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MAMMALIAN RESPONSE TO GLOBAL WARMING ON VARIED TEMPORAL SCALES

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Paleontological information was used to evaluate and compare how Rocky Mountain mammalian communities changed during past global warming events characterized by different durations (350, ~10,000–20,000, and 4 million years) and different per–100-year warming rates (1.0°C, 0.1°C, 0.06–0.08°C, 0.0002–0.0003°C per 100 years). Our goals were to determine whether biotic changes observed today are characteristic of or accelerated relative to what took place during past global warming events and to clarify the possible trajectory of mammalian faunal change that climate change may initiate. This determination is complicated because actual warming rates scale inversely with the time during which temperature is measured, and species with different life-history strategies respond (or do not) in different ways. Nevertheless, examination of past global warming episodes suggested that approximately concurrent with warming, a predictable sequence of biotic events occurs at the regional scale of the central and northern United States Rocky Mountains. First, phenotypic and density changes in populations are detectable within 100 years. Extinction of some species, noticeable changes in taxonomic composition of communities, and possibly reduction in species richness follow as warming extends to a few thousand years. Faunal turnover nears 100% and species diversity may increase when warm temperatures last hundreds of thousands to millions of years, because speciation takes place and faunal changes initiated by a variety of shorter-term processes accumulate. Climate-induced faunal changes reported for the current global warming episode probably do not yet exceed the normal background rate, but continued warming during the next few decades, especially combined with the many other pressures of humans on natural ecosystems, has a high probability of producing effects that have not been experienced often, if ever, in mammalian history.

Key words: climate change, global warming, Holocene, mammals, Miocene, Pleistocene

Predictions about how terrestrial vertebrates will respond to current global warming, projected to occur at rates of 1.4–5.8°C per 100 years (Houghton et al. 2001; Reilly et al. 2001; Schneider and Root 1998; Wigley and Raper 2001), have been based primarily on modern ecological studies (Brown et al. 1997; Harte and Shaw 1995; Kerr and Packer 1998; McCarty 2001; McDonald and Brown 1992; Schneider and Root 1998) or on analysis of data from the Pleistocene–Holocene transition (Graham 1992; Graham and Grimm 1990). Such studies suggest that mammalian communities in a given geographic region will respond to climatic change by altering 1) relative abundance of individuals within species; 2) taxonomic composition as species locally (extirpation) or globally (extinction) disappear or colonize; and 3) species rich-

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TABLE 1.—Global warming episodes compared in this study. ''Projected warming'' is from Intergovernmental Panel on Climate Change (Houghton et al. 2001). ''Current warming'' reflects measured values from 1950 to 2000 (Delworth and Knutson 2000).

Event	Temperature change, ΔT (°C)	Measured over, ΔI (years)	Duration of episode (years)	Standardized rate, (ΔT/ΔI) × 100 years (°C)
Projected warming	1.4–5.8	100	150+ ? (1950–2100+)	1.4–5.8
Current warming	0.70	50	50 (1950–2000)	1.4
Medieval Warm Period	~1	100	350	1.0
Average Pleistocene to Holocene	~5	5,000	10,000	0.1
Mid-Pleistocene	~3 to 4	5,000	20,000–40,000	0.06–0.08
Mid-Miocene Climatic Optimum	~3 to 4	1.5 million	4 million	0.0002–0.0003

ness as rates of extinction, extirpation, and immigration are affected. Other possible effects of environmental change are expression of different phenotypes (not necessarily accompanied by genetic change) as nutritional quality or other environmental factors vary, genetic change through population processes that may or may not be accompanied by phenotypic change (Consuegra et al. 2002; Hadly et al. 2001; E. A. Hadly, in litt.; E. A. Hadly et al., in litt.), and evolution of new species when environmental change induces new selective pressures, fragments species ranges, and encourages dispersal. Changes in speciation rates, like the other factors listed in point 3, would contribute to changing species richness.

As strong as the circumstantial evidence is that the current global warming episode will affect (and perhaps already is affecting) mammals in these ways, 2 uncertainties remain. First, what is the sequence of events and expectable extent of change as the duration of a warming event continues over time spans that are long by ecological standards (i.e., hundreds, thousands, and millions of years)? Second, are ecosystems already experiencing such a fast rate of global warming that the resulting biotic changes are fundamentally different from those that characterized past warming episodes?

Our goal here is to explore these questions and thereby more reliably understand the trajectory of biotic change that mammals will experience as a result of the current global warming episode. We establish the background rate of temperature change for the past 60 million years and, within that context, assess how mammalian species and communities changed during 4 previous warming events: Medieval Warm Period (MWP; 100-year scale), 2 different glacial–interglacial transitions (GIGT; 1,000-year scale), and the Mid-Miocene Climatic Optimum (MMCO, million-year scale; Table 1). The resulting information provides a useful baseline for recognizing what is ''normal'' for rates of climate change and accompanying faunal dynamics and whether currently observed faunal changes reflect a unique response to global warming or fall within the range of background noise in the context of the last 60 million years.

