
The evolution of density-dependent dispersal

Justin M. J. Travis¹, David J. Murrell² and Calvin Dytham^{2*}

¹*Department of Biology, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, UK (jmtravis@ic.ac.uk)*

²*Department of Biology, PO Box 373, University of York, York YO10 5YW, UK (djm113@york.ac.uk)*

Despite a large body of empirical evidence suggesting that the dispersal rates of many species depend on population density, most metapopulation models assume a density-independent rate of dispersal. Similarly, studies investigating the evolution of dispersal have concentrated almost exclusively on density-independent rates of dispersal. We develop a model that allows density-dependent dispersal strategies to evolve. Our results demonstrate that a density-dependent dispersal strategy almost always evolves and that the form of the relationship depends on reproductive rate, type of competition, size of subpopulation equilibrium densities and cost of dispersal. We suggest that future metapopulation models should account for density-dependent dispersal.

Keywords: metapopulation; lattice model; competition; condition dependent; equilibrium density; individual-based model

1. INTRODUCTION

Understanding the conditions under which different dispersal strategies evolve has been of interest to evolutionary ecologists for over 20 years (see, for example, Hamilton & May 1977; Comins 1982; Olivieri *et al.* 1995; Doncaster *et al.* 1997; Travis & Dytham 1999; Dieckmann *et al.* 1999). Today, even more than before, an appreciation of the forces driving different dispersal strategies is important. We live in a world where almost every landscape is becoming increasingly fragmented, disturbed and degraded. More and more species are being forced to adapt to a life in a 'metapopulation' and a recurrent question in metapopulation ecology relates to the likely persistence of populations living in fragmented, patchy landscapes. Dispersal is a key element of an organism's life history and the form of dispersal exhibited by an organism influences its performance in a particular landscape (Neuhauser 1998). Almost all models investigating the consequences of dispersal on metapopulation dynamics have assumed dispersal to be independent of population density (e.g. Gonzalez-Andujar & Perry 1993; Hassell *et al.* 1995; Lindenmayer & Possingham 1996; Rohani *et al.* 1996).

A large body of empirical work suggests that for many species dispersal rate depends on local population size. A positive relationship between population density and the rate of dispersal has been observed in spiders (Duffey 1998), insects (Berger 1992; Denno & Peterson 1995; Fonseca & Hart 1996; Rhainds *et al.* 1997, 1998), echinoderms (Rosenberg *et al.* 1997), mammals (e.g. Berger 1987; Krebs 1992; Sinclair 1992), and birds (e.g. Watson *et al.* 1984; Nilsson 1989; Veit & Lewis 1996). Negative density-dependent effects on dispersal have also been observed, mainly for mammals (e.g. Wolff 1997; Diffendorfer 1998; Diffendorfer *et al.* 1999).

Despite this wealth of empirical evidence suggesting that density-dependent dispersal is a frequently exhibited strategy, relatively few metapopulation models incorporate it (but see Csilling *et al.* 1994; Ruxton 1996; Saether *et al.* 1999). In one recent exception, Saether *et al.* (1999) showed that different density-dependent strategies influence both the establishment and the rescue effects in the local dynamics of metapopulations, and thus alter the likelihood of metapopulation extinction. Exactly the same assumption of density-independent dispersal has been made in almost all models investigating the evolution of dispersal (e.g. Comins *et al.* 1980; Travis & Dytham 1998). Two recent exceptions to this trend are provided by the work of Janosi & Scheuring (1997), who identified evolutionarily optimal thresholds for dispersal in a metapopulation model, and Ezoe & Iwasa (1997) who used a patch occupancy model to investigate the evolutionarily stable strategy proportion of dispersing offspring under different environmental conditions.

In this paper we develop a model that allows linear density-dependent dispersal strategies to evolve. We investigate how changes to the reproductive rate, the type of competition and subpopulation equilibrium density affect the form of dispersal that is selected.

