Article:

Conradt, L, Zollner, P A, Roper, T J et al. (2 more authors) (2003) Foray search: An effective systematic dispersal strategy in fragmented landscapes. The American Naturalist. pp. 905-915. ISSN: 1537-5323

VOL. 161, NO. 6 THE AMERICAN NATURALIST JUNE 2003

Foray Search: An Effective Systematic Dispersal Strategy in Fragmented Landscapes

L. Conradt,[1,3,*] P. A. Zollner,[2] T. J. Roper,[3] K. Frank,[4] and C. D. Thomas[1]

1. Centre for Biodiversity and Conservation, School of Biology, University of Leeds, Leeds LS2 9JT, United Kingdom;
2. Forestry Science Laboratory, Rhinelander, Wisconsin 54501-9128;
3. School of Biological Sciences, University of Sussex, Brighton BN1 9QG, United Kingdom;
4. Department of Ecological Modelling, Centre for Environmental Research (UFZ Leipzig Halle), POB 2, D-04301 Leipzig, Germany

Submitted April 30, 2002; Accepted November 14, 2002; Electronically published June 10, 2003

ABSTRACT: In the absence of evidence to the contrary, population models generally assume that the dispersal trajectories of animals are random, but systematic dispersal could be more efficient at detecting new habitat and may therefore constitute a more realistic assumption. Here, we investigate, by means of simulations, the properties of a potentially widespread systematic dispersal strategy termed "foray search." Foray search was more efficient in detecting suitable habitat than was random dispersal in most landscapes and was less subject to energetic constraints. However, it also resulted in considerably shorter net dispersed distances and higher mortality per net dispersed distance than did random dispersal, and it would therefore be likely to lead to lower dispersal rates toward the margins of population networks. Consequently, the use of foray search by dispersers could crucially affect the extinction-colonization balance of metapopulations and the evolution of dispersal rates. We conclude that population models need to take the dispersal trajectories of individuals into account in order to make reliable predictions.

Keywords: colonization dynamics, dispersal behavior, dispersal patterns, habitat fragmentation, metapopulation ecology.

Dispersal of individuals has crucial implications for populations. In ecological terms, it affects the dynamics and persistence of populations (Levins 1969; Hanski 1998; Dieckmann et al. 1999; Schwartz et al. 2002), the distribution and abundance of species (Reed et al. 2000), and community structure (Bell 2001). In evolutionary terms, it determines gene flow between populations (Aars and Ims 2000) and influences local adaptation (Case and Taper 2000), speciation (Raxworthy et al. 2002), and the evolution of life-history traits (Travis and Dytham 1998; Dieckmann et al. 1999). In short, there is hardly any ecological or evolutionary process that is not affected by dispersal. Little, however, is known empirically about the search strategies that dispersing animals employ to detect new habitat (Koenig et al. 1996; Armsworth et al. 2001), as a consequence of which existing population and evolution models almost always fall back on the "default" assumption of random dispersal (i.e., correlated random walks; e.g., Hanski 1998; Travis and Dytham 1998; Dieckmann et al. 1999; Hanski and Moilanen 2000; Armsworth et al. 2001; Byers 2001). Such models ignore the possibility that, by using nonrandom, systematic dispersal strategies, animals could achieve higher dispersal efficiency and success (Zollner and Lima 1999; Armsworth et al. 2001). This, in turn, could result in population dynamics and gene flow patterns different from those generated by random movements (Zollner and Lima 1999; Conradt et al. 2000). Models based on the assumption of random dispersal also often predict unrealistically high dispersal losses (Lande 1988; Hanski and Zhang 1993).

Hitherto, the main reason for assuming random dispersal movements is that evidence of systematic dispersal is lacking (Zollner and Lima 1999). However, Conradt et al. (2000, 2001) reported that dispersers of two butterfly species search for suitable habitat systematically by flying in a succession of progressively larger ellipsoidal loops ("forays") away from and back to their starting point (fig. 1). The same type of search strategy (which we will term "foray search") has been reported in many other animals, including other insects (Wehner and Srinivasan 1981; Hoffmann 1983; Mueller and Wehner 1994; Durier and Rivault 1999; A. Seymour, personal communication: *Plebejus argus*), mammals (Wiggett et al. 1989; Christian 1993; Sun 1997; E. Revilla, personal communication: *Lynx lynx*; P. A. Zollner, unpublished data: *Peromyscus leucopus*), and birds (Koenig et al. 2000; D. Jordano, personal commu-

---

* Corresponding author; e-mail: l.conradt@sussex.ac.uk.

Am. Nat. 2003. Vol. 161, pp. 905–915.

