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Modelling Dispersal Behaviour on a Fractal Landscape

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Abstract

We use a spatially explicit population model to explore the population consequences of different habitat selection mechanisms on landscapes with fractal variation in habitat quality. We consider dispersal strategies ranging from random walks to perfect habitat selectors for two species of arboreal marsupial, the greater glider (*Petauroides volans*) and the mountain brushtail possum (*Trichosurus caninus*). In this model increasing habitat selection means individuals obtain higher quality territories, but experience increased mortality during dispersal. The net effect is that population sizes are smaller when individuals actively select habitat. We find positive relationships between habitat quality and population size can occur when individuals do not use information about the entire landscape when habitat quality is spatially autocorrelated. We also find that individual behaviour can mitigate the negative effects of spatial variation on population average survival and fecundity.

Keywords: modelling; dispersal behaviour; fractal landscape

1. Software availability

Title	HABITAT, individual based population simulation on a fractal landscape
Language	ANSIC
Availability	source code available on request from first author.

2. Introduction

Many organisms do not move as adults (Wolfenbarger, 1946). In the extreme, entirely sessile animals, like barnacles, are permanently fixed to their substrate. Many mobile animals also limit their movements as adults, restricting long range dispersal to new habitats to the juvenile phase of life. Natal dispersal is crucial to the lifetime reproductive success of an individual, because the location juveniles choose may determine how well they can grow and 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 (Stenseth and Lidicker, Jr, 1992; Haas, 1995). Knowledge of dispersal performance is crucial to understanding biological invasions (Shigesada et al., 1995), and population responses to disturbances (Green, 1989), especially on structured landscapes. We use a spatially explicit population model to explore the population consequences of different dispersal mechanisms on landscapes with continuous variability in habitat quality.

It is important to distinguish between movements at different temporal and spatial scales. At the finest scales, mobile species move on a daily basis to forage, avoid predators, defend territories, find mates, and care for offspring. This sort of movement has been modelled as dif-

fusion (Skellam, 1951), correlated random walks (Kareiva and Shigesada, 1983; Marsh and Jones, 1988), and by detailed simulation (e.g. Jones, 1977). At larger scales, many species undertake large periodic migrations between seasonal habitats that can best meet their needs at different times (Keast, 1968; Stenseth and Lidicker, Jr, 1992). Migrations generally occur along well-defined routes between large regions, and the modelling of the development of such routes is primarily an evolutionary problem over very long time scales. This paper is concerned with natal dispersal, defined as dispersal from the natal home range to a new location which forms the adult home range. Such movements are not incompatible with migration or daily movements, but occur at inter-mediate temporal and spatial scales. However, because natal dispersal occurs infrequently (i.e. once in a lifetime), and is relatively large in scale, empirical data are scarce. Lubchenco et al. (1991) list dispersal as one of the 'intellectual frontiers' of ecology, highlighting the need for further analytical and empirical work in this area.

From the point of view of a juvenile terrestrial vertebrate about to disperse from a natal territory, the location of good quality, unoccupied habitat is unknown. There are two key decisions a dispersing individual must make: in which direction to disperse, and, upon finding an unoccupied site, should the search stop, or is there better quality habitat available? This is a particular instance of a more general problem in operations research, the 'job search problem' (Lippman and McCall, 1977). In ecology, the job search problem has also been used as a model of mate choice (Real, 1991). Most work on the job search problem has ignored the first question, which direction to search in, by assuming that the quality of each job, mate, or home range is independent of the quality of previously encountered possibilities. However, the quality of real landscapes is spatially correlated; if the current territory is good, the neighbouring territories are more likely to be good than bad. When a disperser moves across such a landscape step by step, as in this paper, the quality of subsequent encounters with home ranges is not independent. Furthermore, the direction of movement may influence whether the next unoccupied territory encountered is better or worse than the previous one. Therefore, we assume a simple stopping rule and concentrate on choosing the direction to search in.

Determining the direction a dispersing individual searches depends on the scale at which it can perceive information about the landscape. At one extreme, individuals may know nothing about the landscape beyond their immediate location (e.g. Baur and Baur, 1993). In this case, any direction is as good a place to start as any other. At the other extreme, an animal may be able to perceive large areas of the landscape (e.g. large, wide ranging raptors). For the purposes of this paper, the analysis is restricted to terrestrial vertebrates who move step by step across a landscape. The ecological neighbourhood (Addicott et al., 1987) that determines the scale of our model is a large fraction (say 95%) of the area within which daily resource needs are met; we refer to this as the home range size. We assume that our model individuals can only obtain information about the quality of home ranges immediately next to their current location.

Previous work on dispersal in terrestrial vertebrates (Wolfenbarger, 1946; McCarthy, 1997) has generally assumed that dispersal occurs in a straight line. If dispersal terminates at the first vacancy, and vacancies are randomly distributed, this leads to a negative exponential distribution of dispersal distances. Straightline dispersal is frequently implemented in patch based metapopulation models (Possingham et al., 1994a; McCarthy, 1996). The opposite extreme is to assume that individuals have perfect knowledge of the nearest vacancy. This is also unrealistic.

