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A MODEL TO EXPLAIN ECOLOGICAL PARAPATRY

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Abstract.—Ecological parapatry, in which pairs of largely allopatric taxa abut along common boundaries without hybridization, is often reported but seldom explained. A computer simulation model is developed that shows that parapatry between two species can be maintained by interspecific interaction on a cline of reducing ecological suitability for the competitively stronger species. In the model, a homogeneous environment requires much greater interaction strength to sustain parapatry than does a heterogeneous environment with alternate regions of favorable and poor habitat. The heterogeneous environment of the model is intended to mimic the environment near a well-studied parapatric boundary between two reptile tick species.

Parapatry is a distributional pattern in which pairs of largely allopatric taxa abut along common boundaries (Smith 1955; Key 1982; Bull 1991). It is a widely reported phenomenon from a broad range of taxonomic groups and geographical regions (Mayr 1978; Key 1982; Hillis et al. 1983; Haffer 1986; Hewitt 1988; Bull 1991). Studies of parapatry may contribute to our understanding of speciation, since parapatric taxa may represent the final stage of differentiation to full species (White 1978); to our understanding of community ecology, since parapatry is an opposite state to coexistence; and to our understanding of biogeography, since parapatric boundaries are distributional limits.

Key (1982) divided parapatry into two categories: hybridization parapatry, in which the contacting taxa form a narrow hybrid zone, and ecological parapatry, in which they may have a narrow overlap zone, but no hybrids form. A common explanation for the maintenance of hybridization parapatry is the reduced fitness of interspecies hybrids (Barton 1979; Key 1982; Barton and Hewitt 1985; Hewitt 1988). Computer simulation models have been used to explore this explanation (Nichols 1989).

Mechanisms to explain ecological parapatry, in contrast, have been less well explored. There have been some theoretical models exploring competition along environmental gradients. MacArthur (1972) predicted parapatry in his model of one species replacing another along a cline of resources. An extension of that model (Slade and Robertson 1977) included the requirement of additional re-

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sources to defend territories against the other species and predicted one species replacing another parapatrically but with a gap between the species. There have been few subsequent articles with theoretical models specifically addressing ecological parapatry and none with computer simulations.

Ecological parapatry is generally assumed to result from some ecotonal change (Key 1982) or from interspecific competition (Haffer 1969, 1986). A summary (Bull 1991) of other mechanisms to explain abrupt parapatric boundaries between nonhybridizing species includes predation (Paine 1971; Hairston 1980), parasitism (Cornell 1974), and reproductive interference (Anderson 1977; Ribeiro and Speilman 1986). However, there are few cases of ecological parapatry in which the proposed mechanism has been tested. Existing field tests have led to disagreement (Heller 1971; States 1976) or no conclusion (Key and Balderson 1972; Greenslade 1974; Howard and Harrison 1984a, 1984b; Bull et al. 1989).

A descriptive model published earlier (Bull 1991) proposes a mechanism for the maintenance of ecological parapatry. In the model, the strength of the ecological interaction needed to maintain a parapatric boundary is reduced if the boundary coincides with a region of poorer habitat. The model assumes that two species are spreading toward contact across a landscape of ridges of favorable habitat and troughs of poorer habitat. In this model the terms *ridge* and *trough* denote regions that are favorable or unfavorable for population growth rather than topographical features. Fine-scale mapping commonly shows a pattern in species distributions in which regions of high population density alternate with regions of low population density (Cornell 1974; Carter and Prince 1985; Terborgh 1985; Addicott et al. 1987; Caughley et al. 1987; Kohlmann et al. 1988; Nichols 1989).

In the model, the ridges are further apart than the dispersal distance of either species. In the troughs, populations increase through dispersal from ridge populations and decrease through natural mortality induced by the adverse conditions. Trough populations are sustained if dispersal exceeds mortality. If ecological conditions vary over time, trough populations, in good years, will be large enough to generate their own dispersers and colonize the next ridge. Ridge populations, even with favorable conditions, may occasionally suffer stochastic declines, and even extinction, unless regularly supplied with dispersers from an adjacent trough population.

