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Understanding and predicting how species' distributions will shift as climate changes are central questions in ecology today. The late Quaternary of North America represents a natural experiment in which we can evaluate how species responded during the expansion and contraction of the glaciers. Here, we ask whether species' range shifts differ because of taxonomic affinity, life-history traits, body size or topographic heterogeneity and whether the species survived the megafaunal extinction. There was no difference in range shifts between victims and survivors of the megafaunal extinction. In general, the change in the size of a species' range is not well correlated with any of the ecological or life-history traits evaluated. However, there are significant relationships between some variables and the movements of the centroids of ranges. Differences in the distances shifted exist among orders, although this is probably a result of body size differences as larger bodied species show larger shifts. Although there are a few exceptions, the distance that species shifted their range was weakly correlated with life-history traits. Finally, species in more topographically heterogeneous areas show smaller shifts than species in less-diverse areas. Overall, these results indicate that when trying to predict species range shifts in the future, body size, lifespan and the topographic relief of the landscape should be taken into account.

Keywords: range shifts; Late Pleistocene mammals; body size; life-history traits; ecological traits; climate change

1. INTRODUCTION

The Earth is currently undergoing a period of global warming that is probably attributable to anthropogenic factors (IPCC 2007). The past half-century has produced temperatures higher than anything seen in 1300 years with 11 of the past 12 years between 1995 and 2007 among the 12 warmest on record (IPCC 2007). We are already seeing the effects of these changes on animals and plants in the form of range shifts (Parmesan 1996, 2006; Parmesan *et al.* 1999; Walther *et al.* 2002; Parmesan & Yohe 2003; Thomas 2010), phenology changes (Walther *et al.* 2002; Parmesan 2006; Eppich *et al.* 2009; Moe *et al.* 2009; Bauer *et al.* 2010; Kennedy & Crozier 2010; Wipf 2010; Zhang *et al.* 2010), population declines and extinction (Pounds *et al.* 1999; Parmesan & Yohe 2003; Root *et al.* 2003; Thomas *et al.* 2004; Parmesan 2006). Understanding and making reasonable predictions for what will happen to species as climate change continues is an important step in preparing for the impacts.

Several avenues of research in modern ecology are making progress in understanding the effects of the current climate change. In addition to the numerous studies that are documenting current changes

(see Parmesan 2006 for a review), bioclimatic envelope modelling is being applied to many different groups to make predictions about what will happen to species under different models of predicted climate change (Foody 2008; Jarvis *et al.* 2008; Jeschke & Strayer 2008; Schweiger *et al.* 2008). Bioclimatic envelope modelling uses the current distribution of a species to determine the suite of climatic variables that best predict that distribution. Using different models of climate change, researchers are able to use the resulting distribution model to predict what will happen to a species range in the future. In some cases, a species climate space is expected to disappear and extinction is predicted (Thomas *et al.* 2004).

Palaeoecological data and analyses can provide insights and knowledge that are not possible using the short time scales available to modern ecology. The Pleistocene epoch is characterized by several glacial–interglacial cycles during which the planet warmed and cooled. This provides a natural experiment in which we can observe species responses to climate change and ask about traits associated with that climate change. In particular, the late Pleistocene of North America encompasses the most recent period of glaciation and has a sufficiently detailed record to allow for the estimation of species ranges and their shifts in response to the expansion and contraction of the glaciers. Much of the work done in the late Pleistocene of North America has shown that previous climatic regimes were characterized by communities that have no modern analogues (e.g. Overpeck *et al.* 1992; Roy *et al.* 1995; Graham *et al.* 1996;

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Jackson *et al.* 1997; Jackson & Overpeck 2000; Davis & Shaw 2001; Roy 2001; Williams *et al.* 2001, 2004; Lyons 2003, 2005). Moreover, Williams *et al.* (2001) demonstrated that non-analogue communities are found in regions of non-analogue climate. This suggests that the species found in these communities are expressing some part of their fundamental niche, which is not available to them today and bioclimatic modelling would not accurately predict the past distributions of these species. Therefore, examination of the range shifts of species in response to past climate fluctuations should provide insights not available from the analysis of modern distributions.

One area of inquiry that has not been extensively explored is the extent to which various ecological traits (e.g. body size, taxonomic affinity, life history, etc.) are correlated with the way in which a species shifts its distribution in response to climate change. Roy *et al.* (2001) show that the larger-bodied species of Californian marine bivalves are more likely to shift their ranges in response to climate changes during the Late Pleistocene than were smaller bodied species. However, to our knowledge, similar analyses have not been conducted on other major taxa. Herein, we use the record of the mammals from the US over the last 40 kya to ask five questions related to how species shift their ranges in response to climate change. First, do victims and survivors of the megafaunal extinction show differences in range shifts? Second, are there differences in the responses of mammals belonging to different orders? Third, what is the role of body size? Fourth, are differences in life history correlated with range shifts? Finally, what effect does geographical topography and differences in elevation have on how species shift their ranges?

2. MATERIAL AND METHODS
(a) *Data*
The raw data for these analyses were taken from three different publicly available datasets. The data on mammalian faunas used to construct range were taken from the FAUNMAP database and used the research database exclusively (FAUNMAP Working Group 1994). The FAUNMAP database consists of faunal lists compiled by site locality, and experts on Pleistocene mammals have heavily vetted it. The body sizes were taken from Smith *et al.* (2003), which is a global compilation of body size for extinct and extant mammals from the late Quaternary and the present. Finally, life-history information for extant mammals was taken from a life-history database compiled by Ernest (2003). The life-history variables included were: age at first reproduction, litter size, maximum lifespan, weaning age, gestation length, litters per year, newborn mass and weaning mass.

