

THE GEOGRAPHY OF MAMMALIAN SPECIATION: MIXED SIGNALS FROM PHYLOGENIES AND RANGE MAPS

BENJAMIN M. FITZPATRICK¹ AND MICHAEL TURELLI²

Section of Evolution and Ecology and Center for Population Biology University of California, Davis, California 95616

²E-mail: mturelli@ucdavis.edu

Abstract.—The importance of geographic isolation in speciation has been debated since the 19th century. Since the beginning of the 20th century, the consensus has been that most speciation involves divergence in allopatry. This consensus was based largely on decades of observations by naturalists and verbal arguments against speciation without isolation. Recent attempts to quantify the importance of allopatric versus sympatric speciation using comparative methods called “age-range correlation” (ARC) suggest that allopatric speciation is more common than sympatric speciation. However, very few taxa have been studied and there are concerns about the adequacy of the methods. We propose methodological improvements including changes in the way overlap between clades is quantified and Monte Carlo methods to test the null hypothesis of no relationship between phylogenetic relatedness and geographic range overlap. We analyze 14 clades of mammals, chosen because of the availability of data and the consensus among mammalogists that speciation is routinely allopatric. Although data from a few clades clearly indicate allopatric speciation, divergence with gene flow is plausible in others and many results are inconclusive. The relative rarity of significant correlations between phylogenetic distance and range overlap may have three distinct causes: (1) post-speciation range changes, (2) relative rarity of range overlap, and (3) a mixture of geographic modes of speciation. Our results support skepticism about ARC’s power for inferring the biogeography of speciation. Yet, even if few clades provide clear signals, meta-analytic approaches such as ARC may set bounds on the prevalence of alternative modes of speciation.

Key words.—Age-range correlation, allopatric speciation, parapatric speciation, phylogenies, speciation theories, sympatric speciation.

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Understanding the role of geographic isolation in speciation has always been a central goal of evolutionary biology (Coyne and Orr 2004, ch. 3). Even before Darwin’s (1859) *Origin of Species*, biogeography was viewed as a vital source of information about speciation (e.g., Wallace 1852, 1855). Based on his field observations, Darwin initially stressed the role of geographic isolation (Darwin 1909; Kottler 1978; Sulloway 1979). However, in the 1850s, while developing his “principle of divergence,” he became convinced that density- and frequency-dependent selection associated with biotic interactions were at least as important as abiotic factors in driving natural selection (Ospovat 1981). This argument, coupled with obscure meta-analyses (see ch. IV of *Charles Darwin’s Natural Selection*, Stauffer 1975), led him to conjecture that intraspecific competition might drive speciation, even without geographic isolation (e.g., Darwin 1859, pp. 111–126). Darwin’s logic remains obscure and his conclusions disputed (Sulloway 1979; Browne 1980; Ospovat 1981; Kohn 1985; Mayr 1992; Gould 2002, pp. 224–249; Mayr 2004, pers. comm.). Indeed, by the turn of the 20th century, naturalists studying Lepidoptera, mollusks, fish, birds, and mammals favored allopatric speciation driven by divergent natural selection (e.g., Gulick 1905; Jordan 1905, 1908; Poulton 1908; Grinnell 1914, 1924, 1927). By the mid-20th century, speciation was considered virtually impossible without complete geographic isolation (Mayr 1959, 1963).

This view has been challenged recently by a host of mathematical models and some case studies (Turelli et al. 2001; Drés and Mallet 2002; Coyne and Orr 2004, ch. 4; but see

critiques of the theory by Bolnick 2004 and Gavrillets 2005). These challenges have been effective and few biologists now believe that sympatric speciation is impossible (Coyne and Orr 2004, ch. 4). However, estimating the relative frequencies of different modes of speciation remains elusive. Hence, the debate continues between those arguing that speciation is primarily allopatric (e.g., Coyne and Orr 2004), and those contending that parapatric and sympatric speciation may be common (e.g., Berlocher and Feder 2002).

A few investigators have used meta-analyses to infer the prevalence of allopatric versus sympatric speciation (Lynch 1989; Barraclough et al. 1998; Berlocher 1998; Barraclough and Vogler 2000; Berlocher and Feder 2002). These analyses depend on a predictable relationship between the geography of speciation and the configuration of species’ geographic ranges long after speciation is complete. Response has been mixed. Some writers (e.g., Barraclough and Nee 2001; Vogler 2001; Orr and Turelli 2001; Wiens 2004; Martin and McKay 2004; Palumbi and Lessios 2005; Edwards et al. 2005) cite Barraclough and Vogler (2000) as showing the prevalence of allopatric speciation. In fact, Barraclough and Vogler’s (2000) results were largely inconclusive (see p. 424). Others (Chesser and Zink 1994; Losos and Glor 2003) reject the approach based on the assumption that rapid changes to species’ geographic ranges effectively eliminate any relationship between the geography of speciation and contemporary locations of geographic ranges. Undoubtedly, such range shifts have occurred (Lessa et al. 2003; Lyons 2003), but whether or not they have obscured all information regarding the geography of speciation is not clear.

The more sophisticated age-range correlation, or ARC, methods attempt to account for postspeciation range shifts by hypothesizing that the amount of overlap between two

¹ Present address: Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996; E-mail: benfitz@utk.edu.

geographic ranges depends at first on the geography of speciation but becomes randomized over time due to independent range changes (Lynch 1989; Barraclough et al. 1998; Berlocher 1998; Barraclough and Vogler 2000; Berlocher and Feder 2002). It follows that a statistical relationship will exist between time since divergence (age) and amount of range overlap if three conditions are met. First, a number of pairwise comparisons must be available representing speciation “events” at various times in the geologically recent past, including times for which geographic ranges are informative about the geography of speciation. Second, there must have been a single predominant geographic mode of cladogenesis in the dataset. And finally, there must be enough variation in the amount of pairwise range overlap for a pattern to be detectable. It is not known how often these conditions are met. This can be assessed only by critical application of ARC with clearly articulated null and alternative hypotheses.

After briefly reviewing the history of ARC-related analyses of the geography of speciation, we contribute a new comparative analysis of 14 mammalian clades. We provide several methodological improvements over earlier approaches, but conclude that it is extremely difficult to establish an association between phylogenetic relationships and geographic range overlap. The three conditions outlined above are rarely met in mammals. Although our results do not suggest that sympatric speciation has been common among mammals, they are also inconsistent with “Jordan’s Rule” that sister species almost never have overlapping ranges (Jordan 1905, 1908; Allen 1907; Mayr 1963; cf. Anderson and Evensen 1978; Lynch 1989).

Modern Meta-Analyses Based on Phylogenies and Ranges

The goal of meta-analyses is to produce convincing generalizations from disparate data. Anderson and Evensen (1978) compared range overlaps between 130 putative sister pairs of North American terrestrial vertebrates with range overlaps for 50 nonsister congeners. They found that the sister taxa more frequently exhibited considerable range overlap than did the nonsisters (see their fig. 2), but their conclusions were based on the assumption of vicariant speciation, that is, overlap or parapatry between recently derived sister species results from ranges bleeding together after the vicariance-causing barrier disappears. Lynch (1989) used similar data to infer a relatively low frequency (6%) of sympatric speciation in vertebrates. He explicitly attempted to infer the geography of speciation for various vertebrate clades with complete species-level phylogenies by quantifying range overlap and asymmetry of range sizes. His analysis was presented in part as a critique of earlier biogeographic analyses (such as Anderson and Evensen 1978) which assumed that all speciation is allopatric and hence that range overlap of sister pairs provided evidence for postspeciation dispersal. Lynch’s (1989) analysis of bird speciation was strongly criticized by Chesser and Zink (1994), who noted that in several individual cases, range overlap must represent postglacial range shifts. A common criticism of Lynch’s (1989) approach is that it attempted to infer ancestral ranges, and that such inferences are increasingly unreliable for older sister groups.

