A QUANTITATIVE ASSESSMENT OF THE RANGE SHIFTS OF PLEISTOCENE MAMMALS

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Much attention has been focused on the response of species to the climate change associated with the last deglaciation during the Pleistocene. Generally, species respond in an individualistic manner to climate change, and expand and contract their ranges independently; consequently, community composition is extremely variable over time. Although data are available to examine range shifts of species by mapping species ranges over time, most investigations to date have been qualitative. I quantitatively assessed changes in distributions of species to determine the degree to which species shifted their ranges independently over broad time scales. Data on Pleistocene mammal assemblages from the FAUNMAP database were divided into 4 time periods (Pre-Glacial, full Glacial, Post-Glacial, and Modern). Range shifts were characterized by change in the median position of the range from 1 time period to another, change in range size, and direction of the shift. The degree to which species were shifting their ranges independently of one another was evaluated by examining frequency distributions of each range shift parameter and comparing directions wherein species were shifting their range centroids. Many species are shifting their ranges in similar ways. Many species in each time transition change their range size very little. Species shift their range centroids, on average, between 1,200 and 1,400 km. Moreover, if the United States is divided into quadrats and the direction in which species with those quadrats shift their ranges is examined, it becomes clear that in each quadrat there are some directions that are favored over others. The majority of these distributions in the 2 oldest transitions differ from a uniform distribution. Therefore, the prediction that the individualistic responses of species to climate change should result in nonanalog communities likely is oversimplified.

Key words: climate change, community structure, glaciation, mammals, nonanalog communities, Pleistocene, range shifts, range size

Whether species remain together or change association repeatedly over time is crucial to questions about community structure and to understanding how species respond to climate change. Yet the wealth of information in the fossil record pertaining to this question has not been assessed in a rigorous, comprehensive manner. Nonetheless, examples of species that had sympatric ranges during the Pleistocene, but are now allopatric, have been reported in the literature, and many researchers have concluded that community composition is extremely variable over time. That Pleistocene communities have no analogs among modern assemblages has far-reaching implications for a wide range of disciplines from coevolutionary theory to community ecology (Jackson and Whitehead 1991). Unfortunately, the vast amount of data needed to

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examine range shifts of species and the nature of the analyses done to date (i.e., mapping of species ranges over time) do not lend themselves well to quantitative analyses. Therefore, these conclusions are based largely upon qualitative evaluations (cf. Valentine and Jablonski 1993). Moreover, consequences of the independent movement of species on patterns of species composition at the level of local communities are inferred and are yet to be examined.

Concepts of communities.—In recent years, much attention has been focused on responses of species to the climate change associated with the last deglaciation during the Pleistocene. These responses, typically defined by the way in which individual species have shifted their ranges, are thought to be crucial in elucidating patterns of community organization over time. Historically, there have been 2 main schools of thought on community organization. If communities are incidental sets of species that happen to share the same ecological tolerances, they are "Gleasonian" (Begon et al. 1990; Gleason 1926). However, if communities are composed of strongly interacting sets of species that confer some emergent "superorganismal" properties to the community, they are considered "Clementsian" (Begon et al. 1990; Clements 1936). Evidence for the independent range shifts of species would be taken as support for the "Gleasonian" hypothesis, whereas movements of species en masse would be taken as evidence for the "Clementsian" hypothesis.

Range shifts of species have been examined in a number of taxonomic groups covering terrestrial and marine environments (Coope 1987; Davis and Shaw 2001; Graham 1986; Graham and Grimm 1990; Graham and Mead 1987; Holman 1993; Jackson 1994a, 1994b; Jackson and Whitehead 1991; Overpeck et al. 1992; Potts and Deino 1995; Valentine and Jablonski 1993; Webb 1987; Webb 1981, 1992). The general consensus of these studies has been that species respond in an individualistic manner to climate change, and expand and con-

tract their ranges independently. Moreover, species that previously had overlapping ranges are now allopatric (FAUNMAP Working Group 1996). Therefore, communities are viewed as fluid entities whose membership undergoes extensive reorganization over time, and community structure is deemed "Gleasonian." However, many of these studies are based on a single site or report examples rather than quantitative summaries of their data.

Range shifts.—The focus of paleoecologists on predicting species responses to climate change has led to an increasing suspicion that modern communities have no analogs in the past. One of the most interesting aspects of this pattern is the ubiquitous nature of the individualistic responses of species to deglaciation. Regardless of taxon or continent, examination of the fossil record has shown that species are shifting their ranges at different times and at different rates (A. Baynes and R. T. Wells, in litt. [Australian mammals]; Coope 1987 [British insects]; Davis and Shaw 2001 [North American trees]; Graham 1986; Graham and Grimm 1990; Graham and Mead 1987 [North American mammals]; Holman 1993 [North American herpetofauna]; Huntley 1990 [European plants]; Overpeck et al. 1992 [North American plants]; Potts and Deino 1995 [African mammals]; Spaulding and Van Devender 1977 [conifers in Utah]; Thompson and Mead 1982 [Great Basin plants]; Van Devender and Everitt 1977 [plants in south-central New Mexico]; Webb 1981, 1992 [North American plants]). This has led to the interpretation that the disintegration of communities during the Pleistocene, or coevolutionary disequilibrium, is directly responsible for the end-Pleistocene extinctions (Barnosky et al. 1996; Graham and Lundelius 1984). However, this is much debated; many groups that show independent range shifts did not suffer extinctions (Coope 1987, 1995; Holman 1993).

Despite these differences in interpretation, there are striking similarities among

findings of researchers working on very different groups. Examination of data on fossil mammals from 2,945 localities in the United States has shown that the geographic ranges of individual species shifted at different times and moved at different rates (FAUNMAP Working Group 1996). Moreover, not all species shifted their ranges in ways that indicated a simple tracking of the receding glaciers. Some species (e.g., eastern chipmunk, *Tamias striatus*; montane vole, *Microtus montanus*) show east–west shifts, presumably along a moisture gradient, whereas others (e.g., southern bog lemming, *Synaptomys cooperi*) show predictable northward shifts along a temperature gradient. Notably, Pleistocene communities, although thought to differ from Holocene ones, were organized into similar biogeographic provinces. However, Pleistocene faunas tended to be more variable (FAUNMAP Working Group 1996).

Recent analyses of pairwise associations of mammal species through the Pleistocene found that <3.5% of species pairs exhibited disharmony on a regional level (i.e., allopatric association of previously sympatric species) in any of the time periods examined. The majority of species pairs remained consistently "conjoined" or positively associated with each other throughout the Pleistocene and into the Holocene (Alroy 1999). This implies a pattern inconsistent with previous interpretations of analyses of range shifts. If the majority of species pairs are staying together, one might predict that communities are more stable than previously thought. However, local assemblages were not examined. Species pairs were considered to be conjoined if they occurred in the same biome, and species pairs were not tracked across biomes. The different conclusions drawn from methods used thus far illustrate the need for a quantitative assessment and examination of species range shifts.

Pollen data also have been used extensively to examine range shifts of species (Huntley 1990; Jackson and Whitehead 1991; Overpeck et al. 1992; Webb 1981, 1992), with similar results. However, methods used are much more quantitative than those used in animal studies, and broad generalized conclusions are eschewed. Spruce (*Picea*)–dominated forests show a northward movement from 11,000 to 7,000 years ago, with a subsequent shift south about 4,000 years ago (Webb 1981). Prairies were moving eastward until 7,000 years ago, when they again began moving west, and mixed conifer-hardwood forests show major compositional changes 8,000 years ago (Webb 1981). Although it has been suggested that these patterns are likely to result if the response of individual taxa lagged climate change by different amounts of time, analyses of taxon composition of 2 vegetative regions at 1,000-year intervals indicate that the large areas of nonanalog vegetation coincided with environmental conditions different from any in North America today (Overpeck et al. 1992; Williams et al. 2001).