(b) *Range shift calculations*
Range shifts were taken from previous studies of Late Pleistocene mammalian range shifts and community structure by Lyons (2003, 2005). However, we will briefly review the methods here. The data from FAUNMAP were divided into four time periods following Lyons (2003, 2005) that encompassed

the expansion and contraction of the glaciers: Pre-Glacial (40 000–20 000 radiocarbon years BP), Glacial (20 000–10 000 radiocarbon years BP), Holocene (10 000 years ago to 500 radiocarbon years BP) and Modern (500 radiocarbon years BP to present). The time periods have a 500-year margin of error because of uncertainty in dating (FAUNMAP Working Group 1994). The term radiocarbon years BP refers to uncalibrated dates before present with the present defined as 1950. As a result, the date 3000 BP is equivalent to 1050 BC. The data used in this study were limited to a maximum age of 40 000 BP because the dating of localities older than that in the FAUNMAP database is not reliable (R. Graham 1998, personal communication). The length of the time periods were chosen to correspond as closely as possible with time bins defined by the FAUNMAP working group (1994) and to minimize time-averaging while maximizing our ability to calculate a species' geographic range. Mammalian fossil assemblages represent relatively short amounts of time-averaging, in the order of hundreds to thousands of years (Graham 1993). The time periods chosen here eliminate localities that could not be constrained by these relatively narrow time frames. Because the fossil record does not necessarily preserve all species that coexisted at a particular locality at a given time, some degree of time-averaging is necessary and even desirable to give an accurate representation of an assemblage.

In order to calculate the geographic range of each species in each time period, localities were plotted in an Albers equal area projection and the species occurring in the continental United States in each time period were identified. The area of each species range was calculated as the area (km^2) within a polygon enclosing all localities for a particular species. The centroid of each range was calculated using a Cartesian coordinate system that took into account the shape of the Earth (Lyons 2003, 2005). Various sensitivity analyses were performed and demonstrated that the resulting geographical ranges showed macroecological patterns similar to modern ones suggesting that they were reasonable estimates of species' true geographical ranges (see Lyons 2003, 2005 for additional details).

Range shifts for each of the three time transitions (i.e. Pre-Glacial to Glacial, Glacial to Holocene and Holocene to Modern) were characterized by three parameters: the distance the centroid of the range shifted from one time period to the next (distance was calculated using an equidistant projection), the change in range size (as defined by the log of the percentage of the geographic range size from the previous time period), and the direction of the shift (see Lyons 2003, 2005 for additional details). Because of the difficulty in analysing circular variables such as direction, only the distance of the centroid shift and the change in range size were analysed for their relationship to various ecological traits.

(c) *Estimating life-history characteristics for extinct species*
We used regression equations to estimate life-history parameters for extinct species. In all cases, log mass

was used as the independent variable. Where possible, equations were calculated at the family level and equations with an r^2 value of at least 0.5 were used. If data were insufficient or r^2 values were too low, then we used equations at the order or class level with the highest r^2 values (electronic supplementary material, table S1).

(d) Analyses

In general, the relationship between the range shift parameters and the ecological traits examined in the study were analysed using correlations, *t*-tests and Mann–Whitney *U* tests. Distance was analysed separately from change in range size in all analyses. A Mann–Whitney *U* test was applied to the distribution of range shifts for victims and survivors of the end-Pleistocene megafaunal extinction to determine if there were differences in the way in which species shifted their distributions. Because the majority of species have their last known appearance at the end of the Glacial time period, we only examined differences in range shifts for the Pre-Glacial to the Glacial, or the time period preceding the extinction. Mann–Whitney *U* tests were also used to determine if the different orders of mammals showed different responses to climate change. The comparisons were repeated using Fisher's Protected Least Significant Difference test (PLSD) with a Bonferroni correction applied to the alpha level. The results were similar and only the Fisher's PLSD will be reported. Pearson product–moment correlations were used to evaluate the relationship between range shift parameters, body size and the various life-history traits. They were also used to determine if there was a relationship between the distance shifted and the change in range size. That is, did species that shifted their range centroid longer distances tend to have smaller or larger changes in range size? In order to determine the relative effects of body size and life history on species range shifts, stepwise multiple regression analyses were performed to determine the importance of the many life-history traits on species range shifts.

In order to determine if there was an effect of variation in geographical topography, species were divided into three groups based upon the topography of the USA. Because the western USA is much more mountainous, it has a greater degree of variation in elevation than does the eastern USA. Because the majority of the mountainous area in the USA is west of $100°$ W longitude, it was used as the dividing line. Moreover, the areas chosen for comparison needed to be large enough to encompass the entire range shift of species. This division necessarily includes much of the Great Plains, a relatively flat geographic feature, in the western area. However, this should bias the test against finding differences if topography is important and thus makes the test conservative. Species whose centroid shifts were wholly contained east of $100°$ W were grouped as eastern species. Species whose centroid shifts were wholly contained west of $100°$ W were grouped as western species and those whose centroid shifts crossed the $100°$ W line were grouped as crossers. If topography plays an important role in
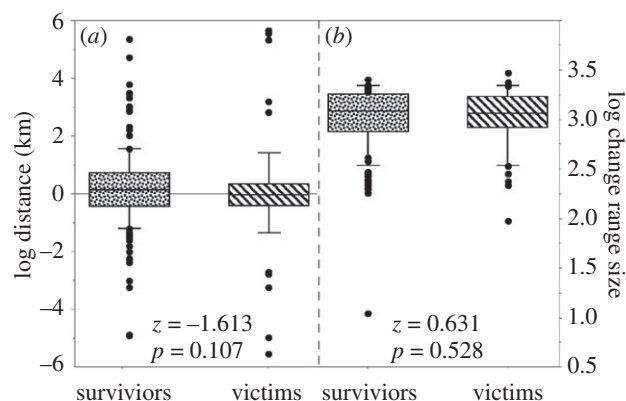
Figure 1. Box plots comparing the range shifts of victims and survivors of the end-Pleistocene megafaunal extinction. Mann–Whitney *U* tests indicate that species that survived the extinction event did not have range shifts that were significantly different in distance shifted (*a*) or change in range size (*b*) compared with species that did not survive. Only the transition from the Pre-Glacial to the Glacial was analysed, as it was the only transition with sufficient numbers of extinct species.

how species shift their range, then we expect western species to show smaller shifts in distance. Because of the greater elevational variation available, it is predicted that they will be able to more easily escape the effects of climate change by shifting up- or downslope and will shift smaller distances overall.

