

Spatially explicit ecological models: population consequences of individual habitat selection mechanisms

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Abstract Organisms that occupy a single territory for their entire adult lifetime must choose as juveniles the location that will determine their lifetime reproductive success. However, juveniles will not normally have global information about the location of high quality, unoccupied habitat. They may only know the quality of the habitat that they are currently moving through, and possibly have knowledge, or an estimate, of the distribution of habitat quality. In addition, there is usually an elevated risk of mortality during dispersal, which increases the incentive to choose a territory quickly. There are many possible ways in which this problem, which is a particular instance of the "job search" problem, could be solved by organisms. In this paper we examine the population consequences of several individual habitat selection mechanisms. We use an individual based, spatially explicit population model of the Greater Glider, *Petauroides volans*. We examine six different dispersal strategies which vary the scale at which individuals sample the landscape, and how choosy they are about the habitat they settle in. The dispersal strategy has a strong effect on the size of the equilibrium population. However, the strategy that achieves the highest population sizes is not evolutionarily stable.

1 INTRODUCTION

Many organisms do not move as adults. In the extreme, there are entirely sessile animals, like barnacles, that are permanently fixed to their substrate. Many mobile animals also limit their movements as adults, restricting long range dispersal to new habitats to juvenile phase of life. This long range dispersal is crucial to the lifetime reproductive success of an individual, because the location juveniles choose will determine how well they can grow and more importantly, reproduce, for the rest of their lives. Despite the importance of this behaviour for population persistence, very little is known about how juvenile organisms disperse and choose new habitats. In this paper we use a spatially explicit population model to explore the population consequences of different habitat selection mechanisms.

From the point of view of a juvenile mammal about to disperse, the location of good quality, unoccupied habitat is unknown. There are two questions that a juvenile must answer. First, which direction to look in? Second, upon finding an unoccupied home range, should the search stop, or is there better quality habitat available? This is a particular instance of a more general

problem, the "job search problem" [Lippman and McCall 1977]. In ecology, the job search problem has also been used to model the process involved in choosing a mate [Real 1991].

Determining which direction to look in depends on the scale at which an individual can obtain information about the landscape. At one extreme, individuals may know nothing about the landscape beyond their immediate location. In this case, any direction is as good a place to start as any other. At the other extreme, they may have information about the habitat quality distribution of the whole landscape.

To decide whether to settle in an available location or keep looking, a dispersing individual needs three pieces of information: the quality of the current habitat, the average quality in the landscape as a whole, and the expected length of time to find an unoccupied home range. All three of these pieces of information may be known, but more likely they have to be estimated by a disperser as it moves through the landscape. The decision is then simple; accept the current home range if it is better than the average quality, discounted by the probability of dying before reaching the next unoccupied home range. The probability of dying depends on the expected length of time to find an unoccupied home range,

Table 1. Baseline life history parameters for the Greater Glider (*Petauroides volans*). All values are per capita rates. Where values have been altered from Possingham *et al.* [1994] the original values are in brackets.

Parameter	Newborn	Juvenile	Adult
Aging related mortality (per year)	0.5	0.15	0.15
Dispersal mortality (per movement)	0.02	--	--
Fecundity (per year)	0	0	0.35 (0.5)

which is determined by the density of individuals in the population.

A dispersal strategy will have ecological consequences at two different levels. First, it will influence the distribution of the population across the landscape. Second, it will influence the lifetime reproductive output of each individual, and consequently the size of the population. We first consider the long term population sizes independently achieved by each of six possible dispersal strategies. Then we consider which of these strategies is likely to be an "Evolutionarily Stable Strategy" [ESS, *sensu* Maynard-Smith 1982], and therefore a candidate for real populations to use.

2 SPATIALLY EXPLICIT POPULATION MODELS AND DISPERSAL

In this section we describe a single species, spatially explicit population model of a population of an Australian arboreal marsupial, greater gliders (*Petauroides volans*). The model is individual based, tracking the location and life history state of all females in the population at one year intervals. The basic spatial unit is a female home range (assumed to be 1.5 ha in size), and all runs of the model are performed on a 33 x 33 grid of home ranges, using a 4-cell von Neumann neighbourhood. We assume that newborns disperse from their natal territories, and settle in an unoccupied home range, or displace another newborn. Territorial battles between newborns are settled randomly, with the resident having no advantage. One year is spent as a juvenile, and neither adults nor juveniles shift territories. Aging, and age related mortality, occurs after dispersal, and before the next year's recruits are born. Life history parameters are given in Table 1, and are taken from Possingham *et al.* [1994]. For our purposes we have altered the adult age-related mortality and fecundity slightly to ensure that populations reached an equilibrium of about 300 individuals after 150 years from any initial population size. This facilitates the comparison of different dis-

persal strategies because we do not need to worry about increasing or decreasing populations. All runs in this paper were 200 years in length, and data for the analyses were collected from either the last 25 years, or only the final year.

