

LINKING LANDSCAPE DATA WITH POPULATION VIABILITY ANALYSIS: MANAGEMENT OPTIONS FOR THE HELMETED HONEYEATER
Lichenostomus melanops cassidix

H. Resit Akçakaya

Applied Biomathematics, 100 North Country Road, Setauket, New York 11733, USA

Michael A. McCarthy and Jennie L. Pearce

Forestry Section, University of Melbourne, Parkville, Victoria 3052, Australia

ABSTRACT

Habitats used by most species are becoming increasingly fragmented, requiring a metapopulation modelling approach to population viability analysis. Recognizing habitat patchiness from an endangered species' point of view requires utilization of spatial information on habitat suitability. Both of these requirements may be met by linking metapopulation modelling with landscape data using GIS technology. We present a PVA model that links spatial data directly to a metapopulation model for extinction risk assessment, viability analysis, reserve design and wildlife management. The use of the model is demonstrated by an application to the spatial dynamics of the Helmeted Honeyeater Lichenostomus melanops cassidix, an endangered bird species endemic to Victoria, Australia. We use spatial data, organized by a GIS, on the habitat requirements of the helmeted honeyeater to define the patch structure. We then combine this patch structure with demographic data to build a metapopulation model, and use the model to analyze the effectiveness of translocations as a conservation strategy for the helmeted honeyeater.

Key words: habitat suitability model; helmeted honeyeater; metapopulation model; population viability analysis; translocation.

INTRODUCTION

Rare and threatened species are adversely affected by changes in the landscape that cause habitat loss and habitat fragmentation. Such changes in the landscape can be brought about by short-term human impact such as change in land-use patterns, or by long-term

impacts such as global climate change. Habitat fragmentation as a result of human impact, as well as the natural heterogeneity of habitats, cause most endangered species to exist in a small number of relatively isolated populations that may occasionally exchange individuals (a *metapopulation*). The difficulty of extrapolating dynamic changes to the metapopulation level from single population models, as well as the need to evaluate management options (such as reserve design, translocations and reintroductions) and to assess human impact (such as increased fragmentation and isolation) at the metapopulation level have made the metapopulation concept one of the most important paradigms in conservation biology (Hanski 1983; Gilpin and Hanski 1991; Burgman et al. 1993).

Models developed for metapopulation dynamics have generally increased in complexity and in the number of factors they incorporate. While the earlier models only regarded each habitat patch either as empty or occupied, recently models that incorporate various components of within-patch dynamics have been developed and implemented as micro-computer software (e.g., Akçakaya and Ferson 1990; Possingham et al. 1992; Lacy 1993; reviewed by Lindenmayer et al.). In all these models, some parts of the landscape are considered habitat patches and the remainder as unsuitable habitat only used for dispersal. In some cases, the species in question has a specific habitat requirement which has sharp boundaries, making patch identification quite straightforward. In other cases, even decisions on the total number of patches may be made differently by different researchers.

Most PVA models do not make explicit use of habitat data organized in geographic information systems (GIS). Recognizing habitat patchiness from a species' point of view requires utilization of spatial information on habitat suitability, in coordination with metapopulation modelling. In this paper we present the prototype of a PVA model that links GIS-generated spatial data directly to a metapopulation model, and demonstrate the use of the model by applying it to the metapopulation dynamics of the helmeted honeyeater.

THE PVA MODEL

The PVA model (Akçakaya 1993) is designed to link GIS-generated landscape data with a detailed metapopulation model for extinction risk assessment, viability analysis, reserve design and wildlife management. The model operates in three steps. First, landscape data are analyzed and the patch structure is exported to a metapopulation model. Second the metapopulation model is built by combining spatial and demographic information. Third, simulations are run to estimate risks. Below we summarize the essential aspects of these three model components.

Landscape data

Spatial data (usually produced by a GIS) may be imported into the model as one or more map layers. Information in different map layers are combined to make a map of habitat suitability indices (HSI). A patch-recognition algorithm is employed to find patches in the HSI map. The spatial structure of the habitat is then exported to a metapopulation model.

