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The Roles of Ecology and Habitat Use in
Explaining Range Shifts by Chipmunks in Yosemite National Park

By

Rachel E. Walsh

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

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in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Eileen A. Lacey, Chair
Professor Justin S. Brashares
Professor Todd E. Dawson

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Abstract

The Roles of Ecology and Habitat Use in
Explaining Range Shifts by Chipmunks in Yosemite National Park

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Doctor of Philosophy in Integrative Biology

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Despite substantial evidence that global climates are changing, predicting organismal responses to such changes poses a vexing research challenge, in part because responses can vary dramatically, even among closely related species. Studies of chipmunks (*Tamias* spp.) in Yosemite National Park provide a unique opportunity to explore the reasons for variation in species-specific spatial and temporal responses to a century of environmental change. Comparisons of historic and modern distributions of these animals indicate that while the Alpine Chipmunk (*T. alpinus*) has experienced a marked upward elevational range contraction over the past century, the Lodgepole Chipmunk (*T. speciosus*) has undergone effectively no change in its elevational range during this period. The reasons for this striking difference in range response are poorly understood. I therefore chose to explore the roles of several biotic factors in shaping patterns of response by these species. Specifically, I focused on habitat specialization and dietary overlap as potential contributors to differences in range response.

I began by selecting three sites in Yosemite National Park where *T. alpinus* and *T. speciosus* co-occur, so that I could compare patterns of habitat use in areas of sympatry between the two species. I carried out live-trapping and radio-tracking of chipmunks at each site during the summers of 2011, 2012, and 2013. I integrated these data with analyses of vegetation cover (NDVI) to quantify interspecific differences in spatial overlap and habitat use. I found that considerable interspecific spatial overlap exists, creating high potential for interspecific competitive interactions to occur. I also report evidence for differences in habitat use, with *T. alpinus* typically found in areas with lower vegetation cover and *T. speciosus* in areas with relatively higher vegetation cover.

Building on the results of the NDVI analyses, I used field-collected microhabitat data to describe characteristics of habitats used by each species in greater detail and to assess degree of specialization in habitat use. I found evidence for interspecific differences in types of habitats used by each species, with lower tree cover and larger amounts of exposed rock in habitats occupied by *T. alpinus*. Interspecific differences also existed in habitat breadth, with higher variation in amount of downed wood in areas used by *T. speciosus*. These results are consistent

with the characterization of *T. alpinus* as a high elevation specialist and suggest that the elevational range contraction reported for this species may reflect habitat tracking.

Finally, I took a longer-term approach by examining evidence for dietary changes and changes in cranial morphology in these species over the past century. Stable isotope analyses of hair samples from modern and historical museum specimens of each species collected at the same localities indicated that signatures of temporal dietary change were more pronounced in *T. alpinus*, although diet breadth did not appear to differ consistently between the study species. Morphometric analyses of crania from these specimens revealed significant temporal 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 *T. speciosus*. These results are consistent with growing evidence that *T. alpinus* is generally more responsive to environmental change than *T. speciosus*. However, the observation of large amounts of dietary change in *T. alpinus* is somewhat inconsistent with expectations based on habitat tracking— if *T. alpinus* has shifted range to remain in similar habitats over the past century, one would expect to see little change in diet. This in mind, our results emphasize the complex and often geographically variable nature of responses to environmental change.

In general, my findings suggest that habitat specialization may be associated with greater response to environmental change. My data underscore the complicated ways in which habitat use and dietary breadth act as contributors to range response. Future studies will build upon my findings to explore how local environmental conditions interact with interspecific differences in ecology and habitat use to generate variation in patterns of range change over time.

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Chapter 1

General Introduction

Anthropogenic climate change is fundamentally impacting organisms across the globe. Studies from multiple ecosystems and geographic regions have revealed climate-driven extinctions and range changes in multiple taxa, including mammals, birds, insects, and plants (Root et al. 2003, Parmesan 2006), and climate change is expected to be one of the leading threats to biodiversity over the next century (Millenium Ecosystem Assessment, 2005). As the impacts of climate change continue to accumulate, a key challenge for biologists will be to accurately predict patterns of organismal response. A popular paradigm used to categorize types of responses states that in the face of changing climate, organisms must move, adapt, or die. Within the first category — movement-based responses — many organisms have undergone distributional changes, frequently shifting their ranges northward or upward in elevation, presumably as they move to track optimal climatic regimes (see Chen, Hill, Ohlemüller, Roy, & Thomas, 2011 for a recent review). However, while many species show distributional shifts that are consistent with climate-based expectations, studies that include multiple species often reveal substantial heterogeneity in response, even among closely related species (Moritz *et al.*, 2008; Tingley *et al.*, 2012; Rowe *et al.*, 2015). Exploring the reasons for this heterogeneity is a major goal of my dissertation, and I focus on the roles of habitat specialization, interspecific competition, and dietary overlap.

I chose to investigate the underlying causes of heterogeneity in range response in two species of chipmunks in Yosemite National Park. Small mammals in the Sierra Nevada region constitute an ideal study system for this work, in part due to extensive work conducted over the past century. This effort has come to be known as the Grinnell Resurvey Project (GRP), a set of paired historical (1914-1920) and modern (2003-2006) surveys that show how elevational ranges of 28 small mammal species have changed over the past 100 years. While many of these elevational range shifts are consistent with climate-based predictions, these analyses have revealed extensive interspecific heterogeneity in patterns of response among species in the Yosemite area. Furthermore, survey results from other regions of California indicate that range responses are spatially variable and that a single species may show different patterns of response in different geographic regions (Moritz *et al.*, 2008; Rowe *et al.*, 2015).

Chipmunks (genus *Tamias*) are one group in which different species exhibited contrasting patterns of range change over the past century. In Yosemite, *T. alpinus* (the Alpine Chipmunk) has undergone a marked upward elevational range contraction and is no longer found at lower elevation sites where it was present historically. In contrast, *T. speciosus* (the Lodgepole Chipmunk) has shown no significant change in its elevational range. Although *T. alpinus* and *T. speciosus* are partially sympatric in many parts of their ranges, they are believed to differ in their 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, from tree line down to the Sierran foothills (Grinnell & Storer, 1924; Best *et al*., 1994; Clawson *et al*., 1994; Waters & Zabel, 1998). These apparent differences in habitat use lead to the expectation that the two species will differ in their sensitivity to the impacts of climate change, with *T. alpinus* predicted to be more impacted than *T. speciosus*. Several previous studies support this hypothesis. First, genetic

analyses indicate that populations of *T. alpinus* have decreased in genetic diversity and become increasingly more isolated from one another over the past century, while such changes have not been observed in *T. speciosus* (Rubidge *et al*., 2012). Second, physiological studies suggest that based on analyses of baseline glucocorticoid levels, *T. alpinus* is more responsive than *T. speciosus* to external stressors such as handling (Hammond *et al*., in prep.). Third, ecological niche models indicate that the elevational range contraction in *T. alpinus* is consistent with changes in climate and vegetation while no comparable climate predictor can be identified for *T. speciosus* (Rubidge *et al*., 2011).

Taken together, these studies of chipmunks provide an important foundation for exploring the impacts of environmental change, although significant gaps exist in our understanding of why these species display such different patterns of range change during the past century. For example, although we know that the two species are partially sympatric in many locations, systematic comparisons of habitat use by each species at these co-occurrence sites have not been conducted. Additionally, the absence of a strong climate predictor for the stasis in range for *T. speciosus* suggests that other factors must influence the distribution limits of this species. Interspecific competition is an especially likely explanation, as competitive interactions between chipmunks have been shown to be associated with range boundaries (Heller, 1971; Chappell, 1978). With these pieces of information in mind, I set out to quantify patterns of habitat use and interspecific spatial overlap in a field setting, and to examine dietary overlap using analyses of museum specimens. The overarching goal of my research was to identify the factors contributing to the interspecific differences in elevational range response observed in these species.

In my first set of analyses (Chapter 2), I examine patterns of interspecific spatial overlap and habitat specialization using a combination of field-collected data on habitat use by each species as well as remotely sensed data on vegetation cover. Evaluating the extent of interspecific spatial overlap in areas of sympatry between *T. alpinus* and *T. speciosus* is an important first step towards assessing the potential for competitive interactions among species to shape responses to environmental change because these data indicate the likelihood that members of each species will come into regular contact with one another. After quantifying patterns of interspecific spatial overlap, I ask whether the study species are using areas that differ with respect to vegetation cover. To quantify vegetation cover, I use remotely sensed imagery to calculate the normalized difference vegetation index (NDVI) for locations at which I either trapped chipmunks or located them during radiotelemetry surveys. NDVI is a common metric for describing the amount of live vegetation cover in an area and is especially relevant for describing differences between *T. alpinus* and *T. speciosus* given the reported habitat associations of each species. Because NDVI data are available at relatively high spatial resolution (30 m), it is also possible to compare the range of NDVI values in areas used by each species and thus to assess the breadth of habitats used by each species.

Although comparisons of NDVI offer general insights into one habitat feature that is likely to be important to my study species, these measurements do not capture other, more fine scale habitat differences that are likely to distinguish *T. alpinus* and *T. speciosus*. For example, *T. speciosus* is reported to use trees more readily than other *Tamias* species, including climbing well up into tree canopies (Best *et al.*, 1994). It is therefore reasonable to expect that tree canopy height

would differ in areas used by *T. alpinus* versus *T. speciosus*– a difference that would not be detectable based on NDVI values. To obtain information about specific microhabitat and vegetation characteristics (Chapter 3), I used detailed field-collected surveys of microhabitat variables to assess differences between habitats used by *T. alpinus* and T. *speciosus.* These data provide a more comprehensive understanding of interspecific differences with respect to an array of microhabitat and vegetation features and indicate the degree of habitat specialization for each of these species.

Given the expected differences in habitat use between *T. alpinus* and *T. speciosus* as well as temporal changes in vegetation in the Yosemite region (Thorne *et al.*, 2008; Lutz *et al.*, 2009; McIntyre *et al.*, 2015), it is logical to predict that the observed patterns of range change are associated with changes in the diets of the study species. My third set of analyses (Chapter 4) focused on using stable isotope analyses to assess dietary differences and to relate those differences to changes in skull morphology. In keeping with the observation that *T. alpinus* exhibits a higher degree of ecological specialization, I predicted that dietary changes should be more pronounced in *T. alpinus*. However, given that *T. alpinus* is a greater habitat specialist, it is possible that it will reveal little change in its diet if the upward contraction of its range reflects tracking the distributions of specific dietary items. To test these predictions, I obtained hair samples from historical and modern chipmunk specimens housed in the Museum of Vertebrate Zoology and analyzed those samples using stable nitrogen (δ^{15}N) and carbon (δ^{13}C) isotope ratios to capture information about diet. These analyses were integrated with data collected by chapter co-author Ana Paula Assis on changes in skull morphology from a spatially and temporally comparable set of chipmunk specimens. Because skull morphology is influenced by environmental conditions (e.g. Caumul & Polly, 2005; Eastman, Morelli, Rowe, Conroy, & Moritz, 2012; Grieco & Rizk, 2010; Millien et al., 2006; Pergams & Lawler, 2009), patterns of change in skull structure can generate insights into the effects of environmental conditions on the study species. I found greater evidence of both dietary and morphological change for *T. alpinus,* an outcome that, again, is consistent with the characterization of this species as more sensitive to the impacts of environmental change.

In general, my dissertation work contributes to our understanding of the processes underlying patterns of range change in response to changes in environmental conditions. I confirm that habitat specialization is associated with a stronger response to environmental change and I demonstrate the potential for interspecific competitive interactions to influence patterns of spatial response. Collectively, my analyses emphasize the utility of integrating multiple lines of evidence into analyses of the effects of climate change and underscore the critical role of baseline historical data as a foundation for identifying and interpreting patterns of change. Ideally, future research will continue to explore the links between a species' biology, its spatial relationships with closely related taxa, and responses to environmental change in order to improve our ability to tackle the daunting task of conserving biodiversity in the face of climate change.

Chapter 2

Understanding range shifts by small mammals in Yosemite National Park: spatial overlap and habitat use in areas of sympatry between Alpine and Lodgepole Chipmunks

Introduction

Although there is little doubt that climate change is impacting biodiversity (Parmesan & Yohe, 2003; Parmesan, 2006; Root, Price, Hall, & Schneider, 2003), considerable uncertainty exists regarding how different species are expected to respond. A growing body of literature on diverse taxa and geographic regions is emerging to support the assertion that, in the face of changing climate, organisms must move, adapt, or die. Within the first category of movement-based responses, many organisms have undergone distributional changes, frequently shifting their ranges poleward or upward in elevation, presumably as they move to track optimal climatic regimes (see Chen, Hill, Ohlemüller, Roy, & Thomas, 2011 for a recent review).

While numerous studies document patterns of spatial response, the underlying processes driving these distributional shifts often remain unclear. Existing empirical work includes examples of spatial responses in mammals (Hickling *et al.*, 2006; Moritz *et al.*, 2008), birds (e.g. Brommer, 2004; Hickling et al., 2006; Hitch & Leberg, 2007; Tingley, Monahan, Beissinger, & Moritz, 2009; Zuckerberg, Woods, & Porter, 2009), insects (e.g. Chen, Hill, Shiu, et al., 2011; Hickling et al., 2006), and plants (e.g. Kelly & Goulden, 2008; le Roux & McGeoch, 2008; Lenoir, Gégout, Marquet, de Ruffray, & Brisse, 2008; Parolo & Rossi, 2008), among other taxa (Chen *et al.*, 2011a). Additionally, model-based work attempts to predict or explain how species will shift ranges in response to change in climate, and why those changes might occur (Thomas *et al.*, 2004; Guisan & Thuiller, 2005; Thuiller *et al.*, 2005; Hijmans & Graham, 2006). Central to both model-based and empirical studies are investigations of how changes in environmental characteristics such as temperature and precipitation might explain the observed distributional changes (Chen et al. 2011, McCain & Colwell 2011, Rapacciuolo et al. 2014). However, although abiotic variables such as climate are certainly important in driving patterns of distributional change, biotic interactions can also play a role in shaping responses to climate change. For example, organisms may depend on other species for food, hosts, or habitat, or may interact competitively with other species. The ecological literature widely acknowledges that these types of biotic forces are key in structuring communities (Connell, 1983; Schoener, 1983; Minchella & Scott, 1991; Fox & Brown, 1993; Morin, 2011), and a growing body of work within the climate change literature has begun to investigate the importance of biotic interactions (Araújo & Luoto, 2007; Tylianakis *et al.*, 2008; Gilman *et al.*, 2010; Hellmann *et al.*, 2012; Staudinger *et al.*, 2013).

Given the increasing emphasis on the role of biotic interactions in responses to climate change, we chose to investigate two types of interactions in a system where patterns of distributional change have already been documented in relation to changes in climate. Specifically, we investigated the importance of habitat specialization and spatial overlap in the context of understanding heterogeneous patterns of elevational range change in chipmunks (genus *Tamias*) in Yosemite National Park. This system is particularly well suited to our study questions because in addition to a solid foundation of work on chipmunk habitat use, behavior, and physiology, an extensive data set on recent elevational range changes is available (habitat use:

Best, Clawson, & Clawson, 1994; Clawson, Clawson, & Best, 1994; Grinnell & Storer, 1924; Heller & Gates, 1971; behavior: M. A. Chappell, 1978; Heller & Gates, 1971; range shifts: Moritz et al., 2008; physiology: Chappell, Calvo, & Heller, 1978). Within our Yosemite region, a re-survey of small mammal communities (circa 100 years after the original faunal surveys of this region by Joseph Grinnell) revealed that many species altered their ranges in response to climate change. However, these results also showed that heterogeneity in responses exists, with even closely related (i.e. congeneric) species responding differently. This tendency is clear among the six species of chipmunks that occur in Yosemite. In particular, the Alpine Chipmunk (*T. alpinus*) has undergone a pronounced upward range contraction and is now absent from lower elevation sites that it occupied 100 years ago. In contrast, the partially sympatric Lodgepole Chipmunk (*T. speciosus*) has shown essentially no change in its elevational range (Moritz et al., 2008; Rubidge et al., 2011). The explanation for this striking difference is poorly understood, and our goal was to explore the influence of biotic factors on generating this interspecific difference in range response.

We began our investigation by quantifying patterns of interspecific spatial overlap between our two study species, with the goal of determining whether they co-exist on a microspatial scale, or whether they show fine-scale habitat partitioning. Given that our two study species are noted to be present in sympatry at several sites in Yosemite (Moritz *et al*., 2008; Rubidge *et al*., 2011), we expected to find extensive overlap between *T. speciosus* and *T. alpinus*. These initial analyses provided a foundation not only for comparing differences in microhabitat use between the two species, but also to examine how habitat characteristics differ in zones of overlap with heterospecifics versus zones of exclusive use by a single species. We were particularly interested in interspecific differences in microhabitat use, as previous observers have noted that the two species differ in the degree to which they use forested areas—and that these behavioral differences cannot be sufficiently explained by differences in morphology (Grinnell & Storer, 1924; Clawson *et al*., 1994). However, these accounts are primarily based on opportunistic observations of chipmunks and do not systematically compare *T. alpinus* with *T. speciosus*. In addition to observational data, a modeling study (Rubidge *et al*., 2011) suggests that climate variables are sufficient to explain *T. alpinus'* elevational range contraction, but not adequate to explain the stasis in *T. speciosus'* elevational range. Considering both this result and the observed differences in habitat use, we expected that *T. alpinus* would specialize on areas with low tree cover, while *T. speciosus* would use habitats irrespective of level of tree cover. We tested this hypothesis by selecting three co-occurrence sites in Yosemite (all of which were also included as part of the historical Grinnell surveys or modern resurvey efforts) where both *T. alpinus* and *T. speciosus* are present.

Overall, by combining information on microhabitat preferences and spatial overlap, we provide an integrated investigation of the impact of multiple biotic factors on species responses to changing climate. Our data generate new insights into the complex, multifaceted challenge of understanding why closely related species may exhibit quite different patterns of response.

Methods
Fieldwork
We conducted trapping and radiotelemetry at three sites in Yosemite National Park where *T. alpinus* and *T. speciosus* co-occur (May Lake, Vogelsang, and Cathedral Lake), as well as at one

site (Glen Aulin) where both species occurred in the historical era, but where *T. alpinus* is no longer present (Figure 1). These sites were also sampled as part of extensive surveys conducted during either historical (1911-1920) or modern (2003-2010) time periods (Moritz *et al.*, 2008). Our focus on co-occurrence sites made it possible to trap and track animals across the transition from areas where primarily *T. speciosus* occurs to areas where *T. alpinus* predominates. From June-September of 2011, 2012, and 2013, we visited each co-occurrence site once per year. We visited Glen Aulin in 2012 only. Durations of visits to each site varied from 2-6 weeks, and we visited sites in the same order each year (May Lake first, Vogelsang second, and Cathedral Lake third, plus a trip to Glen Aulin at the end of the 2012 season).

For trapping, we placed grids or lines of traps to span key habitat transitions (Figure 2). Given the previous reports that *T. alpinus* prefers open, rocky habitats and that *T. speciosus* frequents forested areas, we specifically aimed to trap in habitats with little tree cover and large amounts of exposed rock, as well as forested areas, and areas with intermediate levels of tree cover. Traps were placed in pairs spaced at least 10 m apart. We recorded the location of each pair of traps using a handheld GPS unit. Specific numbers and arrangement of traps within each trapping area varied based on the terrain and availability of suitable trap placement locations (e.g. we avoided areas with standing water or heavy sun exposure). We opened traps around dawn and closed them around or slightly before dusk. The number of trapping days at each site varied from 9-17 at our main co-occurrence sites, with 4 days of trapping at Glen Aulin.

We recorded species and sex for each chipmunk we trapped, and marked each individual with uniquely numbered metal ear tags placed in both pinnae. We outfitted a subset of captured individuals with radio transmitters (model BD-2C from Holohil Systems Ltd.). All individuals fitted with radio collars were adults; whenever possible, we collared approximately equal numbers of male and female individuals.

To conduct radiotelemetry, we first closed all traps, to ensure that the patterns of habitat used we observed would not be influenced by the presence of bait. We used a Yagi antenna and handheld receiver (Communications Specialists model R1000) to track each individual. We recorded a fix when we were able to locate an animal visually or pinpoint its location with confidence (e.g. by walking in a circle around a tree). Whenever we located an individual, we took a GPS point and noted any details we were able to observe about the individual's behavior or location — e.g. if it was foraging, whether it was on the ground or high in a tree, whether other animals were present, etc. To reduce temporal autocorrelation, we waited a minimum of one hour between successive fixes and took a maximum of six fixes per day until a total of 20 fixes per animal had been obtained. This sampling design was intended to provide a snapshot of the types of habitat used by individuals of each species.

All work involving animals followed ASM guidelines (Sikes & Gannon, 2011) and was approved by UC Berkeley's Animal Care and Use Committee.

GIS Analyses
We used ArcMap 10™ software (ESRI, 2015a) to generate visual representations of our data, as well as to produce minimum convex hulls representing either trapping areas or areas used by radiocollared individuals. We used the ESRI World Imagery layer as a basemap (ESRI, 2015b).

For each individual, we then calculated the percentage of its polygon that was overlapped by polygons for conspecific and heterospecific animals.

To quantify the effect of vegetation cover on patterns of habitat use by our two study species, we obtained 30 m resolution Landsat imagery from either the USGS Global Visualization website (glovis.usgs.gov/) or the Web-Enabled Distribution System website (weld.cr.usgs.gov/). Because weather conditions differed between our three study years, we used separate imagery for 2011, 2012, and 2013 to account for the fact that vegetation cover might differ between years with heavier winter precipitation (2011) and drier years (2012 and 2013). For 2011 and 2013, high quality imagery was available for single days during our field season; we selected one image per year that was taken during the middle of our season. For 2012, high quality daily images were unavailable due to a satellite malfunction. We therefore used a seasonal composite image (covering June-August 2012) that had been corrected to fill in gaps created by the malfunctioning satellite component. We created a composite layer using all available bands and used either the NDVI tool in ArcMap 10 or made similar calculations in the statistical program *R* (R Core Team, 2013) to calculate NDVI values for each 30 m raster cell. We then extracted vegetation cover values for either trapping grid polygons or telemetry polygons.

Statistical Analyses
Statistical analyses were carried out in ArcMap 10 or using the program *R* (R Core Team, 2013). In ArcMap, we used the Minimum Bounding Geometry tool to calculate areas of convex hulls and the Intersect tool to calculate overlap between polygons.

To examine patterns of interspecific overlap, we calculated the percent of each individual chipmunk's polygon that was overlapped by conspecific individuals, as well as the proportion overlapped by heterospecific individuals. We did these calculations for each collared individual, generating one conspecific and one heterospecific value per polygon (regardless of whether the focal individual's polygon overlapped with one or many other individuals). We used Wilcoxon rank sum or Mann-Whitney U tests to compare percentage of conspecific and heterospecific overlap by individual members of each study species.

To determine whether values for conspecific and heterospecific overlap differed from random for each of our study species, we applied the following randomization procedure to polygons generated from telemetry data. For each combination of species, site, and year (e.g. May Lake 2012), we used all telemetry points to make a minimum convex hull for that species x site x year combination. We randomly selected sets of coordinates within each of these overall polygons (using the *spsample* function in *R* package *sp* (Bivand, Pebesma, & Gomez-Rubio, 2013; Pebesma & Bivand, 2005) and then moved the centroid for each individual *T. alpinus* or *T. speciosus* polygon to one of these randomly selected locations. We also rotated each polygon at a randomly selected angle. After moving and rotating all polygons, we re-calculated the percentages of each individual's polygon that were overlapped by conspecific and heterospecific individuals. We repeated this process 100 times, then used the values for all 100 iterations to calculate the mean randomly generated percent of conspecific and heterospecific overlap per individual. We used paired Mann Whitney U tests to compare observed and randomly generated percentages of conspecific and heterospecific overlap for members of each species.

To characterize potential interspecific differences in NDVI values, we conducted analyses at the levels of the site, trapping grid, and individual. For our site-level analyses, we extracted NDVI values for areas used only by *T. alpinus*, areas used only by *T. speciosus*, and zones of overlap as determined by telemetry data. For each site x year combination, we randomly selected a maximum of 100 raster cells from each type of area (*T. alpinus* only, *T. speciosus* only, overlap); if a given type of area included less than 100 raster cells, we used all included cells.

We followed the model selection and validation procedures in Zuur et al. (2009) to generate linear mixed effects models (using the package *nlme*; Pinheiro, Bates, DebRoy, Sarkar, & R Development Core Team, 2013) to compare mean NDVI values between the three different types of areas. We began the model selection process by fitting a full linear model with mean NDVI as a response and species, site, and the species*site interaction term as predictors. 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 year 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 or AIC_C), with a correction applied for small sample sizes if n/K < 40 (n = total sample size, K = number of parameters in model) (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 likelihoods for all candidate models (Burnham & Anderson, 2002):

$$w_i = \frac{e^{-0..5*\Delta_i}}{\sum_{r=1}^{R} e^{-0..5*\Delta_i}}$$

In our confidence set of top models we included all of our models with w_i values within 10% of the maximum w_i for that candidate set (following Burnham & Anderson, 2002). In the event that all predictor terms were significant in the full model, we report results for the full model only.

At the level of the trapping grid, we calculated the mean NDVI value for each trapping grid and compared that value to the number of *T. alpinus,* the number of *T. speciosus*, and the proportion of *T. alpinus* captured in that grid (a measure of extent of co-occurrence) using Kendall's tau tests. Finally, at the level of the individual, we extracted NDVI values that corresponded to each individual's telemetry polygon. We used linear mixed effects models (again following procedures from Zuur et al. (2009)) to compare both mean and standard deviation of NDVI values across species and sites. For all cases in which we fit models to our data, we validated our model by visually inspecting plots of residuals to confirm that assumptions of homoscedasticity and independence were met.

Results
Trapping & Telemetry: Over the course of our study, we captured a total of 156 *T. alpinus* and 184 *T. speciosus* (Table 1) and carried out telemetry on 51 individual *T. alpinus* and 59

individual *T. speciosus* (Table 2). Sample sizes for analyses based on telemetry data (Table 2) reflect the number of individuals tracked in each year. As these data reveal, seven *T. alpinus* and two *T. speciosus* were tracked in both 2012 and 2013. While counting these individuals towards both years' sample sizes means that our samples from each year are not fully independent, all repeat animals were tracked across two different years, and had different neighbors in each year. Therefore, we retained repeat animals in both the 2012 and 2013 data sets. For all subsequent telemetry analyses, we included only individuals for which we obtained at least 10 fixes. Number of fixes per animal ranged from 10-32, with a mean of 20 fixes per individual (standard deviation = 3 fixes).

