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Estimating Minimum Habitat for Population Persistence

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Abstract

A central problem for ecological landscape design is to determine how much habitat is needed to ensure persistence of a wildlife population. Various attempts at solving this problem have appeared in the ecological literature over the past six decades. These attempts include patch-scale and landscape-scale ideas, and have incorporated several different processes relating habitat amount to population persistence. In this essay I review these ideas, emphasizing the processes whose rates change with declining habitat amount. I argue that the currently available generic PVA (population viability analysis) models should not be used to estimate minimum habitat for population persistence, because they omit an important process, namely increasing per capita emigration rate and dispersal mortality rate with decreasing habitat amount. I discuss alternative modelling frameworks for estimating minimum habitat for population persistence, and I conclude with some principles for ecological landscape design.

Keywords: dispersal mortality; emigration rate; habitat loss; population viability analysis; Skellam's process.

Introduction: Factors relating habitat amount to population persistence

Population persistence cannot be measured directly, so estimating minimum habitat for population persistence requires a model. There are at least five factors that must be included in any such model. The first two are largely responsible for differences between species in minimum habitat requirements: species need more habitat for population persistence if (i) their individuals have larger area requirements, and (ii) they have lower reproductive rates (Pimm *et al.* 1988; Casagrandi & Gatto 1999; With & King 1999; Fahrig 2001; Vance *et al.* 2003; Holland *et al.* 2005). The other three factors are processes whose rates actually change with changing habitat amount: (i) per capita emigration rate and associated dispersal mortality rate increase with decreasing habitat amount; (ii) the influence of demographic and environmental stochasticity on local extinction rate increases with decreasing habitat amount; and (iii) immigration rate and colonization rate decrease with decreasing habitat amount.

The main reason that the minimum habitat amount for population persistence is difficult to estimate is that the rates associated with these last three factors change with changing habitat amount. In other words, one might estimate emigration rate and dispersal mortality rate, rate of local extinction and immigration and/or colonization rates for a particular species in a particular landscape. However, these values could not be used to estimate minimum habitat requirements for that species, because the rates themselves change with changing habitat amount. In this section I discuss these three processes in more detail.

Increasing per capita emigration rate and dispersal mortality rate with decreasing habitat amount

Possibly the earliest work on the problem of estimating the amount of habitat needed for population persistence is Skellam's (1951) classic paper on dispersal. Skellam argued that there is a **critical patch size**, or a minimum patch size, for population persistence, which is determined by the population's intrinsic growth rate and its dispersal function. Imagine a population in a single, isolated patch (no immigration), with random dispersal. The combination of the dispersal distance and the patch size will determine the probability of an individual dispersing outside the boundary of the patch (i.e. the **per capita emigration rate**). Because the patch is isolated, these emigrants are lost to **dispersal mortality**. The smaller the patch, the larger the per capita emigration rate, because the edge: area ratio of the patch increases with decreasing patch size, which means that a larger proportion of the population is within dispersal range of the edge of a small patch than a large patch. Therefore, there is a minimum patch size (the critical patch size) below which losses through emigration are not balanced by reproduction in the patch, and the population in the patch goes extinct (Fig. 7.1). Note that the existence of a critical patch size is a necessary consequence of geometry; the probability of encountering the patch edge increases with decreasing patch size, no matter what the particular movement behaviour of the organism. Since Skellam's (1951) paper, several studies have evaluated various factors influencing the critical patch size. As summarized by Holmes *et al.* (1994), 'factors that increase movement out of a patch lead to larger critical patch sizes, while factors that decrease movement out of the patch lead to smaller critical patch sizes.'

Landscape-scale models have also demonstrated that emigration rate and dispersal mortality can have a large effect on the amount of habitat needed for

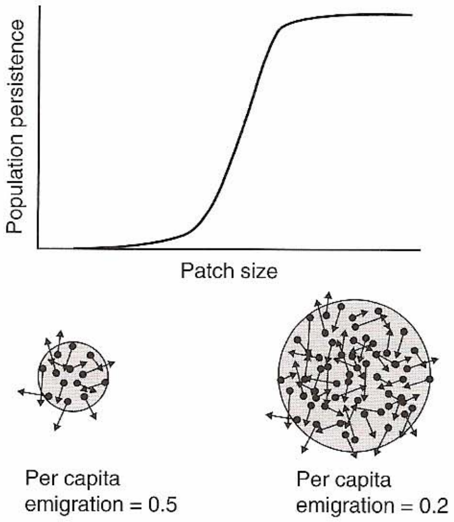

Figure 7.1 **Illustration of the critical patch size concept (Skellam 1951). The per capita emigration rate increases with decreasing patch size, leading to a critical patch size below which reproduction in the patch cannot balance losses from emigration.**