After deciding which species and which geographic section of its range to study, it is necessary to decide which habitat characteristics are important for the species. This can be done, for example, by collecting data at a large number of locations in the landscape. The

data consist of several habitat characteristics that might be important, along with data on the occurrence or abundance of the species at that location. These may then be combined in a multiple regression to rank the factors in terms of their importance for the species, that results in a function that links these habitat characteristics to a habitat suitability index (HSI) function (Pearce et al. 1993). The variables (or arguments) of this function are the habitat characteristics. These may include, for example, percent vegetation cover, percent canopy closure, average age of canopy trees, density of the host plant, amount of rainfall (annual or in certain months), solar radiation, average winter temperature, distance to water, distance to forest edges, elevation, aspect, slope, etc.

Next, it is necessary to know how to relate the HSI to population parameters. The model implemented here assumes a linear relationship between HSI and the carrying capacity. This parameter is a scalar function that relates the carrying capacity of the patch to the total HSI in that patch. The HSI value of all the cells in a patch may be summed, and then rescaled by the linear function to provide the carrying capacity of the patch. If HSI were calculated by multiple regression on census data, they would already be in the correct units, and would not require rescaling if the census represents carrying capacities.

There are two important parameters that provide the link between the HSI function and the metapopulation model. They determine how the species perceives (or reacts to) the patchiness of the habitat. These are threshold HSI and neighbourhood distance, and are used by the patch-recognition algorithm that delineates patches on the HSI map. *Threshold HSI* is the minimum HSI value (as defined by the HSI function) below which the habitat is not suitable for reproduction and/or survival. It is assumed that the species may disperse or migrate through habitat that has a lower HSI than this threshold. *Neighbourhood distance* is used to identify nearby cells that belong to the same patch. Suitable cells (as defined by the HSI threshold parameter) that are separated by a distance less than or equal to the neighbourhood distance are regarded to be in the same patch. It may represent, for example, the foraging distance of the species. Given the same set of habitat maps, the same HSI function and the same scalar function for carrying capacities, a higher threshold HSI and/or a smaller neighbourhood distance will result in a greater number of smaller patches, i.e., a more patchy landscape.

Finally, the spatial data must be organized into input files. Important restrictions are that **(i)** the maps must be in raster format, **(ii)** all layers should be numerical, **(iii)** all should describe the landscape with the same precision (i.e., number of cells in both north-south and east-west directions should be the same), and **(iv)** coverage of all maps should be identical (the corners of the rectangular area described by all maps should be the same). Given all this input information, the model does the following:

- (1) load all maps that describe the habitat components,
- (2) calculate the HSI value for each cell, based on the HSI function,
- (3) find clusters or groups of nearby cells (i.e., within the neighbourhood distance of each other) that have HSI values higher than or equal to the threshold HSI, and label them as patches,
- (4) calculate the total HSI within each patch, and based on this, calculate the carrying capacity of each patch, using the scalar function specified,
- (5) calculate the minimum distance between patches, based on the location and shape of their edges, and
- (6) export the patch coordinates, carrying capacities, and the distances to the metapopulation model.

Metapopulation model

In the second step, the spatial information for the metapopulation is combined with ecological (demographic) parameters of the species. The metapopulation model can incorporate any of the following factors

- + Spatial structure of the metapopulation,
- + Age or stage structure of the populations,
- + Density dependence (crowding effects and Allee effects),
- + Demographic stochasticity,
- + Environmental stochasticity (fluctuations in vital rates or carrying capacities),
- + Temporal trends in carrying capacities of populations (e.g., habitat loss),
- + Local and regional catastrophes,
- + Spatial variation in catastrophe impact,
- + Spatial variation in age structure,
- + Spatial variation in density dependence,
- + Dispersal rates among populations,
- + Age- or stage-dependent dispersal,
- + Density-dependent dispersal,
- + Distance-dependent dispersal,
- + Spatial correlation of environmental fluctuations,
- + Distance-dependent spatial correlations.

