



Environmental influences on spatial and temporal patterns of body-size variation in California ground squirrels (*Spermophilus beecheyi*)

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Abstract

Aim In order to understand how ground squirrels (*Spermophilus beecheyi*) may respond to future environmental change, we investigated five biotic and environmental factors potentially responsible for explaining body-size variation in this species across California. We examined the concordance of spatial patterns with temporal body-size change since the last glacial maximum (LGM).

Location California, western North America.

Methods We quantified body size of modern populations of ground squirrels ($n = 81$) and used a model-selection approach to determine the best variables (sex, vegetation, number of congeners, temperature and/or precipitation) explaining geographical variation in body size among modern populations. We also quantified body size of one fossil population in northern California ($n = 39$) and compared temporal body-size change in *S. beecheyi* at this location since the LGM with model predictions.

Results Body size of modern populations conformed to Bergmann's rule, with larger individuals in northern (wetter and cooler) portions of California. However, the models suggest that precipitation, rather than temperature or other variables, may best explain variation in body size across modern spatial gradients. Our conclusion is supported by the temporal data, demonstrating that the body size of *S. beecheyi* has increased in northern California since the LGM, concordant with precipitation but not temperature change in the region.

Main conclusions Precipitation, rather than temperature, vegetation or number of congeneric species, was the main factor explaining both spatial and temporal patterns of body-size variation in *S. beecheyi*. The integration of space and time provides a powerful mechanism for predicting how local populations may respond to current and future climatic changes.

Keywords

Bergmann's rule, body size, California ground squirrel, climate change, last glacial maximum, North America, precipitation, *Spermophilus beecheyi*.

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INTRODUCTION

Change in body size across geographical and temporal scales is a common way in which species, particularly mammals, respond to environmental variation (Dayan *et al.*, 1991; Hadly, 1997; Ashton *et al.*, 2000; Meiri & Dayan, 2003; Smith & Betancourt, 2006). Numerous studies have identified factors that influence geographical variation in body size within

species, mainly focusing on climatic variables such as temperature and precipitation that may influence the body size of individuals through their effect on physiology (Rosenzweig, 1968; Brown & Lee, 1969; James, 1970; Klein & Scott, 1989; Olcott & Barry, 2000; Yom-Tov, 2001; Yom-Tov & Geffen, 2006). However, few generalizations have emerged, in part because the body size of individuals and populations represents the integration of diverse processes, such as life history

(Brown & Nicoletto, 1991; Brown, 1995; Haskell *et al.*, 2002), species interactions (Dayan *et al.*, 1989) and evolutionary history (Stanley, 1973; Renaud *et al.*, 1999), in addition to physiology (West *et al.*, 1997).

Much less is known about specific factors that drive temporal body-size variation (Tchernov, 1979; Smith *et al.*, 1995; Hadly, 1997). Many studies implicitly assume that if body size varies geographically along a gradient such as temperature, it may vary similarly along a temporal gradient of that variable. Some species, such as the woodrat (*Neotoma cinerea*), show remarkable concordance between spatial and temporal patterns (Brown & Lee, 1969; Smith *et al.*, 1995), whereas results for other species are mixed (Chetboun & Tchernov, 1983; Klein, 1986). For example, Chetboun & Tchernov (1983) found that the average body size of fossil populations of the jird, *Meriones tristrami*, correlated with climatic factors through time, but the relationship between the average body size of modern populations and climate was mixed. A complete understanding of both past and present drivers of body-size variation within species will allow us to make accurate predictions of species' responses to current and future environmental change.

In this study we evaluated biotic and environmental factors that may influence both spatial and temporal patterns of body-size variation within the California ground squirrel, *Spermophilus beecheyi* (Richardson, 1829). We had three overall goals: (1) to determine which biologically relevant variables best explain variation in body size across the modern geographical distribution of this species, (2) to construct a second model explaining variation in body size using time-averaged variables suitable for palaeoenvironmental comparisons, and (3) to document temporal changes in body size within *S. beecheyi* at one location in northern California over the past 20,000 years and determine qualitatively whether those changes are concordant with the modern spatial pattern.

The California ground squirrel was chosen for several reasons. First, California ground squirrels are ecological generalists whose geographical distribution spans a large latitudinal range (c. 17° latitude, Fig. 1; Tomich, 1962) and includes a wide variety of habitats and climates. The variation in their environment is also reflected by behavioural variability, as not all individuals hibernate each year in some parts of their range (Dobson & Davis, 1986). In addition, the geographical range of this species overlaps with the ranges of up to five ecologically similar congeneric species (*S. beldingi*, *S. lateralis*, *S. canus*, *S. mollis*, *S. mohavensis*), and there is high potential for biotic interactions such as competition and character displacement to shape body size within *S. beecheyi* (Chetboun & Tchernov, 1983). Finally, this species is well represented in the fossil record at one location in northern California (Fig. 1), and thus provides an excellent model species with which to investigate body-size variation through both time and space. Two fossil deposits (Potter Creek Cave and Samwel Cave in the McCloud River watershed near Lake Shasta; 40.8° N, 122.3° W) were excavated in the early 1900s, and fossils from these deposits were curated into the University

