

DISTINGUISHING THE EFFECTS OF THE RED QUEEN AND COURT JESTER ON MIOCENE MAMMAL EVOLUTION IN THE NORTHERN ROCKY MOUNTAINS

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ABSTRACT—Red Queen hypotheses maintain that biotic interactions are the most important drivers of evolutionary change, whereas Court Jester hypotheses regard physical-environmental perturbations, such as climate change, as most important. Tests for the biotic effects of climate change that are conducted on too large a geographic scale can falsely reject the Court Jester because climate is so complex its manifestation is in opposite directions in different geographic areas. Consequently, faunal responses vary from place to place, and lumping of data from different climate zones averages out any local faunal responses. Likewise, tests that are conducted at inappropriate temporal scales will not be effective at distinguishing between the Red Queen and Court Jester.

A test at a temporal and geographic scale that takes the above considerations into account suggests a biotic response of mammals to a climatic warming event in the northern Rocky Mountains 18.5–14.0 Ma (the late-Early Miocene climatic optimum). During the environmental perturbation, mammalian species richness possibly increased, faunal turnover was pronounced, and taxa adapted to warm, arid environments became more abundant in numbers of species and density of individuals. The data are consistent with environmental change—the Court Jester—driving evolutionary change at sub-continental spatial scales and temporal scales that exceed typical Milankovitch oscillations. The Red Queen may be active at smaller temporal and geographic scales.

INTRODUCTION

Mammal species and communities have turned over on a repeated basis, witnessed by our ability to recognize at least 39 subdivisions of the Cenozoic based solely on composition of fossil mammal assemblages (Woodburne and Swisher, 1995). A rich literature debates whether this march of morphology and species compositions through time, so well documented not only for mammals but throughout the fossil record, is more strongly influenced by interactions among species (Red Queen hypotheses), or by random perturbations to the physical environment such as climate change, tectonic events, or even bolide impacts that change the ground rules for the biota (Court Jester hypotheses).

Macroevolutionary (Van Valen, 1973) and microevolutionary (Bell, 1982) versions of Red Queen hypotheses, named after Lewis Carroll's Red Queen (originally printed 1871, reprinted 1960 and in several other editions), have been widely discussed in the scientific literature (Lively, 1996). Red Queen hypotheses generally state that biotic interactions are more important than physical-environmental change in driving evolutionary change (see for example McCune, 1982; Kitchell and Hoffman 1991; Pearson, 1992; Vrba, 1993; Alroy, 1996, 1998; Clay and Kover, 1996; Ebert and Hamilton, 1996; Lively, 1996; Rosenzweig, 1996; Lythgoe and Read, 1998; Martin and Fairbanks, 1999; to name but a few).

A class of alternative ideas, here termed Court Jester hypotheses, share the basic tenet that changes in the physical environment rather than biotic interactions themselves are the initiators of major changes in organisms and ecosystems. Some of the more prominent ideas are listed in Table 1. Court Jester hypotheses imply that events random in respect to the biota occasionally change the rules on the biotic playing field. Accelerated biotic response (relative to background rates) is the result.

ANALYTICAL CONTEXT

The purpose of this paper is to explore why it is so difficult to sort between the relative importance of biotic versus abiotic

triggers to evolution, to discuss some scaling issues relevant to the problem, and to present new data on Miocene mammals to help decipher the roles of the Red Queen and Court Jester in evolution. Mammals have fared no better than evidence from any other taxonomic group as a system in which to test the relative influence of the Red Queen and Court Jester. For example, Van Valen (1973), Alroy (1996, 1998), Prothero and Heaton (1996), and Prothero (1999) all have presented evidence that environmental changes, notably climate change, did little to influence faunal turnover patterns in North America in various parts of the Cenozoic. Martin and Fairbanks (1999:44) used Plio-Pleistocene mammalian turnover patterns as support for a "weak" Red Queen. Yet Vrba (1985, 1992, 1993, 1995), Janis (1989, 1993, 1997), Janis and Wilhelm (1993), Webb et al. (1995), Webb and Opdyke (1995), and Barry et al. (1995) just as cogently cited certain groups of mammals in which aspects of evolutionary change correspond well with aspects of environmental change, notably climate and vegetation.

Why has the relative influence of the Red Queen and Court Jester proven so difficult to sort out, even when examined using similar kinds of data (fossil mammals) and at the same hierarchical level of biology (macroevolutionary patterns)? At face value, the procedure for recognizing the Red Queen's or Court Jester's manifestation with these kinds of data is straightforward: (1) postulate an aspect of environmental change that might influence evolutionary patterns; (2) specify how the environmental change would be expected to influence evolution in the taxa of interest, based on reasonable knowledge or inferences about life history traits; (3) document and date faunal patterns; (4) document the timing of the specified environmental change; (5) using appropriate techniques, determine whether the timing of the environmental change corresponds (or does not correspond) to appropriate aspects of the faunal patterns. Straightforward as this approach sounds, it is fraught with all the pitfalls inherent in working with paleontological data, and with potential methodological vagaries that can render generalizations nearly impossible. The paleontological-data problems include: uneven distribution of requisite fossils through time or space; insufficient information to adequately interpret paleoen-

TABLE 1. Examples of Court Jester hypotheses.

Hypothesis	General tenet and study system
Stationary model Stenseth and Maynard Smith (1984)	This model essentially arose out of a mathematical formulation that demonstrates that ecosystems are expected to approach one of two evolutionary modes. One of these is the Stationary Model: “evolutionary stasis, with zero rate of evolution and no extinction or speciation; evolutionary change occurs <i>only in response to changes in the physical environment</i> ” (italics mine) (Stenseth and Maynard Smith, 1984:870). The other plausible condition is the Red Queen model: “a steady state of change (even in a constant physical environment) characterized by continuing evolutionary change, extinction, and speciation.” (Stenseth and Maynard Smith, 1984:870). Thus, Stenseth and Maynard Smith demonstrated that both models are plausible from a mathematical perspective. Their formulation took into account Van Valen’s (1973) Red Queen hypothesis, MacArthur and Wilson’s (1967) theory of island biogeography, and the concepts of species packing and limiting similarity (MacArthur and Levins, 1964; May and MacArthur, 1972). The study system was theoretical.
Habitat theory (Vrba, 1992)	Changes in the physical environment (such as temperature, rainfall, substrate, food, and vegetation cover) in the habitat of a species drive evolutionary change. Seven hypotheses were presented about how species relate to their habitats, and biotic effects of (1) cyclic (Milankovitch-scale) climate change, (2) topographic diversity, (3) latitudinal distribution of speciation and extinction rates during times of climatic stability and (4) climatic cooling, (5) pulsed response of species to physical perturbations, (6) unusually long or intense climatic changes, and (7) how environmental variance affects generalist and specialist species. The model was based primarily on studies of fossil mammals and macroevolutionary theory.
Turnover-pulse hypothesis (Vrba, 1985, 1992, 1993, 1995)	The extreme version holds that <i>initiation</i> of lineage turnover (which includes speciation, extinction, immigration, and emigration) “. . . is exclusively physical Speciation does not occur unless forced by the physical environment . . . most lineage turnover in the history of life has occurred in pulses, nearly synchronous across diverse groups of organisms, and in predictable synchrony with changes in the physical environment. Most of these turnover-pulses are small peaks involving few lineages and/or restricted geographic areas. Some of them are massive and of global extent” (Vrba, 1993:428). “. . . not every lineage undergoes speciation or extinction even during extreme changes in the global environment. . . . Such differences between lineages may be causally influenced by intrinsic biological factors . . .” (Vrba 1993:431). The model derives primarily from studies of fossil mammals and macroevolutionary theory and was listed as one of the hypotheses (Hypothesis 5) in the Habitat Theory.
Traffic light model (Vrba, 1995)	Climatic changes open and close habitat corridors analogous to a biased traffic light that allows more traffic to move in one direction than another. Faunal turnover is therefore expected to be more dramatic in areas that are more frequently opened by a “green light” (Vrba, 1995:27-29). The model was based on studies of fossil mammals, Pleistocene climate change in Eurasia and Africa, and ecological theory.
Relay model (Vrba, 1995)	In response to climate change, “Lineages in contrasting habitat categories have new species starting up (by speciation) at displaced times and old species ending (by extinction) at differing times, rather like runners in a relay race” (Vrba, 1995:29). The model was based on studies of fossil mammals, Pleistocene climate change in Eurasia and Africa, and ecological theory.
Tiers of time (Gould, 1985; Bennett, 1990, 1997)	Based on observations of patterns in the fossil record, Gould (1985) hypothesized that evolutionary processes occur on at least three different scales. The first tier of time is the ecological scale (roughly tens to thousands of years), within which microevolutionary processes (mutation, recombination, selection, drift) and ecological interactions between individuals and populations (competition, predator-prey, parasite-host, etc.) take place. The second tier of time is the geological scale (millions of years), during which macroevolutionary processes such as species sorting occur. Evolution at this scale may or may not be related to physical-environmental changes. The third tier is represented by geologically infrequent catastrophes such as bolide impacts that dramatically change the physical environment and reset the ground rules for the biota. These events are separated by tens to hundreds of millions of years. Bennett (1990, 1997) added another tier, the cyclic climate changes caused by the Milankovitch orbital variations on the scale of ten thousand to hundreds of thousands of years. Bennett (1990, 1997) and Vrba (1992:8, 1993:422; 1995:27) noted that the most common response of species at this tier is to shift geographic ranges.
Coordinated stasis (Brett and Baird, 1995)	“Long-ranging associations of species or biofacies display very minor or no morphological change in most lineages of macrofossils . . . overall patterns of species richness, rank abundance, and guild structure are relatively constant for a particular biofacies” (Brett and Baird, 1995:307) “. . . In contrast, during geologically brief intervals—probably no more than a half million years in duration—major faunal changes occurred in many biofacies more or less simultaneously . . . There seems to be some relationship with major low stands of sea level . . .” (Brett and Baird, 1995:308). “. . . it seems likely that without the episodic perturbations [to the physical environment in the form of sea level changes] and collapse of stable ecosystems there would have been little movement in the history of life” (Brett and Baird, 1995:310). The model is based on empirical study of Silurian to Middle Devonian marine invertebrate macrofossils.
Coevolutionary disequilibrium (Graham and Lundelius, 1984)	Ecosystems develop complex interactions among species during times of environmental stability. Perturbations such as climate change remove keystone species and result in individualistic response of other species, causing ecosystems to significantly restructure. The model was developed from studies of the extinction patterns of late Pleistocene mammals, in an effort to ascribe a mechanism to that extinction event.

