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Morphological and dietary responses of chipmunks to a century of climate change

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Abstract

Predicting how individual taxa will respond to climatic change is challenging, in part because the impacts of environmental conditions can vary markedly, even among closely related species. Studies of chipmunks (*Tamias* spp.) in Yosemite National Park provide an important opportunity to explore the reasons for this variation in response. While the alpine chipmunk (*T. alpinus*) has undergone a significant elevational range contraction over the past century, the congeneric and partially sympatric lodgepole chipmunk (*T. speciosus*) has not experienced an elevational range shift during this period. As a first step toward identifying the factors underlying this difference in response, we examined evidence for dietary changes and changes in cranial morphology in these species over the past century. Stable isotope analyses of fur samples from modern and historical museum specimens of these species collected at the same localities indicated that signatures of dietary change were more pronounced in *T. alpinus*, although diet breadth did not differ consistently between the study species. Morphometric analyses of crania from these specimens revealed significant changes in cranial shape for *T. alpinus*, with less pronounced changes in shape for *T. speciosus*; evidence of selection on skull morphology was detected for *T. alpinus*, but not for *T. speciosus*. These results are consistent with growing evidence that *T. alpinus* is generally more responsive to environmental change than *T. speciosus*, but emphasize the complex and often geographically variable nature of such responses. Accordingly, future studies that make use of the taxonomically and spatially integrative approach employed here may prove particularly informative regarding relationships between environmental conditions, range changes, and patterns of phenotypic variation.

Keywords: chipmunks, climate change, morphometrics, stable isotopes, *Tamias*, Yosemite

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Introduction

Anthropogenically induced climate change is significantly impacting biodiversity on a global scale (IPCC, 2014). Studies from multiple ecosystems across a diversity of geographic regions are revealing climate-driven changes in the distribution of numerous taxa, including extinctions and range shifts for mammals, birds, insects, and plants (Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006; Chen *et al.*, 2011; Staudinger *et al.*, 2013). Such work also indicates that responses to environmental changes vary widely, even among closely related species. For example, although studies of range shifts frequently report general patterns, such as upward contraction of elevational ranges, that are consistent with climate-based expectations, more detailed

inspection of the underlying data reveals that individual species are moving upwards, downwards, or not at all (Le Roux & McGeoch, 2008; Lenoir *et al.*, 2008; Tingley *et al.*, 2012; Rowe *et al.*, 2014). Understanding the reasons for this variability is critical as such differences in response have important implications for preserving current biotic communities as well as predicting future changes to global biodiversity.

Studies of chipmunks (*Tamias* spp.) from the Sierra Nevada mountains of California provide an important opportunity to explore the factors underlying differences in response to changing climatic conditions among closely related (congeneric) species. Comparisons of historic and modern distributions have revealed that while the alpine chipmunk (*T. alpinus*) has experienced a marked upward contraction in elevational range over the past century, the lodgepole chipmunk (*T. speciosus*) has undergone effectively no change in its elevational range (Moritz *et al.*, 2008). Although these species are partially sympatric in many parts of their ranges, they are believed to differ in their

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degree of ecological specialization. While *T. alpinus* is thought to be restricted to high-elevation alpine habitats, *T. speciosus* occurs in a variety of habitats extending from tree line down through several types of forest (Grinnell & Storer, 1924; Best *et al.*, 1994; Clawson *et al.*, 1994). Efforts to model elevational distributions of these species indicate that the upward range contraction of *T. alpinus* over the past century is associated with the changes in abiotic conditions such as temperature (Rubidge *et al.*, 2011; Rowe *et al.*, 2014). In contrast, no clear environmental predictor of the distribution of *T. speciosus* has been identified (Rubidge *et al.*, 2011). More detailed comparisons of these species including detailed analyses of their interactions with environmental conditions have not been made.

As a first step toward identifying ecological and other differences that may have contributed to the distinct elevational responses reported for *T. alpinus* and *T. speciosus*, we examined the patterns of dietary and morphological change in these species over the past century. A species' diet provides a direct link to its environment and has important implications for numerous other aspects of its biology, including physiology, behavior, and morphology. Both *T. alpinus* and *T. speciosus* are omnivorous, with plants as a major portion of their diet (Best *et al.*, 1994; Clawson *et al.*, 1994). Over the past century, the vegetation in montane regions of California has changed significantly with respect to elevational distributions (Crimmins *et al.*, 2011) and relative abundance of individual plant taxa (Kopp & Cleland, 2014), as well as landscape-scale changes in vegetation types and structure (Thorne *et al.*, 2008; McIntyre *et al.*, 2015), suggesting that diets of these chipmunk species also may have changed. The greater ecological specialization of *T. alpinus* predicts that it may have undergone a more extreme dietary shift than *T. speciosus*. Alternatively, given the greater elevational range response by this species, *T. alpinus* may have experienced less dietary change over time if the upward contraction of its range tracks comparable changes in preferred food resources.

In addition to dietary changes that may have occurred, an animal's morphology can change, too. The skull is a complex structure that is involved in multiple essential functions, including protection of the brain, regulation of water loss, and feeding (Hanken & Hall, 1993; Elbroch, 2006). Multiple studies report the correlations between key elements of skull morphology and environmental conditions (Patton & Brylski, 1987; Monteiro *et al.*, 2003; Caumul & Polly, 2005; Grieco & Rizk, 2010), including changes in skull size (Burnett, 1983; Yom-Tov & Nix, 1986; Wigginton & Dobson, 1999; Millien *et al.*, 2006; Eastman *et al.*, 2012), rostral structure (Pergams & Lawler, 2009), and dentition (Caumul &

Polly, 2005) in relation to environmental changes. Identifying causal links between morphology and the environment is more challenging, as relationships may arise due to either adaptive modification of skull structure or genetic drift. Efforts to quantify selection on cranial characters may therefore be useful in elucidating the mechanisms by which environmental conditions bring about morphological change. If *T. alpinus* has experienced greater dietary change over the past century, and if shifts in diet have altered the selection of skull traits, we expect morphology in this species to show a greater variation over time than in *T. speciosus*. If, however, range contraction by *T. alpinus* has resulted in greater conservation of historical diets, then evidence of morphological change may be greater for *T. speciosus*.

To test predictions regarding temporal changes in diet and skull morphology, we compared the specimens of *T. alpinus* and *T. speciosus* collected at the same localities in the central and southern Sierra Nevada over a period of approximately 100 years. Specifically, to examine potential dietary changes, we used stable carbon and nitrogen isotope analyses of hair samples from these specimens to characterize the two-dimensional (C vs. N) diet space that is determined by the combination of food items animals consumed in the historical and modern eras (Ben-David & Flaherty, 2012a). To investigate the changes in morphology over the same time period, we used classic and geometric morphometric techniques to quantify skull size and shape in these specimens. To assess the potential interactions between these traits, we used multivariate statistical models to explore the associations between environmental conditions and the patterns of dietary and morphological change. Our goal was to generate important insights into potentially causal relationships between environment, ecology, and morphology while also advancing our fundamental knowledge of the biology of these two chipmunk species.

Materials and methods

Specimens examined

For both dietary and morphometric analyses, we used specimens of *T. alpinus* and *T. speciosus* housed in the Museum of Vertebrate Zoology at the University of California, Berkeley. Historic museum specimens were collected as part of a California-wide survey of vertebrate fauna conducted by Joseph Grinnell and colleagues from 1911 to 1920. Modern specimens were collected as part of the Grinnell Resurvey Project (GRP), an intensive resampling of Grinnell's historic sites that occurred from 2003 to 2012 (Moritz *et al.*, 2008; Rowe *et al.*, 2014). When available, additional (non-GRP) modern specimens from the same localities were included in our analyses.

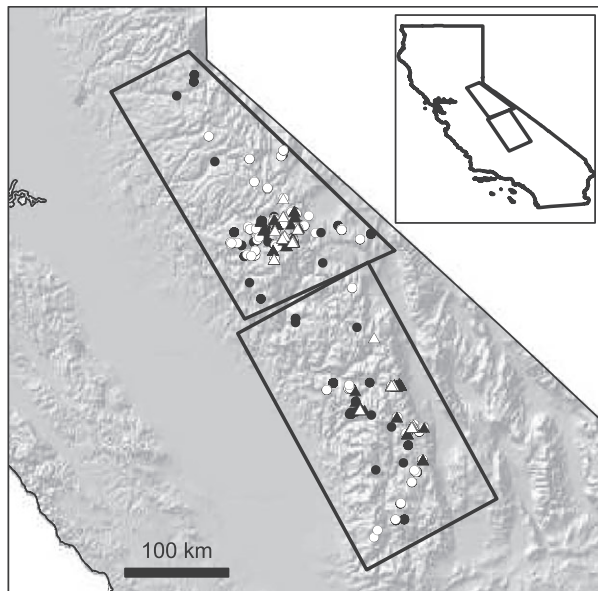


Fig. 1 Location of sampling sites within California. Locations from which we sampled one or more individuals for use in morphological and/or diet analyses are shown in black (historical era) or white (modern era) for *T. alpinus* (triangles) and *T. speciosus* (circles). Black boxes show general areas of GRP sampling for the Yosemite transect (further north) and the Southern Sierras transect. Interspecific overlap exists in both eras, with *T. alpinus* and *T. speciosus* co-occurring at 8 of 47 historical sites and 11 of 43 modern sites.

