

Comparison of climate space and phylogeny of *Marmota* (Mammalia: Rodentia) indicates a connection between evolutionary history and climate preference

Edward Byrd Davis*

Department of Integrative Biology, Museum of Paleontology, University of California, Berkeley,
3060 Valley Life Sciences Building, Berkeley, CA 94720, USA

Palaeobiologists have investigated the evolutionary responses of extinct organisms to climate change, and have also used extinct organisms to reconstruct palaeoclimates. There is evidence of a disconnection between climate change and evolution that suggests that organisms may not be accurate palaeoclimate indicators. Here, marmots (*Marmota* sp.) are used as a case study to examine whether similarity of climate preferences is correlated with evolutionary relatedness of species. This study tests for a relationship between phylogenetic distance and 'climate distance' of species within a clade. There should be a significant congruence between maximum likelihood distance and standardized Euclidian distance between climates if daughter species tend to stay in environments similar to parent species. Marmots make a good test case because there are many extant species, their phylogenies are well established and individual survival is linked to climatic factors. A Mantel test indicates a significant correlation between climate and phylogenetic distance matrices, but this relationship explains only a small fraction of the variance (regression $R^2 = 0.114$). These results suggest that (i) closely related species of marmots tend to stay in similar environments; (ii) marmots may be more susceptible than many mammals to global climate change; and (iii) because of the considerable noise in this system, the correlation cannot be used for detailed palaeoclimate reconstruction.

Keywords: *Marmota*; climate and evolution; mammalian speciation; palaeoclimate reconstruction; geographic information system

1. INTRODUCTION

Biologists have explored the effects of climate change on biological systems since the earliest days of evolutionary theory (Darwin 1859). Many studies have centred on the fossil record, examining trends at the million-year timescale (e.g. Matthew *et al.* 1915; Vrba 1985, 1993; Webb & Opdyke 1995; Prothero 1999; Alroy *et al.* 2000; Barnosky & Carrasco 2002). Extensive work on the extant biota examines the evolutionary and ecological responses of organisms to anthropogenic climate change over time periods ranging from years to decades (e.g. Inouye *et al.* 2000; McCarty 2001; Parmesan & Yohe 2003; Root *et al.* 2003). In general, the work on fossil organisms supports some decoupling of macroevolutionary patterns and climate change, whereas the work on extant species shows distinct biological responses to changing climate.

Palaeontologists have also used the fossil record to reconstruct past climates, working in two different ways: (i) taxonomically, by analogy to living relatives and (ii) ataxonomically, by analogy to similar forms in living organisms (Wing & Greenwood 1993). Taxonomic methods rely upon the geographic ranges of extant species

to construct sets of climate preferences that take the form of qualitative descriptions of preferred habitat or quantitative measures of environmental parameters, such as average temperature or precipitation (Mossbrugger 1999). By projecting these preferences back onto assemblages of fossil organisms, one can construct a band of overlap of climate for all of the species in the assemblage (Mossbrugger 1999; Hernández Fernández 2001; Hernández Fernández & Peláez-Campomanes 2003). Assumptions of these taxonomic methods include correct fossil identification, correct phylogenetic relationships, modern range constraint by climate, and some connection between evolutionary relatedness and climate preferences (Wing & Greenwood 1993; Mossbrugger 1999).

Alternatively, ataxonomic methods assume that organisms evolve morphological adaptations directly in response to environmental variables. By comparing the morphologies of fossil organisms to living organisms, researchers invoke the physical laws that shape organisms through natural selection (Wing & Greenwood 1993). Much of this research has focused on plants (Wolfe 1990; Liang *et al.* 2003), but the approach has also been extended to mammals (Fortelius *et al.* 2002; DeGusta & Vrba 2003).

A fundamental question underlying all of these lines of research is: Do organisms evolve randomly with respect to climate? The answer bears directly on a more specific

* (daviseb@socrates.berkeley.edu).

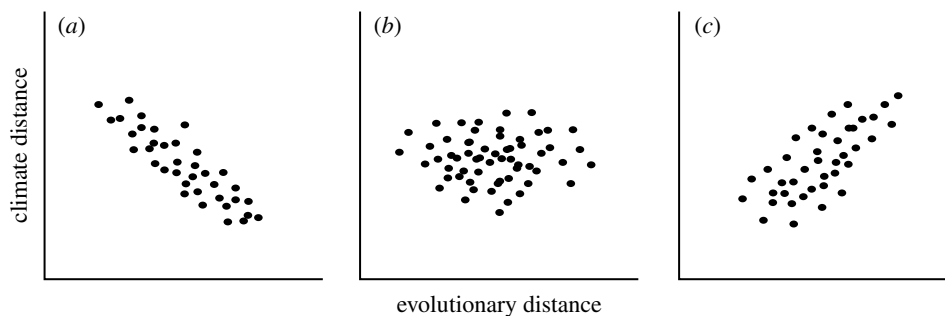


Figure 1. Illustration of the expected results for H_0 and H_1 . For H_0 , two possibilities exist: (a) species are driven apart during speciation, producing a negative correlation between evolutionary distance and climate distance; (b) species disperse randomly through climate space, producing no correlation between the two variables. For H_1 , one possibility exists: (c) species tend to conserve their climate preferences, producing a positive correlation between the two variables.