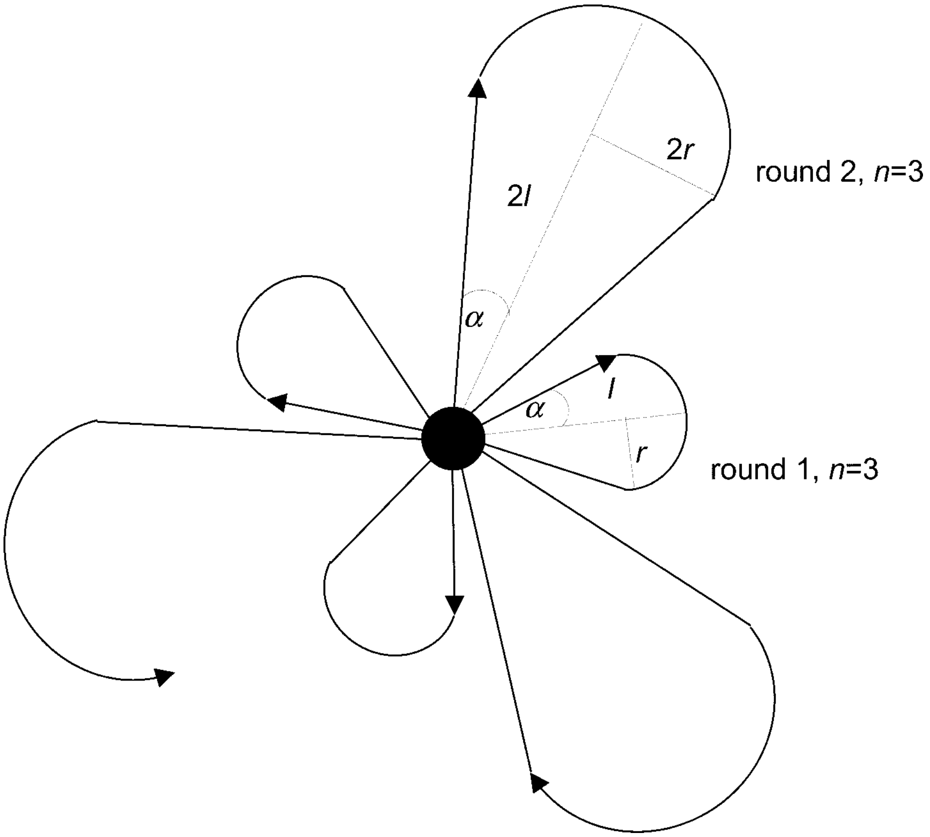

Figure 1: Diagram of foray search pattern. The opening angle α, foray lengths l and $2l$, respectively, and radii r ($r = l/[1+\tan(\alpha)]$) and $2r$, respectively, for a foray of round 1 and a foray of round 2 are shown. In this example, there are $n = 3$ forays per round, after which foray size increases by $+l$ and $+r$. Foray searchers return repeatedly to their starting habitat patch (*filled circle*).

nication: *Columbia livia domesticus*). Although these latter reports either are anecdotal or involve contexts other than dispersal, they imply that foray search is potentially available to dispersers of a wide variety of species. Since dispersal mortalities can be very high (e.g., Lande 1988; Hanski and Zhang 1993; Zollner and Lima 1999), if animals can do better than disperse randomly, they should do so.

Here, we examine the adaptiveness and implications of foray search dispersal by simulating its outcome, by comparison with random dispersal, in fragmented landscapes with different habitat patch densities and even, random, or clumped distribution of habitat patches. For each dispersal strategy, we estimated dispersal efficiency, success, and mortality; energetic constraints; net dispersal distances; and dispersal mortality per net dispersed distance. We were particularly interested in the success of foray search in landscape structures with a clumped distribution of habitat patches (i.e., spatially correlated habitat patches), since these are the types of landscape structures most commonly encountered in nature (Jelinski and Wu 1996).

Methods

Simulated Landscapes

Landscape structures were "infinite" (torus) to avoid boundary effects. They consisted of a matrix of unsuitable habitats (Hanski 1998) in which were distributed 900 circular suitable habitat patches with small, medium, or large radii (11, 15, or 20 units) and three degrees of density (landscape size = 3,000 × 3,000, 6,000 × 6,000, or 12,000 × 12,000 units) in a random (computer-generated Poisson distributions), even (hexagonal pattern), or clumped distribution pattern ("patch configuration"; minimum distance between patches: eight units). Clumping was achieved by distributing patches in a two-dimensional Gaussian distribution around randomly chosen cluster centers (Zollner and Lima 1999) in small, medium, or large clusters (five, 10, or 20 patches) in a closely, medium, or loosely clumped fashion (variance of Gaussian distribution: $\sigma = 40$, 80, or 160 units). In total, 45 different landscape structures were used (table 1). For each landscape structure, 10 different landscapes were generated.

Table 1: Overview of landscape structures that were used in simulations

	Habitat patch density and radius								
	Low			Medium			High		
Patch configuration	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Even	…	X	…	…	X	…	…	X	…
Random	X	X	X	X	X	X	X	X	X
Clumped:[a]									
Closely:									
Small	…	X	…	…	X	…	…	X	…
Medium	…	X	…	…	X	…	…	X	…
Large	…	X	…	…	X	…	X	X	X
Medium:									
Small	…	X	…	…	X	…	…	X	…
Medium	…	X	…	X	X	X	…	X	…
Large	…	X	…	…	X	…	…	X	…
Loosely:									
Small	X	X	X	…	X	…	…	X	…
Medium	…	X	…	…	X	…	…	X	…
Large	…	X	…	…	X	…	…	X	…

Note: An X indicates that a landscape structure was used.

[a] Small, medium, and large refer to cluster sizes in the clumped patch configuration.