MATERIALS AND METHODS

We analyzed superposed assemblages of fossil mammals that spanned each of the 4 past global warming events. This involved comparison of a prewarming and postwarming sample of the mammalian community for each event. Each community sample was time averaged to some degree. Only samples that were similarly time averaged were compared for a given event. In the case of the MWP and GIGT time scales, time averaging enhances fidelity of the fossil sample to the living community from which it was drawn (Hadly 1999). The data were used to assess whether climatic warming coincided with changes in biogeographic ranges, alterations in relative abundance of individuals within a species or species within higher taxa, extinction, phenotypic change, population-level genetic

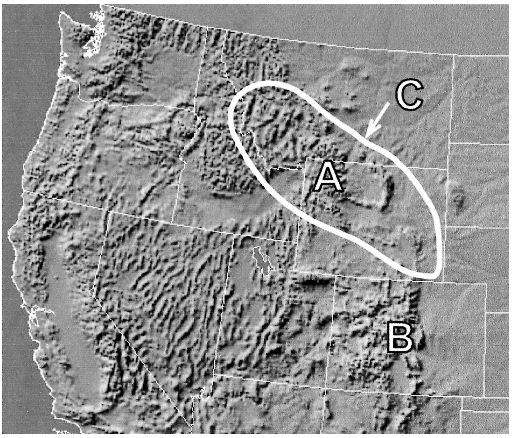

FIG. 1.—Fossil localities. A) Lamar Cave. B) Porcupine Cave. C) Area encompassed by localities used in the analysis of the Mid-Miocene Climatic Optimum (MMCO). Barnosky (2001) and Barnosky and Carrasco (2002) provide a complete listing of the MMCO localities. (Base map from http://fermi.jhuapl.edu/states/us/us_color.gif.)

change (when possible), speciation, and species richness. As with most paleontological data, it was not possible to prove that observed biotic changes that were coincident with climatic change were caused by the climatic change. However, observed faunal responses discussed below were consistent with expectations based on life-history strategies of extant taxa (Barnosky 2001; Hadly 1999). We emphasized superposed samples of fossils from restricted geographic regions because our intent was to understand responses within communities of potentially interacting species. The study area was confined to the northern one-half of the Rocky Mountains in the United States (Fig. 1); any detected response to climate change ultimately depended on how the globally recognized climatic events were manifested in that region. Models summarized by the National Assessment Synthesis Team (2001) suggest that regional climatic effects in our study area will be significant for the current warming episode. Thus, it seems likely that past global warming also would have caused regional climate change in our study area, although this inference becomes less secure for pre-Quaternary times (Barnosky and Carrasco 2002). Sampling itself was dictated by the location of adequate fossil material. Faunal data previously detailed in published studies formed the core for interpretations of biotic change.

Data for the MWP came from Lamar Cave, Wyoming (Hadly 1996, 1997, 1999; Hadly et al. 1998), where >10,000 identifiable mammalian fossils were distributed through 16 stratigraphic levels. Nineteen radiocarbon dates documented that the deposits span the MWP, which lasted from approximately 1,150 to 750 years ago. Warming of ≤1°C occurred within the first 100 years, and the warm event lasted about 400 years, although it was punctuated by some relatively short cooler spells (Broecker 2001; Campbell et al. 1998; Hughes and Diaz 1994).

We compared 2 GIGTs: the last Pleistocene glacial into Holocene interglacial times (which we refer to simply as the ‘‘last GIGT’’) and a mid-Pleistocene transition (‘‘the mid-Pleistocene GIGT’’). Faunal data for the last GIGT in our study area were extracted from the FAUNMAP analysis (FAUNMAP Working Group 1994, 1996) and were augmented by a considerable literature on effects of late Pleistocene climate change on morphological change (e.g., Martin and Barnosky 1993). Faunal data for the mid-Pleistocene GIGT were derived from the Pit sequence in Porcupine Cave, Colorado (Fig. 1), which clearly documents biotic patterns across a glacial–interglacial transition that most likely took place sometime between 750,000 and 850,000 years ago (Barnosky 1998, in press; Barnosky et al. 1996; Bell and Barnosky 2000; Wood and Barnosky 1994).

The last GIGT took place between 10,000 and 15,000 years ago, during which time the average global temperature warmed about 5°C (Schneider and Root 1998). The average warming rate during these 5,000 years (0.1°C per 100 years) was 1 parameter of interest for this analysis. However, this average rate embeds rapid temperature fluctuations (and consequently high warming rates) because much of the warming occurred within a few centuries at the end of the Younger Dryas (Bennett et al. 2000; Blunier and Brook 2001; Clark et al. 1999; Lang et al. 1999; Rodbell 2000; Severinghaus and Brook 1999; Stenni et al. 2001). Hence, Pleistocene global warming events probably are characterized by elevated warming rates for centuries as a glacial period came to an end; then, temperatures stabilized for the 10,000–20,000 years typically spanned by an interglacial.

$\delta^{18}O$ values from deep-sea cores generally reflect temperature and glacial ice-volume. The $\delta^{18}O$ values for the last GIGT appear more or less typical for GIGTs back to about 600,000 years ago, but prior Pleistocene glacial–interglacial shifts demonstrate slightly lower magnitudes of relative warming (Imbrie et al. 1993; Raymo 1997). Consequently, the transition captured by the Porcupine Cave record probably featured a slightly lower warming rate than the latest GIGT (Table 1).

Because the Porcupine Cave project is still in progress, we used only 1 segment of the fauna that has been adequately identified and analyzed and that had adequate taphonomic sampling: the arvicoline rodents (voles, lemmings, muskrats) from the Pit locality (Bell and Barnosky 2000). This sample included about 1,500 specimens distributed through 11 stratigraphic levels (level 1: youngest; level 11: oldest). Additional information from >13,000 curated specimens comprising >130 species of amphibians, reptiles, birds, and mammals is being prepared for publication elsewhere (Barnosky, in press), and to some extent the arvicoline subset is an exemplar of conclusions that are becoming apparent from the larger data set.

