

How large a managed area is needed to protect a threatened animal species? Combining simple dispersal and population models

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Abstract: The size and shape of the managed area for a threatened species to have a stable or growing population is a central issue for conservation management, for example for kiwi, *Apteryx* sp. Combining geometric probability results for retention of juveniles to breed in the protected area with a standard matrix population model allows the creation of an explicit relationship between the minimum area needed and how far juveniles of the species disperse to establish breeding territories. For a given set of demographic parameters for the population, and a rectangular protected area, there is a quadratic relationship between area and dispersal distance. Extensions for a circular protected area, and for a probability distribution on dispersal distance, are considered. The results are applied to kiwi, using established population parameters, giving results that match closely those from a previously published simulation. This approach can provide simple tools, readily implemented in a spreadsheet, for assessment of the size and shape of protected areas needed in conservation management of animals that disperse before breeding.

Keywords: Buffon needle problem; Laplace extension; Leslie matrix; matrix population model; minimum protected area

Introduction

The size and shape of a managed area that allows a threatened species to have a stable or growing population is a central issue for conservation management. In many species, juveniles disperse from their natal areas before breeding. How big a managed area is necessary to allow sufficient recruitment from new generations after dispersal to reverse population decline? For example, the question arises of how large an area of stoat trapping is needed to allow the recovery of local populations of New Zealand's national icon, the kiwi.

Methods for determining the minimum population and area to allow species conservation were reviewed by Shaffer (1981). Of the five methods described (experiments, biogeographic patterns, theoretical models, simulation models, and genetic approaches), the two modelling methods have potential for addressing the impact of dispersal on the size of managed areas needed. Simulation has been the main way of estimating the impacts of effects like dispersal, sometimes involving spatially explicit models (Reed et al. 2002). Simulation allows the solution of complex problems that are not amenable to general theoretical solutions, but can only give answers for the specific scenarios set up in the simulation. Theoretical modelling can lead to more general, mathematical solutions that allow insight into much broader aspects of relationships (Shaffer 1981).

The relationships between dispersal, managed area, and population viability were addressed in relation to kiwi for specific-shaped areas and some dispersal patterns, using simulation by Basse and McLennan (2003), and I will revisit their model as an example.

The key innovation of this paper is that for density-independent dispersal, geometric probability results can be combined with standard matrix population models in a theoretical model. This enables a more general understanding of the relationship between dispersal distance and the size of managed area required for population growth. Laplace's extension to the Buffon needle problem and related results (Laplace 1812; Solomon 1978) are used to derive the probability of retention of dispersing juveniles within a rectangle. This probability model is combined with a matrix model to evaluate the area of management required to support population growth under differing assumptions about dispersal.

Materials and methods

Dispersal model

The probability that a dispersing juvenile will remain within a given region depends on the size and shape of the region and the pattern of dispersal distances. It may also depend on the density of the species, but here I treat dispersal as independent of density. Assume initially

that the dispersal distance is the same for all dispersing juveniles, and that the managed area is rectangular in shape. (I will extend this to a probability distribution on an individual's dispersal distance and to circular shape later.) Results from geometric probability studies can be applied.

Consider the case of dispersal of a fixed distance at a random angle. In Laplace's extension of the Buffon needle problem, let the needle represent the path of a dispersing animal, with one end where it was born or hatched, and the other where it settled to reproduce (Fig. 1). Thus the centre of interest is whether the end point remains in the managed area. For start points randomly distributed (uniformly by area) in the managed rectangle and dispersal distance less than the shorter side of the rectangle, the probability of the end point lying within the rectangle is given by

$$r = 1 - \frac{1}{\pi} \left\{ 2 \left(k + \frac{1}{k} \right) d - d^2 \right\} \tag{1}$$

where $k^2 (\geq 1)$ is the ratio of the lengths of the sides of the rectangle and $d (\leq 1/k)$ is the ratio of the dispersal distance to the square root of the area of the rectangle (Laplace 1812; Solomon 1978).