It is important to note that pollen workers do not assume that all Pleistocene communities are nonanalog. Rather, analog vegetation and nonanalog vegetation are recognized (Edwards et al. 2000; Elenga et al. 2000; Overpeck et al. 1992; Prentice and Jolly 2000; Takahara et al. 2000; Tarasov et al. 2000; Thompson and Anderson 2000; Webb 1981, 1992; Williams et al. 2000, 2001; Yu et al. 2000). Moreover, regions of nonanalog vegetation occur in areas of nonanalog climate (Williams et al. 2001). One reason for this difference is the quality of the data available to plant and animal workers. Pollen workers have a wealth of data on both occurrence and abundance of species. However, the nature of the data makes examination of communities difficult; thus, regions are used. Animal workers often have only single sites with a few species and rarely have abundance data. Recent work by the FAUNMAP Working Group (1996) has changed this inequality. By compiling information from fossil localities of Pleistocene mammals in the United

States into a public-access database, they have made it possible to attempt a large-scale, quantitative analysis of Pleistocene mammalian range shifts. Moreover, it also will now be possible to study the change in mammalian communities over time. This study is the 1st attempt to evaluate range shifts of Pleistocene mammals within a quantitative framework.

MATERIALS AND METHODS

Data.—The information used in this study consists of faunal lists compiled by site locality. The data on mammalian fossil sites is taken from the compilation by the FAUNMAP Working Group (1996) at http://www2.museum.state. il.us/research/faunmap. The FAUNMAP database is divided into 2 entities. One is the archival database that contains all the information the working group was able to gather. The other is the research database, which is a version of the archival database that has been vetted by the experts in the working group. This study uses the research database exclusively.

For the purposes of my study, 4 time periods were chosen to encompass the advance and retreat of the glaciers: Pre-Glacial (40,000–20,000 years ago), Glacial (20,500–9,500 years ago), Holocene (10,500 years ago to present), and Modern (500 years ago to present). Although dates of the different time periods overlap, no data are shared among the time periods. The overlap is due to uncertainty in the dates. The lengths of these time periods were chosen for several reasons. First, dating of localities in the FAUNMAP database >40,000 years is not reliable (R. Graham, in litt.). Second, mammalian fossil assemblages represent relatively short periods of time, on the order of hundreds to thousands of years (Graham 1993). By choosing these time periods, I eliminated localities that could not be constrained by this narrow range of time.

Because the fossil record does not necessarily preserve all species present in a given locality at a particular instant in time, some degree of time averaging will raise the probability that the species found together in a fossil site give an accurate representation of community composition. Species that may not have been fossilized during 1 preservational event may be captured by the next. If time averaging com-

bines the 2 events, we get a more accurate picture of community composition than what the preservation events would give separately (Graham 1993). Conversely, too much time averaging will obscure patterns of community composition because species that never occurred together may be preserved in the same fossil beds. Because of this, a fossil community is analogous to, but not exactly the same as, a modern community.

Determining the degree of time averaging that is acceptable depends on the scale of the study. Greater amounts of time averaging can smooth data and be desirable in large-scale biogeographic analyses (Graham 1993). The time periods chosen in this study allow for the range of sites in each time period to be great enough to calculate distributions and range shifts for the majority of Pleistocene mammals. Because differences in the length and sampling intensity of different time periods may introduce a bias (i.e., inflating richness and geographic ranges), 2 additional intervals were identified (late Glacial, 15,500–9,500 years ago, and late Holocene, 5,000 years ago to present) that were approximately half the length of previously analyzed intervals. Differences between results presented here and those of the shorter time intervals were small (Lyons 2001), indicating that any effects due to the lengths of the chosen time intervals were unlikely to change the results substantially.

Calculation of range shifts.—Localities were plotted in Alber's equal-area projection (D. Rowley, in litt.). Mammals occurring in the continental United States during each of the 6 time periods were identified. The area of each range was calculated as the area (km^2) of a polygon enclosing all localities for a given species. The centroid of each range was calculated using a Cartesian coordinate system that accounted for the shape of the earth. Range shifts were calculated for each of the 4 time transitions (i.e., Pre-Glacial to Glacial, Glacial to Holocene, Holocene to Modern, and late Holocene to late Glacial). Range shifts were calculated for all mammals present in both intervals. Results for the late Holocene to late Glacial transition were compared with those for the Glacial to Holocene transition. Range shifts were characterized by change in the position of the centroid of the range from one time period to another (distance was calculated using an equidistant projection), change in range size (as defined by the natural
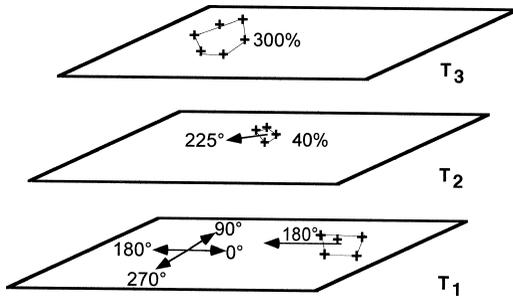
Fig. 1.—Diagram of the calculation of range shifts through time. The ''+'' signs represent the site localities used to determine the range of a species in the given time periods (T_1, T_2, and T_3, where T_1 is the oldest). Lines drawn around the ''+'' signs are convex polygons used to define ranges. Angles of an arrow, defined by a 360° circle, represent the direction of the range shift, and the length of the arrow represents the magnitude of the shift in centroid of the range. Relative spread of the ''+'' signs indicates the geographic size of a range. Expansion or contraction of a range was expressed as a percentage of the range size in a previous time period.

logarithm of the percent change in range area from an older to younger time interval), and direction of the shift (Fig. 1).

A species had to have a measurable range in adjacent time periods for a range shift to be calculated. Therefore, only species with ranges comprising ≥3 localities were used in these analyses. The 1 exception was for a species that was well sampled (>10 localities) in 1 time period and poorly sampled (<3 localities) in the adjacent time period. If a species was found in 1 or 2 localities in the poorly sampled time period, it was assigned a range size of 1 km² and a position in the center of its localities. If the species did not occur in the United States during the poorly sampled time period, the species was judged to have shifted its range into or out of the continental United States and was assigned a range of 1 km² and a position just south of the United States. This assumption was evaluated by conducting analyses without the species that are poorly sampled and was found not to have a significant impact on the conclusions of this study (Lyons 2001). Finally, the direction and distance of range shifts were calculated using range centroids. A range centroid can change position because the entire range moved or be-

cause one or both of the ranges expanded and contracted. To evaluate the effect of using centroids to calculate range shifts, the direction and distance of the shift in the northern and southern limits, and the western and eastern limits of each species range were calculated and evaluated for coordinated movement.

Independence of range shifts.—The degree to which species range shifts were independent of one another (i.e., individualistic) was evaluated by dividing the United States into 8 quadrats of about 10° latitude by 10° longitude. The direction of the centroid shift for all species whose centroid fell in each quadrat was compared. If species shifted their ranges independently, then frequency distributions of the direction of the centroid shifts for each quadrat should not differ significantly from a uniform distribution. One-sample Kolmogorov–Smirnov tests were used to evaluate this hypothesis (Sokal and Rohlf 1981).

RESULTS

Range shifts.—Despite the extensive literature devoted to species responses to glaciation, this is the 1st attempt to quantify the way in which each species in a taxonomic group shifts its range. By characterizing a range shift using 3 parameters (direction, distance, and change in size), I am able to describe species' range shifts in a way that is consistent and comparable across species and time.

Range shifts were calculated for 228 species for the Pre-Glacial–Glacial period (Fig. 2). On average, range size increased from the Pre-Glacial to the Glacial (median change in size = 1.147, median ln change in size = 0.137). Mammals shifted the centroid of their range an average of 1,190 km (median = 1,150 km), and none moved >3,000 km. Centroids of mammalian ranges moved in all directions, with peak movement northwest and southwest.