question: Can taxonomic methods reasonably reconstruct palaeoclimate?

Here, I examine these questions with respect to mammals by examining the relationship between phylogenetic history and climate-space occupied by 12 of the 14 extant species within the marmot (*Marmota*) clade. In response to the first of the questions posed above, two hypotheses remain possible (figure 1). In the null hypothesis, H_0 , the species are diffusing through climate space in such a way that they are either driven apart by competition between close relatives (figure 1a) or drift randomly through climate space (figure 1b). In the alternative hypothesis, H_1 , the species have an association between their climate preferences and their evolutionary history: more closely related species inhabit environments that are more similar to one another than are those inhabited by more distant species (figure 1c). The null hypothesis can be tested statistically through a comparison of the distances between pairs of species in climate space to their phylogenetic distance, as shown by the cartoon plots in figure 1.

The species of *Marmota* are an ideal group for testing these hypotheses because Steppan *et al.* (1999) have produced a thorough molecular phylogenetic reconstruction, and *Marmota* species have evolved life history traits that tie the survival of individuals to climatic parameters. For example, changes in seasonality affect hibernation mortality, a chief cause of death; additionally, individuals alter activity patterns (including date of first emergence and timing of reproduction) in response to air temperature changes (Barash 1989; Inouye *et al.* 2000).

Eight of the extant *Marmota* species live in Eurasia: *Marmota marmota* (exclusively Europe), *Marmota baibacina*, *Marmota bobak*, *Marmota camtschatica*, *Marmota caudata*, *Marmota himalayana*, *Marmota menzbieri*, and *Marmota sibirica*. Six species are native to North America: *Marmota broweri*, *Marmota caligata*, *Marmota flaviventris*, *Marmota monax*, *Marmota olympus* and *Marmota vancouverensis*. The latter two species are restricted to small areas on the Pacific coast: *M. olympus* on the Olympic Peninsula and *M. vancouverensis* on Vancouver Island. Because the ranges of these two species are obviously restricted by geography and not climate, they are not considered in this analysis.

Most species of marmot live in alpine and subalpine meadows, foraging on grass and wildflowers during the

(sometimes brief) summer growing season (Barash 1989). *M. monax*, the woodchuck, lives in the widest variety of habitats, from cultivated land and lowland prairie to forest habitat (Ferron 1996; Kwiecinski 1998). Of all the marmots, *M. camtschatica* occupies the most extreme habitat: harsh, forestless, alpine lands (Barash 1989). The only evidence of competitive exclusion between marmot species is that *M. flaviventris*, the yellow-bellied marmot, is restricted to lower elevations when sympatric with *M. caligata* (Frase & Hoffmann 1980; Barash 1989).

Yellow-bellied marmots, the most extensively studied of all marmot species, provide the best model for climate-related limitations on their geographic ranges. They have two major sources of mortality: predation during the summer months and death during winter hibernation. Hibernation mortality can be traced to the interaction between the length of the growing season and the snowiness of winter. The longer the growing season, the more time the marmots have for feeding, gaining fat reserves that will be consumed during hibernation (Schwartz *et al.* 1998). The snowier the winter, the more insulation the animals will have and the warmer their burrows will be (Svendsen 1974). Mortality is affected by snow at both the northern and southern ends of their ranges: either a late snowmelt or an insufficient insulating blanket of snow will result in increased mortality (Svendsen 1974; Inouye *et al.* 2000). The importance of freezing in hibernacula in ground squirrels other than *Marmota* (e.g. Sherman & Runge 2002) indicates that hibernation mortality is a plesiomorphic natural history trait for *Marmota*.