In the descriptive model, when the two species contact, their interactions may be so weak that they can coexist on ridges. However, in troughs, a weak interaction that marginally increases mortality may be sufficient to change the balance between dispersal and mortality. If mortality now exceeds dispersal, a species cannot maintain trough populations and cannot colonize or sustain populations on further ridges. In this way, a weak interaction, which would be insignificant in homogeneous optimal conditions, may prevent range extension of one species in a heterogeneous habitat. A parapatric boundary would be formed when a trough occurs on an ecotonal cline on which conditions favoring one species are replaced by those favoring the other. The descriptive model concludes that species that might overlap extensively in a homogeneous environment can be prevented from doing so by environmental heterogeneity.

The nature of the interaction between the species is not defined in the model.

It may be any form of interaction in which the presence of one species inhibits population growth in the other. It can include classical interspecific competition, mating inhibition, and indirect interactions via some other species like a parasite or predator.

The descriptive model was developed to explain the abrupt parapatric boundaries between three tick species infesting reptiles. *Aponomma hydrosauri, Amblyomma limbatum,* and *Amblyomma albolimbatum* have allopatric distributions in South Australia, but wherever any two of these tick species meet, they form long parapatric boundaries (Smyth 1973; Bull et al. 1981, 1989; Petney and Bull 1984; Bull 1991). One boundary, near Mount Mary, South Australia, has been mapped in detail for at least 20 km (Bull et al. 1981). Near Mount Mary, *A. limbatum* in the north overlaps with *A. hydrosauri* in the south by less than 1 km (Bull et al. 1981, 1989). *Aponomma hydrosauri* is less tolerant to desiccation (Bull and Smyth 1973), and conditions become gradually drier north of the boundary (Smyth 1973). However, habitat and climate change cannot explain the abruptness of the boundary (Bull et al. 1981), nor can interspecific competition (Bull et al. 1989) or predators (Bull et al. 1988). Near the boundary, transect surveys show alternating regions with high and low levels of infestation on reptile hosts, by both tick species (Bull et al. 1989). We interpret these as regions more or less suitable for tick population growth—the ridges and troughs of the model. Trough sites may result from reduced host density, reduced cover for ticks to avoid desiccation (Petney and Bull 1984), or increased predation (Bull et al. 1988).

In this article, we develop a computer simulation model, incorporating stochasticity, to reflect the descriptive model (Bull 1991). We use the computer simulations to determine whether troughs can sustain parapatric boundaries with reduced interspecific interactions. Specifically, we are interested in whether a heterogeneous habitat generates parapatric boundaries more readily than a homogeneous habitat. Also, we investigate how interactions of competition, dispersal, and environmental heterogeneity influence the likelihood of generating sharp parapatric boundaries. We then compare the predictions of the model with the real structure of the tick boundary on a transect near Mount Mary.

METHODS

The computer simulation model has a grid of 21 rows and 11 columns, which makes up 231 sites where populations can establish. Two species are placed on the grid, species A on row 1 and species B on row 21. The 11 populations of each species each start with 10 individuals.

For each generation, each population cycles through phases of growth, dispersal, and culling. In the growth phase, each population is multiplied by a growth factor. Determination of the value of this growth factor is described in the following paragraphs. Then, in the dispersal phase, a defined proportion of each population disperses from the population site, equally to the four adjacent population sites. Dispersers off the grid, from edge sites, are lost from the system. Any population of less than one individual after dispersal is set to zero. In the culling phase, a carrying capacity between 250 and 500 individuals is randomly derived

for each species, site, and generation. Individuals in excess of the carrying capacity are culled before the growth phase of the next generation. Simulations are run for 500 generations.

Environmental and interaction effects are simulated by their impact on the growth factor. The grid landscape is constructed to contain ridges of favorable habitat and troughs of poor habitat, by setting alternate rows with high and low growth factors. Each species starts on a ridge (high growth factor) but must disperse through a trough (low growth factor) on the adjacent row before reaching the next ridge. In any simulation, maximum values are defined for the growth factors in the ridge and trough rows. The actual factor for each species, site, and generation is a randomly derived value, with a uniform probability density function, between 50% and 100% of the defined maximum.

Superimposed on this landscape is a linear decline in the growth factor for species A with increasing row number. This is to simulate an environmental cline on which the fitness of species A declines gradually as it approaches the end of the grid from where B starts.