Range shifts were calculated for 303 species for the Glacial–Holocene period (Fig. 3). Range size increased, on average, from the Glacial to the Holocene (median change in size = 1.705, median ln change in size = 0.534). Mammals shifted the centroid of
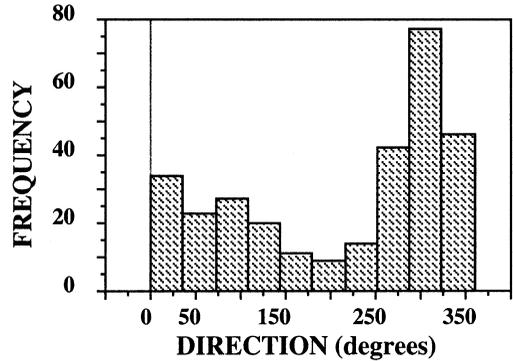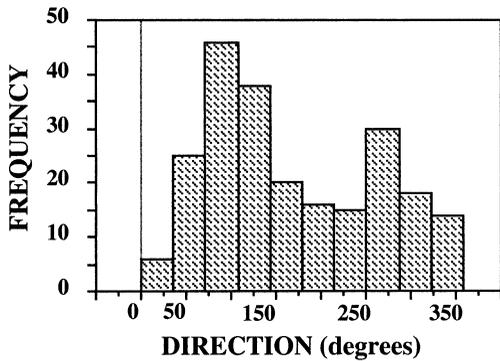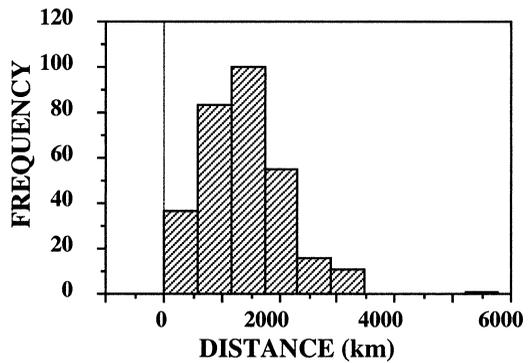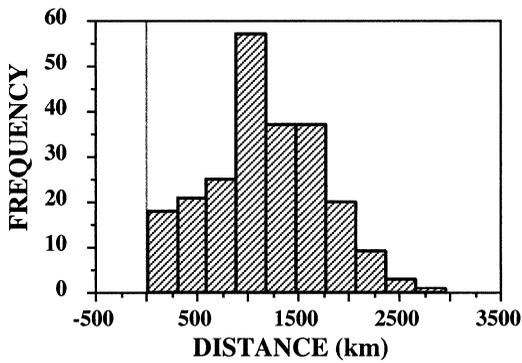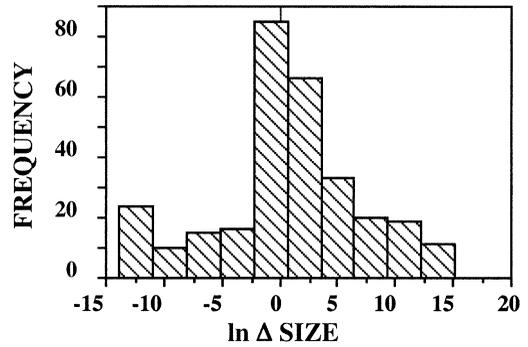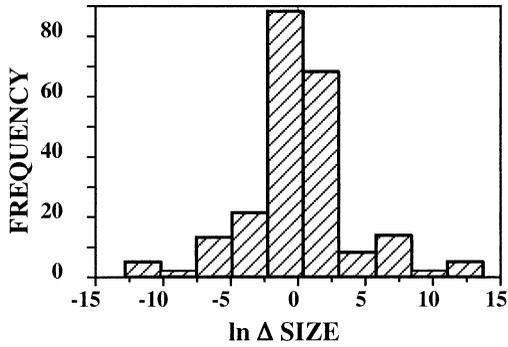
FIG. 2.—Frequency distributions of mammalian range shifts from the Pre-Glacial to the Glacial. Range shifts are described by 3 parameters: ln change in range size (top), distance the centroid of a range moved from 1 time period to the next (middle), and direction of centroid movement (bottom). Direction of a range shift is defined by a 360° circle; thus, 0° is east, 90° is north, 180° is west, and 270° is south.

FIG. 3.—Frequency distributions of mammalian range shifts from the Glacial to the Holocene. Panels as described in Fig. 2.

their range an average of 1,400 km (median = 1,345 km), with 1 subspecies (*Panthera leo atrox*) moving 5,800 km. However, no other species moved >3,200 km. Centroids

of mammalian ranges moved in all directions, with peak movement south and southeast.

Range shifts were calculated for 256 species for the Holocene–Modern period (Fig. 4). Range size decreased, on average, from the Holocene to the Modern (median change in size = 0.255, median ln change in size = −1.367). Mammals shifted the
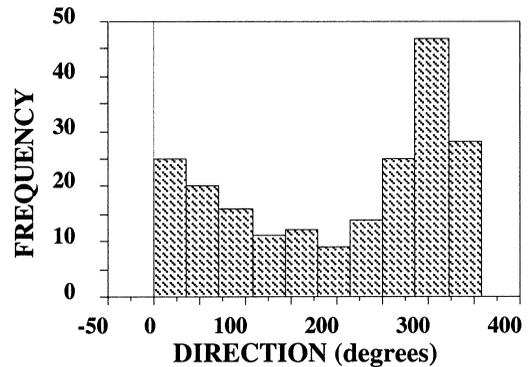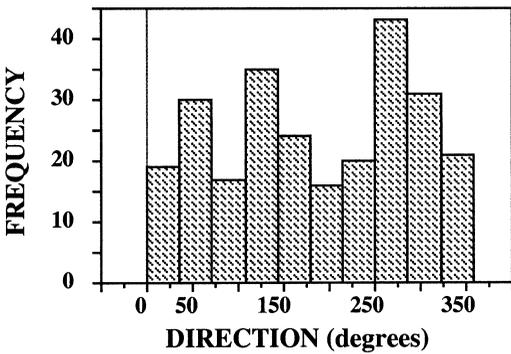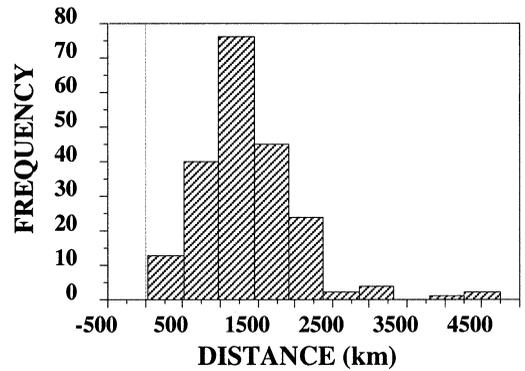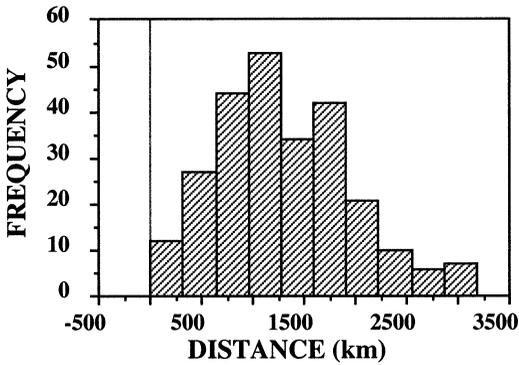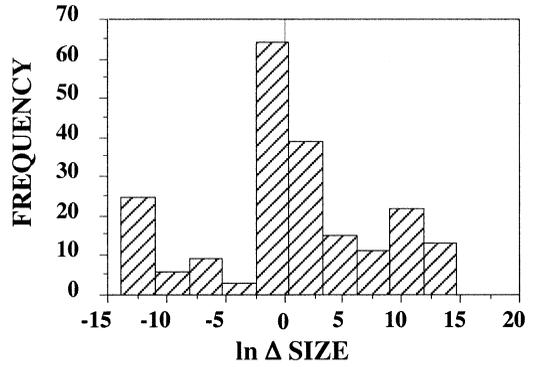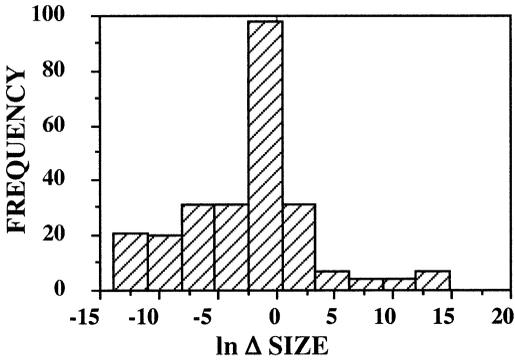
FIG. 4.—Frequency distributions of mammalian range shifts from the Holocene to the Modern. Panels as described in Fig. 2.

