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Behavioral Responses to Climate Change in Chipmunks of the Sierra Nevada

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of the Sierra Nevada

By

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Professor Eileen Lacey, Chair
Professor Wayne Sousa
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Abstract

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Anthropogenic climate change is drastically affecting the lives of animals across the planet, leading many of them to shift their ranges to higher latitudes or elevations. As their environments and habitats are modified, how individual organisms respond to novel conditions and situations will have critical implications for shaping population and species level responses to environmental change. Characterizing both individual behavioral responses to novelty and population-level patterns of demography and life history should provide us with important information elucidating the processes through which organisms are responding to climate change.

Chipmunks (Genus: *Tamias*) in the central Sierra Nevada Mountains of California provide an ideal system for exploring these themes. Over the past century, the alpine chipmunk (*T. alpinus)* has – in apparent response to changing environmental conditions -- experienced a significant upward contraction of its elevational range. In contrast, the partially sympatric lodgepole chipmunk (*T. speciosus*) has undergone no detectable change in elevational distribution during this period. As part of understanding these differences in response, it is critical to examine potential interspecific differences in behavioral response to novelty and to quantify population-level differences in demography that may contribute to the contrasting patterns of range response documented for these animals.

For my first chapter, I examine how individual responses to novelty may inform population-level responses to climate change. Two aspects of behavior that are often used to assess interactions with new environments are exploration and boldness, each of which is expected to influence adaptively important outcomes such as discovery of novel resources. These behavioral attributes may be influenced by degree of ecological specialization, with more specialized species typically thought to display a reduced tendency to interact with novel habitats. To test this prediction, I used open-field assays to compare exploratory behavior and boldness among free-living members of the two focal species of chipmunks. My analyses reveal that while individual *T. speciosus* tend to be bolder and to display greater overall activity than individual *T. alpinus*, measures of exploratory behavior do not differ between species. These findings have important implications for understanding reported differences in the elevational responses of these species to changing environmental conditions in the Sierra Nevada. More generally, these analyses underscore the

potential importance of individual-level differences in behavior in shaping higher-level patterns of response to environmental change.

For my second chapter, I examine how demographic traits vary between my two focal species, as a first step toward determining if such traits can explain population-level patterns of range shifts in response to climate change. Anthropogenic climate change is causing many species to shift their range in response to warming temperatures. However, the demographic mechanisms that drive these changes remain poorly understood. To test the prediction that species with contracting ranges will exhibit demographic vital rates associated with population decline, I analyzed the results of a multi-year mark recapture study of our two focal species. My analyses reveal that sex ratio and reproductive output vary little between species, while body condition varies significantly in both species across localities and capture years, and recapture rate differ significantly, with *T. alpinus* tending to have lower body condition and a lower likelihood to be captured from one year to the next. However, these analyses also reveal that much of the variation detected can be explained by local, site level effects. These results emphasize that in ecologically similar species, even subtle differences in local demographic response may drive long term population dynamics under environmental change.

For my third chapter, I provide the first characterization of the repeatability of individual behavioral responses to novelty in the two focal study species. Repeatability of behavioral responses, often referred to as animal "personality," is thought to be critical in allowing natural selection to shape these aspects of behavior. Accordingly, quantitative estimates of the repeatability offer important insights into the causes and consequences of individual variation in behavior. Using repeated testing of individual free-living alpine and lodgepole chipmunks, I assess the repeatability of the measures of exploration and boldness examined in Chapter 1 and I examine potential correlations between these behavioral responses to determine if, together, they represent a potential behavioral syndrome. Although sample sizes were limited due to the challenges of working with free-living animals, my analyses suggest that exploration is more repeatable than boldness. I found no significant correlation between these behavioral responses, suggesting that they are not linked as part of a single syndrome. Collectively, these findings raise important questions regarding the nature and implications of repeatability in individual behavioral responses to novelty.

Dedication

This dissertation is dedicated to my family, and to my ancestors. In all things, I hope to make those who came before me proud, while building a foundation for those who will come after me to thrive and flourish.

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Introduction

Climate change is having profound effects on ecosystems around the world (Walther *et al.* 2002). While we have extensive evidence of the effects of such change on the distributions of populations and species across the landscape, the mechanisms underlying these patterns remain poorly understood. A commonly observed pattern is for distributions to shift to higher elevations and latitudes (Walther *et al.* 2002; Chen *et al.* 2011; Lenoir and Svenning 2015). Therefore species living in high elevation, alpine environments may be at particular risk due to comparatively higher rates of warming (relative to sea level) as well reduced opportunities to continuing modifying their ranges as they reach to tops of mountains and mountaintop habitats become more scarce (Nogués-Bravo *et al.* 2007; Freeman *et al.* 2018). However, there is considerable heterogeneity in the direction, magnitude, and even the incidence of such range shifts (Mamantov *et al.* 2021), including significant variation in response among closely related species with similar life history attributes (Rubidge *et al.* 2011; Rowe *et al.* 2015).

Basic elements of a species biology that seem likely to affect response to environmental change are body condition, reproductive output, and survival – three critical aspects of an animal's life history that directly inform dynamics and trends at the population level (Sibly and Hone 2002). For cold-adapted, hibernating mammals in particular, climate change has been shown to have a myriad of effects on all of the aforementioned demographic factors (Wells *et al.* 2022). Warming temperatures can have positive effects on body condition and growth, reproductive output, and survival, particularly if warming leads to an increase in the length of the growing season and a net increase in primary production (Eastman *et al.* 2012). Altogether, these conditions can lead to increased survival and growing populations (Paniw *et al.* 2020). However, the lack of precipitation that often accompanies warming in high latitude or high elevation habitats can lead to decreases in vital rates, as decreased winter snowpack provides less insulation for hibernators and leads to drier, less productive active seasons (Sheriff *et al.* 2017). Therefore, while warming can lead to short term increases in vital rates, decreases in precipitation as well as disruptions to phenology may lead us to conclude that, over time, hibernating rodents will see overall negative effects on populations of hibernating mammals, as reflected in the critical demographic traits of growth, reproduction, and survival.

Behavioral traits allow animals to respond quickly to stimuli, including stimuli associated with rapid environmental change (Sih, Ferrari and Harris 2011; Wong and Candolin 2015). Particularly, how individuals behave in novel situations has critical implications for population- and species-level responses to environmental change (Sih, Ferrari and Harris 2011). Within species, individuals may vary in their expression of a number of behavioral traits that can affect how they navigate novel conditions, including differences in boldness and exploratory behavior (Dingemanse *et al.* 2002). Boldness is defined as an individual's propensity for risky behavior (Sloan Wilson *et al.* 1994) while exploration is defined as an individual's readiness to approach a novel object or environment (Réale *et al.* 2007). These behaviors are closely linked and occur within similar ecological contexts, with the result that they are often treated as a single covarying behavioral "syndrome" (Sih, Bell and Johnson 2004; Mazué, Dechaume-Moncharmont and Godin 2015). In a variety of animal taxa, conspecifics may differ in their latency to begin exploring a novel environment as well as in their use of the novel habitat (Wilson and Godin 2009b; Cote *et al.* 2010; Kudo *et al.* 2021). Crucially, a greater tendency to engage with novel surroundings has been shown to facilitate colonization of and initial survival in novel or altered habitats (Atwell *et al.* 2012; Liebl and Martin 2012).

Chipmunks (family Sciuridae; genus *Tamias)* are small-bodied, hibernating mammals that are widespread throughout North America and Eurasia, with their greatest diversity occurring in Western North America (Piaggio and Spicer 2001). The complex topography and diversity of habitats throughout this region, along with a long history of glacial dynamics, has led to complex patterns of diversification of this genus in this landscape (Rubidge, Patton and Moritz 2014). The alpine chipmunk *Tamias alpinus,* is an alpine specialist that is generally found above tree line. In contrast, the lodgepole chipmunk, *Tamias speciosus,* is more of a habitat generalist. In the central Sierra Nevada Mountains of California, the geographic distributions of these species are partially sympatric, with members of both species often co-occurring at the same locality and occupying overlapping home-ranges (Walsh 2015). Where they co-occurr, these species use somewhat different microhabitats, with *T. alpinus* tending to prefer exposed rocky environments and *T. speciosus* tending to occur in more forested, vegetative cover (Walsh 2015). *T. alpinus* is much more specialized for high elevation living than *T. speciosus*, with the former exhibiting a narrower dietary niche and more specialized cranial morphology (Walsh *et al.* 2016). Additional specializations to high elevations include adaptations to hypoxia (Bi *et al.* 2019) and more pronounced physiological responses to acute stress (Hammond, Palme and Lacey 2015), notably response to increased temperatures (Hammond, Palme and Lacey 2018a). Surveys of the central Sierra Nevada region conducted roughly a century apart indicate that *T. alpinus* has seen its altitudinal range decrease in size, with a significant upward contraction of its lower elevational range limit, while *T. speciosus*, has maintained a much larger proportion of its historical range (Rowe *et al.* 2015). The shrinking elevational range for *T. alpinus* has, in turn, led to population fragmentation and a loss of genetic diversity within its current geographic range, with no such changes in population genetic structure observed in *T. speciosus* (Rubidge *et al.* 2012). All together, these contrasts indicate that comparative studies of *T. alpinus* and *T. speciosus* provide an ideal opportunity to evaluate how differences in individual-level behavioral responses and population-level demographic attributes may drive differences in elevational range responses to changing climatic conditions.

Chapter 1: Individual differences in exploration and boldness may inform species-level responses to environmental change in montane chipmunks.

Kwasi Wrensford

Introduction

How individuals behave in novel situations has critical implications for population- and species-level responses to environmental change (Sih, Ferrari and Harris 2011). Within species, individuals may vary in their expression of a number of behavioral traits that can affect how they navigate novel conditions, including differences in boldness and exploratory behavior (Dingemanse *et al.* 2002). Boldness is defined as an individual's propensity for risky behavior (Sloan Wilson *et al.* 1994) while exploration is defined as an individual's readiness to approach a novel object or environment (Réale *et al.* 2007). These behaviors are closely linked and occur within similar ecological contexts, with the result that they are often treated as a single covarying behavioral "syndrome" (Sih, Bell and Johnson 2004; Mazué, Dechaume-Moncharmont and Godin 2015). In a variety of animal taxa, conspecifics may differ in their latency to begin exploring a novel environment as well as in their use of a novel habitat (Wilson and Godin 2009b; Cote *et al.* 2010; Kudo *et al.* 2021). Crucially, a greater tendency to engage with novel surroundings has been shown to facilitate colonization of and initial survival in novel or altered habitats (Atwell *et al.* 2012; Liebl and Martin 2012). Differences in both mean values for these behaviors and the extent to which they vary among individuals may play a significant role in shaping population- and species-level responses to novel environments (Breck *et al.* 2019), thereby contributing to the tendency for some taxa to be more resilient to environmental change, especially anthropogenic change.

Individual responses to novelty may also be influenced by a species' degree of ecological specialization (Ducatez, Clavel and Lefebvre 2015). Typically, more generalist species are expected to exploit a greater variety of ecological habitats, although they may not be the most competitive taxon in any one of the specific habitats that they occupy. In contrast, while more specialist species should occupy a narrower range of habitats, they are expected to be more effective at utilizing the habitats in which they occur (Levins 2020). Adaptation of specialists to a narrower range of extrinsic conditions may leave them more vulnerable to environmental change and, indeed, researchers have reported greater rates of extinction in specialists compared to generalists (Clavel, Julliard and Devictor 2011). The greater vulnerability of specialist species may in part reflect a more limited behavioral toolkit for responding to environmental change (Beever *et al.* 2017). Because natural selection has fine-tuned specialists to experience a relatively limited range of environmental conditions compared to generalists, members of specialist species may be less behaviorally flexible, including being less bold and less exploratory. However, despite the intuitive appeal of this prediction, few empirical studies have examined the relationship between degree of ecological specialization and tendency to explore novel conditions.

Chipmunks (genus *Tamias*) from the Sierra Nevada Mountains of California provide a compelling system in which to explore how individual variation in boldness and exploration shape population- and species-level responses to environmental conditions. In particular, comparative studies of alpine chipmunks (*T. alpinus*) and lodgepole chipmunks (*T. speciosus*) are generating important insights into how behavior, ecology, and physiology intersect to shape responses to changing environments. Although these species are partially sympatric in the northern Sierra Nevada, they vary markedly with respect to habitat use and degree of specialization. While *T. alpinus* is a high-elevation species that tends to occur in exposed, rocky habitats, *T. speciosus* is typically found in a variety of lower elevation, more forested habitats characterized by greater vegetative cover (Walsh 2015). Over the past century, *T. alpinus* has experienced a marked upward contraction of its elevational distribution (Moritz *et al.* 2008) that is associated with a pronounced loss of genetic diversity (Rubidge *et al.* 2012) as well as significant changes in diet and cranial morphology (Walsh *et al.* 2016). In comparison, *T. speciosus* has experienced no significant change in elevational distribution in the central Sierra Nevada (Rowe *et al.* 2015), population genetic structure, diet, or morphology over the same temporal period (Moritz *et al.* 2008; Rubidge *et al.* 2012; Walsh *et al.* 2016). On an individual level, analyses of fecal glucocorticoid metabolites indicate that *T. alpinus* is more physiologically responsive to acute stressors (Hammond, Palme and Lacey 2015) and displays higher baseline levels of glucocorticoid metabolites in hotter habitats than does *T. speciosus* (Hammond, Palme and Lacey 2018a). Collectively, this evidence suggests that *T. alpinus* is more ecologically specialized and more responsive to changes in environmental conditions than *T. speciosus* (Hammond, Palme and Lacey 2018b).