Dispersal Strategies

The random dispersal strategy was a correlated random walk with a change in direction after each step (of one unit) by a random angle

$$\beta = 2\arctan\left[\frac{1-\rho}{(1+\rho)\tan(\Psi)}\right],$$

where Ψ was drawn from a uniform distribution of angles between $-90°$ and $+90°$ and ρ was the degree of correlation. Foray search dispersal was closely modeled on empirical observations (Conradt et al. 2000, 2001). The first foray loop had an opening angle α and a length l (fig. 1). A "round" of forays consisted of n equally sized and evenly distributed foray loops. In each new round, the length of foray loops increased by $+l$. For comparisons between dispersal strategies, we first allowed the dispersal strategies to "adapt" to a given landscape structure by determining the parameter values for ρ (random search) and n, α, and l (foray search) that led to the most efficient dispersals. For random dispersal, this best-adapted search was nearly always a linear random search with $\rho = 1.0$. The one exception was the landscape structure with the fewest, largest, most closely clumped clusters of habitat patches, where the most efficient random dispersal was $\rho = 0.9$. For foray search dispersal, all tested parameter values for n (2–6) and α (11°–45°) were very similar in efficiency in all landscape structures. The values for l that led to the highest dispersal efficiencies are given in table 2.

Simulations

To initiate a simulation, a starting habitat patch and angle were drawn at random. An individual dispersed by using either foray search or random search until it came within perceptive range (small, medium, or large: one, five, 10 units) of a new habitat patch (Zollner and Lima 1999), whereupon it moved straight toward the new patch and the simulation was terminated. For each dispersal strategy, we

Table 2: Parameter values for l of optimal foray search dispersals

	Patch density		
Patch configuration	Low	Medium	High
Even	108	216	432
Random	140	140	140
Clumped:[a]			
Closely:			
Small	70	70	70
Medium	70	70	70
Large	40	40	40
Medium:			
Small	70	70	100
Medium	70	70	70
Large	70	70	70
Loosely:			
Small	140	140	140
Medium	140	140	140
Large	100	100	140

[a] Small, medium, and large refer to cluster size.

simulated 1,000 dispersal events per landscape for 10 replicas of each landscape structure (i.e., 10,000 simulations per dispersal strategy/landscape structure combination).

Dispersal Efficiency, Success, and Mortality

The mean number of dispersal steps (of one unit) that an animal needed to travel until it reached a new habitat patch (i.e., the length of its dispersal trajectory, which was not necessarily the shortest distance between the patches) was used as an inverse measure of dispersal efficiency. We calculated dispersal success depending on a fixed mortality rate of 0.0001, 0.001, 0.01, or 0.1, respectively, per step of traveled distance. The rationale was that dispersers faced higher mortality the more time they spent dispersing, that is, the longer they traveled during dispersal. Dispersal mortality per dispersal event was equal to dispersal success. Although we measured dispersal success only to the first habitat patch encountered, we do not assume that individuals necessarily remain at the first patch. Dispersers might move farther than the first patch (Stamps 2001), particularly when habitat patch quality increases with dispersal distance as a result of spatial autocorrelation (e.g., Hanski 1998) or aggregation of dispersers (i.e., increased competition and danger of inbreeding) in nearby patches. Spatial autocorrelation would be reflected in our simulations by a landscape structure with lower habitat patch density, clumpedness, and cluster size (i.e., patches of low quality would be considered as unsuitable and treated as if they did not exists). Dispersers would stop when they encountered the first (good quality) patch. Local aggregation of dispersers could favor dispersers to make further dispersal attempts. The overall dispersal success (ODS) in a series of dispersal attempts from one encountered patch to the next would be

$$\mathrm{ODS} = \frac{\mathrm{stay} \times \mathrm{success}}{1 - \mathrm{success} \times (1 - \mathrm{stay})}, \tag{1}$$

whereby stay is the probability to stay in a found patch and success is the dispersal success in one dispersal attempt. There are many possible scenarios for the influence of disperser aggregation on patch quality and, thus, on stay. However, because aggregation of dispersers could only be a problem if success was high (i.e., success ≈ 1) and stay at least moderately high, the overall dispersal success (ODS) mainly depends on success (since

$$\frac{d\mathrm{ODS}}{d\mathrm{stay}} = \frac{\mathrm{success} \times (1 - \mathrm{success})}{[1 - \mathrm{success} \times (1 - \mathrm{stay})]^2} \rightarrow 0$$

for success → 1 and

$$\frac{d\mathrm{ODS}}{d\mathrm{success}} = \frac{\mathrm{stay}}{[1 - \mathrm{success} \times (1 - \mathrm{stay})]^2} \rightarrow \frac{1}{\mathrm{stay}} \geq 1$$

for success → 1). Thus, the dispersal success in one dispersal attempt to the first encountered patch is a satisfactory measure with which to compare the success of different dispersal strategies.

Energetic Constraints

At the end of each simulation, we determined the maximum amount of resources that a disperser needed to carry with it at any time in order to disperse successfully, under the assumptions that it needed a fixed amount of resources for each dispersal step that it traveled and that it could replenish its resources every time it returned to its starting habitat patch.

Net Dispersed Distance and Mortality per Net Dispersed Distance

The net dispersed distance in each simulation was defined as the distance between the border of the habitat patch from which the disperser started and that of the habitat patch where the search terminated, and it could be quite different from the distance traveled during dispersal. Mean net dispersed distance was calculated for no mortality and for different per-step mortality rates, in which case only successful dispersers were taken into account. Maximum and standard deviation in net dispersed distance were determined assuming no mortality. Mortality per net dispersed distance was defined as

$$1 - \text{dispersal success}^{1/\text{mean net dispersed distance}}$$

(note that this is different from mortality per dispersal event).

