

# Emergent Properties of Conspecific Attraction in Fragmented Landscapes

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**ABSTRACT:** Attraction to conspecifics may have wide-ranging implications for habitat selection and metapopulation theory, yet little is known about the process of attraction and its effects relative to other habitat selection strategies. Using individual-based simulations, I investigated the emergent properties of conspecific attraction during habitat selection on survival, fecundity, short-term fitness (survival  $\times$  fecundity), and distributions in fragmented landscapes. I simulated conspecific attraction during searching and settlement decisions and compared attraction with random, habitat-based (searching for the presence of habitat), and habitat quality sampling strategies (searching for and settling in high-quality habitat). Conspecific attraction during searching or settlement decisions had different consequences for animals: attraction while searching increased survival by decreasing time spent in nonsuitable habitat, whereas attraction during settlement increased fecundity by aggregating animals in high-quality habitats. Habitat-based sampling did not improve fitness over attraction, but directly sampling habitat quality resulted in the highest short-term fitness among strategies. These results suggest that attraction can improve fitness when animals cannot directly assess habitat quality. Interestingly, conspecific attraction influenced distributions by generating patch size effects and weak edge effects, highlighting that attraction is one potential, yet previously unappreciated, mechanism to explain the widespread patterns of animal sensitivity to habitat fragmentation.

*Keywords:* aggregation, dispersal, edge effect, habitat loss, habitat selection, patch size effect.

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Habitat selection affects several aspects of individual fitness, which can have decisive consequences for many ecological and evolutionary phenomena, from dispersal strat-

egies to speciation (Stamps 2001; Morris 2003; Tonnis et al. 2005). Therefore, the ability to identify and choose the best available habitats should be under strong selective pressure (Jaenike and Holt 1991). In habitat selection theory, individuals are often assumed to behave ideally, to be free to select those habitats where fitness is highest, and fitness is assumed to decline with increasing population density (Fretwell and Lucas 1970). These assumptions are key components of the ideal free distribution (IFD) model of habitat selection and its subsequent extensions (Fretwell and Lucas 1970; Morris 2003). Such models are consistent with distribution patterns for some species (e.g., Kacelnik et al. 1992; Petit and Petit 1996), even though assumptions are often violated (Abrahams 1986; Hugie and Grand 1998). One reason that these assumptions can be violated is that many animals use proximate cues to guide habitat selection (Hildén 1965; Stamps 2001; Dall et al. 2005). Conspecific attraction is one such behavior whereby individuals use the presence or abundance of conspecifics as a positive proximate cue for selecting locations of habitat (Stamps 1988).

Conspecific attraction can have important implications for both habitat selection and metapopulation theory. The process of conspecific attraction challenges habitat selection theory, by suggesting positive density dependence, and metapopulation theory, by altering the likelihood of patch occupancy and extinction (Ray et al. 1991; Stephens and Sutherland 1999; Stamps 2001). Yet despite the recent theoretical (Forbes and Kaiser 1994; Beauchamp et al. 1997; Doligez et al. 2003; Fletcher and Miller 2006) and applied focus on this behavior (Reed and Dobson 1993; Ward and Schlossberg 2004), understanding the role of conspecific attraction in habitat selection has been limited because little is known about the process of conspecific attraction and its costs and benefits relative to other potential strategies (but see Doligez et al. 2003).

The use of conspecifics as positive proximate cues in habitat selection is thought to evolve for at least three ultimate reasons: reduced search costs, reduced settlement costs, and Allee effects (Stamps 2001). These ultimate factors suggest that attraction can occur at different times

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during habitat selection. Reduced search costs can occur if individuals find patches more easily when the patches are already occupied by conspecifics (Stamps 1991; Reed and Dobson 1993), which implies that attraction operates during the search, or dispersal, phase of habitat selection. Reduced settlement costs can occur once individuals find patches if individuals use conspecifics for indirectly assessing habitat quality to guide settlement decisions. Allee effects describe positive relationships between fitness and population size or density (Stephens and Sutherland 1999) and suggest that attraction could occur during either searching or settlement decisions of habitat selection (or both), depending on the reason for the Allee effects (Stamps 2001). Currently, it is unknown whether conspecific attraction while searching, during settlement decisions, or during both has different consequences for animals.

The ultimate factors driving the evolution of conspecific attraction could influence our understanding of whether attraction is equally beneficial in different landscapes. For instance, using a search strategy that incorporates conspecific attraction in fragmented or otherwise heterogeneous landscapes could be more efficient than other commonly assumed movement strategies, such as correlated random walks (Turchin 1998; Byers 2001; Cooper et al. 2002). This is an important consideration because animals likely experience dramatically different landscapes throughout their range, which can influence the evolution of dispersal and habitat selection behavior (Thomas et al. 2001).

It is also unclear whether habitat selection strategies based on conspecifics can lead to large-scale patterns in the distribution of animals, even though such behaviors could help explain observed widespread negative effects of habitat loss and fragmentation (Reed and Dobson 1993). For example, Turchin (1989) modeled and provided empirical evidence for aggregative movement enhancing patch size effects of Mexican bean beetles (*Epilachna varivestis*) on a patchy host plant resource (*Phaseolus vulgaris*). Emergent patterns resulting from conspecific attraction could be highly variable and depend on number of factors, including landscape structure (Lima and Zollner 1996), yet this potential has not been explored.

I use an individual-based, spatially explicit simulation model to examine how conspecific attraction affects the survival, reproduction, and distribution of animals in a landscape context. I address three issues: first, the demographic consequences of using conspecific attraction compared with a random strategy, a habitat-based strategy (using the presence/absence of habitat), and a strategy that directly samples habitat quality; second, whether these consequences vary under different landscape contexts; and third, whether individual decisions based on conspecific

attraction generate emergent patterns in the distribution of animals when patch size, distance from edge, and landscape context vary.

## Methods

### *Fragmented Landscapes*

I generated theoretical landscapes that varied independently in the amount of habitat and degree of fragmentation, using the program RULE (Gardner 1999). In this model, fragmentation describes the configuration of habitat in the landscape, independent of habitat loss, where habitat is more “broken up” in more fragmented landscapes (Fahrig 2003). Each landscape was a  $256 \times 256$  grid that contained suitable habitat in an unsuitable matrix. Each grid cell of suitable habitat was considered a potential territory that only one individual could occupy. Landscapes were generated with 50%, 70%, and 90% of suitable habitat destroyed in the landscape (“habitat loss” hereafter). Thus, the total number of suitable cells in the landscape ranged from 6,554 to 32,768. Four levels of fragmentation were generated by using both simple random (SR) landscapes and fractal landscapes for each amount of habitat loss (i.e., 12 landscape types, with five landscapes per type). For SR landscapes, each cell in the landscape had an independent probability of being suitable habitat, based on the total amount of habitat in the landscape. For fractal landscapes, RULE uses the midpoint displacement algorithm, in which spatial contagion is varied based on a parameter,  $H$ , that ranges between 0 and 1 (Gardner 1999). Landscapes were generated with  $H = 0.0, 0.5,$  and  $1.0$ . When  $H = 1.0$ , landscapes are less fragmented; when  $H = 0.0$ , landscapes are highly fragmented, and SR landscapes are an extreme form of fragmentation (app. A in the online edition of the *American Naturalist*). Patches were delineated using the nearest-neighbor rule, in which patches were defined based on contiguous orthogonal clusters of cells (Gardner 1999).

Within suitable habitat, I varied the relative habitat quality using the same algorithms as for delineating habitat above. Habitat quality was defined as the number of offspring an individual could produce (ranging from 0 to 6) when selecting a location for residency (i.e., fecundity; Pulliam and Danielson 1991). Thus, in SR landscapes, habitat quality was randomly distributed, whereas in fractal landscapes, habitat quality was clumped, and the relative degree of clumping was dependent on  $H$ . Fecundity attained by individuals reflected a site-dependent process (Pulliam and Danielson 1991; Rodenhouse et al. 1997), whereby fecundity was dependent on the location selected and was not influenced by density dependence. The range in habitat quality modeled should be considered a relative measure for eval-

uating the reproductive consequences of different habitat selection strategies. I examined three types of habitat quality within landscapes: “high-quality,” “moderate-quality,” and “low-quality” landscapes, with a greater, equal, and lesser proportion of high-quality habitat, respectively (fig. A1 in the online edition of the *American Naturalist*).

