

Discounting initial population sizes for prediction of extinction probabilities in patchy environments

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ABSTRACT

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Extinction is a major concern in conservation. A most urgent need is to predict the relationship of a population's initial size to its probability of extinction. Previous work has led to a widely accepted conclusion that the larger an initial population size, the less likely the population will go extinct. I used a spatially-explicit simulation model to investigate extinction probabilities of Bachman's Sparrow (*Aimophila aestivalis*) in patchy environments. Contrary to the conventional wisdom, I found that the relationship between extinction probabilities and initial population sizes of the sparrows was not correlated when initial individuals were in several patch types. To make good predictions of the sparrows' extinction rates, I have suggested discounting models which incorporated initial population sizes and initial spatial distributions. The models discounted initial population sizes on the basis of patch characteristics (patch suitability, timing of patch suitability, and duration of patch suitability). As a result, the extinction probabilities decreased with the logarithm of discounted population sizes. The discounting models may have implications for quantitative predictions of extinction chances of other species, since most environments are patchy or spatially-subdivided. The discounting approach may be also useful for evaluating impacts of patchy environments on population dynamics and community structure.

INTRODUCTION

Initial population size is the number of individuals of a population at the beginning of experiments or simulation studies. It is one of the most important factors in determining ecological consequences such as competitive outcomes (Hutchinson, 1978) and population extinction probability.

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For prediction of population extinction probabilities, past investigators have found that the higher initial population sizes, the lower the extinction probabilities are (Shaffer, 1981; Shaffer and Samson, 1985; Harris et al., 1987; Harrison et al., 1988). This conclusion has been drawn from theoretical and simulation models which did not explicitly recognize environmental heterogeneity (e.g., Shaffer, 1978). Because most environments are patchy or spatially-subdivided (Levin, 1976; Wiens, 1976; Kareiva, 1990; Pacala et al., 1990; Hassell et al., 1991), a question to the point is to ask whether this conventional conclusion still holds in a spatially-explicit context. If not, how can population extinction probabilities be predicted? To answer the first question, I have developed a spatially-explicit model which could simulate the population dynamics and extinction chances of Bachman's Sparrow in response to changes of patchy forest structure in a region managed for timber production (Liu, 1992). I will try to answer the second question by proposing discounting models which distinguished and discounted the contributions of various patches to population persistence.

THE SPATIALLY-EXPLICIT SIMULATION MODEL

Bachman's Sparrow is a possibly threatened or endangered species (Pulliam et al., 1992). Its range has declined significantly since the 1930s (Haggerty, 1986). The sparrows breed in various habitats including patchy pine forests of the southeastern United States, which are mostly mosaics of even-aged stands. The pine forests are usually harvested at 20–60-year cycles, depending on desired timber products. Reproductive success of Bachman's Sparrows differs in various stands. In mature (≥ 80 years) and 1–2-year forest stands, a pair of adults produce 3.0 offspring a year, compared to 1.0 offspring in 3–5-year-old stands. No offspring are produced in other age classes and clear-cuts (0-year stands following harvesting) (Pulliam et al., 1992).

In all simulations, the hypothetical landscape for the sparrows to breed was a pine forest of 1000 ha (Fig. 1). I divided the forest into a two-dimensional array of 20×20 hexagonal cells. Each cell was 2.5 ha, which is the average territory size for a pair of Bachman's Sparrow. I assumed that each forest stand was as large as an array of adjacent 2×2 cells (10 ha). In the forest, there were two mature stands and the remaining stands were assigned with equal probability as 0–19-year age classes. All stands were randomly distributed. I further assumed that the mature stands were never harvested, but the remaining stands were managed in rotations of 20 years each.