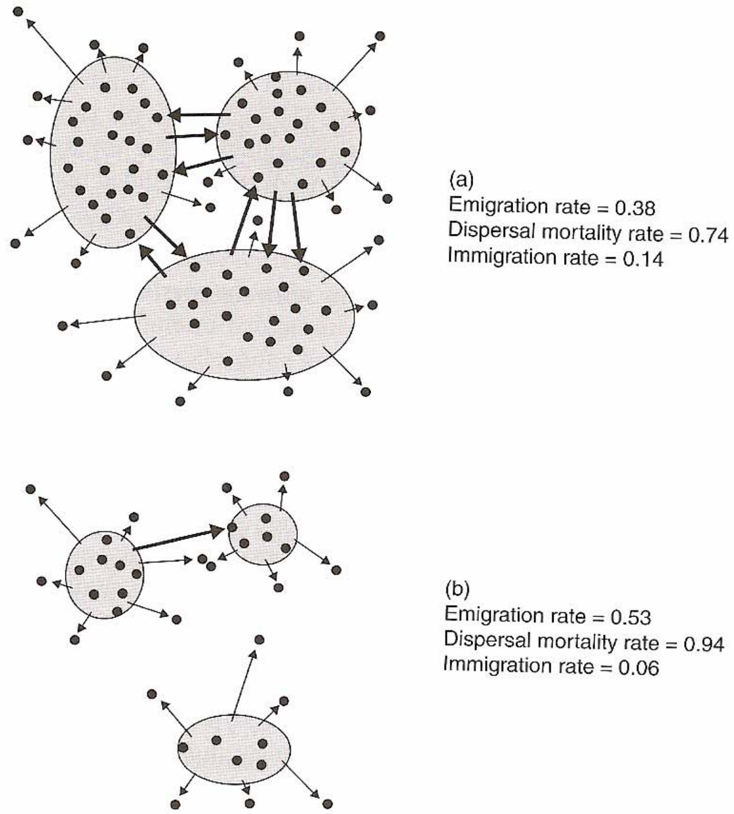

Figure 7.2 **Illustration of the effects of habitat loss on emigration rate, dispersal mortality rate and immigration rate. Ovals are habitat patches. Arrows represent emigration events of individuals between the previous time step and the present. Emigration rate is the proportion of all individuals present in the previous time step that left their patch: (a) 31/82; (b) 18/34. Dispersal mortality rate is the proportion of all emigrants that died without reaching another patch: (a) 23/31; (b) 17/18. Immigration rate is the proportion of all individuals currently present in patches that were in a different patch in the previous time step: (a) 8/59; (b) 1/18.**

population persistence (Casagrandi & Gatto 1999; Fahrig 2001; Flather & Bevers 2002). The rate of loss to the population from dispersal mortality increases with decreasing amount of habitat in the landscape, for the same geometric reasons that create the critical patch size (Fig. 7.2). The less habitat there is, the higher the per capita probability of individuals emigrating from habitat because the edge: area ratio in the landscape generally increases with declining habitat. Also, the less habitat there is, the larger the proportion of these emigrants that die in the matrix without reaching habitat, as shown experimentally by Smith and Batzli (2006). The increase in per capita dispersal mortality rate with decreasing habitat amount affects the amount of habitat needed for population persistence, and needs to be included in any model aimed at estimating minimum habitat for population persistence.

Increasing rate of stochastic extinctions with decreasing habitat amount

Soulé and Simberloff (1986) introduced a very different patch-scale approach to the minimum habitat question, based on the **minimum viable population** (MVP) concept (Shaffer 1981). MVP is based on the idea that population persistence is most strongly related to population size, because extinction is essentially a stochastic event, and the effects of demographic and environmental stochasticity increase with decreasing population size. The MVP is defined as the smallest population that ensures a high probability of persistence (say 95%) over a long time period (say 100 or 1000 generations). Soulé and Simberloff (1986) asked, 'what is the smallest nature reserve that will ensure persistence of a population of interest?' They suggested that one could first estimate the MVP, and then multiply the area requirement of each individual by the number of individuals in the MVP to give the minimum reserve area for MVP. This concept has been used to estimate minimum reserve size for individual species (e.g. Reed *et al.* 1988; Wielgus 2002; Tisdell *et al.* 2005) and groups of species (Pereira *et al.* 2004).