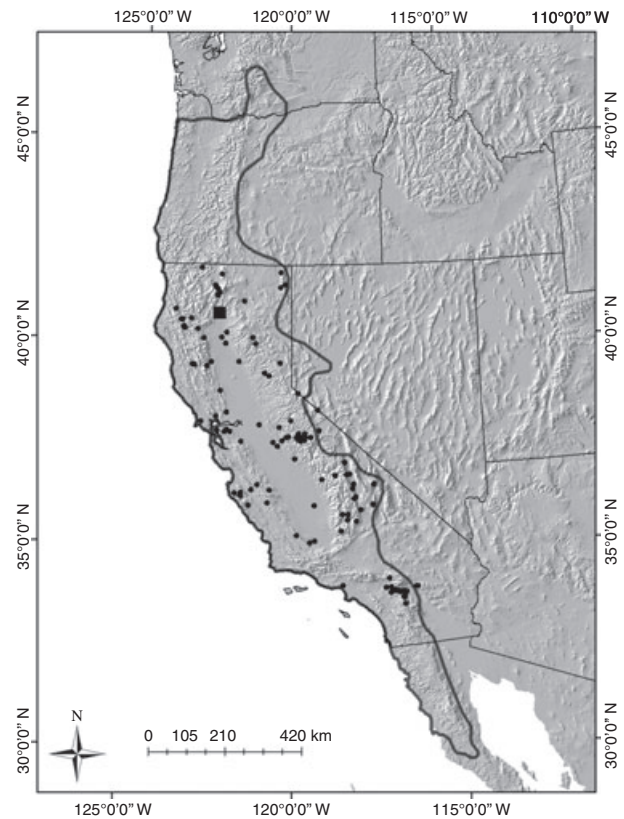


Figure 1 Geographical range of *Spermophilus beecheyi* (thick outline), showing the locations of all California samples measured for the modern study (circles) and Potter Creek and Samwel Caves (square).

of California Museum of Paleontology (Sinclair, 1904; Furlong, 1906). Modern radiocarbon analyses show that the Samwel Cave deposit dates to 17,100–23,600 cal. BC, spanning the height of the last glacial maximum (LGM) in North America (Feranec *et al.*, 2007). Potter Creek Cave is probably a similar age, based on faunal similarity with Samwel Cave (Sinclair, 1904). Both deposits contain numerous ground squirrel fossils, primarily *S. beecheyi* (Kellogg, 1912).

In order to compare body size between modern and fossil specimens, we used the mandibular diastemal length (DL) as a proxy for body size. The mandible is one of the most common bone fragments recovered in the northern California fossil localities, and other studies have shown DL to be well correlated with ecological traits such as the body size of local populations (Smith & Patton, 1988; Hadly, 1997). In general, skull and dental measurements such as DL are particularly useful because they often correlate strongly with body size in mammals (Gould, 1975; Martin, 1990; Meiri *et al.*, 2005).

MATERIALS AND METHODS

We used multiple linear regression models to investigate the first two goals of this paper: to determine which biologically relevant variables explain variation in body size across the

modern geographical distribution of this species; and to construct a model explaining variation in body size using time-averaged variables suitable for palaeoenvironmental comparisons. In this section we first outline the methods used to test the accuracy of DL as a proxy for body size, then review the variables and models used to determine which factors most influence body size. Finally, we address the third goal of the paper (to document temporal changes in body size within this species) by reviewing our calculation of change in the mean body size of *S. beecheyi* over the past c. 20,000 years in northern California.

Spatial analysis

We determined the body size of *S. beecheyi* individuals using modern and historical museum collections from the University of California Museum of Vertebrate Zoology and the University of Washington Burke Museum. We focused on individuals collected in California, which spans most of the range of the species (Fig. 1), because the majority of Oregon and Washington specimens did not have adequate locality information.

Body-size estimation

We measured the DL of *S. beecheyi* of all ages using digital calipers, and validated this measure as a proxy for body size by comparing it with body mass ($n = 205$ specimens) and body length ($n = 395$ specimens) using Pearson's product-moment correlation test (Fig. 2). Seventy-eight individuals were remeasured to quantify the measurement error. All specimens were measured by a single researcher (J.L.B.), negating cross-worker bias. For all subsequent analyses, only adult ground squirrels with adequate locality information and minimal georeferencing error (≤ 10 km) were used. Adult individuals were defined as those specimens in which the lower permanent fourth premolar (P4) was fully erupted and that have probably overwintered at least once (determined based on the date the squirrels were collected and their life cycle; Tomich, 1962).

Variables

We focused on the influence of several variables that may explain variation in body size. First, we examined the relationship between DL and geographical variables such as latitude, longitude and elevation, as these variables (particularly latitude) are used as a proxy for climate in many other studies (Ashton *et al.*, 2000; Meiri & Dayan, 2003). We also examined the influence of four biologically relevant biotic and abiotic variables, all of which have been shown to be important in other studies of body-size variation and that are directly comparable with palaeoenvironmental data: vegetation, number of congeneric species, temperature and precipitation. Sex was additionally included as a variable in all models because differences between males and females may explain a substantial amount of overall variation in body size.