### Habitat Selection Strategies

Using the framework envisioned by Stamps (2001), where habitat selection is viewed as three stages—search, settlement, and residency—I modeled conspecific attraction and compared attraction to random, habitat-based, and habitat quality sampling strategies. While searching and settlement decisions are not mutually exclusive, for modeling it is useful to distinguish these processes to understand how conspecific attraction can influence fitness in patchy landscapes. I modeled three strategies for conspecific attraction: attraction while searching, but random settlement (“conspecific search”); random searching, but attraction during settlement (“conspecific settlement”); and attraction during searching and settlement (“conspecific search and settlement”). I compared these strategies to random search and settlement (“random”); a habitat-based strategy, where animals moved toward suitable habitat while searching but could not perceive habitat quality and thus settled randomly in suitable habitat (“habitat search”); and a habitat quality strategy, where animals could directly assess habitat quality and incorporated this information into searching and settlement decisions (“habitat quality”). For modeling, I envisioned territorial animals, such as migratory birds, searching and settling in habitats that were previously unoccupied in a sequential manner (Fretwell and Lucas 1970; Rodenhouse et al. 1997; Mönkkönen et al. 1999; Stamps et al. 2005). However, the overall approach to the model is general and could be applied to many situations where territorial animals search and settle in patchy habitats in a staggered manner (see Stamps et al. 2005 for a review).

For each habitat selection strategy, the general flow of the model included the following. The search stage began with an individual starting at a random location of suitable habitat within the landscape and then moving. During the search stage, individuals had a fixed mortality rate per time step (0.001 or 0.01) for each habitat selection strategy (Zollner and Lima 1999; Conradt et al. 2003). I considered each time step to reflect approximately one day. These rates result in survival rates from the model being generally similar to survival estimates of some migratory birds during migration (Sillett and Holmes 2002; Menu et al. 2005), and they can be considered relatively low and relatively high search costs, respectively (Stamps et al. 2005). If an individual survived movement, the individual had a chance of settling in the area (settlement stage), if the area

was suitable habitat and unoccupied by other conspecifics. If the individual did not settle, the individual continued moving, and the process was repeated until the individual either settled or suffered mortality. Once an individual settled (residency stage), it occupied that location until the model ended, and it attained fecundity based on the habitat quality in that location. The model then initiated the habitat selection process for the next individual. This was repeated until the model simulated the fates of the total number of individuals, which was equal to the number of suitable cells of habitat in the landscape. Results were summarized when 5%, 10%, 20%, 40%, 60%, 80%, and 100% of the individuals had attempted habitat selection (“population density” hereafter). I focus on relatively low population densities, because emergent properties of attraction can be masked when landscapes become saturated (Wagner 1998).

The process of conspecific attraction requires defining at what scale individuals perceive and use information on conspecifics during habitat selection. The spatial scale that attraction operates could influence the consequences of attraction in landscapes (Lima and Zollner 1996), but this has not been investigated. I addressed this issue by modeling habitat selection for individuals with perceptual ranges of different sizes. I investigated the effect of perceptual range, where individuals perceive and use information on conspecifics within radii of 2, 4, 8, and 16 cells from their current location. Individuals used information within the perceptual range while searching, during settlement decisions, or both.

*Search.* I modeled random search as a correlated random walk. Correlated random walks were simulated where individuals moved in a direction estimated by selecting a random angle from a wrapped Cauchy distribution (Haefner and Crist 1994; Zollner and Lima 1999):

$$\theta_{rt} = \theta_{r(t-1)} + 2 \arctan \left( \frac{1 - \rho_r}{1 + \rho_r} \tan \{ \pi [U(-0.5, 0.5)] \} \right), \quad (1)$$

where  $\theta_{rt}$  is the random direction chosen in time  $t$ ,  $\rho_r$  is the degree of correlation, and  $U$  is a uniform random deviate. Initial simulations revealed that nearly straight paths with  $\rho_r = 0.99$  had higher average survival rates across all model permutations than other correlations (ranging between 0.1 and 0.999; see also Zollner and Lima 1999; Conradt et al. 2003). Therefore,  $\rho_r$  was set at 0.99 for all simulations. The distance moved per time step was a random deviate from a uniform distribution within the perceptual range. However, constraining the distance moved per time step to adjacent cells (Zollner and Lima

1999; Conradt et al. 2003) does not change qualitative results of the model (R. J. Fletcher, unpublished data).

I modeled conspecific search by altering a correlated random walk to bias movement direction toward conspecifics. Individuals first assessed where conspecifics occurred within their current perceptual range and estimated a mean distance-weighted angle to conspecifics,  $\bar{\theta}_{ct}$ . Angles to conspecifics on the perimeter of the perceptual range were given one-tenth the weight,  $w$  [with an exponential decay;  $w = \lambda \exp(-\lambda d_i)/\alpha$ ], of adjacent neighbors. Individuals then incorporated this information into a memory-based search such that individuals used information on both current and previous locations of conspecifics. For the memory-based search, I used a modified linear operator rule if conspecifics occurred in the current time step (McNamara and Houston 1987):

$$\bar{\theta}_{ct} = \bar{\theta}_{c(t-1)}\alpha_c + (1 - \alpha_c)\bar{\theta}_{ct}, \quad (2)$$

where  $\alpha_c$  is the “memory factor” ( $0 < \alpha_c < 1$ ). In this situation, memory is based on the estimated previous angles toward conspecifics, updated relative to the current location. If conspecifics occur within the memory limits of the individual but not in the current perceptual range,  $\bar{\theta}_{ct} = \bar{\theta}_{c(t-1)}$ . However, if an individual traveled for  $t$  time steps without encountering conspecifics so that the memory of the last encountered conspecific drops to <5% of the total acquired information ( $\alpha_c^t < 0.05$ ; McNamara and Houston 1987), the individual proceeded on a correlated random walk (eq. [1]). Given this information, the direction of movement was modeled as:

$$\theta_{ct} = \bar{\theta}_{ct} + 2 \arctan \left( \frac{1 - \rho_c}{1 + \rho_c} \tan \{ \pi [U(-0.5, 0.5)] \} \right), \quad (3)$$

where  $\theta_{ct}$  is the realized conspecific search direction chosen in time  $t$  and  $\rho_c$  can be considered a measure of the overall likelihood of using information on conspecifics. Based on initial simulations that varied  $\alpha_c$  and  $\rho_c$  (from 0.01 to 0.99), individuals using conspecific search with  $\rho_c = 0.5$  and  $\alpha_c = 0.1$  generated higher survival rates on average than those with other correlations. For subsequent simulations, I set  $\rho_c = 0.5$  and  $\alpha_c = 0.1$ .

Finally, to model situations where individuals used either the presence of habitat or habitat quality in searching decisions, I used the same algorithms as for a conspecific-based search, but the animals used different types of information. For a habitat-based search, individuals used the presence of habitat to estimate mean distance-weighted angles to the most habitat encountered within perceptual ranges. For a habitat quality search, individuals used the quality of habitat to estimate mean distance-weighted an-

gles to the best habitat encountered within perceptual ranges.

*Settlement.* Random settlement was modeled as a Bernoulli process with a constant probability of settlement during each time step, conditional on the location being unoccupied and suitable habitat. To accurately compare random settlement to conspecific settlement (see below), the probability of random settlement was equal to the average probability of settlement using conspecific settlement, based on the total number of individuals simulated for each landscape.