Spatial Overlap: Both our trapping and telemetry data confirmed that extensive spatial overlap exists within and between species (Figures 3 & 4). Trapping data revealed that *T. alpinus* and *T. speciosus* were frequently captured within the same trapping grid, including sometimes at the same trap station. Although a substantial amount of spatial overlap was evident, the two species did not overlap completely; at all co-occurrence study sites, telemetry data revealed that certain areas were used exclusively by each of study species. To quantify the extent of heterospecific and conspecific spatial overlap, we analyzed telemetry data gathered during 2012 and 2013 from our three co-occurrence sites (we excluded 2011 due to low sample sizes). Wilcoxon rank sum tests showed that differences existed in between years in proportions of conspecific and heterospecific overlap for several species x site combinations (Conspecific overlap- *T. alpinus* at VO: $W = 58$, $mean_{2012} = 0.761$, $mean_{2013} = 0.325$, $p = 0.0383$; Heterospecific overlap: *T. alpinus* at VO: $W = 57$, $mean_{2012} = 0.509$, $mean_{2013} = 0.233$, $p = 0.048$; *T. alpinus* at CL: $W = 0$, $mean_{2012} < 0.001$, $mean_{2013} = 0.427$, $p < 0.001$). There were no year differences for other species x site combinations (all $p > 0.05$), but because year differences were present in some cases, we separated years for all further comparisons. We then conducted several sets of comparisons, first comparing conspecific vs. heterospecific overlap within a species, and then comparing conspecific or heterospecific overlap between species (Figure 5). For the first set of intraspecific comparisons, we found that in *T. alpinus,* conspecific overlap was greater than heterospecific overlap at May Lake in 2013 and at Cathedral Lake in 2012 and 2013 (ML 2013: $W = 44$, $mean_C = 0.629$, $mean_H = 0.132$, $p = 0.0141$; CL 2012: $W = 64$, $mean_C = 0.864$, $mean_H < 0.001$, $p < 0.001$; CL 2013: $W = 70$, $mean_C = 0.809$, $mean_H = 0.427$, $p = 0.00777$). For *T. speciosus*, conspecific overlap was greater than heterospecific overlap at May Lake and Cathedral Lake in both years (ML 2012: $W = 43$, $mean_C = 0.613$, $mean_H = 0.0513$, $p = 0.0187$; ML 2013: $W = 33$, $mean_C = 0.628$, $mean_H = 0.152$, $p = 0.0194$; CL 2012: $W = 94.5$, $mean_C = 0.433$, $mean_H < 0.001$, $p < 0.001$; CL 2013: $W = 55$, $mean_C = 0.555$, $mean_H = 0.181$, $p = 0.0178$). For our interspecific comparisons of overlap, the only significant difference we found was for conspecific overlap at Cathedral Lakes in 2012 ($W = 72$, $mean_{alpinus} = 0.864$, $mean_{speciosus} = 0.433$, $p = 0.00511$).

Given our finding of substantial spatial overlap between both conspecific and heterospecific individuals, we were interested in determining whether the observed amount of overlap was greater or less than random. For each site x year x species combination, we compared the observed proportions of overlap with the proportions calculated using the randomly moved and rotated polygons (Table 3a). For conspecific overlap in *T. alpinus*, we found that observed overlap was greater than random at two of our three sites (Vogelsang and Cathedral Lake) in 2012 and one site in 2013 (Cathedral Lake). For *T. speciosus* observed conspecific overlap was greater than random only at Cathedral Lake in 2012. All other comparisons for conspecific

overlap were nonsignificant (all p > 0.05).

In contrast to our finding that proportions of conspecific overlap were *greater* than random at some sites, we found that proportions of heterospecific overlap tended to be *less* than random (Table 3b). For *T. alpinus,* observed overlap was less than random at Cathedral Lake in 2012 and at May Lake in 2013; for *T. speciosus*, observed overlap was less than random at May Lake and Cathedral Lake in 2012. All other heterospecific overlap comparisons were nonsignificant.

Habitat use: Model selection revealed that at the level of our study sites, NDVI values were best explained by a model that retained all main predictors. This included site, overlap category (*T. alpinus* only, *T. speciosus* only, or overlap), and the site*overlap category interaction term as fixed effects, plus year as a random effect. The AIC for this model was -3583. Significant differences in NDVI existed between areas used by *T. alpinus* only, *T. speciosus* only, and by both species for all site x year combinations examined except Vogelsang, at which no significant differences were detected for *T. alpinus* only areas and areas of interspecific overlap (Table 4). For all comparisons of *T. alpinus* only versus *T. speciosus* only areas, differences were in the expected direction—that is, NDVI values were higher in *T. speciosus* only areas. Similarly, NDVI values were lower in areas of overlap compared to areas used by *T. speciosus* only. Patterns were less clear for comparisons between areas used by *T. alpinus* only versus areas of overlap, with relative values of NDVI varying across study sites.

Nonparametric correlation tests revealed that the number of *T. speciosus* captured in a grid was positively correlated with NDVI (Kendall's tau test: $\tau = 0.274$, z = 2.5, n = 43, p = 0.0126; Figure 3). Number of *T. alpinus* captured in a grid was negatively related to NDVI, but this correlation was not statistically significant (Kendall's tau test: $\tau = -0.205$, z = -1.82, n = 43, p = 0.0682). Similarly, there was a negative but nonsignificant correlation between NDVI and the proportion of *T. alpinus* captured in a grid (Kendall's tau test: $\tau = -0.214$, z = -1.92, n = 43, p = 0.055).

At the scale of individual telemetry polygons, to reduce heterogeneity in residuals, we log-transformed mean NDVI. We only included 2012 and 2013 data from our three co-occurrence sites in our analyses, choosing to exclude 2011 and Glen Aulin data due to low sample sizes (Figure 6). After completing model selection procedures, our optimal model retained all main predictors (species and site) and the interaction term (Table 5a). Because the two models in our confidence set differed only in the structure of the random effect term, we chose to focus our interpretation on the model with the lowest AIC_C. This model showed that NDVI values for *T. speciosus* polygons were significantly larger than those for *T. alpinus* polygons at Cathedral Lake (coefficient for species parameter = 1.3, p = 0.0002, 95% confidence interval: 1.72-2.28; comparisons for the other two study sites were not significant (Vogelsang: coefficient for species parameter = 1.3, p = 0.0607, 95% confidence interval: 0.988-1.72; May Lake: coefficient for species parameter = 1.16, p = 0.323, 95% confidence interval: 0.864-1.55).

With regard to differences in the range of habitats used by each species, we calculated the standard deviation for NDVI values within each individual's telemetry polygon and compared these values for *T. alpinus* and *T. speciosus* using a linear mixed effects models that included species, site, and the interaction between species and site as fixed predictors, as well as year as a

random predictor and the log-transformed standard deviation of NDVI as a response variable. Our optimal model retained both the main species and site predictors but no interaction term. The AIC_C for this model was 92.6. The species parameter was significant (coefficient for species parameter = 1.31, p = 0.0004, 95% confidence interval 1.14 to 1.52), indicating that standard deviations for NDVI were higher for *T. speciosus* (Table 5b, Figure 7).

Discussion
Our analyses provide convincing evidence that individual *T. alpinus* and *T. speciosus* overlap spatially in parts of their ranges. Both telemetry and trapping data illustrate this extensive overlap, but simultaneously demonstrate that there are areas at all of our co-occurrence study sites that are used only by a single species. Another major finding is that even in areas of sympatry, our two study species use different portions of the habitat. Support for this again comes from both trapping and telemetry data. Specifically, trapping data show a positive correlation between vegetation cover (NDVI) and the number of *T. speciosus* captured in a trapping grid. Telemetry data show that vegetation cover is greater in areas used by *T. speciosus* only than in *T. alpinus*-only areas or zones of overlap. Similarly, comparisons at the level of the individual indicate that at one of our study sites, vegetation cover is greater in *T. speciosus* telemetry polygons. Finally, our data support the hypothesis that *T. alpinus* is more of a habitat specialist, with telemetry data showing higher standard deviations in vegetation cover in *T. speciosus* areas.

While our results generally support our predictions of high interspecific overlap and differential habitat use, our methods do impose limitations on what we can infer with regard to differences between our study species. For example, the limited number of telemetry fixes that we obtained may have captured only a portion of an individual's home range, leading us to underestimate the range of habitats used and also leading to underestimates of the amount of overlap with other individuals. Additionally, while NDVI is useful for quantifying vegetation cover, the 30 m resolution of our data is coarse enough that it does not capture important features relevant to our study species. In particular, *T. speciosus* frequently uses the canopies of tall trees, while *T. alpinus* rarely ascends trees (Grinnell & Storer, 1924; Best *et al.*, 1994; Clawson *et al.*, 1994); while NDVI could capture differences in tree cover, it would fail to capture information on tree height. Finally, while our data allow us to compare habitat use between our two study species, we cannot determine whether the patterns we observed reflect choices by each species, or the outcome of other factors such as competitive exclusion.

Potential for competitive interactions
With regard to interspecific spatial overlap, our results confirm that our two study species are partially sympatric and overlap extensively at a micro-spatial scale. This indicates that members of the two species are likely in frequent contact with one another, and that there are numerous opportunities for competitive interactions to occur. In other chipmunk communities in the Sierra Nevada mountains, competition is a key force in shaping community structure (Chappell, 1978; Heller & Gates, 1971), but the implications of this competition for response to environmental change are not known. Competitive interactions have been suggested to play a role in limiting *T. speciosus*' elevational range (Rubidge *et al.*, 2011). Although laboratory experiments have revealed that *T. speciosus* is subordinate to *T. alpinus* (Heller & Gates, 1971), no field experiments have been conducted with these species to determine if the same relationship applies

in nature. As a result, it is not know to what extent competitive exclusion by *T. alpinus* may be shaping the upper range limit of *T. speciosus*. Additional studies designed to assess patterns of dominance in situ and to quantify the effects of such interactions on each species' spatial distribution are critical next steps toward understanding the importance of competitive interactions in the context of climate-driven distributional changes.

Role of habitat specialization
Our finding that *T. alpinus* uses a different subset of habitats than *T. speciosus* may also be important in understanding differences in the responses of these species to changing environmental conditions. Our data confirm anecdotal reports that *T. alpinus* is typically associated with higher elevation alpine habitats that are characterized by relatively low levels of vegetation cover (Best, Clawson, & Clawson, 1994; Clawson, Clawson, & Best, 1994; Grinnell & Storer, 1924; Heller & Gates, 1971). Thus, even in areas of sympatry, habitat use differs between the study species, creating the potential for differential responses to changes in the same environmental conditions.

Our findings regarding potential differences in the niche breadths of the study species were less conclusive, with evidence for greater habitat specialization by *T. alpinus* varying across study sites. Our analyses, however, were based solely on NDVI, which is a relatively non-specific measure of habitat parameters (Pettorelli *et al*., 2005, 2011; Lengyel *et al*., 2008), especially given the 30 m resolution of our data. It is possible that other habitat features such as the presence of suitable retreat sites or abundant food resources differentially affect the suitability of habitat patches for *T. alpinus* and *T. speciosus*. Additional studies that examine habitat use in greater detail would be valuable.

Implications for elevational range changes
In the context of understanding why range responses vary between *T. alpinus* and *T. speciosus*, our analyses confirm that the two species overlap on the small scale of individual chipmunks. This in turn means that (1) our two study species are experiencing the same general environmental conditions and (2) interspecific competition is a possibility. The latter finding highlights the potentially important role of competition in shaping patterns of distributional change and suggests that future work should explore the influence of competition in more detail. The former point at first seems to imply that given the similarity in environmental conditions, one would expect similar range responses. However, we also found evidence that even in sympatry, our two species use the habitat differently. Given that larger-scale environmental change will impact habitat features (Lutz *et al*., 2009; Dolanc *et al*., 2013; McIntyre *et al*., 2015), this differential habitat use may therefore contribute to shape contrasting patterns of range response. Overall, our findings underscore the complexity of interactions between organisms and their environments, even at very localized scales. Our work provides a critical foundation for future studies that will explore interactions among local environmental conditions, habitat specialization, and interspecific interactions in greater detail.

Figures & Tables
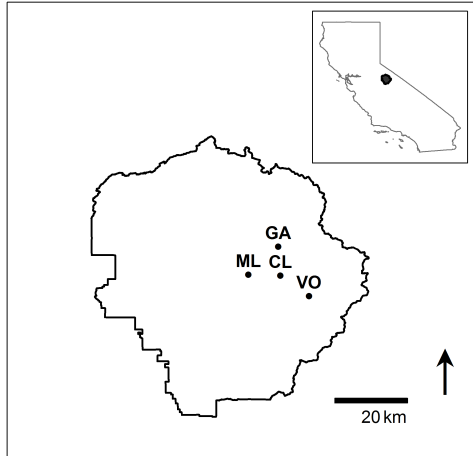
Figure 1: Location of study sites within Yosemite National Park. ML = May Lake, CL = Cathedral Lake, VO = Vogelsang, and GA = Glen Aulin. Inset map shows the location of Yosemite National Park within California.
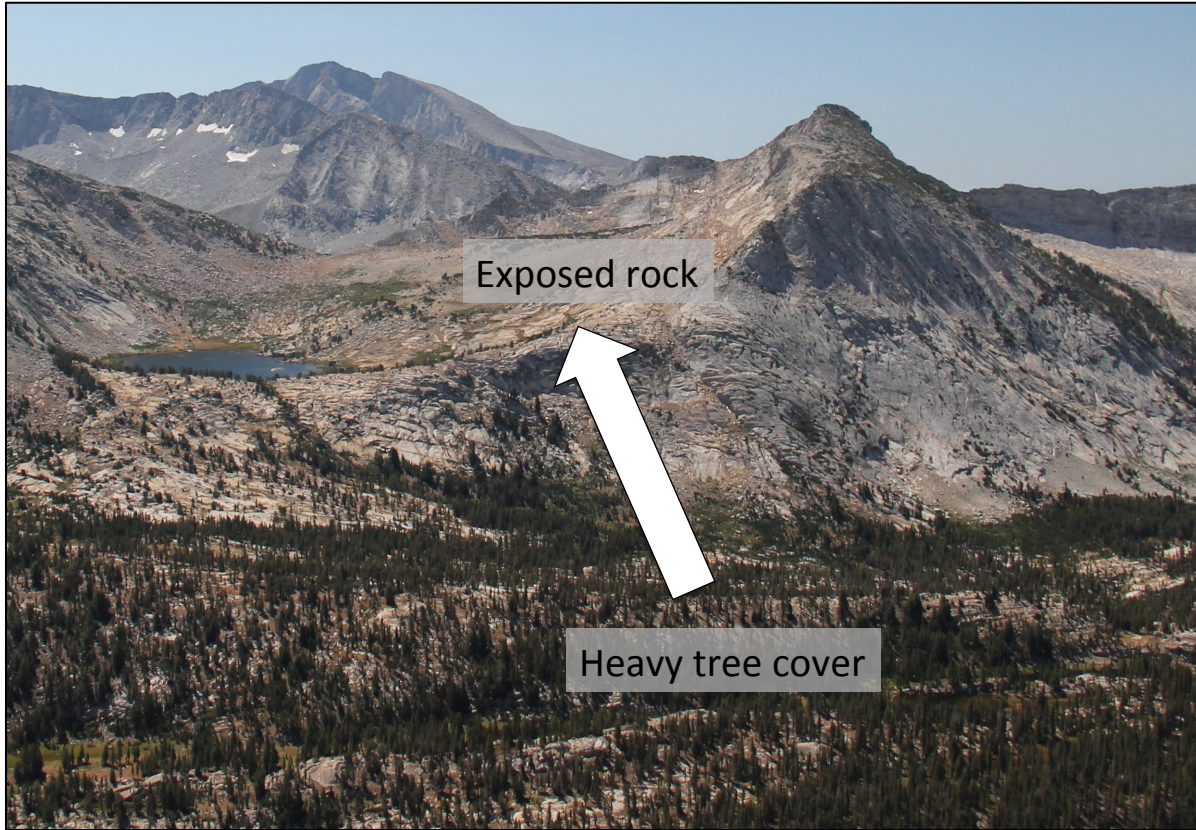
Figure 2: Example of trapping habitat at one co-occurrence site. Traps were placed to span transitions from heavily forested habitat (shown in the lower portion of the photo) to more rocky, exposed habitat (in the upper portion of the photo). (Photo: Michael Hernandez)

Table 1: Sample sizes for trapping

Year	ML	VO	CL	GA
Site				
2011				
T. alpinus	10	10	13	
T. speciosus	20	13	1	
2012				
T. alpinus	9	20	11	N/A
T. speciosus	8	19	23	19
2013				
T. alpinus	12	48	23	
T. speciosus	8	55	18	

Table 2: Telemetry sample sizes by year and site. These data include individuals for which we obtained at least ten fixes.

Year	ML	VO	CL	GA
	Site			
2011				
T. alpinus	1	2	2	
T. speciosus	3	1	1	
2012				
T. alpinus	5	9	8	N/A
T. speciosus	7	9	10	4
2013				
T. alpinus	7	8	9	
T. speciosus	6	10	8	
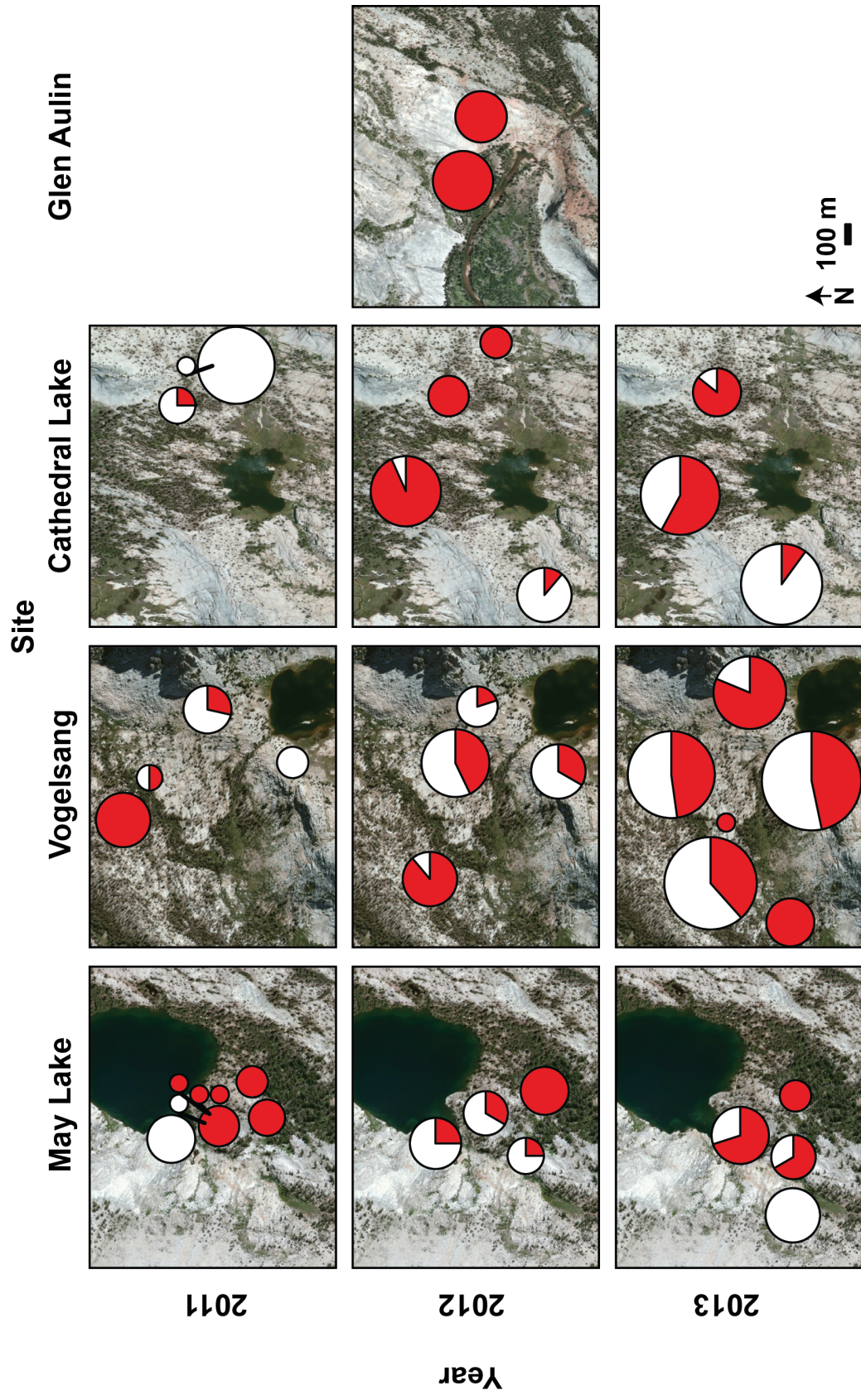
Figure 3: Results of trapping during 2011, 2012, and 2013. Pie charts show the proportion of original captures of *T. alpinus* (white) and *T. speciosus* (red) in each trapping area. Size of each pie is proportional to the total number of individuals captured in that area.

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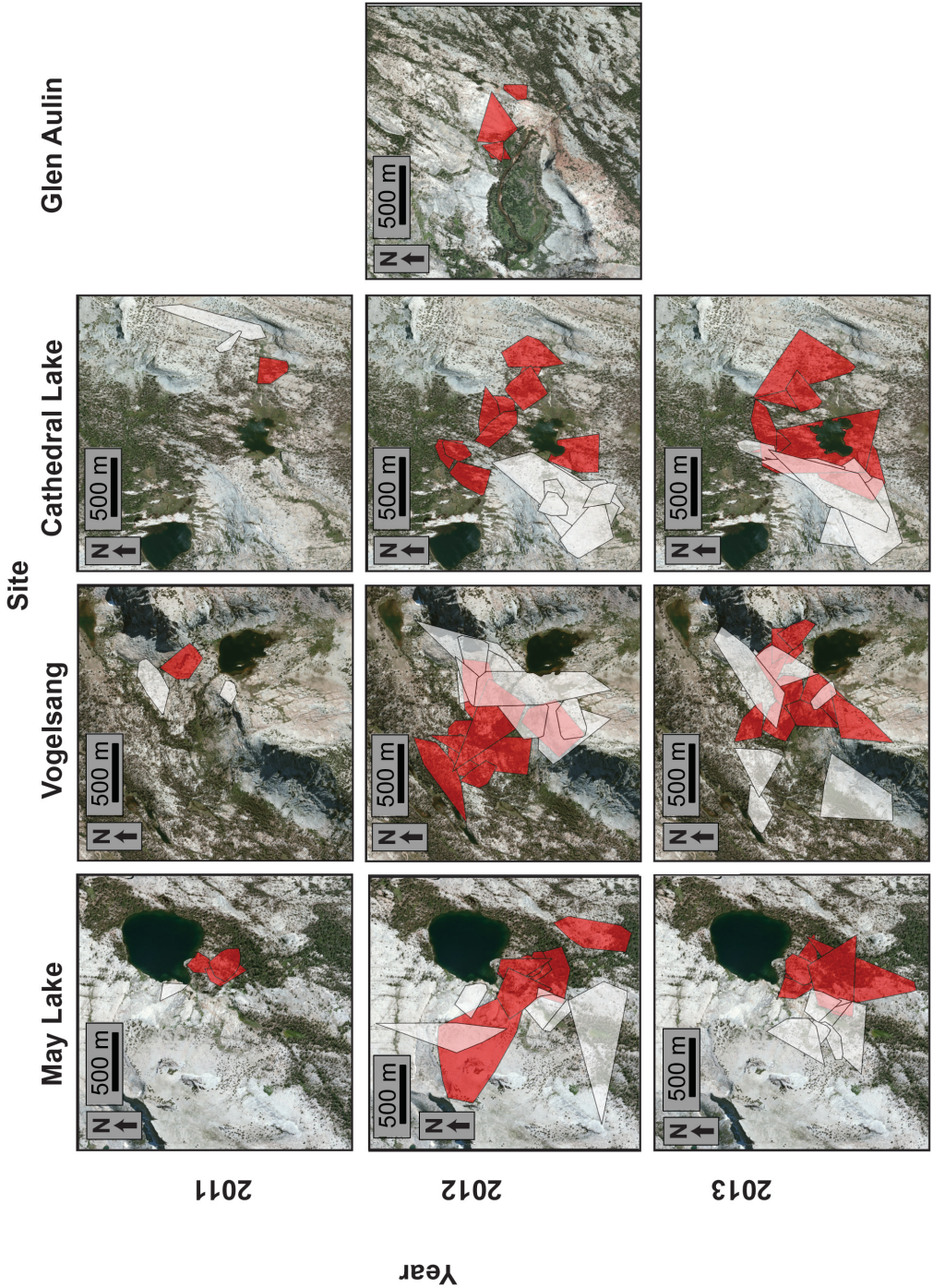
Figure 4: Minimum convex polygons for telemetry data from 2011-2013. Each white polygon represents an individual *T. alpinus*; each red polygon represents an individual *T. speciosus*.

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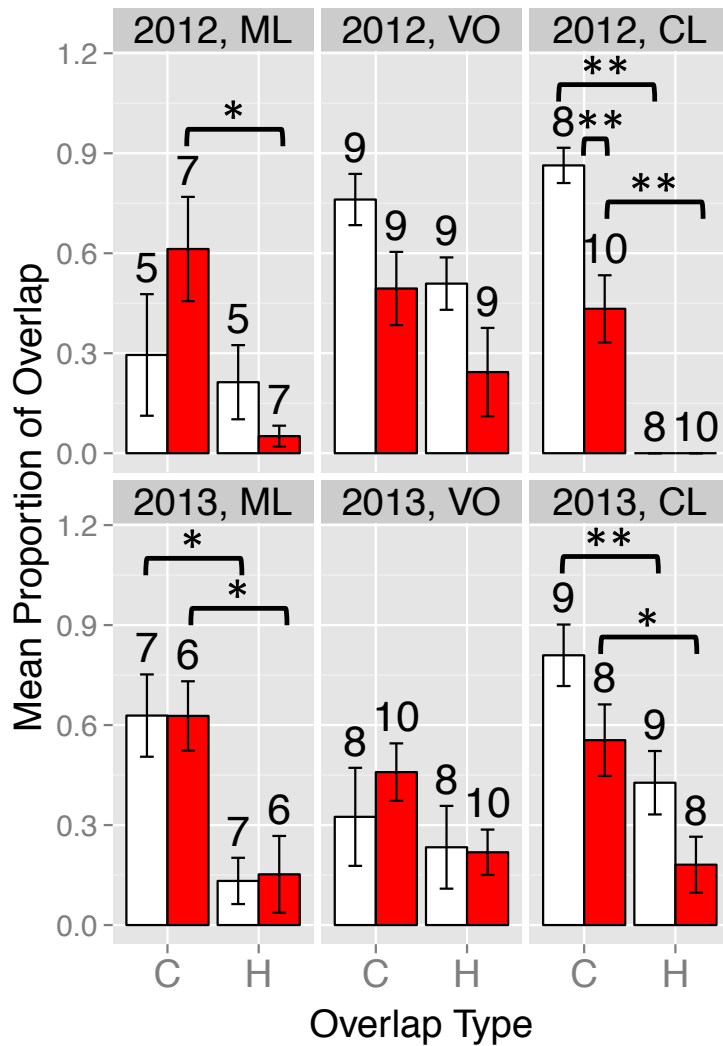
Figure 5: Proportions of overlap at each co-occurrence site in 2012 and 2013. C = conspecific overlap, and H = heterospecific overlap. *T. alpinus* proportions are shown in white; *T. speciosus* is shown in red. Single asterisks indicate comparisons that are significant at the p < 0.05 level, and double asterisks show comparisons that are significant at the p < 0.01 level.