Finally, an interaction effect is added, such that the presence of species A at a population site causes a reduction in the growth factor of species B at that site. Interaction strength is left constant during a simulation of 500 generations. Interaction strength is varied between simulations by varying the amount the growth factor of B is depressed by the presence of A. For this article, interspecific interactions will be referred to as competition, although they encompass any process in which species A reduces population growth of species B. In our simulations, we have asymmetric competition. Species B does not affect species A. Thus, we are simulating the spread of a competitively stronger species into a region in which the ecological suitability for it gradually decreases. This is the situation believed to occur at the tick boundary (Bull 1991).

The distributions of the two species on the grid are examined after 500 generations. Two simulations over 1,000 generations showed unchanged results. We consider the species to be coexisting at a site if both are present and the rarer species contributes at least 5% of all individuals at the site. We count the number of sites where there is coexistence. Three processes can generate a low frequency of coexistence. First, the species may never contact if the dispersal rate is low and the growth factor in the troughs is low. Conditions are too severe to allow the populations to spread. Second, species A can eliminate species B from the grid when competition is high and the growth factor in the troughs is high. There is no impediment to the spread of A. Finally, each species can occupy a different section of the grid, and they can overlap in a few central rows. This is analogous to ecological parapatry. In the simulations, we define parapatry as overlap in fewer than 50 population sites after 500 generations. The arbitrary choice of 50 sites resembles real ecological parapatry, in which a narrow overlap zone separates pure populations of each species. Similar conclusions are reached if we use alternative criteria for parapatry.

For simulations derived in this article, the growth factor on the ridges was 1.6, 1.8, or 2.0 units. With lower values, the two species often failed to spread. With higher values, species A consistently spread across the whole grid. For each ridge

value, we initially simulated a flat homogeneous environment with equal growth factor values in ridge and trough sites. Then we decreased trough values in steps of 0.1 or 0.2 growth factor units in successive simulations. The cline in growth factor for species A was set at 0.015 units per row, for all simulations. Without a cline, species A always spreads over the entire grid (with suitable dispersal and trough conditions), either completely displacing species B if competition is high or coexisting with B at all grid sites if competition is low.

For each combination of landscape conditions, we set dispersal rates at 5%, 10%, 15%, 20%, or 25% of the population. For each combination of landscape conditions and dispersal rates, we varied the competition strength between 0.05 and 0.35 growth factor units, in steps of 0.01 or 0.05 units. For each combination of landscape, dispersal, and competition values we ran two simulations. From these we calculated the average number of sites with coexistence after 500 generations.

To compare the model outcome with a real parapatric boundary, we present data from surveys of one transect across the boundary between two tick species near Mount Mary, South Australia (34°06′ S, 139°26′ E). Each spring since 1982 random encounter captures have been made of host lizards along 47 km of boundary transects (Bull et al. 1989). Over 20,000 capture records have now been made. Each lizard is individually marked, and its location is recorded, together with the number of ticks of each species attached.

Data are presented here for the years 1987–1990, showing the mean number of ticks per lizard in each 100-m segment along 8 km of a north-south transect (transect 1; Bull et al. 1989) where it crosses the boundary. In each year, when a lizard individual is captured more than once, the highest infestation level is used in calculating mean tick load. Data are derived from 350 captures of 289 lizards in 1987, 419 captures of 314 lizards in 1988, 386 captures of 315 lizards in 1989, and 264 captures of 220 lizards in 1990.

RESULTS AND DISCUSSION

Figure 1 shows the results of a typical model simulation. The position reached by species A after 500 generations depends on the habitat quality on the ridges. When initial ridge sites have a maximum growth factor of 2.0, species A usually reaches row 19. With a ridge growth factor of 1.6, species A reaches between row 9 and row 15.

When interaction strength is low, species B is able to extend completely across the grid in most simulations, so the two species overlap extensively. With high ridge values and greater extension of species A, the overlap is more extensive.