To model a settlement process where individuals exhibit conspecific attraction, I envisioned individuals increasing the likelihood of settlement when conspecifics were nearby. Individuals estimated the density of conspecifics within the current perceptual range (pr) as  $\bar{D}_{ct} = \sum_{i=1}^{\text{pr}} (N_i/A_i)w$ , where  $\bar{D}_{ct}$  is the distance-weighted density of conspecifics at time  $t$ ,  $N_i$  is the number of conspecifics at distance  $i$ ,  $A_i$  is the area of habitat at distance  $i$ , and  $w$  is an exponential weighting factor (same as in “Search”). Given this density estimate, I modeled probability of settlement,  $p_{ct}$ , conditional on the location being unoccupied and suitable habitat, as

$$p_{ct} = \gamma \frac{\exp(\beta_0 + \beta_1 \bar{D}_{ct})}{1 + \exp(\beta_0 + \beta_1 \bar{D}_{ct})}, \quad (4)$$

where  $\beta_0$  and  $\beta_1$  are constants that describe the shape of the nonlinear function and  $\gamma$  is a scaling coefficient (fig. B1 in the online edition of the *American Naturalist*). When no conspecifics occurred within the perceptual range, individuals still had a baseline probability of settlement (fig. B1). I also explored a settlement strategy that included conspecific attraction for low densities with avoidance of conspecifics at high densities, but results were similar (app. B in the online edition of the *American Naturalist*).

Finally, for the habitat quality strategy, I modeled settlement using an approach that approximates the IFD at local scales and has been applied to large-scale distributions (Tyler and Hargrove 1997). Individuals directly assess habitat quality at each location and base their settlement decision on the quality of the current location relative to their previous experiences, using a linear operator rule (McNamara and Houston 1987):

$$L_{t+1} = L_t \alpha_q + (1 + \alpha_q) Q_x, \quad (5)$$

where  $Q_x$  is the habitat quality at location  $x$  and  $L_t$  is the estimate of habitat quality in the landscape at time  $t$ . If  $Q_x > L_t$ , then individuals settle in that location, conditional on the location being unoccupied. Each individual started

with the maximum estimate of relative habitat quality for the landscape, and before the commencement of simulating and summarizing habitat selection, each individual moved five time steps to allow each individual to estimate habitat quality in the landscape (Tyler and Hargrove 1997). Based on initial simulations, individuals with a memory factor  $\alpha_q = 0.9$  had higher short-term fitness on average than those with other memory factors across all landscape combinations. Thus, for subsequent simulations I set  $\alpha_c = 0.9$ .

*Estimating Differences among Habitat Selection Strategies*

I focused on four key issues regarding conspecific attraction: first, survival and movement efficiency; second and third, the reproductive and short-term fitness (survival  $\times$  fecundity) consequences of using attraction relative to random, habitat-based, and habitat quality strategies; and fourth, the emergent distribution patterns arising from attraction relative to the random strategy. For each issue, I addressed how landscape structure, perceptual range, mortality rate, and population density influenced the differences among habitat selection strategies.

For each simulation, I summarized the following information related to dispersal success, efficiency, and fitness consequences for individuals in the landscape. Four measures related to dispersal success and efficiency were calculated: per capita survival rate (probability of dispersal success), net distance moved (end location – start location), total time spent dispersing (number of time steps), and the proportion of time spent in the matrix (number of time steps in matrix/total number of time steps). I also estimated the per capita fecundity of successful individuals and the average short-term fitness of individuals. To compare among strategies, I estimated the relative difference in the above rates for conspecific and direct sampling strategies relative to the random strategy as  $(strategy_i - random)/(strategy_i + random)$ ; these relative rates range between  $-1$  and  $1$  (Conradt et al. 2003). I estimated differences among strategies for emergent distributions by separately calculating the frequency of occurrence of individuals as a function of distance from nearest edge and patch size for each landscape. I then investigated whether each strategy caused emergent patch size and edge effects. In simulation modeling, small differences may yield statistical significance because of the ability to produce large sample sizes (Judson 1994; Zollner and Lima 1999). Therefore, for all analyses I focused on the mean square and percent mean square error of factors attained from fully factorial ANOVAs, with the relative differences of survival, fecundity, short-term fitness, and frequency of occurrence as dependent variables. Percent mean square error provides information on the variation explained by different

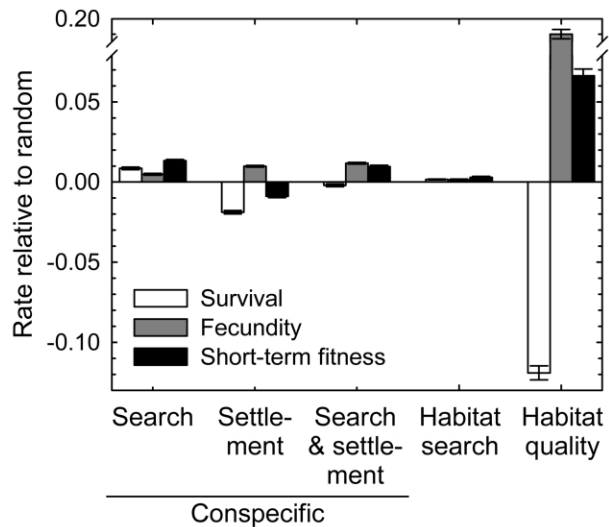
independent variables that is less sensitive to large amounts of replication than other statistics (Tyler and Hargrove 1997). The source code for the model is available from the author upon request.

**Results**

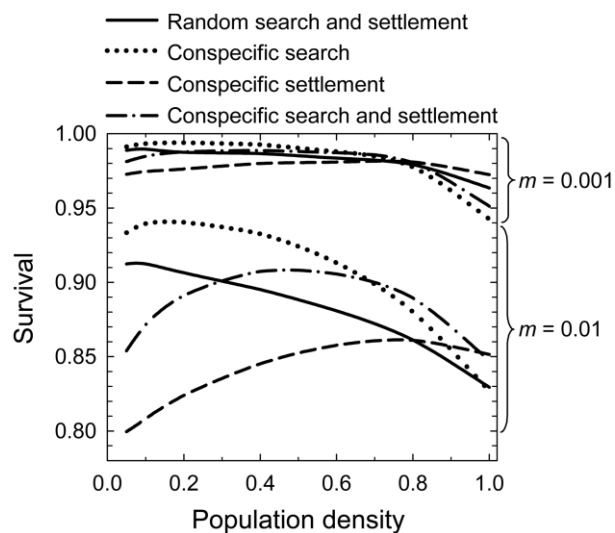
*Survival and Dispersal Efficiency*

Across all model permutations, survival was generally higher for conspecific search than for random habitat selection (figs. 1, 2) because individuals spent less time dispersing and less time in the matrix (app. C in the online edition of the *American Naturalist*). However, when conspecific attraction was incorporated into settlement decisions, survival was generally lower than for random, except at high population densities (figs. 1, 2). This occurred because individuals searched for longer time periods when population density was low, but searching time declined with increasing population density. Habitat-based searching improved survival relative to random but was less efficient than conspecific searching overall, because conspecifics were more refined and aggregated cues than the presence of habitat. The habitat quality strategy resulted in lower survival because individuals searched longer to find high-quality habitat (fig. 1).

Population density, mortality, and landscape structure



**Figure 1:** Estimates ( $\pm 95\%$  confidence intervals) of survival, fecundity, and short-term fitness (survival  $\times$  fecundity) for individuals using different habitat selection strategies relative to random search and settlement across all model permutations. Relative rates were calculated as  $(strategy_i - random)/(strategy_i + random)$ . Relative rates can range between  $-1$  and  $1$ , with positive values indicating greater survival, fecundity, or short-term fitness of a strategy relative to random habitat selection.



**Figure 2:** Survival as a function of population density for different habitat selection strategies and different extrinsic mortality rates ( $m$ ). Results are shown for individuals with moderate perceptual ranges (four-cell radius), in landscapes of moderate habitat loss (30% of habitat remains), and in fragmentation ( $H = 0.5$ ). Population density refers to the proportion of suitable habitat occupied by individuals in the absence of mortality.

influenced the differences in survival among strategies (table 1). Although density dependence was not incorporated into the model, survival rate varied as a function of population density, due to site preemption. When conspecific attraction occurred during settlement, survival was highest at moderate densities, whereas for random settlement, survival declined with increasing density (fig. 2). Relative differences were influenced by mortality rates (table 1), in that differences among strategies were minor when mortality rates were low (fig. 2). Survival was high for all strategies in landscapes with less fragmentation and habitat loss because less time was spent in unsuitable habitat. Relative differences in survival rates increased with habitat loss (table 1; fig. 3A), but few differences occurred with fragmentation, except in SR landscapes (table 1; fig. 3B). Total time spent dispersing and the net distance moved were highly correlated within strategies ( $r > 0.73$ ,  $P < .001$ ; app. C), and these factors explained survival rates both within and among strategies.