3. RESULTS

(a) Is there a relationship between the distance that a species shifts its range and change in the size of that range?

The distance that species shift their ranges and the amount of increase or decrease in their range size are not related in any of the transitions (Pre-Glacial to Glacial: $r = -0.056$, $p = 0.407$; Glacial to Holocene: $r = -0.049$, $p = 0.406$; Holocene to Modern: $r = 0.016$, $p = 0.803$; electronic supplementary material, figure S1). As a result, the two range shift parameters (distance shifted and change in range size) are treated separately in all other analyses.

(b) Are there differences in the range shifts of the victims of the megafaunal extinction event compared with the survivors?

There is no difference in the range shifts for victims versus survivors of the megafaunal extinction for either distance or range size (figure 1). As a result, they are pooled in all subsequent analyses.

(c) Are there differences in the range shifts of different orders of mammals?

Overall, there are very few significant differences in the range shifts of the different mammalian orders (figure 2*a,d* and table 1). When it comes to the distance that species shifted their range centroids, the few significant differences are concentrated in the Carnivora and the Artiodactyla. However, other than carnivores consistently having larger shifts than rodents, there is no systematic pattern to the
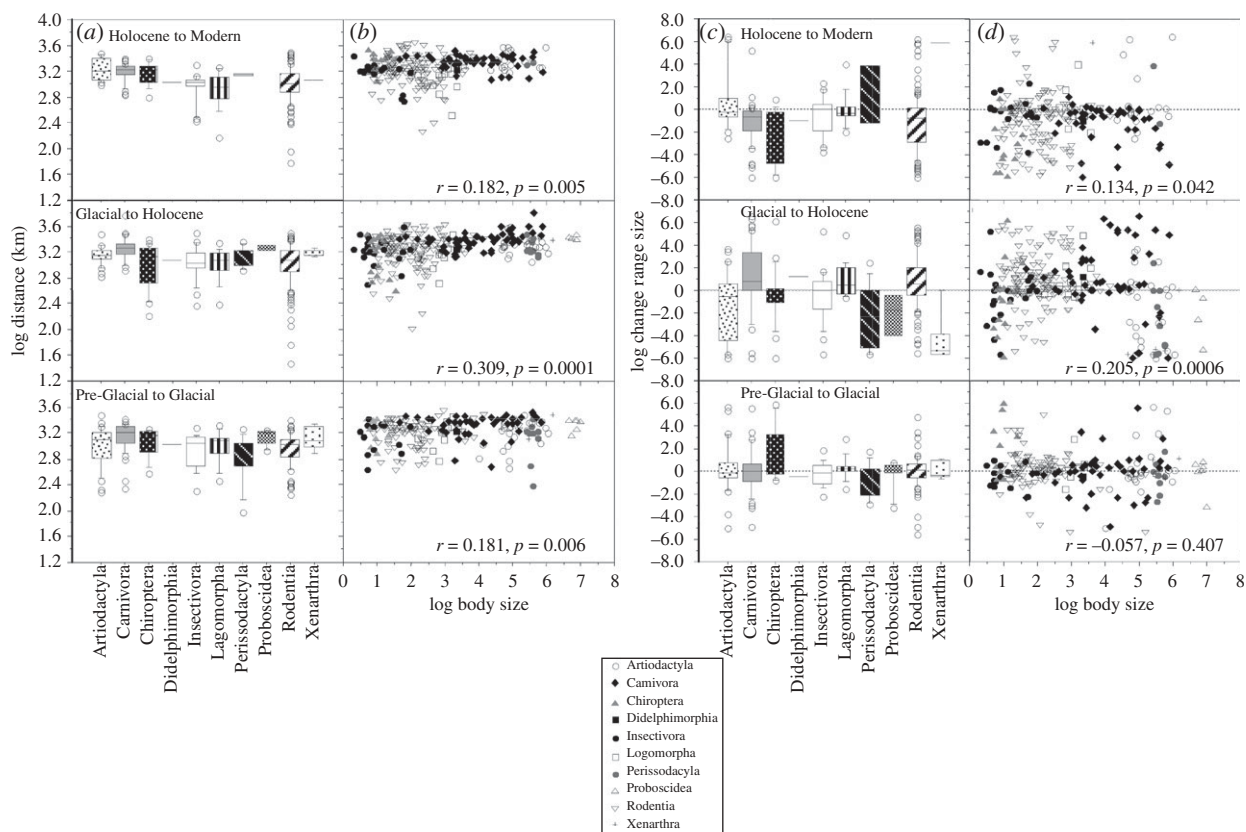
Figure 2. (*a,c*) Box plots comparing the range shifts of the different orders of mammals for each of three time transitions (Pre-Glacial to Glacial; Glacial to Holocene; Holocene to Modern). Log distance is represented in (*a*), and log change in range size is in (*c*). See table 1 and text for details. (*b,d*) Scatter plots showing relationships between the distance a species' range centroid shifted and log body size (*b*) and the log change in range size and log body size (*d*) for each of the three time transitions (Pre-Glacial to Glacial; Glacial to Holocene; Holocene to Modern). Pearson product–moment correlations indicate a significant, positive relationship between distance and body size in each transition. For the change in range size, the correlation with body size was significant for the two younger transitions, but the direction of the correlation differed.

results. The orders with significant differences are not the same from one time transition to the next. Moreover, when distance and size change are plotted against one another and coded as a function of taxonomic affinity, no differences among the orders are readily apparent (electronic supplementary material, figure S1).

(d) *What role does body size play in species range shifts?*

In all time periods, there is a weak positive association between distance shifted and body size (figure 2*b*). However, the relationship is not a straightforward linear one. Rather, the pattern mimics other macroecological patterns in which there is greater variation in the size of the centroid shifts for smaller bodied species than in the shifts for larger bodied species. The maximum distance shifted is consistent across the body size spectrum. However, larger bodied species consistently show larger shifts in distance than do smaller bodied species, and the former do not have shifts as small as the minimum shifts found in smaller bodied species. This pattern is particularly evident in the shifts from the Glacial to the Holocene and the Holocene to the present. The pattern for the Pre-Glacial into the Glacial, when the glaciers are expanding, shows more consistency across the body size distribution.