Table 3: Comparisons of proportions of conspecific and heterospecific overlap for observed and random telemetry data. The means (Mean Obs. and Mean Rand.), sample size (n), test statistic (W), and p-value are reported for each comparison of observed *vs.* random proportions, with significant p-values in bold.

a.) Conspecific overlap

Year	Site														
	ML					VO					CL				
	Mean Obs.	Mean Rand.	n	W	p	Mean Obs.	Mean Rand.	n	W	p	Mean Obs.	Mean Rand.	n	W	p
2012															
T. alpinus	0.295	0.171	5	6	0.787	0.761	0.397	9	0	**0.00915**	0.864	0.309	8	0	**0.0143**
T. speciosus	0.613	0.286	7	4	0.108	0.494	0.353	9	13	0.286	0.433	0.234	10	10	0.0831
2013															
T. alpinus	0.629	0.272	7	2	0.0519	0.325	0.22	8	18	1	0.809	0.403	9	1	**0.0129**
T. speciosus	0.628	0.318	6	1	0.0592	0.459	0.237	10	5	**0.0249**	0.555	0.351	8	5	0.0801

b.) Heterospecific overlap

Year	Site														
	ML					VO					CL				
	Mean Obs.	Mean Rand.	n	W	p	Mean Obs.	Mean Rand.	n	W	p	Mean Obs.	Mean Rand.	n	W	p
2012															
T. alpinus	0.213	0.317	5	11	0.418	0.509	0.377	9	10	0.155	<0.001	0.267	8	36	**0.0143**
T. speciosus	0.0513	0.203	7	28	**0.0225**	0.243	0.426	9	32	0.286	<0.001	0.361	10	55	**0.00592**
2013															
T. alpinus	0.132	0.39	7	27	**0.0346**	0.233	0.251	8	20	0.834	0.427	0.386	9	19	0.722
T. speciosus	0.152	0.288	6	15	0.402	0.251	0.286	10	39	0.263	0.181	0.432	8	32	0.0587

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Table 4: Site-level comparisons of NDVI in areas used by *T. alpinus* only, overlap areas, and areas used by *T. speciosus* only. Estimates are separated by site (ML, VO, and CL), and each cell includes the coefficient estimate, the p-value (bolded if significant at the 0.05 level), and a 95% confidence interval.

	T. alpinus only vs. *T. speciosus* only	*T. alpinus* only vs. overlap	*T. speciosus* only vs. overlap
ML	0.025 **(p = 0.0064)** 95% CI: 0.00701 to 0.0429	-0.0337 **(p < 0.001)** 95% CI: -0.0497 to -0.0176	-0.0586 **(p < 0.001)** 95% CI: -0.0746 to -0.0426
VO	0.0526 **(p < 0.001)** 95% CI: 0.0375 to 0.0677	0.0108 (p = 0.108) 95% CI: -0.00235 to 0.0677	-0.0418 **(p < 0.001)** 95% CI: -0.0577 to -0.0259
CL	0.0873 **(p < 0.001)** 95% CI: 0.0737 to 0.101	0.0213 **(p < 0.001)** 95% CI: 0.00926 to 0.0334	-0.0659 **(p < 0.001)** 95% CI: -0.081 to -0.0508
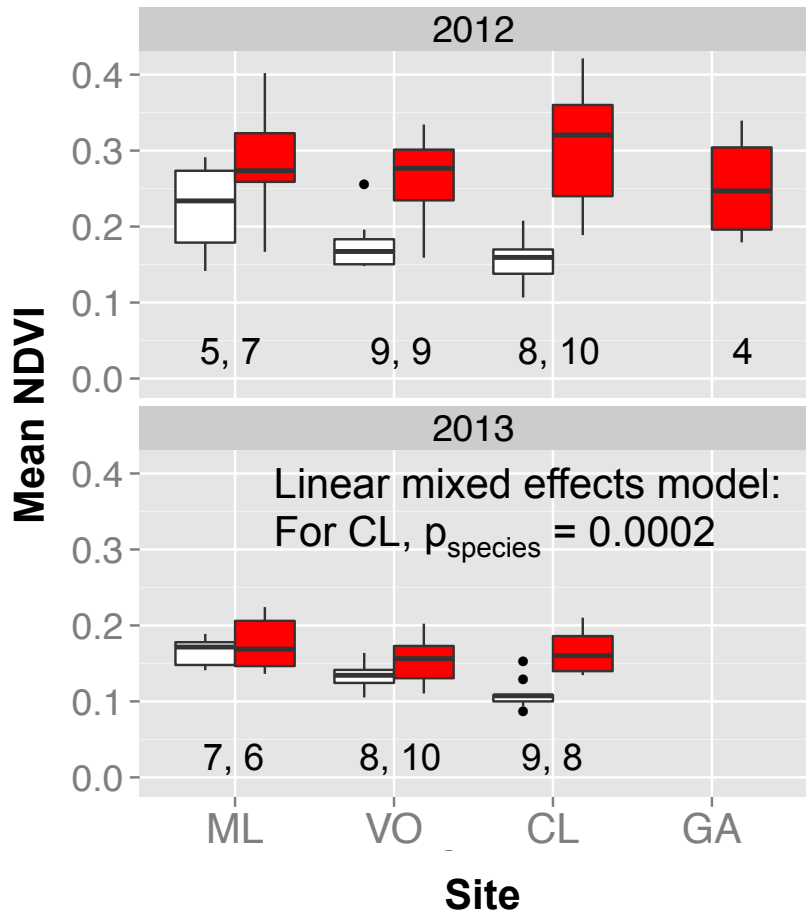
Figure 6: Mean NDVI values in *T. alpinus* and *T. speciosus* telemetry polygons. Individuals are grouped into one boxplot for each unique combination of species, site, and year. (Note: Glen Aulin data are shown here, but were not included in statistical analyses.)

Table 5: Summary statistics for models for models examining the effect of species, site, and year on a) mean and b) standard deviation of NDVI in individual telemetry polygons. Fixed and random effects are listed, as well as 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).

a.)

Response Variable	Predictor variables	Number of Parameters (K)	AIC_C	ΔAIC_C	AIC_C Weight

Mean NDVI	Fixed:
	  Species
	  Site
	  Species*Site
	Random:
	  Year
		9	-2.25	0	0.81

	Fixed:
	  Species
	  Site
	  Species*Site
	Random:
	  Species
	  Year
		11	0.68	2.93	0.19

b.)

Response Variable	Predictor variables	Number of Parameters (K)	AIC_C	ΔAIC_C	AIC_C Weight

Standard deviation of NDVI	Fixed:
	  Species
	  Site
	Random:
	  Year
		6	92.6	0	0.84

	Fixed:
	  Species
	  Site
	  Species*Site
	Random:
	  Year
		8	95.9	3.37	0.16
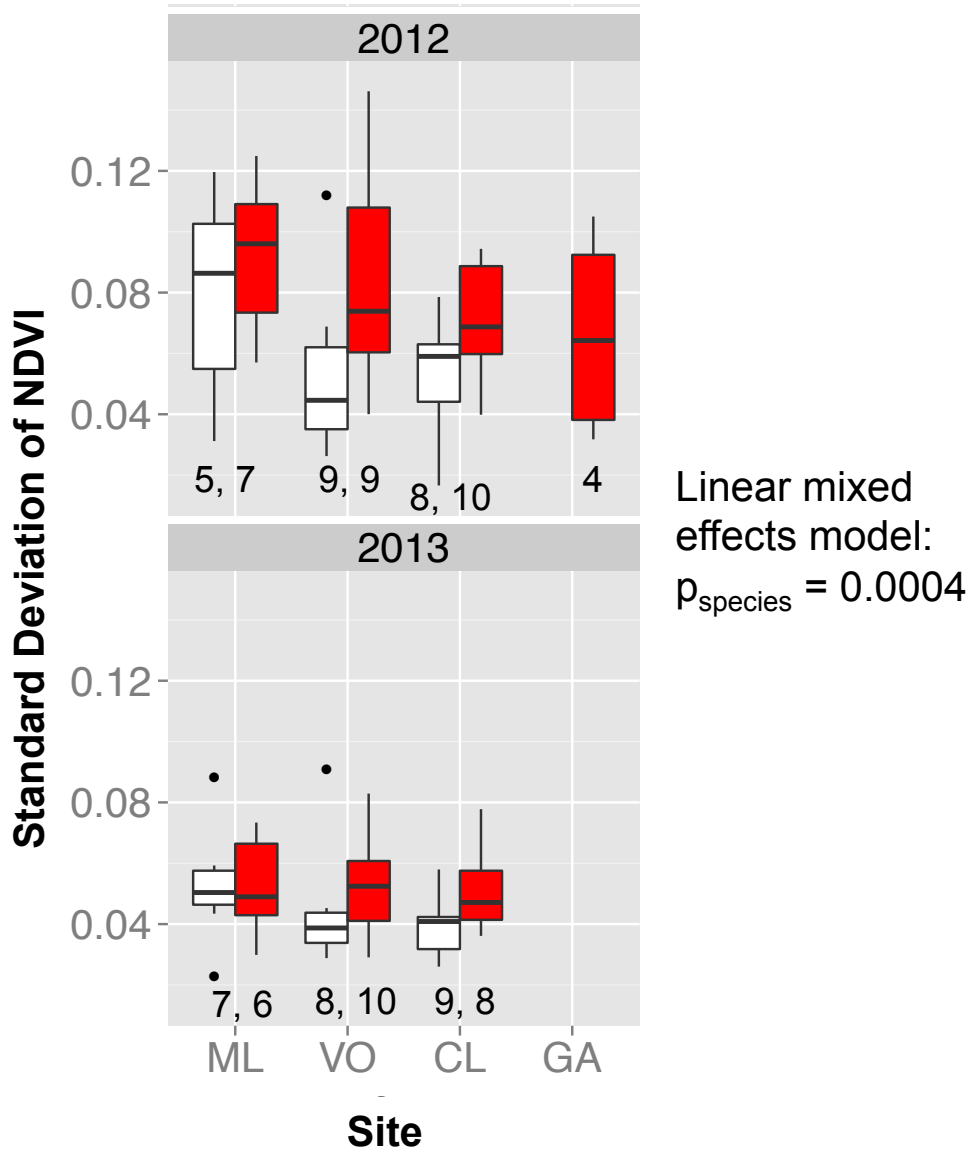
Figure 6: Standard deviations of NDVI values in *T. alpinus* and *T. speciosus* telemetry polygons. Individuals are grouped into one boxplot for each unique combination of species, site, and year. A linear mixed effects model was used to compare NDVI standard deviations between species. The species parameter was significant in this model, meaning that standard deviations in *T. speciosus* are greater for all sites and years (see text for detail). (Note: Glen Aulin data are plotted, but were not included in statistical analyses.)

Chapter 3

Microhabitat use and elevational range change in two sympatric chipmunk species in Yosemite National Park

Introduction:
As evidence for the impacts of climate change on biodiversity accumulates (see Parmesan & Yohe, 2003; Parmesan, 2006; and Root, Price, Hall, & Schneider, 2003 for reviews), there is little doubt that altered climate conditions will have far-reaching consequences for diverse taxa and communities. Distributional changes are one frequently observed example of these consequences, with species ranges moving poleward or upward in elevation, presumably to track optimal climatic regimes (see Chen, Hill, Ohlemüller, Roy, & Thomas, 2011 for a recent review). Although numerous studies provide empirical evidence of climate-driven distributional changes, it remains challenging to generate predictive models that accurately forecast patterns of such responses. In particular, the utility of predictive models that rely on solely on climate information can be limited, as these models ignore other critical parameters and may not account for important ecological differences between species (Araújo & Luoto, 2007; Gilman *et al.*, 2010). For example, taxa vary in the degree to which they are specialized for particular conditions, with specialist species predicted to be more sensitive to the impacts of climate and vegetation change (Warren *et al.*, 2001; Julliard *et al.*, 2004; Jiguet *et al.*, 2007). However, empirical evidence for differences in response between specialists and generalists is scarce, and studies such as Yang et al. (2011) demonstrate that upon close examination, purported habitat specialists may in fact be able to expand into different habitats.

We chose to investigate patterns of habitat use and specialization and their links to elevational range changes in two species of partially sympatric chipmunks in Yosemite National Park. These two species were included in extensive surveys of the region's small mammal community, which provided information on elevational ranges of each species in the historical (1914-1920) and modern (2003-2006) sampling periods (Moritz *et al.*, 2008; Rowe *et al.*, 2015). Survey results from the Yosemite region revealed markedly different patterns of elevational range change in each species over the past century: *Tamias alpinus* (the Alpine Chipmunk) showed an elevational range contraction and is no longer found at lower elevation sites at which it was present historically; in contrast, *Tamias speciosus* (the Lodgepole Chipmunk) showed no significant change in its elevational range. Although *T. alpinus* and *T. speciosus* are partially sympatric in many parts of their ranges, they are believed to differ in their degree of ecological specialization. While *T. alpinus* is thought to be a specialist that is restricted to high elevation alpine habitats, *T. speciosus* occurs in a variety of habitats, from tree line down to the Sierran foothills (Grinnell & Storer, 1924; Best *et al.*, 1994; Clawson *et al.*, 1994; Waters & Zabel, 1998). Niche models of the elevational distributions of these species suggest that the marked upward range contraction of *T. alpinus* over the past century is associated with changes in climate and vegetation (Rubidge *et al.*, 2011).

Although these data are consistent with the hypothesis of greater habitat specialization in *T. alpinus*, few quantitative data are available to test this idea. Analyses using remotely sensed data on vegetation cover (NDVI) indicate that at present, *T. alpinus* uses areas with lower vegetation

cover than does *T. speciosus* (Walsh, Chapter 2), these data provide relatively limited information about habitat characteristics that are likely to be important to individual chipmunks, such as differences in height and growth form of trees and the extent of downed wood in the habitat. Vegetation in the Sierra Nevada region is changing in response to changing climatic conditions (Thorne *et al*., 2008; Lutz *et al*., 2009; Dolanc *et al*., 2013; McIntyre *et al*., 2015) and the resulting habitat modifications are likely to have significant impacts on small, herbivorous mammals such as chipmunks that rely vegetation for food and shelter. For example, tree density is changing in the Sierran region (Dolanc *et al*., 2013; McIntyre *et al*., 2015); given the clear relationships between vegetative cover and the occurrence of our study species, such modifications of the habitat may have significant impacts with respect to range changes in *T. alpinus* and *T. speciosus*.

Given the combination of demonstrated changes to vegetation in the Sierra Nevada, our previous findings that overall vegetative cover differs between areas occupied by *T. alpinus* and *T. speciosus,* and the expected difference in habitat specialization between these species, more detailed data regarding habitat use by these species are required. Accordingly, we set out to gather fine-scale information on microhabitat features and vegetation characteristics, with the goal of determining how these habitat features differ between areas used by *T. alpinus* versus *T. speciosus*. We began by using information from previously published reports of chipmunk habitat use (Grinnell & Storer, 1924; Best *et al.*, 1994; Clawson *et al.*, 1994) and/or own observations to identify potentially relevant variables for inclusion in our analyses. We predicted that *T. alpinus* would occur in areas with fewer tall trees, less tree cover, and larger amounts of exposed rock and, further, that the range of habitat conditions inhabited by this species would be less than that for *T. speciosus*. By identifying fine-scale differences in habitat use and, ideally, linking those differences to longer-term and larger-scale information on patterns of distributional change, our goal was to move beyond documenting how organisms respond to climate change to begin to explain why they respond as observed.

Methods
Study Sites
We conducted live-trapping and radiotelemetry at three sites in Yosemite National Park where *T. alpinus* and *T. speciosus* co-occur (May Lake, Vogelsang, and Cathedral Lake), as well as at one site (Glen Aulin) where both species occurred in the historical era, but where *T. alpinus* is no longer present (Figure 1). Our focus on co-occurrence sites made it possible to trap and track animals across the transition from heavily forested areas to more rocky, exposed areas with little tree cover. From June-September of 2011, 2012, and 2013, we visited each co-occurrence site once per year. We visited Glen Aulin in 2012 only. Durations of visits to each site varied from 2-6 weeks. In addition to allowing us to attain higher trapping and telemetry sample sizes, our multi-year sampling design allowed preliminary assessment of annual variation in habitat use and by the study species.

Trapping & Telemetry
We placed trapping grids or lines of traps to span key habitat transitions. We specifically aimed to set traps in habitats with little tree cover and large amounts of exposed rock, as well as in forested areas and in areas with intermediate levels of tree cover. Traps were placed in pairs with successive trap stations spaced at least 10 m apart. We recorded the location of each pair of

traps using a handheld GPS unit. Specific numbers and arrangement of traps within each trapping area varied based on the terrain and availability of suitable trap placement locations (e.g. we avoided areas with standing water or heavy sun exposure). We opened traps around dawn and closed them around or slightly before dusk. The number of trapping days at each site varied from 9-17 at our main co-occurrence sites, with 4 days of trapping at Glen Aulin.

For each animal captured, we recorded species and sex. Each individual was marked with uniquely numbered metal ear tags placed in both pinnae. We outfitted a subset of the adults captured with radio collars (model BD-2C from Holohil Systems Ltd.). We targeted adult individuals for telemetry and whenever possible, collared approximately equal numbers of male and female individuals.

To conduct radiotelemetry, we first closed all traps to ensure that the data collection would not be influenced by the presence of bait or captured animals in traps. We used a Yagi antenna and handheld receiver (Communications Specialists model R1000) to track each individual until we obtained 20 fixes per animal. To reduce temporal autocorrelation, we waited a minimum of one hour between successive fixes and took a maximum of six fixes per day. This sampling design provided a snapshot of the habitat types used by members of each species but was not intended to generate a comprehensive record of individual home ranges or patterns of habitat use across extended time periods

We recorded a fix when we were able to locate an animal visually or to identify with confidence its location (e.g. by walking in a circle around a tree). Whenever we located an individual, we took a GPS point and recorded any observations of the individual's behavior or location-- e.g. if it was foraging, whether it was on the ground or high in a tree, whether other animals were present, etc.

All work involving animals followed American Society of Mammalogy guidelines (Sikes & Gannon, 2011) and was approved by UC Berkeley's Animal Care and Use Committee.

Microhabitat Surveys
To quantify microhabitat characteristics, we focused on areas within a 5-meter radius of trapping stations or telemetry locations. For trapping stations, we conducted vegetation surveys at all stations at which an adult *T. alpinus* or *T. speciosus* was captured for the first time; in addition, we conducted surveys at a randomly selected subset of stations at which no animals were captured. For telemetry points, we conducted vegetation surveys at 6-8 randomly selected points within the individual areas of activity identified for a subset of individuals of each study species. In selecting individuals for these analyses, we attempted to balance numbers of *T. alpinus* and *T. speciosus* at each site and to include a set of individuals whose areas of activity collectively spanned the range of habitats available at each site.

At each vegetation sampling point, we used ropes and/or flagging to mark the boundaries of our sampling area and recorded information about the biotic and abiotic characteristics of each area. To describe the non-living habitat at ground level, we visually estimated the proportion of the substrate in our sampling area that was covered by rock (e.g. bedrock, boulders, or gravel), leaf litter/decaying plant material, or downed wood. To quantify the vegetative component of the

habitat, we divided the vegetation at each point into different layers based on height and plant type. Tree layers included the tallest canopy layer and the shorter sub-canopy, shrub layers included woody vegetation, and our herbaceous layer included non-woody plants. We recorded the height of all layers, binning tree layers into height categories (>15 m, 10-15 m, 5-10 m, and <5 m) and directly measuring the height of shrub and herbaceous layers. We also estimated the proportion of our sampling area that was covered by each layer.

Given our expectation that tree cover would influence patterns of habitat use by our study species, we collected several additional types of information about standing trees and downed wood at each point. We quantified the number of standing trees (with diameter at breast height >10 cm) within our study plot. We also recorded the dimensions of all large pieces of downed wood by measuring the diameter and length, or length, width, and height of each wood piece. We included all wood pieces for which at least two of the measured dimensions were greater than 10 cm.

Statistical Analyses
All statistical analyses were carried out in the program *R* (R Core Team, 2013). Because many of our variables were correlated with one another, we began by carrying out a principal components analysis (PCA). For further analyses, we used principal component (PC) scores to compare means and standard deviations of habitat characteristics in areas used by each species. PC plots were generated using the package *ggbiplot* (Vu, 2015). We used Kruskal-Wallace tests or Wilcoxon rank sum tests to compare PC scores across years and species. To follow up on analyses using PC scores, we returned to compare individual microhabitat variables. We focused these analyses on telemetry data to eliminate potential biases associated with trapping data. Specifically, during trapping, individuals may be attracted to the bait used in live traps; these biases are not expected to impact telemetry data (Boutin, 1990; Wheatley & Larsen, 2008).

Results
Sample Sizes: We captured a total of 156 different *T. alpinus* and 184 different *T. speciosus*. We collected microhabitat data from the following samples of trapping stations: 76 *T. alpinus* only stations, 95 *T. speciosus* only stations, 40 stations at which both species were captured, and 82 randomly selected stations (Table 1). We carried out telemetry on 51 *T. alpinus* and 59 *T. speciosus*. Telemetry sample sizes reflect the number of individuals tracked in each year; although seven *T. alpinus* and two *T. speciosus* were tracked in both 2012 and 2013. While counting these individuals towards both years' sample sizes means that our samples from each year are not fully independent, all repeat animals were tracked across two different years, and had different neighbors in each year. Therefore, we retained repeat animals in both the 2012 and 2013 data sets. Telemetry fixes were used to identify individual areas of activity, and for each individual that was targeted for microhabitat sampling, we randomly selected locations where fixes were taken to use as microhabitat sampling points. In total, microhabitat data were collected at telemetry fix sites for 170 *T. alpinus* points (mean 5.72 ± 2.4 fixes, range 1-8 fixes per animal) and 233 *T. speciosus* points (mean 6.87 ± 1.36 fixes, range 4-8 fixes per animal) (Table 2). Dividing the vegetation sampling locations according to patterns of use revealed by telemetry data generated the following sample sizes: 111 points in areas used only by *T. alpinus*, 201 points in areas used only by *T. speciosus*, and 84 points in areas used by both species (Table 3).

Principal Components Analysis:
Trapping data: We examined a total of 14 microhabitat measures. The list of all microhabitat variables examined is given in Table 4. We conducted separate PCAs on trapping and telemetry data; for each analysis, loadings for all variables appear in Table 4. For our PCA of data collected at trapping stations, the first, second, and third principal component had eigenvalues of 5.48, 2.3, and 1.6, and explained 39.1%, 16.4%, and 11.6% of the variance, respectively. Construction of a scree plot for all eigenvalues indicated that the explanatory value of the variables examined declined markedly for the remaining parameters measured and we thus proceeded by analyzing only the first three principal components. Based on the loadings of each of our microhabitat variables on PC axes 1-3 (Table 4a), we were able to interpret the general meaning of each axis as follows: PC1 loadings indicate that bedrock cover and rock cover load heavily and negatively on PC1, whereas substrate: litter/duff cover, minimum canopy height, maximum canopy height, canopy cover, subcanopy cover, tree cover, and number of trees load heavily and positively on PC1. We therefore interpreted PC1 to indicate tree vs. rock cover, with high PC1 scores indicating areas with heavy tree cover and low PC1 scores indicating areas with high rock cover. For the second PC, the shrub cover, herbaceous cover, and shrub plus herbaceous cover variables all loaded heavily and positively on this component. This led us to interpret PC2 as representing ground cover. Finally, the sums of lengths of downed wood and volume of downed wood variables loaded heavily and positively on PC3, allowing us to interpret that component as describing the downed wood at a point.

To visualize our results, we plotted PC1-3 scores (Figure 2), including 69% probability ellipses. In these plots, we divided the data according to whether individual points were from *T. alpinus*-only, *T. speciosus*-only, both species, or randomly selected trap stations (Figure 2a).

Telemetry data: For our PCA analyses of microhabitat data collected at telemetry fix locations, the first, second, and third principal component had eigenvalues of 6.24, 2.31, and 1.5, and explained 44.5%, 16.5%, and 10.7% of the variance, respectively. As with our analyses of data from trap locations, scree plots revealed the remaining PC scores to be less informative and thus we chose to proceed with analyses of the first three principal components only. Loadings of each variable on each of the first three principal components (Table 4b) are generally similar to the loadings for measures of the same habitat variables obtained at trapping stations, with the exception that the loadings for shrub cover, herbaceous cover, and shrub plus herbaceous cover variables on PC2 were all negative, rather than positive. Our interpretation of each PC axis was the same as for our analyses of the trap station data.

The results of these analyses were visualized as for microhabitat data obtained from trapping stations. For data obtained from telemetry fixes, however, we divided points into two categories, based on the species of the individual associated with each point (i.e. *T. alpinus* fixes versus *T. speciosus* fixes; Figure 2b). (We later report analyses in which we categorize telemetry points based on their location within a site — i.e. in a *T. alpinus*-only, *T. speciosus*-only, or overlap area — but because the species-based and location-based analyses use the same telemetry data set, we only provide a plot with data grouped according to species.)

PCA Analysis:
For both our trapping and telemetry data sets, we extracted PC1, PC2, and PC3 scores for all points obtained from species co-occurrence sites. We did not include Glen Aulin points because only *T. speciosus* was present at that site. We then tested whether PC scores differ between our two study species as follows:

Trapping: Comparisons of PC scores revealed significant differences among years for PC1 ($H = 10.1$, d.f. = 2, $p = 0.00647$) but no differences among years for PC2 ($H = 3.24$, d.f. = 2, $p = 0.0198$) or PC3 ($H = 1.04$, d.f. = 2, $p = 0.593$). Given the difference among years for PC1, we chose to analyze each year separately in all subsequent comparisons of PC scores. Thus, we used Kruskal-Wallis tests to compare means for PC1, PC2, and PC3 scores among the different categories of trap or telemetry sites (*T. alpinus* only, *T. speciosus* only, both species) at each site in each year. Significant differences were found only for PC1 scores at May Lake and Cathedral Lake in 2012 (ML: $H = 8.28$, d.f. = 2, $p = 0.016$, CL: $H = 8.86$, d.f. = 3, $p = 0.016$) and for PC2 at May Lake in 2012 ($H = 9.16$, d.f. = 2, $p = 0.01$); all other comparisons were nonsignificant.

Telemetry: For our telemetry analyses, we reduced pseudoreplication for individuals with multiple telemetry points by calculating one mean one standard deviation value per individual for PC1, PC2, and PC3 (Table 5); we then used these values in all subsequent comparisons of PC values obtained from telemetry fixes. We found no significant differences between years for mean values for any PC axes (all $p > 0.05$) and thus we pooled data across years for all subsequent analyses. Comparing values across species revealed significant differences in mean PC1 scores at all three study sites (ML: $W = 13$, $n_{alpinus} = 9$, $n_{speciosus} = 14$, $p < 0.001$, VO: $W = 9$, $n_{alpinus} = 14$, $n_{speciosus} = 11$, $p < 0.001$, CL: $W = 0$, $n_{alpinus} = 5$, $n_{speciosus} = 6$, $p = 0.004$). In all cases, PC1 scores were smaller for *T. alpinus* than for *T. speciosus* (Figure 3). No significant differences between species were detected for PC2 or PC3 at any study site (all $p > 0.05$).