Sparrow population sizes at the beginning of simulations were proportional to the number of 1–5-year patches and mature patches. The spatial

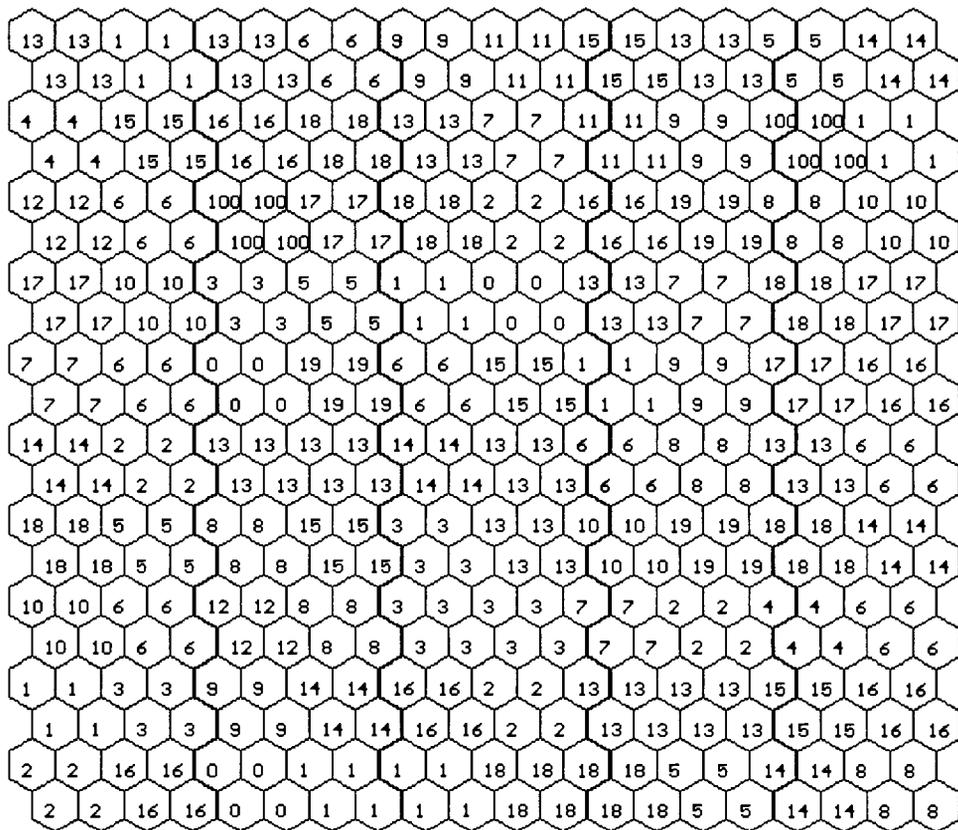


Fig. 1. A sample landscape from the spatially-explicit simulation model. Each hexagonal cell represents 2.5 ha of pine woodlands, which equals a sparrow territory size. Number in each cell is the age of pines.

distributions of initial individuals within each patch type were random. With data from field studies and a literature survey, adult and juvenile survivorships have been estimated as 0.60 and 0.40 respectively in all patches (Pulliam et al., 1992). For simplicity, I just considered a single sex (female) in the simulation model because the sex ratio is 1:1 (Pulliam et al., 1992). If the parents died, one juvenile stayed in its natal patch, but other juveniles had to search for new territories. If there were suitable neighboring patches (mature or 1–5-year stands), a juvenile settled in one of them. Otherwise a juvenile moved into any of the adjacent patches until it found an unoccupied suitable patch, or until it died. The dispersal survivorship was assumed to be 0.90. The forest boundary was constructed to be reflective. When a juvenile reached a forest edge, it moved back to the forest. If a breeding patch became unsuitable, an adult might stay there unless there was one or more suitable neighbors.

The simulation model was coded in Borland C++ 2.0 (an object-oriented programming language) and implemented in a Zenith 386 computer with a math coprocessor. Population dynamics were simulated for 100 years. If no individuals existed before or in the last simulation year, the population was considered extinct. Each simulation run had 100 replicates. The extinction probability was calculated as the ratio of extinction frequency over total replicates (Harris et al., 1987).