Spatial factors such as dispersal (migration) between patches and correlation of environmental fluctuations among populations have important effects on metapopulation persistence and viability (Gilpin 1988; Harrison and Quinn 1989; Akçakaya and Ferson 1990; Akçakaya and Ginzburg 1991; Burgman et al. 1993). In this model, the spatial structure is based on the geographic configuration of populations. Both correlations and rates of dispersal can be specified as functions of the distance between populations. For distance-dependent correlation, distances from the centres of patches are used, whereas for distance-dependent dispersal, minimum (edge-to-edge) distances as imported from the landscape model are used. The two factors, dispersal and correlation, have values that differ among each pair of patches according to their shapes and relative geographic positions, thus making the model spatially explicit.

Factors that effect persistence at the population level include initial distribution (initial number of individuals in each age or stage) (Burgman et al., in press), and density dependence (Ginzburg et al. 1990). Each population in the model can have a different initial distribution, and a different density dependence function. Density dependence may act on survivorships, fecundities, or all vital rates. It may involve a simple ceiling model, logistic-like functions that describe contest- or scramble-type intraspecific competition (including Ricker and Beverton-Holt functions), Allee effects (i.e., density dependence at low population sizes), or Allee effects combined with density dependence at high

population sizes.

Environmental stochasticity is modeled by **(i)** random fluctuations in vital rates (i.e., age or stage-specific fecundities and survivorships), **(ii)** random fluctuations in carrying capacities, and **(iii)** local or regional catastrophes. The random fluctuations can be normal- or lognormal-distributed, and can be correlated among populations. They are assumed to be perfectly correlated among age classes or stages within each population. Catastrophes may have population- or age-specific effects and probabilities, and they may act by decreasing abundances, carrying capacities, or vital rates. Demographic stochasticity is modeled by sampling the number of survivors from a binomial distribution and the number of offspring from a Poisson distribution (Akçakaya 1991).

Risk assessment

The third step is risk assessment. The model can be used to simulate the dynamics and to predict the future of the metapopulation. The results can be expressed as

- + risk of extinction (or any amount of decline),
- + time to extinction (or to any amount of decline),
- + risk of increase or explosion,
- + time to increase or recovery,
- + mean metapopulation trend,
- + expected future fluctuations in metapopulation size,
- + mean trend and expected fluctuations for each population,
- + metapopulation occupancy (number of occupied patches) and its variation,
- + local occupancy (percent of time each population remained extant).

The three dimensions that define the viability of a metapopulation are: **(i)** the probability that a decline will occur (or the metapopulation will become extinct), **(ii)** the amount of decline, if it does occur, and **(iii)** the time it will take the metapopulation to decline to this level (Akçakaya 1992). By giving the risk of decline to various levels (as well as risk of total extinction), and the whole distribution of time to extinction or decline (in addition to the median time to extinction), the PVA model allows complete characterization of the metapopulation viability. The model can be run several times, to analyze the sensitivity of results to input parameters by varying them automatically, to compare management options, or to assess anthropogenic impact by comparing outputs from simulations with parameters for impacted and non-impacted situations.

HELMETED HONEYEATER

We demonstrate the use of the model with an application to the spatial dynamics of the Helmeted Honeyeater, using spatial data organized by a GIS. We use the spatial data to define the patch structure, combine this patch structure with demographic data to build a metapopulation model, and use the model to analyze the effectiveness of translocations as a conservation strategy for the helmeted honeyeater. In this section, we describe the data to be used in this research, and the parameterization of the PVA model.

