Local Movement and Edge Effects on Competition and Coexistence in Ephemeral-Patch Models

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ABSTRACT: For insects exploiting spatially structured arrays of resource patches (host plants, fungi, carrion, etc.), the distribution of individuals among patches can have important consequences for the coexistence of competitors. In general, intraspecific aggregation of consumer individuals over the landscape of patches stabilizes competition. Oviposition behavior of individual females can generate aggregation of larvae across patches and, therefore, strongly influences the outcome of competition between co-occurring species. We used simulation models to evaluate the consequences (for the coexistence of competitors) of different movement behaviors by females before and between oviposition events. Coexistence times increase when females are more likely to travel among neighboring patches than among distant ones. Coexistence times are also longer when females begin egg laying near the site of their emergence. Preoviposition dispersal is, therefore, destabilizing. We also considered responses by females to edges of resource arrays. Edge effects are generally stabilizing, delaying competitive exclusion by increasing larval aggregation, but different responses to edges have dramatically different effects on coexistence. The longest coexistence times occur when edges are "sticky," such that females encountering an edge tend to remain there.

Keywords: clutch size, competition, coexistence, edge effect, oviposition, movement.

Many insects and other mobile consumers exploit resources that occur as small, discrete, and more or less ephemeral patches, such as fungi, fallen fruit, carrion, or annual host plants. Although a single patch (by which we mean an undivided unit of resource, such as one host plant or one mushroom) often supports only one generation of consumers and competition in that patch can be intense, patchy systems can support surprisingly diverse and apparently stable assemblages of species. The frequent existence of strong local competition (e.g., Kneidel 1985; Hanski 1990; Blossey 1995) suggests that resource partitioning is insufficient to explain this observation, and therefore, other mechanisms have been sought that might foster the coexistence of competitors in patchy systems.

Many studies have focused on spatial pattern in patchy systems and, in particular, on the aggregated distributions of consumer individuals among patches. Insects exploiting patchy resources often show strongly aggregated distributions, and in some theoretical models (Atkinson and Shorrocks 1981; Heard and Remer 1997), aggregation can allow extended and even stable coexistence of competitors without resource partitioning. However, there has been much controversy over the mechanisms by which aggregated distributions are generated and over the consequences (for coexistence) of aggregation produced by different mechanisms (Heard and Remer 1997). Because different forms of aggregation may have different consequences, ecologists must explore realistic models that incorporate the mechanisms underlying the distribution of consumers in patchy systems. In this article, we focus on aggregation arising from the movement behavior of females before and between oviposition events.

In a previous paper (Heard and Remer 1997), we considered aggregation arising from the laying of eggs in clutches and examined the effects of behavior that adjusts clutch size in response to costs of travel among patches. In that model, we kept patch choice random, allowing us to focus attention on clutch size behavior without other confounding sources of aggregation. However, random patch choice is not realistic: even if patches are all identical in terms of resource quantity and quality, they will differ spatially for two reasons. First, a female leaving one patch and traveling to another should be more likely to

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choose a neighboring patch than a distant one, either because of behavior minimizing travel costs or because nearby patches are the first to be detected. Whatever the mechanism, localized movement during oviposition generates intraspecific aggregation on a spatial scale somewhat larger than that due to clutch laying and, therefore, introduces neighborhood structure. Second, some patches differ because they are located at the edge of a resource array (a set of patches separated in space from other sets; e.g., a stand of host plants, the fruit shadow of a tree, or mushrooms in a forest fragment). Ovipositing females may respond in a number of different ways when they encounter edges. In this article, we examine some important consequences of local movement and responses to edges for aggregation, competition, and coexistence of species using patchy, ephemeral resources.

Methods

We took a simulation approach to the female movement problem, using a computer program written in QuickBASIC (Microsoft 1988) to examine the effects of oviposition behavior on the coexistence of two competitors in a system of discrete and ephemeral resource patches (for more details, see Heard and Remer 1997). All patches are assumed identical, generations are nonoverlapping, and patches are renewed for each generation of competitors. We focus on the common case where larvae are much less mobile than adults. We ignore, therefore, the possibility of dispersal by larvae.