2. THE MODEL

The model developed incorporates a framework similar to that of models we have used previously to investigate the evolution of dispersal (e.g. Travis & Dytham 1998; 1999). For simplicity, we consider an asexual species. Genotypes differ only in the dispersal strategy that they exhibit: there is no trade-off between dispersal ability and competitive ability. We do consider a cost of leaving the natal site in the form of a probability of dying while dispersing, but reproductive output is otherwise unaffected by the propensity to disperse. The dynamics occur on an $n \times n$ square lattice with periodic boundaries,

* Author for correspondence (cd9@york.ac.uk).

where each site on the lattice can support a subpopulation. All subpopulations have the same equilibrium density. The order of events for individuals in each generation is as follows: birth; local competition; dispersal (or not); reproduction; death.

The most important advance we introduce is the consideration of density-dependent dispersal strategies. Whereas earlier work considered only density-independent rates of dispersal, we now allow for the evolution of any linear density-dependent strategy described by an intercept and slope. The propensity of an individual to disperse depends both on its genotype and the density of its natal patch (i.e. probability of dispersal changes linearly with local patch density).

(a) *Within-subpopulation dynamics*

Within-subpopulation dynamics are described by an individual-based formulation based on Hassell & Comins (1976). Each individual present in the population at time t gives birth to a number of offspring taken at random from a Poisson distribution with mean μ defined as

$$\mu = \left(\frac{N_{t+1}}{N_t} \right),$$

where

$$N_{t+1} = \lambda N_t (1 + a N_t)^{-b},$$

and λ is the rate of increase, a relates to patch quality and b describes the type of competition operating. When $b = 1$ the competition is 'contest' and as b increases, the nature of the competition becomes increasingly 'scramble'. The parameter a is calculated from the following expression:

$$a = (\lambda^{1/b} - 1) / N^*,$$

where N^* is the subpopulation equilibrium density. Using a number drawn from a Poisson distribution to determine how many offspring an adult has causes the model to exhibit demographic stochasticity.

All offspring inherit their dispersal genotype from their parent, but with small independent probabilities, m_i and m_s , of mutation to the intercept and the slope of the density-dependent dispersal strategy respectively. The distance of a mutation away from the parental strategy is given by d_i and d_s , respectively. For all the realizations of the model which we describe in this paper,

$$m_i = m_s = 0.01, \text{ and } d_i = d_s = R/5,$$

where R is a random deviate drawn from the rectangular probability density function with limits -1 and 1 .

(b) *Dispersal*

Dispersal occurs immediately after the within-population dynamics. One feature of our previous models (Travis & Dytham 1998, 1999) was that character space was discrete: a finite number of different dispersal rates could evolve. In the model presented here, character space (the number of possible phenotypes) is continuous and individuals can disperse according to any linear, density-dependent dispersal strategy.

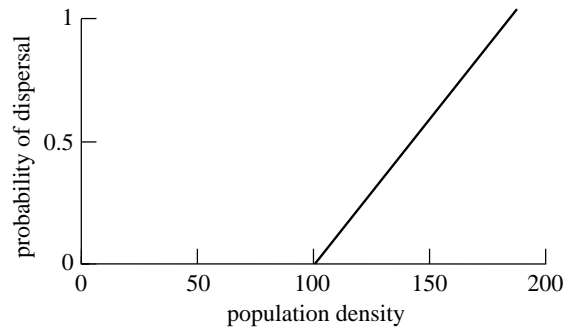


Figure 1. A typical density-dependent dispersal strategy for a system comprising large subpopulations ($N^* = 100$, $b = 1$, $c = 0.05$, $\lambda = 5$).

The probability (P) that any individual will disperse is calculated as follows:

$$P = I + S \left(\frac{N_t}{N^*} \right),$$

where I and S are, respectively, the intercept and slope of the density-dependent dispersal strategy being played by the individual. A positive slope indicates that propensity to disperse increases with density. A negative intercept and positive slope indicates that there is no dispersal at lower densities. Dispersal occurs with equal probability to the eight patches that border on an individual's natal subpopulation. When negative values of P are obtained, the probability of dispersing is interpreted as zero. We include costs of dispersal as follows: a dispersing individual will fail to reach its destination with a probability c .