For size change, there are significant correlations with body size in the two younger time transitions (figure 2*d*). However, the correlations are both weak and inconsistent in direction. Coming out of glaciation, larger species are decreasing range size. Moving from the Holocene to the present, we have a positive correlation with larger bodied species increasing their range size. However, the relationships are very messy and the range of variation in the change in range size for small- and large-bodied species is similar. The greater number of small-bodied species when compared with large-bodied species may drive these results.

(e) *Are life-history parameters correlated with range shifts?*

In each transition, the majority of the life-history traits evaluated had a weakly positive, but significant correlation with the distance that species shifted the centroid of their range (figure 3). There were two consistent exceptions: litter size was never significant and the number of litters per year was negatively correlated with distance. Species with more litters per year had smaller distance shifts. Moreover, there was no difference in the pattern for victims or survivors of the extinction (figure 3, bottom row). Because of the size bias in the extinction, the extinct species tended to be clustered near one part of the life-history trait

Table 1. Fisher's PLSD was used to compare the range shifts of the different orders of mammals. The lower triangle contains the results for distance, and the upper triangle contains the results for change in range size. The value for mean difference is reported and bold indicates significance. A Bonferroni correction for multiple tests was applied. Order names were shortened for convenience: Artio, Artiodactyla; Carn, Carnivora; Chir, Chiroptera; Inse, Insectivora; Lago, Lagomorpha; Peri, Perissodactyla; Prob, Proboscidea; Rode, Rodentia; Xena, Xenarthra.

order	Artio	Carn	Chir	Inse	Lago	Peri	Prob	Rode	Xena
Pre-Glacial to Glacial									
Artio		0.302	−1.459	0.487	−0.044	0.898	0.539	0.230	0.105
Carn	−0.139		−1.761	0.185	−0.345	0.597	0.237	−0.072	−0.196
Chir	−0.040	0.099		1.946	1.416	**2.357**	1.998	**1.689**	1.565
Inse	0.072	0.211	0.112		−0.531	0.411	0.052	−0.257	−0.382
Lago	0.021	0.160	0.061	−0.051		0.942	0.583	0.273	0.149
Peri	0.171	**0.311**	0.211	0.100	0.151		−0.359	−0.668	−0.793
Prob	−0.132	0.007	−0.092	−0.203	−0.153	−0.303		−0.309	−0.434
Rode	0.054	**0.193**	0.094	−0.018	0.033	−0.117	0.186		−0.125
Xena	−0.110	0.030	−0.069	−0.181	−0.130	−0.281	0.022	−0.164	
Glacial to Holocene									
Artio		**−2.751**	−1.064	−1.014	−2.385	1.041	0.677	**−2.298**	2.865
Carn	−0.097		1.687	1.737	0.365	**3.791**	3.428	0.453	**5.616**
Chir	0.151	**0.248**		0.050	−1.322	2.105	1.741	−1.234	3.929
Inse	0.118	0.215	−0.033		−1.372	2.055	1.691	−1.284	3.879
Lago	0.137	0.235	−0.013	0.020		3.426	3.063	0.088	**5.251**
Peri	0.053	0.150	−0.098	−0.065	−0.085		−0.364	**−3.339**	1.824
Prob	−0.121	−0.024	−0.272	−0.239	−0.258	−0.174		−2.975	2.188
Rode	0.136	**0.233**	−0.014	0.018	−0.001	0.083	0.257		**5.163**
Xena	−0.047	0.051	−0.197	−0.164	−0.184	−0.099	0.075	−0.183	
Holocene to Modern									
Artio		1.909	**3.589**	1.237	0.733	−0.635	**1.883**	−5.106	
Carn	0.019		1.680	−0.673	−1.176	−2.544	−0.26	−7.015	
Chir	0.036	0.018		−2.353	**−2.856**	−4.225	−1.706	**−8.695**	
Inse	0.259	**0.240**	0.222		−0.503	−1.871	0.647	−6.343	
Lago	**0.285**	**0.267**	0.249	0.027		−1.368	1.150	−5.839	
Peri	0.057	0.038	0.020	−0.202	−0.229		2.518	−4.471	
Rode	**0.214**	**0.196**	0.178	−0.044	−0.071	0.042			−6.989
Xena	0.132	0.114	0.096	−0.126	−0.153	0.076	−0.082		

space, but they were not restricted in variation in the distance they shifted their ranges.

When it comes to change in range size, there were very few significant relationships with life-history traits in any of the time periods (figure 4). Moreover, there is no consistent pattern among the different time transitions. If a trait shows a significant relationship with change in range size in one transition, then it is not necessarily significant in another transition. Age at first reproduction is significantly correlated with size change in two of the three transitions (i.e. Glacial to Holocene and Holocene to Modern). However, the direction of the correlation changes: it is positively associated with size change as the glaciers were receding, but negatively associated with size change during the transition from the Holocene to present.

When the relationship between body size, life-history traits and the distance that species shifted their distribution were analysed together using a stepwise multiple regression, maximum lifespan was included in the final model in each transition (table 2). Gestation length was also important in the latter two transitions (Glacial to Holocene and Holocene to Modern), whereas weaning age and litter size were also important in the transition as the glaciers were expanding (Pre-Glacial to Glacial). The analyses of the relationship between body size, life history and the change in range size only produced a significant result for the Pre-Glacial to the Glacial. In that transition, body size and litter size came out in the final model. The other two transitions were non-significant (table 3).

(f) *What effect does geographic topography and variation in elevation have on range shifts?*

In all time periods, the distance species shifted their range centroid is consistent with expectations—species in the west have significantly smaller shifts than those in the east or that crossed from one-half of the US to the other. In fact, in all but one case eastern species were not significantly different in the amount they shifted from crossers despite the fact that crossers have the most land area available and could have the largest shifts (figure 5, left-hand column). There are no significant differences for size change (figure 5, right-hand column).