Two areas were targeted for study based on the availability of modern and historical material: Yosemite and the Southern Sierras (Fig. 1). *Tamias alpinus* occurs in both of these areas. Although *T. speciosus* also occurs in both areas, it is represented by two subspecies, *T. s. frater* in Yosemite and *T. s. sequoiensis* in the Southern Sierras.

Evidence of climatic change

To characterize general patterns of climatic change in Yosemite and the Southern Sierras over the past century, we extracted temperature and precipitation data for the capture location of each specimen from the WorldClim database (Hijmans *et al.*, 2005). The capture locality and elevation for each specimen were obtained from the MVZ's Arctos database (<http://arctos.database.museum/>). We used the methods of Moritz *et al.* (2008) to aggregate localities for specimens that were captured within 2 km (linear distance) and 100 m elevation of each other. For each aggregated locality, we used decadal averages from 1900 to 1909 to calculate climatic values for the historical era and decadal averages from 1990 to 1999 to calculate values for the modern era. For each era, mean temperature and precipitation values for the Yosemite transect were obtained by averaging annual mean temperatures and annual precipitation totals across all aggregated localities; the same procedure was used to calculate mean historical and modern climatic values for the Southern Sierras transect. Cli-

matic data from different eras and locations were compared using two-sample *t*-tests, as executed in the statistical program R (R Core Team, 2013).

Dietary analyses

To compare the modern and historical diets of *T. alpinus* and *T. speciosus*, we conducted stable carbon and nitrogen isotope analyses of hair samples collected from museum specimens of these species. These analyses make use of variation in the relative abundance of the stable forms of carbon (^{12}C and ^{13}C) and nitrogen (^{14}N and ^{15}N) laid down in the hair of these animals that has its origin in the diet items they had consumed. The stable isotope composition of different tissues can be used to identify the combination of food resources consumed over different temporal scales (Kelly, 2000; Fry, 2006). For mammals, analyses of the stable isotope composition of hair provide an efficient and biologically appropriate means of characterizing the combination of food resources consumed since the last molt (reviewed in Ben-David & Flaherty, 2012a,b). To characterize the diets of *T. alpinus* and *T. speciosus*, we obtained hair samples from 217 historic and 208 modern specimens of these species housed in the MVZ (Table 1a, Table S1). These individuals represented 74 localities corresponding to or occurring in close proximity to GRP sampling localities. Samples were collected by cutting a small amount ($\sim 1 \times 1$ mm patch) of hair from near the rump of each specimen. After collection, samples were washed in a mixture of methanol and chloroform to remove contaminants (O'Connell *et al.*, 2001) and then air-dried for a minimum of 24 h. Samples were weighed on a microbalance ($+0.000001$ g; Mettler Toledo, Columbus, OH, USA), and 1.4–1.6 mg of material was packaged into tin capsules (Costec Inc., Valencia, CA, USA).

The stable isotope composition of hair is expressed in 'delta [δ] notation' as,

$$\delta^h X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000,$$

where *X* is the element of interest, *h* is the stable isotope with the high mass number, and *R* is the ratio of the heavy to light isotope composition that the sample or standard contains (see Dawson *et al.*, 2002). The final values are expressed in units of part per thousand, or per mil (‰); therefore, C isotope compo-

Table 1 Sample sizes for (a) dietary analyses and (b) morphology

	Historical		Modern	
	Southern Sierras	Yosemite	Southern Sierras	Yosemite
(a)				
<i>T. alpinus</i>	73	33	13	31
<i>T. speciosus</i>	54	57	67	97
(b)				
<i>T. alpinus</i>	75	51	29	38
<i>T. speciosus</i>	83	77	100	221

sition is noted as $\delta^{13}\text{C}$ and N isotope composition as $\delta^{15}\text{N}$. The standard used for carbon was V-PDB (Craig, 1957) and the standard used for nitrogen was air. The reference materials NIST SMR 1547 and peach leaves were used as calibration standards.

Samples were analyzed for carbon and nitrogen contents (% dry weight) and carbon and nitrogen stable isotope ratios by continuous flow isotope ratio mass spectrometry using the CHNOS Elemental Analyzer (vario ISOTOPE cube, Elementar, Hanau, Germany) and IsoPrime 100 mass spectrometer (Isoprime Ltd, Cheadle, UK) housed in the Center for Stable Isotope Biogeochemistry (CSIB) at the University of California, Berkeley. Long-term external precision for C and N isotope analyses in the CSIB is 0.08‰ and 0.11‰, respectively.

Analyses of stable isotope data

To examine dietary differences among our study animals, we generated linear mixed-effects models using the *R* package *nlme* (Pinheiro *et al.*, 2013). Our models included either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ as a response variable and species (*T. alpinus* or *T. speciosus*), era (historical or modern), and transect (Yosemite or Southern Sierras) as fixed effects. Because each of our sampling transects covers a broad altitudinal range (~1615 to 3505 m), we included elevation in our models as a fixed predictor, with the intent of determining whether the patterns of change in isotopic ratios are consistent across elevations. Our models also contained all pairwise interaction terms as fixed effects as well as aggregated collection localities as a random effect. To take into account the fact that isotope ratios and elevation were measured in different units, we scaled and centered all response variables, as well as elevation. Prior to scaling and centering, we corrected $\delta^{13}\text{C}$ values to account for the Suess effect, which describes the decrease in atmospheric $\delta^{13}\text{C}$ ratios over time (approximately -0.015‰ per yr; Keeling, 1979) due to increased fossil fuel combustion.

Following Zuur *et al.* (2009), we began the model selection process by fitting a full linear model for each response variable ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) with species, era, transect, elevation, and all pairwise interactions. Visual inspection of the resulting residuals revealed heteroscedasticity and deviation from normality, leading us to fit linear mixed-effects models that included different variance structures for our predictor variables as well as aggregated collection locality as a random effect. We used AIC-based procedures to compare models with different variance structures for fixed effects and different random effects structures, after which we examined the effects of eliminating nonsignificant fixed predictor variables. For all models, we calculated Akaike Information Criterion values (AIC_C), with a correction applied for small sample sizes (Burnham & Anderson, 2002; Mazerolle, 2014). Once we had generated a candidate set of models for each response variable, ΔAIC_C was calculated by comparing the AIC_C value of each model to the minimum AIC_C across all models in the candidate set. We calculated Akaike weights (w_i) for all models in the candidate set using the following equation, in which the numerator is the Akaike weight for model i and the denominator is the sum of the relative like-

hoods for all candidate models (Burnham & Anderson, 2002):

$$w_i = \frac{e^{-0.5\Delta_i}}{\sum_{j=1}^R e^{-0.5\Delta_j}}$$

In our confidence set of top models, we included all models with w_i values within 10% of the maximum w_i for that candidate set (following Burnham & Anderson, 2002).

To examine the differences in dietary breadth, we calculated variance for nitrogen and carbon isotope ratios and used Brown–Forsythe tests (nonparametric variance tests; Brown & Forsythe, 1974) to compare variances between species or eras.

Morphometric measurements

To characterize the morphological variation in *T. alpinus* and *T. speciosus*, we measured multiple aspects of skull size and shape for 286 historical and 388 modern specimens of these species housed in the MVZ (Table 1b, Table S1). We used only adult skulls in these analyses, defined by full eruption of the permanent premolar 4 and a completely fused basisphenoid–basisoccipital suture. For each skull, three-dimensional coordinates were recorded for 24 cranial landmarks using a Microscribe 3DMX digitizer (Microscribe, IL, USA). To facilitate consistent recognition, the landmarks chosen were positioned at the intersections of sutures or other discrete and homologous cranial features; the specific locations selected were chosen to reflect important developmental and functional relationships among cranial structures while simultaneously capturing overall skull size and shape (Cheverud, 1988; Mar-

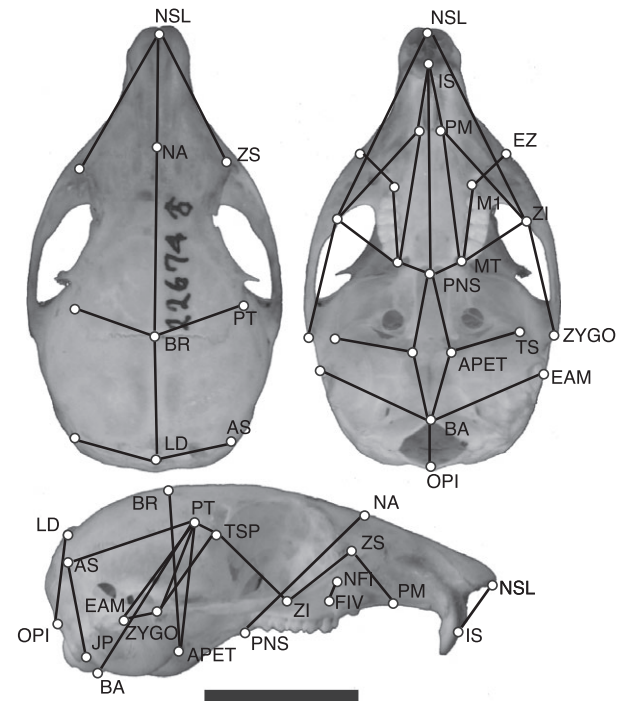


Fig. 2 Locations of landmarks and linear measurements on skulls. Scale bar is 10 mm.

roig & Cheverud, 2001). Coordinates for these landmarks were then used to calculate 38 linear skull measurements (Fig. 2). Bilaterally symmetric measurements were averaged for each individual; if a skull was damaged on the one side, measurements from the intact side only were used in subsequent analyses. All specimens were measured twice, thereby allowing us to assess the repeatability of these data and to estimate measurement error (Lessels & Boag, 1987). The mean of these repeated measurements was used in all subsequent analyses.