In our previous models (Heard and Remer 1997), all patch choices were random, so aggregation resulted only from clutch laying. Here we add two complications: localized movement and behavior at edges. The effect of each is to generate intraspecific aggregation at a neighborhood scale. We are interested in the extent to which different movement behaviors determine whether stable coexistence is possible, and if it is not, in how movement behaviors influence the duration of coexistence. We used simulations instead of analytical models because we considered the transient (short-term) behavior of our models to be just as important as the existence or nature of equilibria (see Heard and Remer 1997).

In each simulation, we begin with adults of two species (100 of each), differing in competitive ability and living on a 10 × 10 array of patches. In our model, these are the only patches in the universe, so we ignore the possibility of consumers moving among multiple arrays (e.g., Kareiva 1982). Each adult is designated male or female with equal probability (in our model, we include, therefore, effects of random sex-ratio variation on the persistence of small populations). Males are not considered

further. For each female, a first patch is chosen at random (except see "Natal Variants" below) and a clutch of c_i eggs (for a female of species i) is laid there. A second patch is then chosen (see below), and a second clutch (again of size c_i) is laid. This continues until the female exhausts her egg supply and is repeated for each female of each species. Choice of a patch is independent of whether, or how many, eggs are already there. We assume that each female has a fixed egg supply (of λ eggs), an assumption met by many, but not all, insects (Büning 1994).

Once all females of both species have laid their eggs, a Hassell-Comins competition equation (Hassell and Comins 1976) determines the number of emerging adults for each species in each patch. This competition model is familiar and flexible and often fits field data well (e.g., Atkinson and Shorrocks 1981). Let y_1 and y_2 be the yield of adults from a patch for species 1 and species 2, respectively; these are the survivors of the e_1 eggs of species 1 and the e_2 eggs of species 2 that were laid in that patch.

$$y_1 = e_1 \left[1 + a(e_1 + \alpha_{12}e_2)\right]^{-b},$$

where $a = 2[(\lambda/2)^{1/b} - 1]/(\lambda K)$. Parameters and equations for species 2 have subscripts 1 and 2 reversed; for simplicity, we assume the two species have identical values of K, λ, a, and b (so these parameters are not subscripted). The factors of two in the expression for a arise because we assumed a 1∶1 sex ratio and allowed only females to lay eggs. The carrying capacity, K, is the number of adults produced each generation by a one-patch system at equilibrium (Heard and Remer 1997), and α_{12} is a competition coefficient expressing the impact of species 2 on species 1. The shape parameter, b, allows for competition functions ranging from pure scramble through pure contest (we used $b = 1$, a value within the range of data for insects with larval competition; Hassell 1975; Shorrocks and Rosewell 1987). Table 1 lists a set of parameter values used for most simulations, chosen so that, without neighborhood structure or edge effects, the superior competitor (species 2) excludes the inferior (species 1) at a moderate rate. The trends in our results are not sensitive to our choice of parameter values: with different parameter combinations, coexistence times change, but trends in coexistence times with changes in oviposition behavior do not.

After considering competition within patches, the program calculated the total number of emerging adults of each species; these adults laid the next generation of eggs. We assumed that consumer pressure does not regulate the dynamics of the patches (donor control), so we held the number of patches constant between generations. This assumption is appropriate for many patchy re-

Table 1: Parameters for the competition models

Parameter	Meaning	Usual value
α_{12}	Interspecific competition strength (superior on inferior)	1
α_{21}	Interspecific competition strength (inferior on superior)	.5
λ	Female fecundity	16
a	Compound parameter: function of λ, b, and K	.21875
b	Shape of completion (scramble/contest)	1 (contest)
c_1	Clutch size, inferior competitor	2
c_2	Clutch size, superior competitor	4
K	Carrying capacity per patch	4

Note: K, λ, a, and b are assumed to be equal for the two species and are, therefore, not subscripted.

sources (e.g., dung, fungi, fallen fruit) but not for others (e.g., annual plants).