It is clear, both intuitively and from Eqn 1, that the best shape of rectangle to maximize r with respect to k is a square, i.e. $k^2 = 1$. The shapes of the curves created from Eqn 1 are shown for a square and two rectangular

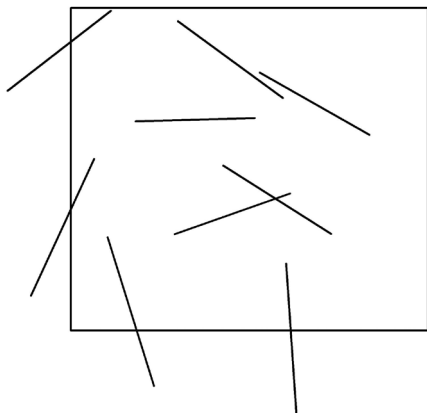


Figure 1. Diagrammatic representation of the Laplace extension of Buffon's needle problem. The box represents the rectangle (the managed area), and the lines represent the needles (the dispersal paths of the animal).

shapes in Fig. 2. Comparing the area of a square and a 2x1 rectangle needed to achieve similar probabilities of dispersal within the region, the rectangle requires a 12.5–20% greater area (in the range $d < 1/\sqrt{2}$).

The fixed dispersal distance assumption can be relaxed readily, by positing a probability distribution on the distance dispersed and integrating Eqn 1. Validity is conditional on the distance being always less than the shorter side of the rectangle. For any probability distribution of dispersal distances (relative to size of the rectangle as for d above) on an interval $[0, 1/k]$ with mean D and variance σ^2 , Eqn 1 becomes

$$r = 1 - \frac{1}{\pi} \left\{ 2 \left(k + \frac{1}{k} \right) D - D^2 - \sigma^2 \right\} \tag{2}$$

The applicability of Eqn 2 is limited in the range of distances allowed. However, upper and lower bounds for the probability that an end point lies within the region can be found when the dispersal distribution goes outside this interval. For example, an upper bound is gained by replacing the probability distribution by one that places all the probability mass from outside the allowable range at the edge point of the range, while a lower bound is given by assuming that the end points fall outside the region in all cases where the dispersal distance is outside the range of validity of Eqn 1.

A circular region is a candidate for a more efficient shape for retention within a region of fixed area. From

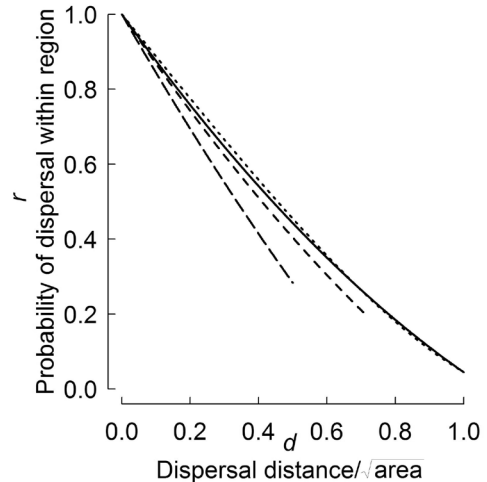


Figure 2. Relationship of probability of dispersers remaining within regions of various shapes for a fixed dispersal distance (scaled by square root of the region's area). Values are only shown within the distance range for which Eqn 1 and Eqn 3 are valid. The solid line represents the square shape. The other lines, in order of increasing dash length, represent the circle, and 2x1 and 4x1 rectangles.

Nahin (2000), for a fixed dispersal distance, with start points randomly distributed (uniformly by area) in a circular region of area A ,

$$r = 1 - \frac{2}{\pi} \left\{ \frac{\sqrt{\pi}}{2} d \sqrt{1 - \left(\frac{\sqrt{\pi}}{2} d \right)^2} + \arcsin \left(\frac{\sqrt{\pi}}{2} d \right) \right\} \quad (3)$$

where, as before, d is the dispersal distance divided by \sqrt{A} , and this is valid for d between 0 and $2/\sqrt{\pi}$ (the diameter of the circle, approximately 1.128). Fig. 2 shows that the shape of the curve from Eqn 3 is barely distinguishable from that for a square of the same area.

A question of interest is when a circle will be more efficient in terms of the area required to gain a given probability of the retention within the region. A circle requires a substantially smaller area when retention probability is large, exceeding 25% at the extreme, but the situation is reversed when retention probability is less than 0.27 (Fig. 3).

In contrast with the situation for a rectangle, the expression in Eqn 3 does not provide a simple relationship when a probability distribution is posited for d . The rest of the paper will concentrate on the rectangular situation.