Barraclough et al. (1998) and Berlocher (1998) introduced a methodological advance that attempted to uncover the biogeography of speciation while explicitly acknowledging that ranges change over time scales significantly faster than cladogenesis. In particular, they extended an idea illustrated in Lynch (1989; figs. 7 and 8), by developing an inference framework to describe how patterns of range overlap in a clade change over time (this approach was later dubbed ARC for “age-range correlation” by Berlocher and Feder 2002). If allopatric speciation is the rule, then range overlap between sister species will start at 0% and the probability of nonzero overlap will gradually increase as ranges change over time. In contrast, if most speciation is sympatric, overlap should start near 100% and tend to decrease with time since divergence. Berlocher (1998) used data from plants that originated by polyploidy, which must involve range overlap (or at least contact) to provide a persuasive positive control for such methodology. He found that sister species inferred to have arisen by polyploidy or recombinational speciation and sister species of phytophagous insects classified as potential “host-shifters” have much greater average range overlap (51–56%) than other “nonshifter” species pairs (14.5% average range overlap). Barraclough and Vogler (2000) found statistically significant positive correlations between overlap and genetic divergence in several animal clades, but they also showed that simulations of randomly placed ranges can produce a similar pattern. This suggests a disconnect between the statistical hypothesis test and the biological question, a problem we address with new methodology below.

At best, ARC methods are informative with regard to a very specific question: what is the relative importance of sympatric versus nonsympatric speciation? In an attempt to differentiate parapatric speciation from purely allopatric divergence, we also consider the geographical distance between ranges of sister groups. Under purely allopatric speciation, we expect to find nonzero distances (geographic gaps as suggested by Jordan 1905) between the ranges of sister species. Whereas under parapatric speciation, sister species ranges abut or slightly overlap immediately following divergence. This dichotomy is imperfect, certain barriers such as rivers may completely isolate populations that would appear on a map to have abutting ranges (e.g., chipmunks in the *Tamias townsendii* group, Gannon and Lawlor 1989). However, a high frequency of near-zero geographic distances between ranges of recently diverged species would call into question the primacy of allopatric speciation and invite research into the concordance of range boundaries with sharp barriers such as rivers or the presence of environmental gradients that may foster parapatric speciation.

Here we present an ARC analysis of 14 mammalian clades. Allopatric speciation has been assumed to be the dominant mode of speciation in mammals (e.g., Alexander and Riddle 2005, p. 376), therefore they provide a valuable test of the ability of ARC to recover the geography of speciation where there is little doubt that allopatry is the rule. Coyne and Orr (2004, ch. 4) presented preliminary range overlap data for seven of our 14 study clades (their figs. 4.5 and 4.6). Those graphs, provided by us, were based on preliminary analyses subsequently found to have an error that tended to produce lower overlap values than the correct analyses presented here.

Although the error affected the quantitative results, our new plots look similar. Coyne and Orr (2004) presented no statistical analyses of those graphs, but concluded (p. 175) that they “. . . provide strong evidence for allopatric speciation, with some observations consistent with parapatric speciation. There is virtually no evidence for sympatric speciation.” We present a much more complete analysis and reach less definite conclusions. In addition to analyzing range overlap, we consider range size asymmetry (as did Barraclough and Vogler 2000) and the geographic distance between spatially disjunct clades. We discuss the natural history of some of the clades analyzed, including some limited fossil data relevant to documenting range changes. We present a null model that generates expected overlaps; and we develop and apply a statistical procedure using randomization and phylogenetically independent contrasts to test the null hypothesis that range overlap between species is uncorrelated with the length of time since their divergence.

METHODS

Clades Analyzed and Data Sources

We worked on mammals because of the availability of good range maps and species-level phylogenetic hypotheses based on genetic data. In addition, as indicated by their relative rarity on islands, mammals (other than bats) are generally less mobile than birds (which also have good range and phylogenetic information), suggesting that mammalian range data may be less affected by postspeciation range shifts. We searched for young clades with complete or near-complete taxon sampling, well-resolved phylogenies and range maps. We focused primarily on approximately “genus level” clades, in part because many phylogenetic studies have focused on genera, which often describe clades of ecologically and morphologically similar species. Table 1 lists the chosen groups and sources of our phylogenetic and range data.

Geographic range data were taken primarily from Hall (1981), Corbet (1978), the *Mammalian Species* accounts published by the American Society of Mammalogists (Table 1; available online from <http://www.science.smith.edu/departments/Biology/VHAYSEN/msi/default.html>), and IUCN status surveys (Chapman and Flux 1990; Nowell and Jackson 1996). For the most part, these maps are coarse summaries of occurrence data and expert opinion. In addition, they are presented at a variety of scales, further complicating comparative analysis. We took these range maps at face value as the best available information on current distributions, and we assume that the inevitable inaccuracies are not biased with respect to our hypotheses. Range maps were digitized and overlaid on a map of the world in ArcView GIS 3.2. A script (available upon request) was written to calculate range areas and overlaps. The degree of overlap between two species was calculated as the ratio of the area of overlap to the area of the smaller of the two ranges (Lynch 1989; Chesser and Zink 1994; Barraclough and Vogler 2000; Berlocher and Feder 2002). This way, if one range is contained within another, overlap is 100%.

Species were recognized according to Wilson and Reeder (1993), unless more recent revisions were available (e.g., from the *Mammalian Species* accounts). We recognize that

taxonomic practices may introduce biases into comparative analyses (Agapow et al. 2004; Isaac et al. 2004). It is not clear whether a net bias exists in the groups we studied, but we assume that any taxon-specific biases are not associated with modes of speciation.

Phylogenetic Inference

DNA data were obtained from GenBank and allozyme data were transcribed from publications. Allozyme-based phylogenies were estimated using Nei's (1972) D and the neighbor-joining algorithm in PHYLIP (Felsenstein 2003). Approximate ages were calculated for each node using molecular clock calibrations given in each source. For each node, we averaged the approximate clock-based ages for each pair using Eq. (1) below. These are intended only as rough guides to divergence times, and they ignore the rate heterogeneity of allozyme divergence. For mtDNA, we used ModelTest (Posada and Crandall 1998) to choose a maximum-likelihood (ML) model for each clade. Maximum-likelihood trees were then estimated in PAUP* (Swofford 1998). If necessary, we resolved polytomies to show maximal range overlap at the shortest distance (in practice, alternative resolutions had no effect on our statistical results). We used age calibrations given in the source papers and Sanderson's r8s program to estimate the ages of nodes on the mtDNA trees (Ribera et al. 2001; Sanderson 1997, 2002). Algorithms for age estimation were chosen using the cross-validation procedure in r8s (Sanderson 2002). Again, these estimates are rough approximations of the length of time over which geographic ranges may have changed since each speciation event. Details on tree and age estimation are given in Appendix Table A1 (available online at: <http://dx.doi.org/10.1554/05-453.1.s1>). We noted no substantive discrepancies between our trees and those reported in the source papers.

Data Analyses

Sympatric versus nonsympatric speciation: ARC

Simply analyzing pairwise range overlap between species within a clade is inappropriate because of nonindependence due to phylogenetic relationships and reuse of species in multiple pairwise comparisons (Felsenstein 1985). Barraclough and Vogler's (2000) solution was a node-based approach, in which each node produces a comparison between clades that are assigned ranges equal to the union of the constituent species ranges. This practice, also used by Lynch (1989), requires that all species ranges within a clade be known and has been criticized by Chesser and Zink (1994) as an unrealistic “reconstruction” of the ancestral range (see Barraclough and Vogler 2000, Losos and Glor 2003). Instead, we used nested averages of the pairwise overlaps between species in each clade (Fig. 1 and eq. 1 below) and maximum pairwise overlap across each node. These methods do not require complete taxon sampling and do not attempt to reconstruct ancestral ranges. Each node provides an estimate of the average overlap between species after a certain time since speciation. Incomplete taxon sampling reduces sample size and precision, but does not bias estimates of the mean unless taxon sampling is biased (estimates of the maximum,

TABLE 1. Groups included in this study.