Variation in PC scores
For analyses of standard deviations for PC scores, we first conducted nonparametric variance tests (Brown-Forsythe tests; Brown & Forsythe, 1974) to compare variances between the two study species (the width of the bars in Figure 3a). All comparisons for PC1 were nonsignificant ($p > 0.05$ for all sites). For PC2, variances were significantly greater for *T. alpinus* at May Lake ($F(1, 21) = 2.05$, $n_{alpinus} = 9$, $n_{speciosus} = 14$, $p = 0.0194$) but did not differ between species at the other two sites (VO: $F(1, 23) = 1.79$, $n_{alpinus} = 14$, $n_{speciosus} = 11$, $p = 0.194$, CL: $F(1, 9) = 3.98$, $n_{alpinus} = 5$, $n_{speciosus} = 6$, $p = 0.0772$). For PC3, variances were significantly greater for *T. speciosus* at May Lake and Vogelsang (ML: $F(1, 21) = 6.22$, $n_{alpinus} = 9$, $n_{speciosus} = 14$, $p = 0.021$, VO: $F(1, 23) = 5.65$, $n_{alpinus} = 14$, $n_{speciosus} = 11$, $p = 0.0262$).

The above tests assessed whether variances in PC scores differed at the species level. We also used Wilcoxon rank sum tests to determine whether variances in PC scores for individuals (obtained by averaging across telemetry fixes for the same animal; Figure 3b) differed between species. These analyses revealed that standard deviations for PC1 scores differed only at Vogelsang ($W = 1$, $n_{alpinus} = 14$, $n_{speciosus} = 11$, $mean_{alpinus} = 1.07$, $mean_{speciosus} = 2.42$, $p < 0.001$). In contrast, all comparisons of PC2 scores were nonsignificant (all $p > 0.05$) but standard deviations for PC3 scores were significantly greater for T. speciosus at all sites (ML: $W = 23$, $n_{alpinus} = 9$, $n_{speciosus} = 14$, $mean_{alpinus} = 0.499$, $mean_{speciosus} = 1.42$, $p = 0.024$; VO: $W = 25$, $n_{alpinus}$

= 14, $n_{speciosus}$ = 11, mean$_{alpinus}$ = 0.5, mean$_{speciosus}$ = 0.921, p = 0.0106, CL: W = 0, $n_{alpinus}$ = 5, $n_{speciosus}$ = 6, mean$_{alpinus}$ = 0.532, mean$_{speciosus}$ = 1.34, p = 0.004).

Comparisons based on study species use
When vegetation data recorded at telemetry locations were parsed according to whether they occurred in *T. alpinus* only areas, *T. speciosus* only areas, or areas of interspecific overlap (for each individual with radio fixes occurring in more than one of these categories, we calculated a separate mean and standard deviation value for each applicable category), we found no significant differences between means or standard deviations between years (Kruskal-Wallis tests, all p > 0.05) and thus we pooled data from all years. Using this pooled data set, comparisons of PC1, PC2, and PC3 values revealed significant differences in mean PC1 scores at all three sites (ML: H = 12.9, d.f. = 2, p = 0.016; VO: H = 17, d.f. = 2, p < 0.001; CL: H = 7.47, d.f. = 2, p = 0. 0239) (Figure 4). Mean PC2 scores differed only at Cathedral Lake (H = 7.76, d.f. = 2, p = 0.0206) and all comparisons of mean PC3 scores were nonsignificant. Post-hoc pairwise comparisons (Wilcoxon rank sum tests with p-value adjustments using the Holm method; Holm, 1979) of categories for PC1 at Vogelsang revealed that PC1 scores in *T. speciosus*-only areas were greater than in either *T. alpinus*-only or overlap areas (*T. alpinus* vs. *T. speciosus* areas: W = 9, $n_{alpinus\ only}$ = 13, $n_{speciosus\ only}$ = 11, $p_{adjusted}$ < 0.001; *T. speciosus* vs. overlap: W = 13, $n_{speciosus\ only}$ = 11, $n_{overlap}$ = 15, $p_{adjusted}$ < 0.001).

Analyses of standard deviations for these data revealed significant differences for PC1 at Vogelsang (H = 14.6, d.f. = 2, p < 0.001), and for PC3 at all sites (ML: H = 9.5, d.f. = 2, p = 0.00868; VO: H = 8.91, d.f. = 2, p = 0.0117; CL: H = 10.2, d.f. = 2, p = 0.00605). No significant differences in standard deviations were detected for PC2. Post-hoc pairwise comparisons of categories indicated that standard deviations for PC1 at Vogelsang were greater in *T. speciosus*-only areas than in *T. alpinus*-only or overlap areas (*T. alpinus* vs. *T. speciosus* areas: W = 6, $n_{alpinus\ only}$ = 13, $n_{speciosus\ only}$ = 11, $p_{adjusted}$ < 0.001; *T. speciosus* vs. overlap: W = 21, $n_{speciosus\ only}$ = 11, $n_{overlap}$ = 15, $p_{adjusted}$ = 0.00282). For all sites, standard deviations for PC3 were greater in *T. speciosus*-only areas than in *T. alpinus*-only areas (*T. alpinus* vs. *T. speciosus*- ML: W = 17, $n_{alpinus\ only}$ = 9, $n_{speciosus\ only}$ = 14, $p_{adjusted}$ = 0.0317; VO: W = 24, $n_{alpinus\ only}$ = 13, $n_{speciosus\ only}$ = 11, $p_{adjusted}$ = 0.0316; CL: W = 0, $n_{alpinus\ only}$ = 5, $n_{speciosus\ only}$ = 6, $p_{adjusted}$ = 0.019;) or areas of overlap (*T. speciosus* vs. overlap- ML: W = 17, $n_{speciosus\ only}$ = 14, $n_{overlap}$ = 7, $p_{adjusted}$ = 0.0235; VO: W = 24, $n_{speciosus\ only}$ = 11, $n_{overlap}$ = 15, $p_{adjusted}$ = 0.0154; CL: W = 0, $n_{speciosus\ only}$ = 6, $n_{overlap}$ = 6, $p_{adjusted}$ = 0.013).

Single Variable Comparisons:
Building upon the results of our PCA analyses, we examined variation in values for 14 individual microhabitat variables identified as important by the PCA results. Because the interpretation of PC axes and loadings of variables were similar for our trapping and telemetry analyses, we restricted our single variable comparisons to vegetation data collected at radio telemetry fixes. For each variable, we used Wilcoxon rank sum tests to compare mean values for the study species at each site. Here, we report preliminary comparisons for a subset of three variables, selected because they loaded heavily on either the PC1 or PC3 axis (Figure 5); results for the remaining variables can be found in Supplementary Table 1. Percentage of rock substrate was greater for *T. alpinus* at all study sites (ML: W = 25, mean$_{alpinus}$ = 9.91, mean$_{speciosus}$ = 7.91, $p_{adjusted}$ = 0.024; VO: W = 130, mean$_{alpinus}$ = 9.6, mean$_{speciosus}$ = 6.88, $p_{adjusted}$ = 0.001; CL: W =

130, mean$_{alpinus}$ = 10.3, mean$_{speciosus}$ =5.81, p$_{adjusted}$ = 0.001). In contrast, the number of trees was greater for *T. speciosus* at all sites (ML: W = 0, mean$_{alpinus}$ = 0.486, mean$_{speciosus}$ = 2.37, p$_{adjusted}$ = 0.004; VO: W = 6, mean$_{alpinus}$ = 0.572, mean$_{speciosus}$ = 0.279, p$_{adjusted}$ = 0.001; CL: W = 6, mean$_{alpinus}$ = 1.06, mean$_{speciosus}$ = 5.01, p$_{adjusted}$ = 0.001), while the volume of downed wood was greater for *T. speciosus* at two of the three sites (ML: W = 0, mean$_{alpinus}$ = 0.0688 m^3, mean$_{speciosus}$ = 0.472 m^3, p$_{adjusted}$ = 0.065; VO: W = 10, mean$_{alpinus}$ = 0.0649 m^3, mean$_{speciosus}$ = 0.348 m^3, p$_{adjusted}$ = 0.008; CL: W = 10, mean$_{alpinus}$ = 0.125 m^3, mean$_{speciosus}$ = 0.727 m^3, p$_{adjusted}$ = 0.008).

Discussion

Overall, our data indicate that *T. alpinus* and *T. speciosus* use different microhabitats, even in areas where these species co-occur at the level of individual areas of activity. Our findings support the hypothesis that *T. alpinus* is a high altitude habitat specialist that occurs in a more restricted range of microhabitats than *T. speciosus*. Support for this conclusion comes from several lines of evidence. First, qualitative inspection of our PCA plots revealed that T. alpinus occupies a narrower range of habitats than *T. speciosus*. Second, analyses of the microhabitat at trapping locations indicated that while habitat characteristics did not differ between *T. alpinus* trap stations and stations at which both species were captured, *T. speciosus* were captured at stations with a wider range of microhabitat values. Finally, analyses of microhabitat at telemetry fix locations revealed greater variation values for *T. speciosus*. Collectively, these findings indicate that differences in microhabitat use are evident among the study species.

Importance of different habitat parameters

Given our interpretations of the PCA axes examined, our findings suggest that *T. alpinus* occurs in areas with less tree cover and more exposed rock. Our analyses of individual microhabitat variables related to rock cover and number of trees support this conclusion by indicating that habitats used by *T. alpinus* are characterized by rockier substrates and fewer trees. This outcome was obtained for analyses based on data collected at telemetry fix locations as well as from analyses of captured localities from a subset of study sites. With regard to vegetation structure, while number of trees was a significant descriptor of microhabitat differences between *T. alpinus* and *T. speciosus*, the nature of understory vegetation appeared to be less important. This finding is consistent with observations indicating that both species forage on herbaceous plants and shrubs that grow close to the ground (Grinnell & Storer, 1924; Best *et al.*, 1994; Clawson *et al.*, 1994).

Breadth of microhabitats used

In addition to finding interspecific differences in the amount of tree and rock cover, we found apparent evidence of differences in the breadth of the habitats used. Specifically, our analyses of the vegetation present at radiotelemetry fix locations indicated that *T. speciosus* occurs in areas characterized by a wider range of quantities of downed wood. While variation in the amount of downed wood did not differ between areas used by *T. alpinus* only and areas used by both species, areas used only by *T. speciosus* were characterized by a greater range of volumes of downed wood. These results are consistent with the categorization of *T. speciosus* as more of a habitat generalist and suggest that this species is capable of using areas with wider ranges of habitat characteristics.

Implications for understanding range shifts

Considering our findings in the context of the differences in patterns of elevational range shifts reported for the study species (Moritz *et al.*, 2008), it is possible that the elevational range contraction documented for *T. alpinus* represents habitat tracking, meaning that the lower distributional limit of this species has moved upward as critical elements of its habitat have shifted upwards in elevation. Additional support for this argument comes from ecological niche modeling indicating that vegetation type is an important predictor of distributional change in *T. alpinus* (Rubidge *et al.*, 2011). In contrast, *T. speciosus*, which uses a wider range of habitats, does not appear to be limited elevationally by vegetation parameters. While detailed information on elevational range shifts of most plant species at our study sites is not available, evidence from other areas of California reports climate-driven upwards elevational range shifts in a diversity of plant species (Kelly & Goulden, 2008), as well as temperature-associated changes in abundances and elevational ranges of several alpine plant species (Kopp & Cleland, 2014). Furthermore, changes in the distribution of vegetation types have been reported throughout the Sierra Nevada mountains, suggesting that our study sites have likely seen (and will continue to see) shifts in features of the plant community (Thorne *et al.*, 2008). However, isotopic analyses of chipmunk diets throughout the Sierra Nevadas shows that signatures of dietary change do not necessarily parallel elevational range shifts (Walsh, Chapter 4), emphasizing that the relationship between chipmunk habitat use and vegetation is complex. Further work is necessary to determine which habitat and vegetation features most strongly influence distributions of our study species.

With regard to future efforts to understand the differences in elevation range responses in these species, given that there is extensive spatial overlap between *T. alpinus* and *T. speciosus* at multiple locations in the Sierra Nevada (Chapter 2), it would be useful to extend comparisons of habitat use to include sites where only *T. speciosus* occurs; such analyses would generate important insights into the extent to which microhabitat use by this species is influenced by the presence of *T. alpinus*. A second productive direction for future research will be to explore how changes in vegetation interact with other types of environmental change, such as changes in abiotic factors, fire regimes, and agricultural or other forms of anthropogenic land use. Changes in aspects of forest structure such as increases in tree density have been reported in our study region and have been linked to altered patterns of precipitation (Dolanc et al., 2013; McIntyre et al., 2015, see also Lutz, van Wagtendonk, & Franklin, 2009), suggesting that climate change is likely to impact species such as *T. alpinus* that do not use areas with heavy tree cover. Patterns of climate change, however, are variable on a local scale and may vary between different regions of California (Rowe *et al.*, 2015). As a result, understanding the impacts of these heterogeneous patterns of climate change will be key to understanding heterogeneity in species range changes.

Conclusions

In summary, our work has demonstrated that patterns of microhabitat use differ between *T. alpinus* and *T. speciosus* and that these differences are consistent with the description of *T. alpinus* as a greater habitat specialist than *T. speciosus*. Our findings have identified several specific aspects of the habitat that appear to differ between these species, even in areas in which these taxa co-occur at the scale of individual areas of activity. This information will be critical in future efforts to explore the role of habitat use and habitat limitations in shaping responses by the study species to environmental change. At the same time, improved understanding of the degree of ecological specialization of each study species should facilitate efforts to link data regarding

changes in biotic as well as abiotic factors to patterns of elevational range change in these taxa. We hope that future studies of response to environmental change will make use of our data and, more generally, the demonstrated importance of this type of information when attempting to predict species responses to environmental conditions.

Figures & Tables
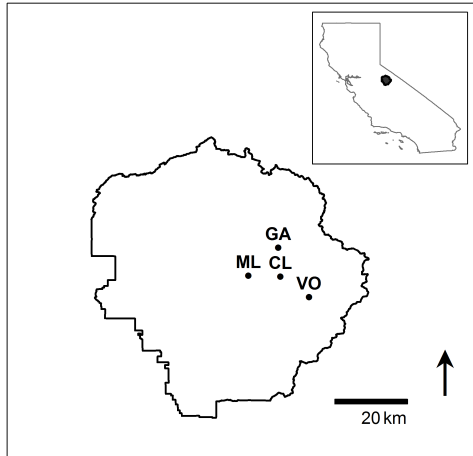
Figure 1: Location of study sites within Yosemite National Park. ML = May Lake, CL = Cathedral Lake, VO = Vogelsang, and GA = Glen Aulin. Inset map shows the location of Yosemite National Park within California.

Table 1: Trapping microhabitat sample sizes by year and site.

Site				
Year	ML	VO	CL	GA
2011				
T. alpinus	6	10	11	
T. speciosus	11	11	1	
Both	2	1	0	
Random	6	16	9	
2012				
T. alpinus	5	10	4	N/A
T. speciosus	10	8	18	10
Both	0	7	2	N/A
Random	10	6	12	7
2013				
T. alpinus	9	8	13	
T. speciosus	4	10	12	
Both	3	21	4	
Random	12	1	3	

Table 2: Telemetry microhabitat sample sizes by year and site.

	Site			
Year	ML	VO	CL	GA
2011				
T. alpinus	4	9	0	
T. speciosus	13	5	0	
2012				
T. alpinus	21	44	7	N/A
T. speciosus	47	48	12	17
2013				
T. alpinus	22	28	30	
T. speciosus	31	29	30	

Table 3: Telemetry microhabitat sample sizes by category, year, and site.

Year	ML	VO	CL	GA
		Site		
2011				
T. alpinus	4	9	0	
T. speciosus	13	5	0	
Overlap	0	0	0	
2012				
T. alpinus	19	22	7	N/A
T. speciosus	43	38	12	
Overlap	5	34	0	
2013				
T. alpinus	20	17	14	
T. speciosus	26	24	23	
Overlap	7	16	22	

Table 4: a) Trapping data PCA results and b) telemetry data PCA results.
a) Trapping Data

Variable	PC1	PC2	PC3
Substrate: bedrock cover	-0.263	-0.257	-0.092
Substrate: rock cover	-0.352	-0.201	-0.111
Substrate: litter/duff cover	0.358	-0.129	-0.036
Minimum canopy height	0.308	-0.052	-0.019
Maximum canopy height	0.341	-0.027	-0.008
Canopy cover	0.302	0.000	-0.209
Subcanopy cover	0.296	-0.035	-0.144
Tree cover	0.366	-0.017	-0.223
Shrub cover	0.002	0.441	-0.121
Herbaceous cover	-0.021	0.498	0.134
Shrub + herbaceous cover	-0.014	0.647	0.019
Number of trees	0.319	-0.024	-0.166
Sum of lengths of downed wood	0.182	-0.074	0.620
Volume of downed wood	0.137	-0.069	0.647

b) Telemetry Data

Variable	PC1	PC2	PC3
Substrate: bedrock cover	-0.251	0.261	-0.014
Substrate: rock cover	-0.338	0.215	-0.051
Substrate: litter/duff cover	0.351	0.115	-0.035
Minimum canopy height	0.319	0.081	-0.102
Maximum canopy height	0.348	0.073	-0.124
Canopy cover	0.319	0.103	-0.194
Subcanopy cover	0.292	0.101	-0.086
Tree cover	0.356	0.118	-0.178
Shrub cover	-0.003	-0.405	-0.161
Herbaceous cover	0.049	-0.501	-0.026
Shrub + herbaceous cover	0.034	-0.635	-0.126
Number of trees	0.316	0.022	-0.006
Sum of lengths of downed wood	0.186	-0.059	0.628
Volume of downed wood	0.159	-0.052	0.676
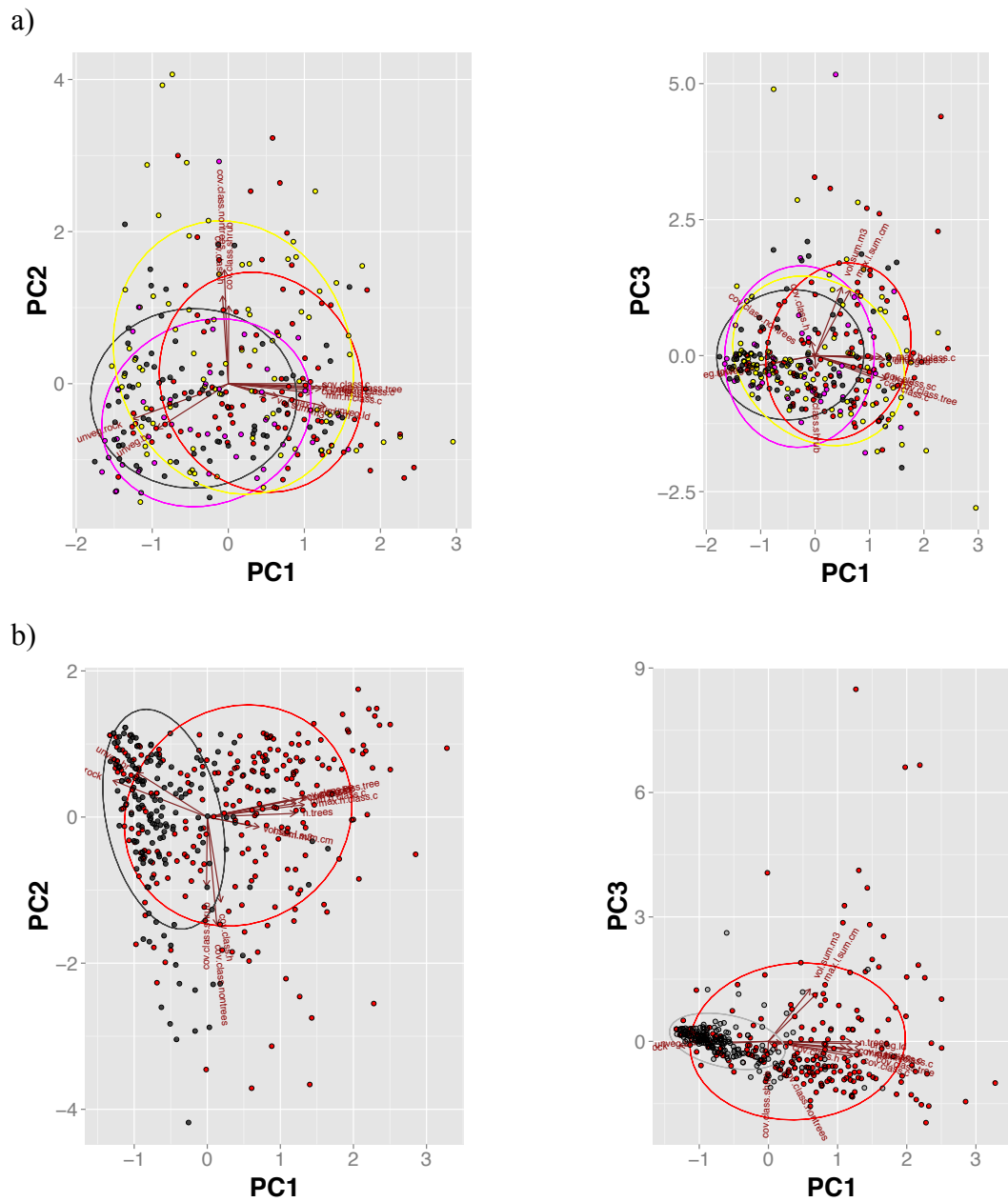
Figure 2: a) Trapping and b) telemetry PCA plots. For each set of figures, plots for PC1 and PC2, as well as PC1 and PC3 are shown. For the trapping PCA, *T. alpinus* trap stations are in gray, *T. speciosus* trap stations in red, both species trap stations in pink, and random trap stations in yellow. The telemetry PCA shows *T. alpinus* points in gray and *T. speciosus* points in red.

Table 5: Means ± standard deviations of PC1-3 scores for each species, at each study site.

Site	PC1	PC2	PC3
ML			
T. alpinus	-1.70 ± 1.39	-0.364 ± 1.28	-0.089 ± 0.499
T. speciosus	0.566 ± 2.1	0.241 ± 1.15	0.0134 ± 1.42
VO			
T. alpinus	-1.32 ± 1.07	0.149 ± 1.2	-0.015 ± 0.5
T. speciosus	0.827 ± 2.42	0 ± 1.55	-0.079 ± 0.921
CL			
T. alpinus	-1.3 ± 1.64	0.414 ± 1.31	0.044 ± 0.532
T. speciosus	2.39 ± 2.45	0.236 ± 1.42	0.171 ± 1.34

a.)
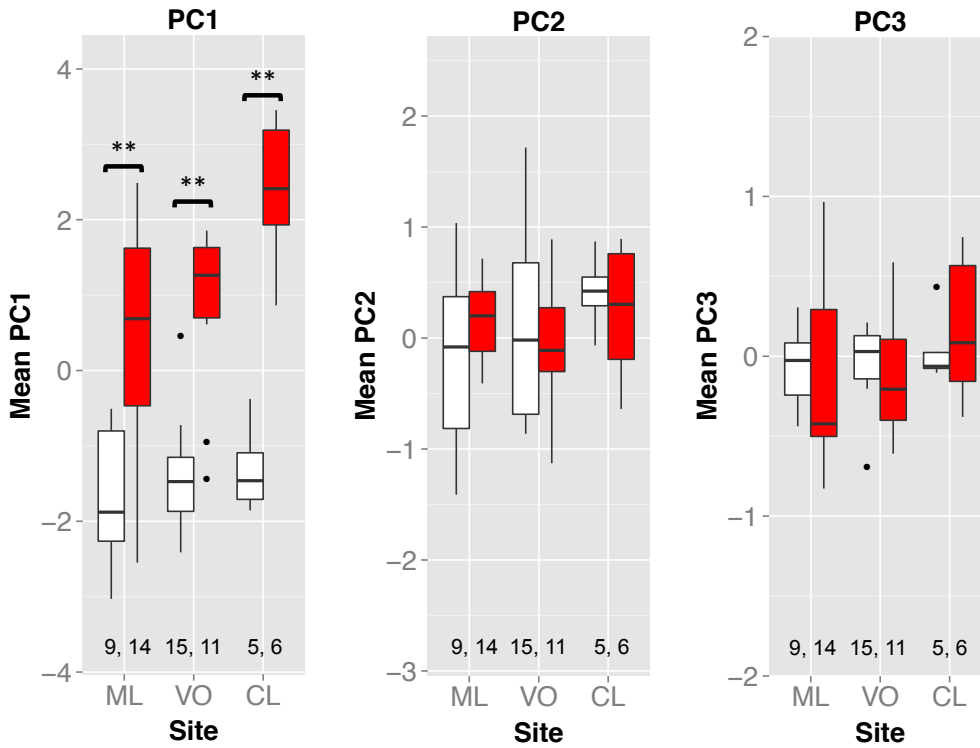
b.)
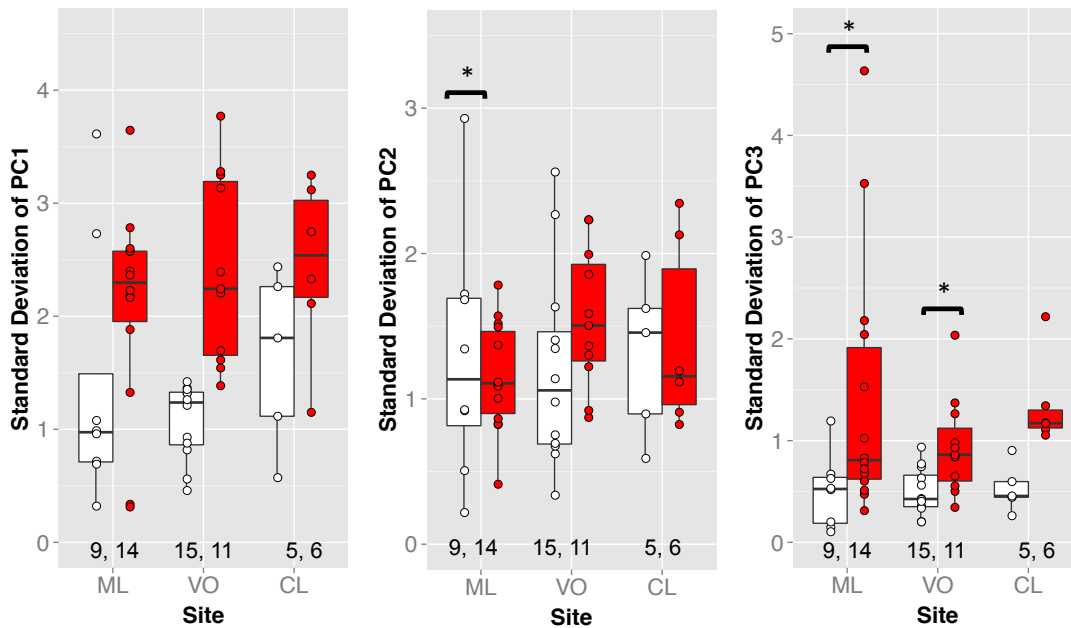
Figure 3: a.) Mean and b.) standard deviations of PC1, PC2, and PC3 scores for telemetry points at the three co-occurrence sites (ML = May Lake, VO = Vogelsang, CL = Cathedral Lake). White bars show *T. alpinus* data; red bars show *T. speciosus* data. Sample sizes for each site and species appear at the bottom of each plot. Single asterisks indicate differences that are significant at the 0.05 level; double asterisks indicate significance at the 0.01 level. Dots in standard deviation plots represent individual animals.