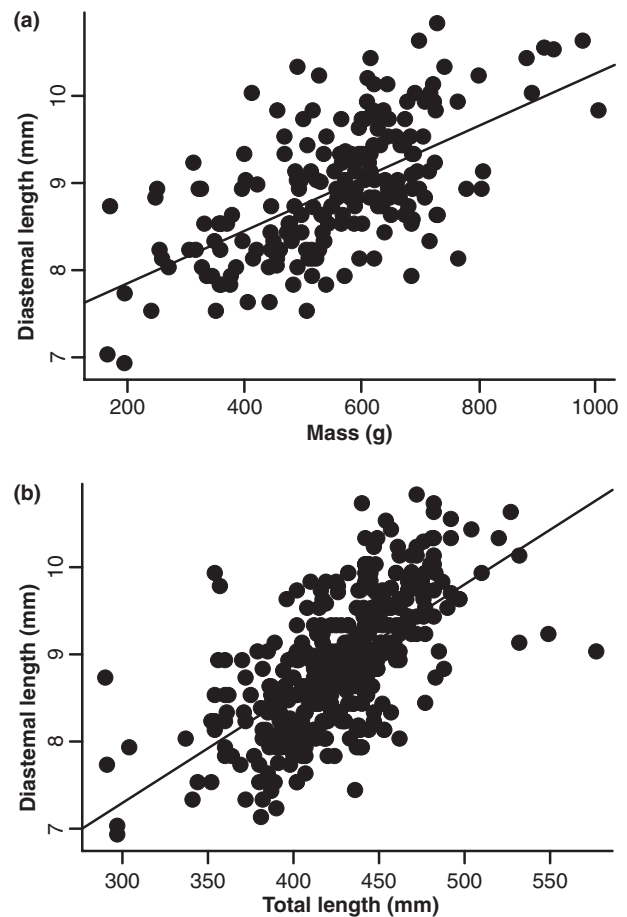


Figure 2 Diastemal length is significantly correlated with (a) body mass ($n = 205$, $r = 0.611$, $P < 0.001$) and (b) total length ($n = 395$, $r = 0.637$, $P < 0.001$) in *Spermophilus beecheyi*. The best-fit line based on linear regression is depicted.

1. Sex: we did not separate males and females in the primary analyses in order to compare our results with the palaeontological record, where males and females of this species cannot be distinguished based solely on mandible. However, we tested for differences between sexes in the slope of the regression between body size and the final variables in each model using a *t*-test (Zar, 1999). We also determined whether males and females responded similarly to spatial gradients in the other variables by reanalysing the annual model (see Models) individually for each sex.
2. Vegetation: we used a geographical information system (GIS) to associate the locality of each specimen with a vegetation type, using the CALVEG GIS layer that describes vegetation within California based on 1977 Landsat images (<http://frap.cdf.ca.gov/data/frapgisdata/select.asp>). This layer categorized vegetation into 28 vegetation types, such as coastal scrub, ponderosa pine forest or perennial grassland.
3. Number of congeners: there are presently five congeneric species within the geographical range of *S. beecheyi*: *S. beldingi*, *S. canus*, *S. lateralis*, *S. mohavensis* and *S. mollis* (Patterson *et al.*, 2005). These five species are roughly half the body size of

S. beecheyi but ecologically similar with regard to life history, habitat and resource use (Nowak, 1991). Thus the number of congeneric species potentially interacting with an individual provides a rough estimate of the magnitude of ecological pressure (e.g. competition for food) that may influence variation in body size within local *S. beecheyi* populations (Chetboun & Tchernov, 1983). We used GIS to tally the number of congeneric species whose geographical range intersected the locality of each specimen.

4. Temperature: we associated weather stations with specimens by determining the closest weather station to each specimen (up to 50 km distance) within ± 200 m elevation. We constrained our data set based on elevation as well as straight-line distance in order to account for the large differences in elevation (and therefore climate) in some parts of the geographical range of *S. beecheyi*. Fewer stations were used in the seasonal model (see Models) due to gaps in the seasonal temperature data. Our reliance on weather stations

means that these data capture broad weather and climate values rather than precise conditions at the site of collection. Both year-of-collection weather data and normalized climate data were available for California. The weather data consisted of monthly minimum, maximum and mean temperatures at a weather station from each year, dating to the late 1800s in some cases (Williams *et al.*, 2005). We determined the average temperature over the approximate lifetime of an individual by averaging the monthly temperature data from the year the individual was collected and the prior year. We then calculated the average seasonal maximum and minimum temperatures for use in the seasonal model (Table 1c). Seasonal variables, particularly seasonal maxima and minima, are more relevant to natural populations than annual measures because they determine an animal's sensitivity to climate more accurately (Badgley & Fox, 2000; O'Keefe, 2007). The climate data consisted of normalized temperature values, calculated as averages of

Table 1 Multiple linear regression models of environmental factors related to body-size variation.

	Model	Variables	Var. R^2		RSE	Adj. R^2	Significance
(a)	Geographic $n = 237$	Longitude	0.2630	–	0.6306	0.2736	***
		Latitude	0.2490	+*			
		Elevation	0.0008	–			
(b)	MAM Geographic $n = 237$	Longitude	0.2630	–***	0.6352	0.2630	***
(c)	Full seasonal $n = 65$	Sex	0.1592	**	0.5641	0.3610	**
		Total fall precipitation	0.1298	+			
		Vegetation category	0.1965				
		Total winter precipitation	0.1425	+*			
		Total spring precipitation	0.1188	–			
		Fall maximum temperature	0.0100	+			
		Winter maximum temperature	–0.0157	–			
		Spring maximum temperature	0.0113	+			
		Summer minimum temperature	–0.0124	+			
		Fall minimum temperature	–0.0159	–			
		Spring minimum temperature	–0.0158	+			
		Total summer precipitation	0.0077	+			
		Summer maximum temperature	0.0164	–			
		Winter minimum temperature	–0.0152	+			
		Number of congeners	–0.0147				
(d)	MAM seasonal $n = 65$	Sex	0.1592	***	0.5969	0.2844	***
		Total winter precipitation	0.1425	+***			
(e)	Full annual $n = 81$	Vegetation category	0.1748	**	0.5870	0.3594	***
		Sex	0.1561	***			
		Total annual precipitation	0.0451	+			
		Mean annual temperature	–0.0102	–			
(f)	MAM annual $n = 81$	Number of congeners	–0.0116	–	0.6570	0.1974	***
		Sex	0.1561	***			
		Total annual precipitation	0.0451	+*			

Model, name and sample size of model; Variables, variables included in each model; Var. R^2 , adjusted R^2 value for the variable when regressed alone with body size, followed by the sign of the partial regression coefficient of that variable with body size when included in the model and the significance of that variable in the model; RSE, residual standard error; Adj. R^2 , adjusted R^2 for the model; Significance, significance of the model.