environmental changes; insufficient ability to reliably date environmental changes and/or faunal patterns; insufficient knowledge to predict how specified environmental changes might be expected to influence extinct (or even extant) taxa. In effect, these and other “data problems” affect steps 3, 4, and 5 enu-

merated above. Methodological vagaries tend to affect steps 1, 2, and 3, but can be minimized by specifying the kind of environmental change with as much precision as possible, the temporal and geographic scale over which the environmental change acts, the aspect of the biotic pattern (i.e., morphology,

diversity, speciation rate, extinction rate, etc.) that is hypothesized to respond (or not respond), and the mechanism that would link biotic response to the environmental change.

SCALING ISSUES

Climate proxy data are available in many forms through the geological record, and for that reason most studies that examine the interplay between environmental perturbations and mammalian faunal patterns focus on climate as the forcing function. Climate change is a complex phenomenon. To understand its effect on faunal patterns, the attribute(s) of climate postulated to affect the biota must be specified, a relevant geographic scale must be identified (as explained below), and the scale at which the biota is analyzed must be commensurate with the geographic scale and specified climatic attributes. In most previous studies, the global temperature curve indicated by oxygen- and/or carbon-isotope stratigraphies is compared to continental-level diversity patterns of terrestrial, non-volant mammals in North America or world-wide (Janis, 1993; Webb and Opdyke, 1995; Alroy, 1996, 1998; Prothero and Heaton, 1996; Prothero, 1999), or to diversity or phylogenetic patterns of selected groups with continent-wide distributions, most often large ungulates (Vrba, 1985, 1992, 1993, 1995; MacFadden and Hulbert, 1988; Janis, 1989; Janis and Wilhelm, 1993; Webb et al., 1995; Janis, 1997). These broad-scale studies have contributed a tremendous amount of useful information, even though they offer different conclusions about the role of physical perturbations in spurring faunal change, ranging from very little importance (Alroy, 1996, 1998; Prothero and Heaton, 1996; Prothero, 1999) to very great importance (Janis, 1989; Janis and Wilhelm, 1993; Van Valkenburgh and Janis, 1993; Vrba, 1993, 1995; Webb et al., 1995; Janis, 1997). The contradictory conclusions result in part from examining different scales of data, for example, focusing on certain orders of mammals or biogeographic provinces in one case and on all mammals and all provinces in another. Likewise, the climatic attributes and taxonomic attributes that are being compared in the various studies sometimes differ. For example, in some cases the correspondence between the global temperature curve and extinction and/or origination rates might be compared (Alroy, 1996, 1998), whereas in others the attributes of interest are immigration rates in response to climate change (Webb and Opdyke, 1995), or the response of morphological features such as digestive or locomotor adaptations to particular climatic events (Janis, 1989; Janis and Wilhelm, 1993; Van Valkenburgh and Janis, 1993; Webb et al., 1995; Vrba, 1995; Janis, 1997). Particular attributes of climate change and how they mechanistically might influence faunal change are treated at the level of generalities in some studies (Janis, 1989; Janis and Wilhelm, 1993; Webb et al., 1995; Alroy, 1996, 1998; Prothero and Heaton, 1996; Prothero, 1999), whereas they are more precisely specified in others (Vrba, 1993, 1995). Finally, yet other studies examine faunal change through particular, geographically restricted sequences, and compare the timing of change to varying-resolved local or global climate signals (Barnosky, 1993; Barry et al., 1995; Martin and Fairbanks, 1999).

Given that scaling and specificity constraints govern interpretations, what is the 'right' scale at which to study the relative importance of the Red Queen and the Court Jester? For studies that focus on interpreting the effects of climate change, the following considerations are important.

Climate Dynamics and Geographic Scale

A mean change in global temperature does not imply that all parts of the globe, or even one continent, change climatic attributes in the same direction and to the same degree. For example, Atmospheric General Circulation Models suggest that

with a doubling of atmospheric CO₂, aridity (measured as precipitation-evapotranspiration) and mean annual temperature would increase in some parts of the North America, while decreasing or changing little in other parts of the continent (Houghton et al., 1990). Such geographic variability means that detectable changes in a given climatic indicator assessed from the geologic record—such as global mean temperature—would be expected to affect the biota quite differently in different regions of a continent. Therefore, comparing changes in global mean temperature to changes in continental diversity patterns, for example, represents a mismatch in scale, even though both scales are "large". The expected result of such a comparison would be no evidence that climate change influences biotic patterns for the following reason. The set of taxa in one geographic region (for example, the Rocky Mountains) might experience and respond to an increase in mean temperature, while analogous taxa in a different climatic and biogeographic province (for example, in the eastern U.S.) simultaneously experience and respond to a decrease in mean temperature. Because the local climatic effect is in opposite directions, the net biotic response would be expected to be in opposite directions. Multiply this effect by many taxa and many geographic areas, and the "average" biotic response to climate looks like no response, even though in each geographic area there may be a clear effect. On the other hand, if the geographic scale drops to the level that encompasses only one direction of climatic response (e.g., a discrete "climate zone" such as the northern Rocky Mountains, or Colorado Plateau, or southeastern U.S.), the effect of space-averaging biotic responses becomes less of a problem. Vrba (1993:431) implicitly recognized such potential scaling problems in her elaboration of the Turnover-Pulse hypothesis: "... geographic factors may determine that global cooling causes extensive environmental changes in most localities, moderate changes in others, and none in some areas."

Evolutionary and Ecological Theory

A large body of evolutionary literature equates probability of speciation with size of geographic range (see, for example, references in Rosensweig, 1995). Basically, the larger the geographic range of a species, the more likely it will be to cast off new species given enough time because it is more likely that populations will become isolated. Isolation can occur through dispersal at the periphery of a range; larger geographic ranges have larger peripheries, thus increasing the probability of isolates. Isolation can also occur from vicariance events; larger ranges have a greater probability of being "cut" by a vicariance event simply because there is more area onto which to "vicariance knife" can fall (Rosensweig, 1995). Thus, climate change might be expected to increase speciation rates by either encouraging dispersal at peripheries of species ranges, or acting as a vicariance knife that fragments species ranges. An example of the latter would be the Great Basin, where mountaintops now contain "island faunas" that were more widespread during full and late-glacial times (Grayson, 1987; Macdonald and Brown, 1992).

Climate change causes vicariance events because some limits on a species' geographic range are defined by climatic parameters (e.g., Begon et al., 1990; Kareiva et al., 1993; Brown and Lomolino, 1998; Schneider and Root, 1998; Graham, 1999). These can be direct limiters, such as the metabolic cost of surviving through a cold winter or the inability to conserve enough moisture to survive in desert environments (Brown and Lomolino, 1998). Or, climate can limit ranges through an intermediary, such as limiting the vegetation that a mammal species needs for either food or shelter (for example, the association between sagebrush voles and clumps of sagebrush documented by Carroll and Genoways, 1980). By either pathway, a change

in an important climatic parameter would be expected to influence geographic range boundaries of some species. An increase in speciation rate might be detectable if there was a marked increase in range size; conversely, a decrease in speciation rate and/or increase in extinction rate would be expected if geographic range shrank past a critical limit. Increases in immigration rates might also be expected, as might increased extirpation, depending on the nature of the climate change.

Given this logic, climate change could reasonably be expected to produce a detectable change in faunal turnover, which combines speciation, extinction, immigration, and extirpation. However, in order to detect such changes (and in the best cases to sort between them), the geographic area of interest must be large enough to encompass much of the geographic ranges of the species under consideration. Typically, geographic ranges of most mammal species are subcontinental in extent (exceptions are ecological generalists in larger body-size classes, which can extend across much of a continent) (Hall, 1981). Coupling this constraint with the observation that a given climatic forcing produces changes of different direction on different parts of the continent, it follows that the optimal geographic scale on which to study the effects of climate change is a scale small enough to encompass only one major climate zone, but large enough to encompass a variety of species ranges. Examples of areas that fit this criterion would be the Pacific Northwest, the Great Basin, the Northern Rocky Mountains, the Central Rocky Mountains, the Northern Great Plains, the Southern Great Plains, and other areas of such magnitude.