The critical patch size concept and the minimum habitat area for MVP concept are based on very different assumptions about the processes that create a relationship between habitat amount and population persistence. The critical patch size is mainly the result of an increase in the per capita rate of loss of individuals through emigration out of the patch (a net loss from the population) with decreasing patch size. The minimum habitat area for MVP actually makes no assumption about loss of individuals through dispersal mortality; rather, the MVP results from an increase in the effects of demographic and environmental stochasticity with decreasing population size. Both processes are important factors in determining the relationship between habitat amount and persistence of any population.

Decreasing rates of immigration and recolonization with decreasing habitat amount

For at least the past 35 years, ecologists have recognized that populations typically do not occupy single, completely isolated patches. Habitat patches occur within landscapes containing other patches of similar habitat, which may also contain the species of interest. Extinction of the population in a particular patch may be only temporary if immigrants arrive from other nearby patches and recolonize the empty patch. This implies that in many situations the calculation of minimum habitat area for population persistence should be done on a landscape scale, not a patch scale.

The first attempts to determine minimum habitat amount on a landscape scale were derived from the metapopulation model (Levins 1970), and are reviewed in Hanski *et al.* (1996). Here, the question was how many patches are needed for population persistence? Hanski *et al.* (1996) referred to this as the 'minimum viable metapopulation'. All patches were assumed to be the same size. The rate of colonization of empty patches was an increasing function of the number of occupied patches in the metapopulation, so the proportion of occupied patches decreased with decreasing number of patches in the landscape. This led to a minimum number of patches below which the proportion of occupied patches was zero, that is, the population was extinct. This number of patches is the **minimum viable metapopulation**.

The original minimum viable metapopulation formulation assumed all patches were the same size, so it did not include the processes relating patch size to population persistence discussed above. Later formulations do allow for patch size effects on both extinction and colonization (Hanski & Ovaskainen 2003): larger patches are assumed to have higher colonization rates and lower extinction probabilities. The reduced extinction probability in larger patches is assumed to be due to reduced effects of demographic and environmental stochasticity with increasing patch size (and presumably increasing population size). More recent metapopulation models (e.g. Drechsler *et al.* 2003) recognize that the probabilities of both extinction and recolonization of a patch population should also depend quite strongly on the rate of immigration to the patch. Immigration rate should depend on the size of the recipient patch as well as the number of patches that are within the dispersal range of the recipient patch, and the population sizes in them, which are assumed to be positively related to the sizes of these patches. Therefore, in these models, both extinction and colonization probabilities of a patch are functions of the number and sizes of other patches within dispersal range of the focal patch.

However, there is an important process missing from these metapopulation models, namely, the increase in losses through emigration and dispersal mortality with decreasing amount of habitat, that is, the process introduced by Skellam in 1951 (here called 'Skellam's process'). This process is also missing from current generic PVA tools, which are based, to varying degrees, on metapopulation models. In the following section I discuss this omission and its implications for using PVA tools for estimating minimum habitat for population persistence.

Misuse of current PVA tools for estimating minimum habitat for population persistence

Several generic computer programs have been developed for estimating population viability at a landscape scale; examples include RAMAS GIS (Akçakaya 2000), VORTEX (Lacy 2000), ALEX (Possingham & Davies 1995) and META-X (Grimm *et al.* 2004). These models are all patch-based, so the landscape is described in terms of the sizes and relative locations of habitat patches. The models allow the user to estimate the viability of a particular species in a particular landscape, by supplying parameter values appropriate for that species. Input parameters include: the maximum number of individuals in each patch, which is a function of patch size and individual area requirements of the species; reproductive rate; mortality rate; and immigration rate to each patch, which is a function of patch size and the number and sizes of other patches within dispersal range of the patch. All of these parameters can be subject to stochastic variation, resulting in demographic stochasticity, and the models all include environmental stochasticity.

Once a PVA model has been parameterized for a particular species in a particular landscape, it is tempting to use that model to evaluate viability of hypothetical populations in different landscape scenarios, representing either different landscapes, or the same landscape in a future where habitat amount and pattern have been altered (e.g. Akçakaya *et al.* 2004; Schtickzelle *et al.* 2005). In principle, one could use such scenarios to estimate minimum habitat requirements for population persistence, by evaluating the viability of the population in hypothetical model landscapes containing different amounts of habitat. The minimum habitat in which the modelled population has a high probability of persistence is then the estimated minimum habitat amount for population persistence.