In this paper we investigate the effect of varying the reproductive rate, the subpopulation equilibrium densities, the type of competition and the cost of dispersal, on the form of dispersal that evolves. The model is initialized by randomly placing 1000 individuals onto the lattice: each individual has $I=0$ and $S=0$ (i.e. no dispersal at any density), and has an equal chance of being in each subpopulation. Each realization of the model runs for 5000 generations, to obtain our values for the intercept and slope we take the mean values of the final population. The results for any particular combination of parameter values use an average taken from ten realizations of the model.

3. RESULTS

Density-dependent dispersal almost always evolved for the conditions we used in our model (figure 1). The only exception to this was for the rather unrealistic case where there is no cost associated with dispersal ($c=0$). When no explicit cost of dispersal is incorporated, the strategy that evolves under a wide range of parameter values is one where individuals always disperse (i.e. intercept ≥ 1.0 and slope > 0.0). This is most often observed when the reproductive rate is high and the type of competition is 'scramble' ($b=10$).

There is a big difference between the results obtained for large and small subpopulation equilibrium densities. When subpopulation equilibrium densities are high ($N^* \geq 100$) the relationship between dispersal probability and population density is robust to changes in

Table 1. Mean density-dependent dispersal strategies for metapopulations with large local populations

($N^* = 100$, $c = 0.01$. When subpopulation size is relatively large the strategy which evolves is largely insensitive to the values of b and λ .)

reproductive rate λ		type of competition, b		
		1	2	10
2	intercept	-1.34	-1.19	-1.37
	slope	1.20	1.05	1.24
5	intercept	-1.30	-1.24	-1.25
	slope	1.15	1.12	1.17
10	intercept	-1.17	-1.27	-1.18
	slope	1.03	1.15	1.07

Table 2. Mean dispersal strategies in metapopulations with small local populations for three types of competition and three reproductive rates

($N^* = 25$, $c = 0.01$. The table clearly shows a reduction in the value of the intercept for both increasing b and increasing λ .)

reproductive rate λ		type of competition, b		
		1	2	10
2	intercept	-0.85	-0.80	-0.89
	slope	0.91	0.85	0.93
5	intercept	-0.69	-0.58	-0.41
	slope	0.79	0.73	0.59
10	intercept	-0.70	-0.44	-0.27
	slope	0.80	0.62	0.49

reproductive rate and the type of competition (see table 1). For a wide range of parameter values the strategy that evolves is one where individuals never disperse until the population they are in reaches the equilibrium density, and always disperse when the population density is higher than twice the equilibrium density. For lower subpopulation equilibrium densities ($N^* = 5, 10$ or 25) the relationship is more complex (see table 2). For higher values of the reproductive rate, λ , the intercept of the relationship increases and the slope decreases slightly (see figure 2a). At higher rates of reproduction dispersal starts to occur at lower densities than for lower values of λ . This effect is strongest for 'scramble' competition (higher values of b). As the value of b is raised, the same effect is seen, with an increase in the values of the intercept and a small decrease in the slope (see figure 2b).

The form of dispersal that evolves is highly dependent upon the cost of dispersal (see figure 2c). As the cost associated with dispersal increases, lower intercepts are selected for. However, there is no such obvious change in the value of the slope that evolves. This result is true for both small and large subpopulations.