Background information

In the past, the helmeted honeyeater (*Lichenostomus melanops cassidix*) was restricted to the tributaries of the Upper Yarra River and Westernport Bay, Victoria. Historically, confirmed colonies of helmeted honeyeaters have been reported from only two areas: the catchments of the Yellingbo area and the Cardinia Creek watershed. The Cardinia population became extinct in the early 1980's and the last remaining population at Yellingbo declined to fewer than 70 birds in 1989. An important reason for decline of the species has been loss of forest habitat and there are many related problems including competition from other bird species, particularly bell miner birds, loss of habitat resulting from eucalypt dieback and fires, and high rates of nest predation (Backhouse 1987; Menkhurst and Middleton 1991; Smales et al. 1990). At Yellingbo, helmeted honeyeaters forage almost exclusively in swamplands composed of alternating stands of *Eucalyptus camphora*, with a mixed understorey of *Phragmites*, *Carex*, *Cyperus* and *Juncus* species, and teatree thickets (predominantly *Leptospermum lanigerum* and *Melaleuca squarrosa*). Historically, the Helmeted Honeyeater has also been found in riparian forests characterized by *Eucalyptus viminalis* with a mixed shrub understorey.

The helmeted honeyeater is a territorial bird. In order to breed, a pair must establish a territory from which all other birds are aggressively excluded. Generally, the minimum age of breeding is 2 years. Average number of immature birds of each sex raised per pair is about 0.48. The number of young raised per pair follows a Poisson distribution and the assumed sex ratio (females:males) is 1:1. Survival is approximately the same for males and females and is equal to 0.76. Because of the small number of birds and the relatively short study period, the level of environmental variation is not clear. It seems to be rather small, on the order of 10% (coefficient of variation) for both fecundity and survival (McCarthy et al., in press). Dispersal (migration) distances are greater in females than in males. Of birds that attained breeding territory, mean dispersal distance is 0.5 km for males and 1.9 km for females. In the model described below, we modeled only the female population.

One of the potential conservation measures available for the recovery of helmeted honeyeaters is the translocation of individuals from one of four closeby colonies to another area where they will be isolated from the catastrophes (such as fire) that may affect the current colonies. There are many factors which make the design of a translocation program difficult. For example, should breeding or non-breeding birds be translocated? What is the cost of translocation to the source population in terms of elevated extinction risks? Given this cost, does the overall extinction risk of the metapopulation decrease or increase with translocation? The model will be used to address these and similar questions.

Landscape data

Since the Helmeted Honeyeater is thought to utilize the swampland and riparian communities differently, two separate HSI functions were found by analyzing the landscape data with logistic regression (Pearce *et al.* 1993). For the riparian community that we will concentrate on, this logistic regression analysis gave the function

$$\text{logit}(p) = \ln(p/(1-p)) = -2.989 + 1.307 W + 0.181 E + 0.409 B,$$

where p is the probability of occurrence, W is the presence or absence of ground water, E is

the number of *E. camphora* stems per 25 m², and *B* is an index (scaled 0 to 5) of the amount of decorticated bark (Pearce *et al.* 1993). The following HSI function was obtained by rearranging the above formula

$$\text{HSI} = 1 / (\exp(2.989 - 1.307 W - 0.181 E - 0.409 B) + 1)$$

The HSI threshold parameter was based on habitat the birds now occupy. Although helmeted honeyeaters generally use territories with HSI > 0.5, some locations have HSI values as low as 0.3. Therefore 0.3 was used as the HSI threshold.

Foraging distance is based on the observations of the field biologists who study helmeted honeyeaters. They regard territories within 200 metres to be in the same colony ("in social contact"). However, the daily foraging distance for a bird is within its territory (about 50-100 metres) (D. Franklin and I. Smales, pers. comm.). Therefore we used 100 metres (2 cells) for the foraging distance.

The constant that relates the carrying capacity of each patch (*K*[*i*]) to the HSI values was determined in the following way. The total number of breeding females was 22. The number of floaters (non-breeders) will be about 0.5 times this number, giving a total of 33 females. The sum of all HSI's within current helmeted honeyeaters territories is 30.0. Dividing this number with the number of females gives 1.1 as the scaling factor. Therefore we used the formula $K[i] = 1.1 \cdot \sum \text{HSI}[i]$, where the summation is over all cells in the patch.