SIMULATION RESULTS: EFFECTS OF HABITAT HETEROGENEITY ON THE RELATIONSHIP BETWEEN POPULATION SIZE AND EXTINCTION PROBABILITY

Traditionally, population size is counted as the total of individuals in all patches. In my simulation model, individuals in mature patches and 1–2-year patches produced more offspring than those in other patches. The traditional concept of population size ignores suitability differences among patches, so it may be called “nominal” population size. To understand the consequences of disregarding the variance in patch suitability, I have done simulations with initial individuals in one patch type and in several patch types. The simulation results have shown that if all individuals were initially in one patch type, the relationship of nominal initial population sizes to extinction rates was significantly correlated. For example, when initial individuals were only in mature patches, the Spearman rank correlation coefficient $r_s = -0.94$ ($n = 11$, $P < 0.01$). This is consistent with the conventional theory that higher initial population sizes result in lower chances of extinction. If individuals were initially in several types of patches, however, there was no correlation between nominal initial population sizes and extinction probabilities (see Fig. 2, Spearman rank correlation coefficient $r_s = -0.1182$, $n = 11$, $P \gg 0.05$).

The above results are due to the differences in spatial distributions of initial populations. In the case that individuals initially were in one patch type, the initial population was made up of individuals in patches with the same reproductive success. When individuals initially were in several types of patches, however, the initial population was composed of individuals with different reproductive success, and individuals in poor patches (with low reproductive success) were treated the same as those in good patches (with high reproductive success). The discounting models below were attempts to differentiate individuals in various patches.

THE DISCOUNTING MODELS

Population persistence may be influenced by three patch characteristics: patch suitability (how suitable is a patch?) (Pulliam, 1988; Pulliam and

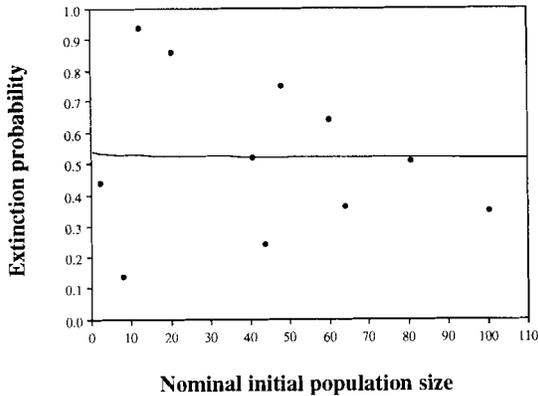


Fig. 2. The relationship between extinction probabilities and nominal initial population sizes of Bachman's Sparrow in patchy environments was not correlated at all. Note that the fitting curve was almost parallel to X -axis.

Danielson, 1991; Pulliam et al., 1992), timing of patch suitability (when is a patch suitable?) (Liu, 1992), and duration of patch suitability (how long is a patch suitable?) (Liu, 1992; Pulliam et al., 1992). In my simulation model, patch suitability was measured in terms of reproductive success because I assumed that all other conditions were the same for individuals in different patches except that reproductive success varied.

I proposed a discounting approach to differentiate individuals in various patches. That is, individuals in poorer patches were discounted as equivalents to a certain number of individuals in the best patches so that all individuals after discounting were essentially the same. In the following, I will demonstrate the discounting models and procedures. Steps 1 and 2 below will integrate temporal characteristics of patches (timing of patch suitability and duration of patch suitability), step 3 will incorporate spatial difference in patch suitability, step 4 will calculate discounted population sizes in one patch, and step 5 will compute discounted population sizes in all patches.