Influence of Landscape Features and Per-Step Mortality on Differences between Dispersal Strategies

To investigate the effects of habitat patch density, habitat patch configuration (patch distribution type; cluster sizes and degree of clumpedness where appropriate), per-step mortality rate, perceptive range, and habitat patch size on the differences between the two dispersal strategies with respect to dispersal efficiency, dispersal success, maximum amount of transported fuel, mean net dispersed distance, and mortality per net dispersed distance, we used regression models and defined the relative difference between strategies as

$$\text{difference between strategies} = \frac{\text{value for foray search} - \text{value for random search}}{\text{value for foray search} + \text{value for random search}}.$$

Results

Dispersal Efficiency, Success, and Mortality

In landscape structures with a clumped or even distribution of habitat patches (but not in landscapes with a random patch distribution), foray searchers were notably more efficient in detecting new habitat than were random dispersers (fig. 2). This was particularly so when overall habitat patch density was low and when clusters of patches were few, large, and closely clumped (tables 3–7). Dispersal success was accordingly higher, and thus dispersal mortality per dispersal event lower, for foray searchers than for random dispersers in landscapes with clumped or even distribution of habitat patches, particularly when patch density and mortality rate per step of traveled distance were low (fig. 2; tables 3–7).

Energy Constraints

In all landscape structures, because foray search dispersers could replenish energy reserves each time they returned to their starting habitat, they needed to carry with them smaller quantities of resources (e.g., energy reserves) during dispersal attempts than did random dispersers (fig. 2), particularly when patch density was low and when clusters of patches were few, large, and closely clumped (tables 3–7). The quantity of resources needed for a particular foray would be predeterminable for the animal in question because it would depend on the trajectory length of the foray.

Dispersal Distances and Mortality per Net Dispersed Distance

Foray dispersal led to lower net dispersed distance away from the natal habitat and higher dispersal mortality per net dispersed distance by comparison with random dispersal, especially when habitat patch density was low (fig. 2; tables 3–7). The maximum distance that foray dispersers reached (in 10,000 simulations per landscape structure, in 45 landscape structures) was on average only 3.9% (±0.7% SE) that of random dispersers, and the standard deviation of net dispersed distance/mean net dispersed distance was significantly smaller for foray dispersers (0.486 ± 0.020 SE) than for random dispersers (1.328 ± 0.010 SE; *t*-test: $t = 37.5$, $\mathrm{df} = 89$, $P < .0001$).

Discussion

By comparison with random dispersers, foray search dispersers were more efficient and more successful in detecting new habitat and had an overall lower mortality rate per dispersal event in landscape structures with a clumped or an even distribution of habitat patches. Landscape structures with a clumped distribution of habitat patches are the most common structures in nature for the following reasons: resource distributions tend to be spatially correlated (Jelinski and Wu 1996; Qi and Wu 1996; Hutchings 1997); even if two or more essential resources were distributed randomly but on different spatial scales, the overlap distribution of such resources would be clumped, leading to clumped distributions of suitable habitat (Oline and Grant 2001); and finite landscapes with random distribution of habitat patches are effectively similar to (infinite) landscapes with clumped distribution of habitat patches (see Zollner and Lima 1999). Thus, our results suggest that foray search is a more efficient dispersal strategy than random dispersal in the majority of natural landscapes. While landscape structures with an even distribution of habitat patches are generally less common, they could play an important role in the dispersal of territorial animals that search for vacant territories (e.g., Christian 1993), since territories tend to be evenly spaced (e.g., Doncaster and Woodroffe 1993).

The primary strength of foray search lies in the fact that search effort is initially concentrated in the vicinity of the start point but then gradually expands to further distances. In this respect, foray search resembles certain other highly effective search strategies, such as Archimedean spirals (Zollner and Lima 1999), that have been proposed on theoretical grounds. In addition, foray search has at least two further important advantages, namely, that foray dispersers regularly return to their starting habitat patch and that the shape of the search pattern can be fine-tuned through evolution to a particular landscape. The first property enables foray dispersers to reorient themselves periodically (Mueller and Wehner 1994; Durier and Rivault 1999) and to postpone or abandon futile dispersal attempts (Christian 1993; Conradt et al. 2000). It also enables them to replenish resources (Conradt et al. 2001) so that they need only to carry with them smaller, predeterminable quantities of resources during dispersal. This could be important in many species in which the necessity for carrying provisions is a limiting factor to dispersal (Nunes et al. 1999; Zollner and Lima 1999). Adaptive fine-tuning of foray search explains its greater success in landscapes with an even distribution of habitat patches, since in such landscape structures the position of neighboring patches is relatively predictable. Random dispersers have a much lower scope for adaptive fine-tuning to a particular land-