For assessing biotic changes during global warming events on a million-year time scale, we examined northern Rocky Mountain mammal faunas through the MMCO. As interpreted from the Atlantic $\delta^{18}O$ curve (Miller et al. 1987; Zachos et al. 2001a), the MMCO began 18.5×10^6 years ago, peaked at 17×10^6 years ago, and continued until 14.5×10^6 years ago. Estimates for the magnitude of warming from $\sim 18.5 \times 10^6$ to 17×10^6 years ago range from 1 to 5°C, with 3–4°C being the most common (Buchardt 1978; Janis 1993; Miller et al. 1987; Schoell et al. 1994; Wolfe 1994; Woodruff et al. 1981; Wright et al. 1992; Zachos et al. 2001a; Zubakov and Borzenkova 1990), yielding an average warming rate of around 2°C per million years. As with average rates during the Pleistocene, this overall warming trend embedded more rapid temperature fluctuations at shorter time intervals, notably at least 3 cold excursions (Woodruff et al. 1981) and judging from detailed records that are slightly older, probably also embedded Milankovitch-scale climatic oscillations (Zachos et al. 2001b). Mid-latitude mean annual temperature during the MMCO was as much as 6°C higher than present (Flower 1999; Wolfe 1994). Locally, within the northern Rocky Mountains, the MMCO was manifested by a warm, wet time $19–17 \times 10^6$ years ago, followed by increasing aridity from 17×10^6 to 14×10^6 years ago (Barnosky and LaBar 1989; Burbank and Barnosky 1990; Fields et al. 1985; Thompson et al. 1982). Time intervals of interest include the Arikareean land-mammal age divided from oldest to youngest into Ar1 ($\sim 27.5 \times 10^6$ to 30×10^6 years ago), Ar2 ($\sim 24 \times 10^6$ to 27.5×10^6 years ago), Ar3 ($\sim 21 \times 10^6$ to 24×10^6 years ago), Ar4 ($\sim 19 \times 10^6$ to 21×10^6 years ago); Hemingfordian divided into He1 ($\sim 17.5 \times 10^6$ to 19×10^6 years ago) and He2 and 3 ($\sim 16 \times 10^6$ to 17.5×10^6 years ago); and Barstovian divided into Ba1 ($\sim 14.5 \times 10^6$ to 16×10^6 years ago), Ba2 ($\sim 12.5 \times 10^6$ to 14.5×10^6 years ago), and Ba3 ($\sim 11.5 \times 10^6$ to 12.5×10^6 years ago) as given by Woodburne and Swisher (1995). The fossil data set resulted from synthesizing information from >90 localities in Wyoming, Montana, and Idaho, which included >300 species. The Rocky Mountain data were interpreted in the context of larger geographic patterns that included an additional >600 localities and >400 species from the adjacent northern Great Plains and Northwest. Details about included localities, methods of estimating species richness, and other indices of faunal change were explained by Barnosky (2001) and Barnosky and Carrasco (2002).

To determine the relationship between the time during which temperature change is measured and rate of temperature change, we used published oxygen-isotope curves and other paleotemperature proxies to infer past temperature changes. Temperature inferences were those of the authors of the included studies (Bradley 1999:figure 6.12—for the 10,000- to 100,000-year time scales; Houghton et al. 1990:figure 7.1—for 100- to 100,000-year time scales; Zachos et al. 2001a:figure 2—for the million-year time scale). Global mean annual temperature measurements from 1860 to 1990 were used to calculate rates during intervals of 5–50 years (Houghton et al. 1990:figure 11). Using enlarged versions of published figures, temperature values were read off of the curves or bar graphs at each appropriate time (e.g., each year, decade, century, millennium). The observed temperature change was divided by the number of years during which the change took place to yield an average rate of temperature change (°C/year). Those rates were standardized to per–100-year