Group	Genetic data	Species	Distribution
<i>Chaetodipus</i> (Pocket mice)	mtDNA (Alexander and Riddle 2005)	14	North America (Hall 1981; Schmidly et al. 1993; MS ^a 384, 418, 297, 517, 419, 320, 484, 420, 385)
<i>Dipodomys</i> (kangaroo rats)	Allozyme (Patton et al. 1981)	13	
	mtDNA (Alexander and Riddle 2005)	14	North America (Hall 1981; Schmidly et al. 1993; MS 324, 369, 339, 232, 323, 389, 326, 381, 353, 354, 51, 311)
Felidae (wild cats)	Allozyme (Johnson and Selander 1971; Hamilton et al. 1987)	11	
	mtDNA (Johnson and O'Brien 1997)	33	World wide (Nowell and Jackson 1996; Sunquist and Sunquist 2002)
<i>Gazella & Antelope</i> (gazelles)	mtDNA (Rebholz and Harley 1999)	14	Africa, Middle East, India (Haltenorth and Diller 1980; MS 491, 490, 518)
<i>Geomys</i> (plains pocket gophers)	mtDNA (Jolley et al. 2000)	10	North America (Hall 1981; MS 36, 382, 383, 170, 86, 35)
Mormoopidae (ghost-faced bats)	mtDNA (Van Den Bussche et al. 2002)	8	Central and South America (Smith 1972; Eisenberg 1989; Redford and Eisenberg 1992; Eisenberg and Redford 1999)
<i>Myotis</i> (little brown bats)	mtDNA (Ruedi and Mayer 2001)	19	North America, South America, Eurasia (Hall 1981; Corbet 1978; Eisenberg 1989; Redford and Eisenberg 1992; Eisenberg and Redford 1999)
<i>Ochotona</i> (pikas)	mtDNA (Yu et al. 2000)	21	Holarctic (Smith et al. 1990)
<i>Orthogeomys</i> (pocket gophers)	Allozyme (Hafner 1991)	7	North America (Hall 1981)
<i>Perognathus</i> (pocket mice)	mtDNA (Alexander and Riddle 2005)	9	North America (Hall 1981; Schmidly et al. 1993)
<i>Peromyscus boylii</i> group (deer mice)	mtDNA (DeWalt et al. 1993; Tiemann-Boege et al. 2000)	17	North America (Hall 1981; MS 48, 161, 49, 596, 161)
<i>Sorex</i> (shrews)	mtDNA (Fumagalli et al. 1999; Odachi et al. 2001)	21	Holarctic (Hall 1981; Corbet 1978; Odachi et al. 2001; MS 524, 215, 554, 528, 231, 296, 337, 27, 155, 143, 2, 131, 212, 131)
	Allozyme (George 1988)	26	
<i>Spermophilus</i> (ground squirrels)	mtDNA (Herron et al. 2004)	17	North America (Hall 1981)—analysis restricted to exclusively North American clade (S2, 3, 4, 5 of Herron et al. 2002)
	Allozyme (Levenson et al. 1985)	18	North America + 1 Eurasian species (Hall 1981; Corbet 1978; MS 478, 444, 460, 452, 466, 469, 468, 443, 472, 476, 437, 399, 436, 411, 438, 390)

^a MS numbers refer to *Mammalian Species* accounts (most are available online from <http://www.science.smith.edu/departments/Biology/VHAYSSSEN/msi/default.html>).

however, will tend to be biased downward in poorly sampled groups). The nested-average calculation illustrated in Figure 1 can be expressed compactly as follows. Suppose node i separates clades C_1 and C_2 , we quantified the average overlap at node i by

$$\bar{o}_i = \sum_{j \in C_1} \sum_{k \in C_2} \left(\frac{1}{2}\right)^{n_{jk}-1} o_{jk} \quad (1)$$

where the double sum is over all species in the two clades, o_{jk} denotes the overlap between species j and k , and n_{jk} is the number of nodes separating the two species on the tree. We use this rather than computing overlaps between the union of ranges within sister clades, because it discriminates between patterns of overlap that are indistinguishable in the Barraclough and Vogler (2000) method. For example, consider sister species A and B and a more distant species C. If C overlaps 100% with A and 0% with B, the union method gives an overlap of 100% between C and the clade A + B, whereas the average overlap is 50%. Our averaging refines the method suggested by Berlocher and Feder (2002; adopted

from Coyne and Orr 1989), which equally weights all pairwise comparisons across a node without taking phylogenetic nesting into account.

We fit linear regression lines to plots of mean and maximum range overlap versus relative node age. Parametric tests of statistical significance are inappropriate because the data are not identically distributed (deeper contrasts, involving averages or maxima, certainly follow different distributions than sister pairs). In addition, the null hypothesis of no relationship between divergence time and overlap does not necessarily correspond to a null hypothesis of slope = 0. If overlap is rare, deeper nodes are more likely to exhibit overlap by chance because they sample more species and are therefore more likely to pick up rare events or extreme values. We used Monte Carlo simulations to estimate the distribution of slopes and intercepts under the null hypothesis of no phylogenetic signal. This null hypothesis was simulated by randomizing ranges among species in each group (Maddison and Slatkin 1991). Randomization was accomplished by permuting the rows of the overlap matrix and ordering the col-

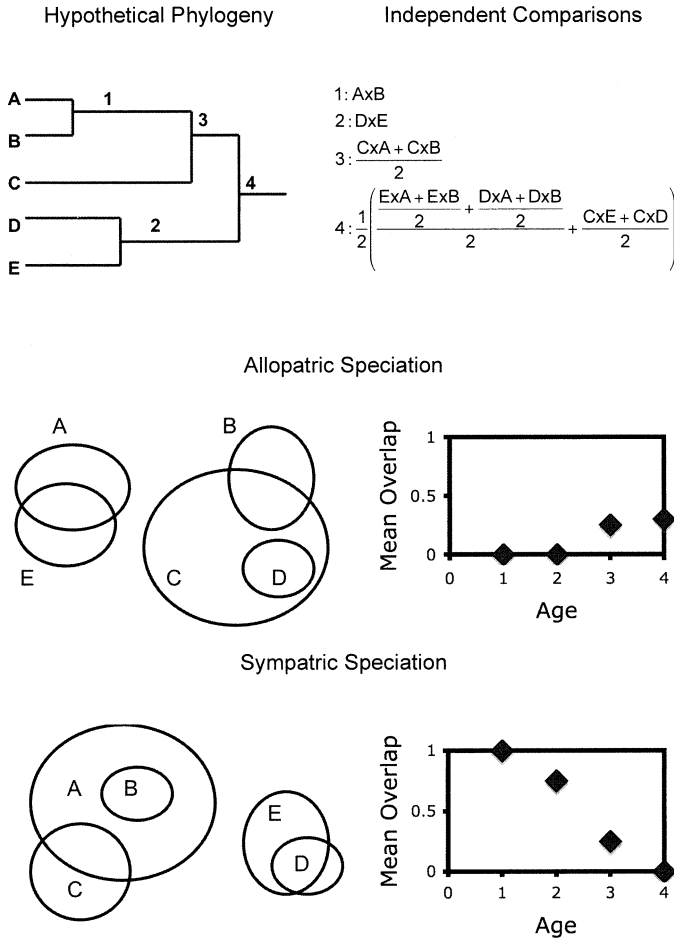


FIG. 1. Age-range correlation (ARC) analysis (Berlocher and Feder 2002). Our independent comparisons are nested averages equivalent to Felsenstein's (1985) independent contrasts (Fitzpatrick 2002), not the simple unweighted averages used by Berlocher and Feder (2002).

umns into the same permutation, as in the Monte Carlo Mantel test (Dietz 1983). We fitted linear regression lines to 10,000 Monte Carlo replicates for each clade. We recorded the fraction, f , of randomized datasets with greater intercepts and slopes than the observed data and estimated two-tailed P -values as $2 \times \text{minimum}(f, 1 - f)$. For comparison, we also analyzed our data with Barraclough and Vogler's (2000) methods, using the union of ranges for clade comparisons and performing parametric regressions to determine statistical significance.

If a significant age-range correlation is present, then more recently diverged pairs of clades are likely more informative about the geography of speciation. If the regression intercept is significantly greater than 0.5 and the slope is negative, we would infer that sympatric speciation is the most frequent mode of speciation in the group. If the intercept is significantly less than 0.5 and the slope is positive, we would infer that allopatric speciation is most common. If the intercept is less than 0.5 but the slope is negative, we would consider the result inconclusive (similarly if the intercept is greater than 0.5 and the slope is positive). For inconclusive results (those just mentioned and cases of no significant ARC), we

asked whether the frequency of overlap in the group as a whole is lower or higher than a random expectation as follows.

Sympatric versus nonsympatric speciation: observed versus expected overlap

Lack of phylogenetic signal need not imply that the geography of speciation cannot be recovered. For instance, groups with no range overlap between any species pair show no pattern of increasing overlap with phylogenetic distance, yet strongly support allopatric speciation (Losos and Glor 2003). To quantify the extent of range overlap within a clade, we propose two "Jordan indices," denoted J_{ALL} and J_{CON} , which are the proportion of pairwise species comparisons and node contrasts, respectively, that show no overlap. (One could compute an index, J_{SIS} , using only sister species, but our analyses and those of Anderson and Evensen (1978), Lynch (1989, fig. 8), and Berlocher (1998, fig. 8.4) suggest that this would not alter our conclusions.)

