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Behavioral tradeoffs when dispersing across a patchy landscape

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A better understanding of the behavior of dispersing animals will assist in determining the factors that limit their success and ultimately help improve the way dispersal is incorporated into population models. To that end, we used a simulation model to investigate three questions about behavioral tradeoffs that dispersing animals might face: (i) speed of movement against risk of predation, (ii) speed of movement against foraging, and (iii) perceptual range against risk of predation. The first investigation demonstrated that dispersing animals can generally benefit by slowing from maximal speed to perform anti-predatory behavior. The optimal speed was most strongly influenced by the disperser's energetic reserves, the risk of predation it faced, the interaction between these two parameters, and the effectiveness of its anti-predatory behavior. Patch arrangement and the search strategy employed by the dispersers had marginal effects on this tradeoff relative to the above parameters. The second investigation demonstrated that slowing movement to forage during dispersal may increase success and that optimum speed of dispersal was primarily a function of the dispersing animal's energetic reserves, predation risk, and their interaction. The richness (density of food resources) of the interpatch matrix and the patch arrangement had relatively minor impacts on how much time a dispersing animal should spend foraging. The final investigation demonstrated animals may face tradeoffs between dispersing under conditions that involve a low risk of predation but limit their ability to perceive distant habitat (necessitating more time spent searching for habitat) and conditions that are inherently more risky but allow animals to perceive distant habitat more readily. The precise nature of this tradeoff was sensitive to the form of the relationship between predation risk and perceptual range. Our overall results suggest that simple depictions of these behavioral tradeoffs might suffice in spatially explicit population models.

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Dispersal between patches within a fragmented landscape may be an important determinant of population viability (Taylor et al. 1993, Alder and Nuernberger 1994, Koenig et al. 1996), as illustrated by many spatially explicit population models that simulate the movements and fates of dispersing animals in virtual landscapes (SEPMs; Dunning et al. 1995, Letcher et al. 1998). These SEPMs recognize that population dynamics can be linked to spatial environments through animal movements (Marsh and Jones 1988, Turchin 1996, Zollner and Lima 1999a). Indeed, SEPMs are valued in conservation planning efforts because of their utility in contrasting future management scenarios (Liu et al. 1995, Turner et al. 1995, Lindenmayer and Possingham 1996). However, the validity of SEPMs in these applications will be limited (Bart 1995, Ruckelshaus et al. 1997) until we better understand the behavior of dispersing animals (Lima and Zollner 1996, South 1999, Russell et al. 2003). For example, if a SEPM fails to account for the fact animals can increase dispersal success by changing their search strategy (Zollner and Lima 1999a, Conradt et al. 2003) or dispersal speed (below),

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then the model may make erroneous predictions about the implications of management strategies.

Unfortunately, much of the empirical data on dispersal that is needed to parameterize SEPMs are not available (Conroy et al. 1995, Ims 1995, Belisle and Desrochers 2002). In fact, we know little about how animals make dispersal-related decisions at the landscape-scale, nor do we have a good sense of what the relative effectiveness of different options might be for animals facing such decisions (Railsback et al. 1999, Armsworth et al. 2001). Some studies have assessed homing behavior following translocation (Pither and Taylor 1998, Belisle and St. Clair 2001, Bakker and Van Vuren, 2004) or the movements of animals in response to taped vocalizations (Desrochers and Hannon 1997, Sieving et al. 2000, Harris and Reed 2002) to improve our understanding of how animals respond to landscapes. Other studies have measured the movement responses of organisms to micro-landscapes in ecological model systems to assess how spatial patterns of habitat affect animal movement (Wiens et al. 1997, McIntyre and Wiens 1999a, b). These approaches provide insights about behavioral responses to specific landscape features or arrangements at relatively short time intervals, but, landscape-level dispersal events are likely to take place over much longer periods of time and involve interactions with numerous landscape features.

Understanding landscape scale dispersal will undoubtedly improve the way dispersal success is represented in SEPMs (Belisle and St. Clair 2001, Belisle et al. 2001). Simulation models can be valuable tools to explore the dispersal-related consequences of behavioral rules across longer time frames and large-scale landscape arrangements (Gustafson and Gardner 1996, Tischendorf et al. 1998, Gardner and Gustafson 2004). Here, we use simulation modeling to explore how long distance, dispersal-related behavioral decisions are influenced by parameters such as the risk of predation, energetic reserves, search strategy used, and landscape configuration. Conceptually, we are modeling a searcher that leaves its natal patch and moves through inhospitable matrix in search for a new patch of suitable habitat. Our approach is motivated by work on small forest-dwelling mammals moving across agricultural fields in search of forest fragments (Zollner and Lima 1997), but the results should be applicable to many ecological systems.

The general model

We used a computer simulation (Zollner and Lima 1999a) in which an animal leaves a habitat patch to search for a new patch while moving across inhospitable matrix (Ricketts 2001). The searcher is successful if it reaches a new patch without depleting its reserves, leaving the landscape, or dying (Tischendorf and Fahrig 2000). We do not consider the more complex aspects of habitat selection, such as conspecific densities, that may lead to several successive movements between patches (Stamps 2001). However, the behavioral rules animals use to make such multiple movements should be well characterized by simulations of single moves between patches (Ries and Debinski 2001, Conradt et al. 2003).