Is this a valid use of PVA models? The first step in answering this is to ask whether these tools contain at least the minimum set of five factors discussed above, which are necessary components of any model aimed at estimating minimum habitat for population persistence. On inspection of the PVA tools, one finds that all of the models lack one important factor: Skellam's process, that is, the increase in per capita emigration rate and dispersal mortality with decreasing habitat amount. The most recent model, META-X, actually predicts a monotonic increase in population persistence with increasing 'emigration' from patches (Grimm *et al.* 2004) (Fig. 7.3a). This is opposite to the predictions of models that explicitly include emigration from patches (Casagrandi & Gatto 1999; Fahrig 2001; León-Cortés *et al.* 2003) (Fig. 7.3b–d). This difference is due to the fact that in META-X 'emigration' is only used to calculate the immigration or colonization resulting from emigration. Emigration itself, with its associated losses to dispersal mortality, does not actually occur in this model. Even though emigration from patches is necessary for immigration to and colonization of other patches, the overall effect of emigration on population persistence can easily be negative when these factors are weighed against dispersal mortality (Casagrandi & Gatto 1999; Fahrig 2001; León-Cortés *et al.* 2003). Because the generic PVA tools do not include one of the processes responsible for the negative effects of habitat loss on population persistence, they must underestimate the minimum habitat needed for population persistence, and they should therefore not be used for this purpose.

It has been suggested that this is a moot point because PVA models really should not be used to provide quantitative estimates of population viability at all; they should only be used qualitatively to compare different management options (landscape scenarios) for their relative impacts on viability (D.B. Lindenmayer, personal communication; L. Tischendorf, personal communication; H.R. Akçakaya, personal communication). The argument is that there must be huge uncertainty associated with any population viability estimate, because estimating viability entails long-term extrapolation based on current parameter values. Small errors in current parameter estimates are propagated and compounded over time, and true parameter values can change over time. Both of these lead to great uncertainty in viability predictions. While this is true, it does not obviate the need for models that can be used to estimate minimum habitat for population persistence. Managers need to know how much habitat will ensure population persistence and, because viability cannot be measured directly, models are the only option. We need models that are unbiased and that contain reasonable estimates of uncertainty and error propagation, so that careful decisions on landscape design can be taken. Current PVA

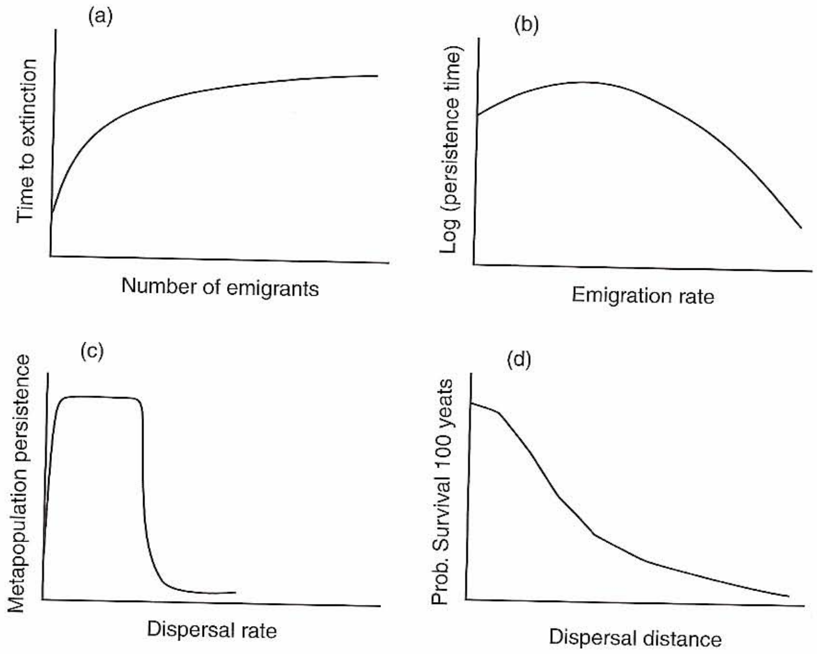

Figure 7.3 **Relationship between emigration and population persistence from four models. (a) In META-X, population persistence is a monotonically increasing function of emigration, due to increasing colonization. Redrawn from Grimm *et al.* 2004, with permission. (b) Population persistence generally decreases with increasing emigration rate, due to increasing dispersal mortality, except at very low emigration rates (Fahrig 2001). Redrawn from Fahrig (in press), with permission. (c) Metapopulation persists only at low to moderate dispersal rates, and not at higher or very low dispersal rates. Curve inferred from Figure 1a, at intrinsic rate of increase = 0.4, in Casagrandi and Gatto (1999). (d) Metapopulation persistence decreases with increasing dispersal distance; in this model dispersal rate from patches is an increasing function of dispersal distance. Redrawn from León-Cortés *et al.* 2003, with permission.**