One possible reason for a lack of phylogenetic signal in range overlap is that overlap is rare, even for distantly related species. In such cases, the question arises, is overlap too rare to be consistent with frequent sympatric speciation? A conservative test is whether overlap is less common than expected if geographic ranges are random with respect to each other. We implemented this by comparing observed values of J_{ALL} to various null distributions obtained by simulating random placement of ranges of the observed sizes. Specifically, we ask what is the probability that randomly placed ranges show J_{ALL} values as large or larger than those observed. Because sympatric speciation should systematically promote range overlap between close relatives, high J_{ALL} values argue against pervasive sympatric speciation.

The null distribution of J_{ALL} depends on the range shapes allowed and the size of the potential area for ranges. As demonstrated below, the results are sensitive to whether randomly placed ranges include gaps and less sensitive to range shape. With gaps, the results are extremely sensitive to assumptions about minimal fragment sizes. Expected overlaps also depend strongly on the size of the area assumed to be available for individual ranges. For example, if the null hypothesis is that ranges could be anywhere in North America, expected overlap will be lower than if ranges are restricted to specific biomes. Lacking a model from which to estimate available areas for our species, we used the range of the entire clade (the union of the individual species ranges). Letcher et al. (1994) took a similar approach to test for competitive exclusion. However, their analysis was explicitly limited to habitat types inhabited by both species of a pair.

To explore alternative null distributions, we considered two extremes: fully connected ranges with idealized shapes, either circles or squares, and fragmented ranges, with different minimum fragment sizes. For the "circle" model, we assumed that circular ranges were randomly placed within a circle of area equal to that of the union of all ranges analyzed within a clade. We randomly placed circular ranges with areas equal to those of the species analyzed, then calculated J_{ALL} for 10,000 random range placements. We performed analogous simulations using squares for the total available area

and the individual ranges. As an alternative to these compact ranges, we performed some simulations with fragmented ranges. As discussed below, the results depended critically on the minimum range-fragment size allowed. These simulations were performed by setting a minimum fragment size (some fraction of the smallest range size within a clade), treating the entire area as a number of urns of this size, then assigning each species to a random set of these urns, proportional to its range area. Again, 10,000 random placements were simulated and the distribution of J_{ALL} tabulated.

Parapatric versus allopatric speciation

For those groups showing evidence that sympatric speciation is rare, the question remains whether allopatric and parapatric speciation can be distinguished using ARC. Previous authors have shied away from this question (Lynch 1989; Barraclough and Vogler 2000). Lynch (1989) cited the arguments of Wiley (1981) and Cracraft (1982) that it is virtually impossible to differentiate parapatric from allopatric speciation. We agree that abutting ranges are consistent with either parapatric divergence or secondary contact after allopatric speciation. However, if most recently diverged species ranges are separated by geographic gaps, allopatric speciation is more likely than parapatric speciation. Therefore, we also analyzed the minimum straight-line distance between ranges (defined as zero for overlapping ranges). Parapatric speciation will result in very small mean and maximum distances between recently diverged clades. As ranges shift over time, some will come to overlap more (zero distance) and some will become much more distant, resulting in an increase in the mean and maximum. Allopatric speciation is also likely to result in sister species with fairly close ranges (Wallace 1855; Jordan 1908; Cracraft 1982; Lynch 1989), while average and, particularly, maximum distance should increase as ranges shift independently. However, the y-intercept should be near or below zero for parapatric speciation, but may be significantly positive if species arise in geographic areas separated by gaps.

Peripheral isolates

If allopatric speciation is pervasive, the relative sizes of the ranges of sister clades may indicate whether or not speciation often begins with peripheral isolates versus a more symmetrical, “dumbbell” model of isolation (Futuyma 1998, fig. 16.1). Highly asymmetrical range sizes have been proposed to indicate peripheral-isolates speciation (Lynch 1989; Barraclough and Vogler 2000). Therefore, we performed ARC on the asymmetry of range sizes for datasets that were credibly consistent with allopatric speciation. Asymmetry was calculated as the area of the larger range divided by the area of the smaller. If most speciation occurs when a small isolated fragment diverges from a widespread ancestral population, then most recently derived sister-species pairs will include one with a very small range and one with a large range; asymmetry between sisters is maximal. As ranges change through time, asymmetries between more distantly related species will take on a wider range of values. Under peripheral-isolates speciation, minimum range size asymmetry should decrease with time while the maximum pairwise

asymmetry is expected to remain high. Therefore, we analyzed mean and minimum range size asymmetry to test for phylogenetic signal consistent with peripheral-isolates speciation.

RESULTS

Sympatric versus Nonsympatric Speciation

Age-range correlation

We analyzed data for 237 species belonging to 14 clades (Table 1). For four clades, our analysis of slopes indicated that we could reject the null hypothesis of no phylogenetic signal in the degree of overlap between species within clades (*Myotis*, *Ochotona*, *Peromyscus*, and *Tamias*; Table 2). However, no regression slopes remain statistically significant after a Bonferroni correction, and they do not all trend in one direction. In the same four groups, intercepts were significantly different from their null expectations, with three remaining significant after Bonferroni adjustment (Table 2). There is no significant trend for slopes or intercepts to be greater or less than their null expectations. *Peromyscus* (deer mice) support the predictions of allopatric speciation (overlap increases with increasing depth in the tree and the intercepts of the regression lines are lower than expected, and well below 0.5). In *Myotis* (little brown bats), the opposite pattern holds with higher range overlap occurring between closely related species and an intercept above 0.5, features expected under sympatric speciation. For *Tamias* (chipmunks) and *Ochotona* (pikas), the slopes are less positive than expected according to our permutation tests, but their signs depend on whether average or maximum overlaps are considered and the intercepts are below 0.5. These results offer no clear support for any dominant mode of speciation.

Some groups show clear support for nonsympatric speciation despite their lack of phylogenetic signal (Table 2, Figs. 2, 3). The gophers, *Geomys* and *Orthogeomys*, show virtually no overlap at all. This is also true for gopher clades not analyzed here due to unresolved phylogenies (*Cratogeomys* [Demastes et al. 2002], *Thomomys* [Patton and Smith 1981; Smith 1998]). The *Gazella*, *Dipodomys* (mtDNA), and *Spermophilus* data may also be interpreted this way; overlap appears too rare to allow a powerful test of the hypothesis that overlap is less rare deeper in the tree (fig. 3). In contrast, the bats (Mormoopidae and *Myotis*) show what is expected for animals with very high dispersal. Overlap is often very great and appears random with respect to relative node age (Fig. 3).

Limiting our analysis to putative sister species did not result in any statistically significant signal (Appendix Table A2 available online at: <http://dx.doi.org/10.1554/05-453.1.s2>). We pooled across clades, creating datasets of 20 sister species with allozyme data and 63 with mtDNA data, and performed simple regression analyses of overlap, distance between ranges, and range size asymmetry versus estimated divergence time. This analysis is weakened by incomplete taxon sampling in some groups, uncertainties in our estimated phylogenies, and significant potential errors in estimates of relative divergence time associated with inconsistent calibrations and rates of molecular divergence across clades.