Step 1. To differentiate contributions of timing of patch suitability to population persistence, I proposed a model (Eq. 1) to discount reproductive success in patch i at time t .

$$DB(i,t) = \frac{B(i,t)}{T(i,t) + 1} \quad (1)$$

where $DB(i,t)$ is the discounted reproductive success of patch i at time t , $B(i,t)$ is the nominal reproductive success in patch i at time t , and $T(i,t)$ is the number of years that patch i has been unsuitable at time t since its first

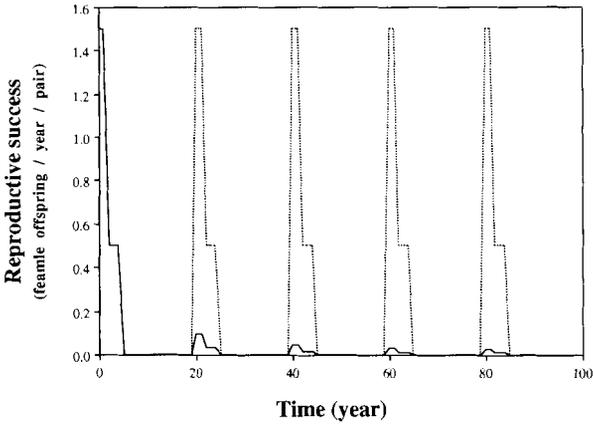


Fig. 3. Periodic dynamics of reproductive success of Bachman's Sparrow in an initial 1-year patch during a period of 100 years (five forest rotations). The dash line (\cdots) indicates the nominal reproductive success, while the solid line (---) refers to the discounted reproductive success. In each rotation, the patch was suitable for the first five years. During the first rotation, the discounted reproductive success was equal to the nominal reproductive success. For the last four rotations, the discounted reproduction success became smaller and smaller.

time of being suitable. I discounted the nominal reproductive success based on two facts: (1) The longer the uninhabitable time period, the less chance that an individual can survive; (2) Even if an unsuitable patch becomes suitable later, the chance for the newly suitable patch to be occupied is lower than a continuously suitable patch (Liu, 1992). I will give an example to show how this model works. For an initial 1-year patch (Fig. 3), the first five years in each rotation were continuously suitable, the remaining 15 years were not (no offspring could be produced). Therefore, there was no discount of reproductive success for initial 1-year patches in the first five years of the first rotation, while the discounted reproductive success during the first five years of the second, the third, the fourth and the fifth rotation was $1/16$, $1/31$, $1/46$ and $1/61$ of the nominal reproductive success respectively because the patches were suitable again after being unsuitable for 15, 30, 45 and 60 years.

Step 2. To consider the duration of patch suitability, I added up discounted reproductive success (Eq. 2) for the time period of interest.

$$CDB_i = \sum_{t=0}^m DB(i, t) \quad (2)$$

where CDB_i is the cumulative discounted reproductive success in patch i , $DB(i, t)$ is the discounted reproductive success in patch i at time t , and m is the last time interval in simulations.

TABLE 1

Relative cumulative reproductive success (RCDB_{*i*}) in patches of different age classes

Initial age of patches (year)	RCDB _{<i>i</i>}
1	0.0339
2	0.0241
3	0.0142
4	0.0109
5	0.0077
Mature (≥ 80)	1.0000

Step 3. In order to compare suitability of one patch with that of other patches, I calculated relative cumulative discounted reproductive success with maximum cumulative discounted reproductive success as a baseline (Eq. 3).

$$\text{RDCB}_i = \frac{\text{CDB}_i}{\text{CDB}_{\max}} \quad (3)$$

RCDB_{*i*} is the relative cumulative discounted reproductive success (or relative suitability) in patch *i*; CDB_{*max*} is the maximum cumulative discounted reproductive success among all patches. That is, CDB_{*max*} = MAX (CDB₁, CDB₂, ..., CDB_{*i*}, ..., CDB_{*n*}), where *n* is the number of patches. The relative suitability ranges from 0 to 1. As presented in Table 1, a mature patch had relative suitability of 1. This is because it was always suitable and had high nominal reproductive success. An initial 1-year patch had lower relative suitability because of three reasons: (1) It was suitable for only five years and unsuitable for fifteen years in each rotation (recall that each forest rotation was 20 years long). (2) Although its nominal reproductive success during the first two years of each rotation was as high as that of a mature patch, the nominal reproductive success during the next three years was just one-third the nominal reproductive success of a mature patch. (3) All of the nominal reproductive success was discounted except for the first five years of the first rotation. An initial 2-, 3-, 4-, and 5-year patch had even lower relative suitability (Table 1). Besides the reasons (1) and (2) mentioned above, the nominal reproductive success was discounted earlier because an older initial patch became unsuitable sooner.