tools do make some attempt to estimate uncertainty in model predictions; however, they are all biased because they omit Skellam's process.

Because of this bias, I suggest that current PVA tools should not even be used for qualitative comparisons of different landscape scenarios with different habitat amounts. Users of the models are generally unaware of the bias, because there is no mention of it in the documentation for any of the PVA tools. In comparing different scenarios, managers naturally favour those whose PVA runs indicate long-term persistence (e.g. Larson *et al.* 2004; Wintle *et al.* 2005). This may create a sense of false confidence in the effectiveness of the proposed management. If managers knew that the true expected population persistence for the scenarios under consideration was much lower than estimated by the PVA tools, possibly even outside the range of estimates provided, they might look for other options.

Alternative modelling approaches for estimating minimum habitat for population persistence

How would one build a model to estimate minimum habitat for population persistence? A possible starting point would be to take an existing PVA model and add to it the missing pieces, namely, increasing per capita emigration rate with decreasing patch size, and increasing dispersal mortality rate with decreasing habitat amount. The available PVA tools are patch-based. This means that the user provides input parameter values for each patch. Because patches are not all equivalent, that is, they differ in size and location, one needs to have information or make assumptions about how patch size and location affect the parameter values, and then use this information to adjust the values depending on the actual patch sizes and locations. For example, one may assume a particular functional relationship between immigration rate to a patch and the size of that patch, and the distances to and sizes of potential donor patches. These assumptions would be used to estimate the immigration rate for each patch. Similarly, one would need a functional relationship between patch size and emigration rate. The most appropriate way to measure patch size – for example, as its area, or perimeter or linear dimension – would depend on the dispersal behaviour of the organism (Hambäck & Englund 2005). The point here is that in such a patch-based model, the relationships between the parameter values and patch sizes and locations must be included as input assumptions in the model, so they must be known *a priori* by the researcher.

A completely different modelling approach for estimating minimum habitat for population persistence is the individual-based, grid-based 'landscape population model' (e.g. Fahrig 2001; reviewed in Fahrig, in press). These models represent the landscape as a spatial grid containing habitat and non-habitat cells, over which the population is distributed. Individuals are tracked through time as they move, give birth and die. The probabilities of an individual giving birth or dying depend on whether the individual happens to be in a habitat cell or a non-habitat cell. As for patch-based models, variation in habitat quality can be included by assigning cell-specific carrying capacity, reproduction and mortality values. An individual's movement probability, direction and distance also depend on whether it is in a habitat or non-habitat cell, and perhaps on the distribution of habitat and non-habitat cells within some neighbourhood. None of these probabilities or movement rules is a function of the size or location of the patch that a cell happens to be in. Therefore, the relationship between emigration and immigration and patch sizes and locations are not included as input assumptions of the models, but they emerge as model output. Even the simplest movement algorithms – for instance, movement occurs with a given probability in a random direction to a random distance – produces as output: (i) the negative relationship between patch size and per capita emigration rate from patches; (ii) increasing dispersal mortality with decreasing amount of habitat on the landscape; (iii) the positive relationship between patch size and per patch immigration rate; and (iv) higher immigration rates to patches that have more large patches nearby (i.e. are less isolated).