FIG. 5.—Frequency distributions of mammalian range shifts from the late Glacial to the late Holocene. Panels as described in Fig. 2.

centroid of their range an average of 1,310 km (median = 1,215 km), and none moved >3,200 km. Centroids of mammalian ranges moved in all directions, with no discernable directionality in movement.

Range shifts were calculated for 207 species for the transition from the late Glacial to the late Holocene (Fig. 5). The range of variation in change in size was substantial (±14 ln units), but the majority of species had a change in size clustered around 1–2 ln units (median change in size = 1.367, median ln change in size = 0.313), and range size increased, on average, from the late Glacial to the late Holocene. Mammals shifted the centroid of their range an aver-

age of 1,355 km (median = 1,240 km). The centroids of mammalian ranges moved in all directions, with peak movement south and southeast.

Range-shift parameters for change in the area and distance the centroid moved were compared using 1-way analysis of variance to determine if there were significant differences between time transitions. The change in area differed between time transitions (F = 22.938, $d.f.$ = 2, 781, P < 0.001). A posteriori comparisons using a Bonferroni correction indicated that these differences are due to a decrease in range size from the Holocene to the Modern, whereas range size increased slightly in the other 2 transitions (Glacial to Holocene–Holocene to Modern: mean difference = 3.022, P < 0.001; Glacial to Holocene–Pre-Glacial to Glacial: mean difference = 0.453, P = 0.351; Holocene to Modern–Pre-Glacial to Glacial: mean difference = −2.570, P < 0.001). The average distance a species shifted its centroids also differed significantly among time transitions (F = 6.673, $d.f.$ = 2, 784, P = 0.001). A posteriori comparisons using a Bonferroni correction indicated that those differences were due to species shifting their range centroids farther in the transitions from the Glacial to the Holocene than in the transitions from the Pre-Glacial to the Glacial (Glacial to Holocene–Pre-Glacial to Glacial: mean difference = 209.051, P < 0.001). There were no other significant differences in the distances the species shifted their centroids (Glacial to Holocene–Holocene to Modern: mean difference = 89.802, P = 0.106; Holocene to Modern–Pre-Glacial to Glacial: mean difference = 119.249, P = 0.452 [to be considered significant, P values were <0.017]).

Shifts of range limits.—A range centroid could change position because the entire range moved or because the latitudinal or longitudinal limits expanded or contracted. To evaluate the effect of using centroids to calculate range shifts, the direction and distance of the shift in the northern and south-

ern limits of each species range were calculated and compared with the direction and distance of centroid shifts. This was done for all species in each time transition and by eliminating species that left the United States from one time interval to the next. A *G*-test of independence (Sokal and Rohlf 1981) also was performed on the shifts of range limits for each time transition to determine the degree to which particular methods for changing the size of range or the distance a centroid moved were favored in each time period. North–south limits were evaluated separately from east–west limits.

During the Pre-Glacial to Glacial period, species shifted the northern limit of their range an average of 816 km (median = 683 km) and the southern limit of their range an average of 632 km (median = 296 km). Movement of northern and southern limits was primarily in northern and southern directions (Lyons 2001:figure 2.6). Species shifted the western limit of their range an average of 771 km (median = 649 km) and the eastern limit of their range an average of 623 km (median = 324 km). Movement was in all directions (Lyons 2001:figure 2.6), with no differences in north–south limits (G = 0.383, P > 0.05) and east–west limits (G = 0.00009, P > 0.05). Shifts in northern and southern limits were independent of one another, as were shifts in eastern and western limits, indicating that species were changing their ranges in complex ways and not simply moving the entire range to a more favorable location.

During the Glacial–Holocene period, species shifted the northern limit of their range an average of 1,274 km (median = 1,096 km) and the southern limit of their range an average of 981 km (median = 669 km). Species shifted the western limit of their range an average of 1,177 km (median = 995 km) and the eastern limit of their range an average of 1,164 km (median = 993 km). Movement of latitudinal and longitudinal limits was in all directions (Lyons 2001:figure 2.7), with no differences in

north–south limits ($G = 0.093$, $P > 0.05$) and east–west limits ($G = 0.528$, $P > 0.05$). Shifts in northern and southern limits were independent of one another, as were shifts in eastern and western limits. Latitudinal and longitudinal limits of species ranges were differentially affected by species responses to glaciation.

During the Holocene–Modern period, species shifted the northern limit of their range an average of 1,042 km (median = 802 km) and the southern limit of their range an average of 1,072 km (median = 910 km). Movement occurred in all directions but primarily in the north and south (Lyons 2001:figure 2.8). Species shifted the western limit of their range an average of 960 km (median = 715 km) and the eastern limit of their range an average of 969 km (median = 705 km). Movement was in all directions (Lyons 2001:figure 2.8), with no differences in north–south limits ($G = 1.026$, $P > 0.05$) but with significant differences in east–west limits ($G = 6.340$, $P < 0.05$). Shifts in northern and southern limits were independent of one another. However, shifts in which the eastern and western limits expanded away from one another were less common than the other 3 possible combinations of shifts. Average range size decreased from the Holocene to the Modern. These results indicate that a contraction of longitudinal limits contributed to this pattern.

During the late Glacial–late Holocene period, species shifted the northern limit of their range an average of 1,347 km (median = 1,118 km) and the southern limit of their range an average of 969 km (median = 680 km). Species shifted the western limit of their range an average of 1,226 km (median = 1,041 km) and the eastern limit of their range an average of 1,114 km (median = 888 km). Movement of latitudinal and longitudinal limits was in all directions (Lyons 2001:figure 2.9), with no difference in north–south limits ($G = 0.265$, $P > 0.05$) and east–west limits ($G = 0.105$, $P > 0.05$). Shifts in northern and southern limits were

independent of one another, as were shifts in eastern and western limits. As in the Glacial to Holocene transition, latitudinal and longitudinal limits of species ranges were differentially affected by species responses to glaciation.