Marmots are social rodents, using group survival strategies to live in harsh environments. The least social species is *M. monax* (the woodchuck), individuals of which remain solitary throughout most of their lives (Barash 1989; Kwiecinski 1998). Woodchucks can survive solitary hibernation because they live in low-elevation or low-latitude environments that have deep soils, which provide better insulation than the rocky, thin soils of high-elevation or high-latitude environments (Ferron 1996). Other species range from moderately social (most Eurasian species) to extremely social (*M. marmota* and *M. camtschatica*; Barash 1989; Ferron 1996). Barash (1989) found that a higher level of socialization was linked to more severe winters, both intraspecifically and interspecifically, because social *Marmots* can hibernate in

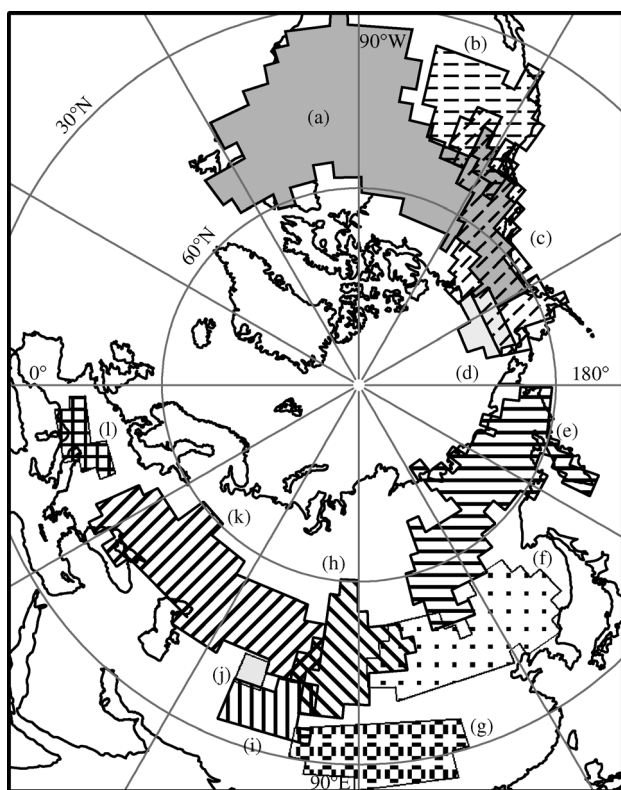


Figure 2. Maps of 2.5° grid cells included for each species of *Marmota*: (a) *M. monax*; (b) *M. flaviventris*; (c) *M. caligata*; (d) *M. broweri*; (e) *M. camtschatica*; (f) *M. sibirica*; (g) *M. himalayana*; (h) *M. baibacina*; (i) *M. caudata*; (j) *M. menzbieri*; (k) *M. bobak*; (l) *M. marmota*.

groups, keeping burrows warmer (Arnold 1988; Blumstein *et al.* 2004).

2. METHODS

In order to derive climate data for the species of *Marmota*, I began with the geographic range maps of Hall (1981) for North American species and Steppan *et al.* (1999) for Eurasian species. To convert the maps to a uniform projection, they were scanned and transformed into geographic coordinates (latitude and longitude) in a geographic information system (GIS) using ArcInfo's (ESRI 2003) *ArcEdit* utility.

The climate data (Shea 1986) are mean monthly values of temperature and precipitation for 1950–1979. Each data point marks the monthly value for a single cell within a 2.5° latitude/longitude grid. These data were entered into a 2.5° latitude/longitude point array using *ArcMap* and *ArcEdit* (ESRI 2003). Using that point array as a guide, I created a set of 'rectangular' *Marmota* species ranges that included all 2.5° grid cells that contain any part of the range of each species (figure 2). The final set of climate data for each species represents the group of 2.5° cells that contain any part of the species range as derived from the original sources. Because they include data from areas that may have small populations of a species, these climate data sets represent a liberal estimate of the species' tolerances, which makes for a conservative test of my hypotheses—that any differences observed between species are likely to be real, as the noise introduced by this method reduces the degree to which differences would be observed. The east-west distance represented by a degree of longitude

decreases as latitude increases, so I calculated weighted mean values by weighting each cell by its percentage of the total geographic area for the species. This prevented the northern areas, which are covered by more grid cells, from contributing excessively to the mean values for each species. This correction amounted to no more than 5% for any precipitation value and 1 °C for any temperature value.

The period over which the climate data were averaged roughly corresponds to the period of time over which data were gathered to construct the North American range maps (Hall 1981; Shea 1986). Ranges for Eurasian species come from studies over a similar time period (e.g. Zimina & Gerasimov 1973), compiled by Steppan *et al.* (1999). Because there is evidence of environmental control over marmot mortality, I assumed that the geographic distributions shown in these maps reasonably reflected the climate tolerances of each species. Although I recognize that biotic interactions with plant resources, competitors and predators will also potentially affect species ranges, these interactions, especially those with plant resources, are also likely to be influenced by climate. While we still have much to learn about the connection between the geographic response of mammals and climate change, published studies suggest the response can be very rapid (McCarty 2001; Barnosky *et al.* 2003; Root *et al.* 2003); thus the importance of using climate and range data from the same time periods. Unfortunately, coordinating the climate and range data requires the use of a dataset that has rough geographic resolution. The improvement of this resolution is an important avenue for future study.