When interaction strength is high, there is low overlap, usually 10–20 population sites, or one to two rows of the grid. Overlap tends to be slightly higher when dispersal is higher. To some extent, this condition is an artifact of the order of events in the model. The reporting of population status is after dispersal. It is before the next generation of growth, which is when the interaction would reduce population size. The artifact may be biologically realistic, because natural dis-
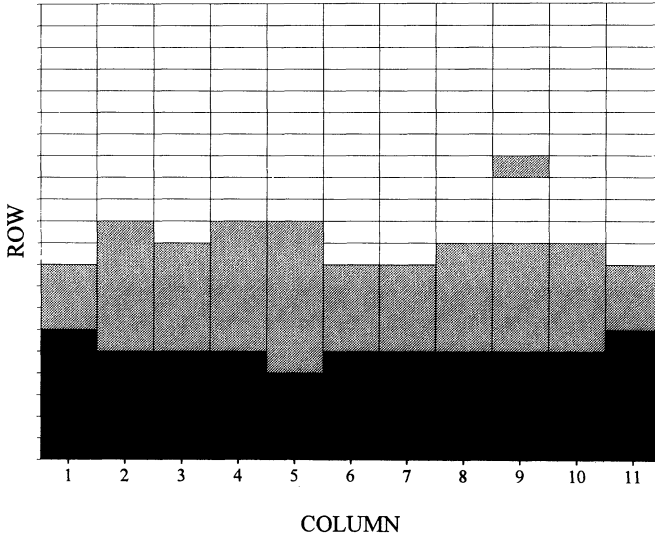
FIG. 1.—The positions of the two species on the grid after 500 generations in a simulation with a growth factor of 1.8 on ridges and 1.2 in troughs. For this simulation, dispersal rate was set at 15%, and competition strength was 0.21 growth factor units (see text). Sites where one species made up over 95% of the total individuals are represented by black or white grid cells. Gray is used to indicate cells with both species present. The overlap in this simulation was 54 sites.

persal will always generate overlap even if the dispersers cannot subsequently breed.

For each set of grid parameters, there is a narrow range of competition levels over which the simulation results change from extensive overlap to low overlap (fig. 2). Results from over 2,000 other simulations with various combinations of ridge and trough growth factor values are not shown. We define a threshold level of competition as the smallest amount of competition required to maintain parapatry (fewer than 50 population sites with overlap). The threshold competition levels for different grid conditions are summarized in figure 3. Each point on each graph in figure 3 is derived from a graph similar to those shown in figure 2.

Heterogeneity in the grid increases as the troughs deepen relative to the ridges (going from right to left on the X-axis). With increased heterogeneity, the threshold level of competition decreases. That is, less competition is needed to sustain parapatry in an environment with troughs and ridges of ecological suitability than in a homogeneous environment in which troughs and ridges have equal growth factors. The greater the heterogeneity, the smaller the competitive strength needed. This effect is greater for lower ridge values. The ecological interpretation of this result is that parapatry is more likely to be generated by interspecific interaction in a more heterogeneous habitat and in conditions that are more marginal for the species.

In our computer model, simulations with higher dispersal need lower levels of
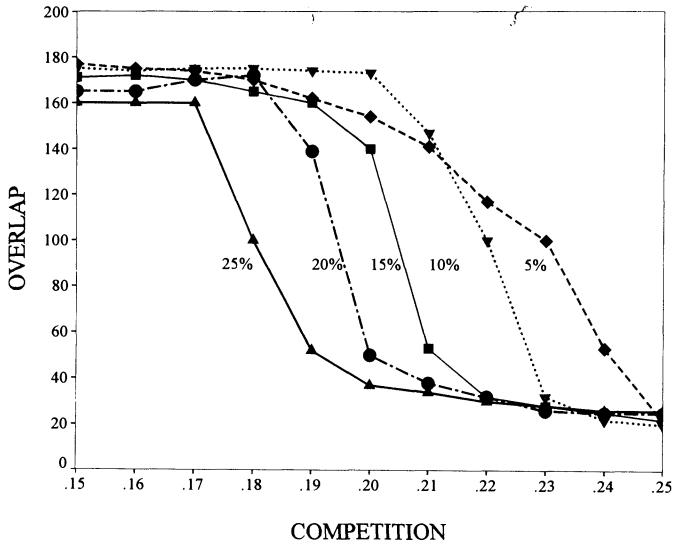
Fig. 2.—The effect of varying competition strength on the amount of overlap after 500 generations in simulations in which the growth factor is set at 1.8 on ridges and 1.2 in troughs. The five lines represent different dispersal rates. The dispersal rates are indicated to the left of each line. Data for each combination of ridge and trough conditions were generated, but only this example graph is shown.

competition to sustain parapatry in the heterogeneous environments (fig. 3). We ascribe this to the fact that high dispersal from small populations may reduce those populations to a size at which a low level of competition can have a major impact. Populations with lower dispersal will have larger residual size after dispersal and will be more robust to competitive inhibition. Our computer model may be unrealistic in maintaining a constant proportion of dispersers independent of density.