Whether patch-based models or individual-based, grid-based models will be more useful for estimating minimum habitat amount for persistence of a real species will depend on which type of model is easier to parameterize for that species. The basic requirements for parameterizing these two model types are very different and are summarized in Table 7.1. In general, patch-based models require functional relationships between population parameters (rates of reproduction, mortality, emigration, immigration) and patch characteristics (patch size, shape) and the amount and distribution of habitat in the landscape. Variances in these parameter values are also needed, so that the effects of stochastic variation can be included. Individual-based, grid-based models require relationships between probabilities (probability of reproduction, mortality, movement, movement directionality) and the individual's location (in habitat, in matrix, at a habitat–matrix boundary). It seems likely that individual-based models will be easier to parameterize for species such as large animals that can be followed individually, for example using radiotelemetry, to determine movement behaviour in matrix, in habitat and at habitat–matrix boundaries, and to determine mortality rates in matrix. This could also be done for some small animals where experimentation to determine parameter

Table 7.1 **Comparison of the parameters needed in a simple patch-based model and a simple individual-based, grid-based model, adequately to represent the processes that determine the relationship between population persistence and amount of habitat on a landscape.**

Process	Parameters needed for patch-based population model	Parameters needed for individual-based, grid-based model
Reproduction and mortality in habitat, and individual area requirements	Per capita reproduction and mortality rates or intrinsic population growth rate, and associated variance(s); carrying capacity as a function of patch size	Expected number of offspring per individual per time step and probability of dying per time step; carrying capacity per habitat cell
Emigration (should increase with decreasing amount of habitat)	Proportion of individuals emigrating from each patch, as a function of patch size and shape, and associated variance	Movement rules in habitat – probability of moving per time step, directionality of movement, distribution of movement distances – and probability that an individual leaves habitat when it encounters the edge
Dispersal Mortality (should increase with decreasing amount of habitat)	Proportion of dispersers that die, as a function of the amount of habitat available within dispersal range of the donor patch	Movement rules in matrix – probability of moving per time step, directionality of movement, distribution of movement distances – and probability of dying per time step in matrix
Immigration (should decrease with decreasing amount of habitat)	Proportion of surviving emigrants from all other patches arriving in the recipient patch, as a function of the distances to and sizes of potential donor patches and the size and shape of the recipient patch, and associated variance	Probability of individuals entering a patch on encountering its edge

values is possible (e.g. Goodwin & Fahrig 2002). Patch-based models may be more appropriate for species such as birds, where individuals are hard to follow and large-scale experimentation is not practical. To estimate the parameter values for a patch-based model one would need measures of emigration and immigration for patches of different sizes and shapes and situated in landscapes containing different amounts of habitat. Of course, the best (though most data intensive) choice is to build both patch-based and individual-based, grid-based models; decisions based on predictions from several models with very different structures are more robust (Burgman *et al.* 2005).

Finally, it is important to note that the factors discussed here are only the minimum set of necessary ingredients in any model aimed at estimating minimum habitat for population persistence. There are many additional factors that will be important in some situations, depending on the biology of the species of interest. For example, space use by the animal may change in various ways with decreasing habitat amount, due to conspecific attraction (e.g. Gautier *et al.* 2006; Nocera *et al.* 2006), increasing territory sizes (e.g. Lindenmayer *et al.* 2001) or altered emigration rates depending on the type of matrix that is adjacent to the habitat (Collinge & Palmer 2002). Species interactions may also be affected by habitat loss (Melian & Bascompte 2002): predation rates can either increase or decrease (Rushton *et al.* 2000; Schneider 2001: Swihart *et al.* 2001; Ryall & Fahrig 2006), and the strength of competitive interactions can either increase or decrease (Tilman *et al.* 1994; Klausmeier 2001). Because such factors can alter population viability (Lindenmayer *et al.* 2003), models for estimating minimum habitat for population persistence need to be flexible enough to allow incorporation of such effects when needed.

Principles

1. An important question in ecological landscape design is how much habitat is needed for population persistence? Virtually any ecological management plan includes as one of its objectives the assurance that particular species of interest and/or importance will not disappear from the landscape. Because habitat availability is the most important determinant of population persistence, to meet this objective managers need to know how much habitat is needed for persistence.
2. Answering this question (How much habitat is needed for population persistence?) requires a model, because population persistence cannot be measured directly.
3. Any model aimed at estimating minimum habitat for population persistence must include at least the following five factors: (i) individual

area requirements; (ii) reproductive rate; (iii) increasing per capita emigration rate and dispersal mortality rate with decreasing habitat amount (Skellam's process); (iv) increasing effects of demographic and environmental stochasticity with decreasing habitat amount; and (v) decreasing colonization and immigration rates with decreasing habitat amount.

4 Current population viability analysis (PVA) tools should not be used to estimate minimum habitat for population persistence, because they omit Skellam's process, that is, increasing per capita emigration rate and dispersal mortality rate with decreasing habitat amount. Use of current PVA tools for estimating minimum habitat would result in underestimates of the amount of habitat needed for population persistence.

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