A dispersal strategy will have ecological consequences at two different levels. First, it will influence the lifetime reproductive output of each individual, because home range quality determines fecundity and survival as a reproductive adult. Second, it will influence the distribution of the population across the landscape, and consequently the total size of the population. The life history of a species may influence the consequences of different dispersal strategies. Therefore, we parameterise our model for two species of Australian arboreal marsupials, the greater glider (*Petauroides volans*), and the mountain brushtail possum (*Trichosurus caninus*), which differ in their reproductive and survival rates. We first consider the long term population sizes that result from a range of possible dispersal strategies, on a variety of landscape structures. Then we explore the individual level causes of variation in equilibrium population size under different dispersal strategies.

3. The species

Tall eucalypt forests in southeastern Australia are inhabited by several arboreal marsupial species. Many of these are of conservation concern, because their habitats are threatened by timber harvesting. We chose to model two species, the greater glider (GG, *Petauroides volans*), and the mountain brushtail possum (MBP, *Trichosurus caninus*), because we have accumulated life history data, habitat requirements, and model parameters from other studies (Table 1; Lindenmayer et al., 1990; Possingham et al., 1994a). MBP are omnivorous, may sometimes forage on the ground (How, 1983), and prefer wet forests. GG are entirely folivorous, consuming only eucalypt leaves (Hume et al., 1984), and prefer tall open forest. Both species have patchy distributions in other-wise contiguous forest (Lindenmayer et al., 1990). Females are solitary occupants of their territory, although female MBP may share their territory with a male (Lindenmayer, 1997). GG have higher first t year survival and greater fecundity, while MBP have higher juvenile and adult survival, and mature later.

TABLE 1

Baseline life history parameters for the greater glider and mountain brushtail possum. Parameters for each species are presented as stage-structured projection matrices (Caswell, 1989). The top row is the probability that a given stage produces a female offspring each year. The subdiagonal entries are the probabilities of surviving to reach the next stage. The value in the bottom right corner is the probability of surviving from year to year as an adult. D is the probability of surviving dispersal, and is given in the text. For GG the exponential population growth rate, calculated as the leading eigenvalue of the matrix, is 1.057, and for MBP it is 1.027, assuming $D = 1.0$.

	GG			MBP				
	N	J_1	A	N	J_1	J_2	J_3	A
Fecundity	0	0	0.49	0	0	0	0	0.4
Survival	$0.55D$			$0.3D$				
Survival		0.85	0.85		0.85			
Survival						0.9		
Survival							0.95	0.95

4. The model

The model was individual based, tracking the location and life history state of all females in the population at one year intervals. We ignored males in this implementation. The basic spatial unit was a female home range. All runs of the model were performed on a 33 x 33 grid of home ranges, using a six-cell hexagonal neighbourhood. There were four important components to the model: the landscape of continuously variable habitat quality, the population of individuals, the connection between habitat quality and vital rates (survival and fecundity) of individuals, and the dispersal rules used by individuals to move around on the landscape. We describe each of these components in turn.

In cellular automata models, the cells that can be influenced by the state of a particular cell are referred to as the neighbourhood. In our model, the neighbourhood was defined as the cells which an individual could reach in a single dispersal step. In theory, the geometry of the neighbourhood does not influence the outcome of cellular automata models (Durrett and Levin, 1994), as long as suitable weighting functions are chosen for the probabilities of movement between cells. We chose a hexagonal neighbourhood to provide the widest range of

directional choices with equal intercell distances, obviating the need for weighting movement probabilities. We tested four-cell von Neumann (Tyre et al., 1997), and eight-cell Moore neighbourhoods, and the results are not significantly different. The landscape was implemented as a single dimensional array, with offset kernels constructed in advance to allow the landscape to be accessed as either an orthogonal or hexagonal grid. Each offset kernel was an array containing information about how far to move up or down the array to move in a given direction. Moving up one row of the landscape translated to moving up the array by the width of the landscape and so on. For hexagonal grids, whether the current row was odd or even affects the kind of shift required for between row movement. Retrieving information about neighbouring territory involved three steps: (1) determining whether the current territory is on an edge and whether the row is odd or even, (2) choosing a direction, and (3) using the offset kernel to determine how far up or down the array the desired territory occurs.

Each home range on the landscape had an associated habitat quality. We wanted random landscapes with controllable amounts of spatial autocorrelation. Fractal surfaces can be constructed with a midpoint displacement algorithm (Saupe, 1988). This algorithm creates a surface with a specific fractal dimension ($H = 2.9$ or 2.5). The higher the fractal dimension is, the more ‘fragmented’ the landscape, with high quality home ranges split into a larger number of smaller patches (Fig. 1). The range of floating point values output by the fractal algorithm was linearly scaled to the integer range 0–100.