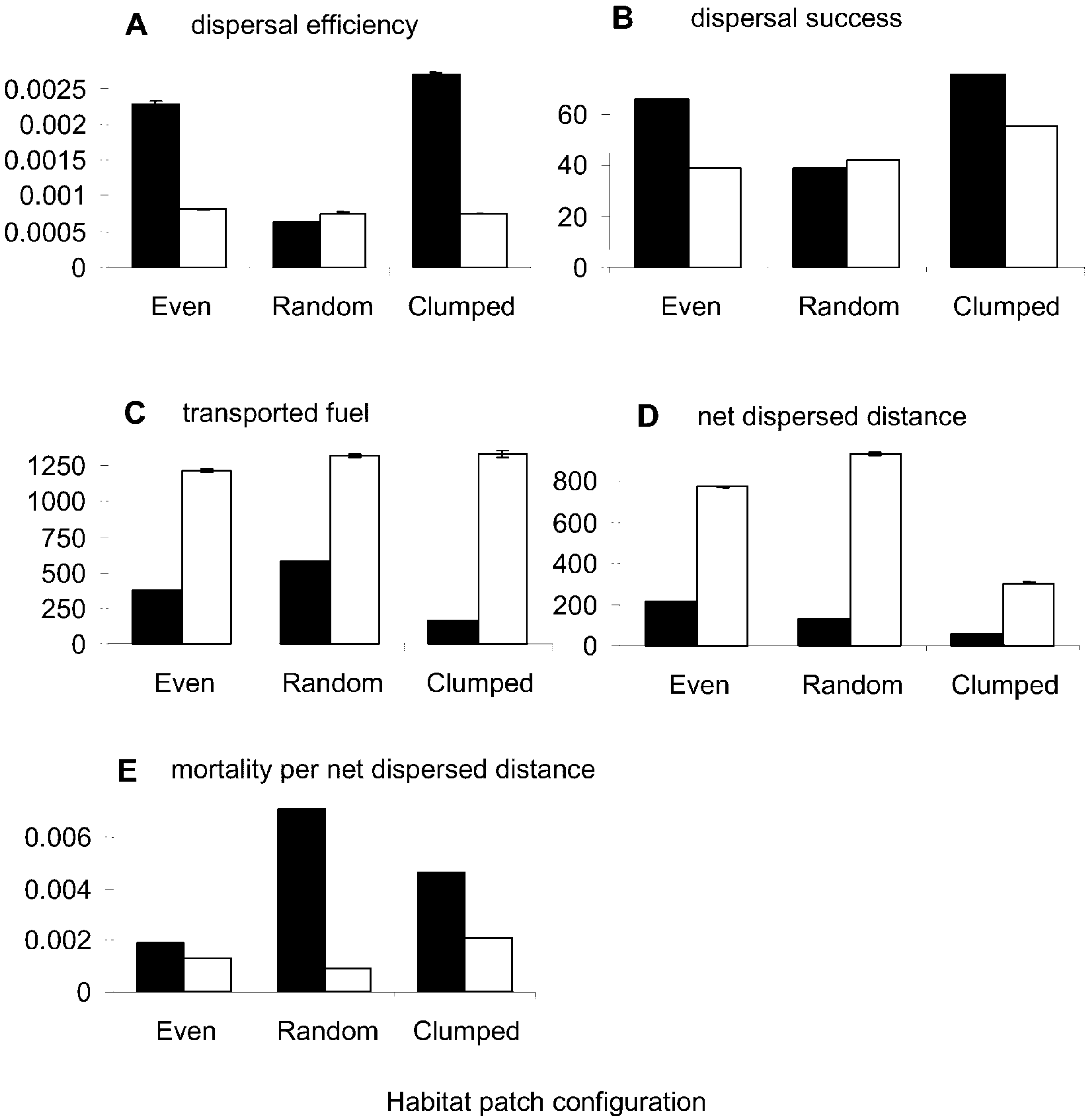

Figure 2: Examples of (*A*) dispersal efficiency (i.e., 1/mean number of traveled steps ± SE), (*B*) dispersal success, (*C*) maximum amount of transported dispersal fuel (±SE), (*D*) mean net dispersed distances (±SE), and (*E*) mortality rate per net dispersed distance for foray searchers (*filled columns*) and random searchers (*open columns*). Results are shown for dispersers with a medium perceptive range in landscape structures with an even, random, or clumped (with medium cluster size and medium degree of clumpedness σ^2) distribution of habitat patches, with medium patch radius at medium habitat patch density and a per-step mortality rate of 0.001 (where applicable).

scape because of the large random element in their search pattern. In conclusion, the fitness advantages of foray search, relative to random dispersal, should make it a preferred strategy for species that have the capacity to implement it.

Foray search dispersal has two important consequences that are especially relevant to models of population dynamics and evolution in fragmented landscapes. These are that it leads to lower net dispersed distance away from the natal habitat and to higher dispersal mortality per net dispersed distance, by comparison with random dispersal. This means that relatively isolated habitat patches with

Table 3: Regression model with respect to difference in dispersal efficiency between strategies

Model	Parameter estimates	*F*	df	*P*	Interpretation
+Patch configuration	Clumped: −.761 Even: −.400 Random: +.083	18.70	2, 42	<.0005	In landscapes with even and clumped distribution of patches, foray search is more effective than random search, but not in landscapes with random distribution of patches
+Patch density in clumped landscapes	+5,383	22.27	1, 41	<.0001	In landscapes with clumped patch distribution, the lower the patch density was, the larger was the difference between strategies
+Degree of clumpedness (σ)	+.0034	62.06	1, 40	<.0001	In landscapes with clumped patch distribution, the closer clumped patches were (i.e., the smaller *s*), the larger was the difference between strategies
+Cluster size	−.0151	26.10	1, 39	<.0001	In landscapes with clumped patch distribution, the larger patch clusters were, the larger was the difference between strategies