Simulated animals traveled through an idealized landscape containing 100 suitable patches embedded in inhospitable matrix. Animals travel a distance of one "step" per time interval unless they slow their movement (travel some fraction of a step per time interval) for other reasons (below). All patches were the same size (10 steps in radius), and were placed within an 1100 by 1100 step area in the center of a 1510 by 1510 step landscape. Three distributions of 100 habitat patches were used in the simulations: uniform, random, and clumped. These distributions were used in our previous application of this simulation (Zollner and Lima 1999a) with average nearest patch distances (edge to edge) of 100.00, 50.37, and 27.19 steps for uniform, random, and clumped landscapes, respectively.

We expressed predation risk as the per time interval probability of death; animals slowing to engage in vigilance or foraging traveled only a fraction of a step per time interval. Our simulations were run with three different per time interval predation risks (0.0001, 0.001, 0.01), which were chosen to cover a range from relatively safe to great risk. Energetic reserve levels in our model represent the maximum number of time intervals available for search before starvation. Three energetic reserve levels were chosen to encompass the range from reserve-constrained search to no effective risk of starvation: low (500 time intervals), intermediate (3000 time intervals), and high (50 000 time intervals). Unless stated otherwise, all simulations were conducted at a baseline perceptual range of 5 steps (distance at which patches could be perceived). The movement of dispersers was modeled with a correlated random walk in which the parameter ρ described the relative straightness of the search path; $\rho = 0$ indicates a purely random walk and $\rho = 1$ indicates perfectly straight search (Zollner and Lima 1999a).

To estimate the probability of successful dispersal, we simulated 10 000 attempts at dispersal for each combination of parameters investigated. For each individual simulation run, a new landscape configuration, and a new starting patch were generated randomly according to the conditions being simulated. An animal's first move was directly away from the center of the patch (starting at the patch's edge), and its subsequent movements through continuous space were determined by the search strategy being modeled (Zollner and Lima 1999a). Each searcher moved until it either reached a new patch or left the landscape, and its trail across the landscape was recorded. Trails that left the landscape or

exceeded energetic reserve capacity represented failed dispersal. The probability of successful dispersal (D) for each of the remaining (viable) search trails was calculated as $D=(1-P)^T$, where P is the per time interval predation risk and T is the number of time intervals covered by the trail. The probability of successful dispersal for each combination of parameters was estimated as the average value of D across all 10 000 replicates (including zeros for nonviable trails).

The large number of simulated dispersal attempts presented a philosophical problem with using inferential statistical analyses (Judson 1994); nearly any noticeable difference between probabilities is likely to be statistically significant. Thus, we elected to focus our statistical interpretation not on P values but on the relative strength of the various parameters and their interactions as determinants of behaviors that maximized dispersal success. We assessed the relative contribution of each parameter and interaction by examining the magnitude of the F values for these effects in the ANOVAs.

The remainder of this paper is divided into 3 separate sections that cover different behavioral tradeoffs. In all cases the simulated animals faced risks of starvation and predation during dispersal. In the first section we examine the tradeoff between speed of movement and the risk of predation while dispersing. In the second section we examine the tradeoff between speed of movement and slowing to forage (increasing energetic reserves). The tradeoff between perceptual range and risk of predation while dispersing is the subject of the final section.

Anti-predatory behavior and speed of movement during dispersal

Rationale

Empirical studies indicate that dispersal increases the risk of predation faced by an animal (Larsen and Boutin 1994, Van Vuren and Armitage 1994, Waser et al. 1994, Sakai and Noon 1997). Nonetheless, most animals have an array of behavioral options to help ameliorate such risks of predation (Lima 1998). In particular, dispersing animals may reduce their risk of predation by slowing down to be vigilant for predators (McAdam and Kramer 1998, Sharpe and Van Horne 1998). Many animals have been observed stopping frequently while moving (Anderson et al. 1997, Wiens et al. 1997), and some have hypothesized that this stop-and-go movement pattern serves to reduce risks of predation via enhanced vigilance (McAdam and Kramer 1998, Kramer and McLaughlin 2001, Vasquez et al. 2002). Animals also may change their movement patterns to use available cover (Wigget and Boag 1989, Stapp and Van Horne 1997), to reduce the ability of predators to detect them (Brillhart and Kaufman 1991, Roche et al. 1999), to increase their ability to detect predators (Sharpe and Van Horne 1998), or to increase their ability to escape (Schooley et al. 1996). All of these anti-predatory behaviors, including vigilance, are likely to increase the amount of time that it takes to travel a given distance. We thus examine how the optimal amount of time that a dispersing animal devotes to anti-predatory vigilance during dispersal is influenced by baseline risk of predation (in absence of such anti-predatory behavior), energetic reserves, efficiency of anti-predatory behavior, efficiency of the search strategy for finding new patches, and the configuration of patches in the landscape.

Methods

In order to examine the tradeoff between vigilance and speed of movement, the general model was modified as follows. A dispersing animal did not necessarily move a distance of one step for each time interval. Instead, simulations were run in which animals moved 0.01, 0.2, 0.4, 0.6, 0.8 or 1.0 step per time interval (greater precision was used to produce figures). Step lengths under one unit represented the allocation of time to anti-predatory behavior during movement, under the assumption that movement and anti-predatory behavior are mutually exclusive (McAdam and Kramer 1998). We assume here that dispersing animals do not feed while crossing the matrix. Dispersal success was calculated as described in the general model section.