Overall, the results of the computer simulation model confirm the previously published descriptive model (Bull 1991). Parapatry can be maintained with less interspecific interaction in a heterogeneous environment than a homogeneous one. We suggest the models provide a mechanism for the maintenance of parapatric boundaries in general and for the reptile tick boundary in particular. More generally, we suggest that the impact of interspecific interactions can be variable depending on the heterogeneity of the landscape over which the species are interacting.

In the field survey, the north-south transect near Mount Mary crosses the parapatric boundary between *Aponomma hydrosauri* in the south and *Amblyomma limbatum* in the north. Figure 4 shows the abrupt transition from one tick species to the other across less than 1 km on the transect. Further north on the transect, there is allopatric *A. limbatum;* further south, allopatric *A. hydrosauri* (Bull et al. 1981, 1989). The overlap zone of the two species is restricted to the region of the transect shown in figure 4. The fine distribution pattern shows a consistent pattern close to the parapatric boundary with alternate regions of high
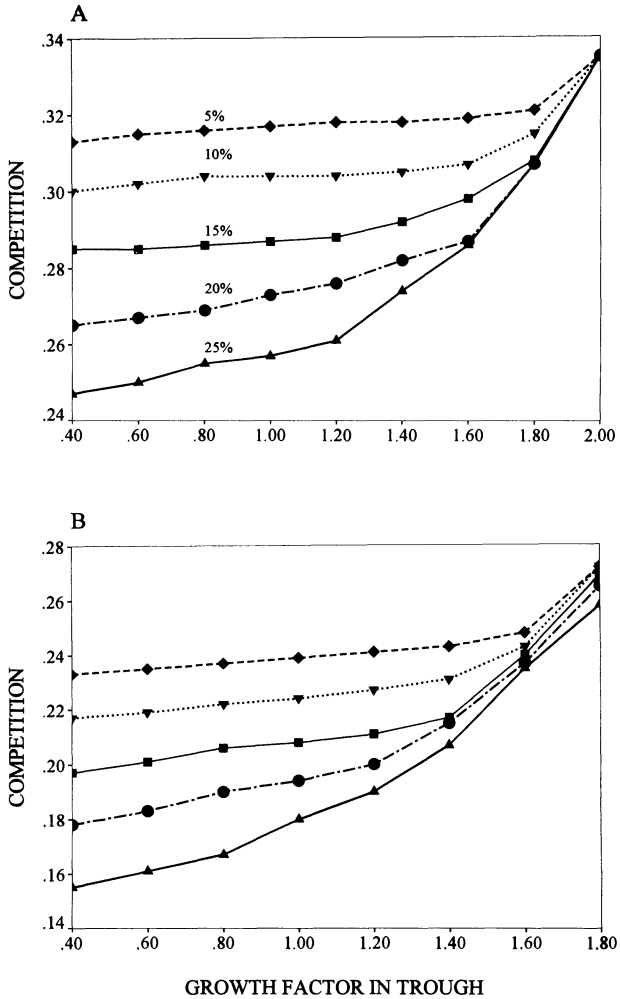
Fig. 3.—The threshold strength of competition above which overlap after 500 generations was fewer than 50 sites, as a function of the growth factor in troughs. Simulations were run with a growth factor on ridges equal to (A) 2.0, (B) 1.8, and (C) 1.6 growth factor units. The five lines on each graph represent different dispersal rates. Dispersal rates are indicated above each line in A, and equivalent symbols are used throughout. In each graph, the right-hand value shows a homogeneous environment in which growth factors in ridge and trough sites are equal. Environmental heterogeneity increases to the left.

and low tick abundance. We suggest that these are analogous to the ridges and troughs of the computer model. We do not yet know what ecological factors generate the troughs, but reduced understory cover, reduced host density, and increased predation may all contribute.