Note: Model examines the influence of patch density, patch configuration, patch radius, perceptive range, cluster size, degree of clumpedness, and per-step mortality rate on the relative difference between foray search and random dispersal (negative parameter estimates indicate higher efficiency of foray searchers). Only significant factors (at $\alpha = 0.05$) are shown. The model explained 90.9% of the total variance in difference between strategies.

long distances to other patches (e.g., as is often the case at the margins of metapopulations) are less likely to be reached by foray search dispersers than they would be by random dispersers. Therefore, their recolonization rates would be expected to be reduced by foray search dispersal, which could in turn have a negative effect on the extinction-recolonization balance of a population network (Levin 1969; Hanski 1998). This will be especially so in highly fragmented landscapes with low habitat patch densities that contain many isolated habitat patches. In landscapes of this type, foray search dispersal could have long-term negative effects on the dynamics and survival of a network of populations, even if it is favored by individual selection in the short term.

The fact that foray searchers face higher costs in terms of mortality for reaching distant, isolated habitat patches, even though their average mortality (per dispersal event) is lower, could influence the evolution of dispersal rates if the mortality cost for long-distance foray search dispersers outweighs the reproductive benefit of colonizing isolated, uninhabited habitat patches (Travis and Dytham 1998) or mating into isolated, inbred populations (Ebert et al. 2002). Thus, evolution might favor lower dispersal rates in metapopulations of foray searchers than would be

Table 4: Regression model with respect to difference in dispersal success between strategies

Model	Parameter estimates	*F*	df	*P*	Interpretation
+Patch configuration	Clumped: +.129 Even: +.181 Random: ±0	17.90	2, 171	<.0001	In landscapes with even and clumped distribution of patches, foray search is more successful than random search, but not in landscapes with random distribution of patches
+Per-step mortality in clumped landscapes	−.926	26.61	1, 170	<.0001	In landscapes with clumped patch distribution, the lower per-step mortality was, the larger was the difference between strategies
+Patch density in clumped landscapes	−853	21.12	1, 169	<.0001	In landscapes with clumped patch distribution, the lower patch density was, the larger was the difference between strategies

Note: Model examines the influence of patch density, patch configuration, patch radius, perceptive range, cluster size, degree of clumpedness, and per-step mortality rate on the relative difference between foray search and random dispersal (positive estimates indicate higher success of foray searchers). Only significant factors (at $\alpha = 0.05$) are shown. The model explained 35.9% of the total variance in difference between strategies.

Table 5: Regression model with respect to difference in maximum transported fuel between strategies

Model	Parameter estimates	*F*	df	*P*	Interpretation
+Patch configuration	Clumped: −.764 Even: −.309 Random: −.189	8.24	2, 42	<.001	In all landscape structures, foray searchers needed to transport less fuel than did random searchers
+Patch density	+3,333	52.44	1, 41	<.0001	The lower the patch density was, the larger was the difference between strategies
+Degree of clumpedness (σ)	+.0018	22.29	1, 40	<.0001	In landscapes with clumped patch distribution, the closer clumped patches were, the larger was the difference between strategies
+Cluster size	−.0070	4.66	1, 39	<.05	In landscapes with clumped patch distribution, the larger patch clusters were, the larger was the difference between strategies

Note: Model examines the influence of patch density, patch configuration, patch radius, perceptive range, cluster size, degree of clumpedness, and per-step mortality rate on the relative difference between foray search and random dispersal (negative estimates indicate lower resource-carrying requirements for foray searchers). Only significant factors (at $\alpha = 0.05$) are shown. The model explained 79.6% of the total variance in difference between strategies.

predicted by models based on random dispersal. This could further decrease the recolonization rates of isolated habitat patches. Additionally, dispersal strategies such as foray search raise the prospect of selection working not only on dispersal rate but also on the type of search strategy employed. In particular, when landscape structures are changing through human influence, populations might do best if their members can modify their dispersal strategy according to changes in the environment (Thomas et al. 2001).

Consequently, we suggest that foray search dispersal could be a more realistic assumption for many population models than is random dispersal. One of the most compelling empirical arguments against the assumption of random dispersal is that spatially explicit models that are based on this assumption and that use data from particular populations predict unrealistically high dispersal mortalities (Lande 1988; Hanski and Zhang 1993). These high dispersal mortalities neither are supported by empirical evidence nor could be sustained in theory (i.e., it would never pay individuals to disperse). What we know so far is that random dispersal is a poor predictor of dispersal success in these models because individuals get lost in space in large numbers (Lande 1988; J. Leon-Cortes, J. J. Lennon, and C. D. Thomas, unpublished data), while foray searchers, by the nature of their search strategy, should not get lost. Thus, the assumption of foray search dispersal is at least a promising candidate for improving these models. Whether by using the assumption of foray search dispersal we can predict the observed patterns in the relevant populations remains to be seen. However, several authors have suggested that population models must be based on realistic assumptions about the dispersal behavior and trajectories of individuals if they are to make predictions that are accurate enough to be applicable to real-world cases (Sutherland and Dolman 1994; Armsworth et al. 2001).

