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PATTERNS OF PARAPATRIC SPECIATION

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Abstract.—Geographic variation may ultimately lead to the splitting of a subdivided population into reproductively isolated units in spite of migration. Here, we consider how the waiting time until the first split and its location depend on different evolutionary factors including mutation, migration, random genetic drift, genetic architecture, and the geometric structure of the habitat. We perform large-scale, individual-based simulations using a simple model of reproductive isolation based on a classical view that reproductive isolation evolves as a by-product of genetic divergence. We show that rapid parapatric speciation on the time scale of a few hundred to a few thousand generations is plausible even when neighboring subpopulations exchange several individuals each generation. Divergent selection for local adaptation is not required for rapid speciation. Our results substantiates the claims that species with smaller range sizes (which are characterized by smaller local densities and reduced dispersal ability) should have higher speciation rates. If mutation rate is small, local abundances are low, or substantial genetic changes are required for reproductive isolation, then central populations should be the place where most splits take place. With high mutation rates, high local densities, or with moderate genetic changes sufficient for reproductive isolation, speciation events are expected to involve mainly peripheral populations.

Key words.—Centrifugal speciation, holey adaptive landscapes, mathematical modeling, parapatric, peripatric.

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The geographic range sizes of most species are much larger than the typical dispersal distances of individuals (or gametes). This creates an opportunity for the generation and maintenance of extensive genetic differences among geographic populations of the same species in spite of migration. Several factors contribute to these processes. Because each specific mutation is a very rare event, whereas the number of possible mutations is enormous, different mutations will appear in different geographic areas. Mani and Clarke (1990) refer to this factor as ''mutational order.'' Additional divergence will be created by stochastic factors affecting survival and reproduction, which are commonly referred to as ''genetic drift.'' Finally, variation in abiotic and biotic conditions can result in systematic differences in selection regimes that operate in different parts of the species range to augment geographic differentiation. Extensive geographic variation is well documented for most species (e.g., Endler 1977; Avise 1994). A classical example of extreme geographic differentiation are ''ring species'' (e.g., Mayr 1942, 1963; Wake 1997), where genetic differences between some neighboring populations result in strong reproductive isolation.

Generation of geographic variation is a necessary step in most scenarios of speciation. Here, we concentrate on parapatric speciation, that is, speciation with some gene flow between neighboring subpopulations. Increasing amounts of data suggest that rapid and extensive speciation is possible without complete geographic isolation (e.g., Endler 1977; Rice and Hostert 1993; Palumbi 1994). We will consider populations living in a habitat subdivided into discrete patches. Analysis of ecological and genetic processes in spatially fragmented populations is a subject of metapopulation biology (e.g., Hastings and Harrison 1994; Hanski and Gilpin 1997). Here, we study possibilities for speciation in metapopulations. As a consequence of accumulating genetic differences, a subdivided population may eventually split into reproductively isolated groups (new species). Two topics will be investigated here: (1) the waiting time until the first split (speciation); and (2) the location of the first break. A priori, the waiting time until speciation can be anything from a very short one until effectively infinite. We will try to develop some quantitative estimates of this time and evaluate their dependence on different parameters including mutation and migration rates, subpopulation size, genetic architecture, and the geometric structure of the habitat. A priori, reproductive isolation can arise between any neighboring subpopulations. We will evaluate how probable are splits at different positions across the species range. In particular, we will consider whether it is peripheral populations that tend to split off or whether speciation results from major changes in the middle of a species range.

There are several reasons why these questions are extremely important. First, they are relevant for identifying and understanding the general patterns and processes of biological evolution, speciation, and the origin and maintenance of biodiversity (e.g., Rosenzweig 1995; Futuyma 1997; Brown and Lomolino 1998). Second, they concern an old and unsettled dispute regarding the relative importance of central and peripheral populations in speciation. In his theory of peripatric speciation, Mayr (1954, 1963) singled out peripheral populations as the primary source of new species. According to Mayr, peripheral populations have higher probability of splitting off because they have smaller sizes, experience different selection regimes, and are less affected by migration. In contrast, in his theory of centrifugal speciation, Brown (1957) argued that central populations are the main source of genetic novelty and, thus, should be the place of the origin of new species. Both Mayr and Brown described numerous examples that apparently fit their corresponding schemes. Mayr's theory has been largely accepted by biologists, whereas Brown's theory has been largely ignored in evolutionary literature (but

see Frey 1993; Rosenzweig 1995). No attempts have been made to consider both scenarios within a single framework. Third, both questions are relevant for understanding species range size distribution. Species range size distribution (i.e., the frequency distribution of the number of species exhibiting geographic ranges of different sizes) provides a very useful summary of the spatial patterns of biodiversity (e.g., Gaston 1996, 1998). This distribution is a product of several processes, of which speciation together with extinction and the temporal dynamics of the range sizes of species during their lifetimes are the most important (Gaston 1998). Fourth, the question on how the sister species arising after a speciation event split the geographic space between them is closely related to the problem of ecological niche breakage between different species (e.g., Sugihara 1980; Nee et al. 1991; Takeshi 1993). In the dynamical models considered below the only resource to be divided by new species is geographic space. However, because the geographic range of a species can be viewed as a spatial reflection of its ecological niche (Brown and Lomolino 1998), insights provided by these models may be useful for thinking about patterns of splitting of other resources among species. Finally, recent years have seen an explosive accumulation of molecular data and development of statistical methods directed toward reconstruction of evolutionary history from these data. The importance of spatial aspects in molecular processes is reflected in the emergence of phylogeography as a branch of molecular evolutionary biology (Avise et al. 1987; Avise 1994, 1998) and in the application of species-level phylogenies for detecting the geographic patterns of speciation (Barraclough and Vogler 2000). The development of theoretical models focusing on the dynamics of speciation in spatially distributed populations that would complement data analyses is especially important given the ineffectiveness of experimental manipulations in studying speciation.