Figure 3 shows three trajectories that describe how the slope and intercept evolve through the phase space to an attractor. If both slope and intercept start with values of zero, there is an initial increase in both. This is because

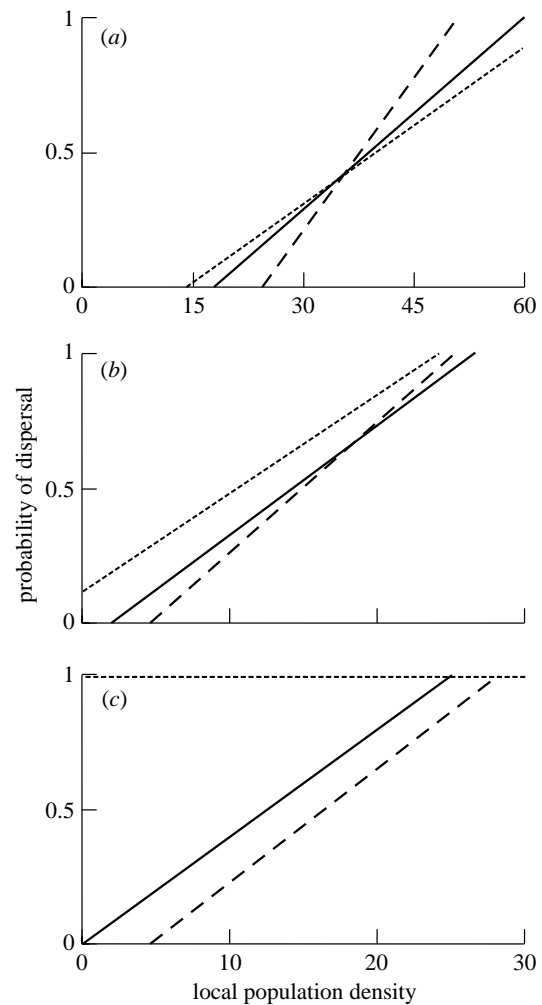


Figure 2. A comparison of the relationships obtained for different parameter values. Only one parameter is varied in each graph. (a) The reproductive rate is varied: $\lambda = 2$ (dotted line); $\lambda = 5$ (solid line); $\lambda = 10$ (dashed line), but all other parameters are kept constant ($c = 0.1$, $b = 10$, $N^* = 25$). (b) The form of competition is varied: $b = 1$ (dotted line); $b = 2$ (solid line); $b = 10$ (dashed line), other parameters are constant ($c = 0.1$, $\lambda = 10$, $N^* = 10$). (c) Cost of dispersal varied: no cost (dotted line); $c = 0.1$ (solid line); $c = 0.5$ (dashed line), other parameters constant ($b = 1$, $\lambda = 5$, $N^* = 10$). When there is no cost of dispersal all individuals disperse at all densities.

some dispersal is better than none and can be achieved with slope or intercept above zero. After a period, the strategy becomes more refined and the trajectory reverses its direction in the intercept axis and tracks back towards, and eventually into, an area of negative intercepts (i.e. no dispersal at low densities). The slope continues to increase until eventually a stable point is reached with a negative intercept and a positive slope.

4. DISCUSSION

The results show clearly that density-dependent dispersal strategies should evolve under almost all conditions. This result met with our expectations. Individuals in patches below their equilibrium densities are likely to be more successful if they produce offspring that remain in their natal patch. Other, nearby patches may have population densities greater than those in the natal patch

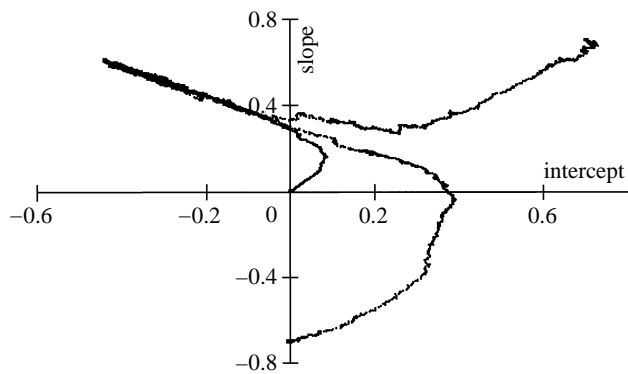


Figure 3. The trajectories taken by the mean intercept and mean slope of a population over 5000 generations from three different initial values for slope (S) and intercept (I). All trajectories are generated with the same parameter values: $\lambda = 5$, $c = 0.05$, $b = 1$ and $N^* = 100$.