In this article, we have concentrated on foray search dispersal as an alternative to random dispersal. Two other systematic search strategies that have been suggested for dispersal are Archimedean spirals (Mueller and Wehner 1994; Zollner and Lima 1999) and dispersal along habitat corridors or landscape features (Vermeulen 1994; Irms 1995; Boudjemadi et al. 1999; Tikka et al. 2001; see also Bell 1991 for a review). While Archimedean spirals could

Table 6: Regression model with respect to difference in mean net dispersed distance between strategies

Model	Parameter estimates	*F*	df	*P*	Interpretation
Constant	Clumped/random/ even: −.612				Foray searchers dispersed less far than random dispersers
+Per-step mortality rate × patch configuration	Clumped/even: +5.491 Random: +3.211	66.12	2, 222	<.0001	The lower the mortality rate per step of total path length was, the larger was the difference between strategies

Note: Model examines the influence of patch density, patch configuration, patch radius, perceptive range, cluster size, degree of clumpedness, and per-step mortality rate on the relative difference between foray search and random dispersal (negative estimates indicate lower net dispersed distances of foray searchers). Only significant factors (at $\alpha = 0.05$) are shown. The model explained 60.9% of the total variance in difference between strategies.

Table 7: Regression model with respect to difference in mortality per net dispersed distance between strategies

Model	Parameter estimates	*F*	df	*P*	Interpretation
+Patch configuration	Clumped/even: +.260 Random: +.582	20.83	1, 178	<.0001	Foray searchers had a higher mortality per net dispersed distance than did random searchers
+Per-step mortality rate	−2.928	38.28	1, 177	<.0001	The lower the mortality rate per step of total path length was, the larger was the difference in mortality per net dispersed distance between dispersal strategies
+Degree of clumpedness (σ)	+.0015	11.75	1, 176	<.001	In landscapes with clumped patch distribution, the less closely clumped patches were (i.e., the larger *s*), the larger was the difference between strategies
+Cluster size	−.0092	5.16	1, 175	<.05	In landscapes with clumped patch distribution, the smaller the clusters were, the larger was the difference between strategies
+Patch density in clumped landscapes	+1,179	4.74	1, 174	<.05	In landscapes with clumped patch distribution, the higher patch density was, the larger was the difference between strategies

Note: Model examines the influence of patch density, patch configuration, patch radius, perceptive range, cluster size, degree of clumpedness, and per-step mortality rate on the relative difference between foray search and random dispersal (positive estimates indicate higher mortality for foray searchers). Only significant factors (at $\alpha = 0.05$) are shown. The model explained 50.9% of the total variance in difference between strategies.

in theory be very efficient at detecting new habitat patches (Zollner and Lima 1999), it is doubtful whether real animals have the navigational skills to implement them (for discussion, see Dusenberg 1992; Mueller and Wehner 1994; Zollner and Lima 1999). Systematic search along habitat corridors or along particular landscape features has been observed and could be very efficient in particular cases (Broekhuizen et al. 1986; Vermeulen 1994; Tikka et al. 2001). However, such a search strategy could only lead to high habitat patch detection in adequate landscape configurations (e.g., Boudjemadi et al. 1999), making it of less general relevance than the other systematic search strategies. Moreover, individuals might disperse along landscape features in order to be able to retrace their steps (Serra-Cobo et al. 2000) rather than because such a search strategy leads to higher patch detection efficiency per se. In this case, movement along landscape features could even be part of dispersal forays if unsuccessful individuals turned back. Since empirical information on systematic search strategies is still very scarce, it is possible that further systematic search strategies will be suggested in the future.

Acknowledgments

We thank C. Wissel for comments and advice on the work, which was supported by a Royal Society Fellowship to L.C. and a Training and Mobility of Researchers network grant from the European Union to C.D.T.

Literature Cited

Aars, J., and R. A. Ims. 2000. Population dynamic and genetic consequences of spatial density-dependent dispersal in patchy populations. American Naturalist 155: 252–265.

Armsworth, P. R., M. K. James, and L. Bode. 2001. When to press on or turn back: dispersal strategies for reef fish larvae. American Naturalist 157:434–450.

Bell, G. 2001. Ecology: neutral macroecology. Science (Washington, D.C.) 293:2413–2418.

Bell, W. J. 1991. Searching behaviour. Chapman & Hall, London.

Boudjemadi, K., J. Lecomte, and J. Clobert. 1999. Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. Journal of Animal Ecology 68:1207–1224.

Broekhuizen, S., C. A. Hoff, F. van 't Maaskamp, and T. Pauwels. 1986. The importance of hedgerows for leading migrating badgers *Meles meles* (L., 1758). Lutra 29: 54–65.

Byers, J. A. 2001. Correlated random walk equations of animal dispersal resolved by simulation. Ecology 82: 1680–1690.

Case, T. J., and M. L. Taper. 2000. Interspecies competition, environmental gradients, gene flow, and the coevolution of species' borders. American Naturalist 155:583–605.

Christian, S. F. 1993. Behavioural ecology of the Eurasian badger (*Meles meles*): space use, territoriality and social behaviour. Ph.D. thesis. University of Sussex.

Conradt, L., E. J. Bodsworth, T. J. Roper, and C. D. Thomas. 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. Proceedings of the Royal Society of London B, Biological Sciences 267:1505–1510.

Conradt, L., T. J. Roper, and C. D. Thomas. 2001. Dispersal behaviour of individuals in metapopulations of two British butterflies. Oikos 95:416–424.

Dieckmann, U., B. O'Hara, and W. Weisser. 1999. The evolutionary ecology of dispersal. Trends in Ecology & Evolution 14:88–90.