Analyses of morphological variation

All statistical analyses were conducted using the computer program *R* (*R* Core Team, 2013). To analyze our morphological data set, we first assessed the variation due to sex and age class, as these variables were not of interest in the current study. To control for age, skulls were assigned to one of the following categories based on the extent of tooth wear: (1) no signs of wear, (2) moderate signs of wear or (3) extensive signs of wear. We then conducted a MANOVA that included these age and sex categories; the residuals from this test were used in all subsequent analyses for which a significant result was obtained. Using the pooled within-groups covariance matrices from the MANOVA, we performed a principal component analysis; all traits loaded positively on the first principal component (PC1), and thus, this axis was used as an estimate of allometric skull size. To assess the temporal changes in skull size, we generated a linear model using PC1 as the dependent variable and era (historical or modern) as an independent variable. To explore the potential variation in size changes in different regions of the skull, we divided the traits examined into those associated with the rostrum and those associated with the neurocranium; separate PC1 scores were calculated for each of these cranial regions.

To evaluate the changes in skull shape, it was first necessary to reconcile the two different (anterior and posterior) views used to digitize landmarks. We used the *R* function *unifyVD* to combine both sets of coordinates into a single configuration based on the locations of nine shared landmarks and by minimizing the sum of squared deviations between both views (Rohlf & Bookstein, 1990); the locations of any missing lateral landmarks were estimated by reflecting from one side of the skull to the other with the *R* function *AMP*. Because landmarks for each skull were recorded twice, we used the mean of these values, as calculated after rotating and translating the landmarks using a least-squares superimposition algorithm (generalized Procrustes analysis with no correction for scale effect; Bookstein, 1997; Zelditch *et al.*, 2012). We then removed the asymmetric component of skull shape using the *Osym* function in *R* (Klingenberg *et al.*, 2002), after which we performed a separate Procrustes superimposition for each species, thereby removing the scale (isometric size) from the data sets (Bookstein, 1997; Zelditch *et al.*, 2012). The cumulative result of these manipulations was to produce skull images with the same configuration and without missing values. As with linear measurements, we then removed fixed effects (age, sex) that were not the focus of this study, in this case by using the overall mean for each trait to center the group means. To evaluate

shape changes between the historical and modern eras, we estimated the Mahalanobis distance (MD) and the Procrustes distance (PD) between the mean shapes for each era (Zelditch *et al.*, 2012). To assess the significance of temporal shape changes, we performed a Procrustes ANOVA between the shape coordinates, with the significance estimated through a permutation test (Goodall, 1991). All of these analyses were conducted in *R* with the packages *shapes* (Dryden, 2013), *geomorph* (Adams & Otárola-Castillo, 2013), and the functions *AMP*, *unifyVD*, and *Osym* developed by A. Haber (available at <http://life.bio.sunysb.edu/morph/soft-R.html>).

To explore the evolutionary process(es) responsible for observed morphological changes over time, we used Lynch's (1990) genetic drift test. This test is derived from the neutral model of phenotypic evolution (Lande, 1976, 1979) and is used to determine whether observed divergence of phenotypic traits is significantly different from that expected if mutation and drift are the primary evolutionary forces underlying this divergence (Lynch, 1990). We used the log-transformed linear measurements to calculate morphological rate of change, denoted as Δ ,

$$\Delta = \frac{\text{var}_B(\ln z)}{[t \text{ var}_W(\ln z)]}$$

where var_B and var_W are the observed between- and within-era components of phenotypic variance for log-transformed measurements obtained from the mean squares generated by an ANOVA, with era as the independent variable and t is the elapsed time in generations between historical and modern samples. We compared Δ -values calculated for each trait to those expected if selection was acting on the trait in question; values $<10^{-4}$ are consistent with the effects of stabilizing selection and higher than 10^{-2} are consistent with directional selection. We used a 1-year generation time (Ingles, 1965), and t was estimated by subtracting the average year for the historical era from the average year for the modern era for each aggregated collection locality sampled.

Relationship between dietary and morphological change

To explore the relationship between patterns of change in diet and morphology, we conducted nonparametric correlation tests (using Kendall's tau) to determine whether morphological measurements and stable isotope ratios were correlated within each combination of species \times era \times transect.

Results

Climatic variation

Our analyses of historical (1900–1909) and modern (1990–1999) climate data revealed no significant changes in mean annual temperature over time for either the Yosemite or Southern Sierra study areas. Mean annual temperature in the Southern Sierra has remained approximately 4.4 °C over the past century (historical mean = 4.45 °C, modern mean = 4.43 °C,

$t = 0.0274$, $n_{\text{historical}} = 33$, $n_{\text{modern}} = 21$, $P = 0.978$), with mean annual temperature in Yosemite remaining approximately 4.9 °C over the same period (historical mean = 4.9 °C, modern mean = 4.88 °C, $t = 0.0331$, $n_{\text{historical}} = 44$, $n_{\text{modern}} = 46$, $P = 0.974$). In contrast, total annual precipitation has decreased at both sites over the past century. Specifically, annual precipitation has decreased by 232 mm in the Southern Sierras and by 220 mm in Yosemite; changes at both sites were significant (Southern Sierras: historical mean = 985 mm, modern mean = 753 mm, $t = 2.81$, $n_{\text{historical}} = 33$, $n_{\text{modern}} = 21$, $P = 0.007$; Yosemite: historical mean = 1272 mm, modern mean = 1052 mm, $t = 3.23$, $n_{\text{historical}} = 44$, $n_{\text{modern}} = 46$, $P = 0.002$).

Dietary variation over space and time

As a first step toward characterizing potential dietary changes over space and time, we plotted historical and modern values for $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ for each species and for both sampling transects (Fig. 3). We found that historical means ranged from 1.96 to 7.53‰ for nitrogen isotope composition ($\delta^{15}\text{N}$) and -17.1 to -22.5‰ for

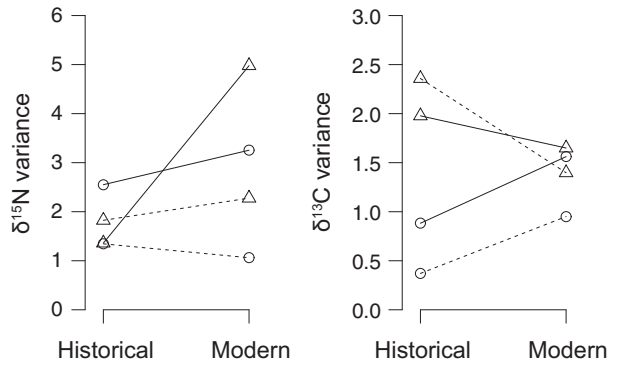


Fig. 4 Patterns over time of variance in (a) $\delta^{15}\text{N}$ and (b) $\delta^{13}\text{C}$ isotope ratios. Triangles represent *T. alpinus*; circles represent *T. speciosus*. Connections between historical and modern variances are shown for each species, with dotted lines connecting Southern Sierra specimens and solid lines connecting Yosemite specimens.

carbon isotope composition ($\delta^{13}\text{C}$), with modern means of 0.443–7.63‰ for $\delta^{15}\text{N}$ and -18.6 to -22.2‰ for $\delta^{13}\text{C}$. Visual inspection of these data suggested that although some of the animals that comprised the data sets (e.g.,

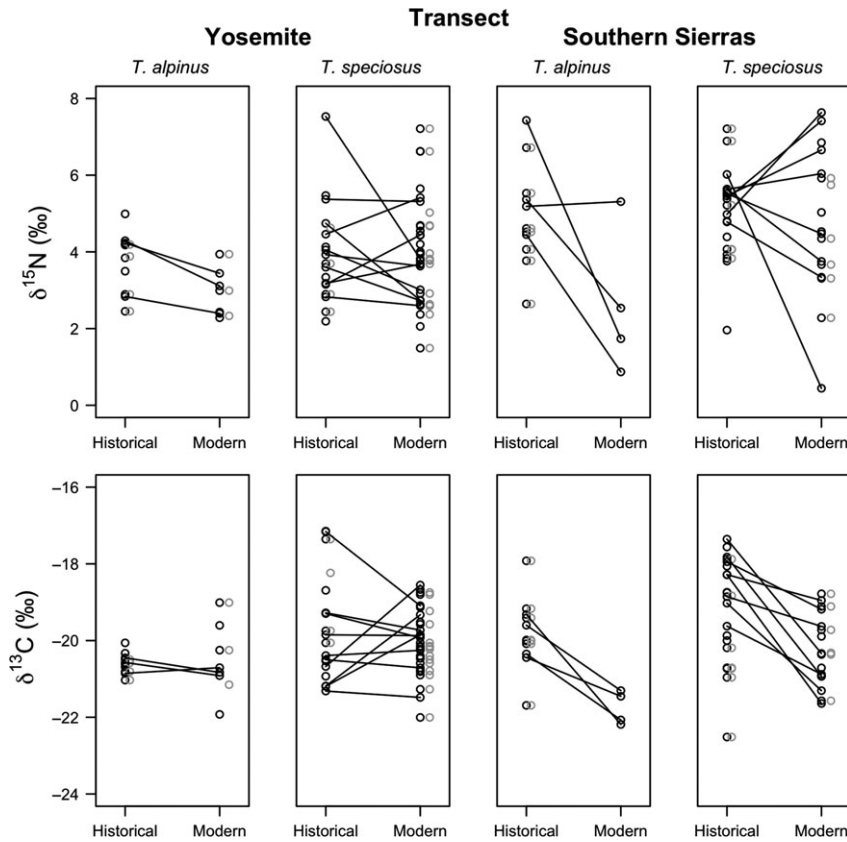


Fig. 3 Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios for GRP sites. Each point represents the mean value for all specimens from a single GRP site. Sites for which specimens were collected in both the historical and modern eras are shown in black, with a line connecting the historical and modern means. Data for sites that include specimens from one era only are plotted in lighter gray.