If dispersing animals are moving slower to be vigilant for predators, then there should be a corresponding decrease in the risk of predation per move. Thus the per time interval risk of predation was calculated as $r=PS^b$, where S is the proportion of a time interval allocated to movement (time not spent vigilant), P is the baseline risk of predation while moving (in absence of anti-predatory behavior; i.e. $S=1$), and b is a constant. This constant b determines the extent to which predation risk is reduced by vigilance (reduction in movement rate). When $b>1$ there are diminishing returns in the reduction of predation risk with continued slowing for vigilance. This means that a small degree of slowing from maximum speed can yield a relatively large reduction in the risk of predation. Increasing values of b indicate increasingly effective vigilance. Conversely, when $b=1.0$, an animal will reduce its per time interval risk of predation in proportion to the degree of slowing, thus slowing for vigilance will not change the net risk of predation the animal experiences. When $b<1.0$ it will always be optimal for animals to disperse as quickly as possible without any time spent being vigilant for predators. Values of $0.0<b<1.0$ do result in increasing rates of return in terms of vigilance gains for slowing but these

returns are not great enough to make it profitable for animals to slow dispersal.

We used a fully factorial design to examine the influence of the following parameters on the optimal time allocated to vigilance while moving through the matrix: baseline risk of predation, energetic reserves when dispersal was initiated, a range of six correlated random walks, three patch configurations, and four measures of the effectiveness of vigilance (Table 1). All possible combinations of these parameters were run (10 000 replicates) for animals that spent $S = 0.01$, 0.2, 0.4, 0.6, 0.8, or 1.0 of each time interval moving and dedicating the remaining time to vigilance. For each combination of parameters we assessed which of these levels of S maximized dispersal success for each combination of parameters (S*). S* values were then used as response variables in a fully factorial ANOVA to quantify the relative influence on S* of each parameter and all 25 of the interactions of these parameters. The emphasis of this analysis was not to examine statistical significance as defined by P values. Rather, conclusions about the relative sensitivity of S* to the parameters and their interactions were determined by considering the relative magnitude of the F values.

Results and discussion

Two of the parameters we investigated and one interaction term explained most of the variation in S* (Table 2). Initial energetic reserves had the greatest influence on S*. Over the range of energetic reserves simulated, animals with limited energetic reserves (500 time intervals) could not afford to slow dispersal for anti-predatory vigilance, whereas animals with large (50 000) and intermediate (3000) energetic reserves could afford considerable vigilance without risking starvation (Fig. 1a). For animals with the greatest reserves (50 000 time intervals) dispersal success was greatest when it slowed dispersal by 90% to be vigilant ($S^* = 0.1$) whereas an animal with limited reserves (500 time intervals) maximizes success by going as fast as possible without vigilance ($S^* = 1.0$; Fig. 1a). The baseline risk of predation explained the second largest portion of the variation in S* (Table 2). Animals that faced greater risks when moving through the matrix gained the most by slowing to be vigilant, and animals facing minimal risks had little to gain by doing so (Fig. 1b). The only interaction that explained more than 2.5% of the variation in S* was that between the two most important parameters: baseline predation risk and energetic reserves. The interaction reflects the fact that animals with moderate to high energetic reserves facing a high risk of predation increased their dispersal success by slowing to be vigilant; this option was not feasible for animals with low energetic reserves, or not valuable for animals facing low predation risks.

Table 1. Variables and values used in the examination of optimum speed of movement when trading speed of movement against vigilance for simulated dispersers.

Effectiveness of anti-predatory behavior (b)	1.1, 2, 3, 9
Baseline predation risk per time interval (P)	0.0001, 0.001, 0.01
Energetic reserves	50 000, 3000, 500 time intervals
Patch arrangement	uniform, random, clumped
Search strategy	degree of correlation in random walk $\rho = 0.8$, 0.85, 0.9, 0.95, 0.99, 1.0

Table 2. F values and partial R^2 values from a fully factorial ANOVA testing for parameters influencing the optimal speed of movement for virtual dispersers slowing movement to decrease risk of predation. Values are shown for all main parameters and interactions where partial $R^2 > 0.025$.

Source	DF	F value	Partial R^2
Energetic reserves	2	509436	0.5446
Risk of predation	2	225087	0.2406
Energetic reserves × risk of predation	4	21447	0.0459
Effectiveness of vigilance	3	10010	0.0161
Search strategy	5	2460	0.0066
Patch arrangement	2	813	0.0009

The effectiveness of vigilance (b), the efficiency of the search strategy used (ρ), and the pattern of the patches in the landscape had relatively minor influences ($R^2 < 0.025$) on S* (Table 2). The relatively small influence of b was surprising and suggests that as long as $b > 1$, variation in b will have only a minor influence on S* (Fig. 1c). The relatively small influence of efficiency of search suggests that the search strategies we examined were efficient enough such that the variation among them did not strongly influence S* ($\rho \cong 0.95$ is optimal for these simulations). Note, however, that the efficiency of search will dramatically influence the overall probability of dispersal success (Railsback et al. 1999, Conradt et al. 2003) even if it has a minimal effect on S*; the same holds for the effectiveness of vigilance. Indeed, values of ρ below the range we investigated result in search paths that are highly redundant and less efficient and ultimately a $\rho = 0$ results in truly random search (Zollner and Lima 1999a). Similarly, the differences in patch arrangement that we investigated may not have been great enough to influence S*, but will influence dispersal success. Other researchers have documented both strong (Wennergren et al. 1995, Goodwin and Fahrig 2002a) and weak (Gustafson and Gardner 1996, Morales and Ellner 2002) behavioral effects of differences in patch arrangement in simulated landscapes.