Model

We will use a model introduced by Gavrilets et al. (1998) and studied analytically in Gavrilets (1999). We consider finite subdivided populations of sexual haploid individuals different with respect to a large number of linked diallelic loci. The restriction to haploids is for computational simplicity. Evolutionary factors included are mutation, recombination, migration, genetic drift, and selection. To decrease the number of parameters, we used some symmetry assumptions. Mutation rates were equal for forward and backward mutations and across loci. Recombination rates between adjacent loci were equal, and recombination events took place independently of each other. The population was subdivided into subpopulations of equal size. We assume that there are no systematic differences in environmental conditions between different subpopulations and no asymmetries in migration regimes. Migration is restricted to neighboring populations only (Kimura and Weiss 1964), and the migration rate between any two neighboring subpopulations is the same. The only difference between peripheral and central subpopulations will be that the former have fewer of neighboring subpopulations than the latter. Thus, in peripheral demes, individuals encounter individuals from the same population more often than in central demes. To reflect the idea that reproductive isolation arises simultaneously with genetic divergence, we posit that an encounter of two individuals can result in mating and viable and fecund offspring only if the individuals are different in no more than K loci. Otherwise the individuals do not mate (premating reproductive isolation) or their offspring are inviable or sterile (postmating reproductive isolation). In this formulation, any two genotypes different in more than K loci can be considered as sitting on opposite sides of a hole in a holey adaptive landscape (Gavrilets 1997a,b, 1999, 2000; Gavrilets and Gravner 1997). At the same time, a population can evolve to any reproductively isolated state by a chain of single-locus substitutions. Threshold K characterizes the minimum genetic change necessary for reproductive isolation. The neutral case (no reproductive isolation) corresponds to K equal to the number of loci. Migration patterns were specified by a migration matrix M with elements m_{ij} defining the probability that an individual from subpopulation i encounters an individual from subpopulation j.

Most previous theoretical studies of nonallopatric speciation consider only some stages—mostly initial or final—of the speciation process, assume very high levels of initial genetic variation and very strong disruptive selection, and posit that the trait under selection pleiotropically controls mating preferences (e.g., Felsenstein 1981; Kondrashov 1986). A distinctive feature of our simulations is the consideration of the complete process of speciation starting with a monomorphic population and ending with complete reproductive isolation. We do not invoke disruptive ecological selection to explain speciation concentrating on genetic factors. Effects of the differences in selection regimes between subpopulations on the patterns of speciation in the model under consideration are discussed in Gavrilets (1999). Among previous theoretical studies of parapatric speciation, the most similar approach is that in Manzo and Peliti (1994), which is based on Higgs and Derrida's (1992) model. There are two major differences between our model and that in Higgs and Derrida (1992). In our model, individuals encounter each other randomly, whereas in Higgs and Derrida's model individuals are actively searching for mates that are similar genetically. The second difference concerns the range of mutation rates used. Here, the rate of mutation per organism is small. In Higgs and Derrida's model, the mutation rate per locus is on the order of one divided by the population size, but the number of loci is assumed to be infinite. This results in an unrealistically high rate of mutation per organism, which in turn makes the process of accumulation of reproductive isolation reversible no matter how far it has already advanced. A minor difference is that in our model the genetic change necessary for reproductive isolation is defined in terms of the number of different genes, rather than the proportion of different genes, as in Higgs and Derrida's (1992) model.

Parameters

In Gavrilets et al. (1998), we reported results for a very limited set of parameter values. In particular, only a single configuration of parameters was used within the framework

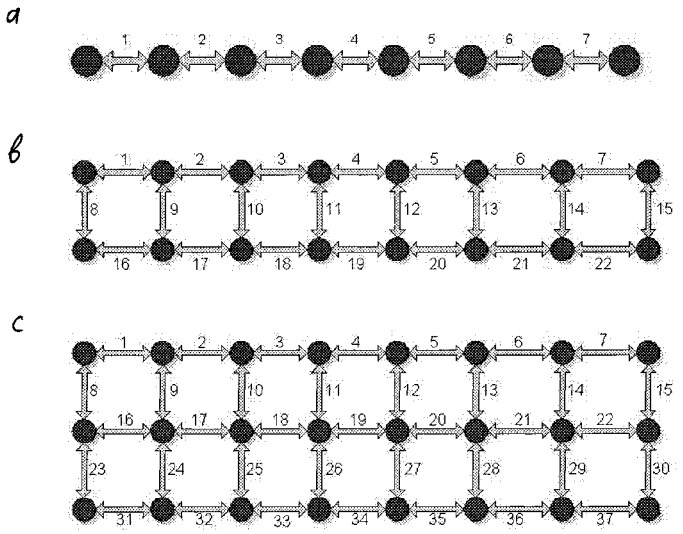

FIG. 1. Stepping-stone models: (a) 1×8 system; (b) 2×8 system; and (c) 3×8 system. Connections between neighboring subpopulations are numbered.