The climate data (Appendix A) describe the distribution of average monthly temperature (°C) and precipitation (mm/month) values for each species. Tracing these average values through a year describes the annual climate cycle experienced by a species (Graham 1984; Wood & Barnosky 1994). These annual cycles reflect the length of the growing season and the minimum and maximum temperature months experienced by the species, which are important to marmot survivorship.

In order to compare these climate data to phylogenetic distance data from Steppan *et al.* (1999), I calculated standardized Euclidian distances between each of the species pairs, based upon their monthly temperature and precipitation averages (Appendix B). Calculating the standardized Euclidian distance has two steps. First, I normalized the climate data to the range [0, 1]. That is, for each variable (January temperature, August precipitation, etc.), I transformed the data so that the observed range extended from zero to one. Normalizing the distances removes any artefact that might be introduced by the scales; this way, the results would be identical whether the climate data were analysed with precipitation as mm/month or inches/day, and the temperature data as °C, K or °F. Alternatively, standardizing these data by their means and standard deviations produces results commensurate with those presented here. Secondly, I calculated the root of the sum of the squared differences between each of the standardized climate variables for each pair of species. I regressed the data against the maximum likelihood (ML) distances, based on mitochondrial cytochrome *b* sequences published by Steppan *et al.* (1999) using JMP IN 4.0.4 (SAS 2002; Appendix B, figure 3). In order to test for

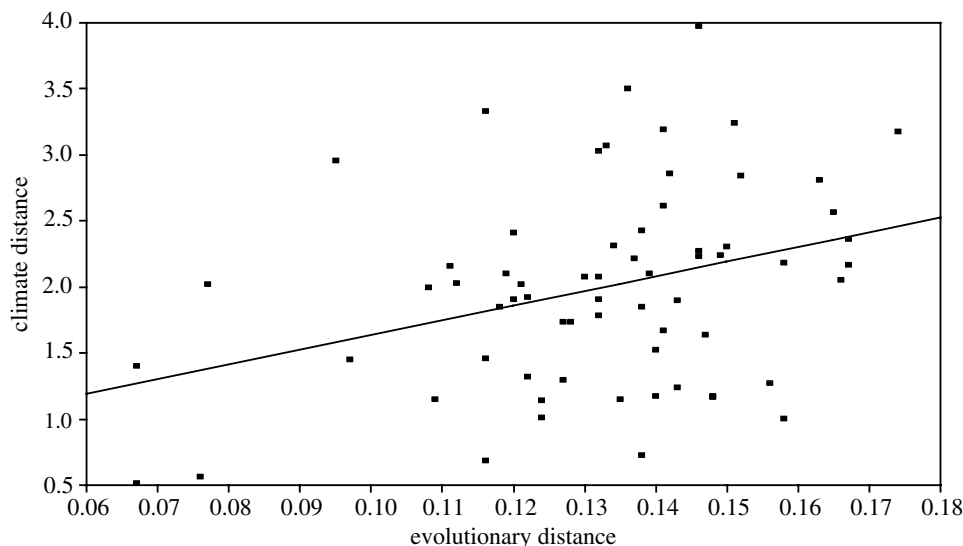


Figure 3. Regressions of Euclidian climate distance against maximum likelihood evolutionary distance. Each point represents a pair of species of *Marmota*, with ML distances on the x-axis and climate distances on the y-axis. See text for sources of distance data. $R^2=0.114$, reflecting the large spread of the data relative to the regression line.

the significance of the differences between the two distance matrices, I performed a standard Mantel test (Mantel 1967), and I used the program Congruence among distance matrices (CADM) (Legendre & Lapointe 2004) to perform a rank-based Mantel test (Mantel & Valand 1970).

3. RESULTS

The regression of Euclidian climate distance against ML distance from Steppan *et al.* (1999) for all included species of *Marmota* produces an R^2 of 0.114 (figure 3). Significance of correlation between the distance data cannot be properly estimated with linear regression because the points are interdependent. Following the methods of Mantel (1967), I calculated $Z=35.51 \pm 0.33$ (value $\pm$ s.e.) for the two matrices. The predicted $Z=34.76$; consequently $t=2.27$, and with 11 d.f., $p=0.022$, which rejects the null hypothesis of incongruence between the matrices. The program CADM (Legendre & Lapointe in press) produced a similar result. A Mantel test on ranked distances with 9999 permutations produced $p=0.038$.