The major implication of these results is that a few relatively simple parameters may determine most aspects of optimal movement behavior. Our results suggest that

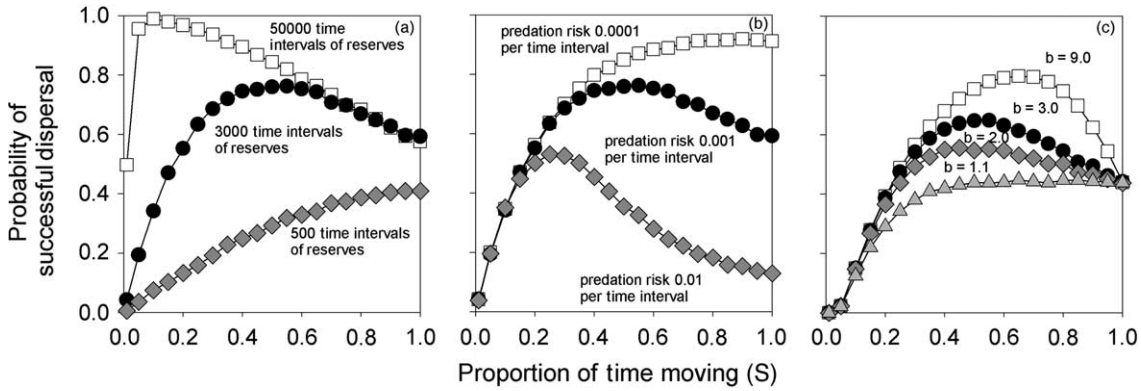

Fig. 1. Illustrative cases of the probability of successful dispersal as a function of speed of movement when animals can slow to be vigilant for predators. (a) Effect of energetic reserves for a disperser facing a baseline per time interval predation risk of 0.001, and effectiveness of vigilance at b = 3.0. (b) Effect of baseline risk of predation for a disperser modeled with moderate energetic reserves (3000 time intervals), and effectiveness of vigilance b = 3.0. (c) Effect of effectiveness of vigilance (b) for a disperser with high energetic reserves (50 000 time intervals) facing a high risk of predation per time interval (0.01). For all cases the patches were randomly distributed across the landscape and dispersers used a correlated random walk with $\rho = 0.95$.

empirical experiments should initially focus on quantifying basic aspects of the constraints that animals face, such as the energetic reserves they have when dispersal is initiated, the risk of mortality they face while dispersing, and the interactions of these parameters. Specifically, it may be insightful to replicate experimental landscape (Goodwin and Fahrig 2002b) and translocation (Bakker and Van Vuren 2004) experiments that assess movement patterns while manipulating energetic reserves (McIntyre and Wiens 1999a) or the perceived predation risk that the focal animals experience. Finally, it is clear that the risk of predation is an important and often unappreciated parameter in SEPMs (Ruckelshaus et al. 1997, Letcher et al. 1998). Those landscape-level models that do not consider the predation risk that animal's face during dispersal may make erroneous predictions, especially with respect to estimating the probability of successful dispersal.

Time spent feeding while dispersing

Rationale

Energetic reserves can strongly influence the decisions animals make about when to disperse (Danielson and Klaas 1995, Nunes and Holekamp 1996, Nunes et al. 1998). Clearly, energetic reserves may be crucial to an animal's dispersal success, especially when the habitat through which the animal is dispersing contains little or no food (Gardner and Gustafson 2004). However, if the matrix is suitable for foraging, a dispersing animal may be able to lower its risk of starvation by slowing to feed during dispersal. Presently, landscape-level population models have failed to consider this possibility (Armsworth et al. 2001).

Feeding during dispersal will be worthwhile only when the animal can increase its energetic reserves by doing so. The viability of foraging during dispersal will to a large extent be a function of the energetic richness of the matrix habitat and the animal's ability to acquire that energy. However, even in a relatively rich matrix, stopping to forage will increase dispersal times (Russell et al. 2003). Thus, slowing down to forage may not increase an animal's probability of successful dispersal unless it has limited energetic reserves and faces a low risk of predation.

In this section, we examine how the optimal amount of time devoted to feeding in the matrix is influenced by the richness of the matrix, initial energetic reserves, the baseline risk of predation, patch arrangement within the landscape, and the search strategy used.

Methods

To examine the tradeoff between movement and foraging, the general model was modified as follows. Animals moved distances ranging from 0.01–1.0 step per time interval. Step lengths < 1 unit represent the allocation of time to foraging during dispersal. We assume further that time spent foraging detracts from the directed movements expected in dispersing animals. Animals dispersing in these simulations faced a constant risk of predation per time interval irrespective of how they allocated time to foraging or moving.