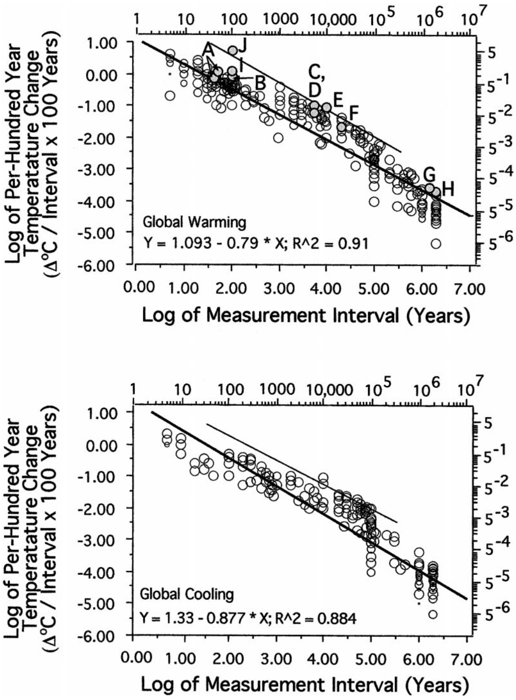

FIG. 2.—Per–100-year temperature-change values plotted as a function of the interval of time during which the temperature change is measured. Top: Warming rates. Bottom: Cooling rates. Open circles show inferred measurements taken from the following sources: intervals of 1–130 years (Houghton et al. 1990:figure 11); 90–900 years (Houghton et al. 1990: figure 7.1, bottom); 1,000–10,000 years (Houghton et al. 1990:figure 7.1, middle); 10,000–130,000 (Bradley 1999:figure 6.12); 100,000–900,000 years (Houghton et al. 1990: figure 7.1, top); 1,000,000–2,000,000 years (Zachos et al. 2001a:figure 2). Shaded circles in the top graph demarcate per–100-year temperature-change values for the following observed, past, or projected global warming episodes: A) global warming measured from 1950 to 1990 (lower dot—Houghton et al. 1990) and from 1950 to 2000 (upper dot—Delworth and Knutson 2000:figure 1); B) Medieval Warm Period (Broecker 2001; Campbell et al. 1998; Hughes and Diaz 1994); C) Pleistocene–Holocene glacial–interglacial transition (upper circle—Schneider and Root 1998); D) mid-Pleistocene glacial–interglacial transition (lower circle—Raymo 1997); E and F) Paleocene Methane Event, highest and lowest estimates, respectively (Katz et al. 1999); G) Mid-Miocene Climatic Optimum (Barnosky 2001; Barnosky and Carrasco 2002; Zachos et al. 2001a); H) Late Oligocene Warming (Barnosky and Carrasco 2002; Zachos et al. 2001a); I and J) lowest and highest estimates, respectively, for global warming during the next 100 years (Houghton et al. 2001; Reilly et al. 2001; Schneider and Root 1998; Wigley and Raper 2001). Dark lines show regressions for the global average; light lines show regression for data from Greenland only (Johnsen et al. 2001). Note that such local records exhibit higher values of temperature change than the globally averaged record. Statistics for the Greenland regressions: warming, y = 2.169 − 0.848 × x (r^2 = 0.793); cooling, y = 1.68 − 0.745 × x (r^2 = 0.728).

temperature-change values in the equation: (temperature change)/(number of years during which the change took place) × 100 years. This facilitated comparison of how much change in temperature a given rate would produce in 100 years. Finally, the per–100-year temperature-change values were plotted in log–log space against the interval length that produced the rate. Precision was limited by the accuracy of the original authors in transforming original raw data onto published graphs and then by our extraction of a value from the published illustrations. However, the limited precision inherent in this technique was sufficient for understanding the general relationship.

RESULTS AND DISCUSSION

Comparison of Warming Rates

The plot of per–100-year temperature-change values against the time interval during which the temperature change was measured indicated a clear scaling effect: the shorter the interval of time during which temperature change was measured, the faster the apparent rate of change and consequently the higher the per–100-year temperature-change value (Fig. 2). This is because short-term changes in one direction tend to be balanced by changes in the opposite direction as time accumulates, analogous to what has been observed for evolutionary rates (Gingerich 1993, 2001).

The relationship also arises because warm (or cool) episodes are characterized by both rates and durations. The rate is the magnitude of change (i.e., the difference in temperature between the beginning and end of the temporal interval of concern) divided by the length of the temporal interval. In the case of a warm episode, the duration is the time beginning with an increase in warming rate. The duration ends with the onset of cooling that leads to a sustained return to conditions that are at least as cool as those that preceded the initial warming rate change. An important consideration is that the warming rate does not necessarily remain constant throughout the warm episode. More typically, rates of warming may be high at the beginning of the episode and then decrease so that the mean rate for the entire warm episode is only a fraction of the rate that characterized the beginning of the warming episode. For example, locally, rapid temperature changes were exemplified by analyses of gases from Greenland ice cores (GRIP and GISP2 cores—Dansgaard et al. 1993; Jouzel 1999). These analyses suggested that a 16°C rise occurred in Greenland within decades to centuries about 70,000 years ago (Lang et al. 1999) and that a ~9°C rise occurred about 15,000 years ago (Blunier and Brook 2001; Jouzel 1999; Severinghaus and Brook 1999). Such fluctuations exemplify Dansgaard–Oeschger events, which are more or less cyclic millennial-scale climate oscillations that characterized much of the last glacial at least in Greenland and the North Atlantic. Each cycle was marked by a very rapid warming rate initially, then about 500–1,500 years during which the temperature decreased nearly back to the cool values that were characteristic at the end of the previous cycle, and then a prolonged cool period that lasted from a few hundred to a few thousand years (Blunier and Brook 2001). Particularly relevant to our study is the information that the Greenland cores yield about rates of climate change at the last GIGT. At about 15,000 years ago, the Dansgaard–Oeschger event noted above (D-O 1—Blunier and Brook 2001) resulted in a ~9°C temperature rise within about 50 years (Severinghaus and Brook 1999). Therefore, the warming rate was 9°C per 50 years (equating to a per–100-year temperature-change value of 18.0°C). By 13,000 years ago, the temperature again had cooled, removing all the 9°C increase of D-O 1. As interpreted from the GISP2 core, about 13,000–10,000 years ago (the last GIGT), the temperature rose ~12°C but has exhibited little, if any, net rise since (Dansgaard et al. 1993). Therefore, the per–100-year temperature-change value measured only across the actual glacial–interglacial transition was 0.4°C (i.e., a rate of 12°C per 3,000 years), whereas the per–100-year temperature-change value averaged over the entire warm episode was substantially lower at 0.09°C (a rate of 12°C per 13,000 years). Although the magnitude of local change in Greenland was higher than the global average (Fig. 2), such data strongly suggest that most warming occurs at the beginning of a warm episode. Such ‘‘frontloading’’ of warming rates also is evident on longer time scales. Most of the warming of the MMCO took place within the 1st one-third of the episode; then, warm temperatures held steady for about 3 million years before rapid cooling reduced global temperatures to below their pre-MMCO average (Zachos et al. 2001a).