For comparison, we also used Barraclough and Vogler's

TABLE 2. Linear regression analyses of percent overlap vs. estimated node age. Parameters under “Randomization Tests” were fitted by least squares with statistical significance determined by Monte Carlo resampling. For each group there are two entries; the top one is the analysis of average overlap, the bottom is of maxima. For comparison, we also present parametric regressions on arcsine-transformed overlaps calculated using the range merging procedure of Lynch (1989) and Barraclough and Vogler (2000). n is the number of species in each dataset; J_{ALL} is the fraction of all pairwise comparisons with zero overlap; J_{CON} is the fraction of nodes across which there are no overlapping species; $f(\text{greater})$ is the fraction of 10,000 Monte Carlo replicates with greater slopes or intercepts than the observed value.

	n	J_{ALL}	J_{CON}	Randomization tests				Parametric	
				Intercept	$f(\text{greater})$	Slope	$f(\text{greater})$	Intercept	Slope
Allozyme data									
<i>Chaetodipus</i>	13	0.47	0.08	0.167 0.199	0.521 0.568	0.066 0.552	0.362 0.308	0.395	0.087
<i>Dipodomys</i>	11	0.58	0.30	0.239 0.330	0.353 0.679	-0.128 0.336	0.609 0.288	0.358	0.339
<i>Orthogeomys</i>	7	0.95	0.83	-0.002 -0.002	0.952 0.480	0.034 0.034	0.048 0.520	-0.002***	0.034
<i>Sorex</i>	26	0.69	0.28	0.322 0.294	0.048 0.097	-0.332 0.704	0.893 0.853	0.351	0.435
<i>Tamias</i>	18	0.74	0.29	0.127 0.334	0.219 0.023*	-0.084 0.123	0.784 0.977*	0.252	-0.029
mtDNA data									
<i>Chaetodipus</i>	14	0.49	0.23	0.161 0.096	0.486 0.752	0.001 0.040	0.462 0.325	0.017	0.060
<i>Dipodomys</i>	14	0.67	0.38	-0.020 -0.283	0.872 0.954	0.016 0.102	0.212 0.063	-0.540*	0.148***
Felidae	33	0.67	0.25	0.432 0.231	0.025 0.029	-0.003 0.005	0.963 0.973	0.403	0.002
<i>Gazella</i>	14	0.79	0.54	0.023 -0.036	0.726 0.576	0.001 0.008	0.253 0.452	0.149	0.0002
<i>Geomys</i>	10	0.98	0.89	0.015 0.031	0.045 0.045	-0.0002 -0.0004	0.955 0.955	0.044***	-0.001
Mormoopidae	8	0.43	0.29	0.819 0.707	0.093 0.128	-0.006 -0.001	0.905 0.966	0.983	-0.006
<i>Myotis</i>	19	0.63	0.06	0.613 0.701	0.004** 0.000***	-0.002 -0.0003	0.826 0.996**	0.882	-0.003
<i>Ochotona</i>	21	0.74	0.25	0.429 0.426	0.005* 0.002**	-0.005 0.001	0.991* 0.995*	0.592	-0.002
<i>Perognathus</i>	9	0.53	0.13	0.303 0.068	0.103 0.224	-0.025 0.044	0.928 0.726	-0.082	0.070
<i>Peromyscus</i>	17	0.68	0.56	-0.004 -0.145	0.955 0.9998***	0.002 0.014	0.117 0.004**	-0.270***	0.016***
<i>Sorex</i>	21	0.74	0.20	0.279 0.191	0.066 0.187	-0.001 0.011	0.716 0.225	0.206	0.008
<i>Spermophilus</i>	17	0.78	0.31	0.035 -0.250	0.488 0.774	0.001 0.011	0.392 0.104	-0.053***	0.004*
<i>Tamias</i>	23	0.80	0.18	0.204 0.282	0.000*** 0.010*	-0.002 0.002	0.995* 0.993*	0.281*	0.0002

* $P < 0.05$; ** $P < 0.01$ (Bonferroni critical value for five tests); *** $P < 0.004$ (Bonferroni critical value for 12 tests).

(2000) methods (union of ranges and parametric regression) to analyze our data (Table 2). As expected, this yields more positive slopes than our method, but only the *Dipodomys* (mtDNA) and *Peromyscus* data show “significant” slopes after Bonferroni adjustment.

Discrepancies between mtDNA and allozymes

Three of the four clades for which we had both mtDNA and allozyme data show striking discrepancies between the two analyses. For pocket mice (*Chaetodipus*) and chipmunks (*Tamias*), the mtDNA data indicate some recently diverged pairs with significant range overlap, suggesting sympatric or parapatric speciation. However, when the phylogenies are estimated with allozymes, the putative sister species with overlapping ranges appear rather distantly related. For kangaroo rats (*Dipodomys*), the pattern is the reverse; allozymes

reveal great overlap for one apparently recently diverged pair which appear more distantly related from mtDNA.

Disagreement between mtDNA and allozymes may indicate introgression of mtDNA (cf. Rieseberg and Wendel 1993; Shaw 2002), or imperfect relationships between phylogenetic topologies and allozyme distances. Allozyme-based trees generally deviated significantly from a molecular clock, but this does not necessarily invalidate their estimated topologies.

Observed versus expected overlap

The Jordan indices, J_{ALL} and J_{CON} (Table 2), are the proportion of pairwise species comparisons and node contrasts, respectively, that show no overlap. Pairwise overlap is generally rare (high J_{ALL}), but across most nodes in most trees there is at least some overlap (low J_{CON}), because a few

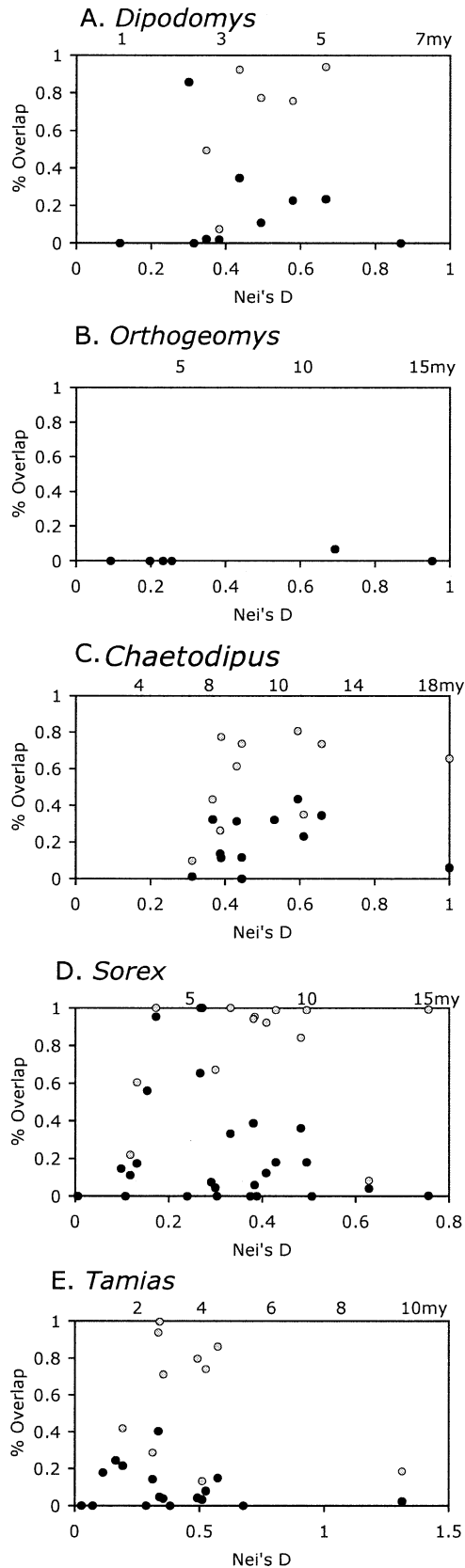


FIG. 2. Allozyme data: average (black circles) and maximum (grey circles) range overlap versus genetic distance across nodes in each group's phylogeny. Approximate time is given along the top of each panel.

broadly distributed species in each clade overlap with several more-restricted species. Thus, overlap between closely related mammal species may generally be too rare to allow meaningful analyses of the relationship between overlap and phylogenetic relationships. A more important question, however, is whether overlap is too rare to be consistent with a high frequency of sympatric speciation.

The analyses of our null models for J_{ALL} produced both expected and counterintuitive results. Table 3 summarizes the outcomes for our models of continuous circular and square ranges. As expected, the gophers show significantly more allopatry than expected by chance. In contrast, *Peromyscus*, which showed a strong ARC signal, did not produce a significantly large J_{ALL} , and the allozyme analysis of *Tamias*, which showed a significant ARC when extrema were analyzed, showed a significantly low level of allopatry. This reflects the fact that most chipmunks are found in the mountains of western North America, whereas a few species are widely distributed in eastern North America and one in Siberia. Thus, the shared available area is very large. Two clades, *Spermophilus* and *Gazella*, which showed no significant ARC, showed a significantly high values of J_{ALL} , supporting the interpretation that the lack of ARC significance reflects relatively little range overlap for any level of divergence and hence a lack of statistical power. For *Gazella* and *Spermophilus*, as for the more extreme case of the gophers *Orthogeomys* and *Geomys*, our null model of random ranges provides statistical support for allopatric speciation, even though the ARC analyses do not. Most unexpected were the significantly high values of J_{ALL} for clades that showed clearly ambiguous ARC results, *Felidae*, *Myotis*, and *Sorex* (mtDNA). These clades, like *Tamias*, are spread over multiple continents, so the significantly high allopatry values reflect the geographic isolation of subclades. For such old and widely distributed clades, the null model of random placement is inappropriate.