If a dispersing animal slows to forage during dispersal, then it should experience an increase in energetic reserves. The change in an animal's energetic reserves for each time interval was calculated as $C = M * (1 - S) - 1$ where M is the richness of the matrix (below) through which the animal is moving, and S is the proportion of time allocated to movement during

dispersal. In a matrix with a richness of $M = 1.0$, a dispersing animal can only break even energetically if it spends all of its time foraging ($S = 0$). For $M > 1$, an animal can at least maintain its reserves if it slows to or below the break-even point ($S = (M - 1)/M$). This break-even point is reached at progressively greater values of S as M increases. Thus, an animal moving through a richer matrix can allocate less time to foraging while still maintaining its energy reserve.

We examined optimal feeding efforts as influenced by the parameters in Table 3. All combinations of the levels of these parameters were simulated (10 000 independent replicates) for dispersers that spent 0.01, 0.2, 0.4, 0.6, 0.8, or 1.0 of each time interval moving, while dedicating the remaining time to feeding. We then determined which of these S values maximized dispersal success (S*) for each combination of parameters and used those values in a fully factorial ANOVA. Conclusions about the relative importance of these parameters and their interactions were based upon F values.

Results and discussion

Two parameters and two interaction terms explained most of the variation in optimal time spent foraging (S*) while dispersing (Table 4). S* was most sensitive to energetic reserves. Dispersing animals with minimal energetic reserves gained much by stopping to forage whereas those with high energetic reserves have no reason to do so (Fig. 2a). The next most important parameter was the baseline risk of predation. In general, animals slowed to forage to a greater extent as baseline risk of predation declined (Fig. 2b). The third most important determinant of optimal time spent foraging was the interaction of these two parameters. This interaction reflects the fact that stopping to feed increased dispersal success only for dispersers with relatively low energetic reserves that faced relatively low risks of predation. Dispersers with either great energetic reserves or facing high risks of predation gained relatively little by slowing to forage. This general result is consistent with observations that goldenrod beetles in experimental landscapes move more slowly across habitat with anti-predatory cover if it contains food than when it is devoid of food (Goodwin and Fahrig 2002b), and by the observation that food-deprived darkling beetles cross experimental landscapes more slowly because they stop to feed (McIntyre and Wiens 1999a).

Table 3. Variables and values used in the examination of optimum speed of movement when trading speed of movement against foraging for simulated dispersers.

Richness of matrix (M)	6, 3, 2, 1.5, 1.25
Risk of predation per time interval (P)	0.0001, 0.001, 0.01
Energetic reserves	50 000, 3000, 500
Patch arrangement	uniform, random, clumped
Search strategy	degree of correlation in random walk $\rho = 0.8, 0.85, 0.9, 0.95, 0.99, 1.0$

The final term that explained a substantial fraction of the variation in dispersal success was the interaction of energetic reserves with predation risk and matrix richness. The importance of this interaction reflects the fact that the interplay of energetic reserves and predation risk also is influenced by matrix richness. Animals dispersing across a rich matrix can satisfy their energetic demands with less time dedicated to foraging than can animals dispersing across a poor matrix; that is, S* increases with an increase in matrix richness (Fig. 2c). This somewhat counterintuitive result reflects the fact that an animal should not forage beyond that needed to maintain a minimal energy balance; building an energetic surplus in the matrix would be done at a cost of increasing the time spent exposed to predation with no corresponding lowering of the risk of starvation. Note further that an animal should not adopt S lower than the break-even speed [$S = (M - 1)/M$], because gaining energetic reserves adds little to dispersal success given our assumptions. In fact, it may be preferable to slowly lower energy reserves in order to speed up dispersal as long as sufficient reserves are maintained to allow the animal to successfully establish at the new patch (Stamps 2001). Anecdotal support for an effect of matrix richness can be found in observations that Florida scrub lizards (*Sceloporus woodi*) move more slowly through poorer quality matrix (Hokit et al. 1999).

The optimal tradeoff between speed of movement and foraging during dispersal was relatively insensitive to the search strategy employed, and to the patch arrangement within the landscape (Table 4). This result suggests that as long as the matrix is rich enough ($M > 1$) to allow profitable foraging, S* is largely determined by energetic reserves and predation risk. However, as mentioned earlier, factors that have a minor influence on S* may still have major impacts on dispersal success, warranting further investigation.

When to disperse: trading off perceptual range against the risk of predation

Rationale

The distance at which a dispersing animal can perceive remote habitat (its perceptual range) should be an important determinant of its dispersal success (McIntyre and Vaughn 1997, Andreassen et al. 1998, Conradt et al. 2000). An animal's perceptual range might be limited by its relevant senses such as vision (Yeomans 1995) or olfaction (Schooley and Wiens 2003) and it also may be a function of its body size (Mech and Zollner 2002) and

Table 4. F value and partial R^2 from a fully factorial ANOVA testing for factors influencing the optimal speed of movement for virtual dispersers slowing movement to forage in matrix. Values are shown for all main parameters and interactions where $R^2 > 0.025$.