To test the hypothesis that ecological specialists are less likely to interact with novel habitats, we compared measures of exploratory behavior and boldness for free-living *T. alpinus* and *T. speciosus* from the Eastern Sierra Nevada Range of California. More specifically, we used open field trials, which are a commonly employed assay intended to characterize individual response to novel environments (Archer 1973; Walsh and Cummins 1976), to test the prediction that individual *T. alpinus* are less bold, less active, and less exploratory under experimental conditions than individual *T. speciosus*. To test the prediction that behavioral variability should be reduced in more specialist species, we also compared the variance in each behavioral metric examined, predicting that the more specialist *T. alpinus* will exhibit less variation in behavioral responses than generalist *T. speciosus.* These analyses add to our growing understanding of the biology of these taxa and generate new insights into potential relationships among ecological specialization, individual behavior, and species-level differences in response to environmental change. Because behavior is a critical mechanism through which animals respond to immediate conditions, these analyses also offer important insights into how behavioral differences between even closely related species may contribute to pronounced variation in response to changing environments.

Methods

Study Animals and Sites

Free-living alpine *(T. alpinus)* and lodgepole (*T. speciosus)* chipmunks were captured at 3 localities in Mono County, California, during July-August of 2019-2022 (Fig 2). Trapping sites were selected based on the reported occurrence of both species at each locality (Rowe *et al.* 2015). All animals were captured using Sherman traps baited with peanut butter, oats, and/or commercial birdseed. Traps were opened at dawn, checked approximately every 4–6 h, and closed at dusk. Upon first capture, each animal was uniquely marked by inserting a numbered metal ear tag (Monel 100S, National Band and Tag Company) into one pinna; beginning in 2020, each animal was also marked by inserting a PIT tag (Bio Medic Data Systems, Inc.) beneath the skin at the nape. Each individual captured was weighed, its sex determined, and standard external measurements (e.g., body length, tail length) were taken. We defined adults as individuals with scrotal testes or conspicuous (post-lactation) mammae (Loew 1999; Hammond, Palme and Lacey 2015; Lyons *et* *al.* 2017); in contrast, males that lacked abdominal testes and females that displayed no visible nipples were considered juveniles. Non-destructive tissue samples (a sliver of ear pinna) as well as fecal pellets and a sample of fleas were collected for use in ongoing studies of these animals. Upon completion of these procedures, individuals were released at the point of capture. All procedures involving live chipmunks conformed to the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes, Care and Mammalogists 2016) and had been approved by the Animal Care and Use Committee at the University of California, Berkeley.

Behavioral Assays

Free-living adult *T. alpinus* and *T. speciosus* captured during this study were used as subjects in open-field tests. Long used in laboratory settings, these tests are increasingly employed in field studies (Martin and Réale 2008). The arena used for open-field tests in this study consisted of a 1 x 1 x 1.22 m free-standing enclosure, the walls of which were constructed of heavy grade plastic sheeting supported by PVC tubing (Fig 3). Given the height of the walls and the inability of the animals to scale the plastic sheeting, the top of the arena was left open. One wall of the arena contained a ground-level opening just large enough to insert one of our live-traps, such that each test animal could move directly from a trap into the arena. A GoPro Hero 6 camera was positioned above the arena to digitally record activity anywhere on the arena floor.

Only adults that had already been captured and marked were used in open-field tests; use of recaptured animals minimized any potential confounds associated with the marking and tissue sample collection procedures (see above) applied to individuals captured for the first time. Adult chipmunks identified as recaptures (i.e., possessing an ear or PIT tag) were returned to the traps in which they had been caught for 5-20 min prior to participating in tests. To begin a test, the trap containing an animal was placed adjacent to the arena, with the door of the trap inserted through the opening at the base of one wall of the arena (Fig 3). The trap was opened, after which the animal was allowed to enter the arena of its own volition; recording began as soon as the trap was opened. Preliminary trials revealed that individuals typically entered the arena after just a few seconds; animals that had not yet entered the arena after 1 min were removed from the trap by tilting the trap vertically and placed in the arena. We recorded whether an individual entered the arena on its own or was prompted for our later analyses of boldness. Trials continued for a total of 10 min, after which the researcher redirected the focal individual back to the open trap, which was closed once the animal was inside; each individual was then released at the location at which it had been captured.

Quantifying Behavioral Responses

Digital recordings of open-field trials were analyzed using the observational software BORIS (Friard and Gamba 2016). A complete list of the behavioral metrics considered is given in Table 1. We focused our analyses on a subset of metrics that have been linked to boldness, activity, and exploration in previous studies of rodents. These measures included latency to enter the arena, which is thought to reflect boldness (Wilson, Godin and Ward 2010), and the proportion of time spent moving, which provides a measure of overall activity (Gould, Dao and Kovacsics 2009). To quantify exploratory behavior, we measured the proportion of time that each animal spent on the edge versus in the center of the arena, with the edge defined as being within one chipmunk body length of the walls of the arena (Fernandez et al 2004).

Statistical Analyses

All statistical analyses were conducted in the program R 4.1.1 (R Development Core Team, 2008). For our continuous behavioral data, we used the boxCox function in the MASS package in R to determine transformation parameters using maximum likelihood estimation (Hawkins and Weisberg 2017). We determined that, while Latency and Proportion of time spent on the edge of the arena did not require transformation, Proportion of time spent active was log-transformed. To provide an initial assessment of interspecific differences in response during open-field tests, we conducted two-sample comparisons of mean values for the three focal behaviors monitored (latency to enter, proportion of time moving, proportion of time on edge,). Parametric statistical tests were used unless the data failed to meet the associated assumptions of normality and homoscedasticity, in which case non-parametric tests were used.

To explore potential interspecific differences in response more fully, we also conducted a series of multivariate analyses. All models included species, sex, and capture locality as fixed effects. Sex was included because previous studies of boldness and exploration in closely related species have found sex differences in these focal behaviors (Montiglio *et al.* 2012); capture locality was included to assess potential inter-population differences in response during trials. Because latency to enter the arena consisted of time-to-event data that were truncated at an upper threshold of 60 seconds, we used a Cox proportional hazard model to analyze differences between the study species with regard to this behavioral response (Therneau 2015, 2022). In our Cox-proportional hazard models, we analyze latency to enter the arena as our response variable, but whether or not an individual entered the arena without prompting represented as a binary outcome. In contrast, potential interspecific differences in the other focal behaviors examined (proportion of time moving, proportion of time on the arena edge, total area used) were assessed using generalized linear models constructed in R. We used Q-Q plots to assess the distribution of our response variables before building models and used the fitdistr function in R to determine the appropriate distribution for our Generalized Linear Models when we detected deviations from normality. To determine if variability in responses differed between the study species, we performed a Bartlett's Test for equal variance. However, we found no statistically significant differences in mean variances between species ($P > 0.1$).

Results

A total of 45 open field trials were analyzed for this study. The *T. alpinus* ($N = 20$) used in these trials were captured at two different localities that were located approximately 4 kilometers apart; the *T. speciosus* ($N = 25$) used were captured at three different localities that were located at least 4 kilometers from each other. Additional information regarding the individuals included in our analyses are provided in Table 2.

Latency to enter arena

Across all trials, most individuals entered the arena in less than a minute, however 62.5 % of *T. alpinus* failed to enter during our experimental window, while only 28.5% of *T. speciosus* failed to enter during our experimental window. A two-sample Cox-proportional model found a significant difference between species in the probability of entering the arena, with *T. speciosus* tending to enter sooner than *T. alpinus* (P = 0.046; Figure 4). However, we found no significant difference between species in the likelihood of entering the arena before one minute had elapsed in our multivariate Cox Proportional Hazard analysis ($p > 0.1$), nor did we find a significant effect of the covariates of locality and sex.

Proportion of time in motion

While in the test arena, members of both study species engaged in a variety of locomotive behaviors, including walking, running, jumping, and attempting to climb the arena walls. When these measures of activity were pooled, the mean proportion of time active for *T. speciosus* (17.05 ± 0.176%) was significantly greater than that for *T. alpinus* (13.9 ± 0.235%; Mann-Whitney U test, U = 91, N = 45 $p < 0.05$; Fig. 4c). However, we found no statistical difference in variance between species (Levene's Test, $p > 0.1$). Consistent with this, species was a significant predictor of proportion of time active in a linear model that also included locality and sex ($P < 0.01$, Table 3).

Proportion of time on edge of arena

When not active during trials, members of both study species tended to position themselves against the edge of the arena, typically with their bodies in contact with the arena walls. On average, the proportion of time spent at the edge of the arena by *T. alpinus* (82.7 ± 29.1%) was greater than that for *T. speciosus* (69.7 ± 17.2 %); this difference was significant (Mann-Whitney U, U = 33, p = 0.016 ; Fig. 4b). However, we found no statistical difference in variance between species (Levene's Test, $p > 0.1$). Similarly, species was a significant predictor in a linear model that also included sex and locality ($p < 0.001$; Table 3).

Discussion

Our analyses indicate that some, but not all, behavioral responses monitored during open arena trials differed between our study species. We saw differences in the proportion of time spent on the edge of the arena which was significantly greater in *T. alpinus,* while the proportion of time active was significantly less. While on average *T. speciosus* tended to enter the arena more quickly than *T. alpinus,* and a two-sample Cox Proportional Hazards model showed this difference was statistically significant, this effect goes away in a multivariate analysis including locality and sex. Collectively, these findings suggest that *T. alpinus* interacts less with novel environments, an outcome that is consistent with predictions based on the greater ecological specialization of this species compared to *T. speciosus*. Across our behaviors, we saw little difference in behavioral variance between species. This could be due to the very large degree of variance in our data, where any difference would be difficult to detect. Overall, at least among chipmunks from the Sierra Nevada Mountains, the degree of ecological specialization appears to be a predictor of behavioral response to novel environmental conditions.

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Interspecific differences in activity

Our data reveal that during open arena trials, individual *T. speciosus* tended to be more active than individual *T. alpinus*. This finding is consistent with previous studies of these species indicating that although mean activity budgets are similar, *T. speciosus* displays much greater variability in daily activity (Hammond, Palme and Lacey 2018b). Measures of an individual's overall activity are thought to capture information regarding physiologically critical parameters such as energy expenditure and metabolism (Green *et al.* 2009). Studies of other rodent taxa (Careau *et al.* 2009;

Montiglio *et al.* 2010; Bergeron *et al.* 2013) as well as birds (Dingemanse *et al.* 2003; van Oers *et al.* 2004) and fish (Jones and Godin 2010) suggest that activity levels under novel or unfamiliar conditions tend to follow two distinct patterns: very active, neophilic individuals versus less active, neophobic animals. The functional significance of these differences in behavior remain poorly understood (Gharnit *et al.* 2020), with evidence indicating that both fast and slow types may confer adaptive advantages to individuals (Jones and Godin 2010; Bergeron *et al.* 2013). Future research on *T. alpinus* and *T. speciosus* should explore the contexts in which differences in activity occur to identify the conditions that favor one pattern over the other. Studies of such behavioral differences in free living animals – coupled with measures of physiological processes such as metabolic rate – should increase our understanding of the adaptive value of differences in activity in novel environments.

Interspecific differences in boldness and exploration

Our data indicate that *T. alpinus* tended to be slower to enter the arena and to spend a greater proportion of time on the arena edge compared to be *T. speciosus.* These findings suggest that, overall, members of the latter species tend to be bolder and more exploratory, an outcome that is consistent with predictions regarding interspecific differences in behavior based on the relative degree of ecological specialization displayed by our study taxa. Although we focused on just two potential measures of boldness and exploration (Wilson, Godin and Ward 2010), it seems likely that each of these terms reflects a suite of phenotypic traits that are associated with response to perceived risk and, indeed, some authors have argued that boldness and exploration should be treated as a single behavioral syndrome (Mazué, Dechaume-Moncharmont and Godin 2015). As with activity patterns, the adaptive value of differences in boldness-exploration may vary; while greater boldness-exploration has been shown to enhance survival in novel habitats in some species (Atwell *et al.* 2012), in others these tendencies are associated with less plastic responses to altered environmental conditions (Kudo *et al.* 2021). Accordingly, additional studies are required to understand how the adaptive significance of boldness-exploration outcomes vary across taxa and ecological contexts.

In additional to behavioral attributes, variation in boldness and exploration may be associated with physiological traits such as differences in activity of the hypothalamic pituitary adrenal (HPA) axis, the neuroendocrine pathway that modulates response to external stressors (Reeder and Kramer 2005). For example, studies of Eastern chipmunks indicate that bolder individuals show decreased HPA activity compared to less exploratory conspecifics (Montiglio *et al.* 2012). With regard to our study species, *T. speciosus* has been shown to have lower mean baseline levels of fGC metabolites compared to *T. alpinus* (Hammond, Palme and Lacey 2015, 2018a) suggesting that at the interspecific level, greater boldness and exploration are associated with downregulated HPA activity. Future analyses will explore these relationships at an intraspecific level to determine if individual-level variation in behavioral response to novel environments is accompanied by similar patterns of HPA activity. While researchers document sex differences in boldness and exploration in a variety of texa , we see no effect of sex on our focal behaviors. In addition to clarifying links between behavior and adaptively important physiological processes, these analyses should generate important insights into potential relationships between intra- and inter-specific level differences in response to novelty.