and the expected reproductive output of offspring moving to those patches will be lower than if they remain at home. Conversely, individuals in patches well above equilibrium density will do best by producing mainly dispersing offspring. This is for two reasons. By producing some dispersing offspring kin competition in the natal patch is reduced, and nearby patches may have lower densities so the expected reproductive success of individuals moving to those patches will be higher than for individuals that do not disperse. Lemel *et al.* (1997) suggest that an evolutionarily stable dispersal rate should permit the spatial homogenization of fitnesses. The density-dependent strategy that evolves in this model appears to be doing likewise: after dispersal the difference in subpopulation density between patches is much reduced. The evolution of the dispersal strategy can be seen in figure 3. For example, from a starting point where $S=0$ and $I=0$, both dispersal variables increase, as any dispersal is better than none. However, as more individuals disperse the strategy becomes more finely tuned, and the intercept reverses its direction and becomes negative so that dispersal occurs only after a threshold density, around the subpopulation equilibrium density, has been reached.

The cost involved in dispersing is critical in determining the relationship between population density and probability of dispersal. For almost all species it would seem likely that there is some cost to dispersal, whether it is due to a risk of mortality while moving, or the risk of not finding a suitable destination site, or through costs associated with developing wings or seeds that disperse better. With density-independent dispersal it has been found that incorporating higher costs of dispersal leads to a reduction in propensity to disperse (Travis & Dytham 1998). We wanted to ascertain whether the slope, the intercept, or both, are affected by increased dispersal costs for the case of density-dependent dispersal. Our results suggest that whenever dispersal has a cost then we should expect the frequency at which it occurs to vary with population density. As the cost of dispersing increases, the form of the density-dependent relationship changes. With a low cost, the effects of density are relatively weak; an individual has a good chance of surviving if it disperses. As the cost of dispersal increases however,

the density at which dispersal is first apparent also increases; unless at very high densities it pays an individual to stay where it is and compete for whatever resources are available (figure 2c). From our results, we predict that the strongest forms of density-dependent dispersal should be observed in species where the cost of dispersal is greatest.

It is interesting that there is a difference in the results for small and large subpopulations. For a subpopulation equilibrium density of 100 the form of dispersal to evolve is largely insensitive to reproductive rate or the form of competition. This is not the case for smaller subpopulation equilibrium densities. In smaller subpopulations demographic stochasticity is far more important. Here, interactions between demographic stochasticity, the reproductive rate and the type of competition determine the form of the relationship that evolves. For a population size near 100 the many stochastic events affecting each individual will average out over the population as a whole, such that the population's behaviour approaches that described by a set of deterministic equations. At these higher densities it appears that the cost involved in dispersing is the dominant factor (of those we included) determining the relationship between population density and probability of dispersal. We expect that deterministic models investigating the evolution of linear density-dependent dispersal strategies would also reach this conclusion.

For smaller subpopulation equilibrium densities the form of dispersal depends on both the reproductive rate and the type of competition. As the type of competition becomes increasingly 'scramble', there is a higher probability of dispersal even at low population densities. As b is increased, the probability of patches becoming empty increases owing to the less stable population dynamics generated by the 'scramble' competition. This greatly increases the benefits of dispersing: dispersers are now far more likely to colonize empty sites, experience less competition and consequently have higher expected reproductive success. With higher values of b it becomes advantageous for a small proportion of offspring to disperse even at low population densities. Holt & McPeck (1996) suggested that chaotic dynamics should favour higher rates of density-independent dispersal, although other work (Travis & Dytham 1998) shows that this may not always be the case. The main conclusion to be drawn from this study is that where dispersal is density dependent we should expect chaotic dynamics to favour increased probabilities of dispersal at relatively low subpopulation densities. It is less clear what happens at higher densities, and to establish that perhaps requires a study of the evolution of nonlinear density-dependent relationships.