3. DISCUSSION

Understanding and predicting species range shifts as climate changes in the future is a critical area of ecology today. There are many analyses of modern data that have already found shifts in response to
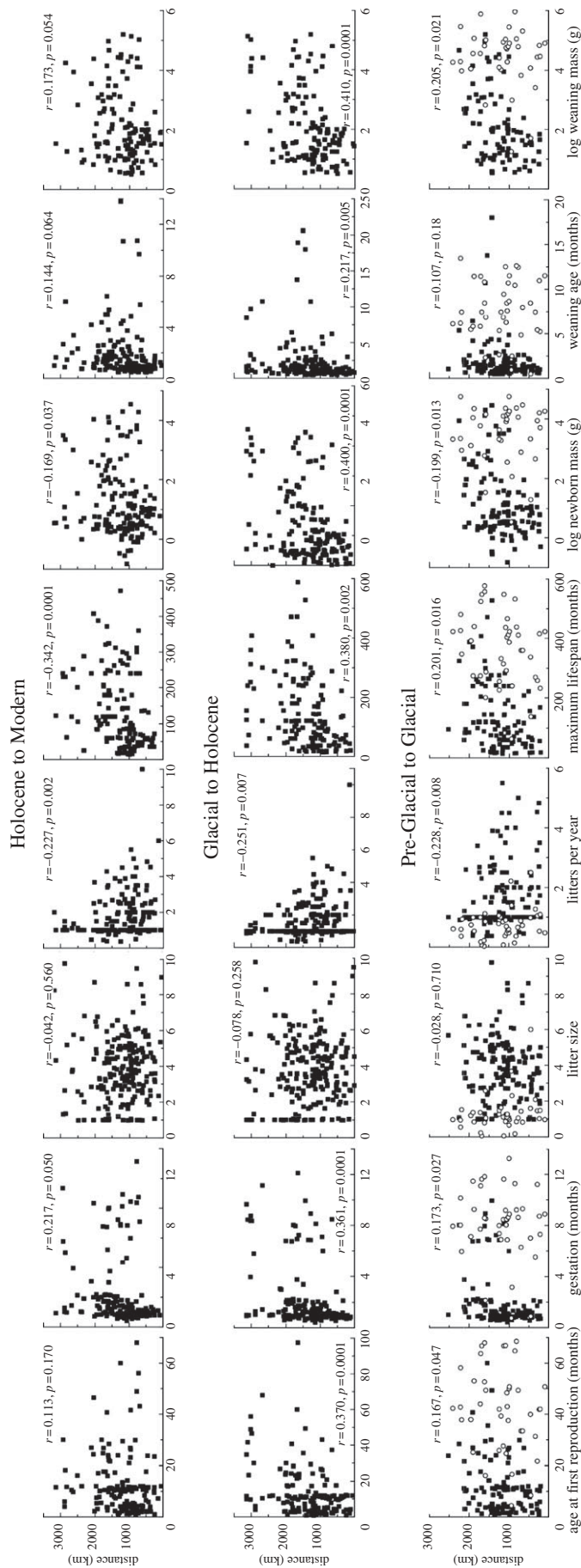
Figure 3. The relationships between shifts in range centroids and life-history traits for all transitions. The eight life-history traits are: age at first reproduction, litter size, maximum lifespan, weaning age, gestation length, number of litters per year, log newborn mass and log weaning mass. Pearson product–moment correlations were used to determine significance.
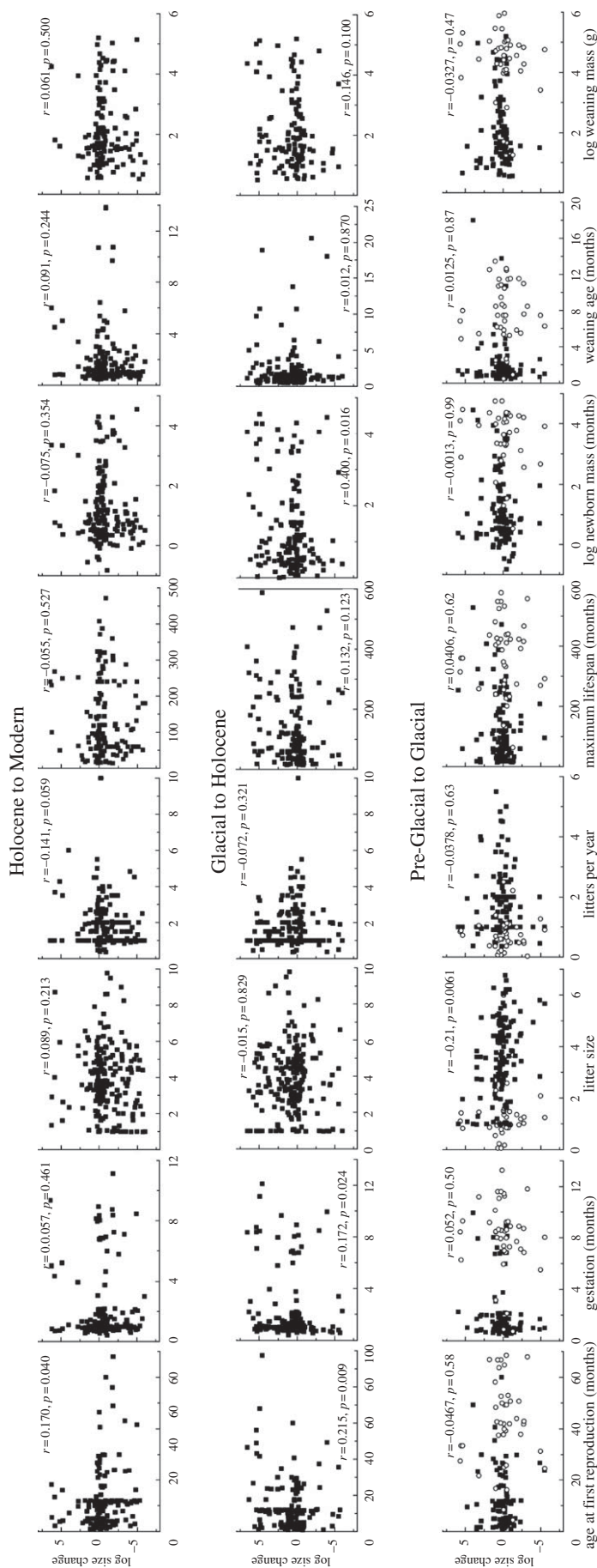
Figure 4. The relationships between log change in range size and life-history traits for all transitions. The eight life-history traits are: age at first reproduction, litter size, maximum lifespan, weaning age, gestation length, number of litters per year, log newborn mass and log weaning mass. Pearson product–moment correlations were used to determine significance.