#### *Reproductive and Total Short-Term Fitness Consequences*

Strategies incorporating conspecific attraction or habitat quality generally resulted in higher fecundity than random, with individuals directly sampling habitat quality attaining the highest overall fecundity (fig. 1). The habitat-based strategy only slightly increased fecundity over random hab-

itat selection. Habitat loss, fragmentation, and habitat quality in landscapes influenced the relative differences in fecundity (table 1), with relative differences diminishing when individuals used landscapes with more suitable habitat, less fragmentation, or a greater proportion of high-quality habitat (fig. 4).

Conspecific search and habitat quality strategies generally resulted in higher total fitness than random, yet conspecific settlement resulted in lower short-term fitness, due to lower survival rates (fig. 1). Relative differences in short-term fitness were influenced by population density, mortality rates, and landscape structure (table 1). Relative short-term fitness for most strategies increased with habitat loss and fragmentation, except in the most fragmented (SR) landscapes. For example, fitness was mainly influenced by habitat fragmentation (table 1) for the habitat search strategy, which performed poorly relative to random in SR landscapes (fig. 5). Conversely, fitness for the habitat quality strategy was highest in SR landscapes, because of the high amount of spatial heterogeneity in habitat quality. The effects of population density and mortality rates were dependent on the habitat selection strategy employed (fig. 5).

#### *Emergent Spatial Patterns*

Differences in overall frequency of occurrence between conspecific strategies and random habitat selection were predictably influenced by factors influencing survival rates of individuals (table 2). If attraction occurred during habitat selection, patch size and edge effects occurred, whereby individuals were less likely to occur in small patches or close to edges (fig. 6). Patch size and edge effects were strongest for strategies that included attraction during settlement (fig. 6A, 6C). Population density consistently influenced patterns: at very low densities, no patch size or edge effects occurred because few conspecifics existed to bias habitat selection (fig. 6B).

#### **Discussion**

Incorporating conspecific attraction into decisions greatly alters how habitat selection influences population dynamics and patterns of distribution. This simple behavioral rule can reduce search costs when incorporated into dispersal and can increase fecundity when incorporated into settlement decisions. In doing so, attraction influences where animals move, their likelihood of selecting habitats, and their fitness during habitat selection. The consequences of this behavior can be complex, yet this complexity can be explained by whether attraction occurs during movement or settlement, the search costs (mortality

**Table 1:** ANOVA summary for factors influencing survival, fecundity, and short-term fitness of individuals using conspecific and direct habitat sampling strategies relative to a random search and settlement strategy

Source	df	Conspecific search		Conspecific settlement		Conspecific search and settlement		Habitat search		Habitat quality	
		MS	%MS	MS	%MS	MS	%MS	MS	%MS	MS	%MS
<b>Survival:</b>											
Density	1	.05	20.3	.73	36.1	.14	29.8			4.43	42.3
Frag	3							.01	23.9	1.69	16.1
Loss	2	.04	18.2								
Mortality	1	.07	30.3	.77	37.7	.11	22.9			2.35	22.5
Density × mortality	1			.34	16.6	.15	32.0				
Frag × mortality	3							.01	16.7		
<b>Fecundity:</b>											
Density	1			.03	25.1					2.93	10.5
Frag	3	.03	20.1			.10	36.9			9.25	33.3
Loss	2	.02	10.4			.03	10.2				
Quality	2									9.32	33.5
Density × frag	3			.01	10.1						
<b>Short-term fitness:</b>											
Density	1	.21	21.6	2.75	40.7	.46	24.9			22.84	30.4
Frag	3							.01	10.3	28.97	38.6
Loss	2	.23	23.9								
Mortality	1	.20	21.0	2.23	33.0	.34	18.5			7.57	10.1
Density × mortality	1			1.14	16.8	.57	30.8				

Note: Only factors contributing to more than 10% of total mean square (MS) error are reported. For all factors reported,  $P < .0001$ . Density = population density; frag = habitat fragmentation; loss = habitat loss; quality = habitat quality.

rates) during habitat selection, density dependence, and landscape context.

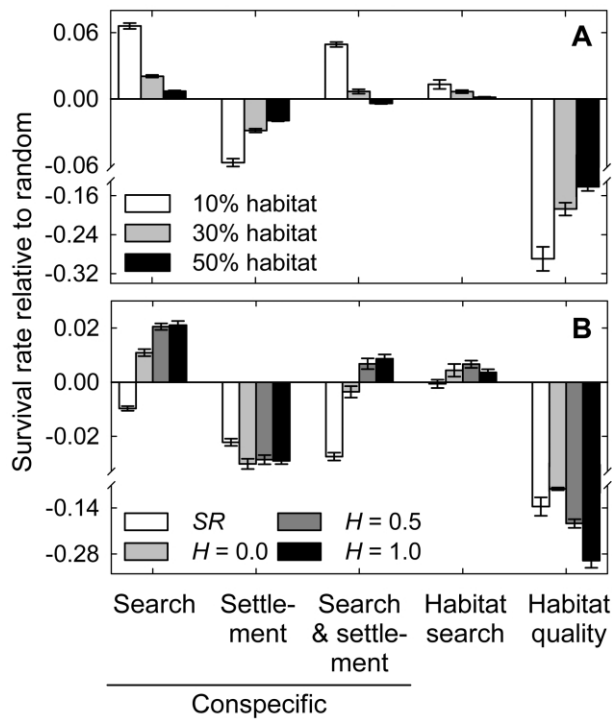
*Attraction as a Strategy for Habitat Selection*

Individuals using conspecific attraction while searching generally incurred lower mortality and slightly greater fecundity than individuals using random habitat selection, which resulted in higher short-term fitness than most other strategies. Search strategies that incorporate social cues increase fitness by decreasing the likelihood of dispersal out of patches containing conspecifics and directing movement through the matrix to nearby occupied patches (see also Cooper et al. 2002). While some have argued that conspecifics could be used while searching for habitat (Stamps 1991; Muller 1998), this potential depends on the scale at which conspecific cues are available to dispersing animals. Such information may be limited to small spatial scales for some animals, but for others, such as some insects and songbirds, cues of conspecifics (e.g., pheromones, song) can be perceived at great distances and could provide important information to guide movement through landscapes (Naguib 1996; Schneider 1999).

When conspecific attraction occurred during settlement decisions, many patterns emerged relative to random habitat selection, all of which were highly density dependent.

Using a two-patch model, Doligez et al. (2003) argued that if attraction occurs during settlement decisions, then this strategy should increase fitness only when conspecifics are honest indicators of habitat quality, which should occur in a frequency-dependent manner (see also Beauchamp et al. 1997). My model suggests that this strategy could result in higher fitness than other strategies only at relatively high population densities, where cues of conspecifics abound to guide settlement decisions. Animals undergoing declining population size could thus suffer from using conspecific attraction. Nonetheless, this strategy may increase fitness for all individuals in a population in situations when settlement costs are greater than the variation in habitat quality in the landscape (Mönkkönen et al. 1999) or when attraction is caused by Allee effects, where individuals receive some sort of social fitness benefit from settling near other conspecifics (e.g., Fletcher and Miller 2006).