The artificial landscape was constructed with a mid-point displacement algorithm [Saupe 1988], that creates a surface with a specific fractal dimension ($H = 2.1$). The particular dimension chosen is immaterial for our present purpose; all we need is an irregular surface with spatially autocorrelated values of habitat quality (Figure 1). The floating point values on the landscape were then scaled to the integer range 0-99. The annual aging mortality in each home range $p_{x,i}$ was then modified with this value according to

$$\ln\left(\frac{p_{x,i}}{1-p_{x,i}}\right) = a\left(\frac{Q_x}{Q} - 1\right) + \ln\left(\frac{p_i}{1-p_i}\right) \quad (1)$$

where a is the effect of habitat quality on survival, Q_x is the habitat quality value in home range x , Q is the average habitat quality on the

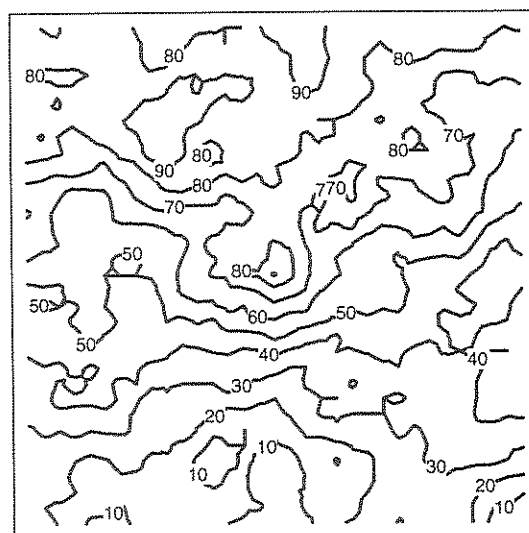


Figure 1 Contour map of artificial landscape.

landscape, and p_i is the annual mortality rate of age class i (Table 1). We used $a = 0.2$, which means the mortality of adults ranged from 0.177 in the poorest habitat to 0.126 in the best habitat.

Very little is known about how individuals make choices about where to move on a heterogeneous landscape during dispersal. The two questions about where to move and when to stop outlined in the introduction translate into variation in the scale of sampling, and whether or not to reject low quality habitat. We examine a total of six different dispersal strategies: three different scales of sampling and individuals that either accept all habitat, or reject low quality habitat.

We have three sampling scales, "random walkers" (RW), "hill climbers" (HC), and "global dispersers" (GD). The random walker limits the scale of sampling to the current home range. These individuals choose one of four neighbouring territories at random to move to. The hill climbers sample at a larger scale by examining all the neighbouring home ranges. They move in the direction of the highest quality, and they break ties at random. They also choose randomly if all surrounding territories are worse than the current home range. Finally, they reduce their estimate of the quality of occupied neighbouring home ranges by the number of steps they have taken; the longer they look for unoccupied habitat, the less fussy they get. This prevents hill climbers from getting stuck on local quality peaks that are already entirely occupied. Global dispersers sample at the scale of the entire landscape by moving to a randomly chosen home range. These individuals experience no sequential correlation of habitat quality as they move.

The two different selection methods are "acceptors" (A) and "rejectors" (R). Acceptors always settle in the first unoccupied territory they encounter. They move through occupied territory. Rejectors also move through occupied territory. In addition, they reject unoccupied home ranges if

$$\frac{F(1 - p_{\text{current}})}{p_{\text{current}}} < \frac{F(1 - p_{\text{expected}})}{p_{\text{expected}}} (1 - d)^s \quad (2)$$

where F is the annual probability of giving birth to a female offspring, p_x is the annual probability of mortality in that home range, d is the probability of dying during a dispersal step, and s is the expected number of steps needed to reach the next unoccupied home range. The right hand side is the expected number of offspring produced in

the average habitat, discounted by the probability of surviving to reach the next unoccupied habitat.

A complete dispersal strategy is referred to in the results with a combination of the abbreviations given above, eg. hill climbing rejectors are HCR.

3 RESULTS

3.1 Dispersal Strategy Affects Population Size

There are substantial differences between dispersal strategies in the long term equilibrium population sizes (Table 2). HCA, HCR, and GDA have the lowest long term populations. The highest population size is achieved by GDR, while both types of RW have intermediate population sizes that are more than double the size of HC populations. A large population size is "good" at the population level, because it reduces the likelihood of extinction. Dispersal strategy can influence long term reproductive success at two points in the current model. First, it affects the degree of habitat selection, and consequently the survival rate of settled individuals. Second, it affects the amount of time spent looking for habitat, and the degree of competition for space during dispersal.