of stepping-stone systems. Here, we significantly extend the range of parameter values studied by considering 243 parameter configurations. The following is a list of parameter values used: rates of mutation per locus per generation: $\mu = 0.00005$, 0.0001, and 0.0002; the minimum genetic change necessary for reproductive isolation: $K = 10$, 20, and 30; subpopulation size: $N = 50$, 100, and 200; migration rate: $m = 0.04$, 0.06, and 0.08; geometric structure of the habitat: 1×8, 2×8, and 3×8 stepping-stone systems (see Fig. 1). Here, migration rate m was defined as the probability that an individual from a ''central'' deme encounters an individual from a different subpopulation. Thus, the probability to encounter an individual from a specific neighboring subpopulation is $m/2$ in 1×8 stepping-stone models, $m/3$ in 2×8 stepping-stone models, and $m/4$ in 3×8 stepping stone models. Two parameters did not change throughout the simulations: the number of loci ($L = 386$) and the recombination rate between adjacent loci ($r = 0.005$). Theoretical arguments (Gavrilets 1999) and additional simulations not reported here suggest that changing L and r will not strongly affect our conclusions. Note that the values of μ used here are somewhat higher than current estimates of the mutation rates per locus, which are typically on the order of 10^{-5} (Griffiths et al. 1996; Futuyma 1997), whereas the values of K are within the range of estimates of the minimum number of genes involved in reproductive isolation (Singh 1990; Wu and Palopoli 1994; Coyne and Orr 1998).

Statistics

Classical population biology focuses on single biological units, such as specific haplotypes (or genotypes). The population state is usually described in terms of the distribution of the frequencies of these units. When a large number of loci (or sites) are considered simultaneously, such an approach is not very informative because many haplotypes are very likely to be unique or absent. Here, instead of focusing on individuals, we focus on the differences between individuals and describe the population state in terms of the distribution of genetic distances between individuals. By genetic distance between two sequences representing two genotypes we mean the number of loci (sites) by which the sequences differ. This is a standard Hamming distance. As summary statistics, we use the average genetic distances within (D_w) and between (D_b) subpopulations. In the neutral case, these genetic distances are proportional to the corresponding coalescent times (Hudson 1990).

Numerical Procedure

We performed individual-based simulations. Each individual was represented as a binary string of length L. We used the following procedure for generating the next generation for a subpopulation. First, we randomly chose an individual from the subpopulation. Individuals were chosen with equal probability $1/N$. Then, we chose a subpopulation from which a second individual of the potential mating pair will be taken. Subpopulations were chosen with probabilities specified by the migration matrix M. Then, we randomly chose an individual from that subpopulation (individuals were chosen with equal probabilities $1/N$). We calculated the number of loci the two individuals are different at, d. We disregarded both individuals and returned to the first step if $d > K$ (the pair of individuals are reproductively isolated). We simulated crossover to produce an offspring if $d \leq K$. This was repeated until all N offspring were generated for all subpopulations. For generating random numbers with a given distribution, we used a linear algorithm described in Vose (1991).

The simulations started with all individuals identical. During the first 1000 generations there were no restrictions on migration between subpopulations and the whole population evolved as a single randomly mating unit. One thousand generations was sufficient for the population to reach a state of stochastic equilibrium. Starting with generation 1000, restrictions on migration were introduced. Restrictions on migration results in genetic differentiation of subpopulations, which possibly leads to speciation. In some runs, the average genetic distances between neighboring subpopulations, D_b, exceeded those within subpopulations, D_w, but both stayed below K, meaning that matings between individuals from neighboring subpopulations took place and were fecund. Although individuals from geographically separated populations could be reproductively isolated, the population as a whole formed a single genotypic cluster in the genotype space. This regime was interpreted as no speciation. In other runs, the average genetic distances between an adjacent group of populations and their neighbors started steadily increasing after some transient time (which can be very short). These distances exceeded K, meaning that encounters between individuals from different groups did not result in viable and fertile offspring. Evolutionary changes in one group of subpopulations did not affect other subpopulations. Thus, different groups form separate genotypic clusters in genotype space became reproductively isolated and undertook changes as evolutionary independent units. This regime was interpreted as speciation according to any of the species concepts common in the literature (e.g., Templeton 1989; Mallet 1995; Avise and Wollenberg 1997). Figures 1, 2, and 3 in Gavrilets