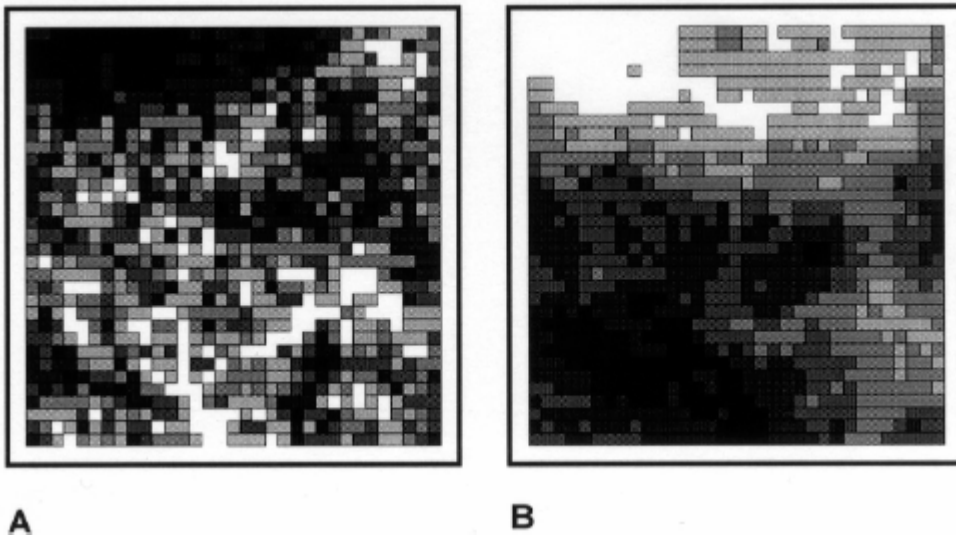


Fig. 1. Example fractal landscapes. Each cell is a territory. White cells are the 10% poorest cells, black the 10% best (i.e. the portion of the landscape above \hat{Q}). Other contour breaks are at 30%, 50%, and 70%: (A) $H = 2.9$, (B) $H = 2.5$.

Distributions of habitat quality generated with higher fractal dimensions were narrower under this transformation. This was because the range of floating point values is larger at larger fractal dimensions. We ignored the slight error on odd rows of the landscape grid resulting from converting the square grid output by the fractal algorithm to the hexagonal grid used in the model.

The population was implemented as a singly linked list of individuals. There were three different processes that occur within a year: birth, dispersal, and aging. Within a year, all individuals were checked sequentially to determine if they give birth. Newborn animals were attached to their mothers until dispersal, at which time they were placed in a queue. Dispersal follows birth and occurs sequentially with individuals being removed from the queue and allowed to move until they settle. There was a per-step probability of dying, which means that the probability of surviving dispersal is:

$$D = (1 - d)^n \quad (1)$$

where d is the per-step probability of mortality ($d = 0.01$ for all runs), and n is the number of steps taken before settling. Note that n was different for every individual.

It also depended on the local density of individuals, because in crowded conditions vacancies were rarer. This was the only point at which density dependence enters the model. The specific movement algorithms we used are described below. Dispersing individuals settled only in unoccupied territories under the assumption that older individuals (i.e. dispersers from previous years) were able to repel inexperienced territorial invaders without significant cost to themselves. If a cell was occupied by an individual of similar age, the resulting territorial dispute was settled randomly, with neither individual having an advantage (50% win/loss). The loser went back into the dispersal queue to continue dispersing from the disputed location.

It was possible that resolving birth, dispersal, and mortality events sequentially, rather than simultaneously, introduces a bias towards certain individuals. The initial order of individuals in the linked list was not important, because individuals were distributed at random on the landscape. Individuals only interact with each other during the dispersal phase. We tested the effect of the initial position within the dispersal queue, and found no systematic bias in the final quality of habitat located, or the number of times a territorial dispute occurred. Bias would only occur if the first individual to settle in an unoccupied territory had an advantage over later arriving individuals. This probably occurs in real animals, but not in the current model.

The variable landscape influenced individuals through either their probability of surviving from one age class to the next, or their probability of giving birth to a daughter. Both of these vital rates are probabilities, and are bounded between 0 and 1. The logistic, or log odds, transformation scales a probability onto the real number line (bounded by $\pm\infty$). We then assumed that habitat quality had a linear effect on the log odds of survival or reproduction. The annual probability of giving birth to a daughter in each home range $p_{x,i}$ was modified by the local habitat quality, Q_x , according to

$$\ln\left(\frac{2p_{x,i}}{1 - 2p_{x,i}}\right) = b\left(\frac{Q_x}{\tilde{Q}} - 1\right) + \ln\left(\frac{2p_i}{1 - 2p_i}\right) \quad (2)$$