Ecological specialization and response to novelty

The range of environmental conditions to which a species is exposed may be an important determinant of how individuals respond to novel conditions. For species adapted to diverse environments, selection may have favored individuals that are relatively quick to engage with new settings compared to members of species that are adapted to a more limited suite of environmental conditions. For example, sympatric species of African striped mice (genus *Rhabdomys)* display clear variation in exploration profiles that appear to parallel the range of habitats in which they occur (Mackay and Pillay 2021). Species that are particularly adept at surviving in urban habitats tend to be ecological generalists (Miranda et al. 2013, Ducatez et al. 2018), with members of urban populations tending to be bolder, more neophilic, and quicker to explore than their rural conspecifics (Break et al. 2019, Evans et al. 2010, Atwell et al. 2012, Biondi et al. 2020). Our findings from Sierran chipmunks are generally consistent with this pattern, with the more ecologically diverse *T. speciosus* tending to be bolder and more exploratory than the more ecologically specialized *T. alpinus*. We expect, however, that characterizing species as either generalists or specialists is too simplistic to capture the full range of ecological factors contributing to differences in responses to novel environments.

Implications for Response to Environmental Change

Characterizing individual-level variation in phenotypic traits is critical to understanding population- and species-level responses to environmental change. Differences in individual responses – including differences in boldness and exploratory behavior – provide the foundation for natural selection to act. Over time, such selection may lead to the population- and species-level differences that are common targets for studies of response to environmental change (Miller *et al.* 2020). Individual-level differences in behavior may be particularly important, given that changes in behavior are often one of the first means by which animals can respond to changing conditions, with effects on behavior being evident before demographic or other impacts become apparent (Wong and Candolin 2015). A growing number of studies are revealing relationships between anthropogenic environmental change and behavior (Kearney, Shine and Porter 2009; Gaynor *et al.* 2018), including environmentally mediated differences in traits such as activity, boldness, and aggression (Zhao and Feng 2015). Such traits may, in turn, affect critical demographic and spatial outcomes such as expansion into novel habitats (Dingemanse *et al.* 2007) and changes in species' distributions (Walther *et al.* 2002). Much of our understanding of population and species level responses to environmental change relies on simplistic models where individual organisms are treated as identical, models that often fail to reliably describe species' biology (A. Lee-Yaw *et al.* 2022). Incorporating species traits, like behavior, may better equip our models to more accurately predict responses to environmental change (Angert *et al.* 2011). Therefore, studies of individual-level behavioral variation can serve as indicators of changing environmental conditions, while generating insights needed to understand and potentially predict population- and species-level responses to anthropogenic environmental change.

Table 1. Behaviors quantified during open arena trials involving free-living lodgepole and alpine chipmunks. Each behavior considered is defined. Point events refer to behaviors that occur in discrete units (e.g., a jump), while state events refer to behaviors that occur over a more extended period of time or reflect a state of being for the focal animal (e.g., locomotion).

Behavior	Point or State Event	Description
Locomotion	State	Proportion of time spent walking or running
Latency	State	Proportion of time spent in trap before whole body has entered the arena.
Jumping	Point	Using hind limbs to propel animal into the air
Grooming	State	Proportion of time spent grooming body.
Scanning	State	Proportion of time spent moving head while rest of body is immobile
Rearing	State	Proportion of time spent on hind legs.
Urinating/Defecating	Point	Defecation or urination event
Scratch	Point	Using front paws to scratch at walls or floor
Time along Edge	State	Proportion of time spent along the walls of the arena
Climbing	State	Proportion of time spent hanging on arena walls

Table 2. Samples sizes by population for the free-living lodgepole (*T. speciosus*) and alpine (*T. alpinus*) chipmunks included in this study. Only *T. speciosus* were captured at Arrowhead Lake.

	N *T. alpinus*	**N *T. speciosus***	***N Total***
Arrowhead Lake	0	10	10
Saddlebag Lake	15	10	25
20 Lakes Basin	5	5	10
Total	20	25	45

Table 3. Results of generalized linear models used to examine the effects of species on measures of boldness, exploration and activity in free-living lodgepole and alpine chipmunks. For each output variable, species, locality (population) and sex were included as fixed effects, and we report coefficient estimates, confidence intervals, and P values. For latency to enter the arena, we report the results of a Cox Proportional Hazards model, with time to enter the arena (in seconds) as the response variable, with a right-censored threshold of 60 seconds denoting how long individuals were given to enter the arena before being prompted by the researcher. For proportion of time spent active and proportion of time spent on the edge of the arena, we report the results of multivariate generalized linear models.

Latency to Enter the Arena (Cox Proportional Hazard Model)

Predictors	**Estimates**	**CI**	**p**
Species	1.16	0.12 – 11.22	0.899
Locality	0.35	0.04 – 2.84	0.328
Sex	0.48	0.14 – 1.63	0.241

Proportion of Time Spent on Arena Edge (Generalized Linear Model)

Predictors	**Estimates**	**CI**	**p**
Species	0.62	0.24 – 1.01	**0.003**
Locality	0.16	-0.19 – 0.51	0.355
Sex	0.12	-0.08 – 0.32	0.230

Activity: Proportion of Time Spent in Motion (Generalized Linear Model)

Predictors	**Estimates**	**CI**	**p**
Species	**0.22**	**0.08 – 0.36**	**0.003**
Locality	-0.16	-0.48 – 0.16	0.299
Sex	-0.07	-0.26 – 0.11	0.419

Figure Legends

Figure 1. Map of capture localities for the lodgepole and alpine chipmunks used in this study. (A) depicts the general location of these sites in California while (B) indicates the specific localities at which chipmunks were captured for use in open arena trials.

Figure 2. The experimental set up used to conduct open arena trials for free-living lodgepole and alpine chipmunks. **(**A) is a photo of the arena when setup for a trial. (B) is an image of the floor of the arena, with the entrance indicated; study subjects entered the arena from a Trap placed at an opening (entrance) in the bottom corner of one wall of the arena. Also indicated is the digital grid (0.25 by 2.35 m cell size) superimposed on images of the arena floor for data analysis.

Figure 3. Comparisons of behavioral responses of lodgepole and alpine chipmunks during open arena trials. Data on (A) latency to enter the arena, (B) proportion of time at the edge of the arena, and (C) proportion of time active are shown. Box plots depict mean, what, and what for each behavior. Sample sizes for all comparisons are 20 T. alpinus and 25 T. speciosus. Significant contrasts (Mann-Whitney U tests, $p < 0.05$) are indicated by asterisks.

Figure 4. Probability that an individual lodgepole (N = 25) or alpine (N = 20) chipmunk would enter the experimental arena as a function of time. Each animal was allowed up to one minute to enter the arena of its own volition. Curves for the two study species did not differ (stats, $p > 0.05$).

Figure 1.

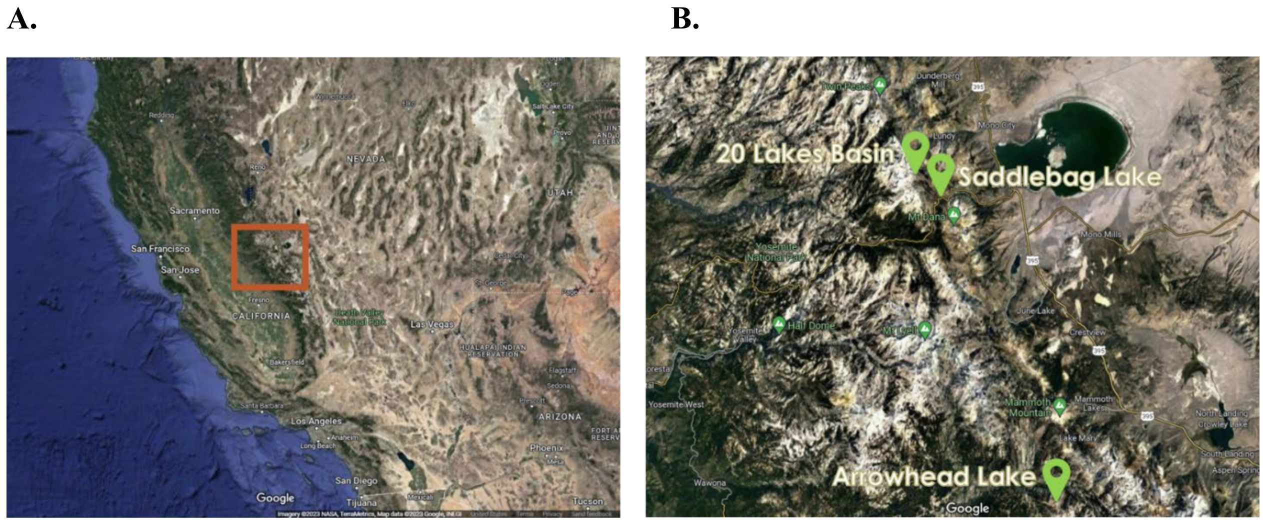

A.
B.
NEVADA
UTAH
Sacramento
San Francisco
San Jose
CALIFORNIA
Fresno
Las Vegas
Bakersfield
Los Angeles
San Diego
ARIZONA
Phoenix
Tucson
Google
20 Lakes Basin
Saddlebag Lake
Mono City
Yosemite National Park
Half Dome
June Lake
Mammoth Mountain
Arrowhead Lake
Google

Figure 2.

A.

B.

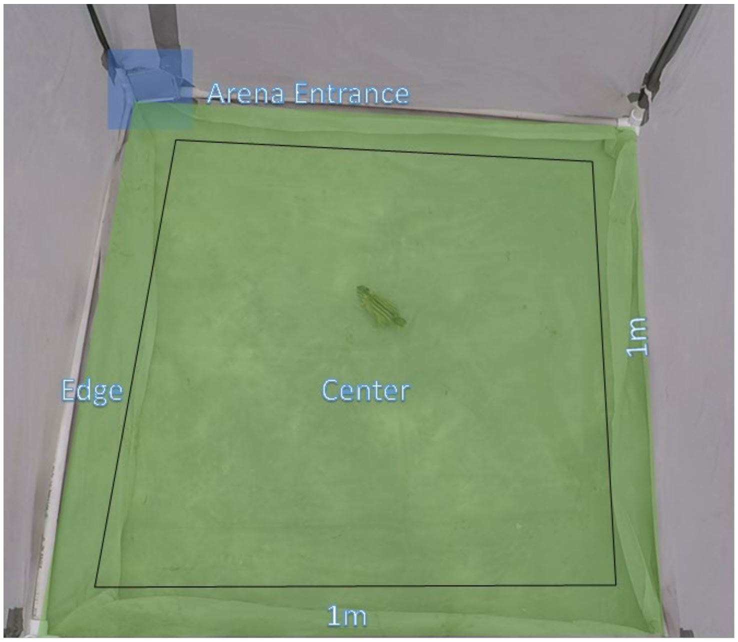


Figure 3. Plot of probability of an individual to enter the arena over time.

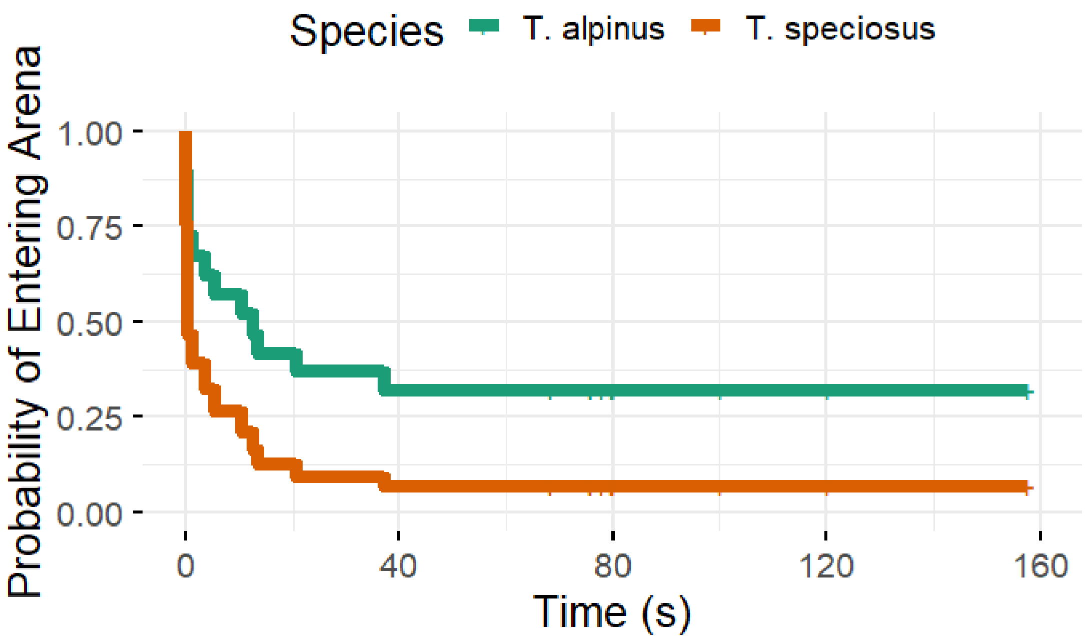
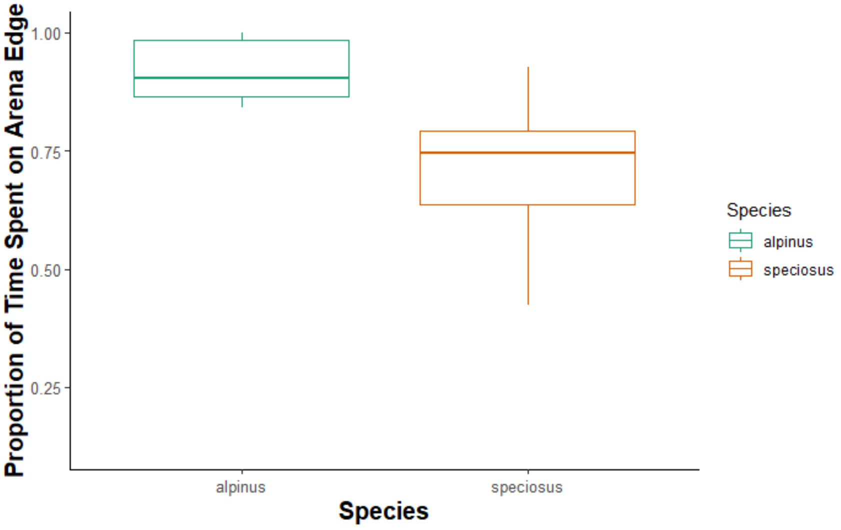
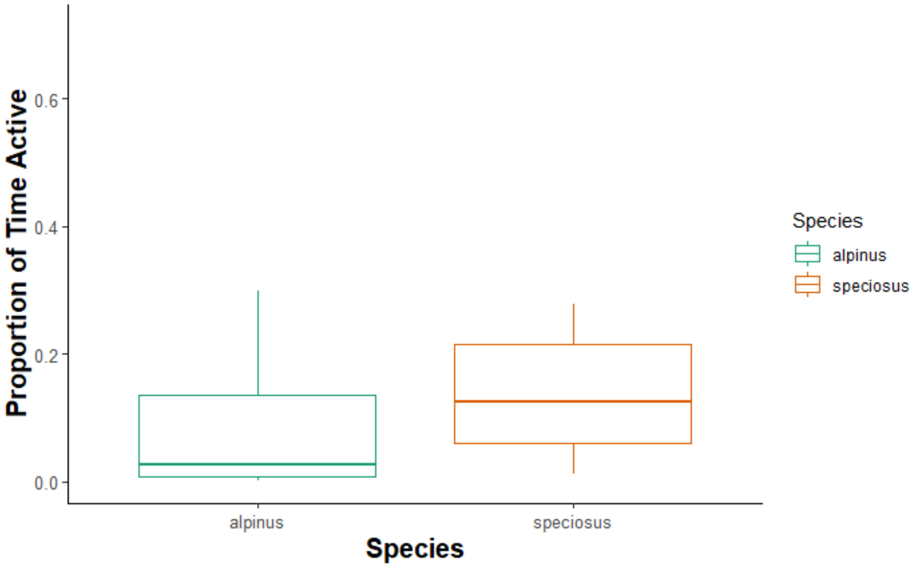