Source	DF	F value	Partial R^2
Energetic reserves	2	98125	0.2633
Risk of predation	2	92769	0.2489
Energetic reserves × risk of predation	4	38508	0.2066
Energetic reserves × risk of predation × matrix richness	16	3456	0.0742
Matrix richness	4	1336	0.0072
Search strategy	5	594	0.004
Patch arrangement	2	333	0.0009

the environmental conditions it experiences during dispersal (Zollner and Lima 1999c). Some studies suggest that perceptual range may be maximal under conditions that also increase the level of predation risk (Stamps 1991) or other sources of mortality such as desiccation (Yeomans 1995). Clearly, animals that can perceive habitat at a great distance will reach their destinations sooner and spend less time searching in the matrix. However, if a greater perceptual range is accomplished by dispersing during conditions that increase the risk of predation, then dispersal success may actually be higher if the animal chooses to disperse under safer conditions with a more limited perceptual range.

In this section, a simple version of the general model is developed to illustrate some important aspects of the decision of when to disperse as influenced by the tradeoff between perceptual range and risk of predation. The model organism here is a small nocturnal forest-dwelling mammal moving across an agricultural matrix, for whom both predation risk and perceptual range increase with ambient illumination (Zollner and Lima 1997, Zollner and Lima 1999c). The modeling approach, however, can easily be applied to other animals and tradeoffs.

Methods

General model was used to determine dispersal success as a simple function of per time interval predation risk and perceptual range (and other parameters below) without explicitly specifying the vigilance or feeding-related tradeoffs (although such parameters could be explicitly incorporated into this approach). The major task here is to derive contour lines of equal probability of dispersal success in the plane defined by all combinations of perceptual range and per time interval predation risk. With these contour lines defined, a constraint curve delineating the relationship between perceptual range and predation risk can then be used to determine the optimal conditions for dispersal (essentially following the method of Levins (1968, below).

Dispersal success was determined for animals facing all possible combinations of 7 different perceptual ranges (5, 20, 40, 60, 90, 125, 150 steps) and 14 different per time interval risks of predation (1.25×10^{-5} to 0.1024, with each successive value double that of the previous). These values were chosen based upon estimates from empirical work on small nocturnal forest mammals dispersing across agricultural fields (Zollner and Lima 1999c unpubl.), and a need to fully characterize lines of equal dispersal success (below). These simulations were performed for all possible combinations of three different degrees of directionality ($\rho = 0.85$, 0.9, 0.99, which cover the range of the most effective random walks, Zollner and Lima 1999b)

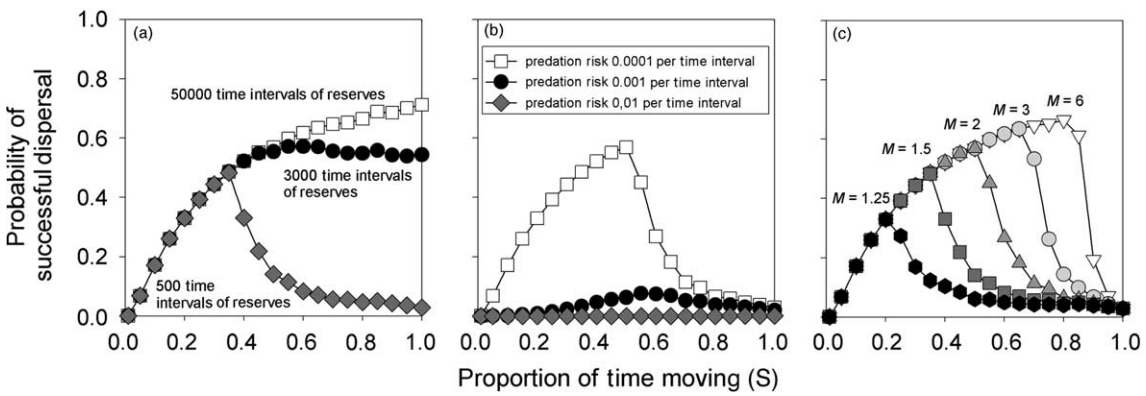

Fig. 2. Illustrative cases of the probability of successful dispersal as a function of speed of movement when animals can slow to forage during dispersal. (a) Effect of energetic reserves for a disperser facing a low baseline per time interval predation risk (0.0001), and a matrix richness of M = 1.5. (b) Effect of baseline risk of predation for a disperser with energetic reserves of 500 time intervals and a matrix richness of M = 2.0. (c) Effect of matrix richness for a disperser with energetic reserves of 500 time intervals facing a low per time interval predation risk (0.0001). For all cases the patches were uniformly distributed across the landscape and dispersers used a correlated random walk with $\rho = 0.8$.

and three different energetic reserve levels (500, 3000, 50 000 time intervals). The randomly arranged landscape described above was used throughout (100 patches 10 steps in width, 2.5% habitat coverage in the landscape).

For each combination of search directionality and energetic reserves, a simple interpolation procedure was used to derive a set of contour lines defining equal probabilities of success (at 10% intervals) in the predation risk – perceptual range plane. Hypothetical constraint curves were then superimposed on these sets of equal success contour lines. The constraint curve intersects a range of contour lines of equal dispersal success; the point of contact with the equal success contour line of greatest value determines the optimal conditions under which to disperse.