Many other components of the distribution are consistent with the model. *Aponomma hydrosauri* is a mesic species (Bull and Smyth 1973) near the arid limit

GROWTH FACTOR IN TROUGH
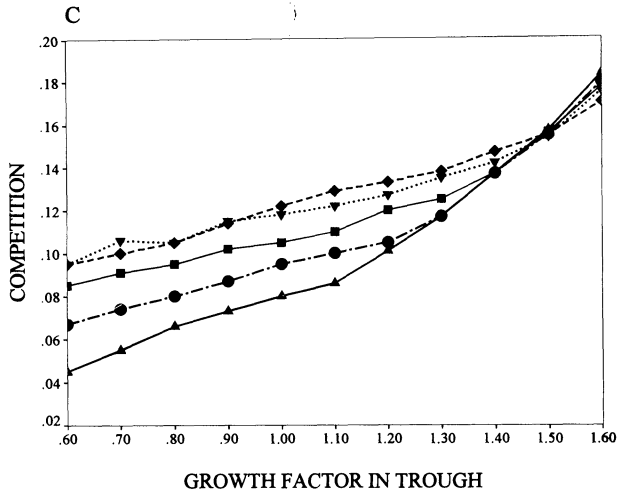
of its range near Mount Mary (Smyth 1973). It can tolerate the drier conditions north of the boundary, but they are less favorable for it (Bull et al. 1981; Petney and Bull 1984). Thus, there is a cline of decreasing fitness for *A. hydrosauri* going north.

Dispersal of these ticks is largely passive, via host movement (Petney et al. 1983), and is less than 600 m (and usually less than 200 m) per generation (Bull 1978, 1987). Figure 4 shows the distance between ridges is 1 km or more, which exceeds the dispersal distance for ticks, consistent with the model.

The model predicts that it is interactions in the trough sites that prevent further overlap between the species. The distributional data show both species coexisting in the central ridge site (locations 0.0–2.0 km), often at high density, but no extension of *A. hydrosauri* into or beyond the trough to the north or of *A. limbatum* into or beyond the trough to the south of that ridge. Thus, the outcome of the model is also consistent with the distributional data.

The model helps explain how the tick boundary is maintained, despite unsuccessful attempts to detect competition (Bull et al. 1989). We suggest that in a heterogeneous environment, weaker interactions in trough sites will be adequate to maintain stable boundaries. Heterogeneous environments may also play a role in maintaining other parapatric boundaries, which remain largely unexplained.

The model also has broader implications for interspecific interactions in which parapatry is not the outcome. Many spatial models of competition show that competing species, which cannot persist together in a closed population, can coexist in a spatially structured environment (Hanski and Gilpin 1991; Nee and May 1992; Tilman 1994). These models are often set in a homogeneous environment. Our model suggests that the result of competition in a spatial environment may vary, depending on the heterogeneity of the environment, and that the predictions of spatial models using a homogeneous background environment may be inappropriate. Other models (Chesson 1985; Pacala and Tilman 1994) consider environmental heterogeneity such that some habitats are more favorable for one
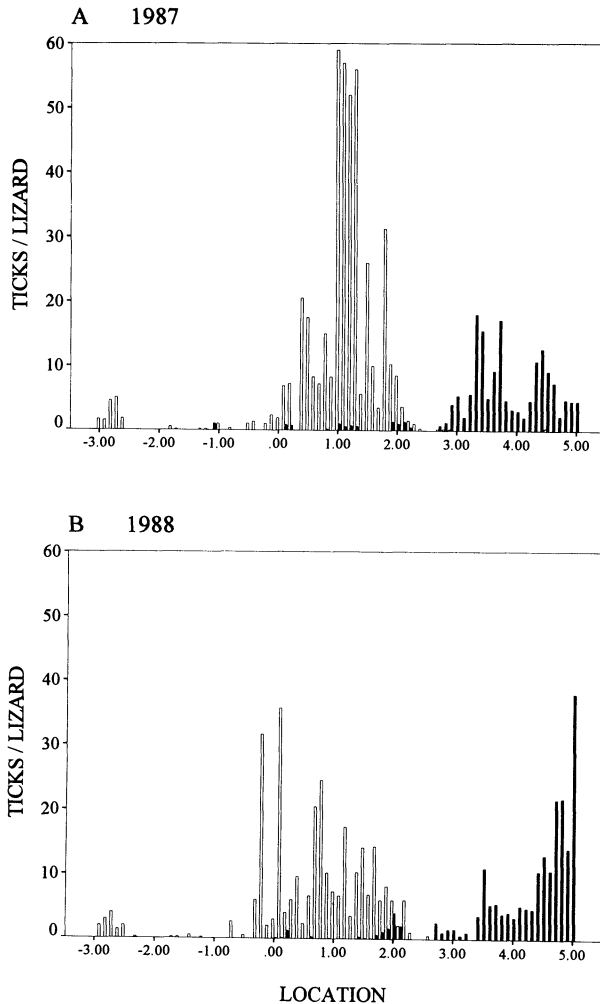
FIG. 4.—The average number of ticks, *Aponomma hydrosauri* (*open bars*) and *Amblyomma limbatum* (*solid bars*), per lizard in each 100-m segment along 8 km of a north-south transect (transect 1) across the parapatric boundary near Mount Mary in (*A*) 1987, (*B*) 1988, (*C*) 1989, and (*D*) 1990. The scale on the location axis is in kilometers. The zero is a reference point (*pipeline corner*); positive values are to the north and negative values to the south of that point.