Categories within the variable Vegetation have been collapsed for the sake of brevity. The R^2 of this variable represents the combined effect of all vegetation types; significance represents the most significant value attained by one of the vegetation types. MAM, minimally adequate model.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

monthly and annual minimum, mean and maximum temperature from 1971–2000 (National Climatic Data Center, 2002). We used mean annual temperature in the annual model (Table 1e).

5. Precipitation: weather stations were associated with specimens as described above. Year-of-collection precipitation data were not available for an adequate number of specimens, so normalized climate data were used instead for all analyses. We calculated total seasonal precipitation values for the seasonal model by summing monthly values by season (Table 1c,d) and used total annual precipitation for the annual model (Table 1e,f).

Models

We used multiple linear regression models to test the ability of three sets of variables to explain variation in body size within *S. beecheyi*. The first regression model (geographical model; $n = 237$) investigated the ability of latitude, longitude and elevation to explain variation in body size (Table 1a,b). We then considered two regression models that incorporated biologically relevant variables only. To determine the best variables explaining modern spatial gradients in body size, we created a model that incorporated biotic and habitat variables as well as seasonal measures of the weather during the lifetime of the individual (seasonal model: $n = 65$; Table 1c,d). Finally, we created a model using biotic, habitat and annual climate variables suitable for palaeoenvironmental comparison (annual model: $n = 81$; Table 1e,f). For this model we focused on annual rather than seasonal measures of climate, and normalized climate rather than year-of-collection values, because palaeoclimatic data are generally integrated over annual to decadal, rather than seasonal, time scales (Daniels *et al.*, 2005). Sample size was restricted in the seasonal and annual models relative to the geographical model by the availability of adequate temperature and precipitation data.

Statistical analysis

We investigated statistically the relative importance of each variable in explaining variation in body size using stepwise deletion of variables according to the Bayesian information criterion (BIC). We used the BIC rather than the Akaike information criterion (AIC) because data exploration demonstrated that the AIC tended to include factors in the final model that were not significant at the $\alpha = 0.05$ level, whereas the final model under the BIC selection process included only significant variables ($P < 0.05$). For each data set we reduced the initial multiple linear regression model that included all variables to a final regression model that included the most significant variables only (the minimally adequate model, MAM; Crawley, 2002). All variables in the final model were significant at $\alpha = 0.05$. Statistical analyses were done in R (ver. 2.2.1; R Development Core Team, 2005). All mean values are reported as mean \pm SD.

Temporal analysis

We measured the right mandibles of all *S. beecheyi* from the Potter Creek Cave and Samwel Cave LGM deposits using the body-size estimation methods outlined above, and combined the results from the two deposits to increase sample size. *Spermophilus* specimens from both localities are associated with extinct Pleistocene megafauna. *Spermophilus* spp. specimens were assumed to be (and probably are) *S. beecheyi* rather than *S. lateralis* or *S. beldingi*, the only other *Spermophilus* that occur in the vicinity of the caves today. The mandibular and dental morphology of *S. beldingi* is distinct from that of *S. beecheyi*, and no *Spermophilus* spp. specimens represented *S. beldingi* (Kellogg, 1912; Howell, 1938), a conclusion we corroborated during our study of the specimens. The lower jaw of *S. lateralis* is morphologically similar to that of *S. beecheyi* but is much smaller in modern samples. One adult *Spermophilus* spp. specimen was excluded from the data set because its DL was more than 6 SD below the mean DL of the LGM sample, and probably represents *S. lateralis*. It was more difficult to separate all LGM adults and juveniles, as the lower P4 was missing in many specimens. However, inclusion of both adults and juveniles in the modern sample did not alter our results (see Results). We used a two-sample *t*-test to compare the body size of *S. beecheyi* from the LGM deposits with modern *S. beecheyi* from the same latitude in California.

To test the influence of the population sex ratio on our results, we calculated the change in body size between the LGM and modern populations, assuming skewed sex ratios of the modern population. We chose sex ratios of 0.56 (14 males, 25 females) and 1.44 (23 males, 16 females) because these are similar to the lower and upper sex ratios, respectively, reported in the literature for *S. beecheyi* (Tomich, 1962; Boellstorff & Owings, 1995). We first calculated a weighted population mean based on the average size of males and females in the real modern sample and assumed that the sample variance was equal to the variance in the original modern sample. We then performed a *t*-test to compare the difference in body size between these populations and the LGM population.

RESULTS

In this section, we first review the accuracy of DL as a proxy for body size. We then summarize the results of the three models considered in the spatial analysis. Finally, we examine temporal changes in the average body size of *S. beecheyi* in northern California.

Spatial analysis

Body-size estimation

The average measurement error was 1.47% of the total DL \pm 0.01 ($n = 78$). The average DL of all modern adult *S. beecheyi* individuals (based on the geographical data set,

$n = 237$) is 8.80 ± 0.74 mm, with a range of 6.80–10.81 mm. DL is significantly correlated with both body mass ($n = 205$; $r = 0.611$, $P < 0.001$) and total length ($n = 395$; $r = 0.637$, $P < 0.001$) in *S. beecheyi* (Fig. 2). Adult males are significantly larger than adult females in this species (difference in mean DL between sexes = 0.61 mm, $t = 6.78$, $df = 202.48$, $P < 0.001$, based on the geographical data set).