Selecting high quality habitat can influence population size by increasing the average lifespan of individuals. The strength of habitat selection shown by a strategy can be determined by comparing the average quality of occupied home ranges with the average quality on the landscape (=53.6). All strategies except GDA show some degree of habitat selectivity, with the strongest habitat selectors being the two hill climbing strategies (Table 3). Note that rejection behaviour does not influence the average quality of habitat, except for GDR vs. GDA. If rejectors were rejecting, the number of unoccupied home ranges visited would be higher for the rejecting strategy than its corresponding acceptor (eg. RWR > RWA). Once an unoccupied home range

Table 2 Population scale results for the six different dispersal scenarios. The value in each cell is the average population size (standard deviation) in the 200th year for 100 replicate runs. For abbreviations see text.

	RW	HC	GD
A	331 (39)	134 (27)	214 (75)
R	331 (38)	138 (28)	408 (58)

is located in a locally crowded landscape, it is accepted because finding another unoccupied home range requires many risky steps. In preliminary runs with movement discounting [2nd term, right hand side of (2)] turned off, rejectors rejected more often, suffered higher dispersal mortality, and ended up with long term population sizes approximately half of those presented here.

Table 3 Individual level results from all individuals dying in the 200th year of all 100 replicate runs. Except for dispersal mortality, only results from successful dispersers are shown, i.e. those that did not die during dispersal. Habitat quality is the minimum and average quality of occupied cells. The maximum quality occupied was 99 for all strategies. # tries is the average number of unoccupied cells encountered before settling. Lifespan is the average (standard deviation) in years. Dispersal mortality is the average proportion of newborns (standard deviation) that died during dispersal.

	RWA	HCA	GDA
Minimum Habitat Quality	14	36	0
Average Habitat Quality	73.1	84.7	52.4
# tries	1.6	2.3	1.1
Lifespan	3.7 (5.9)	4.0 (6.3)	3.5 (5.8)
Dispersal Mortality	0.12 (0.04)	0.18 (0.08)	0.02 (0.02)
	RWR	HCR	GDR
Minimum Habitat Quality	11	36	0
Average Habitat Quality	73.3	84.5	62.8
# tries	1.5	2.2	2.2
Lifespan	3.7 (6.0)	4.0 (6.2)	3.5 (5.8)
Dispersal Mortality	0.12 (0.04)	0.19 (0.07)	0.07 (0.03)

Habitat selection cannot explain the variation in average population size, despite its effect on the average lifespan of successful dispersers (Table 3). With the exception of GDA, there is nearly an inverse relationship between average population size and strength of habitat selection; the strongest habitat selectors (HCA and HCR) have the lowest population sizes.

The second point at which the dispersal strategy could influence population size is during dispersal. The more steps a disperser makes in search of a home range, the more likely it is to die. The higher the population on the landscape, the more difficult it will be to find unoccupied habitat, and dispersal mortality will increase. This density dependent mortality is operating for all strategies in this model; which strategy is used influences the population size at which density dependent mortality starts to take effect. The strength of habitat selection does correspond well with the amount of mortality during dispersal (GDA < GDR < RWA ≈ RWR < HCA ≈ HCR, Table 3). Habitat selectors compete for a limited amount of space. The stronger the habitat selection behaviour, the less space is available, and consequently the smaller the average population size. The anomaly in this explanation is still the fact that GDR has the highest population size of all strategies, and much higher than GDA. GDR does so well at a population level because it selects good habitat by rejection, but does not get stuck in that limited region of the landscape that has high quality.

3.2 Random Walking is an ESS

From an evolutionary point of view, the strategy that will be observed is not necessarily the one that produces the highest average population size. For a strategy to be evolutionarily stable (an ESS), it must provide a higher reproductive rate to individuals using that strategy, both in competition with others using the same strategy, and with other strategies [Mylius and Diekmann 1995]. In other words, it must be both resistant to invasion by alternative strategies, and able to invade a population using an alternative strategy. Formal tests to determine whether or not a strategy is an ESS [Maynard-Smith 1982, Mylius and Diekmann 1995] do not take demographic stochasticity into account. This is important, because in a stochastic environment there is always a chance that an invading alternate strategy fails to succeed simply due to chance. We simulated competition between the six strategies, with offspring having the same dispersal type as their parent. There is no mutation; once a strategy goes

extinct it is considered to have failed to invade or compete.