Demographic data

We modeled only the female population, and used the vital rates summarized above to build a matrix model (see Caswell 1989) in which the individuals are grouped into two stages (juveniles and adults). We assumed the vital rates to be the same in all populations. We used the transition matrix

$$\begin{array}{cc} 0.00 & 0.48 \\ 0.76 & 0.76 \end{array}$$

and 10% coefficient of variation for each vital rate. For each population, we used a different initial stage structure, given by the observed number of birds in each stage (see Table 1). We modeled demographic stochasticity and correlated environmental variation of vital rates, as described above.

The birds breed colonially and those birds that do not have access to a territory join the floating population. Thus, a ceiling-type density dependence was used. Mean dispersal distances were used in an exponential distance-dependent dispersal model (Figure 1). Dispersals were also defined as stage-dependent, since only non-breeding adults migrate. In addition to environmental variability, we assumed a 1% annual risk of regional catastrophes (e.g., fire) which would eliminate the populations entirely.

The demographic data (McCarthy *et al.*, in press) summarized above was combined with the patch structure based on GIS data to complete a spatially-explicit metapopulation model. In addition, we added another patch to the metapopulation to investigate the effectiveness of translocation. For this, we used a potential translocation site. We assumed that this additional population ("new") will have the same vital rates and variabilities and a carrying capacity of 10 females. We also assumed that it would be

independent (i.e., its vital rates will be uncorrelated with those of the other populations), and isolated (i.e., there would be no natural dispersal between the additional population and others), and immune from catastrophes. We simulated the dynamics of the metapopulation after translocating 0, 2, 6, and 10 individuals from the largest colony to this new population, and compared the risk of metapopulation decline in the 50 years for each case. We repeated the simulation with 10 translocated adults by subjecting the new population to catastrophes with the same magnitude (but independent from others). All simulations started with the same total number of individuals and same overall distribution of the total number to two stages. The only difference was in the distribution of the individuals among different populations. The simulations with no translocation started with individuals distributed to the four patches as given in Table 1, while the other started with 2 - 10 individuals in the newly formed population, taken from the largest population. All simulations were run with 10,000 replications.

RESULTS

Patch structure

The map of habitat suitability indices, and the patches identified by the patch-recognition algorithm are shown in Figure 2. The patches identified by the algorithm (A, B, C and E) correspond exactly to 4 of these colonies. One colony (D) was not recognized by the algorithm, since none of the cells around its location seems to have high enough habitat quality. There are three possible reasons for this:

- (1) the sampling strategy used for collecting the spatial data: suitable habitat at this site is rather linear in shape (less than 50 m wide). Structurally it looks similar to the other occupied colonies, but being so narrow, few occupied sites landed in a plot, and those that did are on the edge of the territory, and may not be truly representative of the territory itself;
- (2) habitat quality function: the quality of the habitat obviously depends on many other factors. The HSI function determined by the logistic regression may have excluded a factor that is locally important at the site of this colony.
- (3) historical artifact: there is currently a single pair at this colony site. This pair may have started breeding there when habitat was better, and has not yet left, although the habitat quality now is below that of the other colonies.

The carrying capacities of the identified patches, as calculated from the HSI values, are given in Table 1. Table 1 also gives the initial number of individuals and their distribution among the two stages, as used to in the metapopulation model. One of the patches (A in Fig. 2) has no initial population, since currently there are no breeding pairs in this colony (although it used to be a large colony in the 1970's, and breeding was confirmed as recently as in 1990).