Thus, at longer intervals of measurement, the standardized temperature-change values decrease because reversals in temperature cumulatively cancel each other out and because times of fast change are interspersed with longer times of slower change (Fig. 2). If a global warming event is qualitatively different from the average changes that have characterized the past 60 million years or so, the standardized temperature-change values should plot above the background values. The temperature changes of the MWP, GIGTs, and MMCO do not exceed the background changes that would be expected for temperatures measured during the respective durations, although all plot at the high end of the range (Fig. 2). Therefore, we expect that changes in the studied mammalian communities during the MWP, GIGTs, and MMCO, if resulting from the respective climatic warming events, provide a gauge for mammalian community response to global warming episodes that are at the high end of normal temperature change.

We also plotted measured rates of historic warming (Fig. 2: shaded circles A). So far, these rates do not exceed the background rate. Therefore, the extent to which faunal changes correspond with the 4 past climate changes and with the ongoing global warming episode (e.g., faunal responses summarized by McCarty 2001) probably represents a normal background of community dynamics. (Note that we confine this discussion to climate change and do not consider the effects on ecosystems of current habitat destruction, which unarguably is tremendous.) However, well-founded projections indicate a high probability that current or higher rates of warming will continue for at least a century, with the expectation that mean global temperature will be 1.4–5.8°C higher than today in the year 2100 (Houghton et al. 2001; Reilly et al. 2001; Schneider and Root 1998; Wigley and Raper 2001). If any but the very lowest of those highly probable projections hold true, the per–100-year temperature change will far exceed the background rate of change (Fig. 2: shaded circles I and J). In this light, the background of faunal dynamics we discuss below establishes a valuable context by which to recognize when (and if) human-induced global warming perturbs the system outside the bounds in which it evolved, at which point faunal responses that are outside the normal range might be expected.

Note that climate changes measured or inferred at specific localities may far exceed the global background rate, although such local records still seem to conform to the relationship of rates of temperature change declining as interval length increases (Fig. 2). For example, the 16°C temperature increase noted above at 70,000 years ago reflects a local response in Greenland to a Dansgaard–Oeschger event. Presumably, if this record could be averaged with many simultaneous proxies from throughout the globe, the global temperature increase would appear much lower than 16°C.

The 100-year scale: MWP.—In general, mammalian communities of the northern Rockies, and presumably the rest of the ecosystem in which these communities exist, persisted more or less in their present form for ≥3,000 years (Hadly and Maurer 2001). Within this overall context of community stability, several adjustments characterized the climatic transition into the MWP. The stratigraphic distribution of the taxa at Lamar Cave demonstrated changes in relative abundance of ecologically sensitive taxa in the direction expected, given habitat preferences for these animals today: in open grasslands, voles (*Microtus*) decreased as ground squirrels (*Spermophilus*) increased during the warm time, whereas in closed forests, *Phenacomys* and *Clethrionomys* simultaneously declined (Hadly 1996, 1999; Steele and Hadly 2002). Minor geographic range changes occurred. For example, *Microtus ochrogaster* was absent during xeric intervals and is absent today, but it was present during the mesic interval just before the MWP. Its closest range today is within 200 km. No extinction is evident among mammals in the Lamar Cave record.

To assess potential effects of the MWP on population divergence, sequences of mitochondrial DNA (mtDNA) were obtained from 80 fossil specimens of pocket gophers (*Thomomys talpoides*) and were compared with sequences from surrounding subspecies that presently inhabit the Rocky Mountain region (Hadly et al. 1998). Morphometric criteria indicative of genetic distinctiveness (toothrow length) and ecophenotypic (environmentally induced rather than genetically heritable) variation (diastema length) also were analyzed for the fossil sequence and modern sample (Hadly 1997). Results indicated local genetic stability from 3,000 years ago to the present, but ecophenotypic change coincided with the beginning of the MWP. Species richness as inferred from rarefaction comparisons (Hadly 1999) did not substantially change across the stratigraphic levels that bracketed the transition to the MWP. Population processes such as gene flow have contributed to haplotype turnover as detected in ancient DNA in *Microtus* without evidence of phenotypic change (Hadly et al. 2001; E. A. Hadly, in litt.; E. A. Hadly et al., in litt.). Although there is additional evidence of genetic change in the Holocene, for our purposes the genetic record of response to warming cannot be directly ascertained for earlier warming events.

The 1,000-year scale: GIGT.—In the mid-Pleistocene glacial sediments of Porcupine Cave (best represented by levels 4–5; see Bell and Barnosky 2000:figure 2), there were at least 10 species of voles, lemmings, and muskrats: *Mictomys* cf. *M. meltoni*, *Lemmiscus curtatus*, *Allophaiomys pliocaenicus*, *Microtus paroperarius*, *Microtus meadensis* (synonymous with *Terricola meadensis*), *Microtus* sp. (distinct from *M. paroperarius* and *M. meadensis*), *Mimomys* cf. *M. virginianus*, *P. gryci*, *Phenacomys* sp. (not *P. gryci*), and *Ondatra* sp. *A. pliocaenicus* and *M.* cf. *M. virginianus* were absent in the interglacial deposits (best represented by levels 1–3; see Bell and Barnosky 2000:figure 2), and neither are known from younger deposits elsewhere. *P. gryci* makes its last known appearance in level 3. These data establish extinction and geographic range changes at the climate change within arvicolines.