A simulation ended either when one species became extinct or after 10,000 generations without extinction. We considered a species extinct when it was represented by fewer than two adults, and we report coexistence times in number of generations averaged over 100 simulations. We draw a careful distinction between prolonged but finite coexistence and formal stability. Parameter combinations running 10,000 generations may not be formally stable (in fact, all of our populations are finite and, therefore, eventually doomed to stochastic extinction). However, the absence of formal stability is probably unimportant if extinction requires 10,000 generations, as this far exceeds the expected timescales of environmental perturbations and evolutionary change (Heard and Remer 1997). We use "stabilize" to mean "prolong coexistence" without implying that coexistence lasts forever.

At each generation, we calculated measures of aggregation and competition within and between species. We defined the impact of interspecific competition on a species as the proportional reduction in its population size inflicted by the presence of its competitor (Heard and Remer 1997). For aggregation, we use Ives's index J (Ives 1991), calculated from the number of eggs (not clutches) on each patch: $J = V/M^2 - 1/M$, where M is the mean and V the variance of egg counts across patches. While aggregation and competition indices change slightly from generation to generation in any simulation, for simplicity, we show this data for a single-generation snapshot. We chose to focus on the generation in which the inferior species makes up 30% of the total density. Patterns in aggregation and competition are generally well estab-

lished at this point, and trends in our results are not sensitive to our choice of this particular generation.

Neighborhood Movement

We used three different models to examine the effect of neighborhood (locally restricted) movement by females. In each, initial patch choice for each female is random (except in the natal variants; see "Natal Variants" below), but subsequent choices are not. Instead, a female tends to select a new patch close to its last oviposition site. The algorithms controlling moves between oviposition events differ among the models, but the effect is always to introduce intraspecific aggregation on a neighborhood scale.

Homogeneous Neighborhood Model. With homogeneous neighborhoods, each patch after the first is chosen at random from those patches within d_h array positions (along rows and columns) of the previous one. When $d_h = 10$, there is no neighborhood structure. If $d_h = 1$, there are nine possible patches (including the previous patch, which may be revisited); if $d_h = 2$, there are 25, and so on.

Graded Neighborhood Model. With graded neighborhoods, the probability of a patch being chosen is a linear function (with slope $m \leq 0$) of its distance from the previous patch. This function imposes a distance d_g beyond which no movements occur. When $m = 0$ ($d_g = \infty$), there is no neighborhood structure. As m becomes more negative, a female's likelihood of choosing patches near the previous oviposition site increases. In the extreme ($m = -33$, $d_g = 1$), the next oviposition must occur among the patches immediately adjacent to or on the previous site.

Hierarchical Neighborhood Model. In the hierarchical model, the 10×10 array is divided into four 5×5 clusters. Movement is controlled by specifying the probability (P_{leave}) that a female will leave its current cluster. Patch choice within the cluster is random, and, should a female leave her cluster, patch choice becomes random over all other patches. When $P_{leave} = .75$, there is no neighborhood structure. A decrease in P_{leave} reduces neighborhood size. This model was inspired by models developed by B. Inouye (personal communication).

Natal Variants. In the models described so far, the patch for each female's first oviposition was chosen at random. We refer to these as adult-mixing models because they model emerging adults dispersing freely across the entire array before beginning oviposition. We also modeled consumers lacking preoviposition dispersal, using vari-

ants of each model in which each female's first oviposition visit was made to the new patch closest to the patch from which she emerged. In these natal variants, aggregation patterns are passed on from generation to generation.

Dealing with Edges

In finite arrays (real or modeled), females may encounter edges. In the homogeneous and graded models, and their natal variants, our algorithms specify a direction and distance to be moved; for instance, a female might be instructed to move five patches east when she is only two patches from the east edge. (Edge effects do not occur in our hierarchical model.) We devised three approaches to deal with movement directed beyond an edge, representing different but biologically reasonable ways in which traveling consumers may respond to edges. In all simulations, north/south and east/west movements are concurrent but separate, so that an edge affecting movement along one axis does not affect movement along the other.