We also compared the observed J_{ALL} values to null distributions obtained with extremely fragmented ranges. When the size of the smallest range within the clade was used as the minimum fragment size, the observed J_{ALL} values for every set of data except for *Chaetodipus* (both allozymes and mtDNA) were significantly larger, with $P < 10^{-3}$, than the values expected from the null distribution. However, when the minimum fragment size was set to one-tenth of the smallest range, the observed J_{ALL} values for all groups, including *Chaetodipus*, were deemed significantly large with $P < 10^{-3}$. Given this sensitivity, we assign no biological significance to these results. A problem with the extreme model of fragmentation used is that it assumes no spatial autocorrelation among the fragments. Hence, the smaller the fragments, the more likely they are to be broadly dispersed making random overlaps more likely. In contrast to such dispersion, most of the ranges we analyzed were continuous, so the more fragmented null models (that are easily rejected) are not biologically appropriate.

Parapatric versus Peripatric versus Allopatric Speciation

For groups showing evidence that sympatric speciation is rare (*Geomys*, *Orthogeomys*, *Peromyscus*, *Gazella*, and *Sper-*

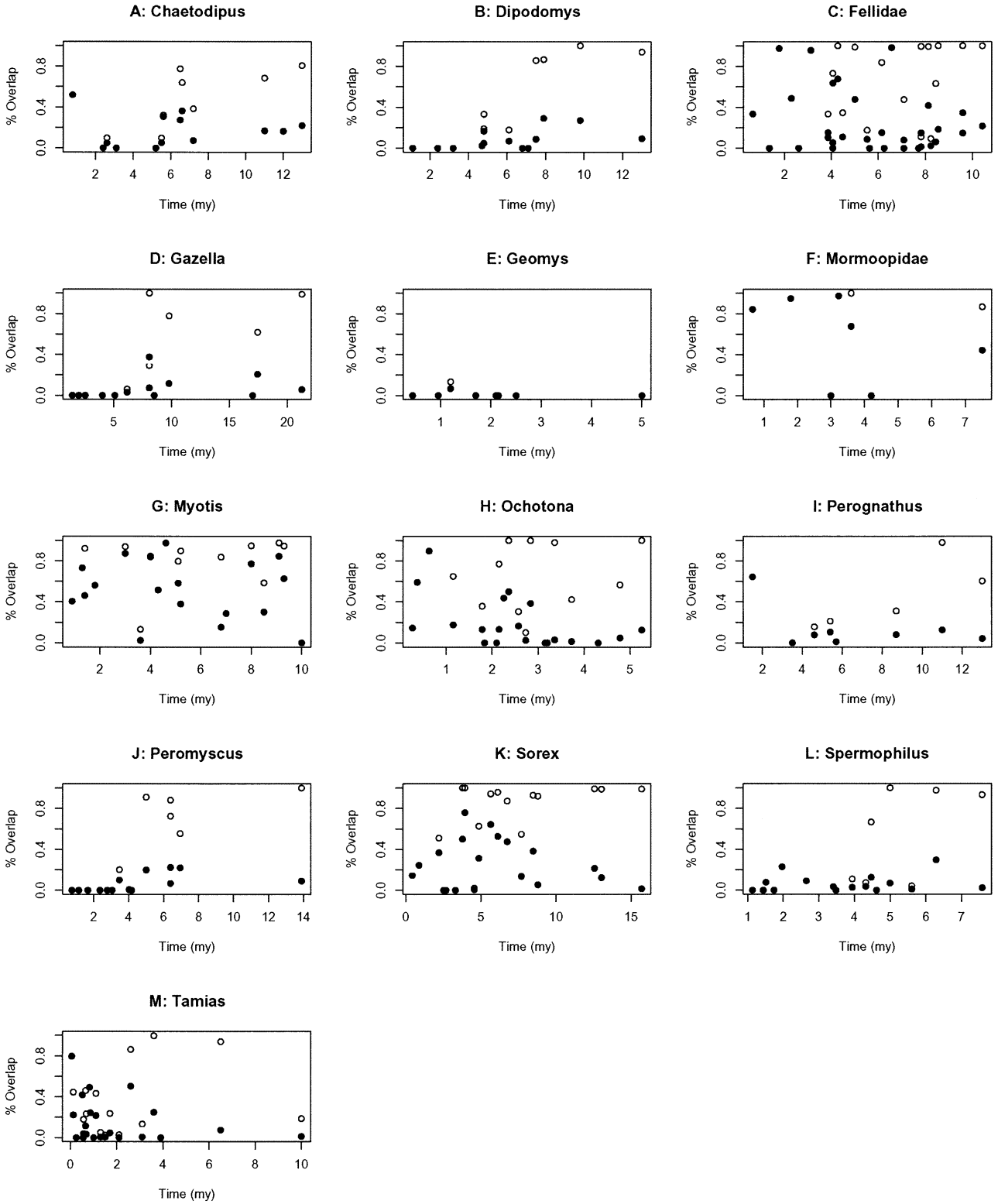


FIG. 3. Mitochondrial DNA data: average (black circles) and maximum (grey circles) range overlap versus approximate age for each node in each group's phylogeny.

TABLE 3. Observed values of J_{ALL} , the fraction of pairs of species in the clade that show no range overlap, compared to two null models: square versus circular ranges. The probabilities are the observed fraction of 10,000 simulations that gave values of J_{ALL} as large or larger than observed.

Taxon (no. of species)	J_{ALL}	$P(\text{circle})$	$P(\text{square})$
Allozymes			
<i>Chaetodipus</i> (13)	0.47	0.96	0.97
<i>Dipodomys</i> (11)	0.58	0.73	0.77
<i>Orthogeomys</i> (7)	0.95	0.000	0.000
<i>Sorex</i> (26)	0.69	0.28	0.33
<i>Tamias</i> (18)	0.74	0.998	0.999
mtDNA			
<i>Chaetodipus</i> (14)	0.49	0.901	0.924
<i>Dipodomys</i> (14)	0.64	0.26	0.24
Felidae (33)	0.67	0.000	0.000
<i>Gazella</i> (14)	0.79	0.001	0.002
<i>Geomys</i> (10)	0.98	0.000	0.000
Mormoopidae (8)	0.43	0.21	0.22
<i>Myotis</i> (19)	0.63	0.000	0.000
<i>Ochotona</i> (21)	0.74	0.79	0.84
<i>Perognathus</i> (9)	0.53	0.054	0.073
<i>Peromyscus</i> (17)	0.68	0.08	0.12
<i>Sorex</i> (21)	0.74	0.000	0.000
<i>Spermophilus</i> (17)	0.78	0.03	0.03
<i>Tamias</i> (23)	0.80	0.999	0.999

mophilus), we analyzed distances between ranges to assess the likelihood of parapatric versus truly allopatric speciation. Although no significant statistical trends were detected (Appendix Table A3 available online at: <http://dx.doi.org/10.1554/05-453.1.s3>), inspection of the data shows a majority of nodes with substantial mean and maximum geographic gaps between species (Fig. 4). This result favors allopatric over parapatric speciation.

For these same groups, we find no evidence that range size asymmetry is maximal between closely related species (Fig. 5). No ARC analyses showed statistically significant trends in mean or minimum asymmetry (Appendix Table A3 available online). Although minima were lower for deeper nodes, the trend was simply consistent with ranges randomized with respect to phylogenetic relationships. Therefore, there is no evidence that peripheral isolates speciation is common in these groups.