Independence of range shifts.—Any species whose range centroid fell within a quadrat was included in the frequency distribution for that quadrat. For every quadrat in each transition, species were shifting in all directions. However, some directions were favored over others (Figs. 6–8). Species occurring within 10° of one another tended to shift their ranges in similar directions in response to climate change. One-sample Kolmogorov–Smirnov tests were used to determine if those distributions were significantly different from the expectation of uniform distributions. For the transition from the Pre-Glacial to the Glacial, distributions for 6 of the 8 quadrats were significantly different from a uniform distribution (Fig. 6; quadrat 1: D = 0.160, *d.f.* = 28, $P > 0.05$; quadrat 2: D = 0.237, *d.f.* = 31, $P < 0.05$; quadrat 3: D = 0.174, *d.f.* = 38, $P > 0.05$; quadrat 4: D = 0.567, *d.f.* = 10, $P < 0.05$; quadrat 5: D = 0.433, *d.f.* = 18, $P < 0.05$; quadrat 6: D = 0.225, *d.f.* = 40, $P < 0.05$; quadrat 7: D = 0.324, *d.f.* = 35, $P < 0.05$; quadrat 8: D = 0.417, *d.f.* = 28, $P < 0.05$). Similarly, for the transition from the Glacial to the Holocene, 6 of the 8 quadrats were significantly different from a uniform distribution (Fig. 7; quadrat 1: D = 0.326, *d.f.* = 19, $P < 0.05$; quadrat 2: D = 0.195, *d.f.* = 26, $P > 0.05$; quadrat 3: D = 0.250, *d.f.* = 38, $P < 0.05$; quadrat 4: D = 0.467, *d.f.* = 15, $P < 0.05$; quadrat 5: D = 0.267, *d.f.* = 20, $P > 0.05$; quadrat 6: D = 0.220, *d.f.* = 50, $P < 0.05$; quadrat 7: D = 0.400, *d.f.* = 95, $P < 0.05$; quadrat 8: D = 0.325, *d.f.* = 38, $P < 0.05$). However, for the transition from the Holocene to the Modern, only 2 of the 8 quadrats were significantly different from a uniform distribution (Fig. 8; quadrat 1: D = 0.103, *d.f.* = 55, $P > 0.05$; quadrat 2: D = 0.104, *d.f.* = 46, $P > 0.05$; quadrat 3: D = 0.126,
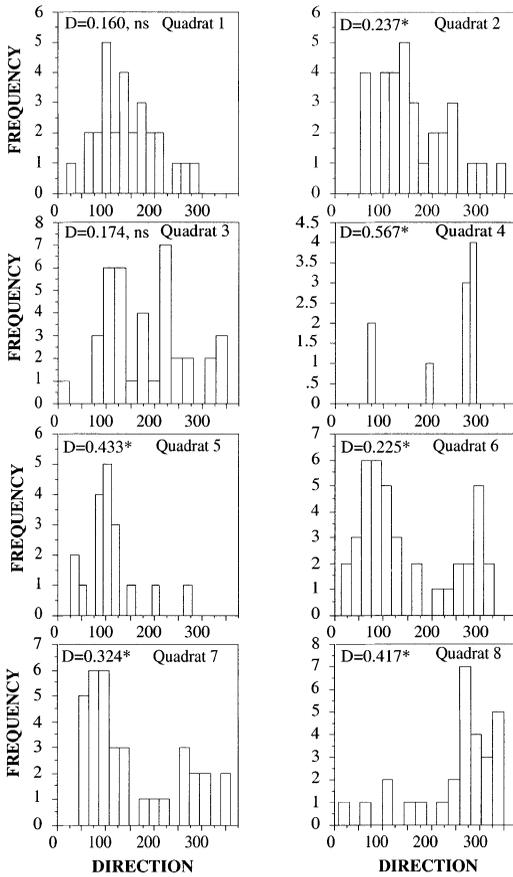
FIG. 6.—Frequency distributions of the direction of centroid shifts for species living within 10° latitude by 10° longitude quadrats in the United States for the transition from the Pre-Glacial to the Glacial. Quadrat 1 is 37.5–47.5°N, 120–110°W. Quadrat 2 is 37.5–47.5°N, 110–100°W. Quadrat 3 is 37.5–47.5°N, 100–90°W. Quadrat 4 is 37.5–47.5°N, 90–80°W. Quadrat 5 is 27.5–37.5°N, 120–110°W. Quadrat 6 is 27.5–37.5°N, 110–100°W. Quadrat 7 is 27.5–37.5°N, 100–90°W. Quadrat 8 is 27.5–37.5°N, 90–80°W. D values are the test statistic for a Kolmogorov–Smirnov 1-sample test (Sokal and Rohlf 1981); asterisk (*) refers to $P < 0.05$; ns = nonsignificant.

FIG. 7.—Frequency distributions of the direction of centroid shifts for species living within 10° latitude by 10° longitude quadrats within the United States for the transition from the Glacial to the Holocene. Descriptions in Fig. 6.

$d.f. = 47$, $P > 0.05$; quadrat 4: $D = 0.267$, $d.f. = 9$, $P > 0.05$; quadrat 5: $D = 0.267$, $d.f. = 9$, $P > 0.05$; quadrat 6: $D = 0.317$, $d.f. = 36$, $P < 0.05$; quadrat 7: $D = 0.229$, $d.f. = 35$, $P < 0.05$; quadrat 8: $D = 0.211$, $d.f. = 18$, $P > 0.05$).

DISCUSSION

The changes in species ranges in response to glaciation during the late Pleistocene are usually described as being individualistic, meaning that species respond independently of one another. That is, they are thought to shift at different times, at different rates, and often in different directions. The key element of an individualistic response is that a species must be shifting its range in a way that is unique to that species. For example, mammals shift along an east–west moisture gradient, whereas others that shift in a north–south fashion
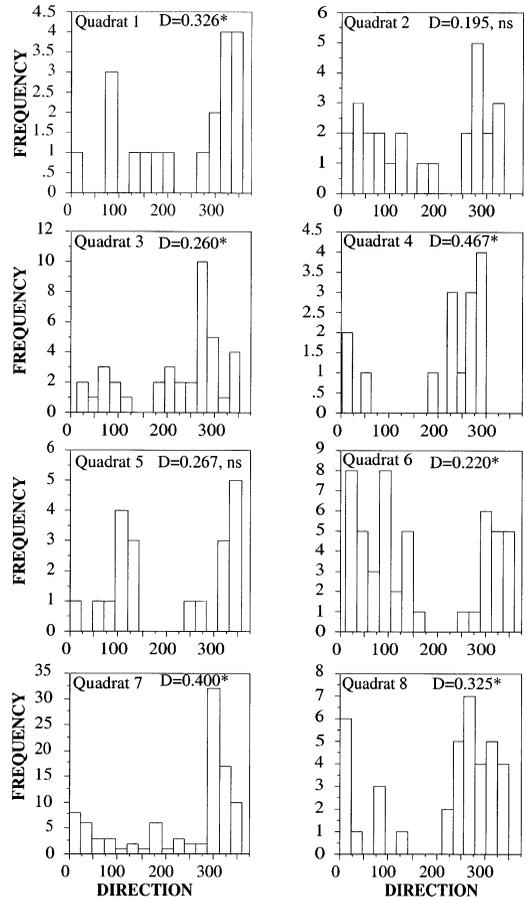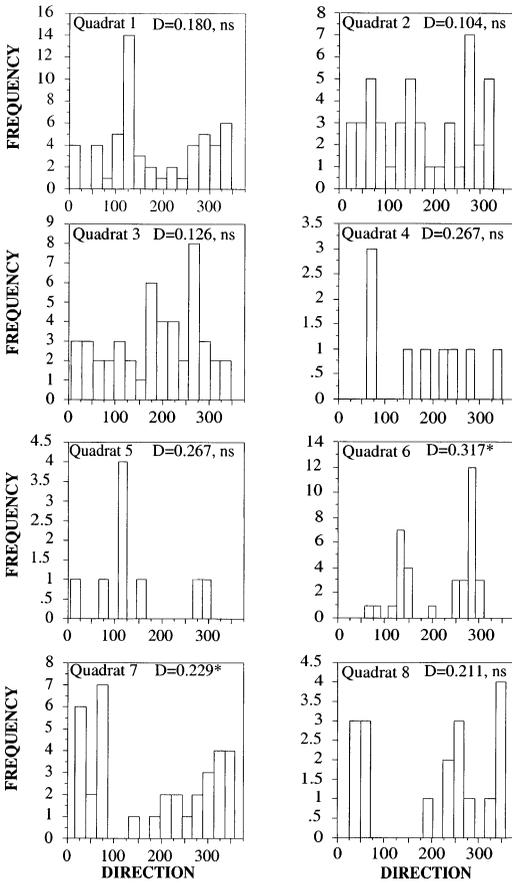
FIG. 8.—Frequency distributions of the direction of centroid shifts for species living within 10° latitude by 10° longitude quadrats within the United States for the transition from the Holocene to the Modern. Descriptions in Fig. 6.

Regardless of whether species shift their ranges en masse due to some emergent property of communities, or independently, but along similar ecological gradients, local assemblage composition through time is unlikely to be as variable as previously thought. For example, even if species shift their ranges independently (Gleasonian), species with similar climatic tolerances may end up in the same place (i.e., results consistent with a weak Clementsian model). The conclusion of the FAUNMAP Working Group (1996) that biogeographic provinces of the Pleistocene were similar to those of the Holocene (although diversity was not), along with Alroy's (1999) conclusion that the majority of species are "conjoined" over time on a regional level, gives tantalizing glimpses into this problem. Both these observations are consistent with predictions that each model of community organization may make about local assemblages. Thus, given the importance of scale and methodology on the conclusions drawn about species association through time, it is likely that patterns of community composition are more complex than previously thought.

Range shifts.—Examples of several mammals that had sympatric ranges but are now allopatric have been reported in the literature (Graham 1986; Graham and Grimm 1990). However, until the advent of large computer databases, a thorough quantitative examination of mammalian range shifts has not been possible. Moreover, the emphasis has been on understanding the subset of species that shifted their range and intermingled with foreign faunas, and little attention has been given to species that show little response. By quantifying range shifts using 3 parameters (change in size, distance, and direction of centroid shifts), a more complete understanding of mammalian community structure is possible. I found that there are many species that show very little in the way of range shifts, indicating that despite the shifting of the specific species documented in the literature,

have been reported in the literature as examples of the individualistic response of species to glaciation (FAUNMAP Working Group 1996). This individualistic response is thought to result in nonanalogous communities. However, little attention has been devoted to the effect of these range shifts on local community composition.