species, some for another species. In our model, the competitive hierarchy remains the same in adjacent ridge and trough sites. Conditions on ridges favor both species, whereas conditions in troughs favor neither. The model of Goldwasser et al. (1994) also retains the competitive hierarchy between three species over all habitats but introduces random spatial variability in habitat quality for all species. Their model shows the inferior competitor occupying more sites in a variable than in a homogeneous environment. In contrast, our model, with environmental variability nonrandomly structured in a ridge and trough system, predicts that

C   1989

D   1990

LOCATION
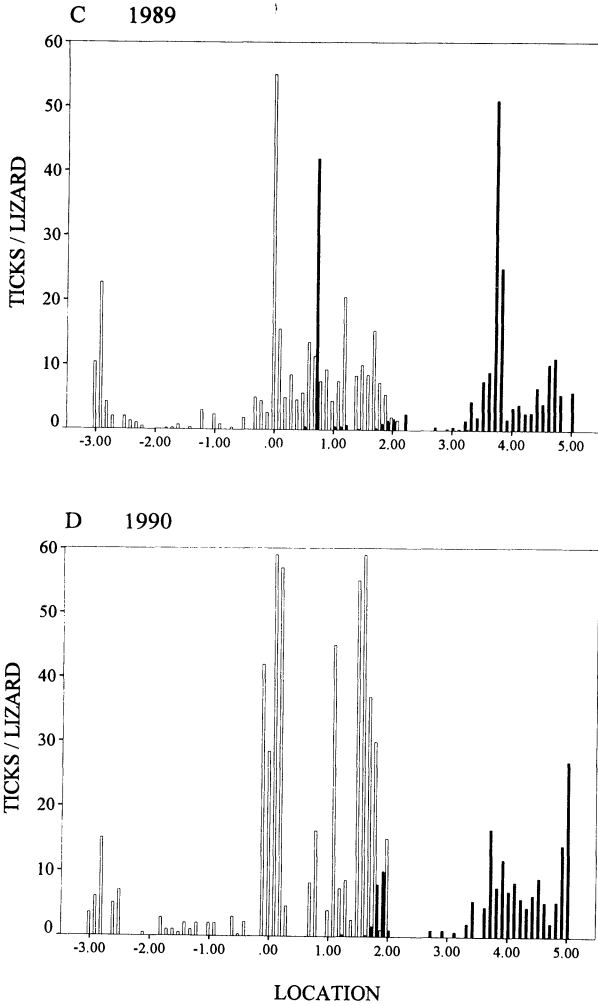
increased environmental heterogeneity reduces the opportunity for the coexistence of competitors. We propose that our model is directly relevant to ecological communities like the Australian reptile ticks with species that actually inhabit environments with ridge and trough structure.

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