DISCUSSION

We found no consistent signal of the geography of speciation. This is surprising given widespread agreement that allopatric speciation is probably the norm in mammals (e.g., Patton and da Silva 1998; Alexander and Riddle 2005; but see Mattern and McLennan 2000). Our failure to detect consistent phylogenetic signal in geographic range overlap suggests that ARC analyses have limited power for many mammals. ARC analyses can be expected to give definitive results only when speciation within a group has been primarily sympatric or allopatric, and when range changes have not erased the evidence. Inconclusive ARC can be expected when diversification involves a mixture of sympatric and nonsympatric speciation, or when range changes have obscured the geography of speciation. Incorrectly inferred phylogenies are another possible source of confusion, especially when intro-

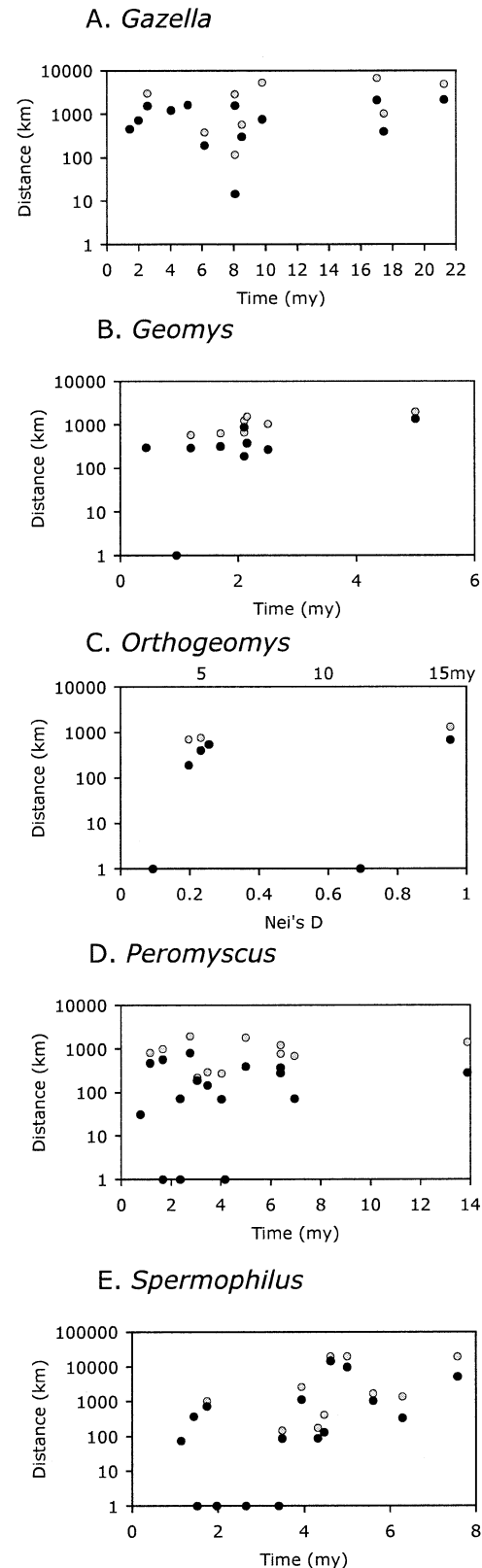


FIG. 4. Average (black circles) and maximum (grey circles) distance between species ranges versus estimated divergence time for each node in the five groups inferred to have high frequencies of nonsympatric speciation. Distance was defined as zero for overlapping ranges.

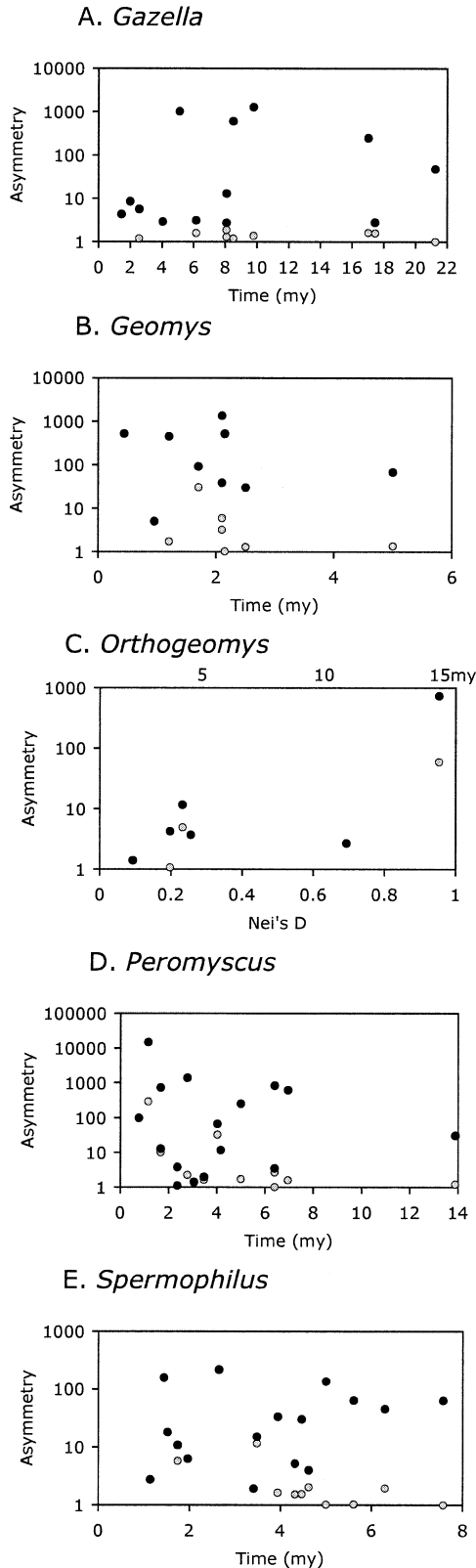


FIG. 5. Mean (black circles) and minimum (grey circles) range size asymmetry versus estimated divergence time for each node in the five groups inferred to have high frequencies of nonsympatric speciation.

gression between distantly related forms makes them appear to be sister species.

Contrary to the nonquantitative statements of early advocates of allopatric speciation, we see “nontrivial” overlap (>10%, after Lynch 1989) in 33–45% of putative sister pairs, and 51–54% of second-level nodes (Fig. 6). These results agree with the qualitative results of Anderson and Evensen (1978) and the quantitative results of Lynch (1989, fig. 8) and Berlocher (1998) who found 46.7% of sister pairs had >10% range overlap when considering groups not expected a priori to have a high incidence of sympatric speciation (i.e., excluding polyploid plants and host-specific phytophagous insects). Further, we found that 14–23% of sister pairs had very high overlap (>50%), similar to Berlocher’s (1998) estimate of 18% of species pairs (see his fig. 8.4).

Speciation clearly seems to be allopatric in gophers (*Cratogeomys*, *Geomys*, *Orthogeomys*, and *Thomomys*), where there is essentially no range overlap for any species pair. Also, there is very little range overlap between young pairs in deer mice (*Peromyscus*), ground squirrels (*Spermophilus*), and gazelles (*Gazella*), and overlap tends to increase with divergence time. However, only in *Peromyscus* is there a significant “phylogenetic signal” of increasing overlap with node age. The remaining groups may be classified as showing inconclusive results. Among these, *Myotis*, *Sorex*, and Felidae are widely distributed across multiple continents. Berlocher (1998) pointed out that clades distributed across multiple continents are not good subjects for ARC studies because ranges in such groups cannot change independently over time. The two groups of bats both show tremendous variation in overlap throughout their phylogenies, including high sympatry at young nodes. This pattern is consistent with the rapid range shifts expected from flying animals (see Lynch 1989; Chesser and Zink 1994; Coyne and Price 2000; Losos and Glor 2003). It is probably uninformative with respect to the geography of speciation events that occurred earlier than the most recent glacial cycle, which almost surely postdates all speciation in these groups. The remaining groups (*Chaetodipus*, *Perognathus*, *Tamias*, *Dipodomys*, *Ochotona*) are small, nonflying, and largely restricted to single, continuous continental areas (the few exceptions in *Tamias* and *Ochotona* do not affect our results). They all occupy geographic ranges that were dramatically impacted by Quaternary ice ages, and most have probably undergone repeated, substantial range shifts more recently than any speciation event. However, the same can be said for gophers, ground squirrels, and deer mice. It has been suggested that ARC may be more informative in continental settings where geographic ranges have been more constant, such as tropical Africa and South America (cf. Lessa et al. 2003).