Incorporating conspecific attraction into searching decisions improved short-term fitness not only relative to a random strategy but also relative to a habitat-based strategy, primarily because individuals enjoyed higher fecundity (see below). Yet directly sampling habitat quality resulted in the highest short-term fitness of the strategies considered. This makes intuitive sense: if animals use conspecifics as cues to guide settlement decisions, these cues will always be imperfect indicators of habitat quality. How-



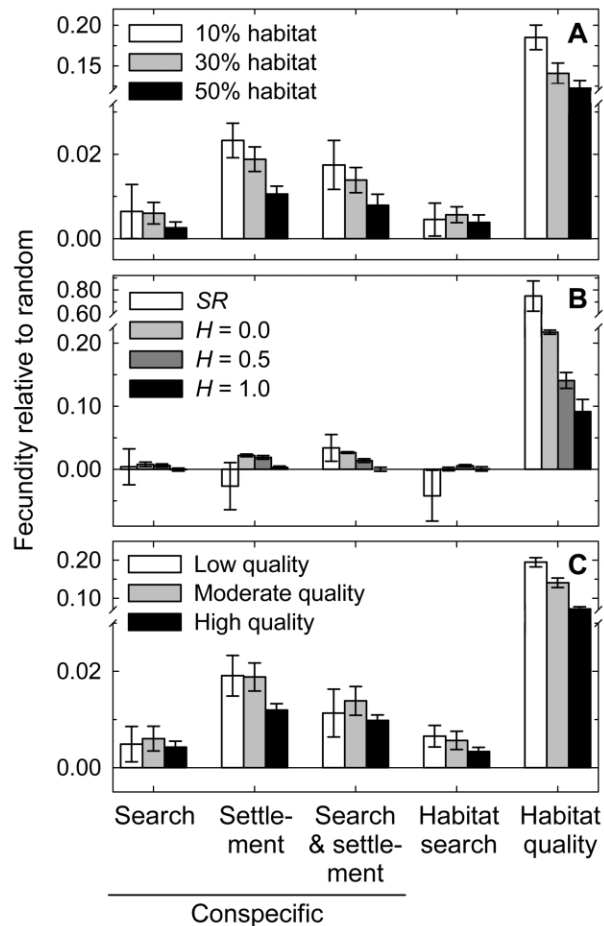
**Figure 3:** Survival for individuals using conspecific attraction and direct sampling of habitat relative to a random habitat selection strategy (relative rate  $\pm$  SE), in which habitat loss (A) or habitat fragmentation (B) influences relative survival rates. A, Example of relative survival rates for individuals when habitat loss varies, where animals have moderate perceptual ranges (four-cell radius) and experience high mortality rates (0.01 per time step) and moderate population density ( $d = 0.4$ ) and landscapes are moderately fragmented ( $H = 0.5$ ). B, Example when fragmentation varies, relative to the example in A, for moderate habitat loss (30% of habitat remains).  $H$  denotes the spatial contagion, or fragmentation, of fractal landscapes (with  $H = 0.0$  being more fragmented and  $H = 1.0$  being less fragmented), while SR denotes simple random landscapes.

ever, if sampling costs differ for direct or indirect assessment of habitat quality, then strategies using less costly sampling, such as conspecifics, could be favored under some situations (Mönkkönen et al. 1999). Moreover, the ability of animals to directly sample habitat quality will often be rare (Danchin et al. 2004; Dall et al. 2005), because perfect information on future fitness during habitat selection could occur only in environments with strong temporal autocorrelation (Doligez et al. 2003) or when the time between the settlement decision and the resulting fitness consequence is exceedingly small.

*Attraction in Fragmented Landscapes*

As the amount of habitat in landscapes declined, conspecific attraction while searching had a stronger positive in-

fluence on survival and resulting short-term fitness relative to a random strategy. Therefore, natural selection could favor this behavior in landscapes with high natural or human-induced heterogeneity, for species using rare habitats, and for individuals in landscapes undergoing rapid habitat loss. However, reductions in movement could counteract survival benefits in the long term, through inbreeding depression and other demographic crowding effects, such as competition. Ray et al. (1991) also proposed



**Figure 4:** Fecundity for individuals using conspecific attraction and direct sampling of habitat relative to a random habitat selection strategy (relative rate  $\pm$  SE), in which habitat loss (A), habitat fragmentation (B), or habitat quality (C) influences relative survival rates. A, Example of relative fecundity rates when habitat loss varies for individuals with moderate perceptual ranges (four-cell radius) and low extrinsic mortality rates (0.001 per time step) in landscapes that are moderately fragmented ( $H = 0.5$ ) and have moderate population density ( $d = 0.4$ ) and moderate habitat quality. B, C, Examples when fragmentation (B) or habitat quality (C) varies, relative to the example in A, for moderate habitat loss (30% of habitat remains).  $H$  denotes the spatial contagion, or fragmentation, of fractal landscapes (with  $H = 0.0$  being more fragmented and  $H = 1.0$  being less fragmented).

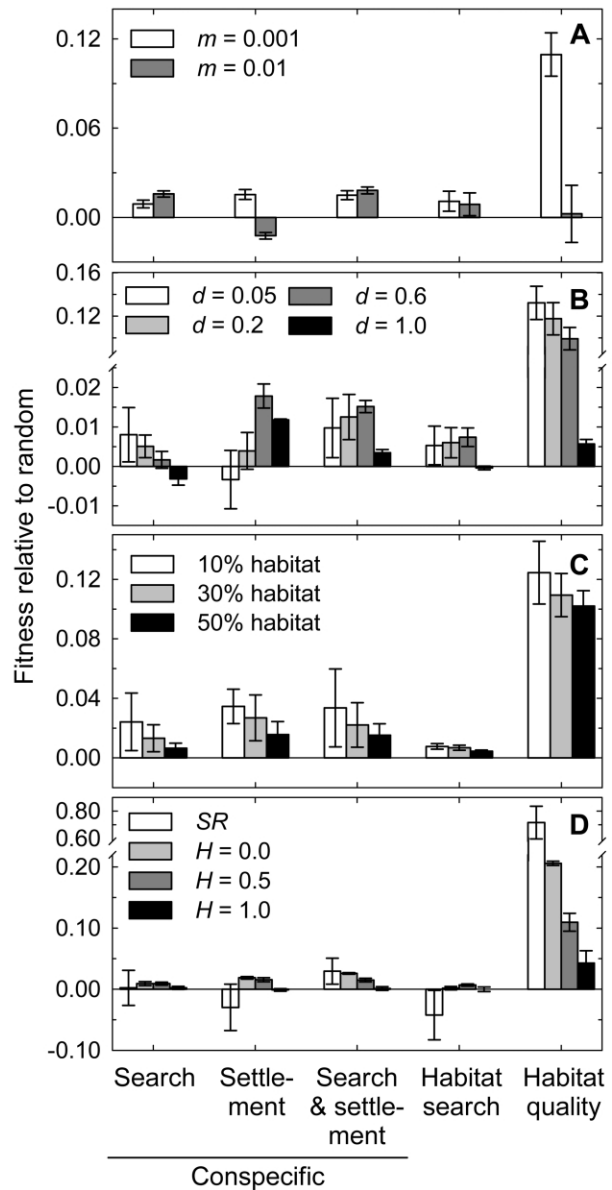
that spatial clumping from attraction would increase the likelihood of environmental stochasticity destroying populations, because many suitable habitats go unoccupied.

The distribution and variation in habitat quality in landscapes influenced relative fecundity for all strategies, although effects were strongest for the habitat quality strategy. When landscapes contained a large proportion of low-quality habitat or when habitat quality was moderately aggregated, strategies incorporating conspecifics into settlement decisions resulted in higher fecundity by individuals aggregating in high-quality areas. In addition, when resources are distributed randomly in landscapes, directly sampling habitat quality can approach an IFD (Tyler and Hargrove 1997). Yet as resources become extremely aggregated, the benefits of both conspecific attraction and direct sampling decline because of less spatial variation in resource distribution.

Emergent distribution patterns of attraction included reduced occupancy in small patches and edge habitat. Although edge effects were relatively weak in the model, it is important to note the scale of the effect: in the model, declines in distribution adjacent to edges are consistent with 50–100-m edge effects for individuals with territories of approximately 0.25–1 ha, which is in general agreement with some empirical estimates (e.g., Ortega and Capen 1999; Fletcher and Koford 2003; Fletcher 2005). While the aggregative nature of attraction could increase vulnerability to extinction (Ray et al. 1991), this vulnerability could be mitigated through individuals avoiding small patches and edge habitat—areas that can contain lower habitat quality and can harbor more predators and invasive species (Ortega and Capen 1999; Chalfoun et al. 2002; MacQuarrie and Lacroix 2003). Larger populations in large patches are also less susceptible to demographic stochasticity, as well as other factors such as susceptibility to invasion (Orrock and Fletcher 2005).