Ecological theory also predicts that as certain climatic parameters change, they might give some species a competitive advantage over other species, resulting in individuals of the competitively favored species to become more abundant. Therefore, changes in relative abundance of individuals within species, and, scaling up, of species within higher taxa (i.e., perissodactyls vs. artiodactyls, or arviculines vs. sciurids), is also an expected response to climate change.

Competitive interactions can also lead to phenotypic change (e.g., character displacement), with or without speciation. Hence, if new climatic regimes bring closely related taxa into sympatry, phenotypic changes within populations may be evident. Further contributing to the potential for phenotypic change is ecophenotypic response. For example, as nutritional quality increases with a longer growing season, populations of species as diverse as pocket gophers (Patton and Brylski, 1987; Hadly, 1997) and big-horn sheep (Guthrie, 1984) demonstrate clearly detectable morphological manifestations.

Temporal Scale

Just as an individual must be able to withstand daily and seasonal variations in weather throughout its life span if it is going to survive and reproduce, a species must be able to withstand “normal” climatic variation that occurs over its lifespan if it is going to remain extant. The median life span of a mammalian species through the Cenozoic is about 1.5 million years (Alroy, 1996). Climate clearly varies considerably on a finer scale than that, most notably exemplified in the approximately 5°C mean global temperature fluctuations that occur on a 100,000 year cycle as a result of the Milankovitch orbital variations (Hays et al., 1976; Imbrie et al., 1993; Schneider and Root, 1998).

Milankovitch orbital variations are most clearly manifested for the Quaternary probably because the orbital parameters combined in a complex way with continental position, elevation, and geochemical feedbacks to finally produce clear glacial and interglacial cycles (Raymo and Ruddiman, 1992). However, the same orbital parameters very likely were effecting climate changes throughout the Cenozoic, albeit without the dramatic

effects of advancing and retreating continental ice sheets. If so, at a minimum, the “typical” mammalian species must have survived at least 10 to 15 Milankovitch cycles. In order for that to happen, a certain amount of resiliency with respect to this “normal” climate change must be built into a typical mammalian species. At the very least, the typical species must be able to track environmental change by migrating, as Vrba (1995) clearly recognized.

How does this resiliency get “built in”? Assume, as the punctuated equilibrium model does (Eldredge and Gould, 1972; Gould, 1982; Gould and Eldredge, 1993), that the speciation event occurs within the first one tenth of a species lifespan. If one favors gradualist models as the primary mode of speciation, the following argument is even more robust. That means that speciation takes place within about 150,000 years in a typical mammalian species. Within that 150,000 years, the probability is high (indeed, almost 100%) that at least one Milankovitch oscillation event will be spanned. If the species is not resilient to that event, it becomes extinct. If the newly formed species is resilient to the first Milankovitch event it encounters, it also will be resilient to all following events of similar or lesser magnitude and of about equal or longer frequency. Because these are the species that survive much longer than 150,000 years, they make up most of our fossil sample. This is because the chance of preservation is a function of the length of time the species survives to be sampled, holding abundance and all other taphonomic factors equal. Thus, it is unlikely that most mammal species in the fossil record will demonstrate an evolutionary response to climatic changes on the order of Milankovitch-cycle events.

This is not a new argument. Gould (1985), Bennett (1990, 1997), and Vrba (1992, 1993, 1995) noted that species must experience out of the ordinary perturbations to their physical environment to show an evolutionary response. The point is that in order to test for a clear biotic response to climate change that includes evolution and extinction, the most meaningful results will be found by focusing on climatic changes that are more pronounced than the typical Milankovitch-scale event.

TESTING THE RED QUEEN AND THE COURT JESTER

In order to test the importance of the Red Queen and Court Jester at the theoretically constrained scale discussed above, this study examines the effect of a specific climate change—global warming—at a temporal scale that exceeds the typical Milankovitch cycle. Response of mammals is examined in a restricted geographic area—the Northern Rocky Mountains (Fig. 1).

The global warming event took place in the late-Early Miocene, from 18.5 to 17 million years ago. The Atlantic $\delta^{18}\text{O}$ curve (Miller et al., 1987) (Fig. 2) demonstrates the Miocene was relatively cool from about 24 to 18.5 Ma, when this late-Early Miocene climatic optimum (Flower and Kennett, 1994; Flower, 1999) began. Although the Pacific $\delta^{18}\text{O}$ curve is less clear in demonstrating the warming event because sampling and correlation is not as good, it also documents warming at 17.5 Ma (Fig. 2). Estimates for the increase in global temperature during this time range from 1–5°C, with 3–4°C the most common (Buchardt, 1978; Woodruff et al., 1981; Miller et al., 1987; Zubukov and Borzenkova, 1990; Wright et al., 1992; Janis, 1993; Wolfe, 1994; Schoell et al., 1994) (Fig. 2). Peak warmth lasted about 2.5 million years (17–14.5 Ma). Thus, the Miocene global warming event was of different character than typical Milankovitch warming events, in that the warming trend was sustained over a much longer time (1.5 million years vs. at most a few thousand years), and resulted in a warm period that lasted on the order of millions rather than tens of thousands of years. It is very likely that typical Milankovitch oscillations continued through the late-Early Miocene climatic optimum; for example,