In the last GIGT geographic range, adjustments may have been more substantial than in the mid-Pleistocene GIGT. For example, sagebrush voles (*Lemmiscus*) and bog lemmings (*Mictomys*) remained sympatric through the mid-Pleistocene GIGT at Porcupine Cave. But by the beginning of the Holocene, sagebrush voles had retracted their range into the Great Basin and sagebrush areas of Wyoming and Montana, whereas bog lemmings retracted their range north into Canada.

Loss of arvicoline species from local communities was comparable at the 2 warming events. The mid-Pleistocene loss (2 or 3 of 10 species or 20–30%) was probably by extinction, and loss at the last GIGT was by extirpation, which removed 2 or 3 (*Dicrostonyx torquatus*, *Mictomys borealis*, and possibly *Microtus xanthagnathus*) of 12 species (17–25%) from the central and northern Rocky Mountain states (Colorado, Idaho, Montana, Wyoming—FAUNMAP Working Group 1994).

Overall, extinction magnitudes are difficult to compare because of the poor mid-Pleistocene record and because it is unclear how much human hunting contributed to large-mammal extinction at the last GIGT (Alroy 2001; Barnosky 1989; Beck 1996; Graham and Lundelius 1984; Martin and Klein 1984). Extinction of large mammals at the late Pleistocene–Holocene transition was pronounced in the central and northern Rocky Mountain states, culling at least 13 species in 13 genera (FAUNMAP Working Group 1994). Comparable data do not exist for the mid-Pleistocene. However, at Porcupine Cave, megafauna such as horses, which became extinct at the end of the Pleistocene, are present both below and above the mid-Pleistocene warming event discussed here (Barnosky, in press).

For the arvicoline rodents, species richness decreased across both examined GIGTs by roughly similar magnitudes (between 17% and 30%). For the mid-Pleistocene GIGT, the reduction in arvicoline diversity contributed to an overall reduction in species richness of small mammals (Barnosky, in press). At the last GIGT, local species richness of mammals very likely decreased through much of North America (Graham 1992) but mainly as a result of extinction of many large mammals rather than small ones.

Relative abundance changes were coincident with climate change at both GIGTs. In the Porcupine Cave deposits, *M. meadensis* and *Microtus* sp. increased, whereas *Mictomys* decreased and *Lemmiscus* remained constant at the mid-Pleistocene GIGT represented by the transition from level 4 to 3 (Bell and Barnosky 2000:figure 10). In the last GIGT, *Dicrostonyx* was locally abundant in Wyoming before warming; near the warming event, it decreased in abundance relative to *Phenacomys* and *Clethrionomys* and then disappeared as *Phenacomys* also became progressively rarer (Walker 1987:355).

Morphologic changes (and therefore by inference genetic changes) in the arvicoline rodents did not seem to vary in any systematic way through the Porcupine Cave sequence, with 1 possible exception, *Lemmiscus*. Specimens referred to *Lemmiscus* are characterized by lower 1st molars that have 4, 5, or 6 triangles as part of their occlusal pattern. The 5- and 6-triangle forms are more abundant in the top 2 interglacial levels 1 and 2. The temporal variation is considerably greater than modern geographic variation, in which all representatives of *L. curtatus*, the only species in the genus, have 5- or 6-triangle molars (A. D. Barnosky and C. J. Bell, in litt.). This pattern possibly indicates that the morphological changes through the stratigraphic sequence reflect genetic changes, but such documentation is beyond the scope of this study. For the purposes of this discussion, however, the relevant point is that 5- and 6-triangle specimens seem to become predominant at the top of the interglacial after the mid-Pleistocene GIGT. Further analyses are warranted to determine whether in fact this provides evidence for a climatically driven effect on genotype.

Several previous studies have documented coincidence of morphologic change in various species with climate change at the last GIGT (e.g., mastodonts—King and Saunders 1984; carnivores, rodents, edentates, and deer—Martin and Barnosky 1993). However, generally these are size changes, which have not been documented to exceed the geographic variation of the species in question. Thus, although the late Pleistocene–Holocene event may have stimulated morphologic changes (usually to a smaller size), evidence for frequent speciation since 15,000 years ago is distinctly lacking for mammals. This accords with studies of sequence divergence in mtDNA, which suggest that although Pleistocene GIGTs were probably important in initiating population-level divergence in mammals, typical mammalian sister species are separated by 2.5–11% sequence divergence or by >1 million years (Avise et al. 1998; Bradley and Baker 2001; Brown et al. 1982), which is much longer than the few thousand years encompassed by a typical GIGT. Some organisms clearly are capable of speciating (and probably have) within time intervals as short as the Pleistocene GIGTs (about 5,000 years), but such examples are rare and do not generally include mammals (Avise et al. 1998; Orr and Smith 1998).