A confounding factor not previously considered is that although the competing hypotheses about community organization (Gleasonian or Clementsian) make different predictions about expected patterns of species range shifts, each could lead to similar patterns of local community composition.

there may be a detectable continuity to the structure of mammalian communities through time.

There is much variation in the degree to which species change the sizes of their ranges in response to climate change (Figs. 3–5). In each of the 3 time transitions, ≥75 species changed their range size less than ±1 ln unit (84 species in the Pre-Glacial to Glacial, 78 species in the Glacial to Holocene, and 75 species in the Holocene to Modern), and ≥117 species changed their range size less than ±2 ln units (137 species in the Pre-Glacial to Glacial, 124 species in the Glacial to Holocene, and 117 species in the Holocene to Modern). Nonetheless, several species in each time transition evinced rather dramatic changes in range size (Figs. 3–5), and in some time transitions as many as 30 species occurred in the largest size-change class (e.g., Fig. 4).

There are several possible explanations for the pattern of change in the range size of late Pleistocene mammals. Despite the rather dramatic changes evinced by some species (e.g., southern bog lemming), other species do not change their range size substantially in response to climate change. Macroecological analyses have shown that there is a relationship between range size and body size in modern North American mammals (Brown 1995), with species with the largest ranges typically being those with the largest body sizes. If this relationship is not unique to the present, then there may be a limit on the degree to which a species can change its range size, which is dictated in some way by its body size or correlates thereof. Although there should be no limit to how small a range can get, small-bodied species may have difficulty increasing their ranges to a very large size. An examination of the relationship between a species' body size and the degree to which it shifts its range in response to climate change should help illuminate this question. Nonetheless, understanding the factors that limit species' ranges is difficult (Brown et al. 1996; Lyons and Willig 1997), and different factors are thought to act in different parts of a species' range. Kaufman and Willig (1998) predicted that abiotic factors such as climatic extremes should have a greater effect in limiting the northern (or temperate) edge of a species' range, whereas biotic interactions such as predation and competition should be mostly limited to the southern (or more tropical) edge of a species' range. If glaciation makes climate more equable, lessening seasonal extremes, it becomes difficult to predict how ranges of species should be affected. Controls on the northern limits of ranges should be lessened. Conversely, the glacier is an absolute barrier that cannot be broached.

Much of the work on the responses of species to climate change during the Pleistocene has concluded that range shifts are individualistic (Coope 1987; Davis and Shaw 2001; Graham 1986; Graham and Grimm 1990; Graham and Mead 1987; Holman 1993; Jackson 1994a, 1994b; Jackson and Whitehead 1991; Overpeck et al. 1992; Potts and Deino 1995; Valentine and Jablonski 1993; Webb 1987; Webb 1981, 1992). However, vertebrate paleoecologists have concentrated almost exclusively on species showing dramatic range shifts. Despite the fact that one of the range shift categories defined by the FAUNMAP Working Group (1996) was "no change in range," little attention has been focused on the degree to which species are remaining in place. The idea that some species show large range shifts, whereas others do not, does not invalidate the hypothesis of individualistic range shifts. It is likely that species that have the phenotypic plasticity to remain in place during climate change do so. Indeed, wood rats (*Neotoma*) change their body size in response to climate change and adapt in place rather than move (Smith and Betancourt 1998; Smith et al. 1995, 1998). Therefore, the range of variation in the change in size of a species range found by this study is unsurprising. Whereas many species show dramatic range shifts during the Pleistocene, others do not.

To truly understand community structure of Pleistocene mammals, as with other taxonomic groups, we must not focus on one type of response to the exclusion of the other.

Another explanation for the pattern of change in range size is that the data used in this study are limited to the continental United States. Many of the species that have been reported in the literature as having dramatic range shifts did so by expanding into Canada as the glaciers receded (FAUNMAP Working Group 1996; Graham 1986). Indeed 2 types of range shift categories identified by the FAUNMAP Working Group (1996) involved movement of species north into Canada and differed only in the speed at which the shift occurred. Although those species are likely to show size changes in the largest size-change classes, the scope of this study (which is determined by the FAUNMAP data) limits the maximum increase to the area of the continental United States. Finally, it should be noted that change in the size of a species range is only 1 possible way that a species can respond to changes in climate.

In any time transition, the average distance that a mammal shifts the centroid of its range is between 1,200 and 1,400 km. These are not insignificant distances. Moreover, the range of distances that mammals shift their centroids is substantial (Figs. 3–5). In each of the 3 time transitions, ≥26 species shifted the centroid of their range <500 km (35 species in the Pre-Glacial to Glacial, 29 species in the Glacial to Holocene, and 26 species in the Holocene to Modern), and ≥78 species shifted the centroid of their range <1,000 km (78 species in the Pre-Glacial to Glacial, 89 species in the Glacial to Holocene, and 91 species in the Holocene to Modern). If we assume that ranges are circular, then the average diameter of a mammalian range is about 850 km. Therefore, a range must, on average, shift >850 km if it is to leave all communities in which it previously had membership.

About one-third of all species in each time transition do not shift that far and will retain at least some membership in previous communities. Although assuming that ranges are circular is a crude approximation, it is a useful thought exercise.

A 2nd complicating factor is that there are many ways in which the centroid of a range can move. In 1 scenario, the range size remains the same, and the entire range shifts. However, the centroid of a range also will move if a range expands or contracts more in one direction than another. For example, as the glaciers recede, a species might expand its range northward without changing its southern limit. In that case, the centroid of the range would shift northward. All membership in previous communities would be retained, and new communities would be added. However, an examination of movement of the latitudinal and longitudinal limits of a species' range indicates that expansion and contraction of these limits are independent in most of the transitions. In the 1 exception, longitudinal limits in the Holocene to the Modern, there are fewer than expected instances in which both longitudinal limits of the range expand outward. Range size decreases during this transition, and this is likely 1 manifestation of that decrease. Nonetheless, in general, movement of the centroid is a good estimate of the direction and distance a range shifts overall (Lyons 2001). Moreover, the distance that a centroid shifts, taken together with the changes in size and direction in which a species' range moves, can be a powerful tool in understanding the effects of range shifts on community composition (Lyons 2001).

In each time transition, species shifted the centroid of their range in all directions, with some transitions showing peaks of movement in certain directions. In the transition from the Pre-Glacial to the Glacial, much of the movement was northwest and southwest. In the transition from the Glacial to the Holocene, much of the movement was south and southeast. Finally, in the

transition from the Holocene to the Modern, species shifted their centroids in all directions, with no discernable peaks in movement. It may seem strange that during the expansion of the glaciers from the Pre-Glacial to the Glacial, species shifted their range centroids northwest, whereas during the withdrawal of the glaciers, species shifted their range centroids south and southeast. However, species in the western United States could leave areas made inhospitable by the glaciers if they moved northwest (e.g., into more maritime areas). Moreover, range centroids could move because of expansion, contraction, or shifting of the range.

Nonetheless, response of species to glaciation does not follow a simple linear tracking model. For example, many species shifted along an east–west gradient in response to moisture (FAUNMAP Working Group 1996). Species that have responded by remaining in place also have been ignored. It is unsurprising that directions in which centroids of species' ranges shift are difficult to explain simply when all species are examined together. Direction of a centroid shift for a species that does not shift its range very far or change its range size very much is likely to contain less useful information than that of a species that shows a dramatic range shift.

Because the degree of time averaging in a fossil site may obscure patterns of community composition, it is important to evaluate the degree to which the length of time periods used in my study affects patterns obtained. The FAUNMAP database contains 2 shorter time intervals, the late Glacial and the late Holocene, that may be used to evaluate the effect of the chosen time periods. These 2 intervals span approximately 5,000 years and cover a time transition comparable with the Glacial to Holocene transition of Lyons (2001). The average change in range size is smaller during the transition from the late Glacial to the late Holocene than for their longer counterparts, but the distance that the centroids of

species' ranges shifted is comparable (Fig. 5).