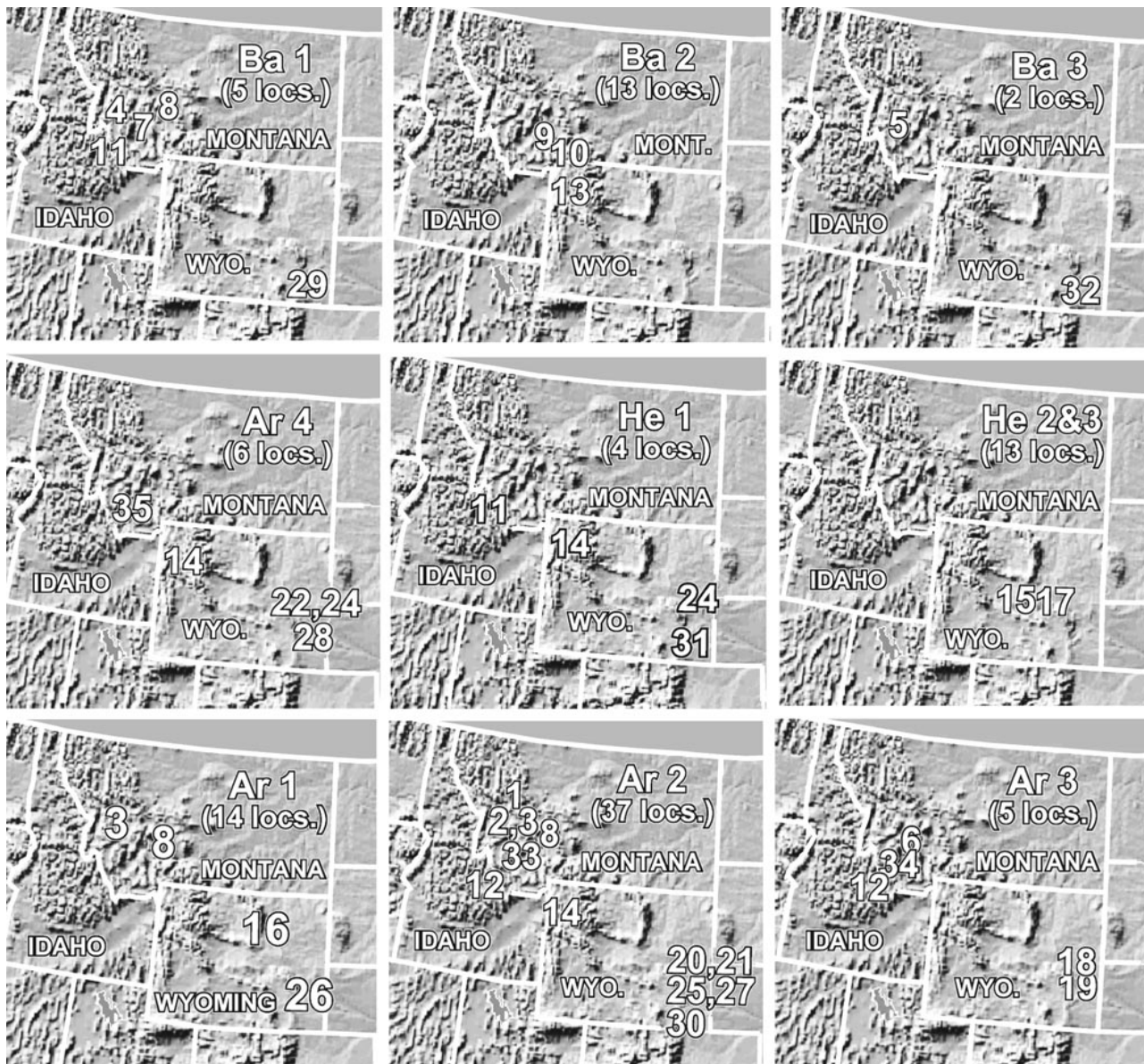


FIGURE 1. Geographic and temporal distribution of the collections that provided the data for this study. Numbers show where collecting areas occur (some collecting areas are represented by the same number if they are geographically too close to separate on these small maps). Some collecting areas contain multiple localities. A "locality" is here considered a restricted stratigraphic horizon or outcrop that has produced abundant specimens. **Abbreviations:** **Ar**, Arikareean; **He**, Hemingfordian; **Ba**, Barstovian; **Cl**, Clarendonian; **locs.**, localities. See Figure 2 for correlation of the biochronologic units with the radiometric timescale. Names of collecting areas are as follows (when a collecting area contains multiple localities, the number of localities is given in parentheses): 1, Canyon Ferry; 2, Tavenner Ranch (in general equates to Middle/Upper Cabbage Patch); 3, Lower Cabbage Patch (11 locs.) and Middle/Upper Cabbage Patch including Tavenner Ranch (25 locs.); 4, Flint Creek; 5, Johnson Gulch; 6, North Boulder; 7, McKanna Spring; 8, Fort Logan (Ar1), Spring Creek 1 (University of Washington Burke Museum [UW] loc. A5867-1, Ar2), Spring Creek 2 (UW loc. A5867-2, Ba1); 9, Anceney; 10, Hepburn's Mesa (9 locs.); 11, Upper Railroad Canyon, Mollie Gulch; 12, Peterson Creek (3 Ar2, 1 potentially Ar3 locs.); 13, Barstovian Colter faunas (North Pilgrim 2, Cunningham Hill, Two Ocean Lake); 14, Arikareean and Hemingfordian Colter faunas (East Pilgrim 5 [He1], East Pilgrim 11 and Saunders Locality [Ar4], Emerald Lake [Ar2]); 15, Split Rock (12 locs.); 16, Darton's Bluff; 17, Devil's Gate; 18, Lower Van Tassel; 19, Raw Hide Buttes; 20, Little Muddy Creek; 21, Willow Creek; 22, Royal Valley; 23, Keeline; 24, Lay Ranch (Ar4) and Jay Em (He1); 25, Bear Creek Mt. East; 26, Lower Sixty-six Mt.; 27, Upper Sixty-six Mt.; 28, Sixteen Mile District; 29, Joe's Quarry; 30, Tremain; 31, Horse Creek; 32, Trail Creek; 33, Woodin; 34, Blacktail Deer Creek; 35, Grasshopper Creek. See Table 2 for a summary of numbers of collecting areas and numbers of localities per time interval. Physiographic base map is modified from Sterner (1995).

between 18.5 and 17.0 million years, the average warming rate of 2°C/Ma embedded at least three cold excursions (Woodruff et al., 1981).

The spatial scale in this study is defined by the Rocky Mountain region of Wyoming, Montana, and Idaho (Fig. 1). Today,

this area of the Northern Rockies typically is recognized as falling largely within one major climate zone (the Highland zone [Brown and Lomolino, 1998]) and is characterized by reasonably similar mean temperature and precipitation in January and July (World Meteorological Organization, 1979). There-

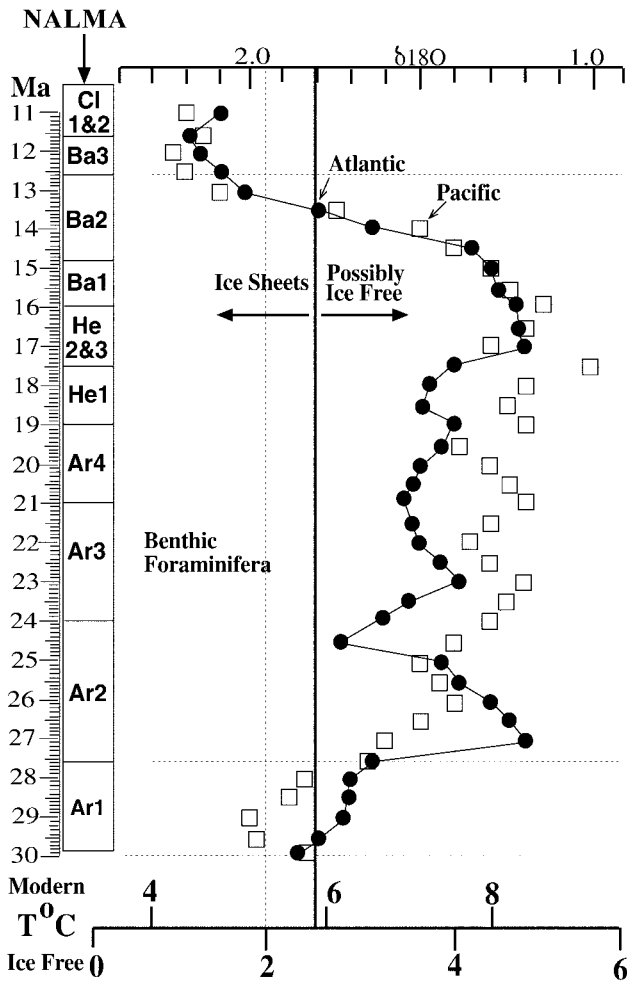


FIGURE 2. Correlation of Land-mammal Ages, radioisotopic chronology (Woodburne and Swisher, 1995), and Miocene oxygen isotope curve (redrawn from Miller et al., 1987). Black dots on the oxygen isotope curve give representative values for benthic foraminifera recovered from cores in the Atlantic Ocean; open boxes indicate values for the Pacific. Because isotopic values depend on both temperature and global ice volume, the temperature scale (T) shows estimates for times when ice volume was high (top "Modern" scale) and low (bottom "Ice-Free" scale). Isotopic values that generally indicate ice-free conditions are on the right side of the vertical line, whereas values typical of high ice volume are on the left side of the line. Note that generally ice-free conditions probably characterized most of the time interval discussed in this paper. **Abbreviations other than those noted in Figure 1:** Ma, megannum; Cl, Clarendonian; NALMA, North American Land Mammal Age.

fore, it is reasonable to suspect that on average, the climatic implications of warming temperature $\sim 3^{\circ}\text{C}$ would be more or less uniform over most of the study area today. While Miocene climate patterns are not well known, paleogeography was similar enough to the present to expect that the study area would have represented a discrete climate zone then as well. Similarly, the present assemblage of northern Rocky Mountain mammal species is distinct from areas to the west, east, south, and north (Hall, 1981), and at least some evidence indicates this distinctiveness in biotic province has persisted (with some minor modifications) since at least Miocene time (Barnosky, 1986).

Within the study area, the Miocene climatic optimum is marked by a warm, relatively wet (but still arid) time between 19 and 17 million years ago, followed by increasing aridity

(presumably indicating a peak in warmth) from 17 to 14 million years ago as interpreted from geochemical, geomorphological, and geological data (Thompson et al., 1982; Barnosky and LaBar, 1989). A Mid-Tertiary unconformity regionally separates 30–18 million-year old (Arikareean and early Hemingfordian Land Mammal Age) deposits from those 17–14 million years old (late Hemingfordian and Barstovian Land Mammal Age) (Fields et al., 1985; Barnosky and LaBar, 1989; Burbank and Barnosky, 1990). It is unclear whether the unconformity developed in response to climate change, tectonic uplift, or some combination of both. In any case, the presence of the Mid-Tertiary unconformity makes it possible to place fossils as older or younger than the local and global warming event independent of biostratigraphic dating. Paleomagnetic or radiometric dating also was used when possible to calibrate the age of fossil assemblages (Fields et al., 1985; Burbank and Barnosky, 1990; Woodburne and Swisher, 1995).

Methods

Taxonomic lists of Miocene (Arikareean through Hemphillian) mammals that occurred within 200 km of the mountainous areas of Montana, Idaho, and Wyoming were compiled from the primary literature and field collections (those largely made by me and deposited in University of California Museum of Paleontology and Carnegie Museum of Natural History). Localities were assigned ages based on stratigraphic position relative to the Mid-Tertiary unconformity, paleomagnetic dating, potassium-argon or argon-argon dating, and biostratigraphic correlation, as determined from the primary literature and my experience collecting in the region. This combination of data generally allowed placing localities with a reasonable degree of confidence into one of the following biochronologic intervals: Arikareean (Ar) 1, Ar2, Ar3, Ar4, Hemingfordian (He) 1, He2&3, Barstovian (Ba) 1, Ba2, Ba3 (Woodburne and Swisher, 1995) (Figs. 1, 2). Lack of chronologic resolution requires that fossils from intervals He2 and He3 be lumped for the purposes of this study. However, this is appropriate since the temporal interval for the lumped He2&3 is as short or shorter than that of most of the other biochronologic intervals (Fig. 2). The taxonomic lists were cross-checked against compilations of other authors (Alroy, 1999; Janis et al., 1998) and discrepancies resolved as appropriate. The resulting data set includes 99 localities distributed through 38 general collecting areas (Fig. 1), and a total of at least 381 species. Data are available from the author upon request, and also are on file at the UCMP.

The warming event is recognized by data independent of the mammalian record as described above. Warming begins in the latter half of He1, continues into the lower part of He2&3, and then maximum warmth lasts into the early part of Ba2. Therefore, if climate change resulted in biotic response, the response should be near the boundary between He1 and He2&3. Because all of the biochronologic boundaries are defined on faunal change, a faunal change by itself does not implicate climate change. To do so, the faunal response should have a different, more pronounced signature at the climatic boundary (between He1 and He2&3). Moreover, the character of the fauna after the climatic warming (e.g., the fauna of He2&3 through Ba2) should be substantially different than the general character before the climate change (Ar3, Ar4, and He1).