Metapopulation dynamics

The risk of decline that this metapopulation faces is represented in two different ways. In Figure 3, the level of decline is fixed at 15 females, and the distribution of times at which

the metapopulation will fall to or below this level are shown as a histogram. The dotted line indicates the median of the distribution, which is about 22.6 years. In Figure 4, the time is fixed at 50 years and the amount of decline is varied. Curve (a) in Figure 4 shows the risk that the metapopulation will decline to various levels anytime within the next 50 years. The levels are expressed as percentages of the total metapopulation abundance at the start of the simulation. Curve (a) indicates that the metapopulation faces about 40% risk of total extinction (100% decline).

Curves (b), (c) and (d) in Figure 4 show the risk of decline following the translocation of 2, 6 and 10 adults, respectively, from the largest population (C in Fig. 2) to the new population. These curves assume that the new population is not subject to catastrophes. Translocating 2 adults decreases the risk of extinction within the next 50 years from 40% to less than 20%, whereas translocating 6-10 adults decreases the risk to less than 10%. The median time to fall below 15 females was 33.7 years, 41.9 years and 41.3 years, following the translocation of 2, 6 and 10 adults, respectively.

Translocating 1 juvenile and 1 adult instead of 2 adults; 2 juveniles and 4 adults instead of 6 adults; and 3 juveniles and 7 adults instead of 10 adults did not change curves (b), (c) and (d) respectively. Similarly distributing the number of individuals to be translocated between the largest (C in Fig. 2) and second largest (E) populations did not change the results.

Curve (e) in Fig. 4 shows the risk of decline following the translocation of 10 adults from the largest population (C in Fig. 2) to the added population, with the assumption that the new population is also subject to 1% annual risk of catastrophes (independently from other populations). The total risk of extinction is about 20%.

DISCUSSION

The patch-recognition algorithm of the model successfully identified the locations of 4 colonies, although it could not identify the location of a single pair nesting away from others. The identified patch structure was then used as input for the metapopulation model, thus providing a link between the landscape data on habitat suitability and demographic data on population dynamics.

Simulations with the metapopulation model indicated that the median time for the metapopulation to fall below 15 females is about 23 years. However, the time-to-quasiextinction distribution in Figure 3 has a high variance and is highly skewed, with a mode around 12 years. The skewed distribution and high variance are typical of time-to-extinction curves (e.g., Levinton and Ginzburg 1984). This common characteristics suggest that using a scalar measure such as the mean to describe the distribution may be misleading. If it is necessary to use a scalar measure of time-to-extinction, the median rather than the mean should be used.

Simulation results summarized in Figure 4 (curve a) imply a relatively high (about 40%) risk of extinction within the next 50 years. This level of risk is similar to those obtained from more detailed simulation models of the same populations (McCarthy et al., in press).

The predicted median time to fall below 15 females (23 years) is probably similar to the length of time it would take for any *E. camphora* planted now to attain the size and structural characteristics suitable for Helmeted Honeyeater occupancy and reproduction. Assuming habitat regeneration or reconstruction was to begin now, and that the important

features of existing habitat could be accurately replicated, then there appears to be a relatively high probability of not being able to increase habitat before the Helmeted Honeyeater population drops to dangerously low levels.

The right end of curve a (Figure 4) is relatively flat, indicating that the risk of declining by 80% or by 100% are about the same. This pattern is characteristic of population dynamics with Allee effects, where the population rapidly goes extinct once it has reached a level as low as 20% of its initial size (i.e., 80% decline). Although we did not explicitly model Allee effects, we believe this pattern has arisen due to the type and rate of dispersal we incorporated into the model. Female helmeted honeyeaters have a relatively high dispersal distance (1.9 km), and they usually do not breed in their natal colony. Thus, the total rate of dispersal of juvenile females from each population is close to 100%. When few populations remain extant and their sizes are very different from each other, such a high rate of dispersal may reduce the metapopulation persistence. This is because the dispersers from the larger to the smaller population will cause the population in the smaller patch to exceed the carrying capacity, hence they will not be able to find sufficient territories. The dispersers from the smaller to the larger population will not be able to fill all vacant territories, resulting in an overall sub-optimal use of resources. This partly results from the assumption of the model that an individual can disperse only once per year.