T. alpinus from the Southern Sierras) showed apparent directional patterns of change in stable isotope composition over time, there were no consistent temporal changes in $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ composition for either sampling locality or study species. Similar plots (Fig. 4) of changes in variance of isotope ratios showed that within species, variance in $\delta^{15}\text{N}$ increased for both *T. alpinus* and *T. speciosus* in the Southern Sierras, with a larger increase observed for *T. speciosus*. Changes were less pronounced in Yosemite, with variance for *T. alpinus* decreasing slightly and variance for *T. speciosus* remaining similar in both eras. For $\delta^{13}\text{C}$, dietary breadth increased for *T. alpinus* in both transects and decreased for *T. speciosus* in both transects. For *T. alpinus*, the amount of increase in variance was similar across both transects, with dietary breadth consistently remaining higher in the Yosemite transect and lower in the Southern Sierras transect. In contrast, for *T. speciosus*, the decrease in dietary breadth was larger in the Southern Sierras than in the Yosemite transect, with the result that dietary breadth was more similar between transects in the modern era (Fig. 4).

To examine quantitatively the effects of species, time period, and sampling transect on diet, we generated a confidence set of seven models for $\delta^{15}\text{N}$ (Table 2a) and seven models for $\delta^{13}\text{C}$ (Table 2b). All models included the same main predictor variables (intercept, species, era, transect, elevation); the models differed only with regard to the retention of interaction terms. Because we were most interested in exploring the effects of the main predictor variables on isotope ratios, we chose to focus on the nitrogen and carbon models with the lowest AIC_C values. ANOVA tests revealed that these models did not differ significantly from others in their respective confidence sets (all *P*-values > 0.05). Estimated coefficients are given in standard units (i.e., standard deviations), using *T. alpinus* as a baseline; as an example, the value of 0.43 in the historical Southern Sierras vs. Yosemite cell for the $\delta^{13}\text{C}$ model (Table 3a) indicates that $\delta^{13}\text{C}$ values for *T. speciosus* are 0.43 standard deviations greater than the corresponding values for *T. alpinus*. For all comparisons involving interaction terms, separate coefficient estimates are reported; in cases with no significant interaction terms, we pooled estimates (Table 3). *P*-values and 95% confidence intervals are also given for all coefficients. Using our top models, we examined the effects of the following factors on the diets of our study animals:

1. *Species*. In both the historical and modern eras, nitrogen and carbon isotope ratios differed significantly between the study species in both the Yosemite and Southern Sierra transects (Table 3a).
2. *Era*. For $\delta^{15}\text{N}$, ratios differed significantly between eras only for *T. alpinus* in Yosemite and the Southern

Sierras; all comparisons for *T. speciosus* were non-significant (Table 3c). For $\delta^{13}\text{C}$, significant differences were found between eras for both species in the Yosemite transect; no significant differences were detected for the Southern Sierras transect (Table 3b).

3. *Transect*. For $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, significant differences in isotope ratios between Yosemite and the Southern Sierras were found for all species \times era combinations (Table 3c).
4. *Elevation*. Elevation was a significant predictor of $\delta^{15}\text{N}$ for all species by transect by era combinations; in contrast, no significant effects of elevation on $\delta^{13}\text{C}$ were detected (Table 3d).

As evident from these analyses, there was a considerable variation in the predictors associated with the variation in isotopic measures of the diets of the study species. To determine whether overall variability in isotopic ratios was greater for the presumably more ecologically generalized *T. speciosus*, we divided our data into four subgroups representing all possible combinations of era by transect (e.g., historical samples from the Southern Sierras). We then used Brown–Forsythe tests (nonparametric variance tests; Brown & Forsythe, 1974) to compare the variances in isotopic ratios for *T. alpinus* and *T. speciosus* within each era by transect category. These analyses revealed that for $\delta^{15}\text{N}$, comparisons of the variance in isotopic ratios between species were significant only for the historical Southern Sierra and the modern Yosemite subsets of data; variance in $\delta^{15}\text{N}$ was greater for *T. alpinus* in the Southern Sierra, but greater for *T. speciosus* in Yosemite (Table 4). For $\delta^{13}\text{C}$, variance in isotopic ratios was greater for *T. speciosus* from both transects in the historic era; no significant differences in variance were found for the modern era (Table 4). Thus, overall, variance in isotopic ratios was greater for *T. speciosus* in 3 of the 4 data subsets for which significant differences in variance were detected (Fig. 4).

To determine whether *T. alpinus* showed greater signatures of change in dietary breadth than *T. speciosus*, we again used Brown–Forsythe tests. We divided our data into subgroups representing all possible combinations of species by transect and compared variances in the historical vs. modern eras. We found that variance in $\delta^{15}\text{N}$ was greater in the modern era for *T. speciosus* ($F(1, 119) = 22.1$, $\text{variance}_{\text{historical}} = 1.36$, $\text{variance}_{\text{modern}} = 4.98$, $P < 0.0001$); no other within-species comparisons for either isotope revealed significant differences between eras.

Morphological variation over space and time

Use of PC1 as a proxy for cranial allometric size revealed a substantial variation in patterns of morpho-

Table 2 Summary statistics for confidence set of models for (a) nitrogen ($\delta^{15}\text{N}$) and (b) carbon ($\delta^{13}\text{C}$) isotope ratios. All models include site as a random effect, as well as the fixed effects listed. The number of parameters (K), AIC_C values (Akaike Information Criterion, corrected for small sample size), and Akaike weights (w_i) are shown for each model (see text for details)

Response variable	Predictor variables	Number of parameters (K)	AIC_C	ΔAIC_C	AIC_C weight
a.) $\delta^{15}\text{N}$	Intercept Species Era Transect Elevation Species*Era	16	951	0	0.315
	Intercept Species Era Transect Elevation Species*Era Era*Transect	17	951	0.00229	0.315
	Intercept Species Era Transect Elevation Species*Era Species*Transect Era*Transect	18	953	1.91	0.121
	Intercept Species Era Transect Elevation Species*Era Species*Transect	17	953	2.03	0.114
	Intercept Species Era Transect Elevation Species*Transect Era*Transect	17	954	3.8	0.0471
	Intercept Species Era Transect Elevation Species*Era Species*Transect Species*Elevation Era*Transect Era*Elevation	20	955	4.62	0.0313
	Intercept Species Era	20	956	5.54	0.0197

Table 2 (continued)

Response variable	Predictor variables	Number of parameters (K)	AIC _C	ΔAIC _C	AIC _C weight
b.) δ ¹³ C	Transect Elevation Species*Era Species*Transect Species*Elevation Era*Transect Transect*Elevation				
	Intercept Species Era Transect Elevation Species*Era Era*Transect Era*Elevation	16	988	0	0.276
	Intercept Species Era Transect Elevation Species*Era Species*Transect Species*Elevation Era*Transect Era*Elevation	18	989	0.663	0.198
	Intercept Species Era Transect Elevation Species*Era Species*Transect Era*Transect Era*Elevation	17	989	1.03	0.165
	Intercept Species Era Transect Elevation Species*Era Species*Transect Species*Elevation Era*Transect Era*Elevation Transect*Elevation	19	990	1.86	0.109
Intercept Species Era Transect Elevation	18	991	2.07	0.0981	

Table 2 (continued)

Response variable	Predictor variables	Number of parameters (K)	AIC _C	ΔAIC _C	AIC _C weight
	Species*Era Species*Transect Era*Transect Era*Elevation Transect*Elevation	14	991	2.34	0.0855
	Intercept Species Era Transect Elevation Species*Era Era*Transect	15	992	3.07	0.0594

logical change over time. For example, while *T. alpinus* from the Yosemite transect increased in size over the past century ($F = 17.98$; $P < 0.001$), *T. alpinus* from the Southern Sierras decreased in size during this same period ($F = 5.80$; $P < 0.05$; Fig. 5). In contrast, no difference in size was detected for *T. speciosus* from either transect over the last century ($P > 0.05$; Fig. 5). Dividing skull characters into those associated with the rostrum (facial region) vs. those associated with the neurocranium (brain case) revealed that the temporal changes in size detected for *T. alpinus* were due primarily to the modification of facial traits (Fig. 6). In *T. speciosus*, the facial – but not the neurocranial – portion of the skull increased significantly in size over time at Yosemite; in contrast, no changes in size for either portion of the skull occurred in this species in the Southern Sierras ($P > 0.05$; Fig. 6). Thus, overall, we detected greater evidence of temporal changes in cranial size for *T. alpinus*, with these changes due primarily to the modifications of the facial portion of the skull.