where b was the effect of habitat quality on fecundity, Q_x was the habitat quality value in home range x , \tilde{Q} was a scaling constant, and p_i was the annual fecundity rate of age class i (Table 1). The 2 in the denominator and numerator of the log odds transformation corrects for ignoring males; the assumed sex ratio is 50/50, so if the probability of reproduction in a year is 1, the maximum probability of having a female offspring is 0.5. \tilde{Q} was the 90th percentile habitat quality, which was an average of 72 ($H = 2.9$) or 70 ($H = 2.5$). The exact distribution of habitat quality values differs between landscapes. \tilde{Q} scales habitat quality to remove any bias between different random landscapes. It ensures that, regardless of the exact details of the landscape, only 10% of the home ranges have fecundity (or survival) rates greater than the parameter value in Table 1. The relationship between b , \tilde{Q} , and fecundity is shown in Fig. 2. When $b > 0$, individuals have increased fecundity when $Q_x > \tilde{Q}$, and decreased fecundity when $Q_x < \tilde{Q}$. We use a similar transformation for the effect of habitat quality on survival:

$$\ln\left(\frac{s_{x,i}}{1 - s_{x,i}}\right) = a\left(\frac{Q_x}{\tilde{Q}} - 1\right) + \ln\left(\frac{s_i}{1 - s_i}\right) \quad (3)$$

We chose a , b and \tilde{Q} to ensure that approximately half of the landscape was occupied at equilibrium, based on preliminary runs ($H = 2.5$, using $\alpha = 3$; see below). We refer to runs where most variation in quality was attributed to survival as ‘survival scenarios’ ($a = 0.6$, $b = 1.0$), and runs where variation was primarily in fecundity as ‘fecundity scenarios’ ($a = 0$, $b = 11$ for GG, 5 for MBP). The fecundity effect parameter b was double the size for GG because this species unmodified parameter was so close to 0.5; smaller slopes did not introduce enough variation in fecundity.

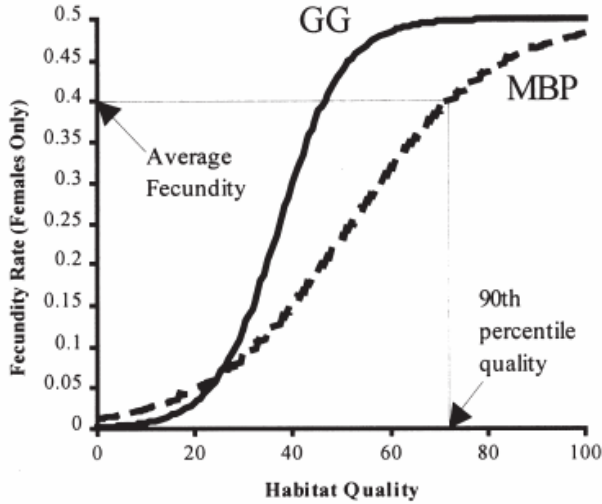


Fig. 2. Plot of Eq. (2) using parameters for MBP ($b = 5$), and GG ($b = 11$). Thin solid lines show the relationship between \hat{Q} and the fecundity parameter for MBP. In the absence of spatial variation all territories would have $p = 0.4$. When spatial variation in habitat quality influences fecundity, most territories (90%) will have fecundities lower than 0.4.

Very little is known about how individuals make choices about where to move on a heterogenous landscape during dispersal. We define our direction selection rule from a beta distribution with a parameter α :

$$P(x) = \int_0^x \frac{\Gamma(2\alpha)}{\Gamma(\alpha)\Gamma(\alpha)} x^{\alpha-1} (1-x)^{\alpha-1} dx \quad (4)$$

where $x = 0.5$ was assigned to the direction in which the greatest increase in territory quality occurs, and $x = 0$ or $x = 1.0$ were the opposite direction. The range $0 \leq x \leq 1$ was then divided up among the six neighbouring cells to provide a table from which a direction can be picked with a uniform random number. Values in the vicinity of 0.5 always result in ‘hill climbing’, or moving towards habitat of increasing quality. When $\alpha = 1$, this rule mimics a uniform random walk, with all directions equally likely. As α increases, the probability of moving ‘uphill’ on the quality landscape increases (Fig. 3). We refer to strategies with $\alpha = 1$ as ‘random walkers’ (RW) and strategies with $\alpha \approx \infty$ as ‘hill climbers’ (HC). Hill climbers did not use Eq. (3) to choose a direction; they always move towards the home range with the greatest increase in quality. Intermediate strategies are referred to using the value of α , or in general as ‘biased random walkers’. Note that this strategy is quite distinct from a ‘correlated random walk’ (e.g. Kareiva and Shigesada, 1983), where the direction chosen is correlated with the previous direction, but has nothing to do with variation in the underlying landscape.