In order to ascertain any faunal differences between the pre- and post-warming time intervals, three major attributes of the fauna were examined: species richness, faunal turnover, and relative abundance of selected ecologically distinct taxa (in terms of number of species within families and abundance of individuals within species). Species richness was examined in three ways: by comparing raw numbers of species in each time interval, standardizing number of species in each interval to spe-

TABLE 2. Species richness and Survival Index (SI) per time interval. Maximum total of species considers indeterminate species as separate species; minimum total of species considers indeterminate species as belonging to one of the other species identified for a given genus. Species per million years and SI are calculated using the minimum total species. The SI shows the proportion of species that extend from the given interval into the next higher interval (see Methods section for further explanation). Adding species for Mountain and Adjacent Plains data does not exactly equal the Total Data set because of the effects of combining indeterminate species when considering data sets separately.

Biochronologic unit	Ar1	Ar2	Ar3	Ar4	He1	He2&3	Ba1	Ba2	Ba3
Duration of interval (10 ⁶ yrs.)	2.2	3.6	3	2	1.5	1.5	1.2	3.2	1
Total data set									
Maximum total species	53	86	45	24	23	53	35	84	19
Minimum total species	44	78	45	23	22	46	32	70	19
Number of species per million years	20	21.7	15	11.5	14.7	30.7	26.7	21.9	19
Species surviving to next interval	19	6	8	10	0	7	9	1	—
Survival index (SI)	0.43	0.08	0.18	0.43	0	0.15	0.28	0.01	—
Total localities	14	37	5	6	4	13	5	13	2
Total general collecting areas	4	9	5	5	4	1	5	3	2
Mountain data set only									
Maximum total species	49	55	19	4	8	53	30	84	7
Minimum total species	40	54	19	4	8	46	30	70	7
Number of species per million years	18.2	15	6.333	2	5.3	31	25	21.9	7
Species surviving to next interval	17	3	1	1	0	4	9	0	—
Survival index (SI)	0.43	0.06	0.05	0.25	0	0.09	0.30	0	—
Total localities	13	32	3	3	2	13	4	13	1
Total general collecting areas	3	6	3	2	2	1	4	3	1
Adjacent plains data set only									
Maximum total species	4	33	27	21	17	0	5	0	12
Minimum total species	4	33	27	20	17	0	5	0	12
Number of species per million years	1.8	9.17	9	10	11	—	4.2	—	12
Species surviving to next interval	0	2	9	8	—	—	—	—	—
Survival index (SI)	0	0.06	0.22	0.40	—	—	—	—	—
Total localities	1	5	2	3	2	0	1	0	1
Total general collecting areas	1	3	2	3	2	0	1	0	1

cies per million years (the quotient of how many species are present in each interval, divided by the length of the interval), and by employing regression, bootstrap and rarefaction analyses to identify the relationship between numbers of identified specimens (NISP) and numbers of identified species (Colwell and Coddington, 1994; Colwell, 1997). Taxonomy follows assignment of authors who reported specimens from the sites listed in Figure 1; in general, the species reflect a morphological species concept. As a crude index of faunal turnover, a survival index (SI) was determined as $SI = (\text{Survivors}/\text{Species Pool})$, where 'Survivors' is the number of species surviving across an interval boundary (i.e., from Ar3 into Ar4), and 'Species Pool' is the number of species found in the lower interval (Ar3 in this example). SI basically measures the proportion of species that persist across temporal intervals: the higher the SI, the more species persist from one interval into the next. Statistics were calculated using Stratview 5.0, Microsoft Excel, and EstimateS 5 (Colwell, 1997).

Results

Species Richness—Table 2 compares the raw numbers of species found in each time interval. A strong correlation exists between species richness and interval of time over which the sample potentially accumulated (Fig. 3A), indicating standardization of the data to species per million years is warranted. Per million year richness peaked during He2&3, and remained elevated through Ba1, at first glance suggesting that an increase in Rocky Mountain mammal standing diversity coincided with the warming event (Table 2). Ecologically, this is consistent with ideas that suggest that diversity increases as a function of net primary productivity (up to a point, after which diversity decreases) (Rosenzweig, 1995). With increasing temperature, NPP generally increases, as long as effective precipitation does not fall below critical levels (Brown and Lomolino, 1998).

However, measures of species richness are strongly depen-

dent on sampling and analytical method (Tipper, 1979; Siegel and German, 1982; Colwell and Coddington, 1994; Rosenzweig, 1995; Colwell, 1997). Is the peak richness observed in He2&3 simply an effect of sampling bias? Given equal time-averaging, two major sampling effects can influence species richness: number of geographic areas that are sampled (more geographic areas correlate with higher species richness), and number of specimens in the sample (more specimens equal more richness, up to a point). Of all of the time intervals considered in this study, He2&3 is represented by the fewest geographic areas: one area in the middle of Wyoming (Fig. 1). Therefore the peak in species richness during He2&3 is not from accumulating species from different sampling areas. Subdividing the data into two geographic groupings within the study area further supports this conclusion (Fig. 1, Table 2). In general, Ar1–4 are well represented by sites within the core of the mountainous area, plus those located on the eastern periphery of the mountain front ("Adjacent Plains" in Table 2). He2&3 and Ba1, however, with the highest per-million-year richness values, are known mainly from core mountain sites only. All else being equal, the greater per million year species richness in the mountains during Ba1 as compared to Ar2 and Ar3 could be due to increased endemism within the mountains proper, because geographic sample coverage in the respective time intervals is similar there.

Assessing the effects of sample size is not straight-forward. One proxy for sample size is number of localities that were collected. By this measure, it is impossible to discount sampling effects as the cause of the diversity peak at He2&3 (Fig. 3B). Numbers of identifiable specimens (NISP) provide a more direct measure of sample size, but the data are not available for all of the localities. Localities for which adequate data were available included Lower (Ar1) and Middle/Upper Cabbage Patch (Ar2) (Rasmussen, 1977), Peterson Creek (Ar2) (Nichols, 1976, 1979), Split Rock (He2&3) (Munthe, 1988 and references