Range Shifts

The likelihood of substantial range changes over the last several million years dictates caution in inferring the geography of speciation from present distributions (Losos and Glor 2003). The lack of age-range correlation in our data may be explained by extensive spatial shifts in geographic ranges after speciation (Barraclough and Vogler 2000). Alternatively, no age-range correlation is expected if mammals have

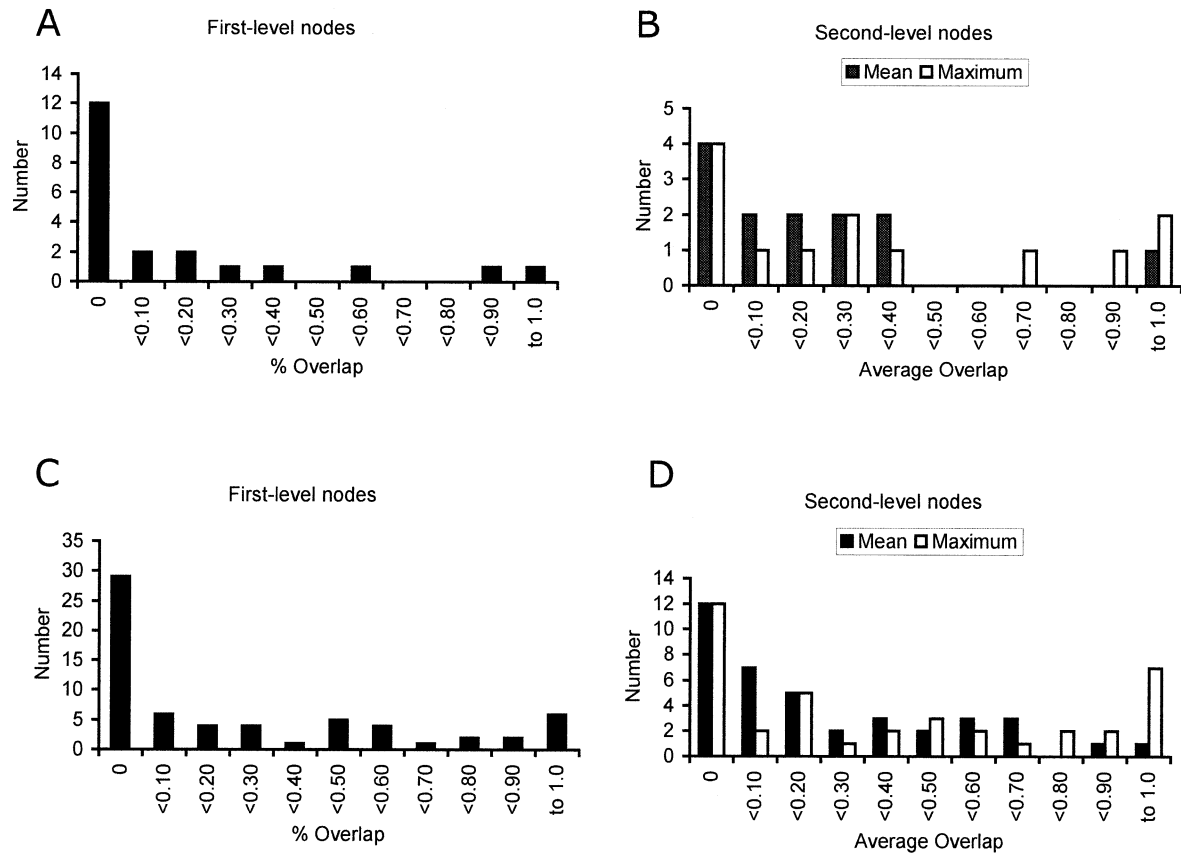


FIG. 6. Frequency distribution of overlaps between sister species (first-level nodes) and second level nodes (i.e., those immediately interior to sister-species nodes [Lynch 1989]) allozyme data (A and B) and mtDNA data (C and D)

diversified by a mixture of sympatric and nonsympatric speciation.

Geographic ranges of extant species have clearly changed over the last 100,000 years (Burton 1995; FAUNMAP Working Group 1996; Bennett 1997, Lyons 2003). According to our crude estimates of divergence times (Figs. 2 and 3) and other analyses (Klicka and Zink 1997; Avise et al. 1998), most mammalian speciation predates this time period. Therefore, extant ranges are most informative with respect to the past if different species ranges shift so that spatial relationships are conserved even as their positions change. That is, if we can discard the assumption that ranges shift independently after speciation. If all species track specific environments that simply shift north-south in response to global climate change, then whole communities should respond en masse (Clements 1936), with sympatric (allopatric) species remaining sympatric (allopatric). This simplistic idea has been justly criticized because many important components of habitat, such as topography or soil characteristics, do not change with climate (Bennett 1997). If species respond more individually, climate change will scramble climatic, physiographic, and edaphic variation and produce novel ecological communities (Gleason 1926). The importance of individualistic versus community-wide concordant responses to climate change is debated and data are scarce. Some authors have made much of a few examples of species that are now allopatric but co-occur in Pleistocene fossil beds; these

have been used to argue that ecological communities do not remain constant through climate changes (reviewed in Bennett 1997). However, these examples involve species that are ecologically quite different (e.g., wood turtle + southern toad; smokey shrew + thirteen-lined ground squirrel + collared lemming) and do not include sister species or even congeners. In a more rigorous, quantitative assessment of mammalian range changes in the Pleistocene, Lyons (2003) found that range shifts were actually quite similar overall, implying that the strict individualistic hypothesis is inadequate to explain Quaternary mammalian distributions. Alroy (1999) found that fewer than 3.5% of mammal species pairs known to co-occur in the Pleistocene no longer co-occur at the level of the biomes described by Brown and Nicoletto (1991). This implies that contemporary range overlap does tend to reflect overlap in the geologically recent past.

We inspected the FAUNMAP database of Pleistocene North American mammal fossils for records of species included in our analysis (FAUNMAP Working Group 1996). If many species pairs that are allopatric today co-occurred in the fossil record, we would have to reconsider the premise that lack of contemporary range overlap between closely related species implies nonsympatric speciation. This is a one-way test; lack of evidence of fossil co-occurrence cannot be taken as evidence that a pair of species did not co-occur (gaps in the fossil record would presumably create many false negatives). However, positive evidence of co-occurrence in the

past can be used to predict co-occurrence in the present. We found 62 fossil co-occurrences of congeneric species pairs for which we have data (one *Chaetodipus*, four *Tamias*, four *Dipodomys*, three *Myotis*, one *Perognathus*, five *Peromyscus*, 23 *Sorex*, and 21 *Spermophilus*). Of these, 60 (97%) also show range overlap today. The two pairs that no longer co-occur both involve *Spermophilus tridecemlineatus* at a single fossil deposit at Wilson Butte Cave 9950 to 14,500 years ago (during the retreat of the Wisconsin glaciation). The eastern limit of *S. tridecemlineatus*' contemporary range is 270 km away (~10% of its current east-west extent). The other two species (*S. beldingi* and *S. townsendii*) still overlap in the area of the deposit. This admittedly limited analysis is entirely consistent with that of Alroy (1999) and suggests that presently allopatric species were not commonly sympatric in the past. That is, the relative position of contemporary geographic ranges may provide some information about the geographic mode of speciation even though ranges have moved.

These data bolster our confidence in inferring allopatric speciation for the few clades whose contemporary ranges seem to clearly indicate predominantly allopatric divergence (e.g., gophers, *Peromyscus*, *Gazella*, and *Spermophilus*). Further, if allopatry and sympatry tend to be conserved even as ranges shift in space, then groups with histories of frequent sympatric speciation ought to show high levels of sympatry, even after considerable time has passed since speciation. Overlap is rarely greater than 50% in the datasets we examined (Figs. 2 and 3). In all five of the allozyme datasets, the regression intercepts for average and maximum overlap are below 34% and 11 of the 13 mtDNA datasets had intercepts lower than 50% (Table 2). The exceptions are the two bat groups. Taken together, the data seem less consistent with frequent sympatric speciation than frequent allopatric speciation. However, for most groups, we could not reject the null hypothesis that current species ranges are independent subdivisions of the clade range (Table 3).

Conclusions

Allopatric speciation is clearly pervasive in a few groups of mammals. Although we find no evidence favoring frequent sympatric speciation, the majority of datasets are simply inconclusive. Age-range correlation analyses revealed no consistent relationship between geographic range overlap and estimated divergence times. This may be interpreted as showing that range shifts over geological time have obliterated most information about the geography of speciation, or that the geography of speciation in mammals has truly been mixed. Our results, like those of Anderson and Evensen (1978), Lynch (1989), Barraclough et al. (1998), Berlocher (1998), and Barraclough and Vogler (2000), are strikingly at odds with the assertions of the early 20th century naturalists, typified by Jordan (1905), who claimed that range data clearly demonstrated the pervasiveness of allopatric speciation. Unfortunately, ARC analyses do not provide the "magic bullet" that will clarify the frequencies of alternative modes of speciation across many clades.

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