Edgeless Arrays. Our first method of dealing with edges was to eliminate them: we allowed a female moving off an edge to reenter the array on the other side. For instance, a female on patch 8 directed east five patches to (nonexistent) patch 13 would land instead on patch 3. Topologically, this is equivalent to wrapping the resource array onto a torus. Biologically, an edgeless 10×10 array is equivalent to a 10×10 focal area taken from a much larger array: a female wrapping around an edge is equivalent to one female leaving the focal area while another arrives. On average, for any focal area in a large array, each female leaving will be replaced by another arriving.

Reflective Edges. A reflective edge is one at which a female directed to move beyond an edge arrives at the edge and then moves back toward the center of the array. Here, a female on patch 8 directed east five patches will move two patches to the edge (patch 10), and then three patches back toward the interior, landing on patch 7.

Sticky Edges. When edges are sticky, a female that would otherwise move past an edge is retained at the edgemost patch. In this case, a female on patch 8 directed to move five patches east will move two patches to the edge and oviposit there. Because the algorithm chooses the direction of movement randomly, once on the edge, a female will remain there for the next oviposition 50% of the time.

Results and Discussion

Within an edge treatment, all models were in agreement when run without neighborhood structure ($d_h = 10$, $m = 0$, or $P_{leave} = .75$). For models with neighborhood structure, we first compare neighborhood models for edgeless arrays and then address edge effects separately.

Neighborhood Structure

Coexistence is extended when each female lays subsequent clutches in a small neighborhood around the first patch she visits. This effect is above and beyond the stabilizing effect of clutch laying itself (Heard and Remer 1997). The details of the behavior producing neighborhood structure are not important; results were qualitatively similar in all three of our models (fig. 1; neighborhood structure is always strongest, i.e., neighborhoods are smallest, to the left). We would expect similar results from more mathematically complicated forms of neighborhood movement, such as diffusion (Kareiva 1982).

Aggregation generated at the neighborhood scale prolongs coexistence in the same way that patch-scale aggregation due to clutch laying does (Heard and Remer 1997): it changes the balance between interspecific and intraspecific competition. Neighborhood movement imposes intraspecific (but not interspecific) aggregation of larvae at the spatial scale of the neighborhood. Aggregation of the superior competitor relaxes its impact on the inferior competitor for two reasons: directly, because aggregation creates spatial variation in the density of the superior competitor, leaving low-density patches as partial refuges from competition; and indirectly, because aggregation intensifies intraspecific competition among superior competitors and, therefore, reduces their mean density. Both effects favor coexistence, although the direct effect of aggregation is generally more important (S. B. Heard and L. C. Remer, unpublished data).

In all three models, the strongest effects of neighborhood behavior are seen when the inferior competitor lays small clutches and the superior competitor lays moderately large ones (fig. 2; cf. bars within groups of four). Small clutch sizes give females more opportunities to move, making movement distance more important, but for the superior competitor, this is partly offset by the stabilizing effect of large clutch sizes themselves (Heard and Remer 1997).