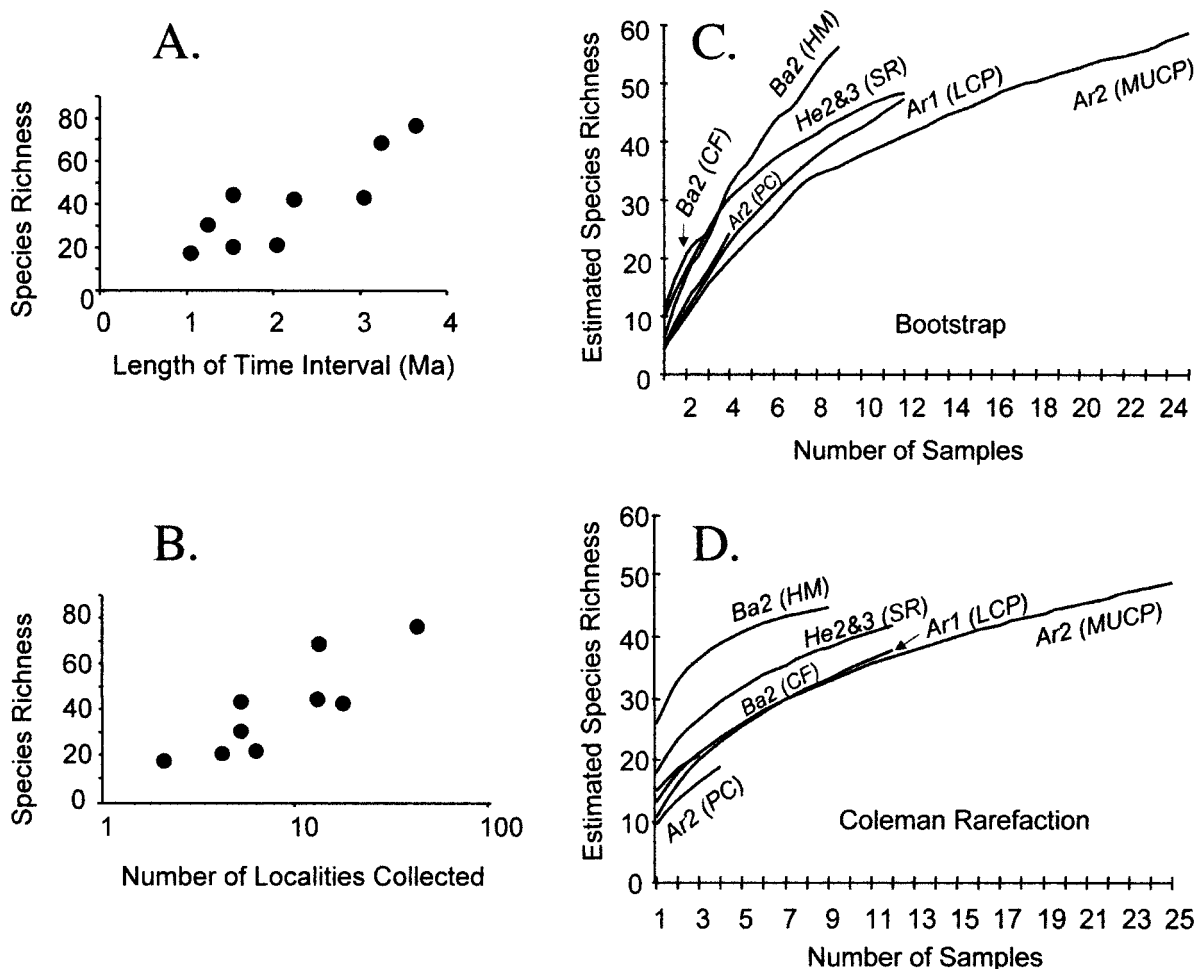


FIGURE 3. Species richness as a function of (A) the maximum time potentially spanned by the samples; (B) the number of localities (on a log scale) at which specimens were collected; and (C and D) the number of identified specimens (NISP) in pooled numbers of samples. The bootstrap (C) and rarefaction (D) curves are statistical estimators of species richness (Coleman, 1997) constructed by selecting a single sample from a specified collecting area, computing richness estimators, then selecting a second sample, adding it to the first, recomputing estimators for the pooled sample, and so on until all samples in the matrix are included. The process was repeated 50 times, with sample order randomized each time. Note that the relative position of curves from the different localities closely corresponds to the NISP of the pooled samples and the number of samples composing the pool, with higher NISP and fewer samples equating with higher, steeper curves. Mean NISP per sample is as follows. Ba2, Hepburn's Mesa, 149.7; Colter 70.3. He2&3, Split Rock, 94.9. Ar1, Lower Cabbage Patch, 23.5; Ar2, Middle/Upper Cabbage Patch, 17.7. Peterson Creek, 16.8. **Abbreviations:** CF, Barstovian Colter faunas; HM, Hepburn's Mesa; LCP, Lower Cabbage Patch; MUCP, Middle/Upper Cabbage Patch; PC, Peterson Creek; SR, Split Rock.

therein, plus UCMP specimen database), Colter faunas (Ba2) (Barnosky, 1986), Hepburn's Mesa (Ba2) (Burbank and Barnosky, 1990, plus unpublished Carnegie Museum collections), and Ancney (Ba2) (Sutton, 1977; Sutton and Korth, 1995) (Fig. 4). For these localities NISP was considered an estimate of number of individuals and used in algorithms of Colwell (1997) to calculate rarefaction and bootstrap estimates of species richness for Ar1, Ar2, He2&3, and Ba2. In interpreting the curves (Figs. 3C, D, 5A, B), it is important to note that NISP clearly overestimates the numbers of individuals sampled and therefore affects the shape of the curves. However, this bias is constant for all of the localities. Although it would not be valid to compare these curves to those produced from accurately sampling individuals from a modern fauna, the curves do provide interesting estimates of species accumulation for the respective paleontological samples. The major trends in Figure 3C and D suggest that the He2&3 localities are more species rich than the Ar1 or Ar2 ones, and that the Ba2 faunas are probably the most species rich (i.e., steeper species accumula-

tion curves and higher y-intercepts). Sampling biases prevent these curves from being taken at face value, however. The relatively low Coleman rarefaction estimate for the Ba2 Colter faunas (Fig. 3D) probably is because the localities include mainly screen-washing sites; thus large-bodied species are not well represented in the sample. Likewise, the low rarefaction value for Peterson Creek (Fig. 3D) probably reflects that only surface collecting built the sample. For all other localities, a combination of screen-washing and surface collecting was used to collect the samples, so collection bias probably is not a problem in comparing them. But these results may be very strongly biased by unequal sample sizes and sample numbers. The relative position and shape of the curves strongly corresponds with total number of specimens (NISP) in the pooled samples (Fig. 3C, D).

In an attempt to remove sample size bias, locality-by-locality species richness of the three time periods also was compared by plotting species richness against logNISP for spatially and temporally discrete localities (Fig. 4). The slopes derived for

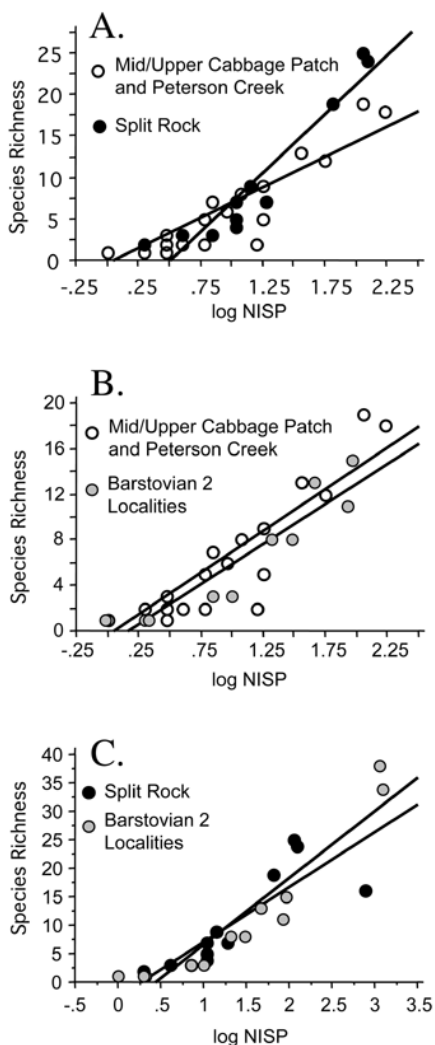


FIGURE 4. Species richness as a function of the log of the number of identifiable specimens (logNISP). **A.** Middle/Upper Cabbage Patch plus Peterson Creek (Ar2) compared to Split Rock (He2&3) localities that contain comparable numbers of specimens (i.e., NISP<200). **B.** Middle/Upper Cabbage Patch plus Peterson Creek (Ar2) compared to Hepburn's Mesa plus Barstovian Colter localities (Ba2) that contain comparable numbers of specimens (i.e., NISP<200). **C.** Split Rock (He2&3) compared to Ba2 localities (Hepburn's Mesa, Barstovian Colter, Anceney) including very large samples (NISP approaching 1,400). The slopes for the Split Rock and Barstovian regression lines in panel C are significantly steeper than the slope for Middle/Upper Cabbage Patch plus Peterson Creek lines in panels A and B. The Split Rock line shown in panel A also is significantly steeper than the Cabbage Patch plus Peterson Creek line. However, when the analysis is confined to NISP<200, the slope of the Barstovian line does not differ significantly from that of the Middle/Upper Cabbage Patch plus Peterson Creek sample as shown in panel B. Regressions for Lower Cabbage Patch (Ar1) samples are not shown, but do not differ significantly from the Ar2 samples. Equations for the illustrated regression lines are as follows. Ar2 Richness (Middle/Upper Cabbage Patch plus Peterson Creek) in panels A and B = $-0.446 + 7.326(\log \text{ NISP})$, $R^2 = 0.836$. He2&3 Richness (Split Rock) in panel A = $-7.37 + 14.265(\log \text{ NISP})$, $R^2 = 0.897$; in panel C, He2&3 Richness = $-2.595 + 9.616(\log \text{ NISP})$, $R^2 = 0.694$. Ba2 Richness (Hepburn's Mesa plus Barstovian Colter) in panel B = $-1.208 + 7.043(\log \text{ NISP})$, $R^2 = 0.877$; in panel C, Ba2 Richness (Hepburn's Mesa, Barstovian Colter, plus Anceney) = $-5.168 + 11.678(\log \text{ NISP})$, $R^2 = 0.882$.

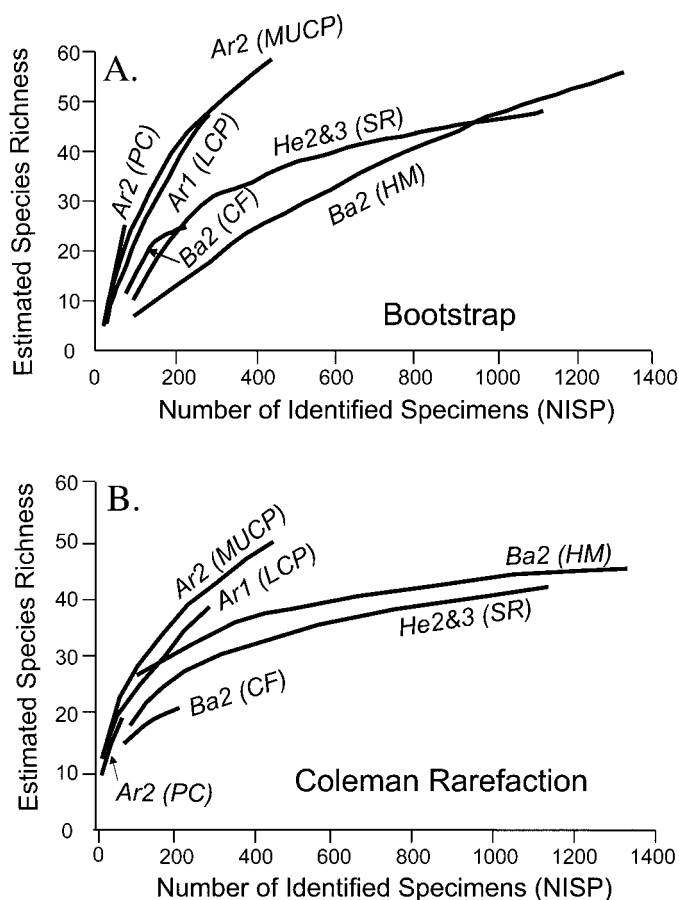


FIGURE 5. Estimated species richness as a function of number of identified specimens (NISP). The bootstrap (**A**) and rarefaction (**B**) estimates were computed as described for Figure 3. Abbreviations as in Figure 3.