In the first test, we placed all six dispersal strategies on the landscape simultaneously in equal numbers (50 of each). We performed 100 runs, each lasting 10,000 years or until there was only one dispersal type left.

In 98 runs, the winning strategy was a random walker, split between rejectors (51) and acceptors (47). The lack of a difference between acceptors and rejectors is consistent with our earlier observation that rejectors do not perform differently from acceptors. In the remaining 2 runs, the GDR strategy and one of the hill climbers were extant at 10,000 years. It is interesting to note that GDR, although it achieves the highest population sizes when growing alone on the landscape, does not compete well against the random walkers.

In the second test, we performed 100 runs of all of the 30 possible pairwise interactions. In each case, one strategy (the resident) was allowed to establish itself in the absence of competition for 200 years, and then the second strategy (the invader) was introduced at 10% of the numbers of the resident. An invasion was counted as successful if either the invading strategy drove the resident extinct, or if it persisted until 10,000 years.

Table 4 Results of pairwise invasion tests. Invading strategies are listed across the top, resident strategies down the side. Values in the table are the number of successful invasions out of 100. To see how well a strategy invades, look down its column; to see how well it resists invasion, look across its row. Table cells are shaded in proportion to the number of successful invasions. Zero successful invasions are left blank for clarity.

	Invader Type					
	RW A	HC A	GD A	RW R	HCR	GD R
RWA				1		
HCA	37			26	5	37
GDA	75	69		66	72	73
RWR	3					
HCR	37	8		33		47
GDR	61	59		61	48	

The pairwise invasions support the observation that global dispersing strategies are not evolutionarily stable (Table 4). Both global rejectors and acceptors were invaded by everything. GDR is able to invade the hill climbing strategies, but this is insufficient to class it as an ESS. The hill climbing strategies are also not evolutionarily stable, given the ability of random walking strategies to invade them. Only the random walking strategies seem to meet the criteria for being evolutionarily stable; they are resistant to everything other than each other, and are able to invade all other strategies. Both RW strategies are more likely to invade either HC strategy, than the other RW. This supports the idea that they are in fact "invading" the HC strategies, in the sense of having a higher reproductive rate. The two RW strategies are more or less equivalent, and so the invasion rate between them is an indication of how often an invasion of that size would be successful.

4 CONCLUSIONS

This paper uses a spatially explicit ecological model to examine whether or not the type of dispersal rule used by individuals influences population dynamics, and what type of rule might be an ESS. This work is unique because it examines continuous variation in habitat quality, as opposed to "patchy" variation where habitat is either available or not [Gustafson and Gardner 1996, Keitt and Johnson 1995]. It also explores strategies that make use of information about the environment to decide where to look for habitat, and whether or not to accept it. The primary conclusion is that individual dispersal behaviour has profound implications for population dynamics, highlighting the need for modellers to be careful in the choice of mechanisms for dispersal.

A second important conclusion from this work is that it is not necessary to have any form of active habitat selection in order to have a relationship between habitat quality and occupancy. The random walking acceptor strategy uses no information about the landscape to make decisions about where to move, or when to stop. They end up in better quality habitat than individuals that move globally simply because they tend to stay in the neighbourhood of areas that favour individual survival. Nonetheless, the relationship between habitat quality and occupancy is weaker for random walkers than for hill climbers. If random walking strategies are indeed used by natural populations of terrestrial mammals, then the use of habitat-occupancy models to reach conclusions about managed populations [Morrison et al.

1992] must deal with an unanticipated source of variation.

Ideally, a dispersal strategy should be an ESS within some reasonable set of constraints. Random walking acceptors are evolutionarily stable, at least within the set of strategies explored in this paper. Furthermore, this strategy is the simplest, and makes no assumptions about what cognitive abilities the disperser has. That it performs as well as, or better, than strategies that are more sophisticated in their use of information for decision making is good news for all modellers that have assumed dispersers use random walks or a variant [eg. Gustafson and Gardner 1996, Keitt and Johnson 1995, McCauley et al. 1996].

Despite this reassurance, it would be dangerous to attribute too much significance to the particular dispersal strategies used in this paper. We have formed a 'neutral landscape model' [With and King 1997] to test the effects on population dynamics of a limited set of dispersal strategies. There are many variations on all of the strategies used here. Moreover, by increasing the strength of the effect of the landscape on survival, and reducing dispersal mortality, it is conceivable that hill climbers would do better. The point is not that these strategies are the only ones, but rather that the choice of strategy, *any* strategy, is one that should be made carefully. The interaction between a continuously heterogeneous landscape and simple dispersal rules has not been explored before, and leads to non-intuitive results.

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