Figure 4. Boxplots of focal behaviors by species.

A. Exploration: Proportion of Time Spent on Edge of Arena



B. Activity: Proportion of Time Spent in Motion



Chapter 2: Inter- and intraspecific variation in demographic traits of co-occurring montane chipmunk species in Central Sierra of California, USA, with implications for their responses to global climate change

Kwasi Wrensford

Introduction

Anthropogenic climate change has drastically affected the lives of organisms across the planet (Parmesan and Yohe 2003). A commonly observed response among taxa is for their ranges to shift to higher elevations and latitudes (Walther *et al.* 2002; Chen *et al.* 2011; Lenoir and Svenning 2015), presumably tracking the abiotic and biotic conditions to which they are adapted. Species living in high elevation, alpine environments may be at particular risk due to comparatively higher rates of warming than sea level, as well as the reduced opportunity to shift their ranges as mountaintop habitats become more scarce (Nogués-Bravo *et al.* 2007; Freeman *et al.* 2018). However, there is considerable heterogeneity in the direction, magnitude, and even the incidence of such range shifts (Mamantov *et al.* 2021), including significant variation in response among closely related species with similar life history attributes (Rubidge *et al.* 2011; Rowe *et al.* 2015).

This variability in observed range shifts suggests responses to climate change are complex and likely to reflect multiple attributes of a species' demography and life history, and their interaction with environmental factors. Basic elements of a species biology that seem likely to affect such responses are body condition, reproductive output, and survival – three critical aspects of an animal's life history that directly inform dynamics and trends at the population level (Sibly and Hone 2002). For cold-adapted, hibernating mammals in particular, climate change has been shown to have a myriad of effects on all of the aforementioned demographic factors (Wells *et al.* 2022). Warming temperatures can have positive effects on body condition and growth, reproductive output, and survival, particularly if warming leads to an increase in the length of the growing season and a net increase in primary production (Eastman *et al.* 2012). This can lead to better foraging success and longer periods of time for foraging, leading to increased fat content and improved body condition (Haigh, O'Riordan and Butler 2012). Warming temperatures and longer growing seasons could also allow individuals to be better prepared for reproduction (Schwartz and Armitage 2005). Altogether, these conditions can lead to increased survival and growing populations (Paniw *et al.* 2020). However the lack of precipitation that often accompanies warming in high latitude or high elevation habitats can lead to decreases in vital rates, as decreased winter snowpack provides less insulation for hibernators and leads to drier, less productive active seasons (Sheriff *et al.* 2017). Researchers have observed long term body mass declines in high alpine species as a result of climate warming (Mason *et al.* 2014). Hibernating mammals also may be a uniquely at risk from climate change than non-hibernating species, as higher temperatures lead to shorter periods of dormancy and decreased overwinter survival (Turbill and Prior 2016). Therefore, while warming can lead to short term increases in vital rates, decreases in precipitation, as well as disruptions to phenology, lead us to conclude that, over time hibernating rodents will see overall negative effects to their populations, reflected in the critical demographic traits of growth, reproduction, and survival. Quantitative measurements of spatial and temporal variation in the density and demographics of species that are experiencing ongoing climate change provide an essential foundation for assessing and predicting the consequences of future environmental change.

Chipmunks (genus *Tamias*) from California's central Sierra Nevada mountains provide an important system to explore the role of demography in shaping interspecific differences in response to climate change (Rubidge *et al.* 2011). The alpine chipmunk *Tamias alpinus,* is a small alpine specialist generally found above tree line, and the larger habitat generalist lodgepole chipmunk, *Tamias speciosus,* overlaps in substantial portions of their distributions, with individuals of each species often co-occurring at the same locality and occupying overlapping home-ranges (Walsh 2015). When co-occurring, these two species use somewhat different microhabitats, with *T. alpinus* tending to prefer exposed rocky environments and *T. speciosus* tending to occur in more forested, vegetative cover (Walsh 2015). *T. alpinus* is much more specialized for high elevation living than *T. speciosus*, exhibiting a narrower dietary niche and more specialized cranial morphology (Walsh *et al.* 2016). While both species are omnivorous and show evidence of varied diets (Best, Clawson and Clawson 1994; Clawson, Clawson and Best 1994), stable isotope data from Walsh et al.,(year?) as well the observed contrast in microhabitat preference, may indicate that the relative abundance and availability of particular key foodstuffs, such as pine seeds, may differ significantly between species. A commonly observed pattern is that species with broader ecological niches tend to have larger geographic ranges (Slatyer, Hirst and Sexton 2013). Species with narrower niche breadths are also predicted to be more sensitive to climate change (Thuiller, Lavorel and Araújo 2005), while species with wide niche breadths are expected to be resilient to climate change (Schwartz *et al.* 2006). *T. alpinus'* adaptations for high elevation extend to the physical environment, exhibiting genetic adaptations to hypoxia (Bi *et al.* 2019), and more pronounced physiological responses to acute stress (Hammond, Palme and Lacey 2015) and environmental stressors in the form of increased temperatures than *T. speciosus* (Hammond, Palme and Lacey 2018a). Surveys of the central Sierra Nevada region conducted roughly a century apart indicate that *T. alpinus* has seen its overall altitudinal range decrease in size, with a significant upward contraction of its lower elevational range limit, while *T. speciosus*, has maintained a much larger proportion of its historical range (Rowe *et al.* 2015) (**Figure 1**). In other regions of its range, *T. speciosus* has seen contraction of its range, particularly in the sky-islands of the San Jacinto range in the south and in Lassen Volcanic National Park in the north, but its Central California Range has remained stable. *T. alpinus*'s shrinking elevational range has led to population fragmentation and a loss of genetic diversity across its current geographic range, with no such changes in population genetic structure observed in *T. speciosus* (Rubidge *et al.* 2012).

Although this suite of genotypic and phenotypic differences is well documented for populations of these species from the central Sierra Nevada, the role of potential interspecific differences in demography in generating the population responses has not been explored. As a first step toward assessing potential demographic factors contributing to interspecific differences in range response, we characterized populations of alpine and lodgepole chipmunks from the central Sierra Nevada Mountains with respect to three of the critical demographic traits outlined above, namely growth, reproduction, and survival. Specifically, we use live-trapping data collected over several field seasons as well as information from museum specimens to explore potential interspecific differences in demography and life history. Based on *T. speciosus's* more generalist ecology, broader dietary niche, and the fact it occupies a greater proportion of its historic elevational range, we predict that populations of this species will generally exhibit higher measures of body condition, survival and reproduction compared to the more ecologically specialized *T. alpinus.*

Our analyses provide the first detailed demographic information regarding potential population-level differences between these species, thereby adding critical information to our growing understanding of the biological attributes that contribute to the observed variation in elevational range responses for alpine and lodgepole chipmunks.

Methods

Study sites

Our three sites, Twenty Lakes Basin, Saddlebag Lake, and Arrowhead Lake, were in the Central Sierra Nevada Mountains in Inyo National Forest (**Figure 2**). These sites were chosen due to reported occurrences of both species (Rowe *et al.* 2015). Twenty Lakes Basin and Saddlebag Lake sites are located at opposite ends of the Saddlebag Lake reservoir. Saddlebag Lake site being an open mountainside with a mosaic of forest dominated by whitebark pine, alpine meadows consisting of grasses, sedges, a diversity of wildflowers and willows, talus slopes, and boulder fields. Twenty Lakes Basin is located within a glacial valley of the Hoover Wilderness Area, dotted with alpine ponds and lakes. While at only slightly higher elevation and with a similar floral community, the protection afforded by the three mountain slopes leads to a slightly more arid environment and more open habitat. Arrowhead Lake is located about 30 miles south of Saddlebag Reservoir, is at slightly lower elevation, and a much different environment characterized by a dense lodgepole and whitebark pine overstory, with a denser understory of herbaceous, riparian plants. These sites represent a region of overlap between our two focal species' elevational range, representing the trailing or "warm" edge of *T. alpinus's* range, and the leading "cool" edge of *T. speciosus's* range. This may have implications for population response to climate change, which we explore further in the discussion.

Study Animals and Trapping Approach

Free-living alpine *(Tamias alpinus)* and lodgepole (*T. speciosus)* chipmunks were captured at each study site during July-August of 2018-2021 (Figure 2). All animals were captured using Sherman traps baited with peanut butter and oats or commercial birdseed. At each site, we deployed 3 gridded trapping arrays covering approximately 400 m^2 each. Distance between grids varied based on site topography and accessibility, but each site had a minimum of 1200 m^2 of area trapped for chipmunks. Traps were opened at dawn, checked approximately every 4–6 h, and closed at dusk. Upon first capture, each animal was uniquely marked by inserting a PIT tag (Bio Medic Data Systems, Inc.) beneath the skin at the nape. Each individual captured was weighed, its sex was determined, and standard external measurements, including snout-vent body length, were taken. We defined adults as individuals with scrotal testes (males) or conspicuous (post-lactation) mammae (females) (Hammond, Palme and Lacey 2015); in contrast, males with abdominal testes and females that displayed no visible nipples were considered juveniles. Non-destructive tissue samples (a sliver of ear pinna) as well as fresh fecal material and fleas were collected for use in ongoing studies of these animals. Upon completion of these procedures, each individual was released at the point of capture. All procedures involving live chipmunks conformed to the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes, Care and Mammalogists 2016) and had been approved by the Animal Care and Use Committee at the University of California, Berkeley.

Museum Data on Reproductive Output

Although live-trapping data provided information regarding the frequency of reproductive females in our study populations, these data did not allow us to assess reproductive output (e.g., number of offspring produced) by members of each study species. To obtain data on reproductive output for each species, we looked at a series of museum specimens collected in Yosemite National Park and Inyo National Forest, the two management areas encompassing previous studies of these two species' range in the Central Sierra Nevada . For each specimen researchers collected reproductive data, along with body size and mass. To assess reproductive output, we used counts of placental scars, a common proxy to estimate litter size in mammals, and has been used successfully in multiple chipmunk species (Sheppard 1969). Information regarding the presence and number of placental scars detected for each female in this sample was obtained from the tag attached to each specimen. (See Appendix for list of specimens and their localities).

Body Condition

To examine potential interspecific differences in individual body condition, we analyzed the relationship between body mass and body length as a proxy for body composition and fat content, which are critical energetic factors for overwinter survival in hibernating mammals (Murie and Boag 1984). Numerous studies of small mammals have used the relationship between body mass and a measure of skeletal body size to estimate body condition (Schulte-Hostedde, Millar and Hickling 2001). For our study populations, measures of individual body mass and snout-vent (body) length were log-transformed, after which we calculated a species-specific Scaled Mass Index (SMI) score using the method outlined in Peig and Green (2009). For each species, the linear relationship between these log-transformed variables was assessed and the slope of the resulting relationships compared between species using a two-way ANOVA analyzing, species, log body length, and the interaction between the two to determine if there is interspecific variation in the relationship between body length and mass. Then, after calculating SMI for each species, we fit a series of ANOVAs for each species, that included capture year and locality as covariates.