Table 2. Results of stepwise multiple regression analyses evaluating the degree to which log body mass (g), age at first reproduction, litter size, maximum lifespan, weaning age, gestation length, litters per year, newborn mass and weaning mass influence the distance a species shifted its distribution.

transition	factors included in final model	standardized beta	significance of factors	overall F	overall p	overall r
Pre-Glacial to Glacial	maximum lifespan	0.357	<0.001	12.179	<0.0001	0.173
	weaning age	0.177	0.016			
	litter size	0.181	0.017			
Glacial to Holocene	maximum lifespan	0.194	0.006	11.735	<0.0001	0.101
	gestation length	0.191	0.007			
Holocene to Modern	maximum lifespan	0.286	<0.0001	8.680	<0.0001	0.080
	gestation length	−0.172	0.017			

Table 3. Results of stepwise multiple regression analyses evaluating the degree to which log body mass (g), age at first reproduction, litter size, maximum lifespan, weaning age, gestation length, litters per year, newborn mass and weaning mass influence the change in a species range size. For the transitions from the Glacial to the Holocene and the Holocene to the Modern, forward entry multiple regressions produced non-significant results.

transition	factors included in final model	standardized beta	significance of factors	overall F	overall p	overall r
Pre-Glacial to Glacial	litter size	−0.325	<0.0001	6.484	0.002	0.069
	log body mass (g)	−0.228	0.013			
Glacial to Holocene	none					
Holocene to Modern	none					

anthropogenic warming (Parmesan *et al.* 1999; Walther *et al.* 2002; Parmesan 2006) and many analyses using species distribution modelling to predict future ranges (Freedman *et al.* 2009; Bassler *et al.* 2010; Morueta-Holme *et al.* 2010). However, less use has been made of the natural experiment provided by the Late Pleistocene glaciation event. Many studies have documented the changes in species distributions and the subsequent effect on community structure (Graham 1986; Graham & Grimm 1990; Overpeck *et al.* 1992; Graham *et al.* 1996; Jackson & Overpeck 2000; Williams *et al.* 2001; Lyons 2003, 2005; Jackson & Williams 2004; MacDonald *et al.* 2008). Less attention has been paid to the species traits associated with range shifts (but see Roy *et al.* 2002). Our study indicates that such analyses can provide fruitful information concerning the way in which species shift their ranges and the factors associated with those range shifts. Moreover, it provides several important conclusions concerning the way in which species shift their distributions in response to climate change.

First, our analyses indicate that there is no relationship between the way in which species change the size of their distribution in response to climate change and the distance that they shift that range (electronic supplementary material, figure S1). This lack of relationship is consistent among the different orders: when range shifts are coded according to taxonomic affinity, the orders all overlap in their range shifts. In addition, change in range size is rarely significantly associated with any of the ecological traits analysed (figures 1, 2, 4, 5; tables 1 and 3). This is consistent with the large literature on the factors that

limit the size and shape of a species' distribution. The factors limiting a species' range are multifaceted and complex (Brown *et al.* 1996; Parmesan *et al.* 2005). It is not surprising that we did not find any straightforward patterns when evaluating the relationship between various ecological traits and the change in species range size. These results indicate that shifting the centroid of a range some distance and changing the size of that range are two independent ways in which species respond to climate change and they are not necessarily affected by the same ecological traits.