4. DISCUSSION AND CONCLUSIONS

These results mean that the association between the two distance matrices is significantly higher than would be expected at random; however, the low R^2 of the regression would not adequately predict the climate distance of a species of known evolutionary distance, eliminating its usefulness for predicting the climate distances of extinct taxa.

On the basis of the results of the Mantel and CADM tests, I can reject the null hypothesis of no relationship between evolutionary distance and climate distance. This means that marmot sister species live in more similar environments than would be expected by chance, implying that daughter species of marmots live in environments

similar to those of their parent species. Thus, the answer to my first question, 'Do organisms evolve randomly with respect to climate?' is no, at least for marmots. The considerable noise in the correlation indicates that, while climate does play a role, it may not be the most important factor shaping the evolutionary history of marmots. This conclusion fits well with the marmot life history traits described in the introduction, because the habitat choices of individuals are constrained by their physical environments, and individuals also endure predation and competition, two factors not accounted for by my analysis.

This result has implications for palaeobiological research, conservation ecology of marmots and palaeoclimatology. My study agrees with other studies of modern systems that tend to find a connection between climate and evolution, and with some palaeobiological studies (Vrba 1985, 1993), but not with other palaeobiological research (e.g. Prothero 1999; Alroy *et al.* 2000). This may be because (i) the taxon-sampling of the clade in this study is nearly complete, as for many modern studies, but unlike many palaeobiological studies; or (ii) changes at the species level do not project to the level of higher taxa that are often studied in palaeobiology. I can assess the importance of incompleteness (the first point) by artificially degrading the data through jack-knifing the analysis: removing three species (75% coverage) results in non-significant results. Incomplete taxon-sampling in the fossil record could account for the discrepancy between modern and fossil studies. More research on temporal, geographic and taxonomic scaling issues would clearly be profitable in resolving conflicting results.

The implication for the conservation ecology of marmots concerns marmot range change and population-level extinction in the face of predicted global warming. The results of Inouye *et al.* (2000) indicate that marmots are already affected by global climate change. My result suggests that closely related species

Table 1. Average monthly precipitation and temperature values for the species of *Marmota*, adjusted for latitudinal change in grid cell size.

<i>Marmota</i>	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
weighted mean precipitation (mm/month)												
<i>M. baibacina</i>	12.00	10.58	13.81	19.90	29.48	37.84	45.63	36.50	23.64	25.51	19.17	17.67
<i>M. bobak</i>	24.48	22.11	22.25	26.47	36.40	44.92	49.45	41.22	31.58	33.29	29.82	29.26
<i>M. broweri</i>	7.61	5.48	4.77	5.14	6.79	13.41	28.41	35.60	22.81	15.40	10.35	7.46
<i>M. caligata</i>	53.54	45.65	43.23	35.46	39.93	49.35	56.90	64.37	64.89	69.81	62.82	61.63
<i>M. camtschatica</i>	19.55	14.44	13.09	15.03	21.44	37.38	53.94	51.24	36.09	28.74	24.56	21.25
<i>M. caudata</i>	28.58	29.80	44.62	40.95	34.58	24.63	36.89	32.74	21.56	15.77	17.59	21.77
<i>M. flaviventris</i>	58.30	42.79	43.80	38.37	40.52	42.07	28.39	30.92	31.41	39.27	49.47	57.16
<i>M. himalayana</i>	10.83	12.23	21.96	38.91	73.23	131.64	195.74	176.23	114.96	42.02	8.67	5.00
<i>M. marmota</i>	65.88	58.30	59.63	59.28	75.06	89.93	81.83	84.95	72.52	70.29	78.87	67.43
<i>M. menzbieri</i>	32.68	23.54	37.68	39.78	28.94	11.50	6.41	5.27	4.90	22.41	26.14	25.78
<i>M. monax</i>	46.99	41.85	48.52	49.73	60.93	74.00	81.06	77.61	70.70	58.90	57.39	51.93
<i>M. sibirica</i>	3.52	3.33	6.26	13.99	25.78	50.83	87.49	76.47	38.81	14.71	7.83	4.85
weighted mean temperature (°C)												
<i>M. baibacina</i>	-16.92	-14.16	-5.03	5.71	13.17	18.98	20.84	18.59	12.75	4.30	-6.36	-13.98
<i>M. bobak</i>	-11.42	-10.59	-4.40	6.48	14.61	19.27	21.20	19.31	13.26	5.51	-2.18	-7.97
<i>M. broweri</i>	-24.38	-26.37	-22.99	-15.29	-4.10	3.75	6.73	6.12	1.88	-7.84	-16.72	-23.72
<i>M. caligata</i>	-15.68	-12.47	-8.15	-0.58	6.76	12.07	14.54	13.13	8.49	0.98	-7.78	-13.56
<i>M. camtschatica</i>	-32.27	-30.16	-21.79	-10.07	2.01	10.94	14.05	11.22	4.26	-8.03	-23.39	-30.45
<i>M. caudata</i>	-2.96	0.12	6.46	13.80	18.55	22.97	24.61	23.42	19.18	12.59	4.96	-0.68
<i>M. flaviventris</i>	-3.22	0.00	2.93	7.78	12.77	16.93	20.58	19.51	15.17	9.79	2.94	-1.14
<i>M. himalayana</i>	-3.51	-1.28	4.05	8.35	12.08	15.08	16.49	16.15	13.01	8.07	2.43	-1.49
<i>M. marmota</i>	0.33	1.70	5.30	9.50	13.62	17.33	19.19	18.43	15.33	10.44	5.32	1.92
<i>M. menzbieri</i>	-5.61	-4.45	2.65	11.06	20.08	24.32	26.54	24.44	17.90	10.35	1.90	-3.07
<i>M. monax</i>	-14.76	-12.01	-6.42	2.02	9.11	14.68	17.68	16.50	11.75	5.46	-3.22	-10.88
<i>M. sibirica</i>	-21.73	-18.00	-8.45	2.71	10.91	17.04	19.15	17.24	10.58	1.68	-10.19	-18.91