Population Sex Ratio

One potentially important determinant of reproductive output is the ratio of adult males to females in a population. In eastern chipmunks, *Tamias striatus*, experimental removal of females from a population led to decreases in male presence in the population (Galloway and Boonstra 1989), implying, in chipmunks, greater female bias in populations leads to higher reproductive output and more viable populations. To analyze adult sex ratio, for each species and locality we determined the proportion of animals captured that were identified as male versus female. We then fit a logistic regression model to assess potential differences in the likelihood of an individual being male or female, with species, year, the interaction between the two, and locality as covariates.

Individual Reproductive Output

As indicated above, data on placental scars were used to estimate the number of offspring gestated by individual females of our study species collected from the study area. Females possessing scars were clearly reproductive adults during the year in which they were collected. Because both study species are highly seasonal breeders that typically produce only one litter of young per year (Best, Clawson and Clawson 1994; Clawson, Clawson and Best 1994), collection dates for specimens lacking scars were used to confirm that non-reproductive females were most likely young of the year that had not yet reached the age of reproductive maturity; these individuals were classified as juveniles for analyses of reproductive output. To assess the proportion of reproductive females present at each locality, we fit a logistic regression model to look at differences in the likelihood of a captured individual being an adult or juvenile, with species, locality, capture year, and the interaction between these variables as covariates. To examine potential differences in the number of young gestated by adult females of each species (i.e., females with placental scars), we fit a series of simple linear models to analyze the effect of species, locality, mass, and capture date on litter size.

Recapture Rates

Recapture of marked individuals from one year to the next is a standard method for estimating annual survival rates for small mammals (Nichols and Pollock 1983). To analyze recapture rates for our study species, we analyzed the percentage of individuals captured during a given field season that had also been captured during the previous year. The accuracy of these estimates depends upon the degree to which all members of a population are captured, particularly during the second in each pair of years. Although not all members of each species were captured at each locality, the same trapping procedure was employed during all years of the study, and we have no reason to expect that it was biased toward greater capture of one study species versus the other. The proportion of animals trapped during each field season that were recaptures from the previous year was examined in relation to species, sex, and localities using a multiple logistic regression.

Statistical Analyses

All statistical analyses were conducted in the program R 4.1.1 (R Development Core Team, 2008). For two sample comparisons, parametric statistical tests were used unless inspection of the data failed to meet the associated assumptions of normality and homoscedasticity, in which case non-parametric tests were used. For larger generalized linear models, we used gaussian distribution for normally distributed, continuous response variables, and binomial distributions for binary response variables. Throughout the text, means are reported ± 1 SD. All p-values are two-tailed unless indicated otherwise.

Results

From 2018 - 2022, we captured 220 individual lodgepole chipmunks (*T. speciosus*) and 71 individual alpine chipmunks (*T. alpinus*) over the course of 500 total trapping events representing 45 trapping days. For *T.* alpinus, average density was approximately 54 individuals/hectare at the Saddlebag Lake Site, and 10 individuals/hectare at Twenty Lakes Basin while average density for *T. speciosus* was approximately 117 individuals/hectare at Saddlebag Lake, 22 individuals per hectare at Twenty Lakes Basin, and 214 individuals/hectare at Arrowhead Lake. In general, there was no conspicuous change in density across successive years of the study, except for a large spike in the number of *T. speciosus* individuals captured at the Arrowhead Lake site in 2020 **(Fig 3)**.

Body Condition

In both species, body mass was significantly positively correlated with snout-vent length. However, that relationship had a much steeper slope in *T. speciosus* (R = 1.2678) than in *T. alpinus* (R = 0.4626) (**Figure 4**). A two way ANOVA with log body mass as a dependent variable, and log body length, species, and the interaction between the two as independent variables, revealed a non-significant trend between Species and body length (P = 0.0678), indicating a trend towards our species having different body length/mass relationships. With our computed Scaled Mass Index (SMI) scores, we found that in *T. alpinus,* mean SMI varied significantly across years at our

Saddlebag Lake site (One-way Anova; P = 0.018). With a Post-hoc pairwise Tukey HSD test, we were able to determine that most of the variation we observed was driven by larger SMI scores in 2022. In *T. speciosus,* we found that in 2019 and 2022, SMI was significantly greater at Arrowhead when compared to Saddlebag Lake (Welch's T Test; 2019 P = 0.05; 2022 P = 0.01). For the years 2021 and 2022, where we were able to compare across all three sites, we found significant differences between year (Tto-way ANOVA; P < 0.001) and Locality (P = 0.0107). Posthoc tests revealed that Arrowhead Lake chipmunks tended to have better body condition, and that 2022 yielded greater body conditions overall (**Figure 5**).

Individual Reproductive Output

Based on data collected from museum specimens, mean litter size for *T. speciosus* (4.05 ± 1.26) was /greater than that of *T. alpinus* (3.75 ± 1.34), although this difference was not statistically significant (P > 0.1) (**Fig 7**). The proportion of females identified as reproductive adults (i.e., had placental scars) did not differ between species; approximately 70% of female specimens from each species displayed placental scars. Data obtained from live trapping were similar in outcome, with no significant difference between species in proportion of reproductive females (P>0.1).

Population Sex Ratio

The ratio of adult females to males in our study populations ranged from 0.26 and 0.8. Consistent with these values, variation in adult sex ratios across years was greater in *T. alpinus* than in *T. speciosus*. We found no statistically significant effect of species on the mean population sex ratio (**Fig 6**) although a non-significant trend effect of year was detected (P = 0.0674) **Table 2**.

Population Age Structure

Although logistic regression revealed that populations of *T. speciosus* tended to have a larger proportion of juveniles in the population. (**Fig 8**), the difference between species was not statistically significant (P>0.05) (**Table 2**).

Recapture Analysis

From 2020-2022, only about 9% of all individuals were recaptured in two successive seasons indicating that overall recapture rates were low. Recapture rates appeared to vary across years. For example, during the 2021 field season, the overall recapture rate was 10% of all individuals; no *T. alpinus* individuals recaptured versus a 10% recapture rate for *T. speciosus*. In contrast, in 2022, the overall recapture rate was 28%, with species-specific recapture rates of 10% for *T. alpinus* and 32.5% for *T. speciosus* being recaptured. When examined as a function of species, approximately 9% of individual *T. speciosus* were recaptured in subsequent years, versus only 4.2% of individual *T. alpinus*. There was little sex difference in recapture rate, with 11.5% of females and 10% of males being recaptured in 2021, and 25% of females and 29% of males being recaptures in 2022. Our logistic multiple regression revealed that in both 2021 and 2022, species was not a significant predictor of recapture probability (P = 0.711; P = 0.8289 respectively), however in 2022, we found marginally significant effects of site (P = 0.057; **Table 3**)

Discussion

As a first step toward identifying the role of potential demographic and life-history differences in shaping elevational responses to environmental change, we compared several metrics of body condition, reproductive output, and survival for partially sympatric populations of alpine and lodgepole chipmunks from the central Sierra Nevada Mountains of California. Our analyses indicate that at these locations, population density tends to be greater for *T. speciosus* than for *T. alpinus*. Despite this difference in abundance and despite reported interspecific differences in elevational range change over the past century (Moritz et. Al. 2009), our analyses revealed few differences between species with respect to body condition, reproductive output, or recapture rate. Instead, the differences that were detected were explained primarily by year and site locality. Thus, based on this initial characterization of demographic and life history parameters, we find no evidence of pronounced differences between alpine and lodgepole chipmunks from the central Sierra.

We found that the relationship between body mass and body length (a proxy for body condition) differed significantly between the study species, with *T. speciosus* displaying a more positive relationship between these parameters. Although multiple factors may contribute to interspecific differences in mass-size relationships, this outcome is consistent with a tendency toward better body condition on *T. speciosus*, particularly among larger (longer) individuals. The slope of the relationship between log mass and log body length falls outside of the range of average relationship described in a review of mammalian mass/body length relationships (Frasier 2015). However, while interspecific patterns may conform to these patterns, intraspecific variation can disproportionately skew mass/body length relationships, particularly in smaller animals (Iskjaer *et al.* 1989). As measured here, body condition is thought to reflect the fat content of an individual, with higher mass to length ratios indicating fatter animals. Among hibernating alpine species, the degree of fat content an individual has is directly related to whether or not they will be able to survive the winter. In 2022, we saw an increase in body condition across all of our sites, which correlated with a significantly wetter year of precipitation the previous winter. This increased precipitation would have increased primary production, and potentially provided a greater degree of forage for the chipmunk populations Future studies of body condition in these species should analyze fat content and body composition more directly to explore the potential role of this variable in other elements of demography and life history, such as survival to the subsequent breeding season (Wells *et al.* 2019).

We found little evidence that reproductive output varied between the populations of alpine and lodgepole chipmunks sampled. More specifically, there was no difference in adult sex ratio between our two focal species, providing no evidence that the proportion of females in a population may contribute to differences in the number of young produced per year. Similarly, although there was some suggestion that populations of *T. speciosus* tend to have a smaller proportion of adults than populations of *T. alpinus*, this difference appeared to be driven largely by one population (Arrowhead Lake) during one year of the study. Thus, we did not find evidence of differences in population age structure (e.g., proportion of reproductive adults) that are expected to contribute to differences in reproductive output. Finally, comparison of data on litter sizes based on placental scar counts from museum specimens failed to reveal evidence of interspecific differences in gestational litter size. Although none of these measures provide direct counts of the individual- and population-level number of young produced per year, the proxies examined during this study fail to suggest that alpine and lodgepole chipmunks at our study sites are distinguished by potentially important differences in reproduction.

The final aspect of demography and life history that we considered was annual survival, as captured in data on the percentage of animals recaptured in successive field seasons. Recapture rates for *T. alpinus* tended to be lower than those for *T. speciosus*, suggesting that annual survival may also be lower for the former species. While more extensive analyses (e.g., longer term, with more extensive annual trapping efforts) are needed to confirm this pattern, decreased year to year survival by alpine chipmunks could reflect challenges associated with environmental conditions at the trailing edge of this species' current elevational distribution in the central Sierra Nevada Mountains. If, as has been proposed, populations of this species are shifting upwards to track the environmental conditions to which the animals are best adapted (Rowe *et al.* 2015) then it is logical to expect that populations at the current lower elevational limit are particularly challenged by environmental changes that have occurred. "Warm" range limits, defined as the boundary of a species' closest to the equator, or lowest in elevation, are governed by much more complex processes than cold limits, especially in regard to climate change (Cahill *et al.* 2014). However, while we have well documented evidence of the relationship between temperature and these range limits, the proximate mechanisms that reinforce these range boundaries remain poorly understood. Species that are able to shift their niche and cope with an altered habitat seem to show lower likelihood of extinction than species who disperse to new habitat (Román-Palacios and Wiens 2020). While additional research is needed to test this hypothesis, such an interspecific difference in annual survival would provide a compelling link between demography and environmentally mediated range change and how those factors may intersect to shape the differences in range response reported for our study species in the central Sierra Nevada.

Implications for Response to Environmental Change

Demographic traits like those analyzed in this study are the driving force behind population dynamics. Understanding how these dynamics interact with climate change is crucial to understanding how species will respond to global change yet their remain relatively few studies, especially in small mammals, that explicitly link climate and demography (Paniw *et al.* 2021). In our study species, historical and modern field survey efforts in the central Sierra Nevada have provided compelling evidence for climate-induced range shifts in *T. alpinus,* with no comparable change evident for *T. speciosus*. However, our initial characterizations of demographic and life history traits failed to reveal differences between these taxa. While our data should be considered preliminary, it is possible that the long-term changes in species elevational ranges are not the result of slow, gradual shifts in population vital rates but instead reflect other intermittent disruptions (e.g., abrupt destruction of habitat) that lead to drastic reductions in populations from which vulnerable species cannot recover. While demographic parameters have important consequences for patterns and rates of population persistence, how these variables interact with both gradual and abrupt patterns of environmental change is likely complex, suggesting that efforts to identify specific demographic contributors may be overly simplistic.

Table 1. Results of generalized linear models analyzing effect of species and other covariates on population sex ratio.

Sex Ratio

Predictors	**Estimate**	**Std. Error**	**Z value**	**P value**
Intercept	1.422e+03	6.465e+02	2.2	0.02782
Species	-1.352e+03	7.459e+02	-1.814	0.06971
Year	***-7.033-01***	***3.200e-01***	***-2.198***	***0.02795***
Locality	***-1.215e00***	***3.960e-01***	***-3.067***	***0.00216***
Saddlebag	3.815e-03	6.474e-01	0.006	0.99530
Species x Year	6.691e-01	3.692e-01	1.812	0.06991

Table 2. Results of generalized linear models analyzing effect of species and other covariates on population age structure.

Age Structure				
Predictors	**Estimate**	**Std. Error**	**Z value**	**P value**
Intercept	-609.4831	1009.5082	-0.604	0.5460
Species	1578.4225	1098.4570	1.437	0.1507
Year	0.3011	0.4996	0.603	0.5468
Saddlebag	***-1.1842***	***0.4874***	***-2.429***	***0.0151***
Twenty Lakes	-0.3536	0.7352	-0.481	0.6306
Species x Year	-0.7809	0.5436	-1.437	0.1508

Table 3. Results of logistic multiple regression analyzing recapture probability as a function of Species, Locality, and Sex in 2021 and 2022 respectively.