*Model Predictions and Limitations*

The model developed here makes two general predictions regarding conspecific attraction. First, attraction should be strongest at moderate to high population densities, because at low densities few cues of conspecifics occur to guide habitat selection. If competition occurs among individuals at high densities, which was not incorporated into the model, then attraction should decline at very high densities. Second, species using attraction should exhibit sensitivity to fragmentation by avoiding small patches, and to a lesser extent edges, in the absence of other factors. The model predicts that if conspecific cues are present in fragmented areas, individuals normally thought to avoid fragmented habitats will settle in these areas. Experiments



**Figure 5:** Short-term fitness (survival × fecundity) for individuals using conspecific attraction and direct sampling of habitat relative to a random habitat selection strategy (relative rate ± SE), in which mortality rate (A), population density (B), habitat loss (C), or habitat fragmentation (D) influences relative survival rates. A, Example of relative fitness rates when mortality varies for individuals with moderate perceptual ranges (four-cell radius), in landscapes that are moderately fragmented ( $H = 0.5$ ) and moderate in habitat loss (30% of habitat remains) and have moderate population density ( $d = 0.4$ ) and moderate habitat quality. B–D, Examples when population density (B), habitat loss (C), or fragmentation (D) varies, relative to the example in A, for animals experiencing low mortality rates (0.001 per time step).  $H$  denotes the spatial contagion, or fragmentation, of fractal landscapes (with  $H = 0.0$  being more fragmented and  $H = 1.0$  being less fragmented).

**Table 2:** ANOVA summary for factors influencing distribution patterns of individuals using conspecific search, conspecific settlement, and conspecific search and settlement relative to a random search and settlement strategy

Source	df	Conspecific search		Conspecific settlement		Conspecific search and settlement	
		MS	%MS	MS	%MS	MS	%MS
Patch size summary:							
Density	1	10.18	24.5	2.83	12.0	10.61	14.6
Frag	2	8.39	20.2			22.49	31.0
Mortality	1			4.33	18.4		
Size	1	6.02	14.5			19.22	26.5
Density × frag	2	4.48	10.8	2.93	12.4		
Density × size	1			3.36	14.3		
Distance from edge summary:							
Edge	1	.91	17.5	1.65	18.8	4.55	39.7
Frag	2					1.80	15.7
Mortality	1			1.14	13.0		
Density × edge	1			.90	10.2		

Note: Only factors contributing to more than 10% of total mean square (MS) error are reported. For all factors reported,  $P < .0001$ . Density = population density; frag = habitat fragmentation; size = patch size; edge = distance from edge. For habitat fragmentation, simple random landscapes were not included in the analysis because of little variation in patch size and distance from edge (table A1 in the online edition of the *American Naturalist*).

could test this prediction by manipulating conspecific cues in fragmented and intact habitats.

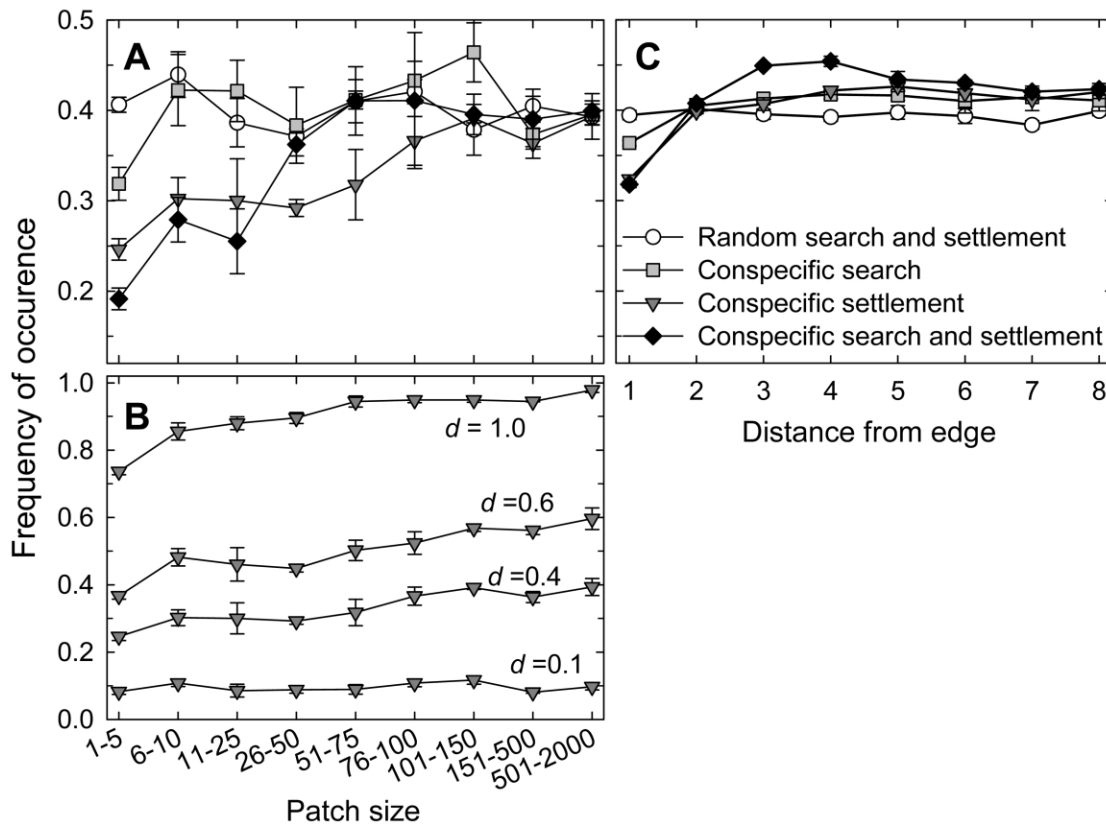
While the model presented here provides a general assessment of the short-term effects of conspecific attraction in fragmented landscapes, it was not intended to simulate the behaviors of specific species (see Dumont and Hill 2001 for an example). Some model parameters would be difficult to estimate in the field, yet I chose this approach to allow full exploration of the potential behavior of conspecific attraction. In addition, for some parameters I used constant values within strategies based on the best average fitness estimate across all model permutations. Such an approach may be appropriate for generalist species or species that have panmictic populations occupying a broad range of environmental conditions. Nonetheless, pilot simulations suggested that the model was not sensitive to changes in many parameters (e.g., changing memory by 20% for conspecific search, habitat search, and habitat quality strategies resulted in a  $<0.001$  change in average survival rates). Investigating long-term effects of conspecific attraction on population dynamics and the evolution of habitat selection may also yield substantial insights into the costs and benefits of this behavior (see Doligez et al. 2003).

### Conclusions

Conspecific attraction can substantially influence the dynamics and distributions of animals, which has

wide-ranging ramifications for the recent theoretical accounts of using socially acquired information and for habitat selection theory (Greene and Stamps 2001; Doligez et al. 2003; Morris 2003; Danchin et al. 2004; Dall et al. 2005). By partitioning when attraction influences habitat selection, the model suggests that the costs and benefits of this behavior differ when used in searching and settlement decisions. Thus, the timing of using socially acquired information may be critically important in the evolution of these behaviors. Furthermore, model results challenge habitat selection theory by suggesting that using conspecifics in habitat selection can result in short-term fitness similar to, or potentially better than, that attained from directly sampling habitat quality in some situations, such as when individuals incur high search costs or in landscapes containing high population densities (fig. 5; see also Mönkkönen et al. 1999).

Results from the model suggest that conspecific attraction is one potential mechanism—previously unappreciated by conservation biologists and landscape ecologists—underlying the effects of patch size and habitat edge that have been observed across many taxa (e.g., Bender et al. 1998; Ries et al. 2004). Predicting the likelihood of these effects will depend on understanding the ultimate factors responsible for attraction and landscape context. While manipulating social cues to attract animals to suitable but unused areas has been suggested (Stamps 1988; Reed and Dobson 1993; Ward and Schlossberg 2004), the efficacy of



**Figure 6:** Examples of emergent distribution patterns (frequency of occurrence  $\pm$  SE) as a function of patch size and distance from edge for different habitat selection strategies. A, C, Examples of patch size (A) and edge effects (C) for individuals with moderate perceptual ranges (four-cell radius) in landscapes that are moderately fragmented ( $H = 0.5$ ), are moderate in habitat loss (30% habitat remains), and have moderate population density ( $d = 0.4$ ). B, Example of how population density influences patch size effects for individuals using conspecific settlement, relative to the example in A.

such an approach remains relatively unknown, particularly in complex situations such as landscapes undergoing habitat loss and fragmentation. Nonetheless, results presented here suggest that conspecific attraction can have strong implications for habitat selection and that these effects can potentially be amplified with ongoing landscape change.