In addition to picking a direction to move in, a complete dispersal strategy must specify what to do in case of ties in quality improvement between two or more directions, what to do on edges, and what to do if all directions are worse than the current location. If two or more directions yield equal increases in habitat quality, the best direction is chosen randomly from among the tied directions. Once a direction was chosen from the beta distribution, if it would take the individual off the edge of the landscape, a new direction was chosen randomly. A random direction was also chosen if all surrounding territories were worse than the current territory. The final component of our general strategy was a rule that applies an increasing penalty to moving in the direction of occupied territories. When individuals initially sample the surrounding territories, they reduce the quality of occupied territories by the number of dispersal steps they have taken. Therefore, the longer individuals spent unsuccessfully looking for good, unoccupied habitat, the less likely they are to move towards occupied territories. In the extreme, this means that hill climbers and biased random walkers acted like random walkers when surrounded by occupied territories, because the decremented quality of all surrounding territories will be less than the quality of the current territory.

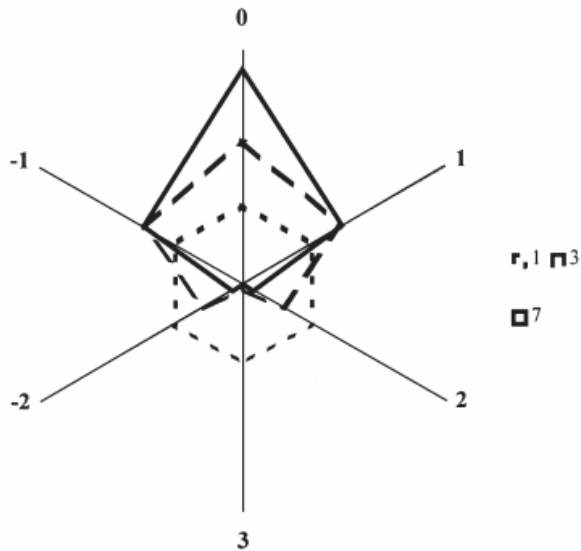


Fig. 3. Effect of the parameter α on the turning distribution. Direction 0 is always in the direction of greatest increase in habitat quality. The dotted line is $\alpha = 1$ (random walkers, RW), the dashed line $\alpha = 3$, and the solid line $\alpha = 7$. Values of $\alpha \gg 7$ are effectively hill climbers. For comparison, the probability of moving in direction 0 when $\alpha = 7$ is 0.46, and when $\alpha = 1$ the probability of moving in any direction is $1/6$ or 0.167.

Our biased random walker strategy relied on local correlations in habitat quality. To determine what happens when there were no local correlations in habitat quality, we examined a strategy referred to as ‘global jumpers’ (GJ). Global jumpers took steps by randomly choosing a territory from the landscape as a whole. This means that the quality of the territory they finally selected was a function only of the frequency distribution of habitat quality, and was not influenced by the spatial distribution of habitat quality on the landscape.

5. Results

As a first step, we confirmed that our different strategies lead to differing degrees of habitat selection on all landscapes and under all life history scenarios. The median (50th percentile) quality of occupied territories should increase when habitat selection is stronger. When there is no habitat selection or spatial autocorrelation in habitat quality, the median of occupied habitat should be equal to the median quality on the entire landscape. This was the case for global jumpers (Fig. 4). By comparison, all other strategies generally led to increased median quality of occupied home ranges ($HC > 5 > RW > GJ$). Ideally, the slopes would be all equal. However, because of the scaling applied to habitat quality values (i.e. 0–100), the maximum possible quality is 100. When the median quality on the landscape was high, the distribution above the median was compressed, and the slope was less than 1.0 (compare HC with GJ). This effect was especially noticeable on landscapes with $H = 2.5$, where the amount of variability in the median landscape quality was higher. Variation between life history scenarios within a particular strategy had no consistent effect on the median quality of occupied habitat.