2021 Recapture Probability

Predictors	**Estimate**	**Std. Error**	**Z value**	**P value**
Intercept	-2.7579	1.15	-2.398	0.0165
Species	0.3788	1.0252	0.369	0.7118
Saddlebag	1.0762	0.8157	1.319	0.1870
Twenty Lakes	-15.1315	1489.6749	-0.10	0.9919
Sex	0.1414	0.7048	0.201	0.8410

2022 Recapture Probability

Predictors	**Estimate**	**Std. Error**	**Z value**	**P value**
Intercept	0.16899	1.12011	0.151	0.8801
Species	-0.21462	.99290	-0.216	0.8289
Saddlebag	*1.46727*	*0.77074*	*-1.904*	*0.0569*
Twenty Lakes	-17.67213	1975.37785	-0.009	0.9929
Sex	0.08113	0.73534	0.110	0.9122

Figure Legends

Figure 1. Comparison of the historic and modern elevational distributions of alpine (T. alpinus) and lodgepole (T. speciosus) chipmunks in the central Sierra Nevada Mountains of California, where these species are partially sympatric. As indicated, while T. alpinus has undergone a significant upward range expansion from historical to modern samples, the elevational distribution of T. speciosus has remained relatively unchanged (Moritz et al. 2008).

Figure 2. Map of capture localities for the lodgepole and alpine chipmunks used in this study. (A) depicts the general location of these sites in California while (B) indicates the specific localities at which chipmunks were captured for use in open arena trials.

Figure 3. Line plot of estimated population trends over the course of the study. Brown lines are speciosus, green lines represent alpinus, while solid lines represent Saddlebag locality, dashed lines represent Twenty Lakes Basin, and dot-dash lines represent Arrowhead lake.

Figure 4. Scatter plot of individual body mass and snout-vent body length. Trendlines for each species are displayed separately in this plot.

Figure 5. Box plotd of body condition by year and by site for A. *T. speciosus* and B. *T.* alpinus.

Figure 6. Histogram of litter sizes in museum specimen females.

Figure 7. Stacked box plots of sex ratio for each species across each capture year.

Figure 8. Stacked bar plots of age structure for each species across each capture year.

Figure 1.

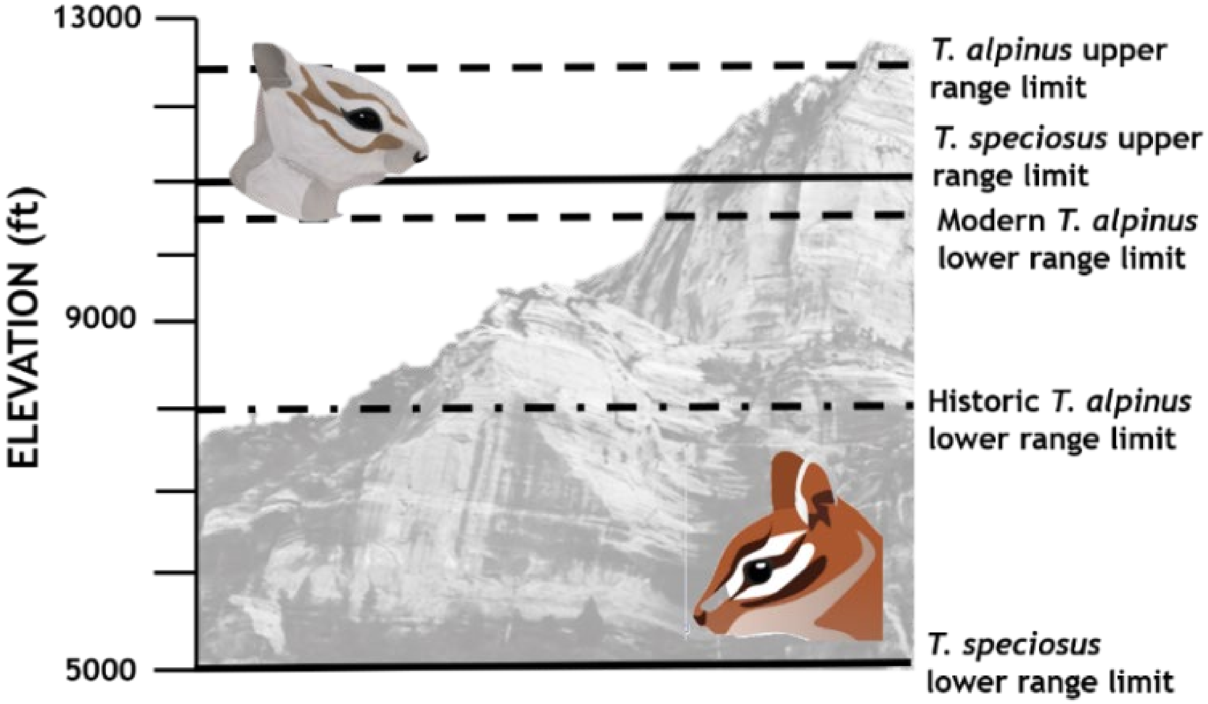
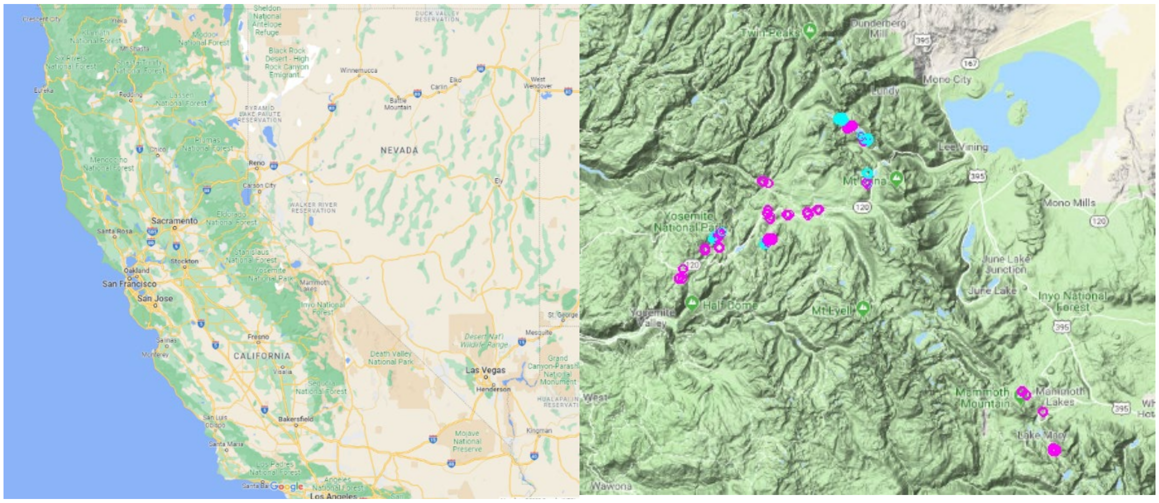
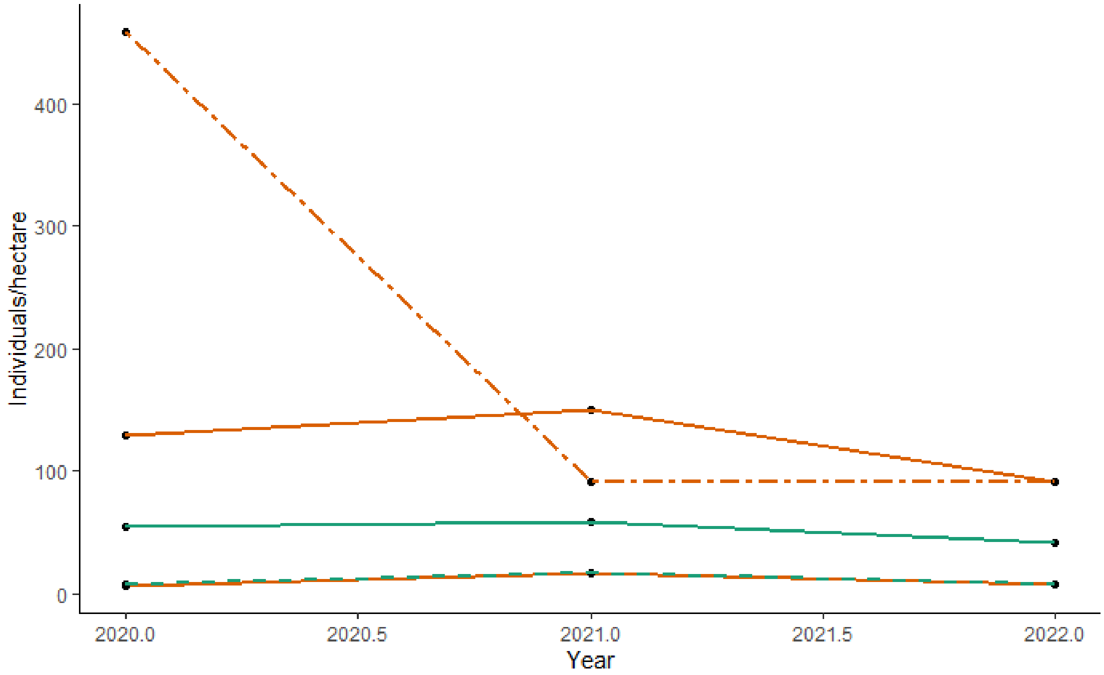

13000
9000
5000
ELEVATION (ft)
T. alpinus upper range limit
T. speciosus upper range limit
Modern T. alpinus lower range limit
Historic T. alpinus lower range limit
T. speciosus lower range limit

Figure 2.



Sacramento
San Francisco
Oakland
San Jose
Stockton
Reno
Carson City
Fresno
Bakersfield
NEVADA
CALIFORNIA
Las Vegas
Henderson
Death Valley National Park
Los Angeles
Twin Peaks
Dunderberg Mill
Mono City
Lundy
Lee Vining
Mt Dana
Mono Mills
Yosemite National Park
Yosemite Valley
Half Dome
Mt Lyell
June Lake Junction
June Lake
Inyo National Forest
Mammoth Mountain
Mammoth Lakes
Lake Mary
Wawona
120
395
167

Figure 3.


Individuals/hectare
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2021.0
2021.5
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Year

Fig. 4

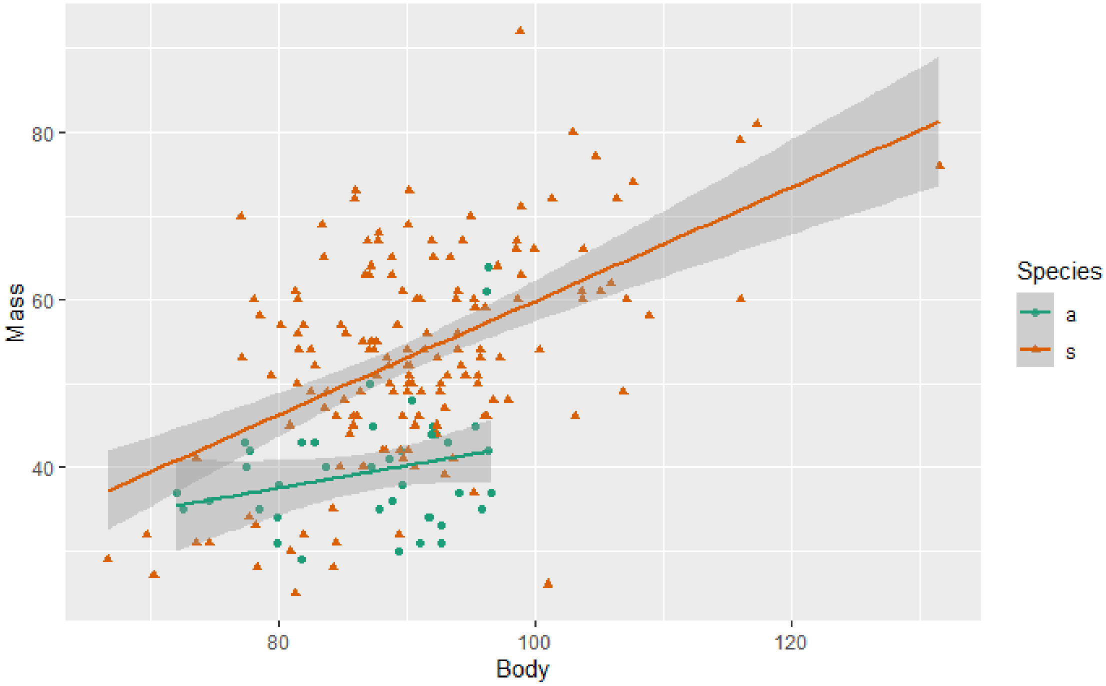
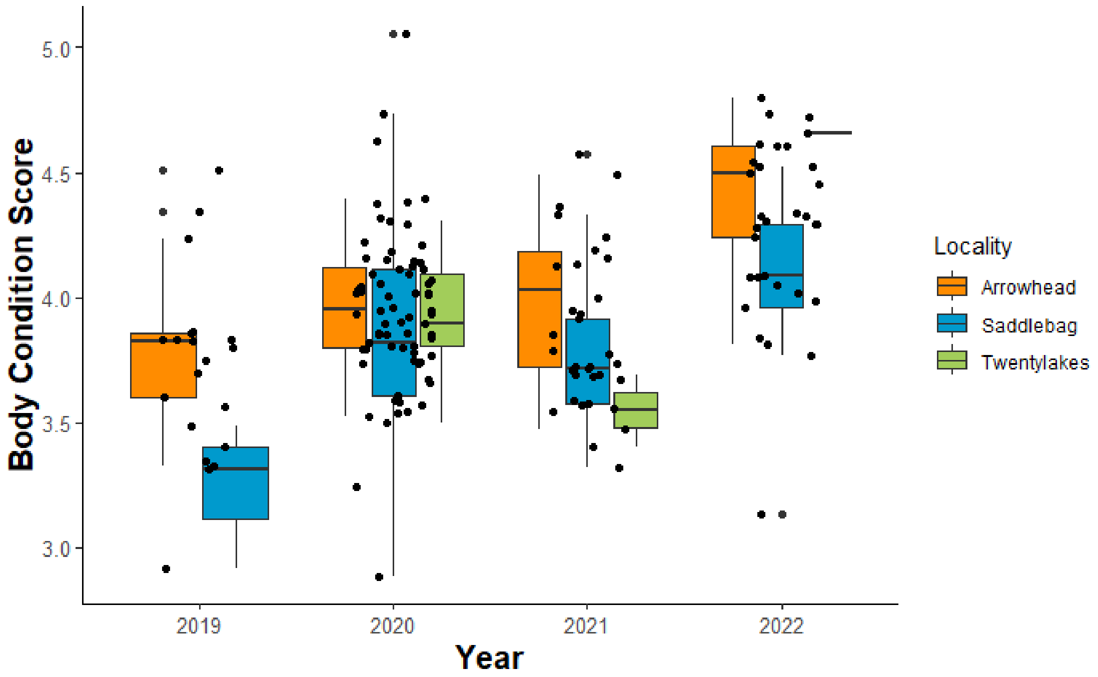