Second, these results indicate that vulnerability to extinction is uncorrelated with how these species were shifting their range. There is no difference in responses of the victims and survivors of the end-Pleistocene extinction event to climate change. However, this result probably says more about the causes of the end-Pleistocene extinction than it does about the effect of degree of extinction risk on range shifts. A necessary correlate of the hypothesis that climate change was a primary driver of the megafaunal extinction (e.g. Graham & Lundelius 1984; Guthrie 2003) is the prediction that victims and survivors respond differently to climate change. It is only reasonable to assume that we would expect to see differences only in the transition during which the extinction occurred and not in other intervals of climate change if, and only if, it can be shown that there was something unique about the climate during the extinction interval that did not occur during other periods of climate change. This extinction event is unique in mammalian history in terms of the magnitude and direction of the
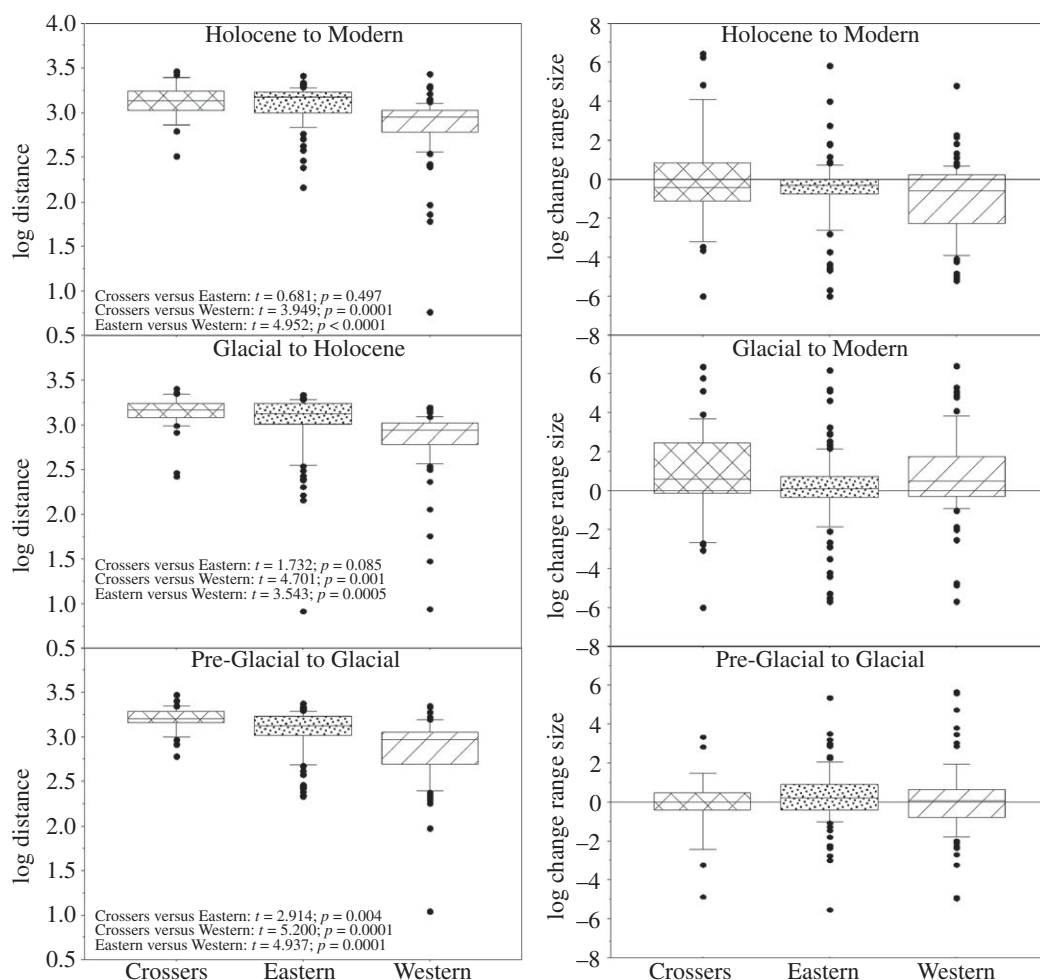
Figure 5. Box plots comparing the range shifts of species whose centroid shifts were wholly contained west of 100° W longitude (Western), species whose centroid shifts were wholly contained east of 100° W longitude (Eastern) and species whose centroid shifts crossed 100° W longitude (Crossers) for each of the three time transitions (Pre-Glacial to Glacial, Glacial to Holocene and Holocene to Modern). Student's *t*-tests were used to determine significance. The comparisons for log distance are in the left-hand column and log change in range size are in the right-hand column.

size bias (Alroy 1999). Therefore, assuming that victims and survivors would show differences only as the glaciers are receding during the last of the many glaciations during the Pleistocene requires the demonstration of something extraordinary and unique about the associated climate event. Otherwise, it is just special pleading. Even under a contrived 'tortoise and hare' scenario, where rapidly shifting species happen to be those that go extinct before shifting as far as they could, whereas slowly shifting species survive to (eventually) make equally large range shifts, requires that we see similar patterns in earlier intervals of climate change. If large-bodied species are vulnerable to extinction as a result of climate change, then we should see an effect during other climate events. In contrast, the hypothesis that anthropogenic factors were the primary driver of extinction has no such corollary predictions (e.g. Martin 1967, 1984; Martin & Steadman 1999). These results give no evidence of the former and thus provide no support for the climate hypothesis. As a result, they cannot easily be interpreted to indicate that species that are at higher risk of extinction owing to natural causes should or should not exhibit differences in their range shifts.

Third, there are no consistent systematic differences in the way in which the different orders of mammals shift their distributions, either for distance or in change in size (figure 2*a*,*c* and table 1). There are significant differences between the Carnivora and some of the other orders in terms of the distance they shift their distribution in each of the time transitions. However, other than Rodentia, the identities of the orders that are significantly different from the Carnivora are unique to each transition. Moreover, any significant differences with respect to change in range size are unique to the time transition and ordinal comparison in question. These results suggest that, in general, the different orders of mammals do not have suites of traits that predetermine a particular type or magnitude of range shift in response to climate change and are consistent with the claim that species range shifts are individualistic (e.g. Gleason 1926; Graham 1986; Graham & Mead 1987; Jackson & Whitehead 1991; Graham *et al.* 1996; Lyons 2003; Williams *et al.* 2004). That is, the way in which a species responds and shifts its distribution in response to climate change is unique to that species and is a function of the multiple factors that impact a species range.

Fourth, body size does play a role in the way in which species shift in response to climate change (figure 2b,d). In all three transitions, there is a weak, but highly significant positive correlation between the distance a species shifted its range centroid and its body size (figure 2b). This relationship is not a straightforward linear relationship, however. Rather it is the type of pattern found often in macroecological studies (e.g. Brown 1995; Gaston 2003). Small-bodied species show a great deal of variation in the distance that they shift their range, with some having range shifts as large as some of the largest species. By contrast, large-bodied species have much less variation in the distance they shifted their range. In general, large-bodied species have large range shifts with only a small number having shifts as small as the minimum shift in small-bodied species. These results are consistent with patterns found in marine invertebrates (Roy *et al.* 2001). Roy *et al.* (2001) analysed the range shifts of Californian marine bivalves from the late Pleistocene and found that large-bodied species are more likely to shift their distribution in response to climate change. Moreover, the difference was not owing to phylogenetic differences, differences in life habit, reproductive mode or larval development.