Step 4. A nominal population size in a patch was discounted according to relative suitability of the patch (Eq. 4).

$$\text{DPS}_i = \text{RCDB}_i * \text{POP}_i \quad (4)$$

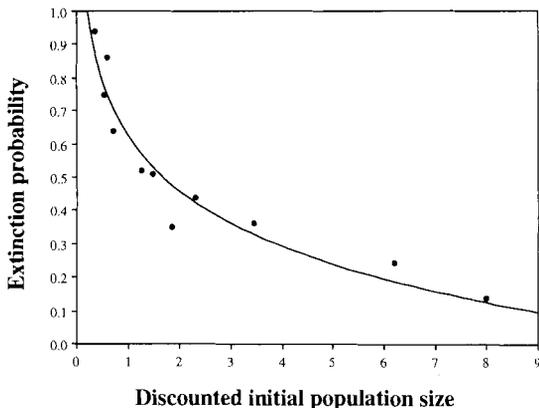


Fig. 4. There was a significant correlation between extinction probabilities and discounted initial population sizes of Bachman's Sparrow in patchy environments. The relationship was described by a logarithm equation, $Y = 0.6229 - 0.5518 \log(X)$, where Y is the extinction probability and X is the discounted initial population size.

where DPS_i is the discounted population size in patch i ; POP_i is the nominal population size in patch i . Relative suitability can tell how many individuals in poorer patches are equivalent to a certain number of individuals in patches with the highest suitability. For example, because relative suitability of initial 1-year patches was 0.0339, 100 individuals in initial 1-year patches were equivalent to 3.39 individuals in mature patches.

Step 5. A total discounted population size (DPS) was summation of the discounted population sizes in all patches (Eq. 5).

$$DPS = \sum_{i=1}^n DPS_i \quad (5)$$

where n is the number of patches.

RESULTS AFTER DISCOUNTING

Nominal initial population sizes presented in Fig. 2 were discounted according to equations (1)–(5). Fig. 4 shows that extinction rates (Y) decreased with the logarithm of discounted initial population sizes (X) ($Y = 0.6229 - 0.5518 \log(X)$, Spearman rank correlation coefficient $r_s = -0.9636$, $n = 11$, $P < 0.01$). This indicates that the discounting models worked very well, because before the discounting there was no correlation between the nominal initial population sizes and extinction probabilities (Fig. 2). The results suggest that initial population sizes alone could not tell extinction probabilities if individuals were initially distributed in various

patch types. The problem was solved through incorporation of patch characteristics with nominal initial population sizes.

DISCUSSIONS AND CONCLUSIONS

The seeding process of initial populations in the simulations was similar to the introduction or reintroduction of populations. The discounting models suggest some management strategies. In order to maintain lower extinction probabilities, it is better to place individuals in mature patches at the very beginning because they were stable and had high quality for the sparrows' reproduction. The sparrows would have much lower chances to successfully keep persistent populations if individuals were seeded in the ephemeral cyclic patches. When breeding patches became unsuitable, no more offspring were produced if the adults could not find suitable patches nearby. Even though the ephemeral patches were suitable again after a long time, they had very low likelihood to be occupied because of insufficient number of offspring.