Table 2. Climate and evolutionary distances between species of *Marmota*. Euclidian climate distances are below the diagonal, maximum likelihood (ML) distances are above.

	<i>M. baibacina</i>	<i>M. bobak</i>	<i>M. brozveri</i>	<i>M. caligata</i>	<i>M. camtschatica</i>	<i>M. caudata</i>	<i>M. flaviventris</i>	<i>M. himalayana</i>	<i>M. marmota</i>	<i>M. menzbieri</i>	<i>M. monax</i>	<i>M. sibirica</i>
<i>M. baibacina</i>												
<i>M. bobak</i>	0.572											
<i>M. brozveri</i>	2.106	2.434										
<i>M. caligata</i>	1.859	1.532	2.573									
<i>M. camtschatica</i>	1.739	2.033	1.008	2.058								
<i>M. caudata</i>	1.465	1.147	3.340	2.281	3.036							
<i>M. flaviventris</i>	1.677	1.155	3.184	1.409	2.816	1.179						
<i>M. himalayana</i>	2.030	1.859	3.250	2.369	2.961	2.163	2.248					
<i>M. marmota</i>	2.619	2.085	3.977	1.645	3.508	2.106	1.274	2.317				
<i>M. menzbieri</i>	1.301	1.015	3.196	2.192	2.850	0.517	1.181	2.420	2.218			
<i>M. monax</i>	1.743	1.330	2.865	0.732	2.315	1.911	1.174	1.929	1.245	1.905		
<i>M. sibirica</i>	0.687	1.158	1.787	2.169	1.457	2.000	2.237	2.023	3.076	1.911	2.086	

of marmots share similar climate spaces. Thus, extreme climate shifts might be expected to similarly affect closely related species. This fits with the North American faunal record from the last 40 000 years, which indicates that geographic range change is a common response to climate change among mammalian taxa, especially small mammals (Graham *et al.* 1996). If deeper time is any indication, however, the majority of mammalian species may not be so directly tied to the physical environment that a rapid climate change will be disastrous (Alroy *et al.* 2000); again, attention to scaling issues is needed.

An important implication for palaeoclimatology is the answer my results provide to my second question, 'Can taxonomic methods reasonably reconstruct palaeoclimate?' The positive correlation between marmot climate preferences and evolutionary relatedness indicates that taxonomic methods may be valid, at least with organisms like marmots that are closely linked to their physical environments. The presence of *M. monax* through several glacial-interglacial cycles at Porcupine Cave, Colorado (Polly 2003; Barnosky *et al.* 2004) is support for this conclusion, as palaeoclimate reconstructions for Porcupine Cave based on other mammals (Wood & Barnosky 1994) indicate that the temperature and precipitation were within the observed range for modern occurrences of *M. monax*.

The correlation between evolutionary relatedness and climate preference for these data is not tight enough to provide a reliable basis for extrapolating palaeoclimate reconstructions from extant species to extinct. That is, one could not determine precisely how similar the climate preference of an extinct species of marmot would be to an extant species based on its evolutionary similarity. My results suggest that, to avoid false precision, palaeoclimate reconstructions based on evolutionary relatedness should be made only on a qualitative basis.