The intensity of the neighborhood effect differs somewhat among our models, but it is often strong. For adult-mixing models, the strongest effects were for the graded model (fig. 1). This is expected because, for the same nominal neighborhood size, graded models generate the
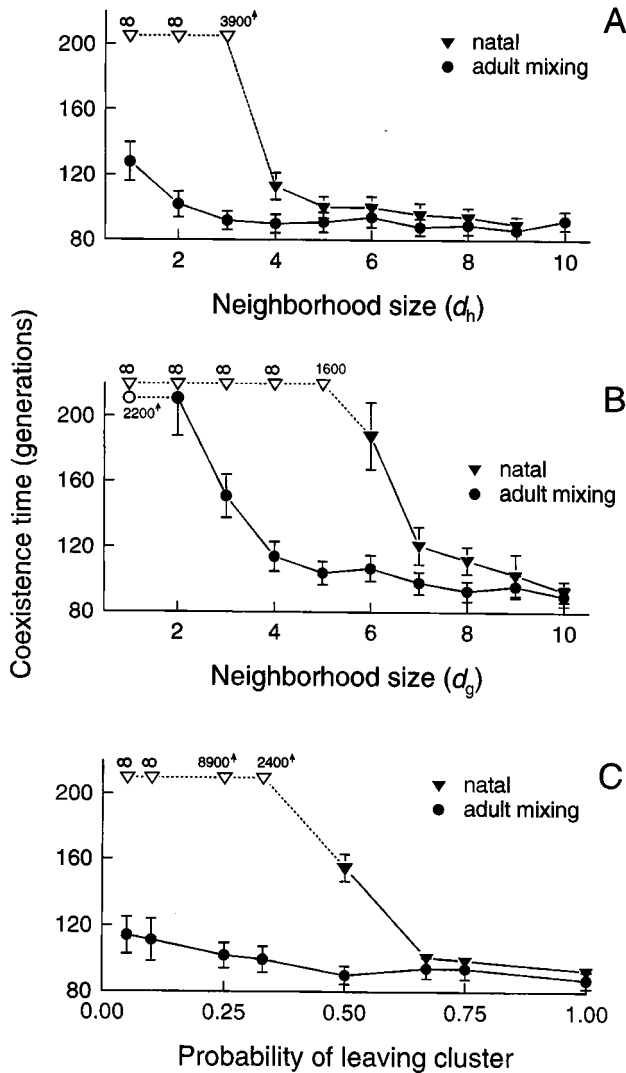
Figure 1: Effects of neighborhood structure on coexistence for three neighborhood models (with adult mixing and natal variants of each). Parameter values as in table 1. Symbols show $\overline{X}$ $\pm$ 2 SE; for filled symbols, bars not shown are hidden by the symbols. Open symbols and dashed lines are not to scale (upward-pointing arrow indicates an underestimate because only some simulations ran to extinction; the infinity symbol denotes 10,000 generations of coexistence in all runs). Neighborhood structure is always strongest to the left. *A,* Homogeneous model; d_h is the maximum movement distance. *B,* Graded model; d_g is the maximum movement distance. *C,* Hierarchical model; increasing the leaving probability means weaker neighborhood structure.
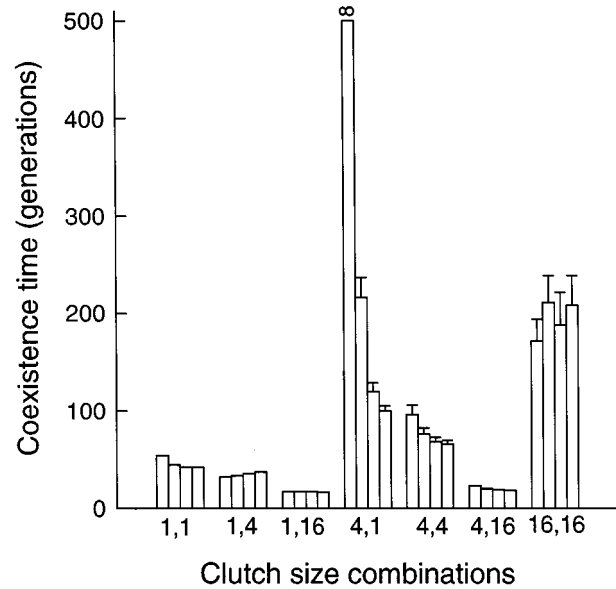

Figure 2: Coexistence times for various clutch size combinations (graded neighborhood model). First clutch size is superior species, second is inferior species. Each group of bars represents neighborhoods of $d_g = 1, 3, 5,$ and 10. Other parameter values as in table 1. Bars show $\overline{X} \pm 2$ SE; errors not shown are <1.4. The symbol for infinity denotes 10,000 generations of coexistence in all 100 runs. For clutch sizes 16 and 16, neighborhood size does not matter because females lay only a single clutch.

most central distribution of larvae around the initial oviposition site.