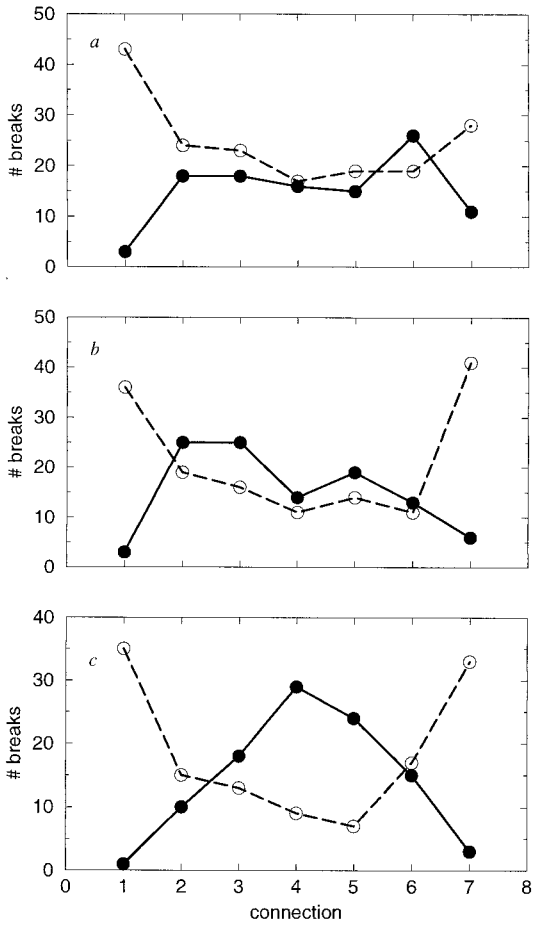

FIG. 2. Effects of mutation rate on the number of breaks observed in 100 runs in 1 × 8 systems with $N = 50$ and $K = 10$: (a) $m = 0.04$; (b) $m = 0.06$; and (c) $m = 0.08$. With a smaller mutation value ($\mu = 0.00005$, black circles, solid lines), central connections are broken more often. With a larger mutation value ($\mu = 0.0002$, open circles, dashed lines), peripheral connections are broken more often.

et al. (1998) illustrate the behavior of the average genetic distances in runs with and without splitting.

We started by performing 10 preliminary runs for each of $3^5 = 243$ parameter configurations. Each run ended whenever an average genetic distance between two neighboring subpopulations exceeded $D_{critical} = K + 10$ or at generation 10,000. The former outcome was interpreted as splitting of the population (the emergence of reproductive isolation between a pair of neighboring subpopulations). Previous experience with running the model strongly suggests that the value of $D_{critical}$ chosen guarantees that splitting is irreversible (for parameter values used). We chose a relatively short time span of 10,000 generations for two reasons. First, we are interested in the plausibility of rapid speciation. Second, only during relatively short time intervals may one assume the constancy of abiotic and biotic environment implied in our model. For each parameter configuration with at least one splitting event in 10 preliminary runs, we made 90 additional runs. To reduce the computation time, in our simulations the average genetic distances were computed only in certain generations, typically every 32nd generation. As a consequence, some runs exhibited more than one split.

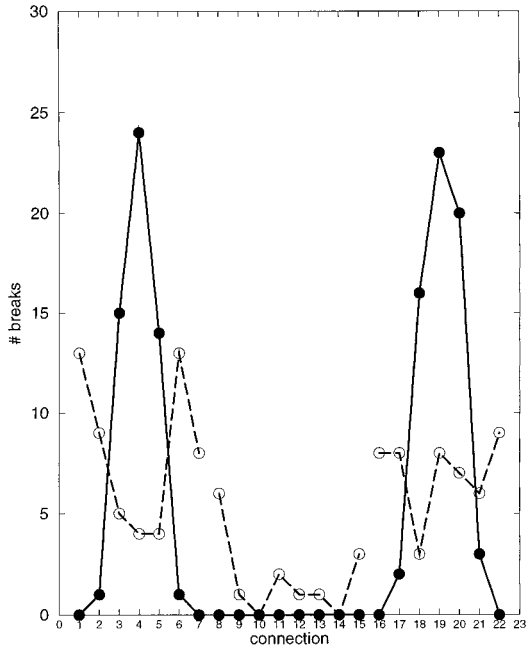

FIG. 3. Effects of parameter K (the minimum genetic change necessary for reproductive isolation) on the number of breaks observed in 100 runs in a 2 × 8 system with $N = 100$, $m = 0.06$, and $\mu = 0.0002$. With smaller K (=10, black circles, solid lines), central connections are broken more often. With larger K (= 30, open circles, dashed lines), peripheral connections are broken more often.

RESULTS

Time until Speciation

The distribution of the time until speciation is nonnormal, strongly asymmetric, and truncated (at time 9000). For these reasons, we used order statistics as statistics of location and dispersion (see Sokal and Rohlf 1995). Table 1 shows the median waiting time until the first split, T_1, together with the 10th and 90th percentiles. Time T_1 was measured from generation 1000, at which time restrictions on migration were introduced. Only runs corresponding to local population size $N = 50$ and $N = 100$ are shown. With $N = 200$, speciation was observed only for the smallest migration rate considered ($m = 0.04$) and the following values of other parameters. In 1 × 8 and 3 × 8 systems, speciation was observed for four combinations of parameters: $K = 20$ or $K = 30$ (moderate and large genetic change necessary for reproductive isolation) and $\mu = 0.0001$ or 0.0002 (moderate and high mutation rates). In 2 × 8 systems, speciation was observed for a single combination of parameters: $K = 30$, $\mu = 0.0002$.

As expected, reducing mutation rate, μ, and/or increasing migration rate, m, always increases T_1. Effects of local population size, N, the amount of genetic change required for reproductive isolation, K, and the system size vary. In general, increasing local population size, N, increases T_1. However, if mutation rate, μ, is small and the population lacks genetic variation necessary to initiate the divergence, then increasing N might help speciation. For example, in 1 × 8

TABLE 1. The median time until speciation, T_1, with the 10th and 90th percentiles (in parentheses for (a) $N = 50$, and (b) $N = 100$. X indicates the corresponding value is larger than 9000. The dates corresponding to $K = 20$ are omitted.