Productive future research should include analyses similar to this one on other animal and plant taxa that exhibit different life history traits and ecological settings, and that are less obviously tied to their physical environments. Such studies are important to assess whether the association between climate similarity and evolution that I found here is the exception or the rule. It would be an important advance if it were possible to use point occurrence data for both evolutionary similarity and local climate to more precisely define the environments that individual organisms experience. Finally, studies that focus on bridging the temporal and geographic gaps that separate neontology and palaeontology (Hadly 2003) would be profitable in resolving the apparent conflict between studies such as the present one, which supports a climate–evolution connection, and palaeobiological work that commonly does not support such a connection.

APPENDIX A See table 1.

APPENDIX B See table 2.

N. C. Arens suggested I look into this problem. A. D. Barnosky has provided extensive editorial help and

mentorship. R. S. Hoffman provided information on sources of Eurasian range maps. C. J. Bell, M. A. Carrasco, R. S. Feranec, C. Graham, B. Kraatz, D. R. Lindberg, B. D. Mishler and A. Shabel all provided constructive criticism. S. S. B. Hopkins also provided constructive criticism and much needed moral support. K. Padian and three anonymous reviewers provided extensive editorial commentary and drastically improved both the methods and content of this paper. This research was completed while I was a Graduate Research Fellow of the National Science Foundation. I received additional funding from the UC Museum of Paleontology and Department of Integrative Biology. GIS software was funded by the MIOMAP Project, supported by NSF grant EAR-0310221 and provided by the UC Berkeley GISC. This is UCMF publication no. 1870.