The simulation results suggest that translocating just 2 adults from the largest population to a new patch might decrease the risk of metapopulation extinction considerably. However, this might be a rather optimistic result, since it is based on the assumption that the additional population is independent from the other populations and immune from catastrophes. We made these assumptions because the patch that can potentially be used for translocation is located in another valley, thus its environment may be independent, especially in terms of fires that may wipe out all populations within the same valley. Relaxing the assumption of immunity from catastrophes increases the predicted risk considerably (compare Fig. 4 curves d and e), but translocation seems to decrease the risk of extinction even if the new population is also subject to catastrophes (compare Fig. 4 curves a and e). However, this result should be interpreted with caution. Although Fig. 4 curves a and e give different risk of total extinction (suggesting an advantage of translocation), the risk of an 80% or less decline is about the same for both cases. This amount of decline corresponds to only about 7 females remaining. Due to the uncertainties of demography at such small population sizes, as well as other uncertainties in the model (such as the carrying capacity of the new population), this result may overestimate the effectiveness of translocation. The metapopulation model discussed in this paper represents the first attempt at linking landscape data on habitat quality to the spatial structure of a metapopulation model for the helmeted honeyeater. Building the model required some simplifying assumptions such as modelling only the females, using a two-stage transition matrix, and allowing only one dispersal per individual per year. As with any model, "relative" results (e.g., whether the species has a higher chance of persistence with or without translocations) are probably more reliable than "absolute" results (e.g., when exactly will the species go extinct), and the model is more useful as a tool to explore different management options and to guide empirical efforts, than as a tool to make exact predictions about the future of the species.

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TABLE 1
Population-specific parameters used in the simulations

Population	K	N(0)	J(0)	A(0)
A	4	0	0	0
B	8	3	1	2
C	24	21	7	14
E	7	9	3	6

K - carrying capacity (as calculated by the patch-recognition algorithm)

N(0) - total initial number of females

J(0) - initial number of juvenile females

A(0) - initial number of adult females

Figures

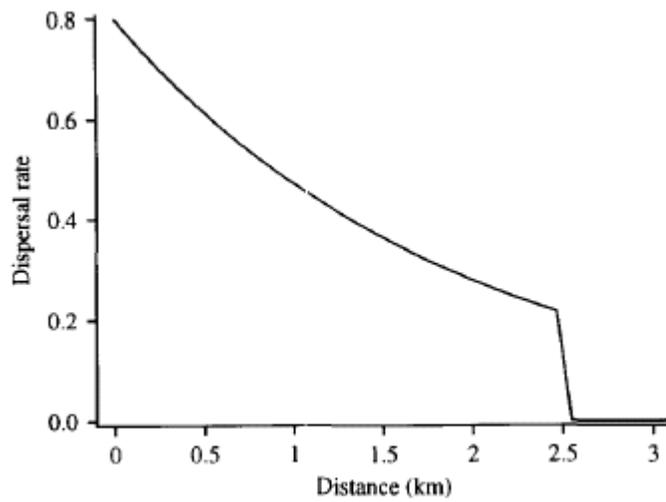


Fig. 1. Dispersal rate of non-breeding females (i.e., the proportion of non-breeding females in the source patch that will arrive at the target patch) as a function of the distance between the two patches.