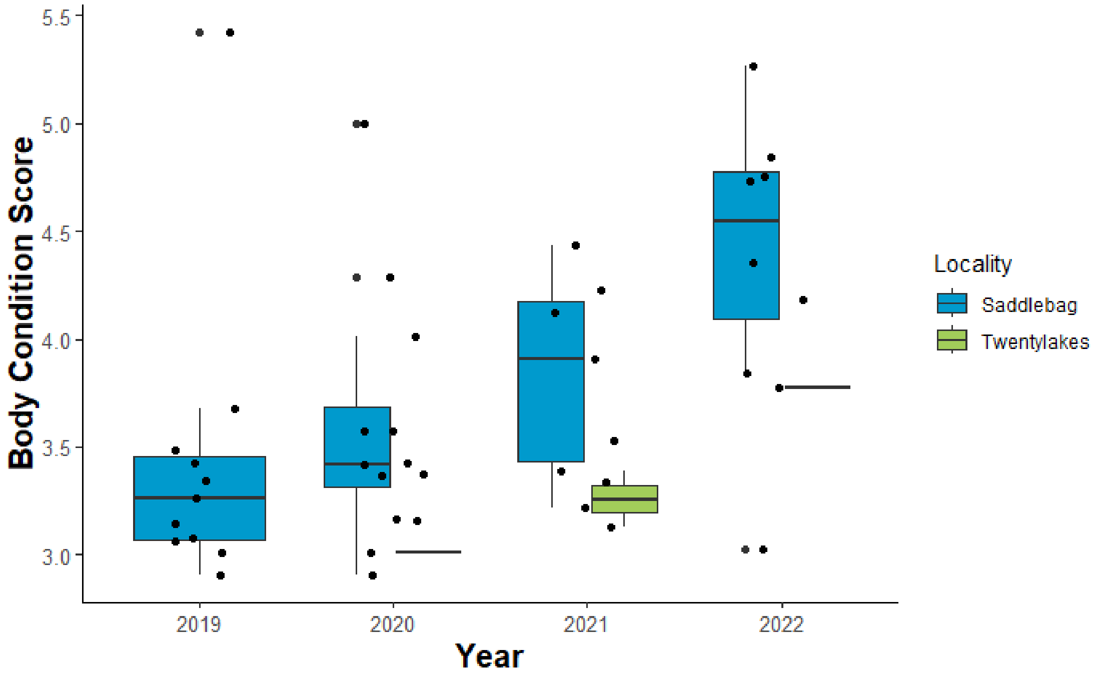
Figure 5.

A.



Body Condition Score
5.0
4.5
4.0
3.5
3.0
2019
2020
2021
2022
Year
Locality
Arrowhead
Saddlebag
Twentylakes

B.



Body Condition Score
5.5
5.0
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3.5
3.0
2019
2020
2021
2022
Year
Locality
Saddlebag
Twentylakes

Figure 6.

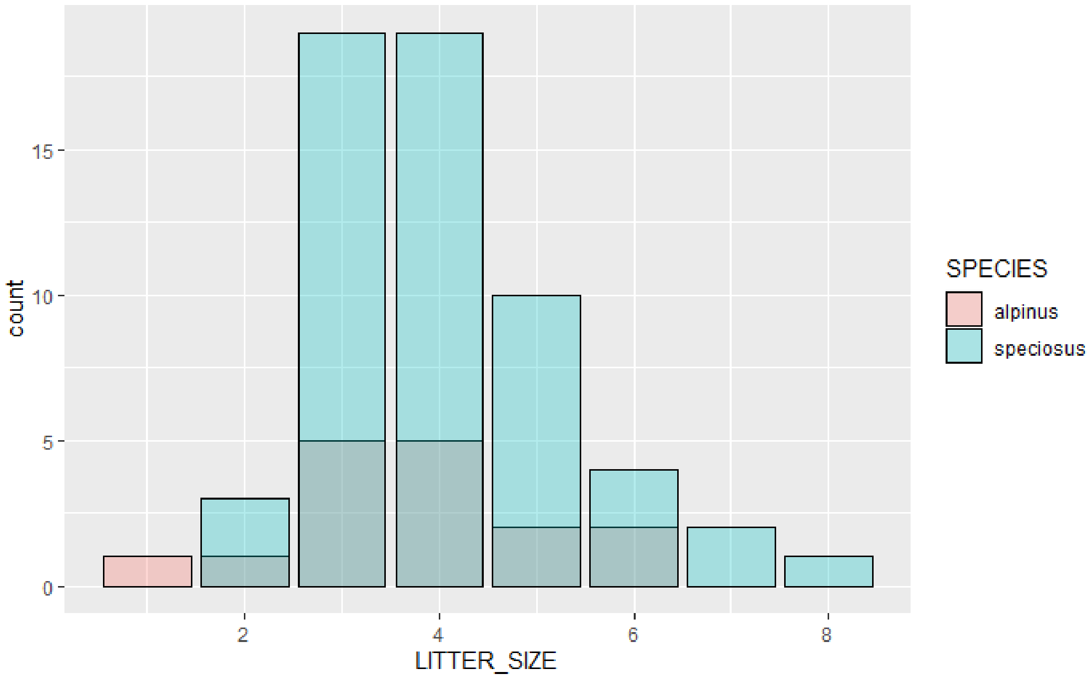

Figure 7

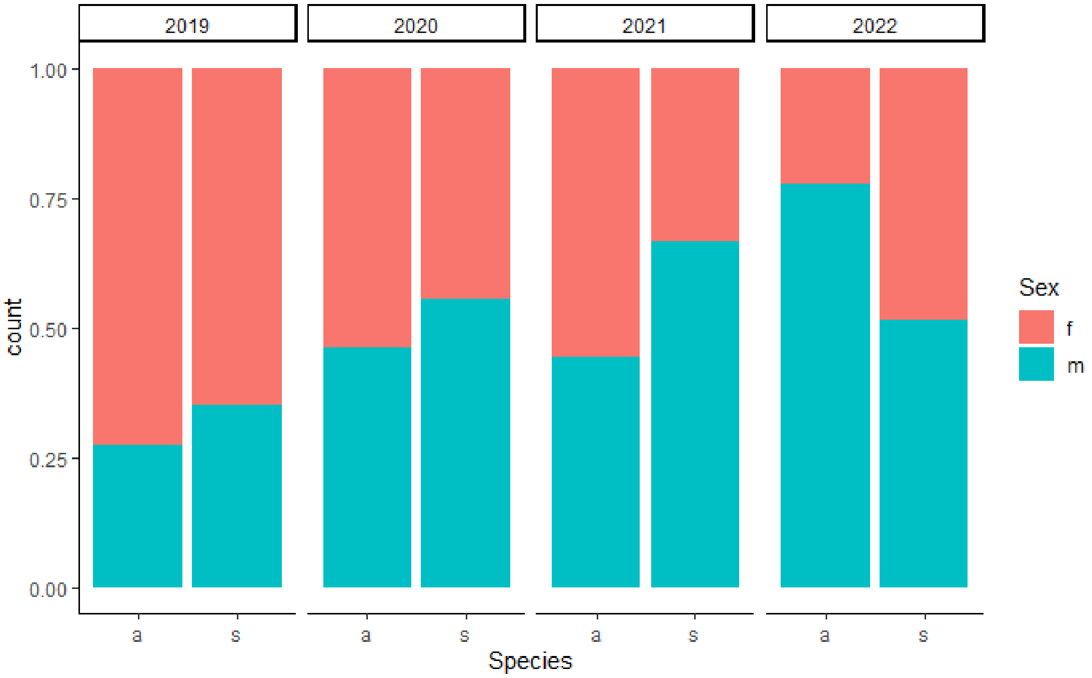
2019
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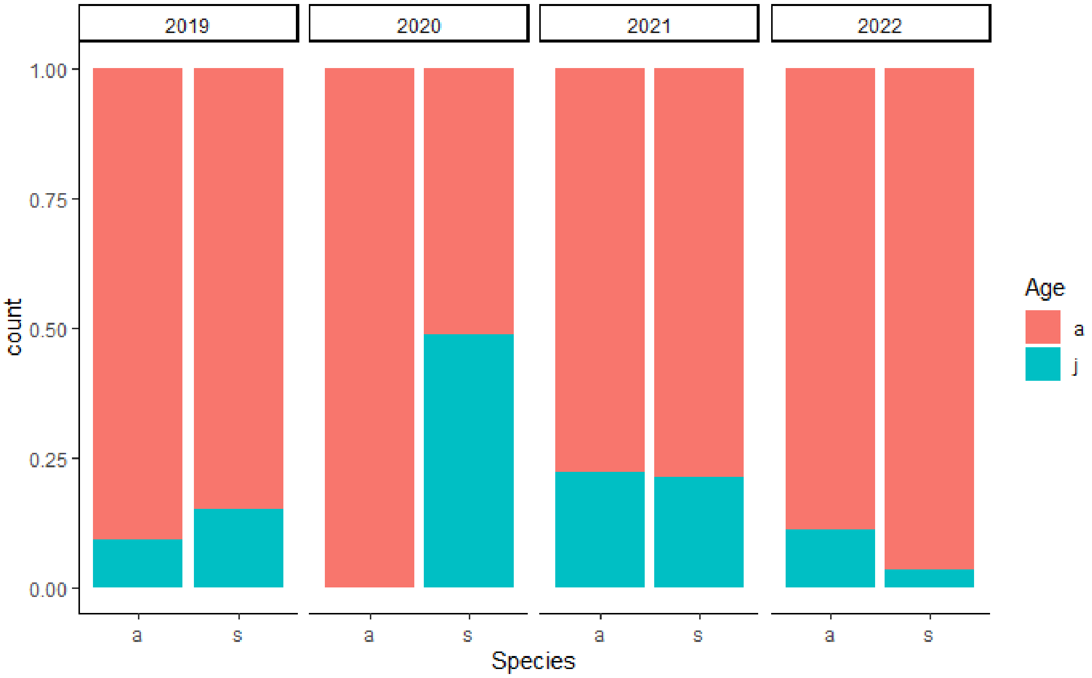
Figure 8.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Chapter 3: Repeatability and Covariance of Exploration and Boldness Behavior in Lodgepole Chipmunks

Kwasi Wrensford

Introduction

Behavioral traits allow animals to respond quickly to stimuli, including stimuli associated with changing environmental conditions (Wong and Candolin 2015). Evolutionary theory predicts that for selection to act on behavioral traits, those traits must be heritable and that individuals in a given environment will display consistency in said behavior – in other words, the behavior is "repeatable" (Dochtermann, Schwab and Sih 2015). Accordingly, behavioral biologists have investigated the consistency of an individual's patterns of behavior, also referred to as animal personality (Dall, Houston and McNamara 2004). Animal personality has been shown to have measurable effects on fitness (Dingemanse and Réale 2005). Like other phenotypic traits, individuals elements of animal personality, such as dispersal and aggression, or exploration and activity, may co-occur under similar conditions and contexts, defined as "behavioral syndromes" (Sih, Bell and Johnson 2004). These relationships between personality traits add further complexity in how selection may act on behavior. Data regarding the consistency or repeatability of personality traits can inform both our understanding of the mechanistic underpinnings (e.g., relative genetic versus environmental control) of behavioral responses and the potential for such responses to provide adaptive solutions to environmental challenges.

Two classes of behavior that have frequently been the focus of studies of personality are boldness and exploration. Boldness is defined as an individual's propensity for risky behavior (Sloan Wilson *et al.* 1994) while exploration is defined as an individual's readiness to approach a novel object or environment (Réale *et al.* 2007). These behaviors have been widely investigated among a diverse array of animal taxa (Dingemanse *et al.* 2002; Martin and Réale 2008; Wilson and Godin 2009a) and are relatively easy to quantify in either the field or laboratory, in a variety of assays such as open field and novel object tests. Within populations, researchers have observed a wide degree of variation in exploration and boldness phenotypes (Bergeron *et al.* 2013). These behaviors are thought to be particularly relevant for animals when responding to changing environmental conditions such as anthropogenic environmental change, as increased response to and engagement with novel resources may allow species to better survive in a changing environment (Cote *et al.* 2010; Atwell *et al.* 2012; Zhao and Feng 2015; Breck *et al.* 2019).