Table 6: Means ± standard deviations of PC1-3 scores for each telemetry point category, at each study site.

Site	PC1	PC2	PC3
ML			
T. alpinus **only**	-1.98 ± 0.851	-0.403 ± 1.01	-0.0388 ± 0.242
T. speciosus **only**	0.638 ± 1.53	0.227 ± 0.481	0.0408 ± 0.714
Overlap	-0.846 ± 1.66	0.252 ± 0.866	-0.224 ± 0.549
VO			
T. alpinus **only**	-1.31 ± 0.833	0.0927 ± 1.06	-0.0139 ± 0.312
T. speciosus **only**	1.2 ± 1.25	-0.0242 ± 0.732	-0.102 ± 0.477
Overlap	-1.21 ± 1.01	-0.13± 0.899	-0.0883± 0.303
CL			
T. alpinus **only**	-1.19 ± 0.837	0.287 ± 0.422	0.0569 ± 0.317
T. speciosus **only**	2.27 ± 0.85	0.0596 ± 0.589	0.172 ± 0.466
Overlap	-0.514 ± 2.56	1.05 ± 0.484	0.0506 ± 0.389
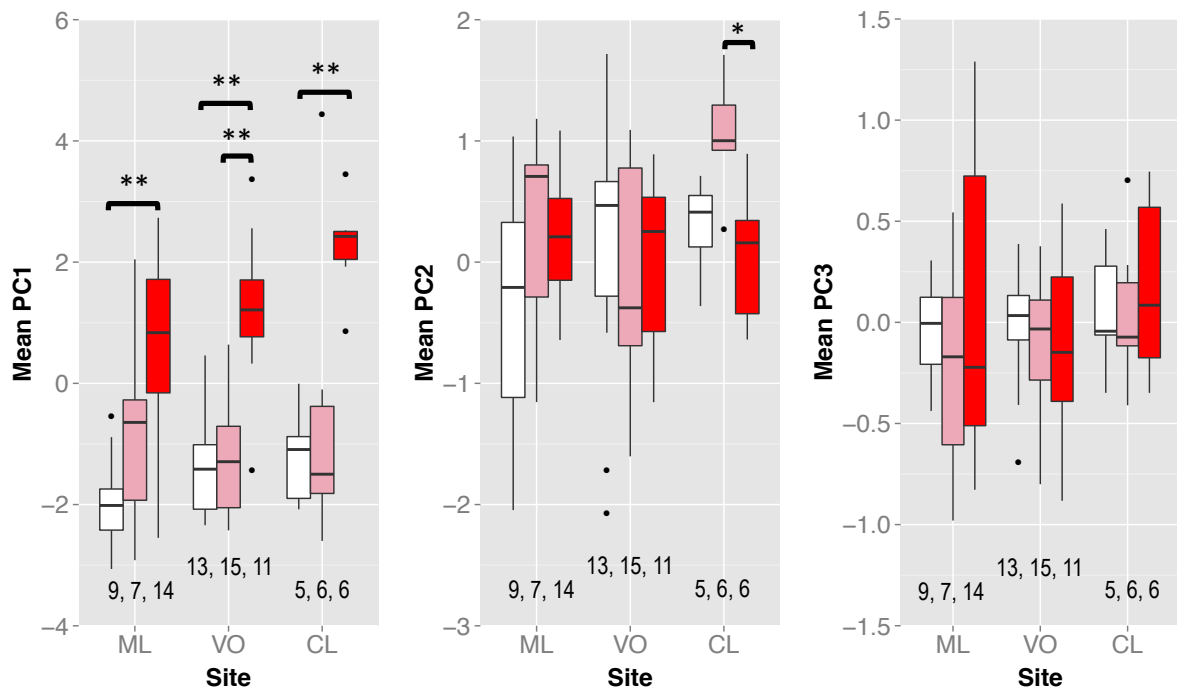
Figure 4: Mean PC1, PC2, and PC3 scores for telemetry point categories at the three co-occurrence sites (ML = May Lake, VO = Vogelsang, CL = Cathedral Lake). White bars represent *T. alpinus* only areas, pink bars represent overlap areas, and red bars *T. speciosus* only areas. Sample sizes for each site and species appear at the bottom of each plot. Single asterisks indicate significant comparisons (p < 0.05), and double asterisks indicate differences that are strongly significant (p < 0.01).
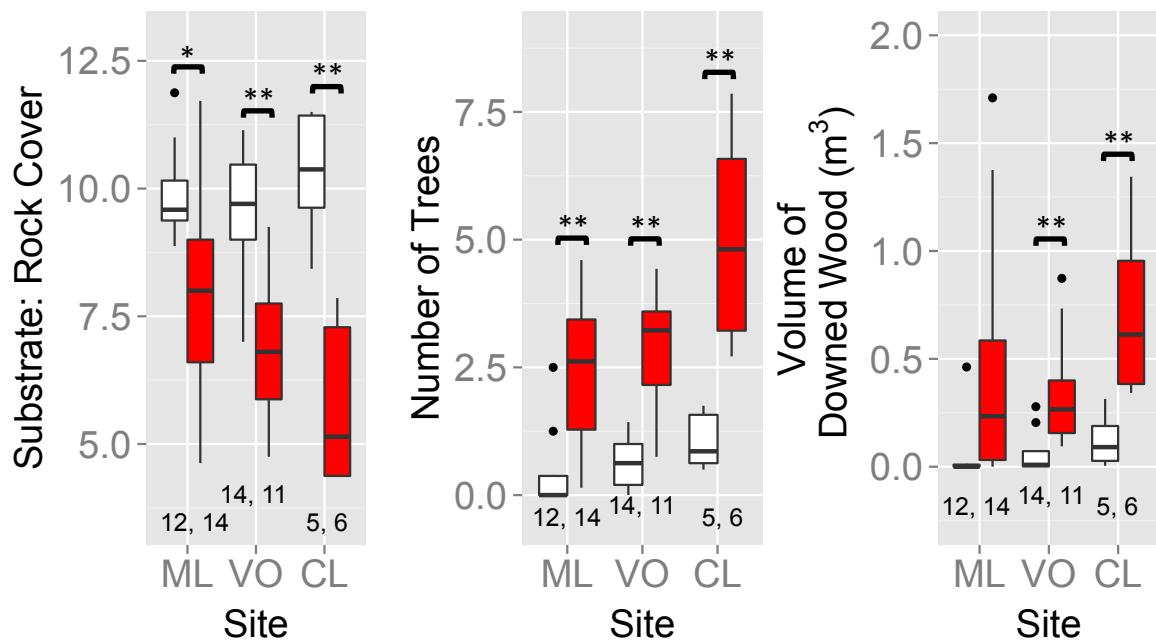
Figure 5: Comparisons of rock cover, number of trees, and volume of downed wood for telemetry point at the three co-occurrence sites (ML = May Lake, VO = Vogelsang, CL = Cathedral Lake). *T. alpinus* points are in white, *T. speciosus* points in red. Single asterisks indicate significant comparisons (p < 0.05), and double asterisks indicate differences that are strongly significant (p < 0.01).

Table 7: Summary of differences in PC scores between different data sets. Check marks indicate significant differences for all sites, and X's indicate nonsignificant comparisons. Cells with both symbols indicate cases in which some comparisons were significant and others were not (with notes about which subsets of comparisons were significant). These data reflect results of comparisons at the species level (see text for details of individual-level comparisons).

Data Set	PC1		PC2		PC3	
	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation
Trapping	✓/✗ ML & CL 2012 only	NA	✓/✗ ML 2012 only	NA	✗	NA
Telemetry (by species)	✓	✗	✗	✓/✗ ML only	✗	✓/✗ ML & VO only
Telemetry (by category)	✓	✓/✗ VO only	✓/✗ CL only	✗	✗	✓

Chapter 4

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

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.*, 2011a; 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.*, 2015). 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 factors underlying differences in response to changing climatic conditions among closely related (congeneric) species. Comparisons of historic and modern distributions of these animals 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 degree of ecological specialization. Specifically, 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 to the Sierran foothills (Grinnell & Storer, 1924; Best *et al.*, 1994; Clawson *et al.*, 1994). Efforts to model the elevational distributions of these species indicate that the upward range contraction of *T. alpinus* over the past century is associated with changes in abiotic conditions such as temperature (Rubidge *et al.*, 2011; Rowe *et al.*, 2015). 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 conducted.

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 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 the elevational distributions (Crimmins *et al.*, 2011) and relative abundances 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 the

diets of these chipmunk species may also 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.

With regard to morphology, the skull is a complex structure that is integrally involved in multiple essential functions, including protection of the brain, regulation of water loss, and feeding (Hanken & Hall, 1993; Elbroch, 2006). Multiple studies have reported correlations between 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). Because such relationships may arise due to either adaptive modification of skull structure or genetic drift, efforts to quantify selection on cranial characters may be useful in elucidating connections between environmental conditions and morphological change. If *T. alpinus* has experienced greater dietary change over the past century, and if shifts in diet have altered selection of skull traits, we expect morphology in this species to show 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 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 diet space that is determined by the combination of food items animals consumed in the historical and modern eras. To investigate 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 potential interactions between these traits, we used multivariate statistical models to explore associations between environmental conditions and patterns of dietary and morphological change. Our goal in conducting these analyses 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.

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 1911-1920. Modern specimens were collected as part of the Grinnell Resurvey Project (GRP), an intensive resampling of Grinnell's historic sites that occurred from 2003-2010 (Moritz *et al.*, 2008). When available, additional (non-GRP) modern specimens from the same localities were included in our analyses. Two areas were targeted for study based on the availability of modern and historical material:

Yosemite and the Southern Sierras (Figure 1). *T. 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/). Because georeferenced collection localities differed among specimens captured from the same local population, 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 1900-1909 to calculate climatic values for the historical era and decadal averages from 1990-1999 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. Climatic 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 and nitrogen laid down in the hair of these animals that has its origin in the diet items they had consumed. 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 A2). These individuals represented 74 localities corresponding to or occurring in close proximity to GRP sampling localities. Samples were collected by cutting a small amount (~ 1 x 1 mm patch) of hair from near the base of the tail 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 hours. Samples were weighed on a microbalance (+0.000001 g; Mettler) and 1.4-1.6 mg of material was packaged into tin capsules (Costec Inc.).

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

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

where X is the element of interest, h is the isotope with the high mass number, R is the ratio of the heavy to light isotope composition that the sample or standard contain (see Dawson, Mambelli, Plamboeck, Templer, & Tu, 2002). The final values are expressed in units of part per thousand, or per mil (‰) and therefore C-isotope composition is noted as $\delta^{13}C$ and N-isotope composition as $\delta^{15}N$. 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.

With regard to diet, 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, 2012b). 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 $\delta^{13}C$ or $\delta^{15}N$ 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 (~1,615-3,505 m), we included elevation in our models as a fixed predictor, with the intent of determining whether 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 $\delta^{13}C$ values to account for the Suess effect, which describes the decrease in atmospheric $\delta^{13}C$ ratios over time (approximately -0.015‰ per year; 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 ($\delta^{13}C$ or $\delta^{15}N$) 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 likelihoods for all candidate models (Burnham & Anderson, 2002):

$$w_i = \frac{e^{-0..5*\Delta_i}}{\sum_{r=1}^{R} e^{-0..5*\Delta_i}}$$

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 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 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 A2). 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, 3-dimensional coordinates were recorded for 24 cranial landmarks using a Microscribe 3DMX digitizer (Microscribe, IL). 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, 1982; Marroig & Cheverud, 2001). Coordinates for these landmarks were then used to calculate 38 linear skull measurements (Figure 2). Bilaterally symmetric measurements were averaged for each individual; if a skull was damaged on 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 these data and to estimate measurement error (Lessels & Boag, 1987). The mean of these repeated measurements was used in all subsequent analysis.

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 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 in the first principal component (PC1) loaded positively and thus this axis was used as an estimate of allometric skull size. To assess 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 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 changes in skull shape, it was first necessary to reconcile the two different (anterior and posterior) views used to quantify landmarks. We used the *R* function *unifyVD* to combine

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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, Swiderski, Sheets, & W.L., 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 datasets (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, 1979; Lande, 1976) and is used to determine if 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 measurements to calculate morphological rate of change, denoted as Δ,

$$\Delta = \frac{var_B(\ln z)}{[t \, var_W(\ln z)]}$$

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 with directional selection acting on the trait in question; values less than 10^{-4} are consistent with the effects of stabilizing selection. We used a one-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 x era x 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, $n_{historical}$ = 33, n_{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, $n_{historical}$ = 44, n_{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, $n_{historical}$ = 33, n_{modern} = 21, p = 0.007; Yosemite: historical mean = 1272 mm, modern mean = 1052 mm, t = 3.23, $n_{historical}$ = 44, n_{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 $\delta^{15}N$ or $\delta^{13}C$ for each species and for both sampling transects (Figure 3). We found that historical means ranged from 1.96 to 7.53‰ for nitrogen and -17.1 to -22.5‰ for carbon, with modern means of 0.443 to 7.63‰ for nitrogen and -18.6 to -22.2‰ for carbon. Visual inspection of these data suggested that although some of the animals that comprised the data sets (e.g., *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 $\delta^{15}N$ or $\delta^{13}C$ composition for either sampling locality or study species. Similar plots (Figure 4) of changes in variance of isotope ratios showed that within species, variance in nitrogen isotope ratios 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 $\delta^{13}C$, 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 (Figure 4).

To examine quantitatively the effects of species, time period, and sampling transect on diet, we generated a confidence set of seven models for $\delta^{15}N$ (Table 2a), and seven models for $\delta^{13}C$ (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 versus Yosemite cell for the $\delta^{13}C$ model (Table 3a) indicates that $\delta^{13}C$ 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 $\delta^{15}N$, ratios differed significantly between eras only for *T. alpinus* in Yosemite and the Southern Sierras; all comparisons for *T. speciosus* were nonsignificant (Table 3c). For $\delta^{13}C$, 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 $\delta^{15}N$ and $\delta^{13}C$, significant differences in isotope ratios between Yosemite and the Southern Sierras were found for all species x era combinations (Table 3c).

(4) *Elevation*. Elevation was a significant predictor of $\delta^{15}N$ for all species by transect by era combinations; in contrast, no significant effects of elevation on $\delta^{13}C$ were detected (Table 3d).

As evident from these analyses, there was considerable variation in the predictors associated with variation in isotopic measures of the diets of the study species. To determine if overall variability in isotopic ratios was greater for the presumably more ecologically generalized *T. speciosus*, we divided our data into four sub-groups 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 nitrogen, 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 nitrogen ratios was greater for *T. alpinus* in the Southern Sierra but greater for *T. speciosus* in Yosemite (Table 4). For carbon, 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 (Figure 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 sub-groups representing all possible combinations of species by transect and compared variances in the historical versus modern eras. We found that variance in nitrogen isotope ratios was greater in the modern era for *T. speciosus* (F(1, 119) = 22.1, variance$_{historical}$ = 1.36, variance$_{modern}$ = 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 size revealed substantial variation in patterns of morphological 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

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size during this same period (F = 5.80 ; p < 0.05; Figure 5). In contrast, no difference in size was detected for *T. speciosus* from either transect over the last century (p > 0.05; Figure 5). Dividing skull characters into those associated with the rostrum (facial region) versus those associated with the neurocranium (brain case) revealed that the temporal changes in size detected for *T. alpinus* were due primarily to modification of facial traits (Figure 6). In *T. speciosus,* the facial — but not the neurocranial — portion of the skull increased 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; Figure 6). Thus, overall, we detected greater evidence of temporal changes in cranial size for *T. alpinus*, with these changes due primarily to 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 to *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 A3, Figure 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 A3). 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 A3, Figure 7).

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 A3, Figure 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 A3, Figure 7). In contrast, in the Southern Sierras, traits that showed significant departures from neutrality were more evenly distributed between the rostrum (50%) and the neurocranium (50%; Table A3, Figure 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 score against either the carbon or nitrogen isotope ratio for that specimen (Figure 8). Kendall's Tau tests to assess whether these correlations were significant showed no significant relationships for either isotope (see Figure 8). In all cases, we 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 both dietary and morphological changes were more pronounced 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., $\delta^{15}N$ values for *T. speciosus*), 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 patterns of change in temperature and precipitation are heterogeneous across our study region (Rowe *et al.*, 2015). 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
T. 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 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 change over time. Thus, elevational range changes by *T. alpinus* over the past century do not appear to be associated with 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) and *Pinus albicaulus* (Whitebark Pine) trees, it typically spends the majority of its time in more open areas (Chapters 2 and 3) 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 quantitative 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— i.e. higher nitrogen isotope in carnivores or omnivores than in herbivores (Post, 2002)— is not possible to predict how *T. alpinus* and *T. speciosus* would be expected 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 variation in nitrogen isotope ratios of chipmunk hairs centers on differences in nitrogen isotope ratios generated by nitrogen fixation by plants. Nitrogen-fixing plant species typically have relatively negative nitrogen isotope ratios, 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 (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 nitrogen isotope ratios 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 carbon isotope ratios, both plant physiology and environmental parameters may contribute to variation in stable isotope ratios. With respect to plant physiology, a primary determinant of carbon isotope composition is photosynthetic pathway: plants using the C3 pathway have highly negative δ^{13}C ratios ($\sim$ -22 to -35‰, mean -27‰) compared to plants that use the C4 pathway ($\sim$ -19 to -9‰), with intermediate δ^{13}C ratios for CAM plants ($\sim$-27‰ 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*. 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 carbon isotope ratios from both our historical and modern chipmunk hair samples are somewhat less negative than the reported mean δ^{13}C ratio of -27‰ for C3 plants, likely reflecting fractionation that occurred as plant material was converted to hair. Fractionation values for this conversion from diet-to-hair in other mammalian species are typically -1 to 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 contribute to the observed δ^{13}C ratios.

Another potential contributor to differences in stable carbon isotope ratios is precipitation. Low levels of precipitation are associated with increased δ^{13}C ratios in C3 plants, due to the effects of water stress on discrimination between the heavy (^{13}C) and light (^{12}C) isotopes of carbon (Fry, 2006; Marshall *et al.*, 2007; Ben-David & Flaherty, 2012). If our carbon isotope ratios reflect water stress on plants consumed by our study organisms, the decreases that we observed in carbon isotope ratios 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.*, 2015), emphasizing the need to explore the relationships between carbon isotope ratios and climate at our study sites on a finer scale.

In sum, 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 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, the diets— in particular the carbon signatures — for the 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 due to tracking of habitats containing 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 the diets of the study 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 morphological change associated with climatic conditions has been observed in a diverse array of rodents (Eastman et al., 2012; Hendry, Farrugia, & Kinnison, 2008; Pergams & Lawler, 2009; Pergams & Lacy, 2008), 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 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, it should perhaps 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 versus 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 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.

Conclusions

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 that have occurred 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.*, in prep.) 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 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.

Figures & Tables:
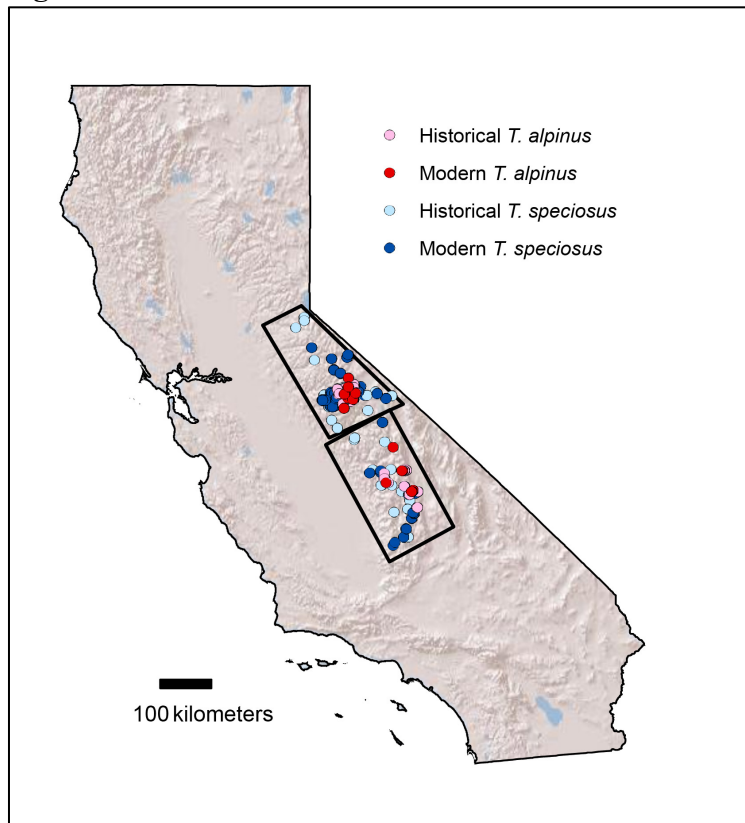
Figure 1: Location of sampling sites within California. Locations from which we sampled one or more individuals for use in morphological and/or diet analyses are shown in pink (historical era) or red (modern era) for *T. alpinus*, and light blue (historical era) or dark blue (modern era) for *T. speciosus*. 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 out of 47 historical sites and 11 out of 43 modern sites.

Table 1: Sample sizes for a. morphology and b. dietary analyses.

a. Dietary analyses

	Historical		Modern	
	Southern Sierras	**Yosemite**	**Southern Sierras**	**Yosemite**
T. alpinus	73	33	13	31
T. speciosus	54	57	67	97

b. Morphology

	Historical		Modern	
	Southern Sierras	**Yosemite**	**Southern Sierras**	**Yosemite**
T. alpinus	75	51	29	38
T. speciosus	83	77	100	221
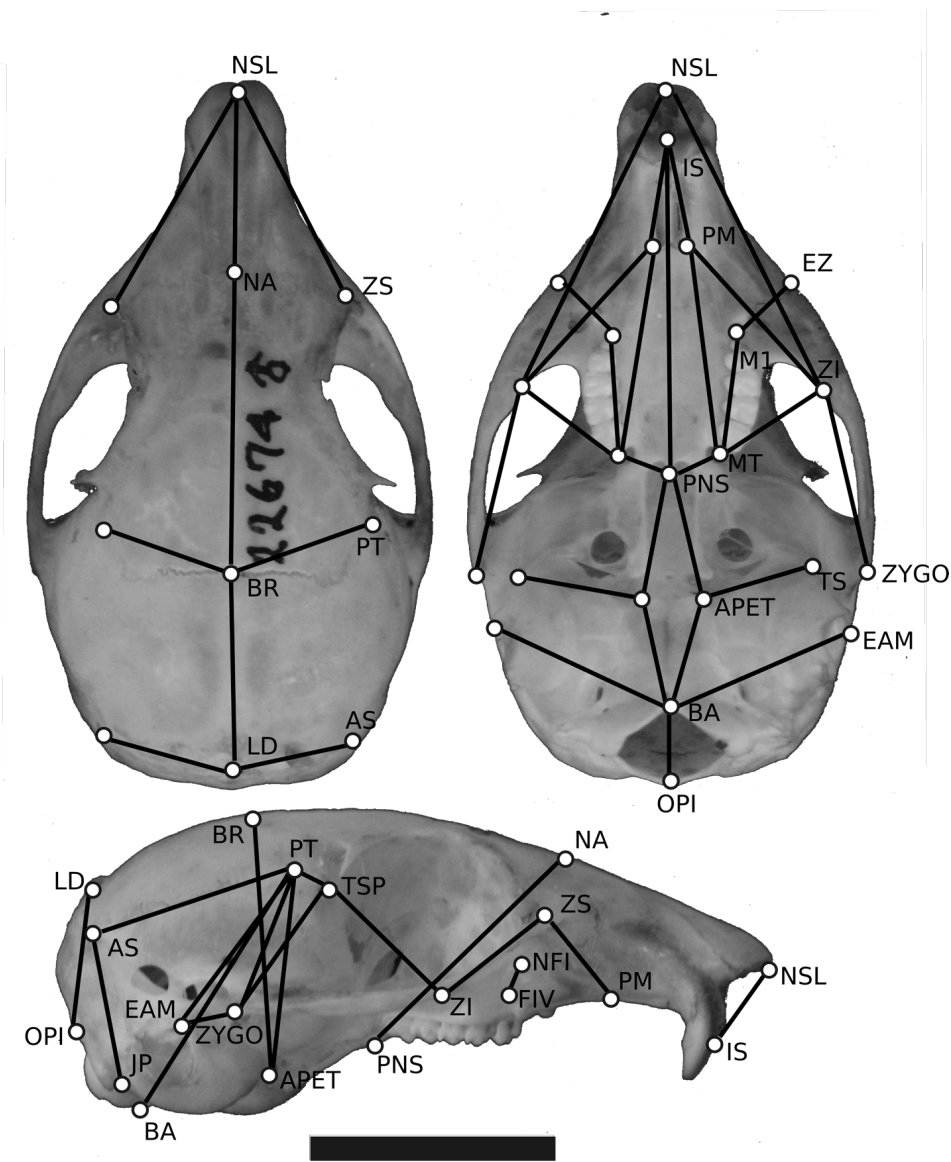
Figure 2: Locations of landmarks and linear measurements on skulls.
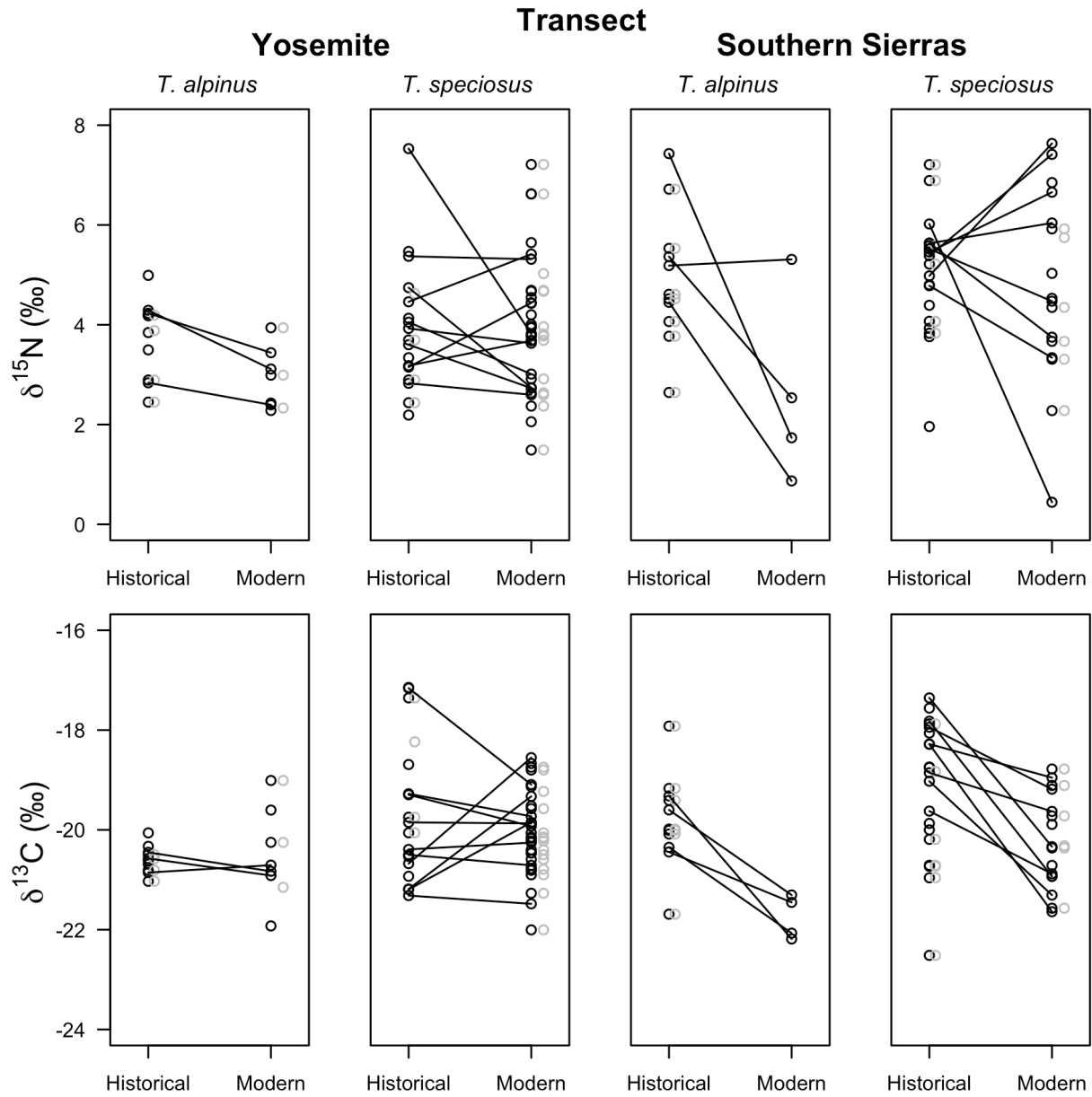
Figure 3: Mean $\delta^{15}N$ and $\delta^{13}C$ ratios for GRP sites. Each point represents the mean value for all specimens from a single GRP site. Sites for which specimens were collected in both the historical and modern eras are shown in black, with a line connecting the historical and modern means. Data for sites that include specimens from one era only are plotted in lighter gray.