With regard to skull shape, all Procrustes ANOVAs were significant, indicating temporal changes in skull shape for both species over the past century (Table 5). The magnitude of shape change, however, differed markedly between the study species. Specifically, the Mahalanobis distance between the mean skull shape for each era was three to four times larger in *T. alpinus* than in *T. speciosus* (Table 5). Similarly, the Procrustes distance between mean historical and modern skull shapes

was almost twice as large in *T. alpinus* compared with *T. speciosus* in both the Yosemite and Southern Sierra transects (Table 5). These data are consistent in suggesting that skulls of *T. alpinus* have undergone more pronounced changes in shape over the past century.

Mechanisms of morphological change over time

Genetic drift tests indicated that for *T. alpinus* in Yosemite, temporal changes in most of the cranial traits examined were greater than expected by drift alone. Indeed, of 38 traits considered, only 6 (15.8%) failed to show evidence of significant departures from neutral patterns of change (drift); patterns of change at the remaining 32 traits were consistent with the effects of directional selection (Table S2, Fig. 7). Of the 6 traits that did not show evidence of departure from neutral expectations, 5 (83.3%) were located in the neurocranium, suggesting that this portion of the skull may have been more subject to modification due to drift. Analyses of *T. alpinus* from the Southern Sierras also tended to reject drift as the process underlying temporal patterns of cranial change, although the number of traits that failed to reject drift (14 of 38, 36.8%) was greater than in Yosemite (Table S2). Further, in the Southern Sierras, traits for which drift was rejected as the mechanism of change were more evenly distributed between the rostrum and neurocranium (Table S2, Fig. 7).

Table 3 Effects of species, era, transect, and elevation on isotope ratios

		Southern Sierras & Yosemite	
(a)			
$\delta^{15}\text{N}$			
Historical		0.507 (<i>P</i> = 0.0039) 95% CI: 0.164–0.851	
Modern		0.972 (<i>P</i> < 0.0001) 95% CI: 0.591–1.35	
$\delta^{13}\text{C}$			
Historical		0.43 (<i>P</i> = 0.0342) 95% CI: 0.368–0.827	
Modern		0.89 (<i>P</i> = 0.0003) 95% CI: 0.416–1.36	
		Southern Sierras & Yosemite	
(b)			
$\delta^{15}\text{N}$			
<i>T. alpinus</i>		-0.676 (<i>P</i> = 0.0027) 95% CI: -1.12 to -0.236	
<i>T. speciosus</i>		-0.211 (<i>P</i> = 0.184) 95% CI: -0.523 to -0.101	
		Southern Sierras	Yosemite
$\delta^{13}\text{C}$			
<i>T. alpinus</i>		-0.462 (<i>P</i> = 0.0915) 95% CI: -1 to 0.0751	0.648 (<i>P</i> = 0.0096) 95% CI: 0.159–1.14
<i>T. speciosus</i>		0.00337 (<i>P</i> = 0.987) 95% CI: -0.413 to 0.42	0.959 (<i>P</i> < 0.0001) 95% CI: 0.542–1.38
		Historical & Modern	
(c)			
$\delta^{15}\text{N}$			
<i>T. alpinus</i> & <i>T. speciosus</i>		-0.528 (<i>P</i> = 0.001) 95% CI: -0.834 to -0.223	
		Historical	Modern
$\delta^{13}\text{C}$			
<i>T. alpinus</i>		-0.58 (<i>P</i> = 0.0007) 95% CI: -0.907 to -0.252	0.529 (<i>P</i> = 0.0091) 95% CI: 0.136–0.922
<i>T. speciosus</i>		-0.591 (<i>P</i> = 0.0007) 95% CI: -0.923 to -0.259	0.529 (<i>P</i> = 0.0091) 95% CI: 0.136–0.922
		Southern Sierras & Yosemite	
(d)			
$\delta^{15}\text{N}$			
Both species, both eras		0.297 (<i>P</i> = 0.0003) 95% CI: 0.137–0.458	
Both transects		Historical	Modern
$\delta^{13}\text{C}$			
<i>T. alpinus</i>		-0.149 (<i>P</i> = 0.183) 95% CI: -0.368 to 0.0703	0.207 (<i>P</i> = 0.0589) 95% CI: -0.0078 to 0.423
<i>T. speciosus</i>		-0.153 (<i>P</i> = 0.175) 95% CI: -0.374 to 0.0683	0.208 (<i>P</i> = 0.0583) 95% CI: -0.00737 to 0.0583

All values are reported in units of standard deviations, with *P*-values in parentheses. Statistically significant *P*-values (<0.05) appear in boldface. 95% confidence intervals (95% CI) for each parameter are also provided. Part a.) of the table (species comparisons) indicates whether there are differences between *T. alpinus* and *T. speciosus* in each transect and era. Each parameter estimate reflects how isotope ratios in *T. speciosus* compared with those in *T. alpinus*. In 3b.), era comparisons indicate whether isotope ratios differ between historical and modern specimens from each species in each transect. Parameter estimates reflect how isotope ratios from modern specimens compared with historical specimens. In 3c.), transect comparisons show how isotope ratios differ between the Southern Sierras and Yosemite transects for each species in each era. 3d.) shows whether elevation has a significant effect on isotope ratios for each group. (See text of Results section for further explanation on each comparison.)

For *T. speciosus*, evidence of departure from drift was less consistent, with animals from both transects displaying a greater percentage of traits (Yosemite: 16 of 38, 42%; Southern Sierras: 20 of 38, 52%) that did not deviate from neutral expectations (Table S2, Fig. 7). In

Yosemite, most (68%) of the 22 traits that deviated from neutrality were in the facial region; patterns of temporal change for these traits were generally consistent with the effects of directional selection (Table S2, Fig. 7). In contrast, in the Southern Sierras, traits that

Table 4 Comparisons of variances in isotope ratios in *T. alpinus* and *T. speciosus*

	Southern Sierras	Yosemite
$\delta^{15}\text{N}$		
Historical	$\text{Var}_{\text{alp}} = 2.55, \text{Var}_{\text{spec}} = 1.36$ $F = 5.14(1, 125), P = \mathbf{0.0251}$	$\text{Var}_{\text{alp}} = 1.35, \text{Var}_{\text{spec}} = 1.82$ $F = 3.12(1, 88), P = 0.0809$
Modern	$\text{Var}_{\text{alp}} = 3.25, \text{Var}_{\text{spec}} = 4.98$ $F = 0.788(1, 78), P = 0.374$	$\text{Var}_{\text{alp}} = 1.06, \text{Var}_{\text{spec}} = 2.28$ $F = 4.48(1, 126), P = \mathbf{0.0362}$
$\delta^{13}\text{C}$		
Historical	$\text{Var}_{\text{alp}} = 0.883, \text{Var}_{\text{spec}} = 1.98$ $F = 12.8(1, 125), P = \mathbf{0.0005}$	$\text{Var}_{\text{alp}} = 0.371, \text{Var}_{\text{spec}} = 2.36$ $F = 14.9(1.88), P = \mathbf{0.0002}$
Modern	$\text{Var}_{\text{alp}} = 1.56, \text{Var}_{\text{spec}} = 1.65$ $F = 0.312(1, 78), P = 0.578$	$\text{Var}_{\text{alp}} = 0.951, \text{Var}_{\text{spec}} = 1.4$ $F = 2.04(1, 126), P = 0.156$

Each table entry gives the variance for *T. alpinus* (Var_{alp}), the variance for *T. speciosus* (Var_{spec}) Brown–Forsythe F -statistic, between-group and within-group degrees of freedom, and the P -value. Significant P -values (< 0.05) appear in boldface.