Geographical model

The geographical data set contained 237 individuals (107 males and 130 females). Overall, extant *S. beecheyi* demonstrated significant variation in body size over the modern geographical gradient (Fig. 3). There was a negative relationship between body size and longitude (Table 1a; Fig. 3a; $F_{1,235} = 85.22$, adjusted (Adj.) $R^2 = 0.263$, $P < 0.001$) and a positive relationship between body size and latitude (Table 1a; Fig. 3b; $F_{1,235} = 79.26$, Adj. $R^2 = 0.249$, $P < 0.001$). There was no relationship between body size and elevation at the scale of the geographical range (Table 1a; Fig. 3c) or at the local scale when latitudes with adequate samples along an elevational gradient were examined (e.g. 33° latitude, $n = 61$, $P = 0.604$; 37° latitude, $n = 54$, $P = 0.213$). The body mass of individuals in the northern and western parts of California was *c.* 1.73 times greater than for individuals in the southern and eastern parts of the state.

Seasonal biotic model

The seasonal data set contained 65 specimens (41 males and 24 females). Twenty-three weather stations were used in the

seasonal analysis; specimens were an average of 22.78 km from a weather station. The ground squirrels in this data set were associated with 14 vegetation types, the most common being urban and agricultural land followed by annual grasslands. Using the BIC we reduced the initial 15-variable model to an MAM with two significant variables: sex and winter precipitation (Tables 1d & 2a; Fig. 4; $F_{2,62} = 13.72$, Adj. $R^2 = 0.284$, $P < 0.001$). The seasonal MAM captured most of the geographical variation in body size; residuals of the model did not show a significant relationship with latitude or longitude (seasonal MAM residuals \approx latitude: $F_{1,63} = 1.119$, Adj. $R^2 = 0.002$, $P = 0.294$; seasonal MAM residuals \approx longitude: $F_{1,63} = 1.942$, Adj. $R^2 = 0.015$, $P = 0.168$).

Annual biotic model

The annual data set contained 81 individuals (46 males and 35 females). Thirty-three weather stations were used in the annual analysis; specimens were an average of 23.30 km from a weather station. The specimens were associated with 18 vegetation types in the annual data set, the most common being urban and agricultural land followed by annual grasslands. The annual MAM included two variables, total annual precipitation (Fig. 5a) and sex, and explained *c.* 20% of the total variation in body size (Tables 1f & 2b; $F_{2,78} = 10.84$, Adj. $R^2 = 0.197$, $P < 0.001$), somewhat less than the full model (Table 1e; Adj. $R^2 = 0.359$). The final annual model did not capture all the geographical variation in body size (annual MAM residuals \approx latitude: $F_{1,79} = 8.976$, Adj. $R^2 = 0.091$, $P = 0.004$; annual MAM residuals \approx longitude: $F_{1,79} = 14.71$, Adj. $R^2 = 0.146$, $P < 0.001$).

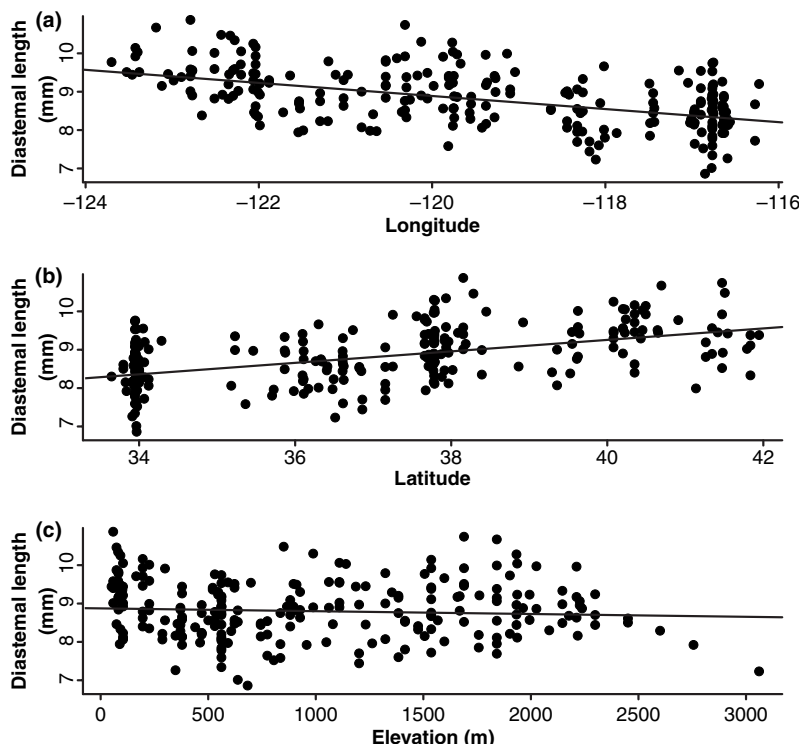


Figure 3 There is (a) a negative relationship between diastemal length (DL) and longitude ($F_{1,235} = 85.22$, Adj. $R^2 = 0.263$, $P < 0.001$); (b) a positive relationship between DL and latitude ($F_{1,235} = 79.26$, Adj. $R^2 = 0.249$, $P < 0.001$); and (c) no relationship between DL and elevation ($F_{1,235} = 1.19$, Adj. $R^2 = 0.001$, $P = 0.276$) in *Spermophilus beecheyi* ($n = 237$).

Table 2 Statistical summary of variables included in the seasonal and annual minimally adequate models (MAM).

	Model	Variables	Coefficient	Error	<i>t</i>	<i>P</i>
(a)	MAM seasonal <i>n</i> = 65	Intercept	8.1232	0.2108	38.532	<.0001
		Sex	0.5648	0.1538	3.673	0.0005
		Total winter precipitation	0.0583	0.0168	3.466	0.001
(b)	MAM annual <i>n</i> = 81	Intercept	8.3494	0.1707	48.903	<.0001
		Sex	0.5896	0.1475	3.998	0.0001
		Total annual precipitation	0.0047	0.0021	2.25	0.0273

Variables, all variables included in the MAM; Coefficient, partial regression coefficient; Error, standard error estimate for the coefficient of each variable. Statistical information for the overall model is included in Table 1.