For large neighborhoods, results for natal variants resemble those of the adult-mixing models. However, for moderate to small neighborhoods, natal variants have greatly extended coexistence, with many parameter combinations running indefinitely (>10,000 generations). In the natal variants, effects of neighborhood size on coexistence are enhanced because the aggregation of eggs produced in the first generation is passed on as a template for initial oviposition in the next generation. In contrast, in adult-mixing models, aggregation must be reestablished each generation. These results suggest that, when dispersal is primarily within resource arrays, the presence in consumer life history of a preoviposition dispersal stage is destabilizing (although dispersal between arrays can be stabilizing; Holyoak and Lawler 1996). This is a new and interesting prediction.

Edge Effects

Because all resource arrays have edges and edges make up a substantial portion of many patchy systems, behavior at edges may have important consequences for population dynamics. We modeled relatively small arrays (100
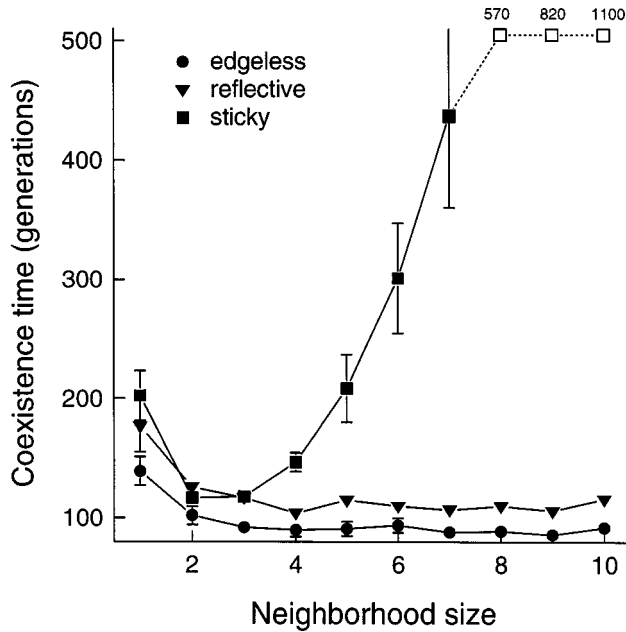
Figure 3: Changes in coexistence times with neighborhood size and edge treatments (homogeneous model). Parameter values as in table 1. Symbols show $\overline{X} \pm 2$ SE; for filled symbols, bars not shown are hidden by the symbols. Open symbols and dashed lines are not to scale.

Figure 4: Edge effects for a range of superior species clutch sizes. Inferior species clutch size 2; homogeneous neighborhood model with $d_h = 7$. Other parameter values as listed in table 1. Symbols show $\overline{X} \pm 2$ SE; for filled symbols, bars not shown are hidden by the symbols. Open symbols and dashed lines are not to scale (upward-pointing arrow indicates an underestimate because only some simulations ran to extinction; the infinity symbol denotes 10,000 generations of coexistence in all 100 runs).

patches) and consequently saw very strong edge effects. The relative importance of edge effects should decrease as the modeled array gets larger.

For all neighborhood sizes, coexistence times were longer for arrays with reflective edges than for edgeless arrays (fig. 3). Sticky edged arrays produced more complex results: for small neighborhoods ($d_h \leq 3$), coexistence times resembled those for reflective edges, but for larger neighborhoods, coexistence times for sticky edges treatments were dramatically longer than for our other treatments (fig. 3). Effects of sticky edges are especially strong when clutch sizes are small (fig. 4) because then individuals move repeatedly and are more likely to encounter and to remain at edges.