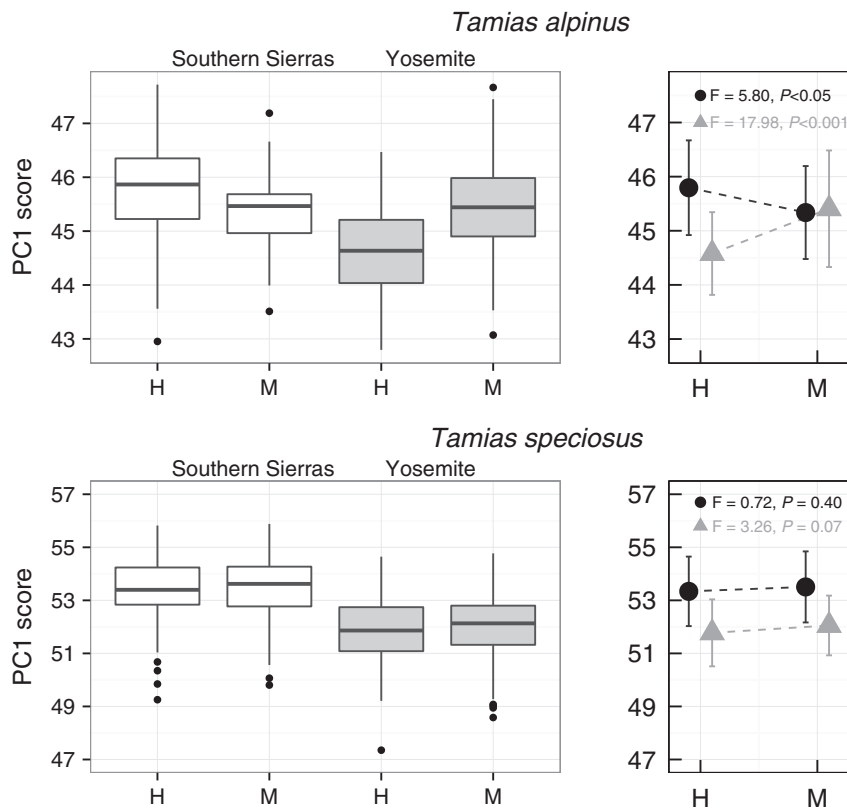


Fig. 5 Patterns of size change over time in *T. alpinus* and *T. speciosus*. PC1 is a proxy for skull size. H = historical era, M = modern era. The right panel graphs combine data for both transects displaying the mean \pm standard deviation observed for PC1 scores in each species. The F -value and P -value for the ANOVA are also displayed on top of the right graphs, with values for the Southern Sierras transect in black and values for the Yosemite transect in gray.

showed significant departures from neutrality were more evenly distributed between the rostrum (50%) and the neurocranium (50%; Table S2, Fig. 7).

Relationship between dietary and morphological change

Given that some of the strongest signatures of morphological change were detected in the facial region, we

focused on facial traits for our examination of correlations with diet. For each specimen for which we had both morphological and dietary data, we plotted its facial traits PC1 scores against either the carbon or nitrogen isotope ratio for that specimen (Fig. 8). Kendall's tau tests to assess whether these correlations were significant showed no significant relationships for either isotope (all P -values > 0.05). In all cases, we

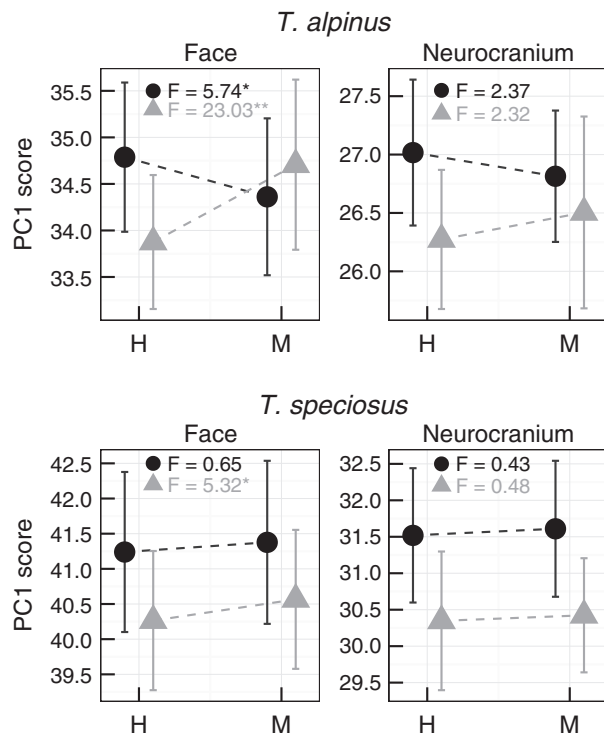


Fig. 6 Patterns of size change in the face and neurocranium regions of the skull. Points shown represent means \pm standard deviation of the observed PC1 scores for each region of the skull in the historical (H) and modern (M) eras. The F -value and P -value for the ANOVA are also displayed at the top of each graph. Data from the Southern Sierras transect are shown in black, and data from the Yosemite transect are shown in gray. * $P < 0.05$, ** $P < 0.001$.

Table 5 Shape changes estimated through Procrustes distance (PD) and Mahalanobis distance (MD)

		MD	PD	F -statistic	P
<i>T. alpinus</i>	Yosemite	4.71	0.010	3.15	0.001
	Southern Sierras	5.30	0.011	3.96	0.001
<i>T. speciosus</i>	Yosemite	1.93	0.006	2.53	0.002
	Southern Sierras	2.65	0.008	4.05	0.001

The F -estimates for the Procrustes ANOVA and respective P -values are also shown in the last columns.

adjusted P -values for multiple comparisons using the Holm method (Holm, 1979).

Discussion

Our analyses indicate that both alpine (*T. alpinus*) and lodgepole (*T. speciosus*) chipmunks have undergone significant changes in diet and cranial morphology over the past century. In particular, information from hair

samples about stable carbon and nitrogen isotope composition of diet as well as morphometric analyses of skull size and shape all revealed evidence of change in our study animals, particularly *T. alpinus* (Table 6). This outcome is consistent with a growing comparative data set indicating that *T. alpinus* has experienced generally greater phenotypic and genotypic change during the past 100 years. For example, while *T. alpinus* has undergone a substantial upward elevational range contraction during this period, *T. speciosus* has experienced no significant elevational range change (Moritz *et al.*, 2008). Concordant analyses of neutral genetic variation in these species indicate that while both overall diversity and gene flow among populations have decreased in *T. alpinus*, no such changes in genetic diversity or structure have occurred in *T. speciosus* (Rubidge *et al.*, 2012). Our findings are consistent with this general trend in that morphological changes were more pronounced in *T. alpinus*, with concordant shifts in diet also occurring more often in *T. alpinus*.

A second striking outcome of our analyses was the marked geographic variation in patterns of dietary and morphological change within each species. For some traits (e.g., $\delta^{15}\text{N}$ values for *T. speciosus*), a significant temporal change was limited to just one sampling transect per species. For others (e.g., skull size in *T. alpinus*), significant temporal changes were detected for both transects, but the direction of change differed between Yosemite and the Southern Sierras. This variability, in particular the different outcomes detected among conspecifics, suggests that changes in environmental conditions over the past century have not been the same throughout the Sierra Nevada. Although our analyses of temperature and rainfall indicated similar overall patterns of change in these environmental parameters over the past ~100 years, more detailed comparative analyses of historical and modern conditions at our sampling transects have revealed that the patterns of change in temperature and precipitation are heterogeneous across our study region (Rowe *et al.*, 2014). Thus, in addition to potential interspecific differences in response, the phenotypic changes reported here likely reflect the effects of local variation in environmental conditions. Accordingly, untangling the causal factors underlying responses to climate change will require detailed knowledge of relationships between environment and phenotype across multiple spatial and taxonomic scales.

Patterns of dietary change

Tamias alpinus is thought to be more of an ecological specialist than *T. speciosus* (Grinnell & Storer, 1924; Best *et al.*, 1994; Clawson *et al.*, 1994). If this contrast is

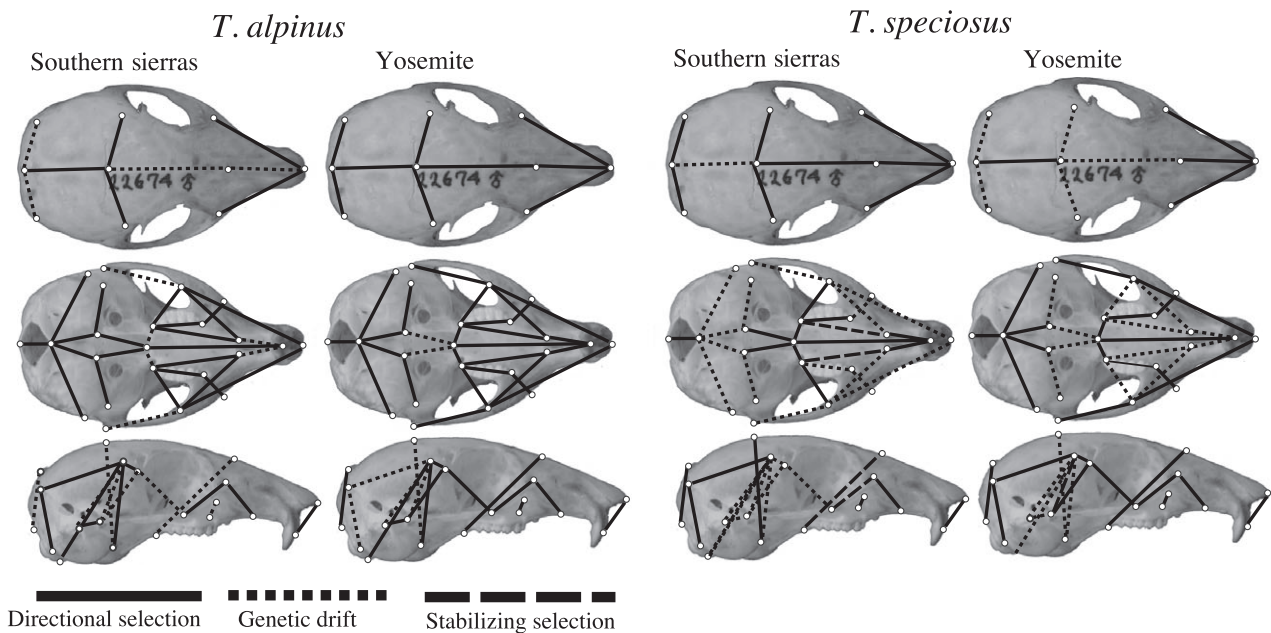


Fig. 7 Patterns of change in linear skull measurements, with the results of genetic drift tests. Solid lines indicate the patterns similar to those expected for changes resulting from directional selection, dotted lines indicate patterns similar to genetic drift, and dashed lines show patterns that are in accordance with a stabilizing selection scenario.