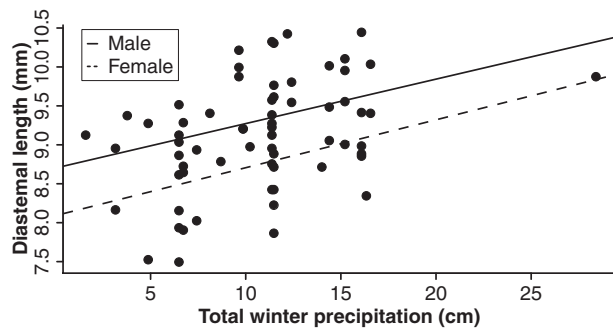


Figure 4 Relationship between diastemal length (DL) and total winter precipitation in the seasonal MAM for both male and female *Spermophilus beecheyi*. There is a significantly positive relationship between DL and total winter precipitation (males: $n = 41$, $F_{1,39} = 6.363$, Adj. $R^2 = 0.118$, $P = 0.016$; females: $n = 24$, $F_{1,22} = 7.255$, Adj. $R^2 = 0.214$, $P = 0.013$). There is no significant difference in the slope of the relationship between DL and total winter precipitation between males and females ($t = -0.007$, $df = 61$, $P > 0.05$).

Differences between sexes

As males were significantly larger than females, we examined whether the patterns noted above were driven by sex. First, we determined the percentage of males associated with each weather station and examined the relationship between the percentage of males at a weather station and the geographical variables. No significant relationship was found between the percentage of males and latitude, longitude or elevation, suggesting that there is no capture bias by sex. Additionally, the slope of the relationship between DL and winter precipitation (seasonal model) or annual precipitation (annual model) was not statistically different between males and females (seasonal model: $t = -0.007$, $df = 61$, $P > 0.05$, Fig. 4; annual model: $t = 0.004$, $df = 77$, $P > 0.05$). Finally, to examine further whether concordance between spatial and temporal comparisons was driven by differences between the sexes, we re-examined the annual model separately for males and females. The body size of both males and females was significantly and positively related to precipitation only (males: $F_{1,43} = 5.938$, Adj. $R^2 = 0.101$, $P = 0.019$; females: $F_{1,31} = 13.86$, Adj. $R^2 = 0.2866$, $P < 0.001$). We did not

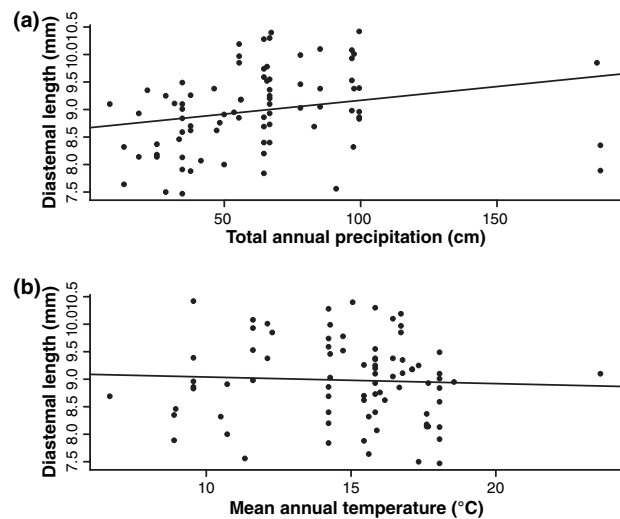


Figure 5 There is (a) a positive relationship between diastemal length (DL) and total annual precipitation ($F_{1,79} = 4.777$, Adj. $R^2 = 0.045$, $P = 0.032$) and (b) no relationship between DL and mean annual temperature ($F_{1,79} = 0.192$, Adj. $R^2 = -0.010$, $P = 0.663$) in *Spermophilus beecheyi* from California ($n = 81$).

re-examine the seasonal model separately for males and females because the statistical power to discriminate between important variables was low due to the large number of variables relative to sample size.

Temporal analysis

The LGM sample contained 39 specimens, with an average DL of $8.90 \text{ mm} \pm 0.63$. The modern sample from the same latitude consisted of 39 individuals (19 males and 20 females) collected from 22 sample localities across 47 years. There was no relationship between DL and longitude or elevation in these individuals. We found that the average body size was significantly smaller in the ancient ground squirrel sample from the LGM than in modern individuals from the same latitude (Fig. 6; $t = -4.000$, $df = 76$, $P < 0.001$). This pattern was robust to age-class effects, because the inclusion of juveniles from modern populations resulted in a similar difference between ancient and modern individuals

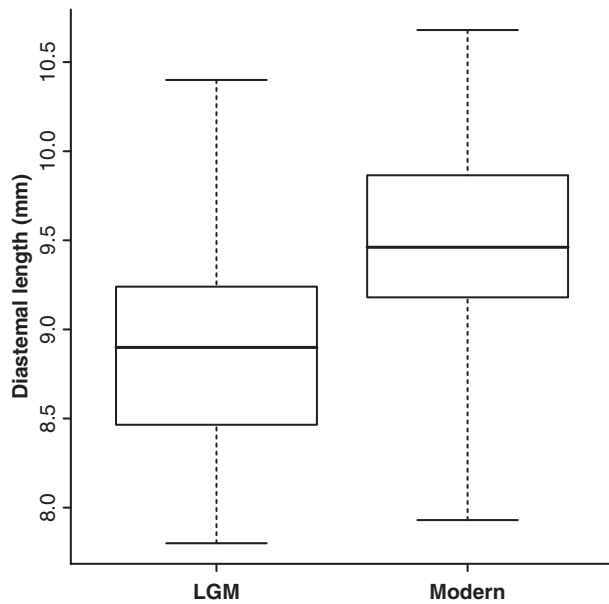


Figure 6 Diastemal length (DL) of *Spermophilus beecheyi* from the last glacial maximum (LGM; $n = 39$) and modern *S. beecheyi* from the same latitude in California ($n = 39$). The mean DL is significantly larger in modern squirrels than in squirrels from the LGM ($t = -4.000$, $df = 76$, $P < 0.001$). The extreme upper and lower horizontal lines represent the upper and lower range of DL, respectively, in each sample. The lower and upper edges of the box represent the first and third quartiles, respectively, and the horizontal line in the middle of the box is the mean DL.

