward the measurement of different parameters should be guided by sensitivity analyses. The more sensitive that time to extinction is to a certain parameter, the more effort should be invested in (further) measurement of that parameter (K. Wiegand et al. 1999). There is a tradeoff with the costs incurred by different measurements. Often, instead of measuring a parameter directly in the field, it might be more effective to measure an additional pattern that can be used to conduct a parameter fit. In a PVA model of a bear by T. Wiegand et al. (1999), for example, mortality proved important, but the authors had only vague information about mortality rates. Mortality was determined by iterating the model with plausible values and comparing simulation results to time series of the number of female bears with cubs of the year, a parameter much easier to measure precisely than mortality rates.

The procedure we propose transfers the effort of constructing spatially explicit models from extensive field measurements toward a high investment in simulation studies. Such studies will require the development of sophisticated models by professional modelers with good biological backgrounds (cf. T. Wiegand et al. 1999). Nevertheless, the approach we propose will reduce the net costs for developing reasonably accurate spatially explicit models. Whether or not the increase in accuracy is worth the greater effort depends, in part, on how much we are willing to pay for a certain expected improvement. We strongly recommend conducting sensitivity analyses of different scenarios to estimate the expected improvement in accuracy. If resources for the development of case-specific models and for necessary field studies are not available, simple best- and worst-case modeling scenarios will be the most that can be done.

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