System	K	m	$\mu = 2 \times 10^{-4}$	$\mu = 10^{-4}$	$\mu = 0.5 \times 10^{-4}$
(a)					
1×8	10	0.04	169 (121, 217)	281 (217, 377)	601 (409, 857)
		0.06	217 (153, 281)	377 (281, 537)	825 (537, 1273)
		0.08	281 (185, 409)	601 (377, 857)	1305 (729, 2425)
	30	0.04	185 (153, 249)	537 (377, 761)	3145 (1785, 7225)
		0.06	249 (185, 345)	697 (473, 985)	X (3993, X)
		0.08	297 (217, 441)	889 (601, 1401)	X (X, X)
2×8	10	0.04	153 (121, 185)	249 (185, 281)	537 (345, 729)
		0.06	185 (153, 249)	377 (281, 537)	1033 (569, 1721)
		0.08	281 (185, 409)	729 (409, 1369)	3113 (1241, 6521)
	30	0.04	153 (121, 185)	377 (313, 505)	1129 (825, 1593)
		0.06	185 (153, 249)	553 (377, 697)	1977 (1081, 3001)
		0.08	281 (217, 377)	841 (569, 1241)	5385 (2265, X)
3×8	10	0.04	121 (121, 121)	217 (153, 249)	377 (281, 505)
		0.06	153 (121, 185)	249 (217, 345)	601 (409, 857)
		0.08	217 (153, 249)	409 (313, 601)	1465 (761, 2361)
	30	0.04	121 (121, 153)	281 (217, 345)	777 (569, 985)
		0.06	153 (121, 185)	409 (281, 505)	1129 (761, 1657)
		0.08	185 (153, 249)	601 (409, 793)	2041 (1177, 4057)
(b)					
1×8	10	0.04	537 (345, 697)	825 (505, 1241)	1897 (1177, 3129)
		0.06	1417 (793, 2649)	3321 (1497, X)	X (5657, X)
		0.08	X (3161, X)	X (X, X)	X (X, X)
	30	0.04	313 (249, 377)	665 (441, 985)	2249 (1337, 4857)
		0.06	537 (377, 793)	1449 (889, 2553)	X (X, X)
		0.08	1209 (665, 2169)	X (2937, X)	X (X, X)
2×8	10	0.04	473 (345, 697)	889 (569, 1273)	3801 (1273, 8505)
		0.06	4585 (1209, X)	X (X, X)	X (X, X)
		0.08	X (X, X)	X (X, X)	X (X, X)
	30	0.04	281 (217, 345)	665 (537, 921)	2201 (1433, 3353)
		0.06	665 (409, 1177)	3865 (1945, 7321)	X (X, X)
		0.08	X (X, X)	X (3097, X)	X (X, X)
3×8	10	0.04	377 (281, 473)	569 (409, 729)	1209 (729, 1849)
		0.06	793 (473, 1529)	5209 (1049, 8985)	X (X, X)
		0.08	X (2201, X)	X (X, X)	X (X, X)
	30	0.04	217 (217, 217)	409 (345, 537)	1433 (921, 1945)
		0.06	345 (281, 409)	1433 (665, 2521)	X (X, X)
		0.08	921 (473, 1753)	X (X, X)	X (X, X)

systems with $K = 30$, $m = 0.04$, and $\mu = 0.00005$ the median time until speciation, T_1, is significantly smaller with $N = 100$ than with $N = 50$ ($P < 0.01$, G-test). Increasing K increases T_1 in populations with $N = 50$, which may lack genetic variation, but decreases T_1 in populations with $N = 100$. In general, increasing the system size (from 1×8 to 2×8 to 3×8) decreases T_1. The reason for this appears to be the increase in the ''opportunity'' for speciation that is the number of connections between neighboring populations to be broken (which is 7, 22, and 37 in 1×8, 2×8, and 3×8 systems, respectively). Increasing population subdivision while keeping the overall population size constant significantly decreases T_1 (in all 27 pairwise comparisons T_1 in 2×8 systems with $N = 50$ is smaller than in 1×8 systems with $N = 100$; $P < 0.001$, two-tailed sign test).

For many species, there is a strong positive correlation between local population density and species range: Species with larger ranges usually have higher local densities as well (e.g., Gaston et al. 1997; Warren and Gaston 1997). The parameter configurations with $N = 100$ in 2×8 systems describe a population that occupies twice as many demes and has a local density twice as large as a population with $N = 50$ in 1×8 systems. In 24 of 25 pairwise comparisons, T_1 is smaller in the latter case than in the former case ($P < 0.001$, two-tailed sign test). This shows that populations with larger range sizes and higher local densities have smaller chances of speciation than populations with smaller range sizes and lower local densities.

A useful parameter in predicting the patterns of neutral variation in subdivided populations is the effective number of migrants per subpopulation per generation, Nm (e.g., Slatkin 1987). We have compared the values of T_1 corresponding to $N = 50$, $m = 0.08$ and those corresponding to $N = 100$, $m = 0.04$ (in both cases $Nm = 4$). Performing 26 pairwise tests for equality of medians (Sokal and Rohlf 1995, ch. 17) results in rejecting the null hypothesis at $P < 0.001$ in 15 tests, at $0.001 < P < 0.01$ in four tests, and at $0.01 < P < 0.05$ in three tests. In four cases the differences were not significant. We conclude that in contrast to the neutral case, in our model the number of migrants per generation, Nm, does not mean much by itself.

Following an anonymous reviewer's suggestion, we also performed multivariate analyses of variance (e.g., Underwood 1981; Sokal and Rohlf 1995) of the data from Table

TABLE 2. The average number of breaks per ''peripheral'' connection versus the average number of breaks per ''central'' connection with standard errors (in parentheses) for (a) $N = 50$, and (b) $N = 100$. X indicates no breaks have been observed for the corresponding parameter values. The dates corresponding to $K = 20$ are omitted.