Our result is consistent with studies that suggest that part of the speciation process involves acquiring enough genetic variation to withstand Milankovitch-scale oscillations in climate (Barnosky 2001; Bennett 1997) and with perhaps the most comprehensive study yet published of speciation patterns in a Pleistocene mammal—the woolly mammoth in Eurasia. Lister and Sher (2001) documented that although climatic extremes may have selected for dental specializations in woolly mammoths, speciation required a complex combination of selection in marginal populations and dispersal that took place through periods of time that ranged from about 300,000 to 500,000 years, spanning several glacial–interglacial cycles.

The million-year scale: MMCO.—The MMCO coincides with several aspects of faunal change in the northern Rockies.

However, on this million-year time scale, these changes also coincide with tectonic activity in the region. Thus, it is difficult to distinguish which aspects of faunal change were directly attributable to global climate change and which were attributable to some rather pronounced changes of the western United States topography during the 4 million years in question. However, of relevance to our study is the fact that no matter what the ultimate cause, it is clear that the northern Rockies experienced a pronounced warming and drying during the MMCO (Barnosky and LaBar 1989; Burbank and Barnosky 1990; Fields et al. 1985; Thompson et al. 1982). It therefore is reasonable to suspect that some local biotic responses within the northern Rockies were influenced by the prevailing local and regional climatic conditions. There is an important caveat with such temporally long and necessarily time-averaged data sets: in addition to a response to local climatic conditions, the faunal patterns also may reflect a complex overprint of other biogeographic and evolutionary processes. Nevertheless, interpreted with this in mind, examination of such data is useful in providing some outside boundaries to the extent of faunal change that might be expected to result from long-term climate changes.

As a 1st approximation as to whether faunal changes at the MMCO exceeded faunal change in older and younger Miocene interval transitions, Barnosky (2001) calculated a survival index (SI) that roughly assessed the combined rate of extinction, pseudoextinction (evolutionary change of ancestor into descendant), and extirpation relative to immigration and speciation: the higher the SI, the fewer species disappeared from one interval to the next. At the transition into the MMCO (He1 to He2 and 3), SI = 0%, indicating that none of the prewarming species survived into the warm period within the study area. In contrast, SI values for earlier- and later-interval transitions in the Miocene all were at least 6% and usually above 15%. None of the prewarming species are known later in the geological record anywhere, suggesting that extinction was widespread. Immigration of species from Eurasia, and accelerated cladogenesis (e.g., in heteromyine rodents and horses), also apparently contributed to the heightened faunal turnover (Barnosky 2001).

Patterns of relative abundance changed dramatically across the warming interval, at the levels of species within higher taxa and numbers of individuals within species (Fig. 3). For example, at the onset of warming, species of heteromyines not only increase from 1 (before warming) to 5 species (after warming) but also dominate the rodent fauna in numbers of individuals after the warming event began (Barnosky 2001). Concurrently, among perissodactyls, the number of horse species increased relative to rhinoceros species. Among artiodactyls, oreodonts decreased relative to camel and antelope species, and the 1st appearance of an antelope species correlates with onset of the warming trend. The decrease in oreodonts appears to have been exacerbated by warming, although the decline of this clade began well before the warming event, so it presumably had an independent cause. All these faunal changes are consistent with increasing abundance of taxa adapted to warmer, drier environments.

Species richness patterns were more difficult to infer from the Miocene data than from the Pleistocene and Holocene deposits. Barnosky (2001) and Barnosky and Carrasco (2002) demonstrated that depending on how species richness was estimated, there may or may not have been an increase in northern Rocky Mountain species richness coincident with the MMCO. However, beta diversity within the Rockies probably increased at that time, although causes other than climate change may have been influential (Barnosky and Carrasco 2002).

CONCLUSIONS

These observations lead to a generalized model of how global warming may affect

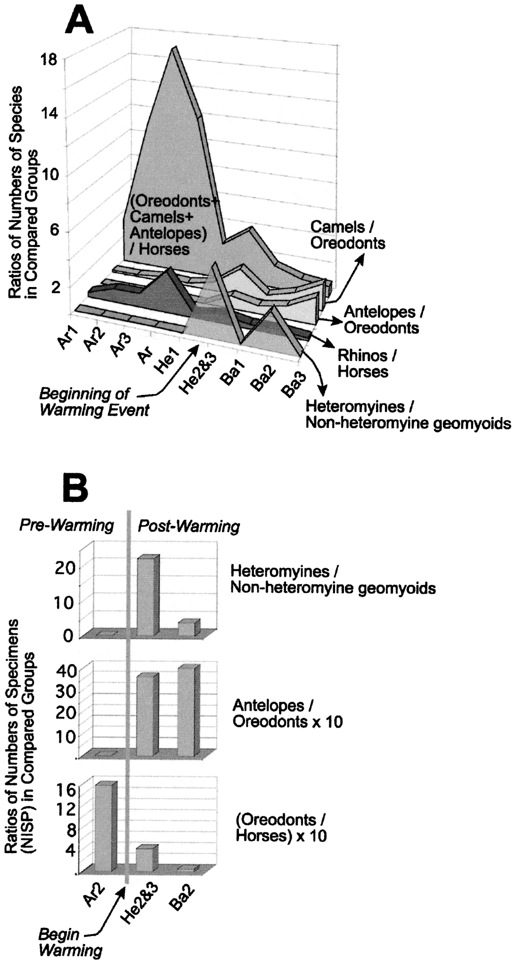

FIG. 3.—Changes in relative abundance of mammals during the Mid-Miocene Climatic Optimum (MMCO). A) Relative abundance of species within higher taxa changes dramatically at the warming event, which begins in temporal interval He1 (see ‘‘Materials and Methods’’). Heteromyine rodents replace nonheteromyine geomyoids, and antelopes, camels, and horses become more dominant relative to rhinos and oreodonts. B) Shifts in the relative abundance of individuals within species; numbers of identifiable specimens (NISP) overestimate actual numbers of individuals but provide a reliable gauge of relative abundance; requisite data for critical time intervals Ar3, Ar4, and He1 do not yet exist, but available data are consistent with a change in abundance at the climate change.