Population model

Matrix population models provide a powerful and increasingly popular approach to analysing the impact of varying demographic parameters on population dynamics (Caswell 2001). Given a matrix of constant population parameters for a population with fixed stages, it is straightforward to derive the condition for population

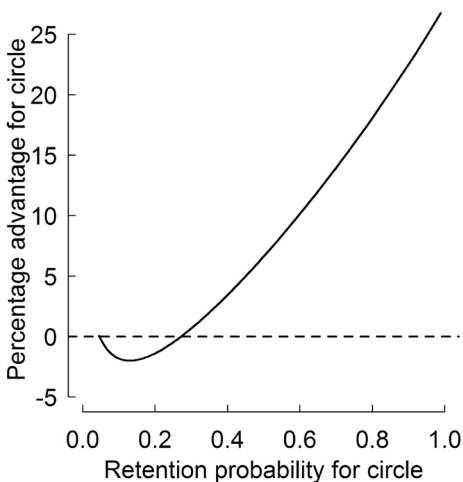


Figure 3. Percentage increase in area required for a square managed area relative to a circle to gain the same retention probability.

growth. Such a population will grow, be stable, or decline depending on whether the net reproductive rate is greater than, equal to, or less than 1 (Caswell 2001). Note that we are not assuming that demographic parameters are actually constant; rather we are assessing a given set of parameters by evaluating what would happen if they were to remain constant (Caswell 2001).

For a population falling naturally into consecutive stages – typically years – a population matrix takes the form of the Leslie matrix (Leslie 1945). Taking a model with n stages, let b_i be the reproduction rate from the i th stage and p_i transition rates from the i th stage to the $(i + 1)$ th stage (for $i < n$). Also let p_n represent survival in the final age class, allowing accumulation of mature individuals here – an extension to a standard Leslie matrix that has $p_n = 0$. For example, a four-stage extended Leslie matrix would be

$$\begin{pmatrix} b_1 & b_2 & b_3 & b_4 \\ p_1 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 \\ 0 & 0 & p_3 & p_4 \end{pmatrix}$$

For an extended Leslie matrix, it can be shown that the net reproductive rate, the average number of offspring that an individual will have during their lifetime, is given by

$$\sum_{i=1}^{n-1} b_i \left(\prod_{j=1}^{i-1} p_j \right) + \frac{b_n \prod_{i=1}^{n-1} p_i}{1 - p_n}$$

Hence, the condition for growth or stability in the population for the extended Leslie matrix is:

$$1 - p_n \leq \frac{b_n \prod_{i=1}^{n-1} p_i}{1 - \sum_{i=1}^{n-1} b_i \left(\prod_{j=1}^{i-1} p_j \right)}$$

The p_i can be decomposed into two parts, actual physical survival itself s_i , and retention in relation to dispersal r_i , so $p_i = r_i s_i$. This becomes useful in considering a population with an age at maturity, m , such that dispersal ceases at this age, and breeding starts. That is $r_i = 1$ for $i \geq m$, and $b_i = 0$ for $i < m$. The condition then becomes:

$$1 - s_n \leq \frac{b_n r \prod_{i=1}^{n-1} s_i}{1 - r \sum_{i=1}^n \left(b_i \prod_{j=1}^{i-1} s_j \right)}$$

where $r = \prod_{i=1}^n r_i$, the overall retention rate, or

$$r \geq \frac{1 - s_n}{b_n \prod_{i=1}^{n-1} s_i + (1 - s_n) \sum_{i=1}^n \left(b_i \prod_{j=1}^{i-1} s_j \right)} \quad (4)$$

For a species that matures at the last age group, the second term in the bottom line of Eqn 4 disappears, giving the intuitively obvious condition for growth, that the mortality rate of breeders ($1 - s_n$) is less than the recruitment to breeders given by the product of breeding, retention, and survival rates.

Putting the dispersal and population models together

We can put the dispersal model together with the matrix model for the population in the managed area developed for Eqn 4, based on an assumption of no migration from outside the managed area, i.e. recruitment of breeders from outside the managed area is negligible. This assumption will often be realistic for threatened species like kiwi.

Combining Eqn 2 and Eqn 4 gives the expression to be satisfied for population growth, on a rectangular managed region with a probability distribution mean D , variance σ^2 , for the relative dispersal distance:

$$1 - \frac{1}{\pi} \left[2 \left(k + \frac{1}{k} \right) D - D^2 - \sigma^2 \right] \geq r_c$$

where r_c is the value for the retention rate given by the right-hand side of Eqn 4 that achieves a constant population.