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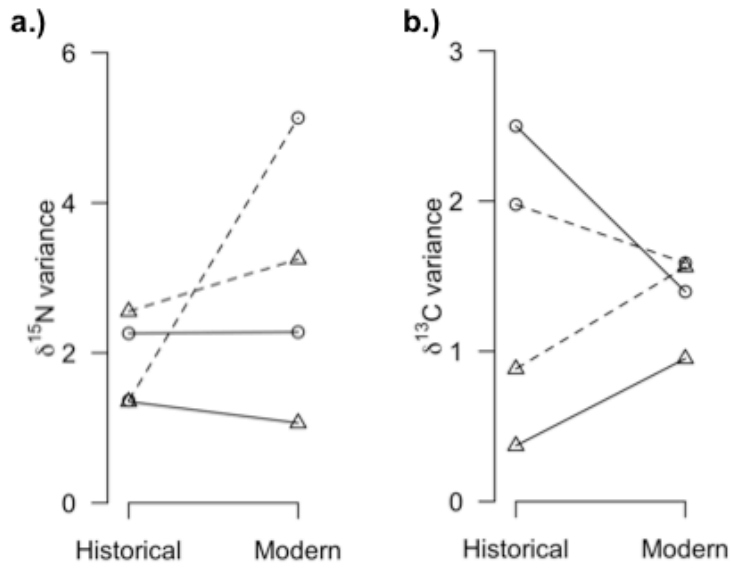
Figure 4: Patterns of over time in variance in a.) $\delta^{15}N$ and b.) $\delta^{13}C$ isotope ratios. Triangles represent *T. alpinus*; circles represent *T. speciosus*. Connections between historical and modern variances are shown for each species, with dotted lines connecting Southern Sierra specimens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

Table 2: Summary statistics for confidence set of models for a.) nitrogen ($\delta^{15}N$) and b.) carbon ($\delta^{13}C$) 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.) $\delta^{15}N$	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

(Table 2a, continued)

Response Variable	Predictor variables	Number of Parameters (K)	AIC$_C$	ΔAIC$_C$	AIC$_C$ Weight
δ^{15}N	Intercept Species Era Transect Elevation Species*Era Species*Transect Species*Elevation Era*Transect Era*Elevation	20	955	4.62	0.0313
	Intercept Species Era Transect Elevation Species*Era Species*Transect Species*Elevation Era*Transect Transect*Elevation	20	956	5.54	0.0197

Response Variable	Predictor variables	Number of Parameters (K)	AIC$_C$	ΔAIC$_C$	AIC$_C$ Weight
b.) δ^{13}C	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

Response Variable	Predictor variables	Number of Parameters (K)	AIC$_C$	ΔAIC$_C$	AIC$_C$ Weight
δ^{13}C	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 Species*Era Species*Transect Era*Transect Era*Elevation Transect*Elevation	18	991	2.07	0.0981
	Intercept Species Era Transect Elevation Species*Era Era*Transect	14	991	2.34	0.0855
	Intercept Species Era Transect Elevation Species*Era Species*Transect Era*Transect	15	992	3.07	0.0594

Table 3: Effects of species, era, transect, and elevation on isotope ratios. All values are reported in units of standard deviations, with p-values in parentheses. Statistically significant p-values (<0.05) appear in bold. 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* compare to those in *T. alpinus*. In 3b.), era comparisons indicate whether isotope ratios differ between historic and modern specimens from each species in each transect. Parameter estimates reflect how isotope ratios from modern specimens compare to historic 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.)

a.) Species Comparisons

$\delta^{15}N$

	Southern Sierras & Yosemite
Historical	0.507 **(p = 0.0039)** 95% CI: 0.164 to 0.851
Modern	0.972 **(p < 0.0001)** 95% CI: 0.591 to 1.35

$\delta^{13}C$

	Southern Sierras & Yosemite
Historical	0.43 **(p = 0.0342)** 95% CI: 0.368 to 0.827
Modern	0.89 **(p =0.0003)** 95% CI: 0.416 to 1.36

b.) Era comparisons

$\delta^{15}N$

	Southern Sierras & Yosemite
T. alpinus	-0.676 **(p = 0.0027)** 95% CI: -1.12 to -0.236
T. speciosus	-0.211 (p = 0.184) 95% CI: -0.523 to -0.101

$\delta^{13}C$

	Southern Sierras	Yosemite
T. alpinus	-0.462 (p = 0.0915) 95% CI: -1 to 0.0751	0.648 **(p = 0.0096)** 95% CI: 0.159 to 1.14
T. speciosus	0.00337 (p =0.987) 95% CI: -0.413 to 0.42	0.959 **(p < 0.0001)** 95% CI: 0.542 to 1.38

(Table 3, continued)

c.) Transect Comparisons

$\delta^{15}N$

	Historical & Modern
T. alpinus & *T. speciosus*	-0.528 (**p = 0.001**) 95% CI: -0.834 to -0.223

$\delta^{13}C$

	Historical	Modern
T. alpinus	-0.58 (**p = 0.0007**) 95% CI: -0.907 to -0.252	0.529 (**p = 0.0091**) 95% CI: 0.136 to 0.922
T. speciosus	-0.591 (**p = 0.0007**) 95% CI: -0.923 to -0.259	0.529 (**p = 0.0091**) 95% CI: 0.136 to 0.922

d.) Elevation comparisons

$\delta^{15}N$

	Southern Sierras & Yosemite
Both species, both eras	0.297 (**p = 0.0003**) 95% CI: 0.137 to 0.458

$\delta^{13}C$

Both transects

	Historical	Modern
T. alpinus	-0.149 (p = 0.183) 95% CI: -0.368 to 0.0703	0.207 (p = 0.0589) 95% CI: -0.0078 to 0.423
T. speciosus	-0.153 (p = 0.175) 95% CI: -0.374 to 0.0683	0.208 (p = 0.0583) 95% CI: -0.00737 to 0.0583

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

$\delta^{15}N$

	Southern Sierras	Yosemite
Historical	Var$_{alp}$ = 2.55, Var$_{spec}$ = 1.36 F = 5.14(1,125), **p = 0.0251**	Var$_{alp}$ = 1.35, Var$_{spec}$ = 1.82 F = 3.12(1,88), p = 0.0809
Modern	Var$_{alp}$ = 3.25, Var$_{spec}$ = 4.98 F = 0.788(1,78), p = 0.374	Var$_{alp}$ = 1.06, Var$_{spec}$ = 2.28 F = 4.48(1,126), **p = 0.0362**

$\delta^{13}C$

	Southern Sierras	Yosemite
Historical	Var$_{alp}$ = 0.883, Var$_{spec}$ = 1.98 F = 12.8(1,125), **p = 0.0005**	Var$_{alp}$ = 0.371, Var$_{spec}$ = 2.36 F = 14.9(1.88), **p = 0.0002**
Modern	Var$_{alp}$ = 1.56, Var$_{spec}$ = 1.65 F = 0.312 (1,78), p = 0.578	Var$_{alp}$ = 0.951, Var$_{spec}$ = 1.4 F = 2.04(1,126), p = 0.156
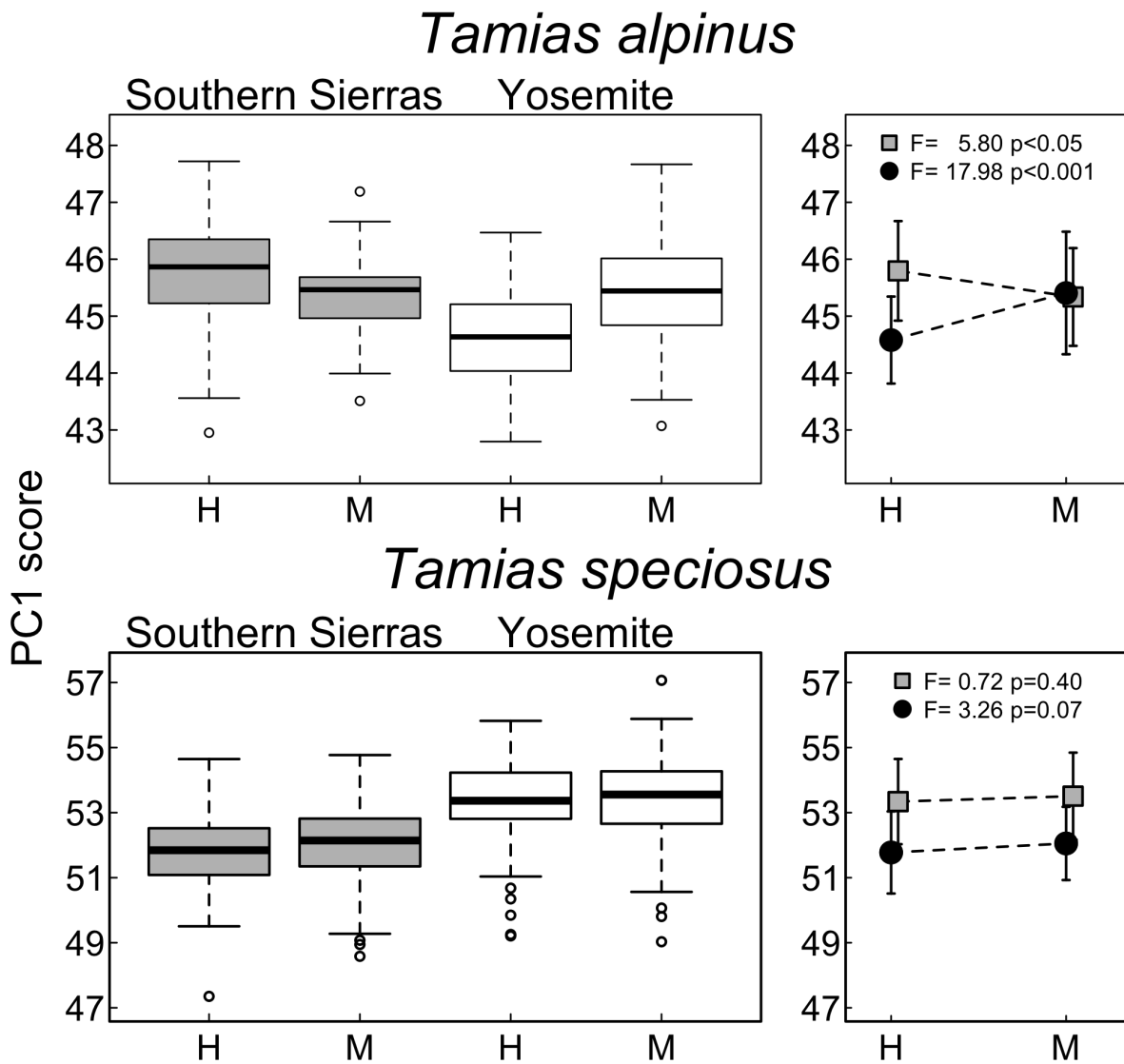
Figure 5: Patterns of size change over time in *T. alpinus* and *T. speciosus*. PC1 is a proxy for skull size. H = historical era, M = modern era. The right panel graphs combine data for both transects displaying the mean ± standard deviation observed for PC1 scores in each species. The F-value and p-value for the ANOVA is also displayed on top of the right graphs, with values for the Southern Sierras transect in gray, and values for the Yosemite transect in black.
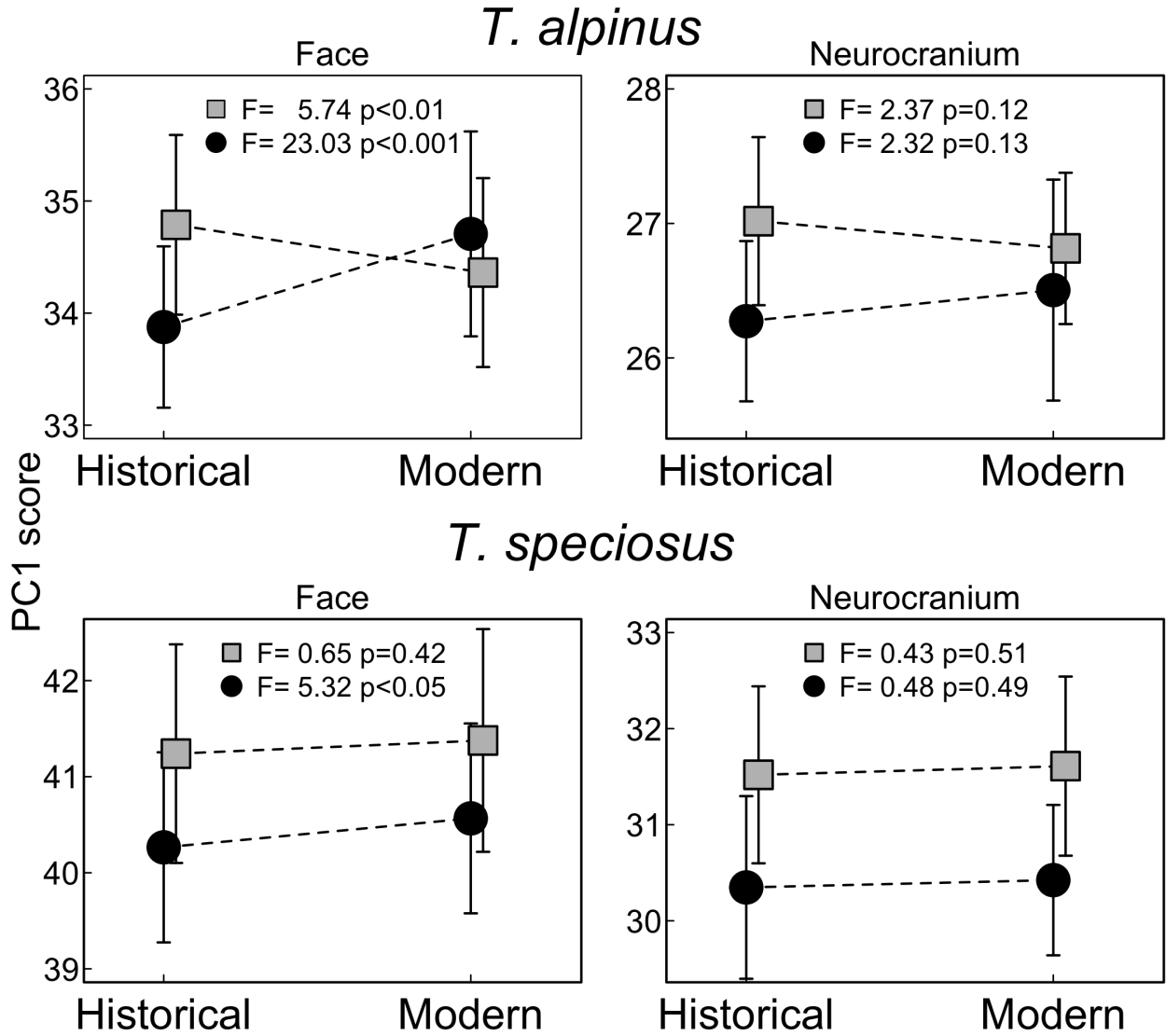
Figure 6: Patterns of size change in the face and neurocranium regions of the skull. Points shown represent means ± standard deviation. The observed F-values and associated p-values are included on each graph. Data from the Southern Sierras transect are shown in gray, and data from the Yosemite transect are shown in black.

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Table 5: Shape changes estimated through Procrustes distance (PD) and Mahalanobis distance (MD). The F-estimates for the Procrustes ANOVA and respective p-values are also shown in the last columns.

		MD	PD	F- statistic	p
T. alpinus	Yosemite	4.71	0.010	3.15	0.001
	Southern Sierras	5.30	0.011	3.96	0.001
T. speciosus	Yosemite	1.93	0.006	2.53	0.002
	Southern Sierras	2.65	0.008	4.05	0.001
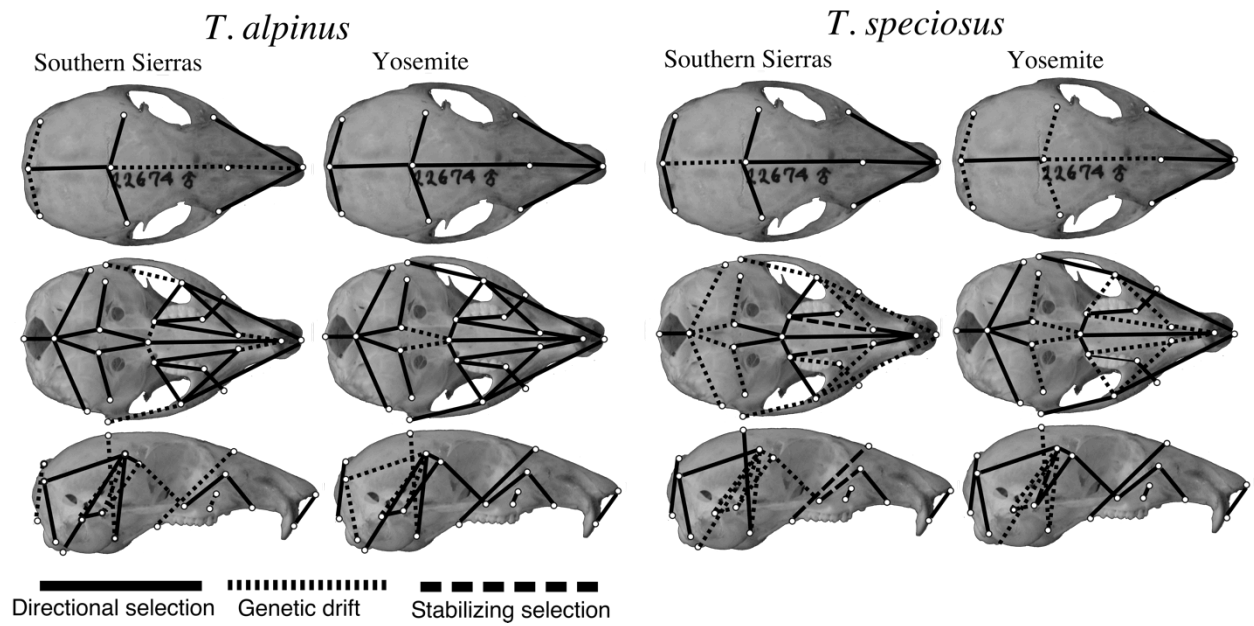
Figure 7: Patterns of change in linear skull measurements, with results of genetic drift tests. Solid lines indicate patterns similar to the expected for changes resulting from directional selection, dotted lines indicate patterns similar to genetic drift, and dashed lines show patterns in accordance with a stabilizing selection scenario.
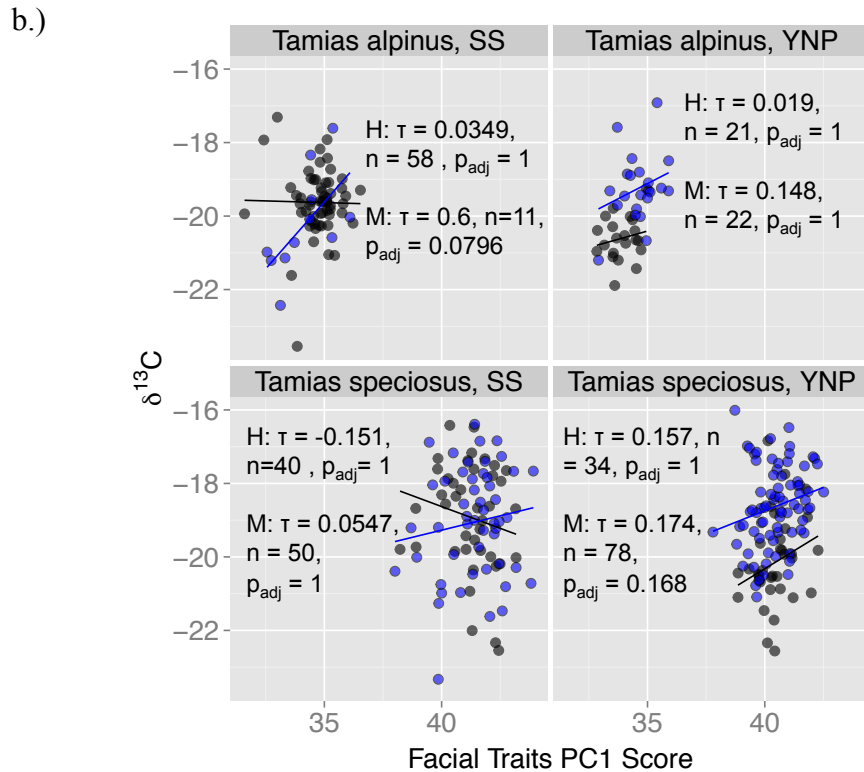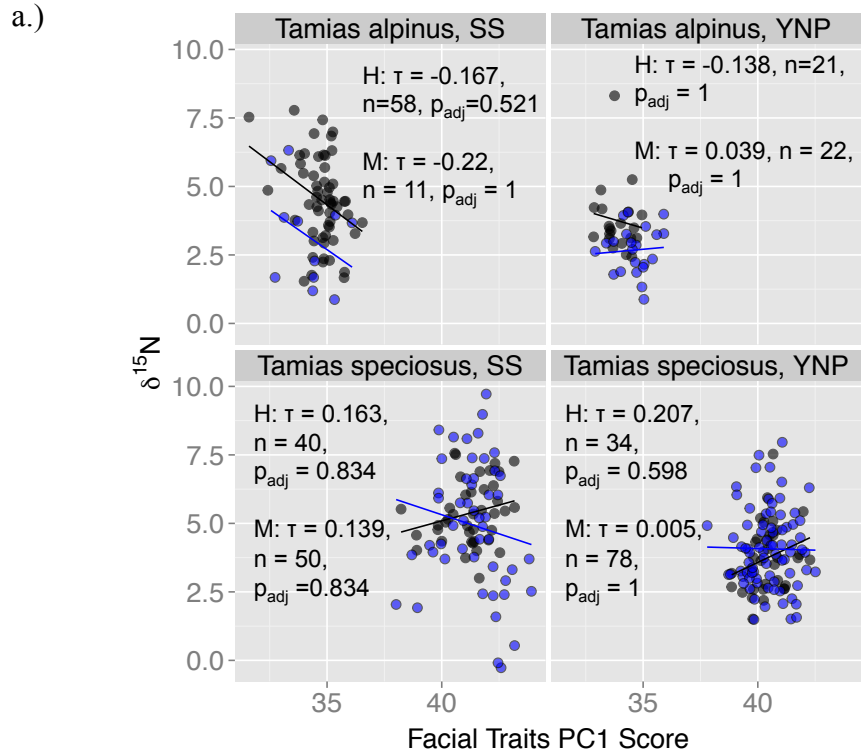
Figure 8: Relationship between facial PC1 scores and nitrogen (Fig. 8a) or carbon (Fig 8b) isotope ratios for each species x transect x era combination. Historic specimens are shown in black, and modern specimens in blue. Results of Kendall's tau tests are reported next to each graph (τ = correlation coefficient, n = sample size, p_{adj} = p-value, with Holm adjustment).

Table 6: Summary of patterns of change in morphology and isotope ratios. All contrasts are for historic and modern samples. Arrows denote significant directional changes from historic to modern material; ns indicates nonsignificant changes. YNP = Yosemite transect, SS = Southern Sierras transect.

Species & location	Morphometric data				Isotopic data	
	Overall skull size	Rostrum size	Cranial Size		$\delta^{15}N$	$\delta^{13}C$
T. alpinus						
YNP	↑	↑	ns		↓	↑
SS	↓	↓	ns		↓	ns
T. speciosus						
YNP	ns	↑	ns		ns	↑
SS	ns	ns	ns		ns	ns

Chapter 5

General Conclusions

As global climates continue to change, a key challenge for scientists is to generate accurate predictions regarding organismal responses. While abundant evidence documents examples of these responses (Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006), the heterogeneity among such findings makes it difficult to understand patterns of response and to predict how species will be impacted by future environmental changes. Given this difficulty, chipmunks in the Sierra Nevada region constitute an excellent study system for exploring factors underlying contrasting patterns of response among closely related species. In this dissertation, I have drawn upon a set of faunal surveys that was initiated by Joseph Grinnell and colleagues in approximately 1911; this work provides a unique and critical baseline against which to compare modern data regarding species distributions. This work has revealed markedly different patterns of elevational range change among the small mammals in the study area, and in particular between my congeneric study species (Moritz *et al.*, 2008), the Alpine Chipmunk (*T. alpinus)* and the Lodgepole Chipmunk (*T. speciosus)*. Ecological niche models (Rubidge *et al.*, 2011) and observational data on patterns of chipmunk habitat use and behavior (Grinnell & Storer, 1924; Heller, 1971; Chappell, 1978; Best *et al.*, 1994; Clawson *et al.*, 1994) have suggested that vegetation and interspecific competitive interactions may be important contributors to this difference in response; my dissertation is the first to compare directly patterns of habitat use and interspecific spatial overlap between my study species in a natural setting. Because my analyses integrate historical data on diet and morphology, they provide an important and almost uniquely direct assessment of ecological response to patterns of environmental change.

Summary of key findings
Overall, my work reveals that *T. alpinus* and *T. speciosus* species show a high degree of spatial overlap in areas of sympatry, although multiple differences in microhabitat features differ between areas used by each species (Chapters 2 & 3). With regard to interspecific spatial overlap, my results confirm that the two species co-occur at a fine scale and that *T. alpinus* and *T. speciosus* individuals are likely to come into frequent contact with one another. Previous studies on determinants of range limits between chipmunk species indicate that competitive interactions can be important in shaping species boundaries (Heller, 1971; Chappell, 1978); in conjunction with my finding of extensive spatial overlap, this information suggests the potential for competitive interactions to influence patterns of range response in my study species. Future work to examine the impacts of such competitive interactions on each of my study species will be critical in assessing the importance of such interactions in the context of climate change.