correct, then the variance of the isotopic ratios of *T. alpinus* hair (a reflection of their diet) should be smaller than the variance in ratios for *T. speciosus*. In general, our data support this interpretation. For example, within time periods and transects, three of the four significant contrasts identified resulted from smaller variances for *T. alpinus*, suggesting that this species is characterized by a more specialized diet. If this interpretation is correct, then the significant upward range contraction by *T. alpinus* over the past century (Moritz *et al.*, 2008) may reflect efforts to follow distributional changes in preferred food resources, leading to the prediction that this species should be characterized by less dietary change over time than *T. speciosus*. However, two of three significant contrasts between historical and modern sampling periods occurred in *T. alpinus*, suggesting that the more ecologically specialized species has experienced greater dietary changes in its $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ over time. These changes may be caused by dietary changes (animals consuming new food plants) or changes in the plant isotope ratios over time brought about by a century of environmental changes. When these plants are in turn consumed, they may 'label' chipmunk hair samples with different isotopic signatures today than in the past. Regardless of the reason, the elevational range changes by *T. alpinus* over the past century do

not appear to be associated with strict tracking of specific food resources.

With regard to the potential ecological significance of our stable isotope data, published reports based on observational data of foraging and cheek pouch contents of specimens (Grinnell & Storer, 1924; Best *et al.*, 1994; Clawson *et al.*, 1994) suggest likely food sources of each of our study species. For *T. alpinus*, diets typically include small seeds of sedges and other alpine plants, including forbs, grasses, and rushes, as well as fungi. This species also consumes shrubs such as *Ceanothus* (New Jersey tea), *Ribes* (currant and gooseberry), *Prunus emarginata* (Bitter Cherry), and *Vaccinium* (Blueberry and Huckleberry). Although *T. alpinus* inhabits areas with *Pinus contorta* (Lodgepole Pine), *Pinus albicaulus* (Whitebark Pine) trees, and Foxtail Pine (*Pinus balfouriana*), it typically spends the majority of its time in more open areas (Walsh, 2015) and thus likely does not consume pine seeds with high frequency. In contrast, *T. speciosus* diets frequently include pine seeds, as well as staminate cones or pollen. *Tamias speciosus* also incorporates seeds of grasses, and shrubs such as *Ceanothus*, *Ribes*, *Purshia tridentata* (Antelope-brush), and manzanita into its diet. Additionally, it consumes fungi and arthropods. Both *T. alpinus* and *T. speciosus* have been noted to consume bird eggs (Best *et al.*, 1994; Clawson *et al.*, 1994). Although more detailed quantita-

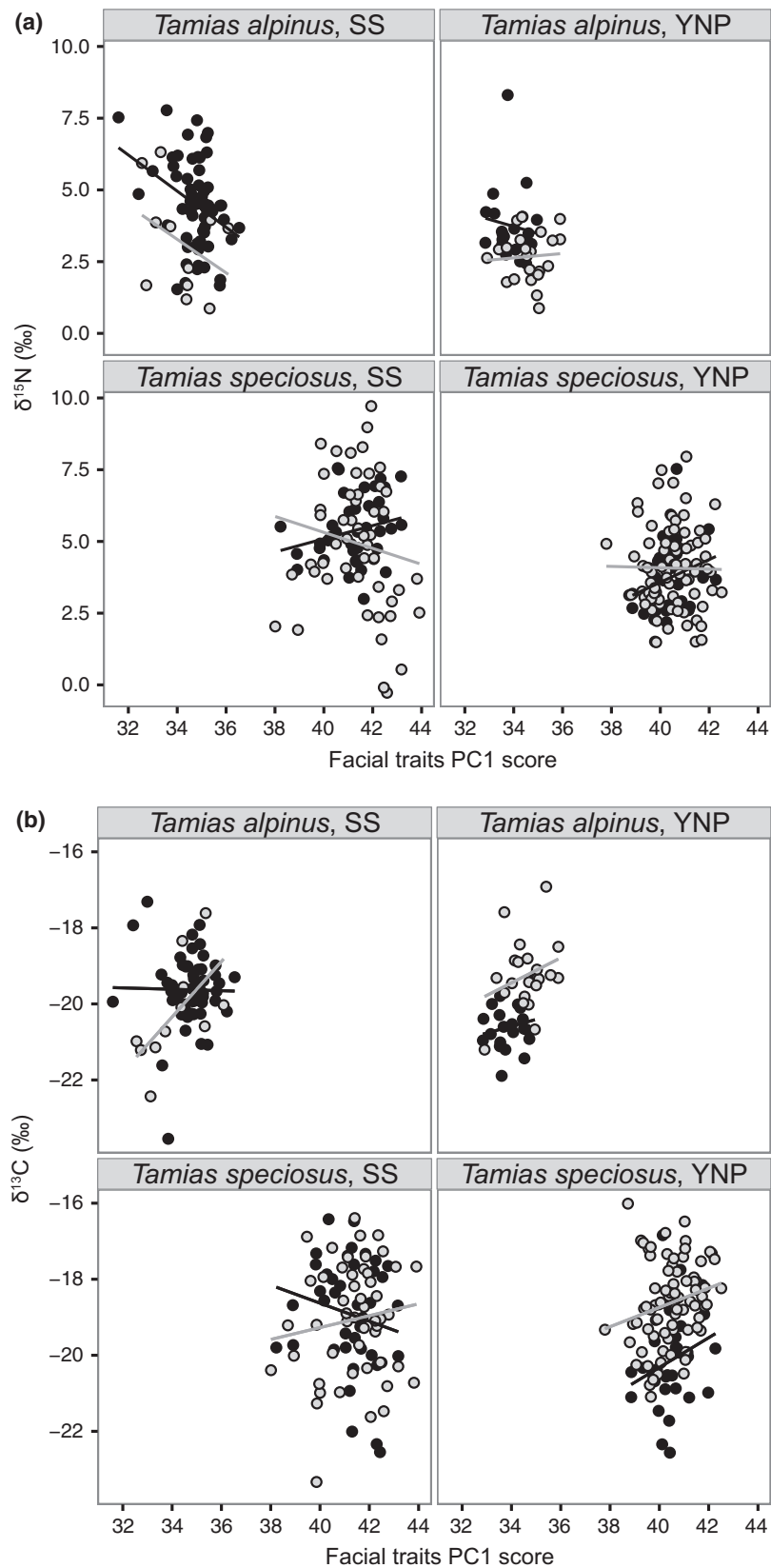


Fig. 8 Relationship between facial PC1 scores and nitrogen (a) or carbon (b) isotope ratios for each Species \times Transect \times Era combination. Historical (H) specimens are shown in black, and modern (M) specimens in gray.

Table 6 Summary of patterns of change in morphology and isotopic ratios

Species & location	Morphometric data			Isotopic data	
	Overall skull size	Rostrum size	Neurocranium size	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<i>T. alpinus</i>					
YNP	↑	↑	NS	↓	↑
SS	↓	↓	NS	↓	NS
<i>T. speciosus</i>					
YNP	NS	↑	NS	NS	↑
SS	NS	NS	NS	NS	NS

All contrasts are for historical and modern samples. Arrows denote significant directional changes from historic to modern material.

NS = indicates nonsignificant changes; YNP = Yosemite transect; SS = Southern Sierras transect.

tive studies (e.g., microhistological analyses) of the diets of these species have not been conducted, these observational records suggest that although the diets of *T. alpinus* and *T. speciosus* are generally similar, they may also be characterized by important differences in the relative abundance of key food resources such as pine seeds or cones.

Given the likely dietary items of our two study species, variation in nitrogen isotope ratios could arise from several sources, including differences in trophic level and degree of consumption of nitrogen-fixing vs. non-nitrogen-fixing plants. Although higher nitrogen isotope ratios are frequently associated with increasing trophic level, that is, higher nitrogen isotope in carnivores or omnivores than in herbivores (Post, 2002), it is not possible to predict how *T. alpinus* and *T. speciosus* would be expected to differ in their degree of insectivory or carnivory. Further investigation into this topic would be useful in determining whether differences in trophic level might exist, especially given the limited and anecdotal information about insect and egg consumption in our study species.

A second explanation for the variation in $\delta^{15}\text{N}$ of chipmunk hair centers on differences in $\delta^{15}\text{N}$ that arise during the process of nitrogen fixation by plants. In general, nitrogen-fixing plant species typically have $\delta^{15}\text{N}$ values near zero ($\pm 2\text{‰}$; Dawson *et al.*, 2002; Craine *et al.*, 2009), whereas non-nitrogen-fixing species typically have more positive nitrogen isotope ratios – on average 2‰ greater than co-occurring nitrogen-fixing species (Kelly, 2000; Marshall *et al.*, 2007). Among the reported components of the diets of each study species, *Ceanothus* is nitrogen-fixing species (Clawson *et al.*, 2004). Several additional nitrogen-fixing species occur

in the study region and are potentially consumed by chipmunks, including *Lupinus* (Lupines) and *Astragalus* (Allen & Allen, 1981). Therefore, the observed decrease in the hair $\delta^{15}\text{N}$ over time could reflect increasing chipmunk consumption of these nitrogen-fixing plant species. A productive avenue for future research would be to integrate surveys of modern plant communities with observations of chipmunk foraging or information on gut contents to determine whether extant individuals are consuming large quantities of nitrogen-fixing plants.