Hence, the condition for asymptotic population growth in terms of D (the mean relative dispersal distance) is

$$D \leq \left(k + \frac{1}{k} \right) - \sqrt{\left(k + \frac{1}{k} \right)^2 - \sigma^2 - \pi(1 - r_c)}$$

and is valid for dispersal distance distributions in the interval $[0, 1/k]$.

For a square region and fixed dispersal distance, d , this reduces to

$$d \leq 2 - \sqrt{4 - \pi(1 - r_c)} \quad (5)$$

Hence, since D and d denote dispersal distance relative to the square root of area, the minimum area for a self-sustaining population is a quadratic function of dispersal distance for a given set of demographic and dispersal parameters.

Application to the North Island brown kiwi

Figure 4 shows a contour plot based on Eqn 5 of the minimum area for a sustainable population in relation to dispersal distance and demographic parameters.

The results can be readily applied to conservation management situations. Populations of North Island brown kiwi *Apteryx mantelli* are under threat with an estimated decline in remaining populations of around 6% per annum, mainly due to stoats preying on chicks (McLennan et al. 1996). To deal with this threat, stoat-trapping operations have been established, some covering hundreds of hectares (100 ha = 1 km²), and others as large as 10 000 ha or more. However, although kiwi are generally faithful to territories as adults, juvenile kiwi can disperse substantial distances. Basse and McLennan (2003) estimate, based on preliminary data for dispersal, that for a dispersal distance of 5 km a minimum managed forest area of 10 000 ha is required for a self-sustaining population of brown kiwi. They use a computer simulation to gain this result, with movement in and out of the managed zone based on simulated populations of individuals. They also show the effects of some alternative values for the key demographic and dispersal parameters. Their estimates of these parameters are based on expert opinion and prior research. Here we apply the simple formulae above to the same problem.

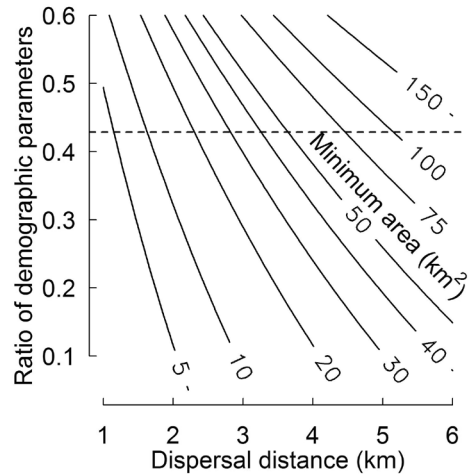


Figure 4. Contour plot of minimum area (km² = 100 ha) of a square managed area for a self-sustaining population, by dispersal distance, and the ratio of demographic parameters given by the right-hand side of Eqn 4. The dashed line corresponds to $r_c = 0.429$, corresponding to the demographic parameters for kiwi used by Basse and McLennan (2003).

For simplicity I combine the juvenile (0–9 months) and subadult (10–13 months) stages of Basse and McLennan (2003) into a single pre-breeder stage, and retain adults as the breeder stage. Taking the pre-breeding stage as equivalent to one year in the formulae and combining the demographic parameters of the two stages make the results almost exactly comparable. The model also assumes that all deaths and dispersals take place at the end of each year modelled, and only the female population is modelled on the assumption of a balanced sex-ratio in the population. In contrast to Basse and McLennan, I assume that insufficient juveniles are bred for there to be any dispersal from outside into the managed area.

Based on the demographic parameters given by Basse and McLennan (2003), I take $b_2 = 0.425$ (females chicks produced per female), and survival rates $s_1 = 0.45$ and $s_2 = 0.918$, giving $r_c = 0.429$ as the critical retention rate, shown as a line in Fig. 4. Calculations from the approach outlined here match the results of the earlier simulation, even though quite different criteria for sustainable populations are used. Additionally, Eqn 5 explains the quadratic relationship of managed area to dispersal distance previously derived empirically. For a dispersal distance of 5 km, Eqn 5 gives a minimum area of over 9400 ha, similar to the just over 10 000 ha given by Basse and McLennan (2003).