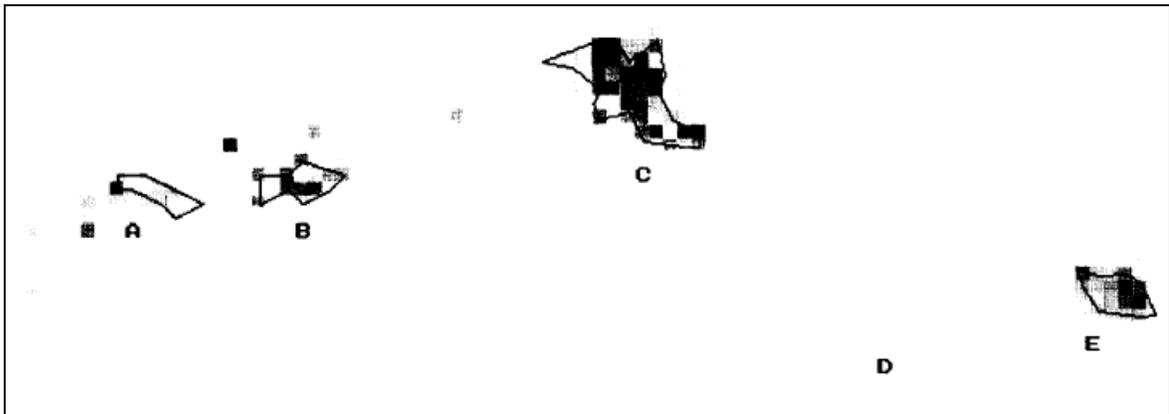


Fig. 2. The map of habitat suitability indices (HSI). The darker the tone, the higher the HSI value. The metapopulation structure identified by the patch-recognition algorithm is shown by the four polygons.

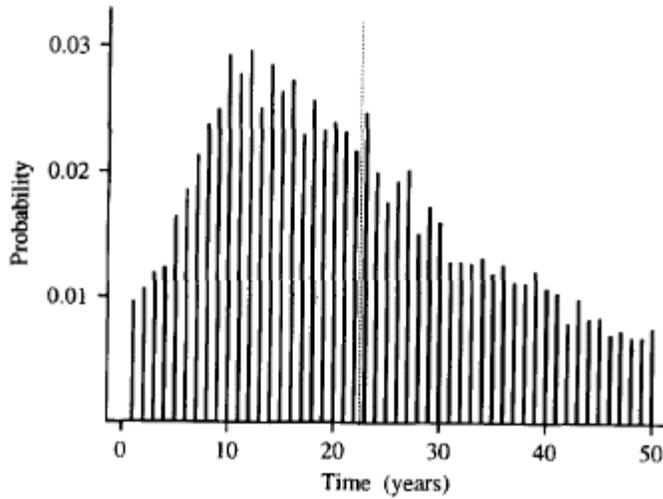


Fig. 3. Number of years required for the number of Helmeted Honeyeater females to fall below 15, given no translocation. The vertical line represent the median of the distribution. The distribution is based on a simulation with 10,000 replications.

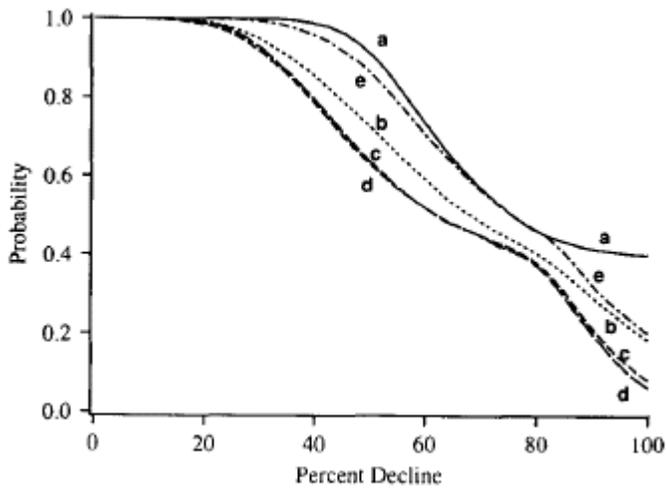


Fig. 4. Probability of a decline in the metapopulation of the Helmeted Honeyeater within 50 years, as a function of the amount of decline. **a**: no translocation; **b**: 2 adults translocated; **c**: 6 adults; **d**: 10 adults; **e**: 10 adults with the "new" population also subject to catastrophes. Each curve is based on a simulation with 10,000 replications.