Ar1 and Ar2 data do not differ significantly. The slope of the He2&3 sample (Split Rock) is significantly steeper (i.e., outside the 95% confidence band) than that of the Ar2 sample (Upper/Lower Cabbage Patch and Peterson Creek), indicating higher richness with a given NISP between about 30 and 200 specimens (Fig. 4A). The slope and mean of the Ba2 curve (Colter, Hepburn's Mesa) do not differ from those of the Ar2 curve for NISP up to about 200 specimens (Fig. 4B). However, when NISP approaches 1000 (which adds Anceney to the Ba2 dataset and anthill localities to the Split Rock dataset), the Ba2 curve steepens such that it is statistically indistinguishable from the He2&3 curve (Fig. 4C). These data support that species richness is highest during He2&3 for localities that have between 30 and 200 specimens, and Ba2 might be richer than Ar1 and 2. However, we do not know how the Arikareean analyses would behave if localities with >200 specimens were discovered and added to the dataset.

To further examine the effect of sample size on locality-by-locality species richness, bootstrap and rarefaction estimates of richness were plotted against sample sizes as averaged from 50 randomizations of sample order (Colwell, 1997). This analysis suggests that the Hemingfordian and Barstovian localities may in fact be less species rich than the Arikareean ones (Fig. 5). Why is this result so different from the locality-by-locality counts (Fig. 4)? The plots in Figure 5 were constructed by successive pooling of individual samples. Thus, the steepness of the curves reflects how many new species are added to the pool

with each new sample. New species will be added quickly and the curve will remain steep if the successive samples come from strata of widely differing age (reflecting evolutionary change as well as new taxa added by immigration) or different environments (pooling ecological assemblages). The Ar1 and Ar2 Cabbage Patch samples potentially span up to 2.2 and 3.6 million years, respectively, though probably somewhat less (Rasmussen, 1977). In contrast, the He2&3 and Ba2 samples temporally pool a maximum of only 1.5 and 1.2 million years, respectively, and probably span less (Sutton, 1977; Barnosky, 1986; Barnosky and LaBar, 1989; Burbank and Barnosky, 1990). Therefore the steepness of the Ar1 and Ar2 curves (Fig. 5) may simply reflect more time-averaging of samples used to construct the curves. The locality-by-locality NISP-richness comparisons (Fig. 4) do not suffer from this potential bias, because the comparison is simply of the numbers of species that occur at single, stratigraphically and spatially discrete localities, without pooling samples. For this reason, the results demonstrated in Figure 4 (increased He2&3 richness) seem less affected by sampling problems and therefore more robust than the bootstrap and rarefaction comparisons with NISP (Fig. 5). Unfortunately, requisite data do not yet exist for NISP-based comparisons of richness in Ar3, Ar4, and He1, which would be necessary to definitively rule out that the change in species richness took place during one of these time intervals. This does not seem likely, however, based on the per-million-year species richness estimates discussed above.

Clearly, the definitive determination of species richness with the available data is a complex issue, the resolution of which requires more fossils and more work. However, the salient point for this paper is that no matter what technique has been tried, richness in He2&3 appears different than that in Ar1 through He1, and Ba1 and Ba2 richness closely approximates that of He2&3. The shift to greater richness (if we believe the per-million year estimates of Table 2 and the locality-by-locality comparisons of Fig. 4) or lesser richness (if we believe Fig. 5) took place between Ar2 and He2&3, and most likely between He1 and He2&3.

Survival Index—The SI (Table 2) varies inversely with the difference in species richness between the lower and upper stratigraphic intervals that are being compared (until the upper-interval species richness is at least equal to the lower-interval one) (Fig. 6). This relates to probability theory, but intuitively is easy to understand because if the lower stratigraphic interval has many more species than the higher one, there is a high probability that a randomly drawn species from the higher stratigraphic interval also will be represented in the lower interval. The more higher-interval species that are also present in the lower interval, the higher the SI. Conversely, if the lower stratigraphic interval has many fewer species than the higher one, there is a high probability that a randomly drawn species from the higher stratigraphic interval will be new, which depresses the SI. Strong deviations from the theoretical curve predicted by this relationship should highlight times when survival of species across interval boundaries was elevated (abnormally low faunal turnover) or depressed (abnormally high faunal turnover) relative to background rates. Figure 6 and Table 2 indicate that an anomalously low SI occurs at the transition from He1 to He2&3, coincident with the late-Early Miocene climatic warming event. An anomalously low SI also characterizes the Ar1 to Ar2 transition for the Adjacent Plains dataset, coincident with an earlier warming event (Fig. 2), but disappears when SI is based on the entire dataset. Therefore apparent faunal turnover at the He1–He2&3 transition for the whole study area was more extreme than between any other two time intervals.

In addition to extinction of pre-existing species, immigration and speciation probably contributed to the elevated faunal turnover across the He1–He2&3 boundary. The two largest mam-

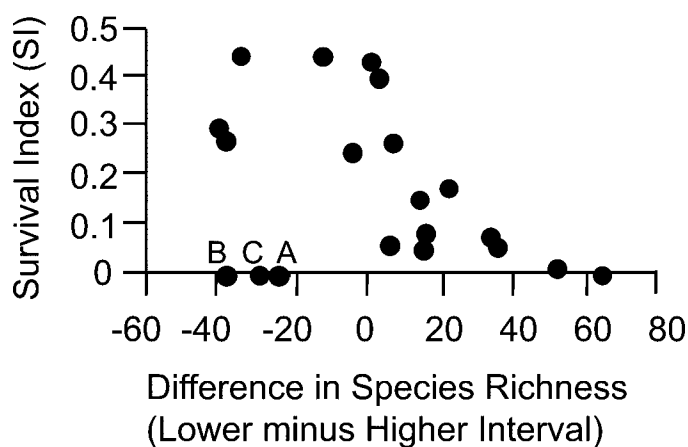


FIGURE 6. Survival Index (SI) as a function of the difference between species richness in adjacent stratigraphic intervals. The difference in species richness is computed as (species richness in the lower stratigraphic interval)—(species richness in the upper stratigraphic interval). Data are from Table 2. Abbreviations: A and B designate the points for the transition between He1 and He2&3 in the entire dataset and the Mountain dataset, respectively; C denotes the transition between Ar1 and Ar2 for the 'Adjacent Plains' dataset. See text for further explanation.

mal interchange events of the entire Miocene took place during He1 (between 18.5 and 19 Ma) and He2 (ca. 17.2 Ma) (according to Woodburne and Swisher, 1995, who distinguish He2 from He3; but note that these two intervals must be lumped into one interval [He2&3] in the present paper for reasons explained in the methods section). Given the uncertainty in correlations, the He1 immigrations conceivably took place as the global warming event commenced. At least four (*Angustidens*, *Oreolagus*, *Leptarctus*, *Aletomeryx*) of the 15 He1 immigrant genera and three (*Petauristodon*, *Mionictis*, *Plionictus*) of the eight He2 immigrants appear in the study area first after inception of the warming event (i.e., during He2&3, Ba1, or early Ba2). Speciation certainly contributed to the equation as well, in taxa ranging from horses to rodents. For instance, MacFadden and Hulbert (1988) showed that cladogenesis of grazing horses initiated at about 18 Ma, peaking near 16 Ma. In the study area, heteromyine rodents increase from zero or one species prior to the warming, to a minimum of five species during He2&3, to a minimum of 11 species during the earliest part of Ba2. Thus, inception of accelerated cladogenesis must have occurred near 17.5 Ma, with a peak between 15 and 16 Ma in both of these groups.

Relative Abundance—Changes in relative abundance were dramatic across the warming interval. For example, during He2&3, heteromyine species increase in number as noted above, and also begin to dominate the rodent fauna in numbers of individuals (Table 3). Concurrently, the ungulate component of the fauna flipped from primarily oreodontids prior to He1 to primarily equids during He1 through Ba3. The artiodactyl fauna decreases in oreodontids relative to camelids and antilocaprids correlative with the warming trend.

All of these faunal changes are consistent with increasing abundance of taxa adapted to warmer, more arid environments. Heteromyine rodents today are known primarily from desert environments. The change in the perissodactyl and artiodactyl faunas, at the morphological level, is from browsers with low-crowned teeth to grazers or mixed feeders with higher-crowned teeth. Generally, grazers occupy open habitats characteristic of arid to semi-arid environments. An increase in the relative pro-

TABLE 3. Number of species and number of identified specimens (NISP) in selected families. Number of species is calculated from combining all localities. NISP represents the total per time period for the following selected localities: Ar1—Lower Cabbage Patch; AR2—Middle/Upper Cabbage Patch and Peterson Creek; He2&3—Split Rock; Ba2—Colter faunas, Hepburn's Mesa, and Anceney. No entry for NISP means that adequate abundance data were unavailable for those time periods. See text for listing of publications and museum collections used in compiling NISP. A single specimen of the heteromyine rodent *Mookomys* reported for Ar2 by Rasmussen (1977) here is considered to represent one of the many geomyids in the Cabbage Patch fauna.