($t = -3.019$, $df = 103$, $P = 0.003$). This pattern was also robust to the effects of sex. In both tests with a skewed sex ratio, modern ground squirrels remained significantly larger than ancient ground squirrels (sex ratio = 0.56: $t = 3.275$, $df = 76$, $P < 0.002$, sex ratio = 1.44: $t = 4.581$, $df = 76$, $P < 0.001$).

DISCUSSION

Spermophilus beecheyi demonstrates a significant amount of geographical, local and temporal variation in body size throughout California (Figs 3–6), and we sought to identify the main factors responsible for this variation. We found that *S. beecheyi* conforms to Bergmann's rule, a pervasive empirical pattern (Ashton *et al.*, 2000; Meiri & Dayan, 2003) first proposed by Bergmann and reframed by Rensch (1938), whereby individuals in colder regions are larger than conspecifics in warmer regions. The mechanism responsible for Bergmann's rule was thought to be energetic limitations related to heat retention and thus environmental temperature (Rensch, 1938; Mayr, 1956), but support for this mechanism has been mixed. While some studies have corroborated the importance of temperature in explaining body-size variation in mammals and birds (Brown & Lee, 1969; Smith & Betancourt, 1998; Ashton *et al.*, 2000), other studies have found that factors such as precipitation, primary production and food availability are more important (Rosenzweig, 1968; James,

1970; Yom-Tov & Yom-Tov, 2005; Yom-Tov & Geffen, 2006). In *S. beecheyi*, temperature does not explain a significant amount of the variation in body size when considered alone (Fig. 5b), and our analyses demonstrate that temperature may not be the best single factor explaining both spatial and temporal patterns of body-size variation.

Correlates of body-size variation

Sex is a significant variable in all our final models (Tables 1 & 2) due to the significantly larger size of males relative to females. However, sex explains local rather than geographical variation in body size. The sex ratio of individuals associated with weather stations does not vary with latitude, and the body size of males and females responds similarly to changes in precipitation, indicating that differences between the sexes do not drive the overall geographical patterns in body-size variation.

We used an explicit model-testing framework to tease apart the relative effects of the four remaining biotic and environmental variables that may explain the geographical pattern of variation in body size exhibited by *S. beecheyi* (temperature, precipitation, vegetation and number of congeners). Similar to the results of Rosenzweig (1968), we found that the presence or absence of congeneric species was not as important as the environmental variables in explaining the modern body-size gradient. Vegetation and temperature also were not significant variables in the final models. Instead, precipitation emerged as the most important variable for explaining variation in body size within *S. beecheyi*.

The seasonal MAM showed that winter precipitation was the most important climatic variable explaining variation in body size across the modern geographical distribution of *S. beecheyi*. The importance of precipitation in our analyses is similar to the findings of James (1970), Wigginton & Dobson (1999) and Yom-Tov & Geffen (2006), who found that precipitation, both alone and in combination with temperature, played a role in explaining variation in body size in birds and mammals. Similar to the mammalian studies by Wigginton & Dobson (1999) and Yom-Tov & Geffen (2006), and in contrast to the avian study by James (1970), our results show that larger individuals of *S. beecheyi* were found in moist rather than dry environments. While particular life-history traits of individual species may tip the balance in favour of temperature vs. precipitation in explaining the pattern, the generality of precipitation as a driver across major taxonomic categories suggests that it must have an important effect on variation in body size.

The results of the annual model were concordant with the seasonal model: the major climatic factor explaining geographical patterns of body-size variation within *S. beecheyi* was precipitation. In the final seasonal and annual models, the relationship between precipitation and body size was positive (Table 2), indicating that increased precipitation was positively related to larger body size in *S. beecheyi*. We chose to measure precipitation rather than primary productivity so that the models were most comparable with palaeoenvironmental data. However, due to the strong correlation between precipitation

and primary production (Fang *et al.*, 2001; Knapp *et al.*, 2006), precipitation may reflect the importance of primary production and overall forage availability in structuring body size within this species, rather than the direct impact of rainfall on organisms. For example, in California grasslands (one of the vegetation types strongly associated with *S. beecheyi*), winter precipitation is positively correlated with March plant cover (Pitt & Heady, 1978) and thus possibly the availability of food resources for squirrels. Other support for the influence of precipitation on body size in ground squirrels in particular includes the amount of snow cover, which influences whether California ground squirrels hibernate or remain active during the winter (Dobson & Davis, 1986), and increased green forage that may lead to greater overwinter fasting endurance (Millar & Hickling, 1990; Humphries *et al.*, 2003). While the specific mechanisms remain anecdotal, the final models demonstrate the ultimate importance of precipitation rather than temperature in structuring variation in body size within this species.

Additional sources of variation

A substantial amount of variation in body size was unexplained in all models. For example, the seasonal MAM captured only 28% of the variation in body size within *S. beecheyi*, leaving 72% unaccounted for in this model. However, our goal was not to explain all sources of body-size variation within this species, but rather to focus on geographical variation in body size. In this regard, the seasonal MAM performed well. The residuals of the final seasonal model did not vary with latitude or longitude, indicating that the seasonal MAM captured most of the geographical variation in body size.