Results and discussion

For all combinations of parameters examined, the contour lines of equal dispersal success in the predation/perceptual range plane had the same overall form (Fig. 3), being generally concave upward. Note, however, that these contour lines eventually become concave downward as perceptual ranges approach a large fraction of the width of the simulated landscape (at such values, an increase in perceptual range does little to increase dispersal success). For simplicity we represent the constraint curve as linear (dashed line) such that a given increase in perceptual range entails a proportional increase in predation risk (Fig. 3). Because we modeled a nocturnal forest rodent dispersing across an agricultural matrix, the endpoints of the constraint curves might be thought of as representing dispersal under the light of a full moon (upper right endpoint) or on a dark, moonless night (lower left endpoint) as suggested by results in Zollner and Lima (1999c).

The situations depicted in Fig. 3 suggest that an animal with low energy reserves and a relatively uncorrelated random walk would do best by dispersing under conditions of high risk and high perceptual range, while the opposite holds for animals with highly correlated random walks and high energetic reserves. Unlike the two tradeoffs investigated earlier, the optimal conditions for dispersal are sensitive to the search strategy (correlation coefficient; e.g. Fig. 3) employed.

The shape of the equal success contour lines and slope of the constraint function are critical to determine the optimal dispersal conditions. With linear constraint functions and concave upward contour lines of equal dispersal success (e.g. as in Fig. 3), one or the other extreme of the constraint function will generally be the optimum. As the slope of the constraint function increases, the animal pays a high cost in terms of predation risk for a given increase in perceptual range, and this favors the low risk–low perceptual range optimum. Similarly, a relatively flat constraint function implies that little additional risk is incurred under conditions of high perceptual range, and this favors dispersal under the high risk–high perceptual range extreme. Strongly concave downward equal success contour lines will generally lead to dispersal at intermediate values of risk and perceptual range; here, an increase in the slope of the constraint function will favor shifts towards one extreme or the other.

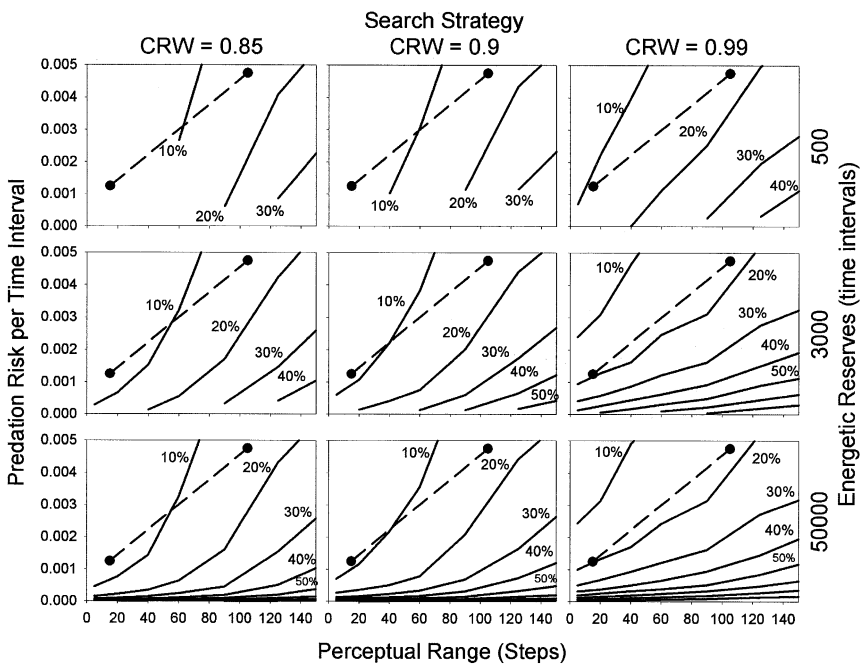

Fig. 3. Constraint curves (dashed lines) and contour lines of equal probability of dispersal success (solid lines) for simulated dispersers facing a tradeoff between perceptual range and predation risk. All scenarios are based upon the disperser moving through a landscape with 100 randomly arranged patches covering 2.5% of the landscape. Contour lines of equal dispersal success are depicted for dispersers using correlated random walks with three different degrees of correlation and three different levels of energetic reserves. Values adjacent to lines of equal success indicate the probability of dispersal success. The solid dots at the end of each constraint line represent the two extreme dispersal options faced by a disperser.

The concavity of the constraint function also is critical here (Fig. 4). A concave upward constraint function implies that predation risk initially increases relatively little with increasing perceptual range (from the low extreme), but that this increase in risk accelerates as perceptual range approaches the maximum extreme. This situation favors dispersal at intermediate values of risk and perceptual range. Alternatively, a concave downward constraint function implies an initial, relatively steep increase in predation risk with increasing perceptual range, which then increases more slowly as the maximum perceptual range is approached. This situation favors dispersal at conditions given by one of the extremes of the constraint function.