Although *T. alpinus* and *T. speciosus* overlap in portions of their ranges, they do not overlap completely— both live-trapping and radiotelemetry data indicate that, within areas of sympatry, there are areas that are used exclusively by only one species. Furthermore, analyses using trapping and telemetry data in conjunction with remotely sensed NDVI data (Chapter 2) and field-collected microhabitat data (Chapter 3) indicate that vegetation cover differs in areas used by each species. In particular, comparisons of microhabitat characteristics (Chapter 3) reveal that *T. alpinus* uses areas with more exposed rock and less tree cover. *T. speciosus*, in contrast, uses microhabitats with a wider range of characteristics. These findings offer support for the

characterization of *T. alpinus* as a greater habitat specialist, and *T. speciosus* as more of a habitat generalist. Further, these findings are consistent with the prediction that specialist species will be more strongly affected by climate change (Jiguet et al., 2010; Julliard et al., 2004; Warren et al., 2001). In the context of elevational range shifts over the past century, this suggests that the elevational range contraction observed for *T. alpinus* may reflect habitat tracking, as habitat in portions of this species' range may have become unsuitable with respect to vegetation cover. Indeed, increases in tree density have occurred throughout Yosemite (McIntyre *et al.*, 2015) which, given the occurrence of *T. alpinus* in less vegetated areas, may indicate a loss of habitat for this species. More detailed investigations of microhabitat features such as vegetation cover at sites where *T. alpinus* extirpations have occurred would be useful in providing additional support for the role of vegetation cover in influencing occupancy of sites by *T. alpinus*.

In addition to showing a higher degree of specialization with regard to habitat use in a field setting, morphological analyses of museum specimens (Chapter 4) are consistent with the designation of *T. alpinus* as more responsive to the impacts of environmental change. However, while *T. alpinus* shows stronger signatures of change in skull morphology, stable isotope analyses of hair from specimens collected in the same areas indicate that the relationship between skull morphology and diet in the study species is complex. Further, given that stable isotope signatures suggest a greater tendency for dietary change in *T. alpinus*, these data appear to contradict the microhabitat data in suggesting that range changes in this species are not due to habitat tracking. The lack of strong associations between changes in diet and changes in morphology reflect the need to investigate further the functional significance of the morphological changes that are described here, as well as the types of changes that have occurred in the plant community over the past century.

Future Directions
Collectively, my results suggest that habitat features are important determinants of differences in species' responses to a changing environment but that there are still significant gaps in our understanding of the processes through which chipmunks interact with one another and with their environment. With respect to analyses of spatial overlap (Chapter 2), it would be especially informative to conduct removal experiments to better understand the extent to which the presence of one study species affects the other. Similarly, information on the frequency and outcome of aggressive interspecific encounters would be useful in evaluating whether one species might competitively exclude the other from certain areas.

Another productive avenue for future research would be to expand my analyses of differences in patterns of habitat use (Chapter 2 & 3) to additional study sites, in particular to areas where either *T. alpinus* or *T. speciosus* occur alone. This approach would generate critical insights into how patterns of habitat use differ in the presence versus absence of heterospecifics, and would clarify the extent to which each species is truly a habitat specialist or generalist.

Regarding the relationship between chipmunk diets and morphological changes (Chapter 4), a key shortcoming of the specimen-based work described here is the absence of plant samples collected in conjunction with hair samples, a shortcoming that limits the ability to draw robust inferences about likely diet items for the study species. Analyses of modern hair and plant samples collected simultaneously are currently in progress (Walsh, unpublished data) and will

prove key in linking information on chipmunk diet and morphology to plant community composition. This information will allow us to better understand which features of the habitat are particularly important for each of our study species and will be invaluable for confirming whether the habitat specialization reported here for *T. alpinus* translates into dietary specialization.

While I have capitalized on the contrast in patterns of range change between *T. alpinus* and *T. speciosus* in Yosemite, data regarding other species of chipmunks and other regions of California have been collected as part of the Museum of Vertebrate Zoology's Grinnell Resurvey Project (2003-present). Increasing the taxonomic and geographic scope of my work will provide a broader perspective on how changes in climate and habitat parameters interact with species' ecology to shape distributional changes. The differing patterns of change in temperature and precipitation revealed by this project, in conjunction with the associated data indicating considerable heterogeneity in patterns of range change among even conspecifics (Rowe *et al.*, 2015) creates a unique opportunity to replicate the analyses described here and to improve understanding of the processes underlying organismal responses to environmental change.

Finally, although I have provided evidence linking habitat use to patterns of elevational range change, it remains difficult to determine whether these elevational range shifts can in turn be attributed to climate change. In particular, I have shown that vegetation cover is relevant especially for *T. alpinus*, but further investigation is necessary to assess how climate interacts with other drivers of environmental change (e.g. fire regimes, anthropogenic land use change), to shape patterns of vegetation change and influence species' distributions. Strengthening our understanding of the mechanisms through which climate impacts organisms will be an important step in disentangling the effects of multiple synergistic drivers of change.

In summary, this dissertation provides important new information regarding the ecological factors contributing to differences in response to environmental change among closely related (congeneric), partially sympatric species of mammals. These analyses represent a critical step toward identifying the processes underlying these responses and provide empirical support for the hypothesis that habitat specialization is associated with greater response to environmental change. Strengthening understanding of the links between pattern and process will be critical as we move beyond documenting *how* species are responding to such change to understanding *why* they are responding in given ways, thereby providing a critical basis for improving our ability to predict future patterns of response.

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Appendices

Appendix for Chapter 3: Microhabitat use and elevational range change in two sympatric chipmunk species in Yosemite National Park

Table A1: Results of Wilcoxon rank sum tests comparing individual microhabitat variables between *T. alpinus* and *T. speciosus* telemetry points. The test statistic (W) is reported for each comparison, along with p-values (adjusted using the Holm method).

Variable	ML W	ML p-value (adjusted)	VO W	VO p-value (adjusted)	CL W	CL p-value (adjusted)
Substrate: bedrock cover	25	0.024	107	0.065	107	0.065
Substrate: rock cover	25	0.018	130	0.001	130	0.001
Substrate: litter/duff cover	0	0.008	15	0.002	15	0.002
Minimum canopy height	0	0.008	1	0.000	1	0.000
Maximum canopy height	0	0.008	1	0.000	1	0.000
Canopy cover	0	0.019	23.5	0.011	23.5	0.011
Subcanopy cover	0	0.018	6.5	0.000	6.5	0.000
Tree cover	0	0.009	17	0.003	17	0.003
Shrub cover	11.5	1.000	66.5	1.000	66.5	1.000
Herbaceous cover	14.5	0.753	51	0.324	51	0.324
Shrub + herbaceous cover	11	1.000	65.5	1.000	65.5	1.000
Number of trees	0	0.004	6	0.001	6	0.001
Sum of lengths of downed wood	2	0.063	6	0.003	6	0.003
Volume of downed wood	0	0.032	10	0.008	10	0.008

Appendix for Chapter 4: Morphological and dietary responses of chipmunks to a century of climate change

Table A2: List of specimens used for stable isotope analyses of diet and morphological analyses. The MVZ number column lists the unique number of each individual specimen. For era, H = historical and M = Modern, and for Transect, SS = Southern Sierras and YNP = Yosemite National Park. The Analyses column indicates whether each specimen was included in stable isotope analyses, morphology analyses, or both.

MVZ Number	Species	Era	Transect	Analyses
11931	*Tamias speciosus*	H	YNP	Morphology
11933	*Tamias speciosus*	H	YNP	Morphology
14775	*Tamias speciosus*	H	SS	Morphology
14776	*Tamias speciosus*	H	SS	Morphology
14780	*Tamias speciosus*	H	SS	Morphology
14784	*Tamias speciosus*	H	SS	Morphology
14786	*Tamias speciosus*	H	SS	Morphology
14790	*Tamias speciosus*	H	SS	Morphology
14791	*Tamias speciosus*	H	SS	Morphology
14792	*Tamias speciosus*	H	SS	Morphology
14793	*Tamias speciosus*	H	SS	Morphology
14801	*Tamias speciosus*	H	SS	Morphology
14810	*Tamias speciosus*	H	SS	Morphology
14815	*Tamias speciosus*	H	SS	Morphology
14820	*Tamias speciosus*	H	SS	Morphology
14822	*Tamias speciosus*	H	SS	Morphology
14823	*Tamias speciosus*	H	SS	Morphology
14824	*Tamias speciosus*	H	SS	Morphology
14826	*Tamias speciosus*	H	SS	Morphology
14827	*Tamias speciosus*	H	SS	Morphology
14828	*Tamias speciosus*	H	SS	Morphology
14831	*Tamias speciosus*	H	SS	Morphology
14835	*Tamias speciosus*	H	SS	Morphology
14836	*Tamias speciosus*	H	SS	Morphology
14841	*Tamias speciosus*	H	SS	Morphology
14843	*Tamias speciosus*	H	SS	Morphology
14844	*Tamias speciosus*	H	SS	Morphology
14847	*Tamias speciosus*	H	SS	Morphology
14852	*Tamias speciosus*	H	SS	Morphology
14855	*Tamias speciosus*	H	SS	Morphology
14856	*Tamias speciosus*	H	SS	Morphology
14857	*Tamias speciosus*	H	SS	Morphology
14858	*Tamias speciosus*	H	SS	Morphology
14861	*Tamias speciosus*	H	SS	Morphology
14863	*Tamias speciosus*	H	SS	Morphology

MVZ Number	Species	Era	Transect	Analyses
14865	*Tamias speciosus*	H	SS	Morphology
14869	*Tamias speciosus*	H	SS	Morphology
14870	*Tamias speciosus*	H	SS	Morphology
14872	*Tamias speciosus*	H	SS	Morphology
14875	*Tamias speciosus*	H	SS	Morphology
14876	*Tamias speciosus*	H	SS	Morphology
14877	*Tamias speciosus*	H	SS	Morphology
14879	*Tamias speciosus*	H	SS	Morphology
14880	*Tamias speciosus*	H	SS	Morphology
14881	*Tamias speciosus*	H	SS	Morphology
14882	*Tamias speciosus*	H	SS	Morphology
14885	*Tamias speciosus*	H	SS	Morphology
14890	*Tamias alpinus*	H	SS	Morphology
14892	*Tamias speciosus*	H	SS	Morphology
14894	*Tamias speciosus*	H	SS	Morphology
14895	*Tamias speciosus*	H	SS	Morphology
14896	*Tamias speciosus*	H	SS	Morphology
14897	*Tamias speciosus*	H	SS	Morphology
14901	*Tamias speciosus*	H	SS	Morphology
14903	*Tamias alpinus*	H	SS	Morphology
14904	*Tamias alpinus*	H	SS	Morphology
14905	*Tamias alpinus*	H	SS	Morphology
14911	*Tamias alpinus*	H	SS	Morphology
14914	*Tamias alpinus*	H	SS	Morphology
14915	*Tamias alpinus*	H	SS	Morphology
14916	*Tamias alpinus*	H	SS	Morphology
14918	*Tamias alpinus*	H	SS	Morphology
14922	*Tamias alpinus*	H	SS	Morphology
14923	*Tamias alpinus*	H	SS	Morphology
14924	*Tamias alpinus*	H	SS	Morphology
14927	*Tamias alpinus*	H	SS	Morphology
14929	*Tamias alpinus*	H	SS	Morphology
14930	*Tamias alpinus*	H	SS	Morphology
14931	*Tamias alpinus*	H	SS	Morphology
14936	*Tamias alpinus*	H	SS	Morphology
14939	*Tamias alpinus*	H	SS	Morphology
14942	*Tamias alpinus*	H	SS	Morphology
14945	*Tamias alpinus*	H	SS	Morphology
14946	*Tamias alpinus*	H	SS	Morphology
14948	*Tamias alpinus*	H	SS	Morphology
14949	*Tamias alpinus*	H	SS	Morphology
14950	*Tamias alpinus*	H	SS	Morphology

MVZ Number	Species	Era	Transect	Analyses
14957	*Tamias alpinus*	H	SS	Morphology
14958	*Tamias alpinus*	H	SS	Morphology
14959	*Tamias alpinus*	H	SS	Morphology
14962	*Tamias alpinus*	H	SS	Morphology
14964	*Tamias alpinus*	H	SS	Morphology
14970	*Tamias alpinus*	H	SS	Morphology
14973	*Tamias alpinus*	H	SS	Morphology
14975	*Tamias alpinus*	H	SS	Morphology
17576	*Tamias alpinus*	H	SS	Morphology
17579	*Tamias alpinus*	H	SS	Morphology
17581	*Tamias alpinus*	H	SS	Morphology
17585	*Tamias alpinus*	H	SS	Morphology
17586	*Tamias alpinus*	H	SS	Morphology
17587	*Tamias alpinus*	H	SS	Morphology
17589	*Tamias alpinus*	H	SS	Morphology
17590	*Tamias alpinus*	H	SS	Morphology
17592	*Tamias alpinus*	H	SS	Morphology
17593	*Tamias alpinus*	H	SS	Morphology
17594	*Tamias alpinus*	H	SS	Morphology
17595	*Tamias alpinus*	H	SS	Morphology
17596	*Tamias alpinus*	H	SS	Morphology
17597	*Tamias alpinus*	H	SS	Morphology
17598	*Tamias alpinus*	H	SS	Morphology
17599	*Tamias alpinus*	H	SS	Morphology
17600	*Tamias alpinus*	H	SS	Morphology
17601	*Tamias alpinus*	H	SS	Morphology
17602	*Tamias alpinus*	H	SS	Morphology
17603	*Tamias alpinus*	H	SS	Morphology
17604	*Tamias alpinus*	H	SS	Morphology
17605	*Tamias alpinus*	H	SS	Morphology
17606	*Tamias alpinus*	H	SS	Morphology
17607	*Tamias alpinus*	H	SS	Morphology
17608	*Tamias alpinus*	H	SS	Morphology
17609	*Tamias alpinus*	H	SS	Morphology
17611	*Tamias alpinus*	H	SS	Morphology
17615	*Tamias alpinus*	H	SS	Morphology
17617	*Tamias alpinus*	H	SS	Morphology
17618	*Tamias alpinus*	H	SS	Morphology
17619	*Tamias alpinus*	H	SS	Morphology
17621	*Tamias alpinus*	H	SS	Morphology
17622	*Tamias alpinus*	H	SS	Morphology
21338	*Tamias speciosus*	M	YNP	Morphology

MVZ Number	Species	Era	Transect	Analyses
22665	*Tamias alpinus*	H	YNP	Morphology
22667	*Tamias alpinus*	H	YNP	Morphology
22668	*Tamias alpinus*	H	YNP	Morphology
22669	*Tamias alpinus*	H	YNP	Morphology
22671	*Tamias alpinus*	H	YNP	Morphology
22672	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22673	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22674	*Tamias alpinus*	H	YNP	Morphology
22675	*Tamias alpinus*	H	YNP	Morphology
22676	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22677	*Tamias alpinus*	H	YNP	Morphology
22678	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22679	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22680	*Tamias alpinus*	H	YNP	Morphology
22681	*Tamias alpinus*	H	YNP	Morphology
22682	*Tamias alpinus*	H	YNP	Morphology
22684	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22685	*Tamias alpinus*	H	YNP	Morphology
22686	*Tamias alpinus*	H	YNP	Morphology
22687	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22689	*Tamias alpinus*	H	YNP	Morphology
22690	*Tamias alpinus*	H	YNP	Morphology
22691	*Tamias alpinus*	H	YNP	Isotopes
22692	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22695	*Tamias alpinus*	H	YNP	Isotopes
22696	*Tamias alpinus*	H	YNP	Isotopes
22697	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22699	*Tamias alpinus*	H	YNP	Morphology
22700	*Tamias alpinus*	H	YNP	Morphology
22701	*Tamias alpinus*	H	YNP	Isotopes
22702	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22703	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22705	*Tamias alpinus*	H	YNP	Isotopes, Morphology
22707	*Tamias speciosus*	H	YNP	Morphology
22708	*Tamias speciosus*	H	YNP	Morphology
22709	*Tamias speciosus*	H	YNP	Morphology
22710	*Tamias speciosus*	H	YNP	Morphology
22711	*Tamias speciosus*	H	YNP	Isotopes
22712	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22713	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22714	*Tamias speciosus*	H	YNP	Morphology
22715	*Tamias speciosus*	H	YNP	Morphology

MVZ Number	Species	Era	Transect	Analyses
22716	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22717	*Tamias speciosus*	H	YNP	Morphology
22718	*Tamias speciosus*	H	YNP	Isotopes
22719	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22720	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22721	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22722	*Tamias speciosus*	H	YNP	Isotopes
22723	*Tamias speciosus*	H	YNP	Isotopes
22724	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22725	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22726	*Tamias speciosus*	H	YNP	Morphology
22729	*Tamias speciosus*	H	YNP	Morphology
22730	*Tamias speciosus*	H	YNP	Morphology
22731	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22733	*Tamias speciosus*	H	YNP	Isotopes
22734	*Tamias speciosus*	H	YNP	Morphology
22735	*Tamias speciosus*	H	YNP	Morphology
22736	*Tamias speciosus*	H	YNP	Morphology
22737	*Tamias speciosus*	H	YNP	Morphology
22738	*Tamias speciosus*	H	YNP	Morphology
22740	*Tamias speciosus*	H	YNP	Morphology
22741	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22742	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22743	*Tamias speciosus*	H	YNP	Morphology
22744	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22745	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22746	*Tamias speciosus*	H	YNP	Isotopes
22747	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22748	*Tamias speciosus*	H	YNP	Morphology
22749	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22750	*Tamias speciosus*	H	YNP	Morphology
22752	*Tamias speciosus*	H	YNP	Morphology
22754	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22761	*Tamias speciosus*	H	YNP	Morphology
22762	*Tamias speciosus*	H	YNP	Morphology
22763	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22764	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22765	*Tamias speciosus*	H	YNP	Isotopes
22766	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22767	*Tamias speciosus*	H	YNP	Isotopes
22769	*Tamias speciosus*	H	YNP	Isotopes
22770	*Tamias speciosus*	H	YNP	Isotopes

MVZ Number	Species	Era	Transect	Analyses
22772	*Tamias speciosus*	H	YNP	Isotopes, Morphology
22773	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23318	*Tamias alpinus*	H	YNP	Isotopes
23319	*Tamias alpinus*	H	YNP	Isotopes
23320	*Tamias alpinus*	H	YNP	Isotopes, Morphology
23321	*Tamias alpinus*	H	YNP	Isotopes
23322	*Tamias alpinus*	H	YNP	Isotopes, Morphology
23323	*Tamias alpinus*	H	YNP	Isotopes, Morphology
23324	*Tamias alpinus*	H	YNP	Isotopes
23325	*Tamias alpinus*	H	YNP	Isotopes
23326	*Tamias alpinus*	H	YNP	Isotopes
23327	*Tamias alpinus*	H	YNP	Isotopes, Morphology
23329	*Tamias alpinus*	H	YNP	Isotopes, Morphology
23330	*Tamias alpinus*	H	YNP	Isotopes, Morphology
23331	*Tamias alpinus*	H	YNP	Isotopes, Morphology
23332	*Tamias alpinus*	H	YNP	Isotopes, Morphology
23334	*Tamias alpinus*	H	YNP	Morphology
23335	*Tamias alpinus*	H	YNP	Morphology
23336	*Tamias alpinus*	H	YNP	Morphology
23337	*Tamias alpinus*	H	YNP	Morphology
23338	*Tamias alpinus*	H	YNP	Morphology
23340	*Tamias alpinus*	H	YNP	Morphology
23341	*Tamias alpinus*	H	YNP	Isotopes
23342	*Tamias alpinus*	H	YNP	Isotopes, Morphology
23343	*Tamias alpinus*	H	YNP	Morphology
23344	*Tamias alpinus*	H	YNP	Morphology
23345	*Tamias alpinus*	H	YNP	Morphology
23346	*Tamias alpinus*	H	YNP	Morphology
23348	*Tamias alpinus*	H	YNP	Morphology
23350	*Tamias alpinus*	H	YNP	Morphology
23383	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23384	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23386	*Tamias speciosus*	H	YNP	Isotopes
23387	*Tamias speciosus*	H	YNP	Isotopes
23388	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23390	*Tamias speciosus*	H	YNP	Morphology
23391	*Tamias speciosus*	H	YNP	Morphology
23393	*Tamias speciosus*	H	YNP	Isotopes
23395	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23396	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23397	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23398	*Tamias speciosus*	H	YNP	Isotopes

MVZ Number	Species	Era	Transect	Analyses
23399	*Tamias speciosus*	H	YNP	Isotopes
23400	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23401	*Tamias speciosus*	H	YNP	Morphology
23402	*Tamias speciosus*	H	YNP	Morphology
23404	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23405	*Tamias speciosus*	H	YNP	Isotopes
23409	*Tamias speciosus*	H	YNP	Morphology
23410	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23411	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23412	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23413	*Tamias speciosus*	H	YNP	Isotopes
23414	*Tamias speciosus*	H	YNP	Morphology
23415	*Tamias speciosus*	H	YNP	Morphology
23416	*Tamias speciosus*	H	YNP	Morphology
23418	*Tamias speciosus*	H	YNP	Morphology
23420	*Tamias speciosus*	H	YNP	Morphology
23421	*Tamias speciosus*	H	YNP	Morphology
23422	*Tamias speciosus*	H	YNP	Morphology
23423	*Tamias speciosus*	H	YNP	Morphology
23424	*Tamias speciosus*	H	YNP	Morphology
23425	*Tamias speciosus*	H	YNP	Morphology
23426	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23427	*Tamias speciosus*	H	YNP	Isotopes, Morphology
23428	*Tamias speciosus*	H	YNP	Morphology
24137	*Tamias alpinus*	H	YNP	Isotopes
24382	*Tamias speciosus*	H	SS	Morphology
24385	*Tamias speciosus*	H	SS	Morphology
24387	*Tamias speciosus*	H	SS	Morphology
25189	*Tamias alpinus*	H	SS	Morphology
25190	*Tamias alpinus*	H	SS	Morphology
25193	*Tamias alpinus*	H	SS	Morphology
25199	*Tamias alpinus*	H	SS	Morphology
25200	*Tamias alpinus*	H	SS	Morphology
25204	*Tamias alpinus*	H	SS	Morphology
25209	*Tamias alpinus*	H	SS	Morphology
25213	*Tamias alpinus*	H	SS	Morphology
25215	*Tamias speciosus*	H	SS	Morphology
25216	*Tamias speciosus*	H	SS	Morphology
25220	*Tamias speciosus*	H	SS	Morphology
25221	*Tamias speciosus*	H	SS	Morphology
25223	*Tamias speciosus*	H	SS	Morphology
25225	*Tamias speciosus*	H	SS	Morphology

MVZ Number	Species	Era	Transect	Analyses
25226	*Tamias speciosus*	H	SS	Morphology
25228	*Tamias speciosus*	H	SS	Morphology
25230	*Tamias speciosus*	H	SS	Morphology
25231	*Tamias speciosus*	H	SS	Morphology
25232	*Tamias speciosus*	H	SS	Morphology
25236	*Tamias speciosus*	H	SS	Morphology
25237	*Tamias speciosus*	H	SS	Morphology
25242	*Tamias speciosus*	H	SS	Morphology
25245	*Tamias speciosus*	H	SS	Morphology
25247	*Tamias speciosus*	H	SS	Morphology
25248	*Tamias speciosus*	H	SS	Morphology
25250	*Tamias speciosus*	H	SS	Morphology
25252	*Tamias speciosus*	H	SS	Morphology
25253	*Tamias speciosus*	H	SS	Morphology
25254	*Tamias speciosus*	H	SS	Morphology
25257	*Tamias speciosus*	H	SS	Morphology
25259	*Tamias speciosus*	H	SS	Morphology
25261	*Tamias speciosus*	H	SS	Morphology
25262	*Tamias speciosus*	H	SS	Morphology
25264	*Tamias speciosus*	H	SS	Morphology
30074	*Tamias alpinus*	H	SS	Morphology
30076	*Tamias alpinus*	H	SS	Morphology
30078	*Tamias speciosus*	H	SS	Morphology
30079	*Tamias speciosus*	H	SS	Morphology
30080	*Tamias speciosus*	H	SS	Morphology
30081	*Tamias speciosus*	H	SS	Morphology
30083	*Tamias speciosus*	H	SS	Morphology
30087	*Tamias speciosus*	H	SS	Morphology
32926	*Tamias speciosus*	H	YNP	Morphology
68989	*Tamias speciosus*	H	YNP	Morphology
85250	*Tamias speciosus*	H	YNP	Morphology
85251	*Tamias speciosus*	H	YNP	Morphology
85252	*Tamias speciosus*	H	YNP	Isotopes, Morphology
88184	*Tamias speciosus*	H	YNP	Morphology
88185	*Tamias speciosus*	H	YNP	Morphology
88186	*Tamias speciosus*	H	YNP	Morphology
94860	*Tamias speciosus*	H	YNP	Morphology
94861	*Tamias speciosus*	H	YNP	Morphology
99010	*Tamias speciosus*	H	YNP	Morphology
99011	*Tamias speciosus*	H	YNP	Morphology
99012	*Tamias speciosus*	H	YNP	Isotopes, Morphology
99013	*Tamias speciosus*	H	YNP	Isotopes

MVZ Number	Species	Era	Transect	Analyses
99014	*Tamias speciosus*	H	YNP	Isotopes, Morphology
99015	*Tamias speciosus*	H	YNP	Isotopes, Morphology
99016	*Tamias speciosus*	H	YNP	Isotopes, Morphology
108999	*Tamias alpinus*	H	SS	Morphology
109001	*Tamias speciosus*	H	SS	Morphology
109002	*Tamias speciosus*	H	SS	Morphology
109003	*Tamias speciosus*	H	SS	Morphology
109005	*Tamias speciosus*	H	SS	Morphology
109007	*Tamias speciosus*	H	SS	Morphology
109008	*Tamias speciosus*	H	SS	Morphology
119131	*Tamias speciosus*	M	SS	Morphology
151374	*Tamias speciosus*	M	YNP	Isotopes
151375	*Tamias speciosus*	M	YNP	Isotopes, Morphology
151378	*Tamias speciosus*	M	SS	Morphology
151379	*Tamias speciosus*	M	SS	Morphology
151380	*Tamias speciosus*	M	SS	Morphology
151381	*Tamias speciosus*	M	SS	Morphology
151382	*Tamias speciosus*	M	SS	Morphology
151383	*Tamias speciosus*	M	SS	Morphology
151783	*Tamias speciosus*	M	YNP	Morphology
161305	*Tamias speciosus*	M	YNP	Morphology
165877	*Tamias speciosus*	M	YNP	Morphology
201265	*Tamias speciosus*	M	YNP	Morphology
201430	*Tamias alpinus*	M	YNP	Morphology
201450	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201451	*Tamias speciosus*	M	YNP	Morphology
201452	*Tamias speciosus*	M	YNP	Morphology
201453	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201454	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201455	*Tamias speciosus*	M	YNP	Morphology
201456	*Tamias speciosus*	M	YNP	Morphology
201457	*Tamias speciosus*	M	YNP	Morphology
201458	*Tamias speciosus*	M	YNP	Morphology
201459	*Tamias speciosus*	M	YNP	Morphology
201460	*Tamias speciosus*	M	YNP	Morphology
201461	*Tamias speciosus*	M	YNP	Morphology
201462	*Tamias speciosus*	M	YNP	Morphology
201463	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201464	*Tamias speciosus*	M	YNP	Morphology
201466	*Tamias speciosus*	M	YNP	Morphology
201467	*Tamias speciosus*	M	YNP	Morphology
201468	*Tamias speciosus*	M	YNP	Isotopes, Morphology