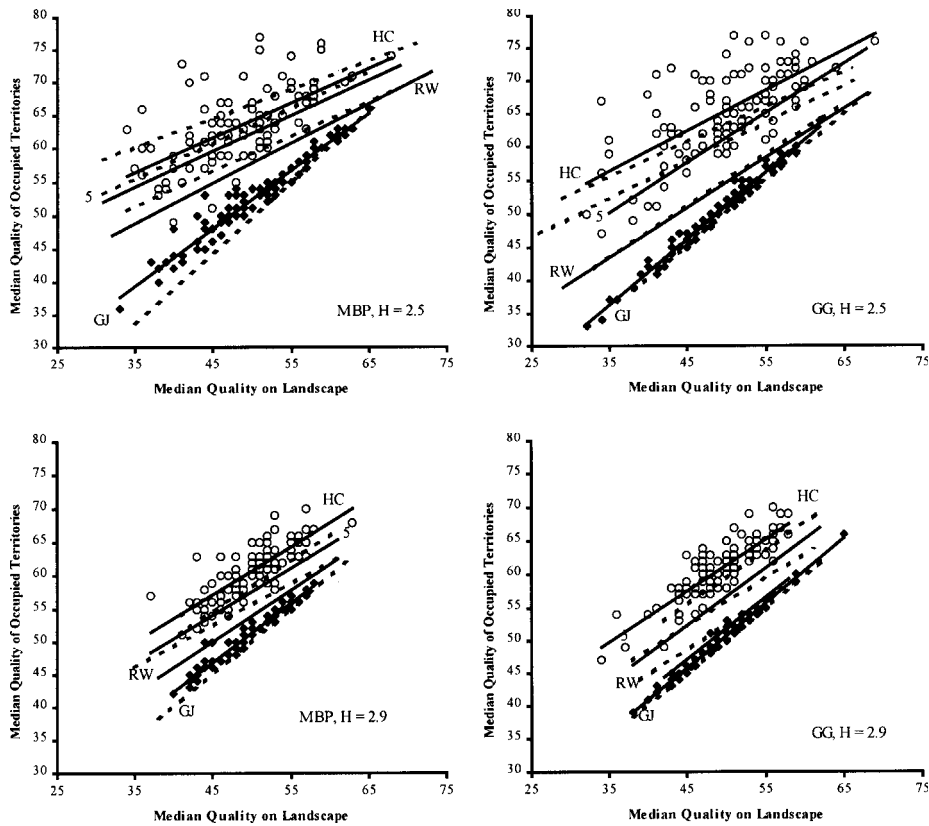


Fig. 4. Effect of different dispersal strategies on the median quality of occupied territories. For clarity, symbols are only plotted for global jumpers (GJ) and hill climbers (HC) in the survival effect scenario. Other strategies shown are random walkers (RW) and biased random walkers with $\alpha = 5$. Lines are independent least squares fitted to each scenario/dispersal strategy combination. Dashed lines are fecundity effect scenarios, and solid lines are survival effect scenarios.

For all parameter values, populations reach a quasi-equilibrium within 100 years. None of the simulated populations went extinct, indicating that the probability of extinction is low. There were substantial differences between dispersal strategies in the long term equilibrium population sizes (Fig. 5). In general, there were higher populations in the absence of habitat selection behaviour (smaller a). Landscape structure and life history values also influence population size, but the magnitude of these effects was much smaller. For both species, and all life history scenarios, fragmented landscapes ($H = 2.9$) had larger populations. The mechanism by which landscape quality influences individuals, either through fecundity or survival, affected population size differently for the different species. MBP had higher population sizes when survival varied across the landscape, and fecundity was constant. GG had higher population sizes when fecundity varied across the landscape, and survival was constant. Random walking GG had either no or reversed differences. These differences within dispersal strategies between different kinds of landscapes, could have arisen either from the interaction between the spatial structure of the landscape and the particular dispersal strategy, or simply from small changes in the distribution of habitat quality under different scenarios and landscapes. We can tease these effects apart by examining the life history performance of individuals at the equilibrium population size.

Dispersal strategy influenced long term reproductive success at two points in the model. Individuals that searched more intensively for better habitat should have tended to end up in higher quality habitat with better survival or reproduction once settled. However, the process of searching for that habitat may have led to increased mortality during dispersal. Fig. 6 shows average fecundity and juvenile survival as a function of dispersal strategy and life history scenario for greater gliders on fragmented landscapes ($H = 2.9$). Mortality during the first year includes both dispersal mortality and aging mortality. Overall, the stronger the habitat selection behaviour was, the less likely individuals were to survive during dispersal (Fig. 6(A)). This was true under both life history scenarios. Dispersal mortality introduced density dependence into the model. When individuals sought high quality territory, dispersers competed for a

smaller number of territories, and dispersal mortality increased at smaller population sizes.

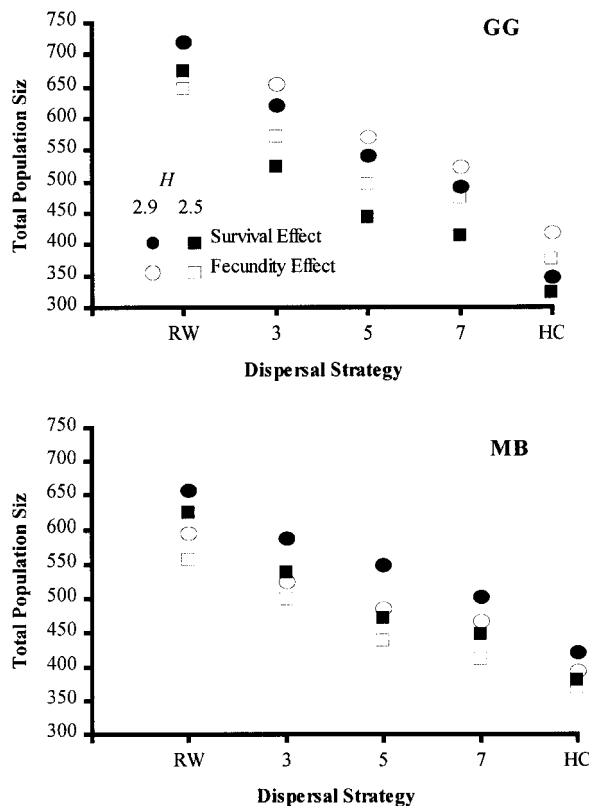


Fig. 5. Effect of habitat selection on total population size at 200 years; x-axis labels are the α in Eq. (2) and Fig. 2. Each point is the average of 100 replicate landscapes with $H = 2.5$ (squares) or 2.9 (circles); standard errors are smaller than the points. GG = greater gliders; MBP = mountain brushtail possum. Note the x-axis scale is not linear; HC (hill climbers) represent an infinite α . RW = random walkers; GJ = global jumpers.