Dispersing animals face an increase in the risk of predation (Waser et al. 1994, Sakai and Noon 1997, but see Yoder et al. 2004), but little is known about perceptual ranges and how they might relate to changes in predation risk. Thus the nature of the above curves cannot yet be specified for any animal, but none of the above scenarios is obviously biologically unrealistic. However, data gathered from the simulated dispersal of white-footed mice (Zollner and Lima 1999c unpubl.) yield some insight into the constraint function that they might face. Dispersal across agricultural fields on dark nights involves a perceptual range of about 15 m and an estimated predation risk of 0.0002 per meter moved (based on total trail length of tracked animals and predator-induced mortality). Under full moonlight, perceptual range increases 5-fold to about 75 m whereas predation risk increases only by a factor of 1.5 to 0.0003 per meter moved. These data suggest a relatively flat constraint curve. Furthermore, it seems likely that white-footed mice would benefit considerably from an increase in perceptual range given their limited perceptual abilities on dark nights, hence their curves of constant dispersal success are probably concave upward as in Fig. 3. These two points suggest that white-footed mice might do best by dispersing on moonless nights or under full moonlight, very possibly the latter.

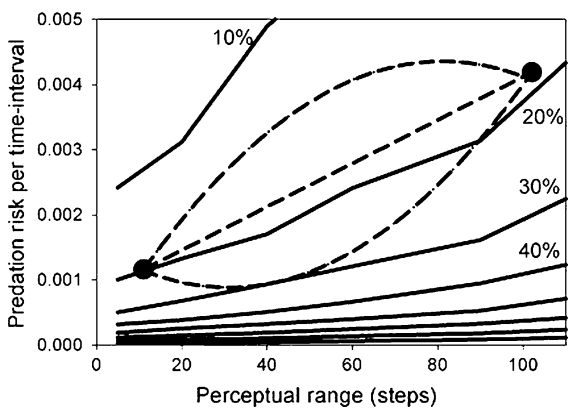

Fig. 4. Nonlinear constraint curves (dashed lines) and contour lines of equal dispersal success (solid lines) for dispersers facing a tradeoff between perceptual range and predation risk. All symbols and points of interpretation are as in Fig. 3. Dispersers were modeled using a correlated random walk with $\rho = 0.99$ and energetic reserves of 50 000 time intervals.

Conclusions

The behavior exhibited by a dispersing animal should be strongly influenced by its own characteristics and the environment in which it travels (Wiens et al. 1997). Such influences are readily apparent in our simulations. For example, a dispersing animal should slow it's movement to be vigilant for predators when it has extensive energetic reserves or travels through riskier environments (assuming vigilance is an effective anti-predator tactic). A dispersing animal should slow dispersal to forage when it has limited energetic reserves, faces low risks of predation, or travel through an energetically poor matrix. The combination of perceptual range and predation risk that maximizes dispersal success is strongly influenced by the tradeoff between these two factors and energetic reserves. These results are by and large intuitive and straightforward, although results suggesting only a minor role for landscape configuration as a determinant of optimal dispersal behavior are surprising. Furthermore, our results suggest that simple treatments of the effects of predation risk and energetic reserves on dispersal behavior might suffice for SEPMs.

Our simulations demonstrate clearly that behavioral tradeoffs can affect dispersal success, but there are limited empirical observations to support or refute our conclusions. More generally, however, several recent studies suggest animals moving across landscapes alter their behavior in adaptive ways. Ruffed grouse (*Bonasa umbellus*) experience higher predation risk in unfamiliar areas and compensate for this increased risk by changing their rates of movements (Yoder et al. 2004). Artificially translocated red squirrels move more slowly in more dangerous clear cuts than in forested cover; lighter squirrels, which may have lower energetic reserves, are more likely to cross those risky gaps (Bakker and Van Vuren 2004). Cottontail rabbits (*Sylvilagus floridanus*), on the other hand, move more quickly in open habitat types (Bond et al. 2001b) and experience higher predation risk if they are moving more (Bond et al. 2001a). These different responses to risky habitat may reflect the effectiveness of anti-predator behaviors: in clear cuts, cover remains available to squirrels and vigilance may be effective, while rabbits in open habitat may have limited options for reducing predation risk. More generally, matrix habitat type is known to alter the effects of habitat isolation for animals as diverse as flea beetles (*Aphthona* sp. Jonsen et al. 2001), newts (*Triturus* sp. Joly et al. 2001) and hazel grouse (*Bonasa bonasia* Aberg et al. 1995); these observations imply that

dispersal behavior may be a function of perceived predation risk, but data of the sort needed to evaluate our models are lacking. Similarly, information on the perceptual range of animals is very sparse, and even less information is available to assess relationships between perceptual range and predation risk (Zollner and Lima 1997, 1999b, c). Another intriguing difficulty with using existing studies to assess our models is the fact that dispersing animals may be in a unique state where they select different solutions to tradeoffs that differ from those chosen by non-dispersing animals (which are often used to simulate dispersal). Such a scenario is suggested by the observation that migrating yellow-rumped warblers (*Dendrocia coronata*) tradeoff predation risk against energetic reserves very differently from non migratory birds (Moore 1994). We therefore suggest that empirical work should focus on dispersing animals to the extent possible.

Understanding how dispersing animals may behave under different circumstances is an important step in the integration of behavioral ecology and landscape ecology (Ims 1995, Lima and Zollner 1996, Wiens 2002). A better theoretical and empirical understanding of decision making during dispersal will help design spatially explicit simulations that better describe the dispersal patterns of real animals (Roitberg and Mangel 1997, Russell et al. 2003). Even though accounting for such behavioral variation may add complexity to SEPMs, it may ultimately enhance the value of this increasingly important class of models (Armsworth et al. 2001, Morales and Ellner 2002).

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