The discounting models may be valuable in predicting extinction probabilities of other species in heterogeneous environments after some modifications. The patch suitability in my models was measured by reproductive success. Although the discounting models performed satisfactorily in this paper, other patch characteristics may be potentially important to other species. For example, if mortality differs in various patches, the discounting models should incorporate it. Another important factor to consider may be patch position, which partially determines the success of locating suitable patches (Harrison et al., 1988).

Many studies have shown effects of patchy environments on population dynamics and community structure (Kareiva, 1990; Hassell et al., 1991). Predicting the effects, however, is very challenging because patches are different in quality (Pulliam and Danielson, 1991). This problem would become simpler if various patch types could be comparable on the basis of a common index. As discussed above, the discounting models first considered the patch variations and then made the patches equivalent to each other so that all patches were compared according to a single measure (relative suitability). It seems promising that the discounting approach would be beneficial to forecasting ecological consequences of patchy environments.

In summary, when initial individuals of Bachman's Sparrow were put in several types of patches in heterogeneous environments, nominal initial population sizes alone could not predict extinction probabilities. Through integrating patch characteristics (patch suitability, timing of patch suitability, and duration of patch suitability), the discounting models discounted

nominal initial population sizes in various patches. The extinction probabilities were then significantly correlated with the discounted population sizes. It is hoped that the discounting models would be applicable to predicting extinction rates of some other species in patchy environments. The discounting approach would also be useful for examining impacts of patchy environments on population dynamics and community structure.

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REFERENCES

- Haggerty, T.M., 1986. Reproduction ecology of Bachman's Sparrows (*Aimophila aestivalis*) in Central Arkansas. Ph.D. Dissertation, University of Arkansas, Fayetteville.
- Harris, R.B., Maguire, L.A. and Shaffer, M.L., 1987. Sample size for minimum viable population estimation. *Conserv. Biol.*, 1: 72–76.
- Harrison, S., Murphy, D.D. and Ehrlich, P.R., 1988. Distribution of the Bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *Am. Nat.*, 132: 360–382.
- Hassell, M.P., Comins, H.N. and May, R.M., 1991. Spatial structure and chaos in insect population dynamics. *Nature*, 353: 255–258.
- Hutchinson, G.E., 1978. *An Introduction to Population Ecology*. Yale University Press, New Haven.
- Karciva, P., 1990. Population dynamics in spatially complex environments: theory and data. *Phil. Trans. R. Soc. Lond. (B)*, 330: 175–190.
- Levin, S.A., 1976. Population dynamic models in heterogeneous environments. *Ann. Rev. Ecol. Syst.*, 7: 287–310.
- Liu, J., 1992. A spatially-explicit model for ecological economics of species conservation in complex forest landscapes. Ph.D. Dissertation, University of Georgia, Athens.
- Pacala, S.W., Hassell, M.P. and May, R.M., 1990. Host–parasitoid associations in patchy environments. *Nature*, 344: 150–153.
- Pulliam, H.R., 1988. Sources, sinks, and population regulation. *Am. Nat.*, 132: 652–661.
- Pulliam, H.R. and Danielson, B.J., 1991. Source, sink, and habitat selection: a landscape perspective on population dynamics. *Am. Nat.*, 137: S50–S66.
- Pulliam, H.R., Dunning, Jr., J.B. and Liu, J., 1992. Population dynamics in complex landscapes: a case study. *Ecol. Appl.*, 2: 165–177.

- Shaffer, M.L., 1978. Determining minimum viable population sizes: A case study of the grizzly bear (*Ursus arctos*). Ph.D. Dissertation, Duke University, Durham, NC.
- Shaffer, M.L., 1981. Minimum population sizes for species conservation. *BioScience*, 31: 131–134.
- Shaffer, M.L., 1990. Population viability analysis. *Conserv. Biol.*, 4: 39–40.
- Shaffer, M.L. and Samson, F.B., 1985. Population size and extinction: A note on determining critical population sizes. *Am. Nat.*, 125: 144–152.
- Wiens, J.A., 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.*, 7: 81–120.