Shifts of range limits.—Characterizing the direction and distance of a range shift is difficult. Species' ranges can be influenced by many factors that affect different areas or aspects in an irregular manner (Brown et al. 1996; Lyons and Willig 1997). Consequently, the centroid of a range may shift in a way that does not adequately describe other aspects of a range shift. One way to assess the degree to which shifts in centroids of ranges characterize the shift in the range as a whole is to examine changes in latitudinal and longitudinal limits.

For each time transition, shifts in the northern, southern, eastern, and western range limits were examined (Lyons 2001: figures 2.6–2.9) for patterns unique to the different groups of mammals. In the transition from the Pre-Glacial to the Glacial, carnivores and artiodactyls are primarily responsible for the large shifts in northern limits, and carnivores are primarily responsible for the large shifts in southern limits. In the Glacial to the Holocene, carnivores and rodents are the groups primarily responsible for the large shifts in latitudinal limits. In the Holocene to the Modern, rodents are primarily responsible for the large shifts in northern limits, and all groups contribute to the large shifts in southern limits. Interestingly, it is typically the larger-bodied mammals that show the largest shifts in their northern and southern limits. The rodents that contribute to this pattern also are large bodied given their phylogenetic constraints (e.g., squirrels, *Spermophilus*, and chipmunks, *Tamias*). Moreover, a large shift in one edge of the range is not necessarily accompanied by a large shift in another edge. Although there is some association between distances that the northern and southern limits of a range shifted in each transition and some association between distances that the eastern and western limits of a range shifted, there is considerable scatter in the data, and these correla-

tions are weak ($r = 0.149$ to 0.543—Lyons 2001:figure 2.13). *G*-tests of independence also show that the expansion and contraction of latitudinal and longitudinal limits of species ranges are independent of one another, except for longitudinal limits of species ranges in the youngest transition.

In my study, shifts in the northern and southern limits of a species range were influenced by more than the responses of species over time. Data used in my study were limited to the United States, but the species likely were not. The pattern of shifts in the northern and southern limits of a species range is a result of the actual shifts of species wholly contained in the United States and the pseudoshifts of species whose actual range extends beyond the borders. During the height of glaciation, this would be less of a problem for shifts in the northern limits of a species' range because few species could live on the glaciers. Shifts in the eastern and western limits are not affected in this manner and represent the actual longitudinal shifts of each species (Lyons 2001:figures 2.6–2.9). However, effects of any potential pseudoshifts were lessened by using centroid shifts. The shift in the centroid of species range was the aggregate of the latitudinal and longitudinal shifts of a range and was likely the best estimate given the data. Moreover, there is no reason to suspect that pseudoshifts should be systematically biased and, at best, should just introduce noise into the signal given by the data.

Independence of range shifts.—The United States was divided into 8 quadrats of 10° latitude by 10° longitude, and the direction of the shifts of all species whose centroid fell within each quadrat was examined. In each quadrat, some directions were preferred over others (Figs. 6–8). However, the preferred direction differed among quadrats. If species were shifting their ranges in a manner consistent with a strict interpretation of individualistic range shifts, then frequency distributions should be flat. Moreover, the direction in which

species shift their centroids is to some degree determined by the particular quadrat within which their centroid resides. For example, species whose centroid occurs within quadrat 1 (northwestern United States; 47.5–37.5°N and 120–110°W) can shift their centroid a small distance in any direction. However, to shift their centroid a large distance, they must move in an easterly or southeasterly direction (otherwise they run into the ocean). Indeed, within the transition from the Glacial to the Holocene, in which climate change is most dramatic, the preferred direction is to the southeast. If the climate or habitat changed enough such that a species was required to shift to survive, there would be little choice about which way to go.

Although range shifts of individual species are likely to be individualistic in that they respond to glaciation in their own way, range shifts of mammals as a group are not individualistic in the strictest sense. For example, the prediction of individualistic range shifts would be that the distributions of directions within each of my quadrats should not be different from a uniform distribution. However, for the 2 oldest transitions, the transitions during which glaciation occurs, 6 of the 8 quadrats do not have uniform distributions (Figs. 6 and 7). In the final transition, only 2 of the 8 quadrats do not have uniform distributions. During the 2 oldest transitions, there is much alteration of the climate associated with glaciation, but the largest shifts in climate were mostly over by the beginning of the Holocene (Bond and Lotti 1995; Dansgaard et al. 1993; FAUNMAP Working Group 1996; Mayewski et al. 1993; Taylor et al. 1993; Thompson et al. 1993; Webb et al. 1993). If climate change was great enough during the 2 oldest transitions to force species to shift their ranges in response, there may have been preferred directions simply because species were limited in where they could move to escape their current conditions. Moreover, because the changes in climate were mostly over by the Holocene,

range shifts from the Holocene to the Modern likely represent the regular background shifting in ranges, rather than a concerted response to climate change. If species were not shifting their ranges to escape unfavorable climatic conditions, then the direction in which a range centroid shifted likely was less important, and thus the distributions within the majority of quadrats would not be expected to be different from uniform (Fig. 8).

Because landmasses are finite, mammals are restricted in the movements they can make. This is reflected in the directions in which the species residing in each quadrat are able to shift their ranges. The species are probably responding individualistically in the truest sense of the word. They are responding to their own cues and at their own rates. However, the bounded nature of landmasses limits directions and distances that they can shift. Therefore, the prediction that the individualistic responses of species to climate change should result in nonanalog communities likely is oversimplified. Certainly, some communities should be nonanalog but not all.

LITERATURE CITED

ALROY, J. 1999. Putting North America's end-Pleistocene megafaunal extinction in context: large-scale analyses of spatial patterns, extinction rates, and size distributions. Pp. 105–143 in Extinctions in near time (R. D. E. MacPhee, ed.). Kluwer Academic Publishers, New York.

BARNOSKY, A. D., T. I. ROUSE, E. A. HADLY, D. L. WOOD, F. L. KEESING, AND V. A. SCHMIDT. 1996. Comparisons of mammalian response to glacial-interglacial transitions in the middle and late Pleistocene. Pp. 16–33 in Paleoecology and paleoenvironments of late Cenozoic mammals (K. M. Stewart and K. L. Seymour, eds.). University of Toronto Press, Toronto, Ontario, Canada.

BEGON, M., J. L. HARPER, AND C. R. TOWNSEND. 1990. Ecology: individuals, populations and communities. 2nd ed. Blackwell Scientific Publications, London, United Kingdom.

BOND, G. C., AND R. LOTTI. 1995. Iceberg discharges into the North Atlantic on millennial time scales during the last glaciation. Science 267:1005–1010.

BROWN, J. H. 1995. Macroecology. University of Chicago Press, Chicago, Illinois.

BROWN, J. H., AND M. A. KURZIUS. 1987. Composition of desert rodent faunas: combinations of coexisting species. Annales Zoologici Fennici 24:227–237.

BROWN, J. H., G. C. STEVENS, AND D. M. KAUFMAN. 1996. The geographic range: size, shape, boundaries and internal structure. Annual Review of Ecology and Systematics 27:597–623.

CLEMENTS, F. E. 1936. Nature and structure of the climax. Journal of Ecology 24:252–284.

COOPE, G. R. 1987. The response of late Quaternary insect communities to sudden climatic changes. Pp. 421–438 in Organization of communities, past and present (J. H. R. Gee and P. S. Gillers, eds.). Blackwell, Oxford, United Kingdom.

COOPE, G. R. 1995. Insect faunas in Ice Age environments: why so little extinction? Pp. 55–74 in Extinction rates (J. H. Lawton and R. M. May, eds.). Oxford University Press, Oxford, United Kingdom.

DANSGAARD, W., ET AL. 1993. Evidence for general instability of past climate from a 250-kyr ice-core record. Nature 364:218–220.

DAVIS, M. B., AND R. G. SHAW. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292:673–679.

DIAMOND, J. M., AND M. E. GILPIN. 1982. Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. Oecologia 52:64–74.