the mammalian component of communities over spans of time that are long by ecological standards and, importantly, establish which faunal responses are normal given the background rate of climate change that has characterized the Cenozoic. As a global warming episode begins, morphologic changes become evident in populations as individuals are affected by nutritional and other ecophenotypically important aspects of their environment. Concurrently, relative abundance of individuals within species changes, leading to slight changes in species ranges as populations expand and contract. Population-level genetic changes may occur from the resulting effects on gene flow and population size. These responses are evident by the time global temperature is elevated 1°C within 100 years and remains so elevated for 400 years (MWP). If global temperature rises 5°C within a few millennia (e.g., the first 5,000 years of an interglacial), extinctions, extirpations, and immigrations lead to clear changes in taxonomic composition of local communities and possibly some reduction in species richness. When warming persists over a million years or so, with global temperature increasing at least 2°C (possibly in some interval of time less than a million years but we cannot be sure from the data), relative abundance of species within higher taxa changes dramatically, and speciation may become important in augmenting species richness of local communities. Concurrently, extinction, immigration, and emigration on this million-year time scale are widespread, leading to a nearly completely new set of species relative to the prewarming time (MMCO). How much such dramatic changes result from the long duration of the warming episode itself, and how much from the accumulation of other biotic influences over such long time periods, remains unclear.

Our model needs to be refined by additional studies of well-dated, stratified fossil deposits that span times of global warming well documented by paleoclimatic proxy data. Even in its current generalized stage, however, important implications emerge from our model and the data on which it is based. First, past warming episodes seem to have been characterized by an initially fast rate of change and then stabilization of rates as global temperatures remained elevated through the duration of the episode. This holds true for all 4 past events discussed in this article. In terms of biotic response, the length of time during which temperature increased and the total duration of the warm episode seem to be important. Elevating global mean temperature at least 1°C in 100 years seems to elicit local biotic response, and the greater the magnitude of initial warming and the longer the warming episode persists, the more biotic change accumulates. The 1st-order response is change in populations and geographic ranges, and the 2nd-order response is extinction of species. The 3rd-order response of rebuilding species diversity through speciation takes much longer than the 1st- and 2nd-order responses.

Second, the kinds of biotic changes that are being reported as currently accruing from climatic change (e.g., Brown et al. 1997; Etterson and Shaw 2001; McCarty 2001; Sæther et al. 2000; Wuethrich 2000) parallel our expectations based on observations of what happened during the MWP and GIGTs and on the similarity in the rate of global warming measured so far compared with the rate of the MWP warming. This is both a cause for consolation and for great concern. The consolation is that interpretations of how global warming influences faunal dynamics are converging from many modern and fossil data sets. Therefore, predictions about how climate change will influence local biotic systems (changes in phenotype, relative abundance of taxa, extinction probabilities, etc.) are becoming increasingly robust. Furthermore, neither the faunal responses that currently are being reported nor the rate of warming so far measured (and we emphasize ‘‘so far measured’’) has yet exceeded what was normal for most of mammalian history. That means that we still have some more or less naturally operating mammalian communities within earth's ecosystems. Mammalian response to the current global warming episode probably is now within the 1st-order response noted above: adjusting phenotypes and minor adjustments in geographic ranges.

Concerns arise with the very high probabilities of continued rapid warming rates through the rest of this century and beyond (Houghton et al. 2001; Reilly et al. 2001; Schneider and Root 1998; Wigley and Raper 2001). Within a few decades, we can expect the rate of global temperature change to have exceeded the norm for mammalian history, even when interval length of measurement is taken into account. As Jackson and Overpeck (2000:193) astutely noted, this will present ‘‘unique challenges to the biota of the planet.’’ When that threshold is crossed, we predict that the 2nd-order response to climate change—extinction and dramatic geographic range changes leading to very different taxonomic compositions relative to what now exists in given localities—will accelerate rapidly. Extinction may well be elevated relative to past warming events, such as the MWP and GIGTs, especially in view of the other human-induced changes that have the net effect of habitat fragmentation on the one hand (various land uses) and homogenization of global biota on the other (introduction of exotic species). Speciation, the 3rd-order response, will not act to maintain diversity because it operates on a much longer time scale than the 1st- and 2nd-order responses.

Besides theoretical implications, our conclusions have an important practical aspect. Biotic systems are resilient within a certain range of rates in global temperature change over periods that are long relative to a human lifetime. We have not exceeded this range of normal rates yet. Thus, there is still hope of conserving natural landscapes that exhibit most of the climate-equilibrated ecosystem dynamics to which mammalian communities have adapted during their long evolutionary history. However, it also is clear that we are on the verge of exceeding the natural variation in rates of global temperature change as global warming continues into the next century. In this light, worldwide efforts to curb duration and acceleration of global warming are critical to conserving natural biotic systems, if ''natural'' is taken to mean conditions within the bounds of typical faunal response and climatic-change rates through the past 60 million years.

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