Why do responses to edges affect coexistence times? The answer lies in patterns of inter- and intraspecific aggregation and competition experienced by the inferior species (the persistence of which determines coexistence time). In our models, intraspecific aggregation (fig. 5A) is generated in two ways: through neighborhood movement by ovipositing females and when females are delayed or stuck at edges. (Interspecific aggregation also increases when females are stuck on edges, but the effect on intraspecific aggregation is stronger.) Patterns of aggregation in turn determine the intensity of competition (fig. 5B). At any neighborhood size, as we move from edgeless to reflective to sticky edge treatments, the ratio
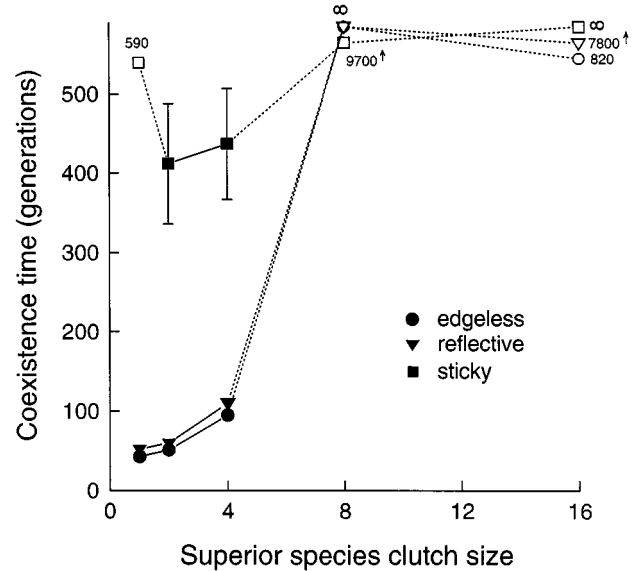
of intraspecific to interspecific competition increases (fig. 5B). As in most models, as intraspecific competition increases in importance relative to interspecific competition, coexistence becomes more likely. The striking difference in the competition ratio for edgeless and sticky boundary treatments at large neighborhoods parallels the difference in coexistence times (fig. 5C) for the same comparison. This difference is smaller for smaller neighborhoods, when females encounter edges less often.

In our models, edge effects result from females encountering edges during movements from the interior of the array. When a landscape contains multiple arrays and females disperse among them, they will also intercept edges when entering an array from outside, and edges may also be sticky with respect to these movements (see fig. 6 in Grünbaum 1998). Such effects should further strengthen the stabilizing effects of edges.

General Discussion

Incorporating individual behavior on spatially structured landscapes can yield valuable insights into the ecology of populations and communities (Lima and Zollner 1996; Roitberg and Mangel 1997). We found that both female movement behavior before and between oviposition
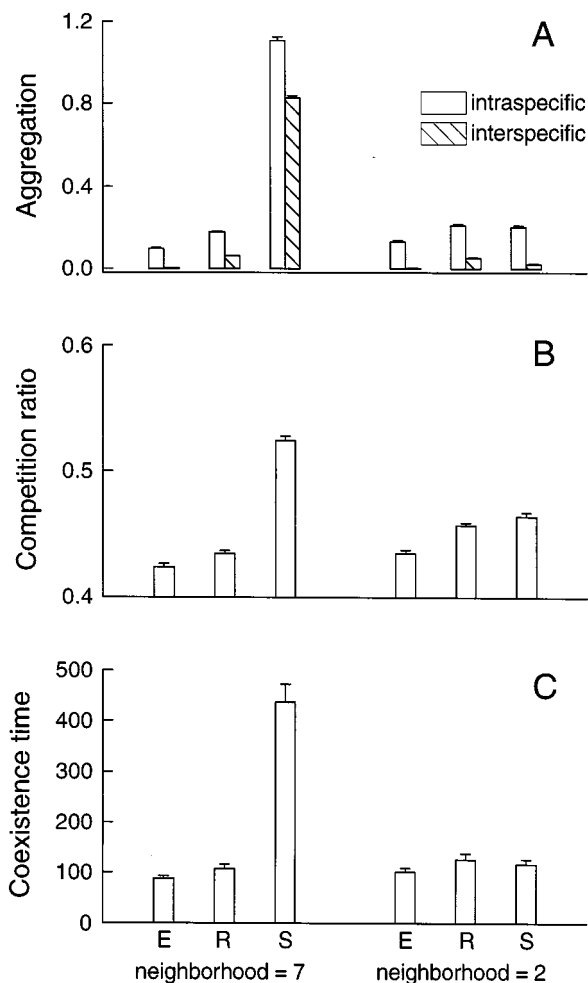
Figure 5: Effects of edge treatments and neighborhood size on aggregation, competition, and coexistence (homogeneous model; for a single generation in which inferior competitors have been reduced to 30% of the total). Parameter values as in table 1. Symbols show $\overline{X} \pm 2$ SE. E = edgeless, R = reflective edges, S = sticky edges. A, Inter- and intraspecific aggregation values. B, Ratio of intraspecific to interspecific competition. C, Coexistence times.

events and responses to array edges can have important and unexpected effects on community dynamics.