System	K	m	$\mu = 2 \times 10^{-4}$	$\mu = 10^{-4}$	$\mu = 0.5 \times 10^{-4}$
(a)					
1×8	10	0.04	35.5 (10.6) vs. 19.7 (3.1)	23.0 (7.1) vs. 13.0 (4.0)	7.0 (5.7) vs. 16.3 (1.5)
		0.06	38.5 (3.5) vs. 13.7 (2.5)	24.5 (0.7) vs. 10.7 (0.6)	4.5 (2.1) vs. 19.3 (5.5)
		0.08	34.0 (1.4) vs. 9.7 (3.1)	14.0 (1.4) vs. 12.3 (4.9)	2.0 (1.4) vs. 23.7 (5.5)
	30	0.04	13.0 (2.8) vs. 20.7 (3.1)	0.0 (0.0) vs. 24.7 (2.5)	0.0 (0.0) vs. 28.0 (9.2)
		0.06	4.5 (0.7) vs. 18.3 (4.5)	0.0 (0.0) vs. 28.0 (9.6)	0.0 (0.0) vs. 9.3 (5.5)
		0.08	3.5 (0.7) vs. 21.3 (2.5)	0.0 (0.0) vs. 30.7 (3.1)	X
2×8	10	0.04	15.0 (1.8) vs. 10.8 (2.6)	13.0 (2.4) vs. 6.2 (1.5)	8.5 (3.8) vs. 4.8 (1.5)
		0.06	12.5 (0.6) vs. 4.7 (1.0)	13.5 (3.3) vs. 2.0 (1.4)	9.5 (2.4) vs. 5.2 (1.9)
		0.08	15.3 (3.0) vs. 0.7 (0.8)	16.0 (3.6) vs. 2.5 (2.0)	4.5 (1.9) vs. 8.8 (2.4)
	30	0.04	10.0 (4.5) vs. 8.2 (1.5)	6.3 (3.6) vs. 9.2 (3.2)	0.0 (0.0) vs. 14.3 (3.8)
		0.06	10.0 (2.3) vs. 10.2 (1.8)	1.0 (0.8) vs. 10.8 (2.8)	0.0 (0.0) vs. 18.7 (4.3)
		0.08	10.8 (1.3) vs. 8.5 (3.3)	1.3 (0.5) vs. 13.8 (3.3)	0.0 (0.0) vs. 14.2 (3.7)
3×8	10	0.04	14.3 (2.2) vs. 7.0 (3.3)	10.8 (3.9) vs. 3.7 (1.8)	9.3 (3.2) vs. 3.0 (2.8)
		0.06	13.0 (2.4) vs. 4.8 (4.6)	13.3 (3.3) vs. 2.3 (3.1)	5.0 (5.2) vs. 2.0 (2.4)
		0.08	14.3 (7.9) vs. 1.7 (2.4)	3.5 (4.0) vs. 1.5 (1.8)	4.0 (4.9) vs. 1.0 (1.7)
	30	0.04	13.3 (7.7) vs. 12.2 (2.2)	6.5 (3.9) vs. 4.8 (1.9)	2.0 (1.4) vs. 6.7 (2.7)
		0.06	12.3 (6.8) vs. 5.5 (2.6)	6.0 (4.5) vs. 3.0 (2.7)	0.0 (0.0) vs. 4.3 (5.0)
		0.08	13.5 (5.8) vs. 3.3 (3.9)	2.5 (3.3) vs. 3.2 (3.5)	0.0 (0.0) vs. 8.3 (10.1)
(b)					
1×8	10	0.04	45.0 (11.3) vs. 2.3 (1.2)	34.0 (9.9) vs. 5.7 (1.2)	8.5 (4.9) vs. 16.7 (3.1)
		0.06	36.0 (1.4) vs. 3.0 (3.6)	14.5 (2.1) vs. 11.3 (1.2)	0.0 (0.0) vs. 4.7 (0.6)
		0.08	10.5 (0.7) vs. 4.7 (2.1)	X	X
	30	0.04	21.5 (0.7) vs. 15.7 (0.6)	3.0 (1.4) vs. 15.3 (3.5)	0.0 (0.0) vs. 31.0 (6.6)
		0.06	8.5 (0.7) vs. 14.7 (2.3)	0.0 (0.0) vs. 25.3 (5.7)	0.0 (0.0) vs. 2.7 (3.1)
		0.08	0.5 (0.7) vs. 20.7 (1.2)	0.0 (0.0) vs. 10.7 (2.9)	X
2×8	10	0.04	8.0 (0.8) vs. 1.0 (2.0)	10.5 (3.9) vs. 0.2 (0.4)	10.8 (4.8) vs. 2.5 (2.2)
		0.06	7.5 (2.6) vs. 0.0 (0.0)	X	X
		0.08	X	X	X
	30	0.04	19.5 (3.9) vs. 7.8 (2.9)	12.3 (4.0) vs. 8.7 (2.1)	0.8 (0.5) vs. 15.0 (5.1)
		0.06	27.3 (5.4) vs. 2.0 (1.1)	1.8 (1.7) vs. 15.7 (5.8)	X
		0.08	7.8 (2.1) vs. 2.8 (1.2)	X	X
3×8	10	0.04	5.5 (6.4) vs. 1.5 (1.6)	5.0 (5.8) vs. 0.8 (1.0)	3.5 (4.0) vs. 0.7 (1.2)
		0.06	6.8 (7.9) vs. 0.0 (0.0)	5.0 (5.8) vs. 0.0 (0.0)	1.0 (1.2) vs. 0.0 (0.0)
		0.08	3.5 (4.0) vs. 0.0 (0.0)	X	X
	30	0.04	11.5 (4.9) vs. 6.5 (7.2)	4.8 (4.5) vs. 2.0 (2.3)	2.0 (2.4) vs. 5.0 (5.7)
		0.06	6.5 (7.7) vs. 2.5 (3.2)	6.8 (9.0) vs. 1.2 (1.6)	X
		0.08	8.5 (10.1) vs. 0.0 (0.0)	X	X