MVZ Number	Species	Era	Transect	Analyses
201471	*Tamias speciosus*	M	YNP	Morphology
201472	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201473	*Tamias speciosus*	M	YNP	Morphology
201474	*Tamias speciosus*	M	YNP	Morphology
201475	*Tamias speciosus*	M	YNP	Isotopes
201476	*Tamias speciosus*	M	YNP	Morphology
201477	*Tamias speciosus*	M	YNP	Morphology
201478	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201479	*Tamias speciosus*	M	YNP	Morphology
201480	*Tamias speciosus*	M	YNP	Morphology
201481	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201482	*Tamias speciosus*	M	YNP	Morphology
201483	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201484	*Tamias speciosus*	M	YNP	Morphology
201485	*Tamias speciosus*	M	YNP	Morphology
201486	*Tamias speciosus*	M	YNP	Morphology
201487	*Tamias speciosus*	M	YNP	Morphology
201488	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201489	*Tamias speciosus*	M	YNP	Morphology
201490	*Tamias speciosus*	M	YNP	Morphology
201492	*Tamias speciosus*	M	YNP	Morphology
201493	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201494	*Tamias speciosus*	M	YNP	Morphology
201495	*Tamias speciosus*	M	YNP	Morphology
201496	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201497	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201498	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201499	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201500	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201501	*Tamias speciosus*	M	YNP	Isotopes
201502	*Tamias speciosus*	M	YNP	Morphology
201503	*Tamias speciosus*	M	YNP	Morphology
201504	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201505	*Tamias speciosus*	M	YNP	Morphology
201506	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201508	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201509	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201510	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201512	*Tamias speciosus*	M	YNP	Morphology
201513	*Tamias speciosus*	M	YNP	Morphology
201514	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201515	*Tamias speciosus*	M	YNP	Isotopes, Morphology

MVZ Number	Species	Era	Transect	Analyses
201516	*Tamias speciosus*	M	YNP	Morphology
201517	*Tamias speciosus*	M	YNP	Morphology
201518	*Tamias speciosus*	M	YNP	Morphology
201522	*Tamias speciosus*	M	YNP	Morphology
201523	*Tamias speciosus*	M	YNP	Morphology
201524	*Tamias speciosus*	M	YNP	Isotopes
201525	*Tamias speciosus*	M	YNP	Isotopes
201526	*Tamias speciosus*	M	YNP	Isotopes
201527	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201528	*Tamias speciosus*	M	YNP	Morphology
201529	*Tamias speciosus*	M	YNP	Morphology
201530	*Tamias speciosus*	M	YNP	Morphology
201531	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201532	*Tamias speciosus*	M	YNP	Morphology
201533	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201534	*Tamias speciosus*	M	YNP	Isotopes
201548	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201549	*Tamias speciosus*	M	YNP	Morphology
201551	*Tamias speciosus*	M	YNP	Morphology
201553	*Tamias speciosus*	M	YNP	Morphology
201556	*Tamias speciosus*	M	YNP	Morphology
201557	*Tamias speciosus*	M	YNP	Isotopes, Morphology
201558	*Tamias speciosus*	M	YNP	Morphology
201560	*Tamias speciosus*	M	YNP	Morphology
201561	*Tamias speciosus*	M	YNP	Morphology
201565	*Tamias speciosus*	M	YNP	Isotopes, Morphology
206396	*Tamias alpinus*	M	SS	Morphology
206397	*Tamias alpinus*	M	SS	Morphology
206412	*Tamias speciosus*	M	SS	Morphology
207199	*Tamias alpinus*	M	YNP	Isotopes, Morphology
207200	*Tamias alpinus*	M	YNP	Isotopes, Morphology
207201	*Tamias alpinus*	M	YNP	Isotopes, Morphology
207202	*Tamias alpinus*	M	YNP	Morphology
207203	*Tamias alpinus*	M	YNP	Isotopes, Morphology
207204	*Tamias alpinus*	M	YNP	Isotopes, Morphology
207205	*Tamias alpinus*	M	YNP	Morphology
207206	*Tamias alpinus*	M	YNP	Isotopes, Morphology
207207	*Tamias alpinus*	M	YNP	Isotopes, Morphology
207208	*Tamias alpinus*	M	YNP	Isotopes, Morphology
207224	*Tamias speciosus*	M	YNP	Morphology
207232	*Tamias speciosus*	M	YNP	Isotopes
207234	*Tamias speciosus*	M	YNP	Isotopes

MVZ Number	Species	Era	Transect	Analyses
207237	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207238	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207239	*Tamias speciosus*	M	YNP	Isotopes
207240	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207241	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207242	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207243	*Tamias speciosus*	M	YNP	Isotopes
207244	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207245	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207246	*Tamias speciosus*	M	YNP	Morphology
207247	*Tamias speciosus*	M	YNP	Morphology
207248	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207250	*Tamias speciosus*	M	YNP	Isotopes
207254	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207257	*Tamias speciosus*	M	YNP	Isotopes
207258	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207259	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207260	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207261	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207262	*Tamias speciosus*	M	YNP	Isotopes
207264	*Tamias speciosus*	M	YNP	Morphology
207265	*Tamias speciosus*	M	YNP	Morphology
207266	*Tamias speciosus*	M	YNP	Morphology
207268	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207269	*Tamias speciosus*	M	YNP	Morphology
207270	*Tamias speciosus*	M	YNP	Isotopes
207271	*Tamias speciosus*	M	YNP	Morphology
207272	*Tamias speciosus*	M	YNP	Morphology
207273	*Tamias speciosus*	M	YNP	Morphology
207274	*Tamias speciosus*	M	YNP	Morphology
207275	*Tamias speciosus*	M	YNP	Morphology
207276	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207277	*Tamias speciosus*	M	YNP	Morphology
207279	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207280	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207281	*Tamias speciosus*	M	YNP	Morphology
207283	*Tamias speciosus*	M	YNP	Isotopes, Morphology
207284	*Tamias speciosus*	M	YNP	Morphology
207285	*Tamias speciosus*	M	YNP	Morphology
208335	*Tamias speciosus*	M	YNP	Morphology
216019	*Tamias speciosus*	M	YNP	Morphology
216020	*Tamias speciosus*	M	YNP	Morphology

MVZ Number	Species	Era	Transect	Analyses
216021	*Tamias speciosus*	M	YNP	Morphology
216270	*Tamias alpinus*	M	YNP	Morphology
216272	*Tamias alpinus*	M	YNP	Morphology
216324	*Tamias speciosus*	M	YNP	Morphology
216325	*Tamias speciosus*	M	YNP	Morphology
216326	*Tamias speciosus*	M	YNP	Morphology
216327	*Tamias speciosus*	M	YNP	Morphology
216328	*Tamias speciosus*	M	YNP	Morphology
216330	*Tamias speciosus*	M	YNP	Morphology
216333	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216334	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216335	*Tamias speciosus*	M	YNP	Morphology
216336	*Tamias speciosus*	M	YNP	Morphology
216337	*Tamias speciosus*	M	YNP	Morphology
216339	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216340	*Tamias speciosus*	M	YNP	Morphology
216342	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216343	*Tamias speciosus*	M	YNP	Morphology
216344	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216346	*Tamias speciosus*	M	YNP	Isotopes
216347	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216348	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216349	*Tamias speciosus*	M	YNP	Morphology
216350	*Tamias speciosus*	M	YNP	Morphology
216351	*Tamias speciosus*	M	YNP	Morphology
216352	*Tamias speciosus*	M	YNP	Morphology
216353	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216358	*Tamias speciosus*	M	YNP	Morphology
216361	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216362	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216363	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216365	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216366	*Tamias speciosus*	M	YNP	Isotopes, Morphology
216367	*Tamias speciosus*	M	YNP	Morphology
216373	*Tamias speciosus*	M	YNP	Morphology
216374	*Tamias speciosus*	M	YNP	Morphology
217178	*Tamias alpinus*	M	YNP	Morphology
217179	*Tamias alpinus*	M	YNP	Isotopes, Morphology
217180	*Tamias alpinus*	M	YNP	Isotopes, Morphology
217181	*Tamias alpinus*	M	YNP	Isotopes, Morphology
217182	*Tamias alpinus*	M	YNP	Morphology
217183	*Tamias alpinus*	M	YNP	Isotopes, Morphology

MVZ Number	Species	Era	Transect	Analyses
217184	*Tamias alpinus*	M	YNP	Isotopes, Morphology
217185	*Tamias alpinus*	M	YNP	Isotopes, Morphology
217186	*Tamias alpinus*	M	YNP	Isotopes, Morphology
217189	*Tamias alpinus*	M	YNP	Isotopes
217191	*Tamias speciosus*	M	YNP	Isotopes, Morphology
217192	*Tamias speciosus*	M	YNP	Morphology
217193	*Tamias speciosus*	M	YNP	Morphology
217196	*Tamias speciosus*	M	YNP	Morphology
217197	*Tamias speciosus*	M	YNP	Morphology
217198	*Tamias speciosus*	M	YNP	Morphology
219224	*Tamias speciosus*	M	SS	Morphology
219986	*Tamias alpinus*	M	YNP	Morphology
219987	*Tamias alpinus*	M	YNP	Morphology
219989	*Tamias alpinus*	M	YNP	Morphology
219990	*Tamias alpinus*	M	YNP	Morphology
219991	*Tamias alpinus*	M	YNP	Morphology
219992	*Tamias alpinus*	M	YNP	Morphology
219993	*Tamias alpinus*	M	YNP	Morphology
219997	*Tamias alpinus*	M	YNP	Morphology
219998	*Tamias alpinus*	M	YNP	Isotopes, Morphology
219999	*Tamias alpinus*	M	YNP	Morphology
220000	*Tamias alpinus*	M	YNP	Isotopes
220001	*Tamias alpinus*	M	YNP	Isotopes
220002	*Tamias alpinus*	M	YNP	Isotopes, Morphology
220010	*Tamias alpinus*	M	YNP	Isotopes, Morphology
220019	*Tamias alpinus*	M	YNP	Isotopes, Morphology
220025	*Tamias speciosus*	M	YNP	Morphology
220026	*Tamias speciosus*	M	YNP	Morphology
220027	*Tamias speciosus*	M	YNP	Morphology
220029	*Tamias speciosus*	M	YNP	Morphology
220055	*Tamias speciosus*	M	YNP	Morphology
220064	*Tamias speciosus*	M	YNP	Morphology
220066	*Tamias speciosus*	M	YNP	Isotopes, Morphology
220067	*Tamias speciosus*	M	YNP	Isotopes, Morphology
220070	*Tamias speciosus*	M	YNP	Isotopes, Morphology
222199	*Tamias alpinus*	M	YNP	Isotopes, Morphology
222200	*Tamias alpinus*	M	YNP	Isotopes, Morphology
222201	*Tamias alpinus*	M	YNP	Isotopes
222202	*Tamias alpinus*	M	YNP	Isotopes
222203	*Tamias alpinus*	M	YNP	Isotopes, Morphology
222207	*Tamias alpinus*	M	YNP	Isotopes
222208	*Tamias alpinus*	M	YNP	Isotopes

MVZ Number	Species	Era	Transect	Analyses
222209	*Tamias alpinus*	M	YNP	Isotopes
222210	*Tamias alpinus*	M	YNP	Isotopes
222211	*Tamias speciosus*	M	YNP	Isotopes, Morphology
222212	*Tamias speciosus*	M	YNP	Isotopes, Morphology
222216	*Tamias speciosus*	M	YNP	Isotopes, Morphology
222217	*Tamias speciosus*	M	YNP	Isotopes
222502	*Tamias speciosus*	M	SS	Morphology
222503	*Tamias speciosus*	M	SS	Morphology
222504	*Tamias speciosus*	M	SS	Morphology
222505	*Tamias speciosus*	M	SS	Morphology
222506	*Tamias speciosus*	M	SS	Morphology
222507	*Tamias speciosus*	M	SS	Morphology
222508	*Tamias speciosus*	M	SS	Morphology
222509	*Tamias speciosus*	M	SS	Morphology
222510	*Tamias speciosus*	M	SS	Morphology
222511	*Tamias speciosus*	M	SS	Morphology
222512	*Tamias speciosus*	M	SS	Morphology
222513	*Tamias speciosus*	M	SS	Morphology
222514	*Tamias speciosus*	M	SS	Morphology
222516	*Tamias speciosus*	M	SS	Morphology
222518	*Tamias speciosus*	M	SS	Morphology
222519	*Tamias speciosus*	M	SS	Morphology
222520	*Tamias speciosus*	M	SS	Morphology
222674	*Tamias speciosus*	M	SS	Morphology
222675	*Tamias speciosus*	M	SS	Morphology
222676	*Tamias speciosus*	M	SS	Morphology
222677	*Tamias speciosus*	M	SS	Morphology
222681	*Tamias speciosus*	M	SS	Morphology
222687	*Tamias speciosus*	M	SS	Morphology
222689	*Tamias speciosus*	M	SS	Morphology
223552	*Tamias speciosus*	M	SS	Morphology
223553	*Tamias speciosus*	M	SS	Morphology
223961	*Tamias speciosus*	M	SS	Morphology
223963	*Tamias speciosus*	M	SS	Morphology
223964	*Tamias speciosus*	M	SS	Morphology
223966	*Tamias speciosus*	M	SS	Morphology
223968	*Tamias speciosus*	M	SS	Morphology
223969	*Tamias speciosus*	M	SS	Morphology
223971	*Tamias speciosus*	M	SS	Morphology
223972	*Tamias speciosus*	M	SS	Morphology
224075	*Tamias alpinus*	M	SS	Morphology
224077	*Tamias alpinus*	M	SS	Morphology

MVZ Number	Species	Era	Transect	Analyses
224078	*Tamias alpinus*	M	SS	Morphology
224079	*Tamias speciosus*	M	SS	Morphology
224080	*Tamias speciosus*	M	SS	Morphology
224081	*Tamias speciosus*	M	SS	Morphology
224082	*Tamias speciosus*	M	SS	Morphology
224083	*Tamias speciosus*	M	SS	Morphology
224084	*Tamias speciosus*	M	SS	Morphology
224085	*Tamias speciosus*	M	SS	Morphology
224087	*Tamias speciosus*	M	SS	Morphology
224158	*Tamias speciosus*	M	YNP	Morphology
224159	*Tamias speciosus*	M	YNP	Morphology
224160	*Tamias speciosus*	M	SS	Morphology
224161	*Tamias speciosus*	M	SS	Morphology
224162	*Tamias speciosus*	M	SS	Morphology
224163	*Tamias speciosus*	M	SS	Morphology
224164	*Tamias speciosus*	M	YNP	Morphology
224165	*Tamias speciosus*	M	YNP	Morphology
224166	*Tamias speciosus*	M	YNP	Isotopes, Morphology
224167	*Tamias speciosus*	M	YNP	Isotopes, Morphology
224168	*Tamias speciosus*	M	YNP	Morphology
224169	*Tamias speciosus*	M	YNP	Morphology
224170	*Tamias speciosus*	M	YNP	Morphology
224171	*Tamias speciosus*	M	YNP	Morphology
224172	*Tamias speciosus*	M	YNP	Morphology
224173	*Tamias speciosus*	M	YNP	Morphology
224174	*Tamias speciosus*	M	YNP	Isotopes, Morphology
224175	*Tamias speciosus*	M	YNP	Morphology
224176	*Tamias speciosus*	M	YNP	Morphology
224177	*Tamias speciosus*	M	YNP	Morphology
224178	*Tamias speciosus*	M	YNP	Isotopes
224178	*Tamias speciosus*	M	YNP	Morphology
224179	*Tamias speciosus*	M	YNP	Isotopes
224179	*Tamias speciosus*	M	YNP	Morphology
224180	*Tamias speciosus*	M	YNP	Morphology
224181	*Tamias speciosus*	M	YNP	Morphology
224182	*Tamias speciosus*	M	YNP	Morphology
224183	*Tamias speciosus*	M	YNP	Isotopes
224183	*Tamias speciosus*	M	YNP	Morphology
224184	*Tamias speciosus*	M	YNP	Morphology
224185	*Tamias speciosus*	M	YNP	Isotopes
224185	*Tamias speciosus*	M	YNP	Morphology
224186	*Tamias speciosus*	M	YNP	Isotopes

MVZ Number	Species	Era	Transect	Analyses
224186	*Tamias speciosus*	M	YNP	Morphology
224187	*Tamias speciosus*	M	YNP	Morphology
224188	*Tamias speciosus*	M	YNP	Morphology
224189	*Tamias speciosus*	M	YNP	Morphology
224190	*Tamias speciosus*	M	YNP	Isotopes, Morphology
224191	*Tamias speciosus*	M	YNP	Morphology
224192	*Tamias speciosus*	M	YNP	Morphology
224193	*Tamias speciosus*	M	YNP	Morphology
224194	*Tamias speciosus*	M	YNP	Morphology
224195	*Tamias speciosus*	M	YNP	Morphology
224196	*Tamias speciosus*	M	YNP	Morphology
224197	*Tamias speciosus*	M	YNP	Isotopes, Morphology
224198	*Tamias speciosus*	M	YNP	Morphology
224199	*Tamias speciosus*	M	YNP	Isotopes, Morphology
224200	*Tamias speciosus*	M	YNP	Morphology
224202	*Tamias speciosus*	M	YNP	Morphology
224203	*Tamias speciosus*	M	YNP	Morphology
224204	*Tamias speciosus*	M	YNP	Morphology
224205	*Tamias speciosus*	M	YNP	Morphology
224206	*Tamias speciosus*	M	YNP	Morphology
224207	*Tamias speciosus*	M	YNP	Morphology
224209	*Tamias speciosus*	M	SS	Morphology
224210	*Tamias speciosus*	M	SS	Morphology
224211	*Tamias speciosus*	M	SS	Morphology
224212	*Tamias speciosus*	M	SS	Morphology
224213	*Tamias speciosus*	M	SS	Morphology
224214	*Tamias speciosus*	M	SS	Morphology
224215	*Tamias speciosus*	M	SS	Morphology
224216	*Tamias speciosus*	M	SS	Morphology
224217	*Tamias speciosus*	M	SS	Morphology
224218	*Tamias speciosus*	M	SS	Morphology
224219	*Tamias speciosus*	M	SS	Morphology
224220	*Tamias speciosus*	M	SS	Morphology
224221	*Tamias speciosus*	M	SS	Morphology
224222	*Tamias speciosus*	M	SS	Morphology
224223	*Tamias speciosus*	M	SS	Morphology
224224	*Tamias speciosus*	M	SS	Morphology
224225	*Tamias speciosus*	M	SS	Morphology
224226	*Tamias speciosus*	M	YNP	Morphology
224227	*Tamias speciosus*	M	YNP	Morphology
224228	*Tamias speciosus*	M	YNP	Morphology
224229	*Tamias speciosus*	M	YNP	Isotopes

MVZ Number	Species	Era	Transect	Analyses
224279	*Tamias speciosus*	M	SS	Morphology
224280	*Tamias speciosus*	M	SS	Morphology
224281	*Tamias speciosus*	M	SS	Morphology
224282	*Tamias speciosus*	M	SS	Morphology
224283	*Tamias speciosus*	M	SS	Morphology
224284	*Tamias speciosus*	M	SS	Morphology
224285	*Tamias speciosus*	M	SS	Morphology
224291	*Tamias speciosus*	M	SS	Morphology
224293	*Tamias speciosus*	M	SS	Morphology
224295	*Tamias speciosus*	M	SS	Morphology
224298	*Tamias speciosus*	M	SS	Morphology
224299	*Tamias speciosus*	M	SS	Morphology
224432	*Tamias speciosus*	M	SS	Morphology
224433	*Tamias speciosus*	M	SS	Morphology
224434	*Tamias speciosus*	M	SS	Morphology
224481	*Tamias alpinus*	M	SS	Morphology
224483	*Tamias alpinus*	M	SS	Morphology
224484	*Tamias alpinus*	M	SS	Morphology
224488	*Tamias speciosus*	M	SS	Morphology
224490	*Tamias speciosus*	M	SS	Morphology
224491	*Tamias speciosus*	M	SS	Morphology
224492	*Tamias speciosus*	M	SS	Morphology
224493	*Tamias speciosus*	M	SS	Morphology
224495	*Tamias speciosus*	M	SS	Morphology
224496	*Tamias speciosus*	M	SS	Morphology
224497	*Tamias speciosus*	M	SS	Morphology
224498	*Tamias speciosus*	M	SS	Morphology
224499	*Tamias speciosus*	M	SS	Morphology
224501	*Tamias speciosus*	M	SS	Morphology
224502	*Tamias alpinus*	M	SS	Morphology
225304	*Tamias alpinus*	M	SS	Morphology
225305	*Tamias alpinus*	M	SS	Morphology
225306	*Tamias alpinus*	M	SS	Morphology
225307	*Tamias alpinus*	M	SS	Morphology
225308	*Tamias alpinus*	M	SS	Morphology
225309	*Tamias alpinus*	M	SS	Morphology
225310	*Tamias speciosus*	M	SS	Morphology
225311	*Tamias speciosus*	M	SS	Morphology
225313	*Tamias speciosus*	M	SS	Morphology
225314	*Tamias speciosus*	M	SS	Morphology
225316	*Tamias speciosus*	M	SS	Morphology
225317	*Tamias speciosus*	M	SS	Morphology

MVZ Number	Species	Era	Transect	Analyses
225318	*Tamias speciosus*	M	SS	Morphology
225319	*Tamias speciosus*	M	SS	Morphology
225320	*Tamias speciosus*	M	SS	Morphology
225321	*Tamias speciosus*	M	SS	Morphology
225323	*Tamias speciosus*	M	SS	Morphology
225324	*Tamias speciosus*	M	SS	Morphology
225325	*Tamias speciosus*	M	SS	Morphology
225326	*Tamias speciosus*	M	SS	Morphology
226162	*Tamias alpinus*	M	SS	Morphology
226163	*Tamias alpinus*	M	SS	Morphology
228177	*Tamias alpinus*	M	SS	Morphology
228178	*Tamias alpinus*	M	SS	Morphology
228179	*Tamias alpinus*	M	SS	Morphology
228180	*Tamias alpinus*	M	SS	Morphology
228182	*Tamias alpinus*	M	SS	Morphology
228183	*Tamias alpinus*	M	SS	Morphology
228185	*Tamias alpinus*	M	SS	Morphology
228186	*Tamias alpinus*	M	SS	Morphology
228187	*Tamias alpinus*	M	SS	Morphology
228188	*Tamias alpinus*	M	SS	Morphology
228189	*Tamias alpinus*	M	SS	Morphology
228190	*Tamias alpinus*	M	SS	Morphology

Table A3: Results of genetic drift tests for morphological traits in the face and neurocranium regions of the skull. Numbers in the body of the table are Δ values (see Chapter 4 text for details), with values in bold indicating traits for which patterns of change rejected drift.

Trait	Region	*T. alpinus*		*T. speciosus*	
		Yosemite	Southern Sierras	Yosemite	Southern Sierras
EAM.ZYGO	Face	**0.1565**	**0.0250**	0.0001	0.0012
EZ.M1	Face	**0.1505**	**0.0193**	**0.0183**	0.0020
IS.NSL	Face	**0.3871**	**0.0191**	**0.1488**	**0.1080**
IS.PM	Face	**0.1061**	0.0002	0.0001	**0.0156**
IS.PNS	Face	**0.3421**	**0.0459**	0.0292	**0.0110**
MT.M1	Face	**0.0205**	**0.0796**	**0.0484**	0.0004
MT.PNS	Face	**0.0926**	0.0043	**0.0992**	**0.0168**
NA.PNS	Face	**0.1429**	0.0059	**0.0330**	*0.0001*
NFI.FIV	Face	**0.1361**	0.0084	**0.2475**	**0.1196**
NSL.NA	Face	**0.0484**	0.0062	**0.2135**	**0.0556**
NSL.ZI	Face	**0.1632**	**0.0297**	0.0400	0.0075
NSL.ZS	Face	**0.1240**	**0.0582**	**0.1300**	**0.0373**
PM.MT	Face	**0.1164**	**0.1526**	0.0010	*0.0001*
PM.ZI	Face	**0.0341**	**0.1057**	0.0093	0.0084
PM.ZS	Face	**0.1554**	**0.1478**	**0.0182**	**0.0281**
PT.ZYGO	Face	0.0007	0.0027	*0.0000*	0.0036
ZI.MT	Face	**0.0423**	**0.0346**	0.0008	**0.0229**
ZI.TSP	Face	**0.1040**	0.0074	**0.0554**	0.0006
ZI.ZYGO	Face	**0.0182**	0.0001	**0.0590**	0.0003
ZS.ZI	Face	**0.0770**	**0.0140**	**0.0129**	*0.0000*
ZYGO.TSP	Face	**0.1169**	0.0005	**0.0406**	0.0067
APET.BA	Neurocranium	**0.0795**	**0.0885**	**0.1361**	0.0020
APET.TS	Neurocranium	**0.0161**	**0.0593**	0.0067	0.0076
BA.EAM	Neurocranium	**0.1001**	**0.0374**	**0.1318**	0.0067
BA.OPI	Neurocranium	**0.0199**	**0.0296**	**0.0778**	**0.1236**
BR.APET	Neurocranium	0.0068	0.0099	0.0018	**0.0790**
BR.LD	Neurocranium	**0.3251**	**0.0158**	**0.0530**	0.0040
BR.PT	Neurocranium	**0.0732**	**0.0860**	0.0035	**0.0136**
JP.AS	Neurocranium	0.0047	**0.2107**	**0.0520**	**0.1168**
LD.AS	Neurocranium	**0.1534**	0.0006	0.0024	**0.0206**
NA.BR	Neurocranium	**0.0130**	0.0063	0.0002	**0.0577**
OPI.LD	Neurocranium	**0.0172**	0.0057	**0.0216**	**0.0503**
PNS.APET	Neurocranium	0.0013	**0.0902**	0.0066	**0.0447**
PT.APET	Neurocranium	**0.0322**	**0.0110**	0.0034	0.0009
PT.AS	Neurocranium	0.0069	**0.0158**	**0.0194**	**0.0412**

Trait	Region	*T. alpinus*		*T. speciosus*	
		Yosemite	Southern Sierras	Yosemite	Southern Sierras
PT.BA	Neurocranium	**0.0377**	**0.0373**	*0.0040*	0.0005
PT.EAM	Neurocranium	**0.0007**	**0.0047**	*0.0060*	0.0008
PT.TSP	Neurocranium, Face	**0.0633**	**0.0480**	*0.0001*	0.0049