At higher reproductive rates dispersal starts to occur at lower population densities and this effect is seen most clearly at higher values of b . For individuals with low reproductive output that are in patches below equilibrium density, there is an advantage to be gained by having sedentary offspring. Offspring in these patches will suffer relatively low levels of competition and by moving they suffer costs of dispersal with limited possible gains. However, for individuals with higher reproductive rates it is not so straightforward. If all their offspring remain the

patch will become crowded and kin competition will be high. For these individuals it is better for some offspring to disperse, simultaneously reducing the level of competition in the natal patch and increasing the chances that a new patch may be colonized. Thus, for reasons of kin competition, it benefits individuals with higher rates of reproduction to start producing dispersing offspring at lower subpopulation densities than individuals with lower reproductive output.

In this paper the relationship between population density and dispersal is constrained to be linear. This was primarily chosen as it represents the simplest case, although we believe that a linear relationship can provide for most likely strategies. An example of density-dependent dispersal that has a similar form to the one shown here is that of bagworm larvae (Rhainds *et al.* 1997). Females of the bagworm, *Metisa plana*, lack wings and disperse by ballooning, releasing a silken thread, which is then caught on the wind. The propensity to balloon is density dependent with a linear relationship. At lower population densities females tend to stay on their natal host plant. This is attributed to the fact that *M. plana* is host specific and the chance of finding a suitable plant is quite small given that movement is dependent on wind conditions (Rhainds *et al.* 1998). Mortality during dispersal is high but this mortality is traded off against a reduction in fecundity due to small size at pupation if the female remains on a densely populated host plant. Another bagworm, *Oiketicus kirbyi*, has a higher rate of dispersal at low density levels. This is attributed to a combination of lower cost of dispersal (lower host specificity) and higher level of competition (Rhainds *et al.* 1998).

Future work should address the evolution of nonlinear relationships. We anticipate that the main difference would be that at population densities well above equilibrium density, the probability of dispersing would remain slightly below unity: a curve would have an asymptote of unity. The same would possibly also be true at very low population densities, with a curve having an asymptote of zero. Johst & Brandl (1997) modelled a form of nonlinear density-dependent dispersal and have shown that under certain circumstances it is favoured over the linear form. However, they only modelled two nonlinear dispersal strategies with no evolution, and it remains unclear what forms of nonlinear density-dependent dispersal are favoured under differing environmental and demographic conditions.

Positive density-dependent dispersal is often easy to explain and usually relates to competition for food or other types of resources, or interference. However, there are also well-documented cases of species showing dispersal occurring more frequently at low population densities (e.g. Birkhead 1977; Lamont *et al.* 1993; Herzig 1995; Kuussaari *et al.* 1998). Negative density-dependent dispersal may occur as a result of the Allee effect (Allee 1931). Recruitment to a population may be low owing to the problems in finding a mate, to social effects such as cooperation or facilitation. For example, female goldenrod beetles, *Trirhabda virgata*, disperse from host plants with a higher frequency when there is a low density of males, than when there is a high density, whatever the local patch quality (Herzig 1995). Incorporating the Allee

effect into models of the evolution of dispersal is outside the scope of this paper, but remains an interesting area for future study.

We thank the organizers and all who attended the workshops on the Evolution of Dispersal in Tvarminne, Finland, and Roscoff, France. We also thank David French for his comments on the manuscript and Isabelle Olivieri and Ophelie Ronce for useful discussions. We are grateful for the helpful comments of two anonymous referees. J.M.J.T. and D.J.M. are supported by Natural Environment Research Council.