1a. We log-transformed the data and used the 10th and 90th percentiles together with the median as replicates. A three-way ANOVA with the factors geometric structure of the habitat, K, and m shows that all three main factors are significant ($P < 0.05$) and that there is no significant interaction. When the factor μ is included in the analyses (in a four-way ANOVA), all the main factors plus all two-way interactions that include mutation were significant. The two-way interaction of geometric structure of the habitat and K was significant as well. This shows that the factor μ (mutation rate) may produce complex interactions with all other factors studied.

Location of the First Break

We calculated the number of breaks observed per each connection in Figure 1 for all parameter configurations used. In general, in 2×8 and 3×8 systems the vertical connections (such as connections 8–15) were broken less frequently than the horizontal ones (such as connections 1–7). Also, in 3×8 systems the internal horizontal connection (connections 16–22) were broken less frequently than external horizontal connections. First, we tested whether the distribution of the location of the first break (LFB) among external horizontal connections deviates from the uniform distribution. The latter is implied in various ''broken stick'' models (e.g., Sugihara 1980; Nee et al. 1991; Takeshi 1993; Barraclough and Vogler 2000). In most cases, the distribution of the LFB significantly deviated from uniformity. Using the G-test (Sokal and Rohlf 1995, ch. 17) the null hypothesis was rejected at $P < 0.001$ in 74 of 149 tests performed; the results were not significant in 48 tests.

Next, we compared the average number of breaks per connection for peripheral and central connections (Table 2). By ''peripheral'' connections, we mean connections 1 and 7 in 1×8 models; connections 1, 7, 16, and 22 in 2×8 systems; and connections 1, 7, 31, and 37 in 3×8 systems (see Fig. 1). By ''central'' connections, we mean connections 3, 4, and 5 in 1×8 models; connections 3, 4, 5, 18, 19, and 20 in 2×8 systems; and connections 3, 4, 5, 33, 34, and 35 in 3×8 systems. In general, the average number of breaks per connection for ''intermediate'' connections (connections 2 and 6 in 1×8 systems; connections 2, 6, 17, and 21 in 2×8 systems; and connections 2, 6, 32, and 36 in 3×8 systems)

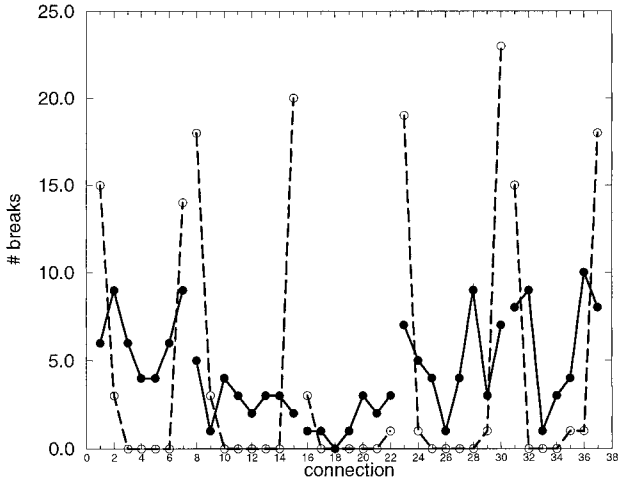

FIG. 4. Effects of subpopulation size, N, on the number of breaks observed in 100 runs in a 3×8 system with $K = 20$, $m = 0.06$, and $\mu = 0.0001$. With smaller N ($= 50$, black circles, solid lines), both central and peripheral connections are broken. With larger N ($= 100$, open circles, dashed lines), only peripheral connections are broken.

was intermediate between those for central and peripheral connections.

To analyze the effects of different parameters on the LFB, we performed a series of pairwise tests. The most general patterns observed concerns the effects of μ, K, and N. Increasing the rate of mutations from the smallest value to the largest value significantly increases the difference between the average number of breaks per peripheral and central connections in 42 of 46 pairs for which data are available ($P < 0.0001$, one-tailed sign test). Thus, decreasing μ shifts the LFB toward central areas, whereas increasing μ shifts the LFB toward peripheral areas. This effect is illustrated in Figure 2. Increasing parameter K from the smallest value to the largest value decreases the difference between the average number of breaks per peripheral and central connections in 38 of 47 pairs for which data are available ($P < 0.001$, one-tailed sign test). Thus, increasing K shifts the LFB toward central areas, whereas decreasing K shifts the LFB toward peripheral areas. This effect is illustrated in Figure 3. Increasing population size from $N = 50$ to $N = 100$ in 2×8 and 3×8 systems significantly increases the ratio of the average number of breaks per peripheral and per central connections. (This ratio increases in 34 of 35 pairs for which data are available; $P < 0.0001$, one-tailed sign test.) Thus, increasing population size shifts the location of first breaks toward peripheral areas. This effect is illustrated in Figure 4. There are no obvious patterns in the effects of migration rate and the system size.