Discussion

The results given here apply to the extended Leslie matrix population model with dispersal prior to breeding. In particular, such a model can be applied for long-lived species as are common in New Zealand wildlife. The results from Eqn 5 could equally be applied to a shorter lived species that disperses before breeding. The result for a standard Leslie matrix population model, without accumulation of population in the last age group, is derived by setting $s_n = 0$. The results of the dispersal model used could also be applied in more general matrix population models, for example where there are more complex transitions between stages, or where some breeding happens before dispersal. In some cases the relationships between dispersal and population growth may be able to be derived analytically. An approach to deriving analytical formulae for net reproductive rate for more general matrix population models is given by de-Camino-Beck and Lewis (2007). Where analytical solutions are not possible, numerical approaches could be applied, with potential for reducing computing effort substantially compared with simulating populations. The model presented here has the advantages of being simple both in concept and solution, and of providing graphs, or simple formulae for use in spreadsheets. These can be readily applied in conservation management without the need for application of significant computational,

mathematical, or modelling skills.

The derivations here depend on a number of assumptions in dispersal and demographic models. Interpretation of the results depends on the plausibility of these assumptions and what happens when the assumptions are violated.

The assumption that dispersal distance is independent of population density is plausible for many threatened species of interest, as they have often suffered substantial reductions in population density from a natural level. In fact, providing the dispersal distance estimates used are appropriate for the current density, even if dispersal distance increases as density increases, the areas derived will be large enough, as the current density will clearly remain sustainable. Similar arguments can be made for plausible impacts of density dependence on demographic parameters.

The analysis presented assumes no effective recruitment into the managed area from outside. This is an important assumption. It is likely to be appropriate for many endangered species. Without management, their populations are already in serious decline, so are unlikely to be producing many dispersing juveniles. For example, in the case of kiwi, Bass and McLennan (2003) take survival from 0 to 9 months as 50% in managed areas and as 5% in unmanaged areas. The impact of recruitment from outside, however small, can only boost the population, and hence will make estimates of minimum area that allow no such recruitment larger than necessary.

Is shape important? A square shape always requires less area than a rectangle to gain the same probability of retention at dispersal. However, the effect will be small for small deviations from squareness. For a 2×1 rectangle the impact is less than 20%. While the contrast between a circle and square can appear large, the large values occur in the cases where retention probabilities are already high, and the managed area is already very large compared with dispersal distances. In many cases, interest will lie in the mid-range of retention rates, where the advantages of one shape over the other are small (less than 10% for a retention rate less than 0.6.) This suggests that for retention rates less than about 0.6, exact shape is not critical, provided that distances from the centre to the edges are reasonably similar, as in a circle or square.

The combination of historical geometrical probability results with matrix population modelling allows the derivation of quite general results for how large a managed area is needed to protect a threatened species that disperses before breeding. These can be readily applied in conservation management as in the kiwi example given. The method provides flexible tools for assessing the trade-offs between options to manipulate population parameters such as survival, dispersal, or recruitment, and the scale on which these need to be implemented to achieve a self-sustaining population.

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References

- Basse B, McLennan JA 2003. Protected areas for kiwi in mainland forests of New Zealand: how large should they be? *New Zealand Journal of Ecology* 27: 95–105.
- Caswell H 2001. *Matrix population models: construction, analysis and interpretation*. 2nd edn. Sunderland, MA, USA, Sinauer. 722 p.
- de-Camino-Beck T, Lewis MA 2007. A new method for calculating net reproductive rate from graph reduction with applications to the control of invasive species. *Bulletin of Mathematical Biology* 69: 1341–1354.
- Laplace PS 1812. *Théorie analytique des probabilités*. Paris, Veuve Courcier.
- Leslie PH 1945. On the use of matrices in certain population mathematics. *Biometrika* 33: 183–212.
- McLennan JA, Potter MA, Robertson HA, Wake GC, Colbourne R, Dew L, Joyce L, McCann AJ, Miles J, Miller PJ, Reid J 1996. Role of predation in the decline of kiwi, *Apteryx* spp., in New Zealand. *New Zealand Journal of Ecology* 20: 27–35.
- Nahin PJ 2000. *Duelling idiots and other probability puzzlers*. Princeton, NJ, Princeton University Press.
- Reed JM, Mills LS, Dunning JB Jr, Menges ES, McKelvey KS, Frye R, Beissinger SR, Anstett M-C, Miller P 2002. Emerging issues in population viability analysis. *Conservation Biology* 16: 7–19.
- Shaffer ML 1981. Minimum population sizes for species conservation. *BioScience* 31: 131–134.
- Solomon H 1978. *Geometric probability*. Philadelphia, PA, USA, SIAM (Society for Industrial and Applied Mathematics) Press.

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