Interestingly, despite the relationship between body size and geographical range found in both modern (Brown 1995; Gaston 2003; Madin & Lyons 2005) and late Pleistocene mammals (Lyons 2005), body size does not have a consistent effect on the change in the size of species ranges (figure 2d). In the oldest transition, the relationship is non-significant. In the transition coming out of glaciation, the relationship is significant, but negative. Finally, in the transition to the present, the relationship is significant, but positive. This result is likely owing to the size of the domain of this study relative to the size of species' geographical ranges. If the geographical area being sampled is smaller than the size of the geographical ranges being estimated, then it can weaken or reverse the magnitude and direction of the body size–range size relationship (Madin & Lyons 2005). In this case, our domain is the continental United States and it is likely that the ranges of many species expand outside of this domain. Although the range sizes estimated in this study show the expected macroecological patterns in terms of range size frequency distributions and body size–range size relationships (Lyons 2005), it is possible that the discrepancy in the results of this analysis is an artefact of the geographical area available for sampling.

Fifth, in each of the transitions, the majority of life-history traits are significantly correlated with the distance a species shifts the centroid of its range (figure 3). However, there are very few significant correlations between life-history parameters and change in range size (figure 4). Interestingly, in all but one case (e.g. Holocene to Modern size change as a function of litters per year), the significant relationships between life-history traits and range shifts are in the same direction as the relationship between body size and the life-history trait in question. For example, in all transitions, there is a positive relationship between maximum lifespan and the

distance a species shifts its distribution (figure 3). Similarly, there is a positive relationship between body size and maximum lifespan. These results indicate that the significant relationships found between life-history and range shift parameters might simply be a function of the relationship between body size and range shifts.

In order to test this idea, we ran stepwise multiple regressions using either log distance shifted or log change in range size as the dependent variable, and log body size and the eight life-history parameters as the independent variables. In all three transitions, maximum lifespan remained in the final model predicting the distance a species shifted the centroid of its range (table 2). In addition, gestation length was important in the two younger transitions (Glacial to Holocene and Holocene to Modern). For the transitions during glacier expansion, weaning age and litter size were also important. Body size was not a significant factor in the final model predicting the distance shifted for any of the transitions. This suggests that although the relationships with life-history traits are in the direction expected if body size was the driving factor, body size is not, in fact, driving the relationships between life history and range shifts. Life-history traits such as maximum lifespan are also important predictor variables. In contrast, for the change in range size, none of the variables were important in the final model for the two younger transitions and only litter size and log body mass were important for the oldest transition (table 3).

The pattern among mammals contrasts with that documented for contemporaneous bivalves by Roy *et al.* (2001). For bivalves, only body size is important and large-bodied species are more likely to shift their distributions than are small-bodied species. Although body size is clearly important for mammals and larger-bodied mammals do have larger range shifts, other traits including maximum lifespan and some reproductive traits are also important predictors of the magnitude of species range shifts.

Finally, our results suggest that the availability of variation in elevational relief is likely to have an impact on species range shifts (figure 5). In particular, in areas with greater topographic variation, species will shift their ranges smaller distances than in areas with less variation. Moreover, this pattern was not mediated by body size. When we compare the body size distributions of species in each of the groups (e.g. Crossers, Eastern and Western) in each of the time periods, we found no consistent relationships (table 4). Species may be shifting their distributions up- and downslope to escape the effects of climate change or they may have smaller shifts because the mountains prove to be an unsurpassable barrier for many species. Alternatively, they may be responding differently because of differences in aridity between the two areas. The western US is generally more arid than the eastern US and some species are thought to be shifting in response to moisture gradients (e.g. Graham *et al.* 1996). In any case, topographic variation also needs to be taken into account when predicting what will happen to species ranges in the future.

Table 4. Comparisons between the body size distributions of species whose range shifts were wholly contained west of 100° W (Western), species whose range shifts were wholly contained east of 100° W (Eastern) and those whose shifts crossed 100° W (Crossers). Bold indicates significance.

comparison	Pre-Glacial to Glacial		Glacial to Holocene		Holocene to Modern	
	t	*p*	*t*	*p*	*t*	*p*
Crossers versus Eastern	**3.037**	**0.003**	0.531	0.596	0.089	0.929
Crossers versus Western	**2.548**	**0.012**	1.665	0.099	1.873	0.064
Eastern versus Western	−0.867	0.387	1.396	0.165	**2.514**	**0.013**

4. CONCLUSIONS

Our results suggest that larger-bodied species are likely to shift their distributions farther in response to climate change on average than will smaller-bodied species. This implies that species that shift longer distances do so because they have a better dispersal ability to do so, and that they are likely to perceive fewer barriers. It also suggests that smaller changes in climate might have a greater effect on perceived environmental changes, forcing them to shift farther. Smaller bodied species might be able to adapt in place more easily (Smith *et al.* 1995, 1998; Hadly *et al.* 1998; Smith & Betancourt 2003) or may perceive the environment at a scale that allows them to find suitable habitat patches more readily. Although larger-bodied mammals will probably have the best ability to shift their distributions as climate changes in the future, they may also have the greatest need to shift their distributions.

Our results also suggest that life-history parameters such as maximum lifespan and some other reproductive traits might influence species range shifts. This might be, as in the case of maximum lifespan, that a longer lifespan will allow for longer shifts over the lifetime of a single individual. This would result in a more rapid shift in range. However, this is speculative and cannot be evaluated with the data or analyses in this study.

Finally, our results suggest that topographic variation has an effect on how species shift their distributions. Species may be taking advantage of variation in elevation to escape the effects of climate change, or mountains may be a barrier to dispersal for many species. If the worst-case scenarios in climate change are borne out (IPCC 2007), then the necessary climate zones at different elevations may disappear. This could effectively doom species that shift up in elevation rather than long distances to ameliorate the effects of climate.

It must be noted that the relationships documented in this study are weak and there is a great deal of variation in range shifts that ecological traits do not explain. Thus, other factors not measured in this study must also contribute to these patterns. For example, habitat preferences, the availability of prey items and the position of barriers are all likely to be important in how species shift their distributions in response to climate change. Nonetheless, the results of this study demonstrate that body size, lifespan and elevational relief are all important factors that contribute to the distance that mammals shifted their distributions in response to the end-Pleistocene climate changes. Body size, life-history traits and geographical topography should be included in future studies designed to predict the responses of mammals to climate warming.

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