Bichronologic unit	Ar1	Ar2	Ar3	Ar4	He1	He2&3	Ba1	Ba2	Ba3
Number of species: all localities									
Non-heteromyine Geomyid species	2	8	2	1	1	1	1	4	0
Heteromyine species	0	0	0	0	0	5	0	11	1
Rhinocerotid species	1	2	1	3	1	2	2	1	1
Equid species	3	2	1	1	3	3	6	3	6
Oreodontid species	9	20	13	10	5	3	5	1	1
Antilocaprid species	0	0	0	0	0	3	3	1	2
Camelid species	1	2	4	2	3	6	2	1	2
Ratios of species in higher taxa									
Heteromyines/other Geomyoids	0	0	0	0	3	5	0	2.75	—
Rhinocerotid/Equid	0.33	1	1	3	0.33	0.67	0.33	0.33	0.17
Antilocaprid/Oreodontid	0	0	0	0	0	1	0.6	1	2
Camelid/Oreodontid	0.11	0.1	0.308	0.2	0.6	2	0.4	1	2
Oreodontid/Equid	3	10	13	10	1.67	1	0.84	0.33	0.17
NISP: Representative localities									
Non-heteromyine Geomyid specimens	0	183	—	—	—	4	—	249	—
Heteromyine specimens	0	0	—	—	—	88	—	939	—
Rhinocerotid specimens	2	3	—	—	—	7	—	3	—
Equid specimens	0	7	—	—	—	12	—	47	—
Oreodontid specimens	9	11	—	—	—	5	—	2	—
Antilocaprid specimens	0	0	—	—	—	18	—	8	—
Camelid specimens	0	0	—	—	—	8	—	18	—
Total NISP for all taxa	282	509	—	—	—	1,139	—	2,261	—
Ratios of NISP in higher taxa									
Heteromyines/other Geomyoids	—	0	—	—	—	22	—	3.77	—
Rhinocerotid/Equid × 100	—	43	—	—	—	58	—	6	—
Antilocaprid/Oreodontid × 10	0	0	—	—	—	36	—	40	—
Camelid/Oreodontid	—	—	—	—	—	16	—	90	—
Oreodontid/Equid × 10	—	15.7	—	—	—	4.17	—	0.43	—

portion of such habitats would be expected under warming scenarios in the northern Rockies.

DISCUSSION AND CONCLUSIONS

Although additional data from Ar3, Ar4, and He1 are desirable to strengthen conclusions, the case study presented here is consistent with physical-environmental change—sustained climatic warming in this case—being very important in triggering ecological and evolutionary change. Changes in species composition, species richness, faunal turnover, and relative abundance of species within families and individuals within species apparently coincided with climatic warming that began in the northern Rockies about 18.5 Ma and peaked around 17 Ma. Mechanistically, all of the changes in the mammals are consistent with what ecological and evolutionary theory would predict from warming the northern Rockies by a few degrees C. Likewise, all of the changes are consistent with such Court Jester models as the Habitat Theory and Turnover Pulse models (Vrba, 1995), but do not fit expectations of a Red Queen-dominated system, which would require no more biotic change at the global warming event than at boundaries between other land-mammal ages that were considered.

This consistency very likely reflects that the study took place at the geographic and temporal scale where Court Jester effects are most likely to be evident: at a geographic scale on the order of an average species range up to a single biotic region or climate zone, and at a temporal scale longer than the Milankovitch scale (Fig. 7A). Tests for the biotic efficacy of climate change that lump data from much larger geographic areas are expected to reject the Court Jester because climate is so com-

plex its response varies in different geographic areas. Consequently, regional faunal responses also will be in varying directions, and lumping of the data from different climate zones averages out any regionally-evident faunal responses. This scaling effect means that absence of evidence for the Court Jester at larger geographic scales (e.g., right portion of Fig. 7A) should not be interpreted as support for the Red Queen, even though the apparent pattern (no more change at climatic events than elsewhere in the record) is consistent with Red Queen hypotheses.

Evolutionary responses of mammals to climate change generally should not be expected on temporal scales that are close to or on shorter time scales than Milankovitch-time scales ($\leq \sim 100,000$ years). This is because species must have the resiliency to withstand at least one Milankovitch-scale oscillation if they are going to survive past 100,000 years, and most mammal species in the fossil record have an average lifespan of around 1.5 million years. Thus, most of our fossil sample is of species that by definition have built-in resiliency to climatic oscillations similar in frequency and magnitude to Milankovitch oscillations. Much of this resiliency may be attributable to the ability to migrate out of areas of unfavorably changed habitat (Vrba, 1992, 1993, 1995), but some of it may well be tolerance of fairly broad climatic conditions, at least for some species.

Also important is the rate of the physical-environmental disruption (Fig. 7B). In general, as the rate of environmental disruption increases, the effect of the Court Jester becomes more important. One of the interesting implications of this function is that the Court Jester can rule at very short time scales, providing the rate of environmental change is substantially higher

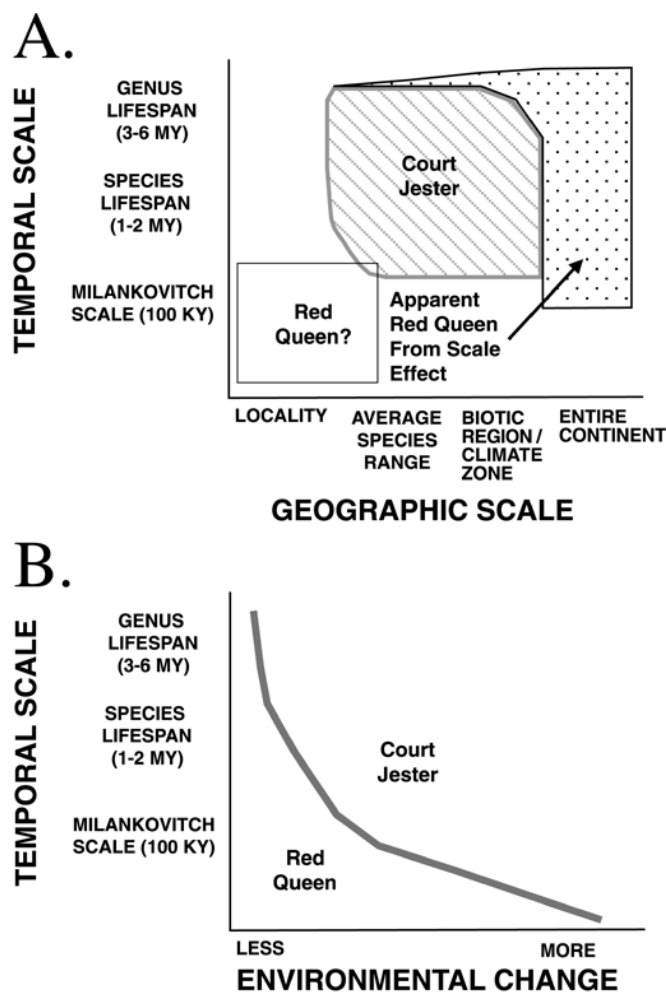


FIGURE 7. **A.** Temporal and geographic scales within which biotic effects of physical environmental change can be detected are represented by the lightly hatched area. The stippled area at the right of the graph covers geographic scales that are so large that biotic response to physical-environmental change is obscured by spatial averaging of local responses that may be in opposite directions. At this scale patterns consistent with the Red Queen do not necessarily reject Court Jester processes. The lower left part of the field in and around the box encompasses scales where Red Queen processes may in fact operate. **B.** Physical-environmental disruptions probably elicit biotic response along a gradient depicted by the heavy gray line. At time-scales and magnitudes to the right of the heavy gray line, the Court Jester probably rules, whereas the Red Queen might be expected to dominate at time-scales and magnitudes to the left of the line.

than the background rate. Examples include bolide impacts—Gould's (1995) third tier of time—and perhaps the global warming event that humans are now accelerating.

These observations do not mean that the Red Queen does not operate: they simply point to productive geographic and temporal scales to look for her. Indeed, Figure 7A suggests that there are theoretical reasons to suspect that the Red Queen dominates at spatial scales that are within the overlapping ranges of individuals and populations, and at temporal scales that are within Milankovitch oscillations. Clearly, interactions between competitors, predator and prey, and hosts and parasites must influence evolution strongly at these scales, just as major changes to the physical environment must influence evolution at geographic and temporal scales, and at rates and magnitudes, that override the day-to-day interactions of individuals and popu-

lations at given localities (Gould, 1985). Indeed, as Ned Johnson remarked (after listening to a lecture expressing these ideas), "Maybe it is time for the Court Jester to marry the Red Queen." That is, perhaps the dichotomy between the two hypotheses is really a dichotomy of scale, and that as we look for ways to travel across biological levels, we will find ways to resolve the dichotomies. For example, Stenseth and Maynard Smith (1984) demonstrated the plausibility of both models by progressing through the ecological time scale, the gene-frequency time-scale, and the speciation-extinction time scale, and Vrba (1992, 1993, 1995) recognized the importance of biotic interactions in determining why different lineages react (or do not react) to environmental changes in different ways.

The theoretical considerations and case study presented here lead to two conclusions. First, the Court Jester very likely is important in driving evolutionary patterns, but only at certain geographic and temporal scales. Therefore any test of the Red Queen or Court Jester must pay particular attention to the scaling effects inherent in the study. Second, robustly differentiating between the Court Jester and Red Queen requires exceptionally good paleontological data sets that adequately sample large parts of biotic provinces through long temporal intervals. In most cases, this will require additional field and taxonomic work, as well as clear documentation of the numbers of identifiable specimens collected from every locality. The presented case study, for example, would be greatly strengthened by increasing the paleontological sample of the northern Rockies for the late Arikareean and early Hemingfordian, and by a comparison of the data from the Rocky Mountains with that of other geographic regions.

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