EDWARDS, M. E., ET AL. 2000. Pollen-based biomes for Beringia 18,000, 6000 and 0 ^{14}C yr BP. Journal of Biogeography 27:521–554.

ELENGA, H., ET AL. 2000. Pollen-based biome reconstruction for southern Europe and Africa 18,000 yr BP. Journal of Biogeography 27:621–634.

FAUNMAP WORKING GROUP. 1996. Spatial response of mammals to late Quaternary environmental fluctuations. Science 272:1601–1606.

GLEASON, H. A. 1926. The individualistic concept of plant association. Bulletin of the Torrey Botany Club 53:7–26.

GRAHAM, R. W. 1986. Response of mammalian communities to environmental changes during the late Quaternary. Pp. 300–313 in Community ecology (J. Diamond and T. J. Case, eds.). Harper & Row, New York.

GRAHAM, R. W. 1993. Processes of time-averaging in the terrestrial vertebrate record. Pp. 102–124 in Taphonomic approaches to time resolution in fossil assemblages (S. M. Kidwell and A. K. Behrensmeyer, eds.). The Paleontological Society, University of Tennessee, Knoxville.

GRAHAM, R. W., AND E. C. GRIMM. 1990. Effects of global climate change on the patterns of terrestrial biological communities. Trends in Ecology and Evolution 5:289–292.

GRAHAM, R. W., AND E. L. LUNDELIUS, JR. 1984. Coevolutionary disequilibrium and Pleistocene extinctions. Pp. 223–249 in Quaternary extinctions: a prehistoric revolution (P. S. Martin and R. G. Klein, eds.). University of Arizona Press, Tucson.

GRAHAM, R. W., AND J. I. MEAD. 1987. Environmental fluctuations and evolution of mammalian faunas during the last deglaciation in North America. Pp. 372–402 in North American and adjacent oceans during the last deglaciation (W. F. Ruddiman and H. E. Wright, Jr., eds.). The Geological Society of America, Boulder, Colorado.

HOLMAN, J. A. 1993. British Quaternary herpetofaunas: a history of adaptations to Pleistocene disruptions. Herpetological Journal 3:1–7.

HUNTLEY, B. 1990. Dissimilarity mapping between fossil and contemporary pollen spectra in Europe for the past 13,000 years. Quaternary Research 33:360–376.

JACKSON, J. B. C. 1994a. Community unity? Science 264:1412–1413.

JACKSON, J. B. C. 1994b. Constancy and change of life in the sea. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 344:55–60.

JACKSON, S. T., AND D. R. WHITEHEAD. 1991. Holocene vegetation patterns in the Adirondack mountains. Ecology 72:641–653.

KAUFMAN, D. M., AND M. R. WILLIG. 1998. Latitudinal patterns of mammalian species richness in the New World: the effects of sampling method and faunal group. Journal of Biogeography 25:795–805.

LYONS, S. K. 2001. A quantitative assessment of the community structure and dynamics of Pleistocene mammals. Ph.D. dissertation, University of Chicago, Chicago, Illinois.

LYONS, S. K., AND M. R. WILLIG. 1997. Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials. Oikos 79:568–580.

MAYEWSKI, P. A., ET AL. 1993. The atmosphere during the Younger Dryas. Science 261:195–197.

OVERPECK, J. T., R. S. WEBB, AND T. WEBB III. 1992. Mapping eastern North American vegetation changes of the past 18ka: no-analogs and the future. Geology 20:1071–1074.

POTTS, R., AND A. DEINO. 1995. Mid-Pleistocene change in large mammal faunas of East Africa. Quaternary Research 43:106–113.

PRENTICE, C., AND D. JOLLY. 2000. Mid-Holocene and glacial-maximum vegetation geography of the northern continents and Africa. Journal of Biogeography 27:507–519.

SMITH, F. A., AND J. L. BETANCOURT. 1998. Response of bushy-tailed woodrats (*Neotoma cinerea*) to late Quaternary climatic change in the Colorado Plateau. Quaternary Research 47:1–11.

SMITH, F. A., J. L. BETANCOURT, AND J. H. BROWN. 1995. Evolution of woodrat body size tracks 20,000 years of climate change. Science 270:2012–2014.

SMITH, F. A., H. BROWNING, AND U. L. SHEPHERD. 1998. The influence of climatic change on the body mass of woodrats (*Neotoma albigula*) in an arid region of New Mexico, USA. Ecography 21:140–148.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry: the principles and practice of statistics in biological research. 2nd ed. W. H. Freeman and Company, New York.

SPAULDING, W. G., AND T. R. VAN DEVENDER. 1977. Late Pleistocene montane conifers in southeastern Utah. Southwestern Naturalist 22:269–286.

TAKAHARA, H., S. SUGITA, S. P. HARRISON, N. MIYOSHI, Y. MORITA, AND T. UCHIYAMA. 2000. Pollen-based reconstructions of Japanese biomes at 0, 6000 and 18,000 ^{14}C yr BP. Journal of Biogeography 27:665–683.

TARASOV, P. E., ET AL. 2000. Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia. Journal of Biogeography 27:609–620.

TAYLOR, K. C., ET AL. 1993. The "flickering switch" of late Pleistocene climate change. Nature 361:432–436.

THOMPSON, R. S., AND K. H. ANDERSON. 2000. Biomes of western North America at 18,000, 6000 and 0 ^{14}C yr BP reconstructed from pollen and packrat midden data. Journal of Biogeography 27:555–584.

THOMPSON, R. S., AND J. I. MEAD. 1982. Late Quaternary environments and biogeography in the Great Basin. Quaternary Research 17:39–55.

THOMPSON, R. S., C. WHITLOCK, P. J. BARTLEIN, S. P. HARRISON, AND W. G. SPAULDING. 1993. Climatic changes in the western United States since 18,000 yr B.P. Pp. 468–513 in Global climates since the last glacial maximum (H. E. Wright, Jr., J. E. Kutzback, T. Webb III, W. F. Ruddiman, F. A. Street-Perrott, and P. J. Bartlein, eds.). University of Minnesota Press, Minneapolis.

VALENTINE, J. W., AND D. JABLONSKI. 1993. Fossil communities: compositional variation at many time scales. Pp. 341–348 in Species diversity in ecological communities: historical and geographical perspectives (R. E. Ricklefs and D. Schluter, eds.). University of Chicago Press, Chicago, Illinois.

VAN DEVENDER, T. R., AND B. L. EVERITT. 1977. The latest Pleistocene and recent vegetation of the Bishop's Cap, south-central New Mexico. Southwestern Naturalist 22:337–353.

WEBB, S. D. 1987. Community patterns in extinct terrestrial vertebrates. Pp. 439–466 in Organization of communities, past and present (J. H. R. Gee and P. S. Gillers, eds.). Blackwell Scientific Publishers, Oxford, United Kingdom.

WEBB, T., III. 1981. 11,000 years of vegetation change in eastern North America. BioScience 31:501–506.

WEBB, T., III. 1992. Past changes in vegetation and climate: lessons for the future. Pp. 59–75 in Global warming and biological diversity (R. L. Peters and T. E. Lovejoy, eds.). Yale University Press, New Haven, Connecticut.

WEBB, T., III, P. J. BARTLEIN, S. P. HARRISON, AND K. H. ANDERSON. 1993. Vegetation, lake levels, and climate in eastern North America for the past 18,000 years. Pp. 415–467 in Global climates since the last glacial maximum (H. E. Wright, Jr., J. E. Kutzback, T. Webb III, W. F. Ruddiman, F. A. Street-Perrott, and P. J. Bartlein, eds.). University of Minnesota Press, Minneapolis.

WILLIAMS, J. W., B. N. SHUMAN, AND T. WEBB III. 2001. Dissimilarity analyses of late Quaternary vegetation and climate in eastern North America. Ecology 82:3346–3362.

WILLIAMS, J. W., T. WEBB III, P. H. RICHARD, AND P. NEWBY. 2000. Late Quaternary biomes of Canada and the eastern United States. Journal of Biogeography 27:585–607.

YU, G., ET AL. 2000. Palaeovegetation of China: a pollen data-based synthesis for the mid-Holocene and last glacial maximum. Journal of Biogeography 27: 635–664.

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