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R. L. Hutto and PPL Montana provided support while this manuscript was written. J. J. Fontaine, J. L. Orrock, E. Revilla, B. A. Robertson, and two anonymous reviewers critically reviewed previous drafts of this manuscript, which greatly improved and clarified the ideas presented here.

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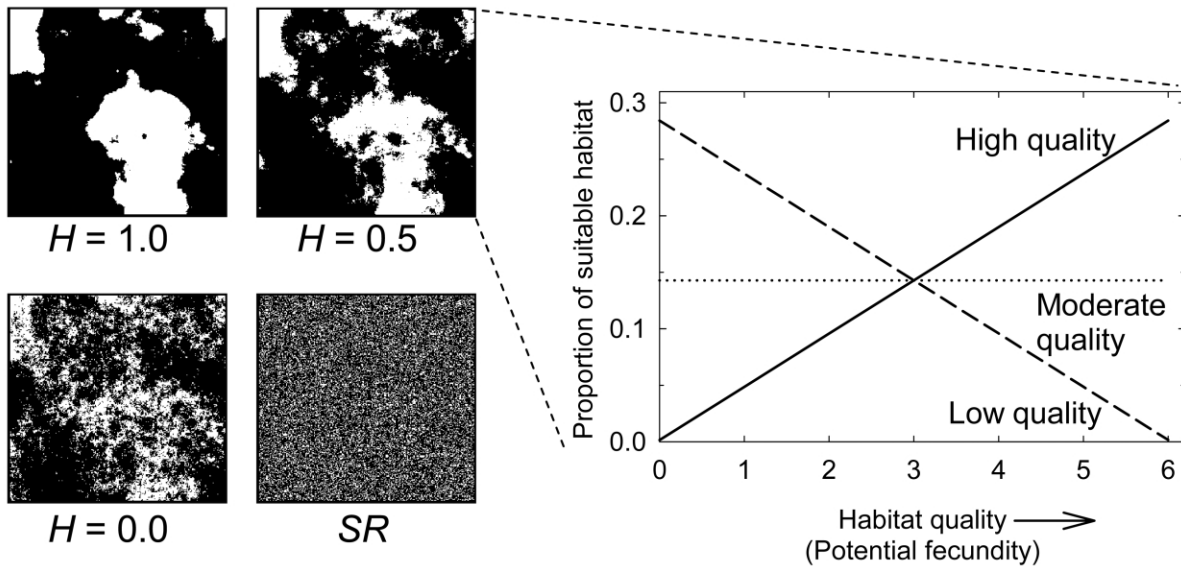
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## Appendix A from R. J. Fletcher, “Emergent Properties of Conspecific Attraction in Fragmented Landscapes”

(Am. Nat., vol. 168, no. 2, p. 207)

### Examples and Characteristics of Fragmented Landscapes Used in Modeling Habitat Selection Strategies



**Figure A1:** Examples of theoretical landscapes used for linking conspecific attraction to fragmented landscapes when 30% of the landscape is suitable habitat and of the variation in habitat quality within suitable habitat (i.e., high-, moderate-, and low-quality landscapes). Suitable habitat is denoted in white; unsuitable matrix is in black. Fragmentation was varied by changing  $H$ , the spatial contagion of the fractal landscape, and comparing these fractal landscapes with simple random (SR) landscapes (Gardner 1999).

**Table A1**

Some physical characteristics of the theoretical landscapes (generated by program RULE; Gardner 1999) used for linking conspecific attraction to fragmented landscapes

Landscape fragmentation, amount of habitat <sup>a</sup>	Mean number of patches	Patch size		Proportion near edge <sup>b</sup>
		Mean	Maximum	
SR:				
10	948.6	2.4	10	1.00
30	3,448.4	3.9	42	1.00
50	2,117.4	13.6	400	1.00
<i>H</i> = .0:				
10	515.2	9.9	1,641	.95
30	796.2	22.2	6,395	.84
50	624.8	50.3	24,984	.72
<i>H</i> = .5:				
10	62.2	102.4	4,302	.44
30	114.6	170.8	10,367	.36
50	113.4	300.9	31,621	.26
<i>H</i> = 1.0:				
10	8	855.5	5,489	.22
30	10	2,086.7	11,597	.15
50	9.8	3,571.6	32,732	.10

<sup>a</sup> SR = simple random (most fragmented); 0.0, 0.5, and 1.0 refer to the spatial contagion (or clumping) parameter, *H*, of fractal landscapes. Five landscapes were generated for each landscape type (*n* = 60 landscapes). Amount of habitat refers to the percentage of suitable habitat in the landscape (a 256 × 256 grid). Thus, the total number of suitable cells (potential territories) in the landscape ranged from 6,554 to 32,768.

<sup>b</sup> Mean proportion of suitable habitat located within two cells of an edge.

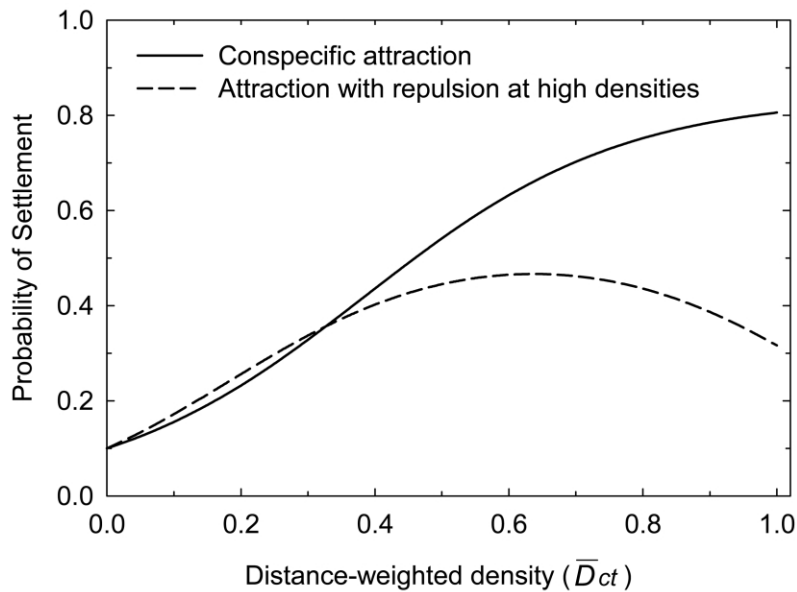
## Appendix B from R. J. Fletcher, ‘Emergent Properties of Conspecific Attraction in Fragmented Landscapes’

(Am. Nat., vol. 168, no. 2, p. 207)