For $\delta^{13}\text{C}$, both plant physiology and environmental parameters may contribute to the variation in carbon stable isotope ratios. With respect to plant physiology, a primary determinant of carbon isotope composition is plant photosynthetic pathway: Plants using the C3 pathway have highly negative $\delta^{13}\text{C}$ ratios (~ -22 to -35‰ , mean -27‰) compared with plants that use the C4 pathway (~ -19 to -9‰), with intermediate $\delta^{13}\text{C}$ ratios for CAM plants ($\sim -27\text{‰}$ to -11‰) (Dawson & Siegwolf, 2007; Koch, 2007; Marshall *et al.*, 2007). Although no C4 plants are present in our study region, several CAM taxa are present, including *Sedum obtusatum* (Sierra Stonecrop) and several species of *Senecio* that are conjectured to possess the CAM pathway. Additional taxa that show low levels of CAM activity are also present, including *Lewisia* and *Calyptridium* (Pussypaws) (Smith & Winter, 1996; Botti, 2001; Besnard *et al.*, 2009; Edwards, 2011; Sage *et al.*, 2011). Mean $\delta^{13}\text{C}$ from both our historical and modern chipmunk hair samples are somewhat less negative than the reported mean $\delta^{13}\text{C}$ ratio of -27‰ for C3 plants, likely reflecting a slight fractionation that occurred as plant material was consumed and converted to hair. Fractionation values for this conversion from diet to hair in other mammalian species are typically -1 to 3 (rarely 5‰) (Ben-David & Flaherty, 2012a), meaning that the range of carbon isotope ratios observed here is consistent with either diets that consist entirely of C3 plants or diets that include a mix of C3 plants and CAM plants. Further surveys of C3 and CAM plant abundance at our sampling localities would be useful in determining the extent to which each of these types of plants contributes to the observed $\delta^{13}\text{C}$ ratios.

Another potential contributor to differences in plant $\delta^{13}\text{C}$ is precipitation. Low levels of precipitation are associated with increased $\delta^{13}\text{C}$ ratios in C3 plants, due to the effects of water limitation and stomatal closure on plant discrimination of the heavy (^{13}C) and light (^{12}C) isotopes of carbon during carbon assimilation (Fry, 2006; Marshall *et al.*, 2007; Ben-David & Flaherty, 2012a). If our plant $\delta^{13}\text{C}$ reflects water limitation in the food plants consumed by our study organisms, the decreases (more negative $\delta^{13}\text{C}$) that we observed in hair

$\delta^{13}\text{C}$ at many sites in the Southern Sierras would suggest increases in precipitation. Similarly, variable patterns of change at sites in the Yosemite region would imply heterogeneous patterns of precipitation change. However, our climate analyses show overall *decreases* in precipitation at our study sites in both the Yosemite and Southern Sierras transects. Other analyses of climate change in these regions reveal extensive local variation in patterns of precipitation change (Rowe *et al.*, 2014), emphasizing the need to explore the relationships between plant and animal $\delta^{13}\text{C}$ and climate at our study sites on a finer scale.

In sum, our stable isotope analyses suggest that *T. alpinus* is more of a dietary specialist than *T. speciosus*, although the extent of this difference varied across sites and sampling eras. These analyses also indicate that while the diets of *T. alpinus* and *T. speciosus* have changed over the past century, patterns of change are not consistent within species, across transects, or between isotopes. As a result, no single factor or suite of factors is clearly associated with temporal changes in the diets of the study species. Over time, diets of our study species have tended to converge, indicating that the foods consumed by these animals today are more similar than they were historically. This change is due primarily to changes in the diet of *T. alpinus*, implying that the observed change in elevational range for this species was not solely due to tracking of particular food resources. While the food resources consumed by each species need to be characterized in greater detail, our data suggest that no simple link exists between patterns of elevational range change and diets of the study species. To this end, we plan to follow up with analyses of modern chipmunk hair samples and potential food items that have been simultaneously collected from a subset of GRP study sites (R.E. Walsh, unpublished data). By applying stable isotope mixing models (Ben-David & Flaherty, 2012a) to this data set, we hope to gain additional insight into the isotopic niche of each species.

Patterns of morphological variation

Our morphological analyses revealed significant changes in skull shape and size over the last century in both study species. The magnitude of these changes, however, was approximately three times greater for *T. alpinus* than for *T. speciosus*, again suggesting greater responsiveness in the former species. Changes in skull morphology were more pronounced for the Yosemite transect, indicating that as with the dietary analyses, relationships between environment and phenotype varied geographically. Rapid morpho-

logical change associated with climatic conditions has been observed in a diverse array of rodents (Hendry *et al.*, 2008; Pergams & Lacy, 2008; Pergams & Lawler, 2009; Eastman *et al.*, 2012), with high-elevation species tending to display increases in body size (Ozgul *et al.*, 2010; Eastman *et al.*, 2012). Although we observed an increase in body size for *T. alpinus* in Yosemite, the converse was observed for this species in the Southern Sierras transect, thereby underscoring the variability and habitat-specific nature of phenotypic responses to environmental change.

In addition to taxonomic and geographic differences in patterns of morphological change, our data revealed that the patterns of change varied among the individual cranial traits examined. The majority of the changes detected were modifications to the rostrum, or facial region of the study species. The rostral region of the skull plays an integral role in multiple fundamental biological processes, including acquisition and initial physical processing of food (Hanken & Hall, 1993; Elbroch, 2006), respiratory water and temperature regulation (Schmidt-Nielsen *et al.*, 1970), intake of multiple modalities of sensory cues (Elbroch, 2006). Given the diversity of functional roles that the cranium plays in rodent biology and given the apparent complexity of the effects of environmental conditions on morphology, perhaps it should not be surprising that the impacts of those conditions differ across cranial structure.

Genetic drift tests indicated that in *T. alpinus* from both Yosemite and the Southern Sierras, most morphological traits examined changed more than expected under a model of neutral change over time. Departures from neutrality were also detected for *T. speciosus* from Yosemite, but not from the Southern Sierras, thereby underscoring the general patterns of greater responsiveness to environmental change by *T. alpinus*. Given that these tests reject neutral mechanisms as explanations for morphological differences over time, the most likely mechanism underlying the observed changes in skull morphology is selection (Lynch, 1990). As with any phenotypic trait, the morphological characters examined likely reflect the effects of both genetic and environmental factors (Falconer & MacKay, 1996), the relative contributions of which remain unknown. Future studies that examine functional relationships between environmental conditions and skull morphology in chipmunks in greater detail as well as studies that quantify the heritabilities of the cranial traits examined (Mousseau & Roff, 1987; Cheverud, 1988) should help to clarify the apparent contributions of genetic vs. environmental factors in generating the morphological changes reported here.

Relationships between dietary and morphological change

Diet has been shown to influence cranial – and in particular rostral – morphology in multiple rodent species (Caumul & Polly, 2005), leading to obvious questions regarding potential associations between the patterns of dietary and morphological change in our study species. While evidence for dietary and morphological change was more pronounced and more consistent for *T. alpinus*, we found little suggestion of consistent, potentially causal relationships between these aspects of the phenotypes of the study species. Overall, the absence of clear relationships between diet and morphology underscores the probable complexity of interactions between genotype, phenotype, and environmental change among the small mammals of the Sierra Nevada over the past century.

Implications for climate change research

Our comparative analyses indicate that both alpine and lodgepole chipmunks have experienced significant changes in diet and skull morphology over the past century. In general, these changes were more evident in *T. alpinus*, suggesting that this species has been more affected by environmental modifications during this period. This outcome is intriguing given a growing body of evidence indicating that *T. alpinus* has experienced greater changes in elevational distribution (Moritz *et al.*, 2008) and genetic structure (Rubidge *et al.*, 2012) over the last ~100 years and is more physiologically responsive to external stressors Hammond *et al.*, 2015 than *T. speciosus*. The reasons for these interspecific differences, including potential causal relationships among changes in environmental conditions, elevational distribution, diet, and skull morphology, have yet to be identified. Although it has been suggested that because *T. alpinus* is more ecologically specialized it should be more affected by changes in environmental conditions than *T. speciosus*, we found that the patterns of temporal change in diet and skull morphology varied markedly within as well as between species, indicating that niche breadth alone cannot explain the observed differences between the study species. Thus, while our data provide important insights into interspecific differences in the effects of environmental change, they also reveal how temporally and spatially complex these responses are. Future studies will build upon our findings to explore how local environmental conditions interact with interspecific differences in ecology, physiology, and morphology to generate the variation in response reported here.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of specimens used for stable isotope analyses of diet and morphological analyses.

Table S2. Results of genetic drift tests for morphological traits in the face and neurocranium regions of the skull.