Behavior governing movement among patches in a resource array certainly varies among species (Kareiva 1983; Antolin and Addicott 1991; Jones et al. 1996; Heard 1998). Dispersal behavior also varies within species, being influenced by factors including wind (Morrow et al. 1989), odor (Bernays 1994), resource array size and density (Heard 1998), landscape features (Munguira and Thomas 1992), population density (Herzig 1995), and female age and reproductive status (Messina 1982). Both the tendency for localized movement and the degree to

which movement approximates simple dispersal models vary among and within species (Kareiva 1983; Antolin and Addicott 1991). We suspect that movement between oviposition events will vary from stepping-stone behavior (movement only between adjacent patches) to movement that is nearly unrestricted in space, and we appeal for more empirical studies of fine-scale female movement. Our models indicate that the degree of neighborhood structure introduced by local movement behavior may be an important parameter influencing a population's likelihood of coexistence with competitors.

Edges of resource arrays are likely to provoke a variety of responses by moving individuals. For instance, among butterflies in roadside vegetation, roads (habitat edges) inhibit movement of some species but stimulate movement of others (Munguira and Thomas 1992). In a number of insect species, individuals execute turns when they leave areas of suitable habitat (Bell 1991), resulting in movement along a continuum from our reflective-edge models (when turn angles are $\approx 180°$) to our sticky-edge models (when turn angles are $\approx 90°$). Movement behavior may contribute (along with plant quality; Cappuccino and Root 1992) to a common pattern in which densities of herbivorous insects are highest along the edges of host plant stands (e.g., Courtney and Courtney 1982); such a pattern was apparent in our sticky edged arrays. Our models predict that behavior at edges will be most important when arrays of patches are small, when females lay multiple clutches (fig. 3), and when neighborhoods defined by female movement are not too small (fig. 4).

The implication that behavior at edges matters to community structure may have important consequences for conservation ecology, at least for species (most likely insects) ovipositing on arrays of resource patches of the kind we have modeled. Habitat fragmentation is a pervasive form of human impact on ecosystems (Soulé 1986), and one result of fragmentation is an increase in the relative amount of edge habitat. Edges have proven different from interior in many aspects of habitat quality (Yahner 1988; Saunders et al. 1991; Matlack 1993), but our models suggest another reason why edges might be different even without differences in patch quality: patches at an edge differ from interior patches in their likelihood of use by mobile consumers following plausible movement rules. The edge effects in our models extend the coexistence of competitors on arrays of patches and do so more strongly as the relative amount of edge increases. This is a novel result, and if borne out empirically, it may have important implications for some management decisions. In cases where species targeted for conservation use arrays of patches in the way we model, movement-mediated edge effects could counterbalance other deleterious

effects of edges. If so, increasing representation of edges (via fragmentation or otherwise) might even increase the likelihood of coexistence within each fragment and so assist in the maintenance of biodiversity.

In general, there are important and sometimes surprising conclusions to be drawn from the integration of individual behavior with the population and community ecology of competition on spatially structured landscapes. Our simple models demonstrate that, in theory, the fine-scale movement behavior of females during oviposition (in particular, how movement is restricted in space and how females respond to array edges) can have significant consequences for the coexistence of competitors. To what extent these local movement and edge effects are important for the dynamics of real communities remains an unanswered question. We do know that consumer movement is often restricted (e.g., Antolin and Addicott 1991), that many consumers respond to array edges (e.g., Bell 1991), and that plants along edges of host plant stands often support high consumer densities (e.g., Courtney and Courtney 1982). The next step is to ask whether fine-scale spatial structure in consumer distribution leads to spatial structure in resource exploitation and in competition, and whether this structure is important for larger- and longer-scale patterns in communities. We are now beginning to address this question with field studies of herbivore attack on experimentally created arrays of host plants.

Acknowledgments

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