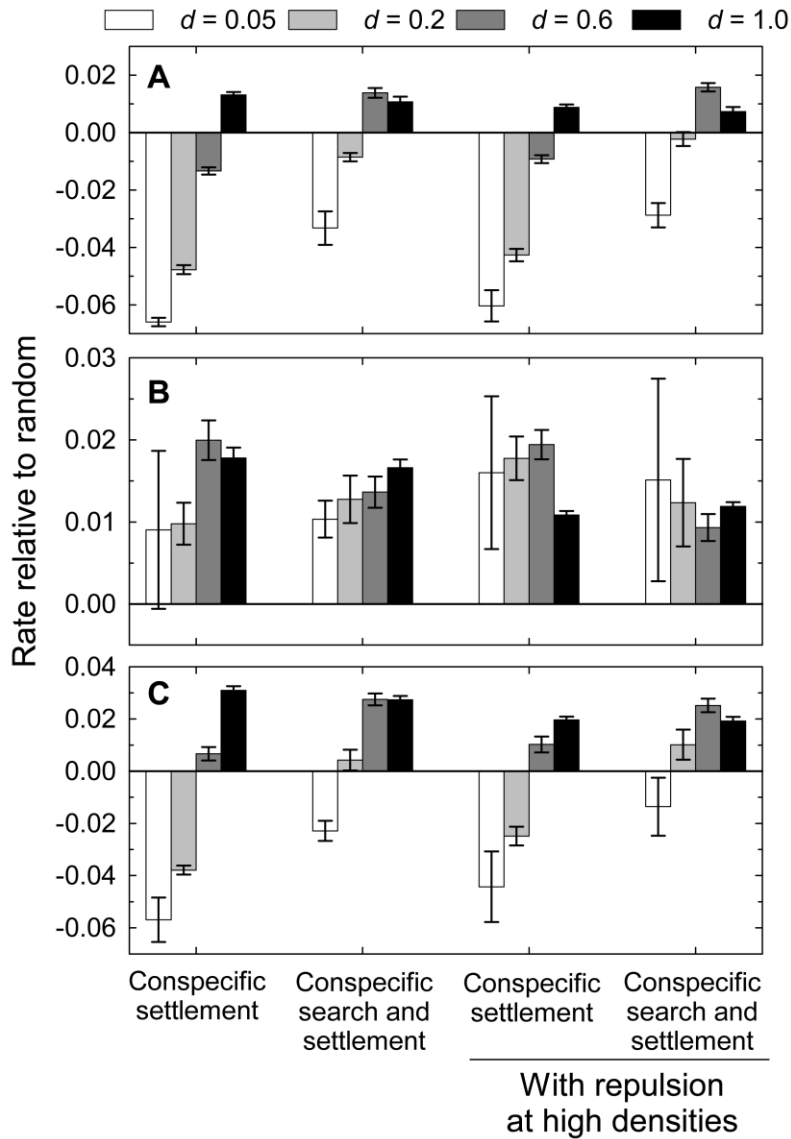
### Influence of Repulsion at High Densities on Conspecific Attraction

When conspecific attraction occurs during habitat selection, it is possible that attraction operates only at low to moderate densities, whereas avoidance operates at high densities because competition with conspecifics for limiting resources may outweigh any potential benefits gained from settling near conspecifics (Fretwell and Lucas 1970; Greene and Stamps 2001; Stamps 2001). To address this potential strategy, I considered a settlement strategy where individuals were more likely to settle in areas with moderate conspecific densities by altering equation (4) to include a quadratic term (fig. B1). I compared this strategy to random search and settlement, where the probability of settlement was set equal to the average probability of settlement for an attraction/repulsion settlement strategy in each landscape.

Incorporating repulsion at high densities either alone or in concert with a conspecific search strategy generally had similar effects as compared to conspecific settlement in the absence of repulsion. Overall, variation in survival rates, fecundity, short-term fitness, and patterns of distribution were explained by the same factors as for conspecific settlement and conspecific search and settlement (see tables 1, 2). However, including repulsion slightly weakened these effects (smaller mean square errors) and generally increased nonlinearity of effects, particularly the effects of population density (e.g., fig. B2).



**Figure B1:** Conspecific attraction during settlement with and without repulsion at high local densities, where the probability of settlement varies as a function of distance-weighted density (the estimated density within the current perceptual range of an individual). Probability of settlement was estimated as  $p_{ct} = \gamma \exp(\beta_0 + \beta_1 \bar{D}_{ct}) / (1 + \exp[\beta_0 + \beta_1 \bar{D}_{ct}])$ . For attraction,  $\beta_0 = -2$ ,  $\beta_1 = 5.2$ , and  $\gamma = 0.839$ . For repulsion at high densities, a quadratic term was added to the above equation:  $\beta_0 = -2$ ,  $\beta_1 = 7$ ,  $\beta_2 = -5.7$ ,  $\gamma = 0.839$ .

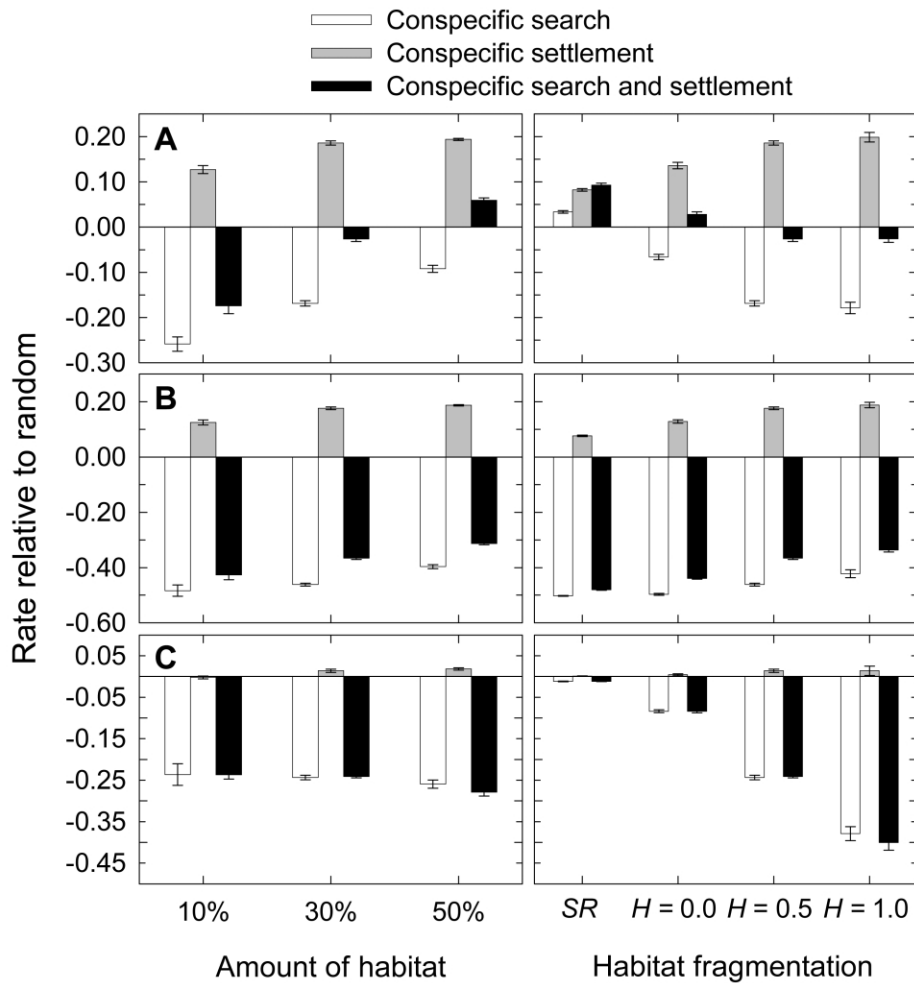


**Figure B2:** Examples of survival (A), fecundity (B), and short-term fitness (C) of conspecific attraction during settlement and attraction with repulsion at high densities relative to random habitat selection as a function of population density ( $d$ ). For each example, results are presented for individuals with moderate perceptual ranges (four-cell radius), in landscapes that are moderately fragmented ( $H = 0.5$ ), have moderate habitat loss (30% of landscape is suitable habitat), and are of moderate habitat quality (equal proportions of low- and high-quality habitat).

## Appendix C from R. J. Fletcher, “Emergent Properties of Conspecific Attraction in Fragmented Landscapes”

(Am. Nat., vol. 168, no. 2, p. 207)

### Influence of Conspecific Attraction on Movement and Dispersal Efficiency



**Figure C1:** Examples of total time spent dispersing (A), net distance moved (B), and the proportion of time spent in the matrix (C) for individuals using conspecific attraction, relative to random habitat selection (relative rate  $\pm$  SE). For panels comparing habitat loss, results are shown for individuals that have moderate perceptual ranges (four-cell radius) and experience high mortality rates (0.01 per time step) in moderately fragmented landscapes ( $H = 0.5$ ). For panels comparing landscape fragmentation, results are shown for individuals that have moderate perceptual ranges (four-cell radius) and experience high mortality rates (0.01 per time step) in landscapes with moderate habitat loss (30% habitat).  $H$  denotes the spatial contagion, or fragmentation, of fractal landscapes (with  $H = 0.0$  being less clumped, or more fragmented, and  $H = 1.0$  being more clumped, or less fragmented), while  $SR$  denotes simple random landscapes.