DISCUSSION

The classical view of speciation is that reproductive isolation arises as a by-product of genetic divergence (Dobzhansky 1937). Here, we focused on parapatric speciation scenario assuming a specific genetic architecture of reproductive isolation that allows for substantial ''nearly-neutral'' divergence leading to fixation of incompatible alleles in different subpopulations. A growing amount of data supports the genetic architecture implied in the model we used (Wu and Palopoli 1994; Orr 1995; Gavrilets 1997a, 2000). A distinctive feature of our simulations is the consideration of the complete process of speciation (from initiation until completion). The time scale for speciation is short (from a few hundred to a few thousand generations), meaning that restrictions on migration between subpopulations do not need to be long lasting. A relatively brief period of reduced migration (or isolation) may be sufficient for initiating significant genetic divergence and evolution of reproductive isolation (cf. Palumbi 1992). It has been repeatedly argued that strong divergent selection is necessary for speciation. Although divergent selection for local adaptation may under certain conditions increase the plausibility of speciation (Rice and Hostert 1993; Schluter 1996; Gavrilets 1999), our results imply that it is not required for rapid speciation.

Many evolutionary biologists appear to believe that very weak migration on the order of one individual exchanged between two populations per generation is sufficient to prevent any genetic differentiation, thus making speciation impossible. However, this conclusion has been only proven for neutral alleles (Slatkin 1987). Here, the highest number of migrants still compatible with speciation was $Nm = 8$ migrant gametes per subpopulation per generation (in models with $N = 200$ and $m = 0.04$ or with $N = 100$ and $m = 0.08$). This together with earlier results in Gavrilets (1999) and Gavrilets et al. (1998) strongly suggest that rapid speciation is possible even when subpopulations exchange several individuals per generation.

Of course, these conclusions should not be interpreted as suggesting that parapatric speciation is inevitable or can be accomplished very easily in general. In our simulations, speciation was observed only for specific sets of parameter values (see Table 1). Extrapolating our data, one can conclude that choosing less ''favorable'' parameter values (e.g., making N or m significantly larger or μ smaller) will make rapid parapatric speciation practically impossible within the framework of the model used. One can only speculate on how modifying the model itself will affect the time until speciation, T_1, which we do not attempt here. At the same time, we expect our qualitative results to be less dependent on the modeling details than quantitative characteristics such as T_1.

Species-Level Characteristics and Speciation Rate

There has been extensive discussion in the literature of the relationships between species-level characteristics, such as local abundance, range size, dispersal ability, and speciation rate (see Stanley 1986, 1990; Rosenzweig 1995; Wagner and Erwin 1995; Chown 1997; Gaston 1998 and references therein). Results presented here allow us to put previous theoretical arguments on firmer grounds. Given all else equal, increasing population range size and the resulting greater subdivision will increase the likelihood of speciation. However, geographic range size is usually positively correlated with local abundance and dispersal ability (e.g., Gaston 1994). In general, increasing local population size and/or migration rate significantly decreases the probability of parapatric speciation. (Increasing local abundance can increase the likelihood

of speciation if a population lacks genetic variation necessary to initiate divergence.) In general, the positive effects of geographic range size on the likelihood of speciation will be overwhelmed by negative effect of population density and dispersal ability. Thus, our model substantiates the claims that species with smaller range sizes (which are characterized by smaller population sizes and reduced dispersal ability) should have higher speciation rates.

Asymmetry of Range Division at Speciation

In most cases, the distribution of the location of the first break significantly deviates from a uniform distribution. Our results on the asymmetries of range division between sister species can be understood in terms of limiting factors. Any speciation event as considered here involves two necessary steps: appearance of new genotypes and breakage of a cohesive group of genotypes into evolutionary independent units. Mutation is a major factor controlling the level of genetic variation. Dispersal of individuals between subpopulations is a major factor preventing the breakage. Central populations are characterized by higher levels of genetic variation than peripheral populations, but the latter are less affected by migration than the former. Thus, if new genetic variation is the limiting factor, then central populations should be where most splits (speciation events) take place. This will happen if mutation rate, μ, is too small if local population size, N, is too small, or too many genetic changes are required for speciation (K is too high). If there is a sufficient amount of genetic variation, which will take place with high μ, high N, and low K, then migration becomes the major factor controlling speciation. In this case, speciation events are expected to involve mainly peripheral populations. Thus, both Mayr's (1954, 1963) and Brown's (1957) arguments are sound, but within their own specific domains.

Some data suggest that splits resulting in sister species with similar ranges are more common than splits producing species with very different ranges (Lynch 1989; Chesser and Zink 1994). This is compatible with patterns expected on the basis that new genetic variation is a major limiting factor in evolution. For a different dataset (Barraclough and Vogel 2000), the overall trend appears to be toward greater asymmetry than expected under a broken-stick null model, providing potential support for the peripatric model of speciation. However, some caution in interpreting such data is necessary because the extent of postspeciational change in geographic range sizes is typically unknown, and extinction of species will strongly influence the distribution of species range size (Gaston 1998).

Patterns of parapatric speciation can be affected by other factors not considered here. In a heterogeneous environment the population will most likely split along geographic areas at which population densities are low, migration is restricted, or selection regimes changes significantly. The importance of spatial heterogeneity of the environment is well recognized (Mayr 1942, 1963; Rosenzweig 1995). Our results clearly show that genetic factors are important as well.

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