Habitat selection reduced post-dispersal mortality when survival varied across the landscape (Fig. 6(B)). However, the magnitude of the increase did not offset the decrease in survival during dispersal. HC cut the effect of spatial variability on first t year survival in half, while decreasing survival during dispersal by > 10% (compare HC with GJ in Fig. 6(A,B)). For both species, the average fecundity was reduced when there was spatial variation in the probability of reproduction. The variation in population size as a function of dispersal strategy was primarily a result of increased density dependence in dispersal mortality.

6. 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. This work is unique because it examines continuous variation in habitat quality, as opposed to ‘patchy’ variation where habitat is either available or not (Keitt and Johnson, 1995; Gustafson and Gardner, 1996). It also explores strategies that make use of information about the environment to decide where to look for habitat. We have formed a ‘neutral landscape model’ (With and King, 1997) to test the effects of a typical span of dispersal strategies on population dynamics. There are many variations on the strategies used here. 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. To the best of our knowledge, the inter-action between a continuously heterogeneous landscape and simple dispersal rules has not been explored before, and leads to non-intuitive results.

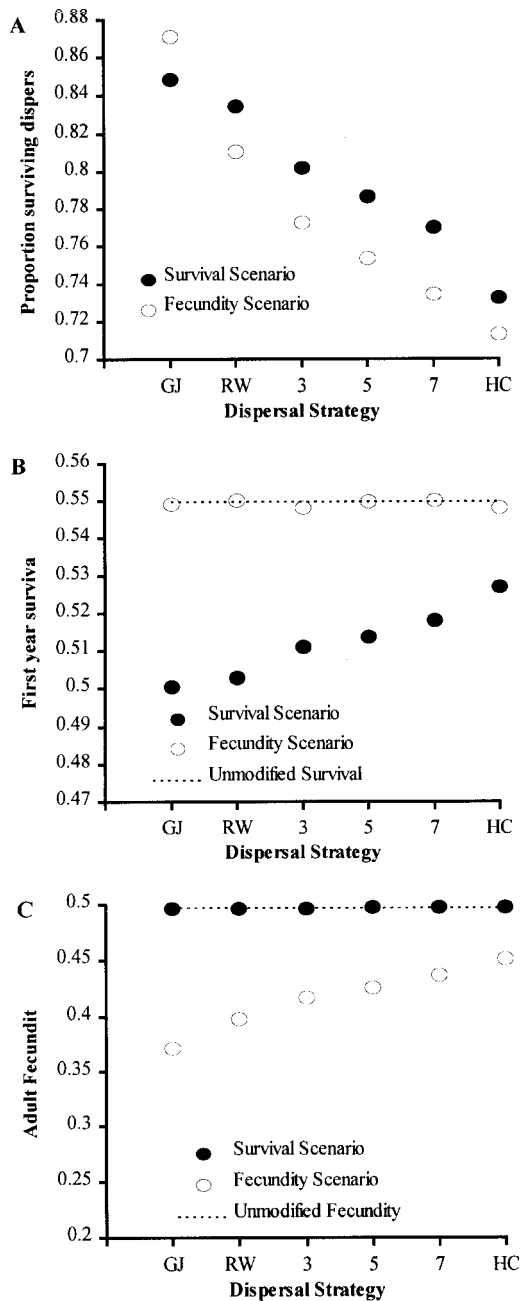


Fig. 6. Life history parameters determined by recording the fate of all individuals born between year 160 and 180. Only results for GG, $H = 2.9$, are shown for clarity. Dashed lines indicate the value input to the model in the absence of spatial variability (Table 1). Symbols as for Fig. 4. Each point is the average of 100 replicate runs, and standard errors are smaller than the points.

The primary conclusion is that strong habitat selection behaviour leads to reduced population sizes. This occurs because of density-dependent mortality while searching for high quality habitat. In short, when all individuals seek the best habitat, and there is insufficient habitat, density-dependence in dispersal mortality arises at smaller population sizes. The stronger the bias in the random walk, the more individuals tend to remain clustered around local centres of high habitat quality, and not venture into poorer quality habitat. Some empirical work has demonstrated that dispersing individuals do tend to remain within high quality habitat during dispersal (Holekamp, 1984; Merriam and Lanoue, 1990; Haas, 1995). Other work has shown that dispersers do compete for limited high quality habitat (Smith and Peacock, 1990).

A second important conclusion from this work is that it is not necessary to have any form of active habitat selection in order to obtain a relationship between habitat quality and occupancy. The random walking strategy does not use information about the landscape to make decisions

about where to move. Animals 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 or fecundity. Nonetheless, the relationship between habitat quality and occupancy is weaker for random walkers than for hill climbers (Fig. 4).