REFERENCES

- Allee, W. C. 1931 *Animal aggregations. A study in general sociology*. University of Chicago Press.
- Berger, A. 1992 Larval movements of *Chilo partellus* (Lepidoptera: Pyralidae) within and between plants: timing, density responses and survival. *Bull. Ent. Res.* **82**, 441–448.
- Berger, J. 1987 Reproductive fates of dispersers in a harem-dwelling ungulate: the wild horse. In *Mammalian dispersal patterns* (ed. B. D. Chepko-Sade & Z. T. Halpin), pp. 41–54. University of Chicago Press.
- Birkhead, T. R. 1977 The effect of habitat and density on breeding success in the common guillemot (*Uria aalge*). *J. Anim. Ecol.* **46**, 751–764.
- Comins, H. N. 1982 Evolutionary stable dispersal strategies for localized dispersal in two dimensions. *J. Theor. Biol.* **94**, 579–606.
- Comins, H. N., Hamilton, W. D. & May, R. M. 1980 Evolutionary stable dispersal strategies. *J. Theor. Biol.* **82**, 205–230.
- Csilling, A., Janosi, M., Pasztor, G. & Scheuring, I. 1994 Absence of chaos in a self-organised critical coupled map lattice. *Phys. Rev. E* **50**, 1083–1092.
- Denno, R. F. & Peterson, M. A. 1995 Density-dependent dispersal and its consequences for population dynamics. In *Population dynamics* (ed. N. Cappuccino & P. W. Price), pp. 113–130. San Diego, LA: Academic Press.
- Dieckmann, U., O'Hara, B. & Weisser, W. 1999 The evolutionary ecology of dispersal. *Trends Ecol. Evol.* **14**, 88–90.
- Diffendorfer, J. E. 1998 Testing models of source–sink dynamics and balanced dispersal. *Oikos* **81**, 417–433.
- Diffendorfer, J. E., Gaines, M. S. & Holt, R. D. 1999 Patterns and impacts of movements and different scales in small mammals. In *Ecology of small mammals at the landscape level: experimental approaches* (ed. G. W. Barrett & J. D. Peles). University of Chicago Press. (In the press.)
- Doncaster, C. P., Clobert, J., Doligez, B., Gustafsson, L. & Danchin, E. 1997 Balanced dispersal between spatially varying local populations: an alternative to the source–sink model. *Am. Nat.* **150**, 425–445.
- Duffey, E. 1998 Aerial dispersal in spiders. In *Proceedings of the 17th European Colloquium of Arachnology* (ed. P. A. Seldon), pp. 187–191. Buckinghamshire: British Arachnological Society.
- Ezoe, H. & Iwasa, Y. 1997 Evolution of condition-dependent dispersal: a genetic-algorithm search for the ESS reaction norm. *Res. Pop. Ecol.* **39**, 127–137.
- Fonseca, D. M. & Hart, D. D. 1996 Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* **75**, 49–58.
- Gonzalez-Andujar, J. L. & Perry, J. N. 1993 The effect of dispersal between chaotic and non-chaotic populations within a metapopulation. *Oikos* **66**, 555–557.
- Hamilton, W. D. & May, R. M. 1977 Dispersal in stable habitats. *Nature* **269**, 578–581.
- Hassell, M. P. & Comins, H. N. 1976 Discrete time models for two-species competition. *Theor. Popul. Biol.* **9**, 202–221.
- Hassell, M. P., Miramontes, O., Rohani, P. & May, R. M. 1995 Appropriate formulations for dispersal in spatially structured models: reply to Bascompte and Sole. *J. Anim. Ecol.* **64**, 662–664.