Doncaster, C. P., and R. Woodroffe. 1993. Den site can determine shape and size of badger territories: implications for group-living. Oikos 66:88–93.

Durier, V., and C. Rivault. 1999. Path integration in cockroach larvae, *Blattella germinica* (L.) (insect: Dictyoptera): direction and distance estimation. Animal Learning and Behaviour 27:108–118.

Dusenberg, D. B. 1992. Sensory ecology. W. H. Freeman, New York.

Ebert, D., C. Haag, M. Kirkpatrick, M. Riek, J. W. Hottinger, and V. I. Pajunen. 2002. A selective advantage to immigrant genes in a *Daphnia* metapopulation. Science (Washington, D.C.) 295:485–488.

Hanski, I. 1998. Metapopulation dynamics. Nature 396: 41–49.

Hanski, I., and D. Y. Zhang. 1993. Migration, metapopulation dynamics and fugitive coexistence. Journal of Theoretical Biology 163:491–504.

Hanski, I., J. Alho, and A. Moilanen. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. Ecology 81:239–251.

Hoffmann, G. 1983. The search behaviour of the desert isopod *Hemilepistus reaumuri* as compared with a systematic search. Behavioural Ecology and Sociobiology 13:93–106.

Hutchings, M. J. 1997. The structure of plant populations. Pages 344–345 *in* M. J. Crawley, ed. Plant ecology. Blackwell Scientific, Oxford.

Irms, R. A. 1995. Movements patterns related to spatial structures. Pages 85–109 *in* L. Hansson, L. Fahrig, and G. Merriam, eds. Mosaic landscapes and ecological processes. Chapman & Hall, London.

Jelinski, D. E., and J. G. Wu. 1996. The modifiable areal unit problem and implications for landscape ecology. Landscape Ecology 11:129–140.

Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology & Evolution 11:514–517.

Koenig, W. D., P. N. Hooge, M. T. Stanback, and J. Haydock. 2000. Natal dispersal in the cooperatively breeding acorn woodpecker. Condor 102:492–502.

Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). Oecologia (Berlin) 75:601–607.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Mueller, M., and R. Wehner. 1994. The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. Journal of Comparative Physiology A 175: 525–530.

Nunes, S., C. D. T. Ha, P. J. Garrett, E. M. Mueke, L. Smale, and K. E. Holekamp. 1998. Body fat and time of year interact to mediate dispersal behaviour in ground squirrels. Animal Behaviour 55:605–614.

Oline, D. K., and M. C. Grant. 2001. Scaling patterns of biomass and soil properties: an empirical analysis. Landscape Ecology 17:13–26.

Qi, Y., and J. G. Wu. 1996. Effects of changing spatial resolution on the results of landscape pattern analysis using spatial autocorrelation indices. Landscape Ecology 11:39–49.

Raxworthy, C. J., M. R. J. Forstner, and R. A. Nussbaum. 2002. Chameleon radiation by oceanic dispersal. Nature 415:784–787.

Reed, D. C., P. T. Raimondi, M. H. Carr, and L. Goldwasser. 2000. The role of dispersal and disturbance in determining spatial heterogeneity in sedentary organisms. Ecology 81:2011–2026.

Schwartz, M. K., L. S. Mills, K. S. McKelvey, L. F. Ruggiero, and F. W. Allendorf. 2002. DNA reveals high dispersal synchronizing the population dynamics of Canada lynx. Nature 415:520–522.

Serra-Cobo, J., M. Lopez-Roig, T. Marques-Bonet, and E. Lahuerta. 2000. Rivers as possible landmarks in the orientation flight of *Miniopterus schreibersii*. Acta Theriologica 45:347–352.

Stamps, J. A. 2001. Habitat selection by dispersers: integration of proximate and ultimate approaches. Pages 230–242 *in* J. Clobert, A. A. Dondt, and J. D. Nichols, eds. Dispersal. Oxford University Press, Oxford.

Sun, C. 1997. Dispersal of young in red squirrels (*Tamiasciurus hudsonicus*). American Midland Naturalist 138: 252–259.

Sutherland, W. J., and P. M. Dolman. 1994. Combining behaviour and population dynamics with applications for predicting consequences of habitat loss. Proceedings of the Royal Society of London B, Biological Sciences 255:133–138.

Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. Davies, M. Musche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. Nature 441:577–581.

Tikka, P. M., H. Hogmander, and P. S. Koski. 2001. Road and railway verges serve as dispersal corridors for grassland plants. Landscape Ecology 16:659–666.

Travis, J. M. J., and C. Dytham. 1998. The evolution of dispersal in a metapopulation, a spatially explicit, individual-based model. Proceedings of the Royal Society of London B, Biological Sciences 265:17–23.

Vermeulen, H. J. W. 1994. Corridor function of a road verge for dispersal of stenotopic heathland ground beetles *Carabidae*. Biological Conservation 69:339–349.

Wehner, R., and M. V. Srinivasan. 1981. Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). Journal of Comparative Physiology A 142: 315–338.

Wiggett, D. R., D. A. Boag, and A. D. R. Wiggett. 1989. Movements of intercolony natal dispersers in the Columbian ground squirrel. Canadian Journal of Zoology 67:1447–1452.

Zollner, P. A., and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. Ecology 80: 1019–1030.

Associate Editor: Rolf A. Ims