The substantial amount of variation remaining can be attributed to age, year of collection and seasonal differences in body size, among other sources. For example, we probably were not able to eliminate all juveniles conclusively, due to our reliance on museum specimens and literature about the timing of ontogenetic shifts in the life cycle of California ground squirrels (Tomich, 1962). Additionally, ground squirrels exhibit substantial differences in body size and weight throughout their lifetime, and even some differences in DL in individuals older than 1 year (Hall, 1926; Tomich, 1962). For example, the average body mass in one population of ground squirrels increased *c.* 67-fold for males and *c.* 56-fold for females between birth and adult stages (Tomich, 1962), compared with a *c.* twofold increase in body mass between southern and northern populations of ground squirrels in California. Finally, specimens were collected over a 100-year period. While no historical changes in body size were found in our data sets, temporal averaging of samples was an additional source of variation. Additional studies of the sources of local variation in body size within this species are clearly needed.

Temporal change in body size

The body size of California ground squirrels in northern California is significantly larger today than during the LGM.

This was the result of a roughly 6% shift in the mean DL of individuals and translates to a *c.* 190-g increase in body mass, based on the DL/body mass relationship shown in Fig. 2. The body-size increase was not the result of a larger number of juveniles in the ancient sample, as adding juveniles to the modern sample did not significantly alter the size increase. It was also not solely the result of differences in the sex ratio of modern and ancient samples, as there is no *a priori* reason to assume that the ancient sample of ground squirrels contained a biased sex ratio. The sex ratio of modern populations of *S. beecheyi* is variable, with several studies reporting sex ratios (males : females) from 0.50 to 1.5 (Evans & Holdenried, 1943; Fitch, 1948; Tomich, 1962; Dobson, 1983; Boellstorff & Owings, 1995). We tested the influence of sex ratio using the modern sample with known body sizes for males and females. In both cases with a skewed sex ratio, even the conservative case of few large males and many small females, the mean body size of modern ground squirrels is still larger than that of squirrels from the LGM. This indicates that it is highly unlikely that variation in sex ratio alone is driving the change in body size between the LGM and today.

There was some amount of both spatial and temporal averaging of body size. The body size of modern specimens was spatially averaged within a latitudinal band encompassing Potter Creek and Samwel Caves due to limited specimens in the immediate vicinity of the caves, so the ground squirrels were sampled from a wide range of elevation and habitat types found locally. Additionally, radiocarbon analyses of the fossil deposits indicate that samples are from the LGM (Feranec *et al.*, 2007), but the deposits span several thousand years (17,100–23,600 cal. BC). However, both spatial and temporal averaging should act to reduce statistical differences in body size between populations sampled from multiple time points and from multiple localities because the variability of the samples would increase.

Overall, the significantly larger body size of modern squirrels is likely to be real, and not due to artefacts of taphonomy, sex or spatial/temporal averaging. Our data do not address whether the increase in body size is due to *in situ* population change or population movement, but both mechanisms of body-size change could be the result of climatic change in the region. For example, a population adapted to higher latitudes could have moved into the region, replacing the population present during the LGM, or the local population could have adapted to the change in precipitation regime, increasing overall size. Ancient genetic sampling to compare the genotypes of the surrounding populations would help to differentiate which of these two hypotheses is most reasonable.

Spatial-temporal comparisons

It remains difficult to make quantitative predictions about temporal body-size change using the annual model because of the lack of quantitative precipitation values in the palaeoenvironmental literature. However, we can make qualitative predictions based on the positive relationship between body

size and precipitation (Table 1f; Fig. 5a). High-quality palaeoenvironmental data such as pollen and charcoal analysis (Daniels *et al.*, 2005), and alkenone sea surface temperatures and CaCO₃ percentage (Barron *et al.*, 2003), are available for the region surrounding Potter Creek and Samwel Caves. All available palaeoenvironmental studies show that the climate at the height of the LGM in northern California was much drier and colder than today (Adam & West, 1983; Mohr *et al.*, 2000; Barron *et al.*, 2003; Briles *et al.*, 2005; Daniels *et al.*, 2005). If we contrast predictions based on temperature vs. precipitation, two of the most common variables postulated to drive variation in body size, we would expect opposite patterns of temporal change in body size. Based on the negative relationship between temperature and body size in our full annual model (Table 1e; Fig. 5b), which is consistent with traditional energetic drivers of variation in body size, we predict that the average body size of modern squirrels would be smaller than that of LGM squirrels. However, our annual MAM contains precipitation as the single factor explaining geographical variation in body size (Tables 1f & 2b) and predicts that ground squirrels are larger on average today than they were during the LGM. The temporal data show that body size has increased in northern California since the LGM (Fig. 6), in support of precipitation as the main driver of body-size change in this species rather than temperature. Thus, while palaeoenvironmental data show that both temperature and precipitation have changed over the past 20,000 years, using ground squirrels as a palaeoenvironmental proxy demonstrates that precipitation changed much more profoundly in northern California than did temperature.

CONCLUSIONS

In summary, *S. beecheyi* shows a strong pattern of body-size variation over both spatial and temporal gradients. Our results suggest that precipitation, rather than temperature, vegetation or number of congeneric species, is the primary factor driving both patterns, and that the processes structuring body size across California today may be responsible for structuring body size over the past 20,000 years. The integration of both spatial and temporal patterns of body-size change provides a powerful mechanism for predicting how local populations may respond to current and future climatic changes. Precipitation is the most reliable factor to use in the case of this species, and possibly of other small mammals, when predicting how body size may change in response to current and future climatic change. Precipitation is underappreciated in studies of future environmental change, in part because it is less predictable than temperature change in many models, but it may emerge that the dynamics of moisture far outweigh the effects of temperature change.

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