- Herzig, A. L. 1995 Effects of population density on long-distance dispersal in the goldenrod beetle *Trirhabda virgata*. *Ecology* **76**, 2044–2054.
- Holt, R. D. & McPeck, M. A. 1996 Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.* **148**, 709–718.
- Janosi, M. J. & Scheuring, I. 1997 On the evolution of density dependent dispersal in a spatially structured population model. *J. Theor. Biol.* **187**, 397–408.
- Johnst, K. & Brandl, R. 1997 Evolution of dispersal: the importance of temporal order of reproduction and dispersal. *Proc. R. Soc. Lond. B* **264**, 23–30.
- Krebs, C. J. 1992 The role of dispersal in cyclic rodent populations. In *Animal dispersal. Small mammals as a model* (ed. N. C. Stenseth & W. Z. Lidicker), pp. 160–175. London: Chapman & Hall.
- Kuussaari, M., Saccheri, I., Camara, M., & Hanski, I. 1998 Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos* **82**, 384–392.
- Lamont, B. B., Klinkhamer, P. G. L. & Witkowski, E. T. F. 1993 Population fragmentation may reduce fertility to zero in *Banksia goodii*: a demonstration of the Allee effect. *Oecologia* **94**, 446–450.
- Lemel, J., Belichon, S., Clobert, J. & Hochberg, M. E. 1997 The evolution of dispersal in a two-patch system: some consequences of differences between migrants and residents. *Evol. Ecol.* **11**, 613–629.
- Lindenmayer, D. B. & Possingham, H. P. 1996 Modelling the inter-relationships between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum, in south-eastern Australia. *Landscape Ecol.* **11**, 79–105.
- Neuhauser, C. 1998 Habitat destruction and competitive coexistence in spatially explicit models with local interactions. *J. Theor. Biol.* **193**, 445–463.
- Nilsson, J. A. 1989 Causes and consequences of natal dispersal in the marsh tit *Parus palustris*. *J. Anim. Ecol.* **58**, 619–636.
- Olivieri, I., Michalakis, Y. & Gouyon, P. 1995 Metapopulation genetics and the evolution of dispersal. *Am. Nat.* **146**, 202–227.
- Rhainds, M., Gries, G. & Chew, P. S. 1997 Adaptive significance of density-dependent ballooning by bagworm larvae, *Metisa plana* (Walker) (Lepidoptera: Psychidae). *Can. Entomol.* **129**, 927–931.
- Rhainds, M., Gries, G. & Saleh, A. 1998 Density and pupation site of apterous female bagworms, *Metisa plana* (Walker) (Lepidoptera: Psychidae), influence the distribution of emergent larvae. *Canadian Entomologist* **130**, 603–613.
- Rohani, P., May, R. M. & Hassell, M. P. 1996 Metapopulations and equilibrium stability: the effects of spatial structure. *J. Theor. Biol.* **181**, 97–109.
- Rosenberg, R., Nilsson, H. C., Hollertz, K., & Hellman, B. 1997 Density-dependent migration in an *Amphiura filiformis* (Amphiuridae, Echinodermata) infaunal population. *Mar. Ecol. Prog. Ser.* **159**, 121–131.
- Ruxton, G. D. 1996 Density-dependent migration and stability in a system of linked populations. *Bull. Math. Biol.* **58**, 643–660.
- Saether, B. E., Engen, S. & Lande, R. 1999 Finite metapopulation models with density-dependent migration and stochastic local dynamics. *Proc. R. Soc. Lond. B* **266**, 113–118.
- Sinclair, A. R. E. 1992 Do large mammals disperse like small mammals? In *Animal dispersal. Small mammals as a model* (ed. N. C. Stenseth & W. Z. Lidicker), pp. 229–242. London: Chapman & Hall.
- Travis, J. M. J. & Dytham, C. 1998 The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. *Proc. R. Soc. Lond. B* **265**, 17–23.
- Travis, J. M. J. & Dytham, C. 1999 Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. Lond. B* **266**, 723–728.
- Veit, R. R. & Lewis, M. A. 1996 Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. *Am. Nat.* **148**, 255–274.
- Watson, A., Moss, R., Rothery, P. & Parr, R. 1984 Demographic causes and predictive models of population fluctuations in red grouse. *J. Anim. Ecol.* **53**, 639–662.
- Wolff, J. 1997 Population regulation in mammals: an evolutionary perspective. *J. Anim. Ecol.* **66**, 1–13.