The reduction in life history parameters in the presence of spatial variation is a consequence of averaging a non-linear function (Chesson, 1981, 1990). There are two ways in which the average of a function of a random variable can be calculated. If $g()$ is the function, and z is the random variable, then the first possibility is to average the random variable, and then apply the function, or $g(E(z))$. The alternative is to take the function of each instance of the random variable, and average the results, or $E(g(z))$. These two quantities will not be identical. The magnitude of the change can be approximated by looking at the expectation of a Taylor expansion of a function at the mean of a random variable (Hilborn and Mangel, 1997, p. 58):

$$E(g(Z)) = g(\mu) + \frac{1}{2} g''(\mu) \text{VAR}(Z) \quad (5)$$

where Z is a random variable with mean μ , E is the expectation operator, and $g(z)$ is the function (or its derivative) evaluated at z . Clearly, if g'' is negative, then $E(g(Z)) < g(E(Z)) = g(\mu)$. In our case, habitat quality is a random variable. When habitat quality does not influence fecundity, we are using an ‘average’ fecundity for all individuals. When fecundity varies spatially, variation above the average quality increases fecundity less than variation below the average quality (Fig. 2). As a result, the average fecundity in the presence of spatial variation is reduced.

We can also explain the different responses of the two species’ equilibrium population size to variation in fecundity (Fig. 5) using Eq. (5). The second derivative of Eq. (2), the response of fecundity to habitat quality, is:

$$\frac{\partial^2 p_{x,i}}{\partial Q_x} = \frac{-1}{2e^{\beta}[(\beta\tilde{b})^2 + \tilde{b}^2]} \quad (6)$$

where

$$\beta = \tilde{b}Q_x - b + \ln\left(\frac{2p_i}{1 - 2p_i}\right)$$

and

$$\tilde{b} = \frac{b}{\tilde{Q}}$$

is always negative when evaluated at \tilde{Q} . Furthermore, the larger b is, the smaller Eq. (6) is in absolute magnitude, and the less effect variability in habitat quality will have on average fecundity. As shown in Fig. 2, the value of b used for GG is larger than for MBP. Therefore, landscape variability will decrease the average fecundity of MBP more. The magnitude of the effect of landscape variability under the survival scenario is equivalent, because a is the same for both species. Under the fecundity scenario, GG have higher population sizes than under the survival scenario, and MBP lower than under the survival scenario, because the impact of variability on average fecundity is greater for MBP.

A final point from this analysis is that behaviour can reduce or eliminate the effects of spatial variation on individual performance. Individuals that use habitat selecting rules tend to obtain higher quality territories, and therefore their populations do not suffer the penalties of non-linear averaging to the same extent as populations of non-selective individuals. This improved individual performance comes at a cost: the density-dependent ceiling that arises through

increased dispersal mortality is lower. Determining the dispersal strategy that is optimal in an evolutionarily stable sense (Maynard-Smith, 1982) is difficult in this model because of the complexity in the landscape, and individual and population level responses to that complexity. The interaction between individually optimal behaviour and spatially variable landscapes is only beginning to be studied (Roitberg and Mangel, 1997), and promises to be interesting.

Although this model has included fine scale spatial variability in habitat quality, we ignored variation in individual phenotypic quality. While this is not an uncommon assumption in population modelling, it is potentially important in the context of the optimal behaviour patterns discussed above. Verhulst et al. (1997) showed that phenotypic variation among great tits (*Parus major*) interacts with the quality of their natal habitat to determine the distance they disperse. High quality birds born in low quality habitat are more likely to disperse long distances. In the context of the current model, this indicates that the assumption of equal competitive ability among new dispersers is false for some species, and will have an influence on the optimal strategy to follow during dispersal. High quality individuals may be better off with a biased or hill climbing strategy, because they will be able to displace other individuals from high quality home ranges. In contrast, low quality individuals may be better off searching for unoccupied territories without regard for their quality.

Recent years have witnessed an explosion of individual based, spatially explicit population models (see review in With and King, 1997). Most have utilised homogenous landscapes without variability. The variability that is introduced is generally binary source/sink variation with patches of useable habitat in an unusable matrix (e.g. Keitt and Johnson, 1995). The effects of this kind of spatial structure are well understood in the context of patch based metapopulation models (Kareiva, 1990; Day and Possingham, 1995). What has not been addressed is the effect of variable habitat quality within otherwise contiguous patches of habitat. Such variability is assumed to have little or no effect on population dynamics. It does have an influence because of non-linear averaging (Chesson and Warner, 1981; Chesson, 1990). Analytical approaches to understanding the effects of spatial variability are limited because they have difficulty accounting for spatial autocorrelation in habitat quality (but see Possingham et al., 1994b), and including the effect of individual behaviour. This model has demonstrated that behaviour and spatial variability interact in interesting and sometimes non-intuitive ways, and that ignoring the interaction may lead to misinterpretations of observations of population dynamics.

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