REFERENCES

- Alroy, J., Koch, P. L. & Zachos, J. C. 2000 Global climate change and North American mammalian evolution. In *Deep time: paleobiology's perspective* (ed. D. H. Erwin & S. L. Wing), pp. 259–288 (Supplement to *Paleobiology* 26). Lawrence, KS: Allen Press.
- Arnold, W. 1988 Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). *J. Comp. Physiol. B* **158**, 151–156.
- Barash, D. P. 1989 *Marmots: social behavior and ecology*. Stanford, CA: Stanford University Press.
- Barnosky, A. D. & Carrasco, M. A. 2002 Effects of Oligo-Miocene global climate changes on mammalian species richness in the northwestern quarter of the USA. *Evol. Ecol. Res.* **4**, 811–841.
- Barnosky, A. D., Hadly, E. A. & Bell, C. J. 2003 Mammalian response to global warming on varied temporal scales. *J. Mammal.* **84**, 354–368.
- Barnosky, A. D., Kaplan, M. H. & Carrasco, M. A. 2004 Assessing the effect of middle Pleistocene climate change on *Marmota* populations from the Pit Locality. In *Biodiversity response to climate change in the Middle Pleistocene: the Porcupine Cave Fauna from Colorado* (ed. A. D. Barnosky), pp. 341–346. Berkeley, CA: University of California Press.
- Blumstein, D. T., Im, S., Nicodemus, A. & Zugmeyer, C. 2004 Yellow-bellied marmots (*Marmota flaviventris*) hibernate socially. *J. Mammal.* **85**, 25–29.
- Darwin, C. 1859 *On the origin of species by means of natural selection, or preservation of favored races in the struggle for life*. London: Murray.
- DeGusta, D. & Vrba, E. 2003 A method for inferring paleohabitats from the functional morphology of bovid astragali. *J. Archaeol. Sci.* **30**, 1009–1022.
- ESRI 2003 *ArcGIS/ArcInfo*. Redlands, CA: ESRI.
- Ferron, J. 1996 How do woodchucks (*Marmota monax*) cope with harsh winter conditions? *J. Mammal.* **77**, 412–416.
- Fortelius, M. *et al.* 2002 Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evol. Ecol. Res.* **4**, 1005–1016.
- Frase, B. A. & Hoffmann, R. S. 1980 *Marmota flaviventris*. *Mamm. Species* **135**, 1–8.
- Graham, R. W. 1984 Paleoenvironmental implications of the quaternary distribution of the eastern chipmunk (*Tamias striatus*) in central Texas. *Quaternary Res.* **21**, 111–114.
- Graham, R. W. *et al.* 1996 Spatial response of mammals to late quaternary environmental fluctuations. *Science* **272**, 1601–1606.
- Hadly, E. A. 2003 The interface of paleontology and mammalogy: past, present, and future. *J. Mammal.* **84**, 347–353.
- Hall, E. R. 1981 *The mammals of North America*. New York: John Wiley and Sons.
- Hernández Fernández, M. 2001 Bioclimatic discriminant capacity of terrestrial mammal faunas. *Glob. Ecol. Biogeogr.* **10**, 189–204.
- Hernández Fernández, M. & Peláez-Campomanes, P. 2003 The bioclimatic model: a method of palaeoclimatic qualitative inference based on mammal associations. *Glob. Ecol. Biogeogr.* **12**, 507–517.
- Inouye, D. W., Barr, B., Armitage, K. B. & Inouye, B. D. 2000 Climate change is affecting altitudinal migrants and hibernating species. *Proc. Natl Acad. Sci. USA* **97**, 1630–1633.
- Kwiecinski, G. G. 1998 *Marmota monax*. *Mamm. Species* **591**, 1–8.
- Legendre, P. & Lapointe, F.-J. 2004 Assessing the congruence among distance matrices: single malt scotch whiskies revisited. *Aust. N. Z. J. Stat.* **46**, 615–629.
- Liang, M.-M., Bruch, A., Collinson, M., Mosbrugger, V., Li, C. S., Sun, Q.-G. & Hilton, J. 2003 Testing the climatic estimates from different palaeobotanical methods: an example from the Middle Miocene Shanwang flora of China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **198**, 279–301.
- Mantel, N. 1967 The detection of disease clustering and a generalized regression approach. *Cancer Res.* **27**, 209–220.
- Mantel, N. & Valand, R. S. 1970 A technique of non-parametric multivariate analysis. *Biometrics* **26**, 547–558.
- Matthew, W. D. 1915 Climate and evolution. *Ann. N. Y. Acad. Sci.* **24**, 171–318.
- McCarthy, J. P. 2001 Ecological consequences of recent climate change. *Conserv. Biol.* **15**, 320–331.
- Mosbrugger, V. 1999 The nearest living relative method. In *Fossil plants and spores: modern techniques* (ed. T. P. Jone & N. P. Rowe), pp. 261–265. London: Geological Society.
- Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change across natural systems. *Nature* **421**, 37–42.
- Polly, P. D. 2003 Paleophylogeography: the tempo of geographic differentiation in marmots (*Marmota*). *J. Mammal.* **84**, 369–384.
- Prothero, D. R. 1999 Does climatic change drive mammalian evolution? *GSA Today* **9**, 1–7.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. 2003 Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60.
- SAS 2002 *JMP IN*. Cary, NC: SAS Institute.
- Schwartz, O. A., Armitage, K. B. & Van Vuren, D. 1998 A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *J. Zool.* **246**, 337–346.
- Shea, D. J. 1986 *Climatological atlas: 1950–1979*, vol. NCAR TN-269 + STR. Boulder, Colorado: National Center for Atmospheric Research.
- Sherman, P. W. & Runge, M. C. 2002 Demography of a population collapse: the northern Idaho ground squirrel (*Spermophilus brunneus brunneus*). *Ecology* **83**, 2816–2831.
- Steppan, S. J., Akhverdyan, M. R., Lyapunova, E. A., Fraser, D. G., Vorontsov, N. N., Hoffmann, R. S. & Braun, M. J. 1999 Molecular phylogeny of the marmots (Rodentia: Scuriidae): tests of evolutionary and biogeographic hypotheses. *Syst. Biol.* **48**, 715–734.
- Svendsen, G. E. 1974 Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. *Ecology* **55**, 760–771.

- Vrba, E. S. 1985 Environment and evolution; alternative causes of the temporal distribution of evolutionary events. *S. Afr. J. Sci.* **81**, 229–236.
- Vrba, E. S. 1993 Turnover-pulses, the red queen, and related topics. *Am. J. Sci.* **293-A**, 418–452.
- Webb, S. D. & Opdyke, N. D. 1995 Global climatic influence on Cenozoic land mammal faunas. In *Effects of past global change on life* (ed. J. P. Kennett & S. M. Stanley), pp. 184–208. Washington: National Academy Press.
- Wing, S. L. & Greenwood, D. R. 1993 Fossils and climate: the case for equable continental interiors in the Eocene. *Phil. Trans. R. Soc. B* **341**, 243–252.
- Wolfe, J. A. 1990 Palaeobotanical evidence for a marked temperature increase following the cretaceous/tertiary boundary. *Nature (London)* **343**, 153–156.
- Wood, D. L. & Barnosky, A. D. 1994 Middle Pleistocene climate change in the Colorado rocky mountains indicated by fossil mammals from Porcupine Cave. *Quaternary Res.* **41**, 366–375.
- Zimina, R. P. & Gerasimov, I. P. 1973 The periglacial expansion of marmots (*Marmota*) in middle Europe during the late Pleistocene. *J. Mammal.* **54**, 327–340.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.