Expression of boldness and exploration are often closely linked and occur within similar ecological contexts. Boldness and exploration are thus often treated as a single co-varying behavioral syndrome (Sih, Bell and Johnson 2004; Mazué, Dechaume-Moncharmont and Godin 2015), underscoring expectations that not only are both traits repeatable on the individual level, but also that patterns of expressions covary within an individual as well. While there is evidence that these traits can covary as a single syndrome (Rodríguez-Prieto, Martín and Fernández-Juricic 2010), this is not the always the case (Clary *et al.* 2014; Kudo *et al.* 2021). Characterizing how patterns of expression differ in these traits should allow researchers to identify the different ecological and evolutionary pressures these behaviors are responding to, leading to improved understanding of how these traits are maintained in a population.

The lodgepole chipmunk (*Tamias speciosus*) from the central Sierra Nevada Mountains of California provide a compelling system in which to explore how individual variation in boldness and exploration shape population. *T. speciosus* is an elevational generalist, typically found in a variety of lower elevation, forested habitats characterized by denser vegetative cover (Walsh 2015). *T. speciosus* have limited physiological responses to acute stressors, showing limited HPA activity in response to being handled by researchers. They also show decreased physiological responses to environmental stress when compared to closely related congeners. In closely related eastern chipmunks, lower HPA activity was associated with greater rates of exploration (Montiglio *et al.* 2012). All this evidence tells us that *T. speciosus*, a habitat generalist, may show consistent and repeatable signs of exploratory and bold behavior.

With the rapidity at which climate change is projected to alter habitat (Parmesan and Yohe 2003), behavior is expected to play a significant role in species' responses to these changes (Beever *et al.* 2017). While the role of exploration and boldness has been explored in other contexts of environmental change, such as urbanization and species invasion, its role in climate change response remains poorly understood. In a previous study of exploration and boldness behavior, we found that during open arena trials, *T. speciosus* tends to be more active and more exploratory than s sympatric congener (Chapter 1). The same analyses suggest that measures of boldness and exploration are not highly correlated, raising the question of whether these traits form a behavioral syndrome in our focal taxa and creating an opportunity for different behavioral mechanisms and plasticity as well as variation in both selective pressures and adaptive consequences to shape exploration and boldness. To date, however, individual-level repeatability of boldness and exploration has not been assessed in lodgepole chipmunks. To address this gap, we quantified the responses of free-living lodgepole chipmunks during successive behavior trials to evaluate the repeatability of these behaviors and to determine if measures of boldness and exploration were correlated. These analyses provide the first information regarding individual repeatability of boldness and exploration in lodgepole chipmunks and should generate critical insights into the potential adaptive values of these behaviors as responses to environmental change., and their relationships.

Methods

Study Animals and Sites

Free-living lodgepole (*T. speciosus)* chipmunks were captured at 3 localities in Mono County, California, during July-August of 2019-2022. Trapping sites were selected based on the reported occurrence of lodgepole and alpine chipmunks at each locality (Rowe *et al.* 2015; Chapter 1); more detailed descriptions of these sites are provided in the Introduction and in Chapter 2. All animals were captured using Sherman traps baited with peanut butter, oats, and/or commercial birdseed. Traps were opened at dawn, checked approximately every 4–6 h, and closed at dusk.

Upon first capture, each animal was uniquely marked by inserting a numbered metal ear tag (Monel 100S, National Band and Tag Company) into one pinna; beginning in 2020, each animal was also marked by inserting a PIT tag (Bio Medic Data Systems, Inc.) beneath the skin at the nape. Each individual captured was weighed, its sex was determined, and standard external measurements (e.g., body length, tail length) were taken. We defined adults as individuals with scrotal testes or conspicuous (post-lactation) mammae (Loew 1999; Hammond, Palme and Lacey 2015; Lyons *et al.* 2017); in contrast, males that lacked abdominal testes and females that displayed no visible nipples were considered juveniles. Non-destructive tissue samples (a sliver of ear pinna) as well as fecal pellets and a sample of fleas were collected for use in ongoing studies of these animals. Upon completion of these procedures, individuals were released at the point of capture. Study sites were sampled continuously for five days, during which individuals may be captured multiple times. All procedures involving live chipmunks conformed to the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes, Care and Mammalogists 2016) and had been approved by the Animal Care and Use Committee at the University of California, Berkeley.

Open-field Tests

Free-living adult *T. speciosus* that had already been captured and marked during this study were used as subjects in open-field tests, which are a commonly employed assay to characterize individual responses to novel environments (Archer 1973; Walsh and Cummins 1976) (Martin and Réale 2008). We focused our analyses on this species and not *T. alpinus* due to the greater abundance and trappability of the former species (Chapter 2). Use of recaptured animals minimized any potential confounds associated with the marking and tissue sample collection procedures (see above) applied to individuals captured for the first time. The procedures used to conduct open-field tests are described in Chapter 1. In brief, the arena used for these tests consisted of a 1 x 1 x 1.22 m free-standing enclosure, the walls of which were constructed of heavy grade plastic sheeting supported by PVC tubing (Fig 1). Given the height of the walls and the inability of the animals to scale the plastic sheeting, the top of the arena was left open. One wall of the arena contained a ground-level opening just large enough to insert one of our live-traps, such that each test animal could move directly from a trap into the arena. A GoPro Hero 6 camera was positioned above the arena to record activity anywhere on the arena floor.

Adult chipmunks identified as recaptures (i.e., possessing an ear or PIT tag) were returned to the traps in which they had been caught for 5-20 min prior to participating in tests. To begin a test, the trap containing an animal was placed adjacent to the arena, with the door of the trap inserted through the opening at the base of one wall of the arena (Fig 3). The trap was opened, after which the animal was allowed to enter the arena of its own volition; recording began as soon as the trap was opened. Preliminary trials revealed that individuals typically entered the arena after just a few seconds; animals that had not yet entered the arena after 1 min were removed from the trap and placed in the arena. Trials continued for a total of 10 min, after which the researcher redirected the focal individual back to the open trap, which was closed once the animal was inside; each individual was then released at the location at which it had been captured.

Due to conducting these trials in free-living, live-trapped individuals, it was not possible to retest all individuals used in open arena trials and the identities of the animals that were retested were determined by the study subjects. Further, although we allowed a minimum of at least 24 hours before retesting an individual, we were unable to standardize time between behavioral trials. Accordingly, time between trials (in days) was included in our subsequent analyses of the repeatability of boldness and exploration.

Quantifying Behavioral Responses

Digital recordings of open-field trials were analyzed using the observational software BORIS (Friard and Gamba 2016). A complete list of the behavioral metrics considered is given in the methods of Chapter 1. We focused our analyses on a subset of these metrics that have been linked to boldness and exploration in previous studies of rodents. These measures included latency to enter the arena, which is thought to reflect boldness (Wilson, Godin and Ward 2010). For individuals that needed to be encouraged to enter the arena , latency to enter was scored as 60 seconds (Martin and Réale 2008). We also quantified the proportion of time that each animal spent on the edge versus in the center of the arena, which is thought to reflect exploration (Gould, Dao and Kovacsics 2009). We defined the edge as being within one chipmunk body length of the walls of the arena.

Statistical Analyses

All statistical analyses were conducted in R 4.1.1 (R Development Core Team, 2008). First, we estimated the repeatability of our two focal behavioral traits. Both traits were non-normally distributed, so we used non-parametric, two sample Pearson Rank-Sum correlation tests to assess R coefficients between values for boldness and exploration from first versus second open arena trials. Using a method described in Nakagawa and Cuthill, we then computed bootstrapped 95% confidence intervals from 1000 bootstraps to determine the statistical significance of our repeatability estimates (Nakagawa and Cuthill 2007).

To determine if measures of individual measures of exploration and boldness were correlated, we conducted a Spearman's Rank correlation test to determine if individual identity predicted the relationship between behavioral traits.

Results

A total of 25 lodgepole chipmunks were subjected to open field tests (Chapt 1). Of those individuals, 9 were tested a second time and are thus included in the analyses of repeatability reported here. The average time interval between trials was 2.1 ± 2.21 calendar days, with intervals ranging from 1-7 days (Table 1). The Arrowhead Lake site was overrepresented in our sample, with ~ 78% of individuals tested coming from that locality.

Individual Repeatability of Behavior

Individuals showed little consistency in latency to enter the arena from first trial to second trial (**Figure 2A**), Boldness behavior, measured as latency time in seconds to enter the arena, had a repeatability estimate (Spearman rank correlation coefficient *R*) of 0.19 across all individuals, indicating low rates of variation explained by individual identity; 95% confidence intervals based on 1000 bootstrap iterations indicated that this value was not statistically significant (CI = -0.7537 - 1.1306; P > 0.1). Exploration had an *R* of 0.310, indicating greater consistency between values for an animal's first and second trials, although this value also was not statistically significant (CI = -1.0913 - 0.4780; P > 0.1).

Correlation of Exploration and Boldness

When individual measures of boldness were compared to those for exploration, we found no significant relationship (Spearman's rank sum correlation test, r = 0.001, N = 9, P = 0.374) between these two measures of behavior. In other words, individuals with high scores for boldness did not consistently receive high scores for exploration and vice versa.

Discussion

Overall, while our measure of exploration tended to be more repeatable than our measure of boldness, neither of these repeatability scores were significant in our study animals. Further, we did not find a significant relationship between our measures of boldness and exploration, suggesting that these traits do not form a behavioral syndrome, decoupling two traditionally correlated behaviors. Low sample size limited our statistical power and thus we interpret these results cautiously; we propose future studies to assess further the potential for selection to act on these behaviors in our focal species. The difficulty in recapturing free-living individuals presents a particular challenge. Although lodgepole chipmunks tend to be more trappable than the sympatric alpine chipmunk (Chapter 2), it was still rare to capture an individual *T. speciosus* a second time and recapturing the same individual a third time to conduct repeatability analysis was even more difficult. Long term studies with well documented and sampled populations should allow more robust assessment of the repeatability of behavior in free-living chipmunks and other mammals. While not statistically significant, our repeatability score for exploration behavior ($R = 0.310$) is close to the average repeatability (0.37) of a variety of taxa reported in (Bell, Hankison and Laskowski 2009).

The repeatability of a trait is critical for determining the potential for selection to act on that trait. However, behavioral traits – particularly complex personality traits – often have a high degree of plasticity, both contextually and developmentally. In yellow-bellied marmots, boldness behavior was only observed as significantly repeatable in yearling marmots, not in juveniles or adults (Petelle *et al.* 2013). Repeated testing of behavior also carries with it the possibility individuals can habituate to experimental conditions. This may lead to an outcome where individuals, under experimental conditions, show little repeatability in a behavior as they habituate to experimental conditions. Both boldness and exploration describe responses to novelty and thus may be particularly subject to effects of habituation. Repeated testing of response to novelty may be difficult if individuals habituate to experimental conditions (Dingemanse *et al.* 2002), such that experimental conditions are no longer perceived as novel. For example, studies in the closely related Eastern chipmunk *Tamias striatus*, revealed that individuals rapidly habituate to repeated standardized tests of exploration (Martin and Réale 2008) and often do not respond to experimental conditions by the third test (Montiglio *et al.* 2010). Individual variation in habituation may yield important information about individual personality as well, as not all individuals may not habituate to behaviors at the same rate. Future analyses that can incorporate individual capture rates and that employ behavioral assays that do not require subsequent captures should improve our understanding of the repeatability of behavioral phenotypes.

Our study found no correlation between our measures of boldness and exploration. While this relationship is well studied in a variety of other taxa, there is increasing evidence that these behaviors may not be correlated in all contexts. Mosquitofish tend to be more exploratory and have higher dispersal tendencies in areas in which they have been introduced (compared to their native range) but show no relationship between invasiveness and boldness (Rehage and Sih 2004). There is also evidence that boldness and exploration may be regulated by different mechanisms. In Richardson's ground squirrels, individuals who were more vigilant when presented with a novel object showed elevated fecal glucocorticoid levels, while exploration was not related to glucocorticoid levels (Clary *et al.* 2014). The relationship between exploration and boldness may also vary over development. In convict cichlids, stress during early life can prevent the formation of a boldness/exploration syndrome (Hope *et al.* 2020). More systematic study of the relationships between these behaviors in a wider diversity of taxa can better inform the mechanisms underlying the relationship, or lack thereof, between boldness and exploration. Clarification of these supporting mechanisms may, in turn, lead to better understanding of when these behaviors should be correlated versus when they are more likely to function independently of one another.

With no evidence of significant repeatability, our findings raise the question of whether selection can act on our focal behaviors. For example, it is possible that these behaviors represent emergent outcomes of underlying cognitive or physiological mechanisms that are the actual targets of selection. In addition, plasticity may be playing a large role, with individuals modifying expression of behavior as environments and contexts change. Variation in plasticity can itself be adaptive, with the slope of change in a given variable across common contexts varying due to a combination of genetic and environmental factors (Dingemanse and Wolf 2013). While repeatability may tell us if a trait is expressed with enough consistency for selection to act, the strength of selection depends on the amount of variation present in the population. In other words, an individual may display significant repeatability in a trait but differ little from other individuals in its population, or an individual may show little consistency in personality, but still exhibit variation well outside of the mean of its population (Dochtermann and Royauté 2019). Therefore, putting individual repeatability of a trait in the context of the total variation of that trait within the population is an important consideration when exploring the potential for natural selection to act. For behaviors that involve response to novelty and have a high potential for plasticity and flexibility, ascertaining how selection may act on these traits is challenging and requires integration of data sets beyond just behavioral responses to repeated testing. Repeated measures of standardized behavioral assays across, rather than within, capture seasons may provide a more biologically relevant repeated measure of boldness and exploration, as has been demonstrated in eastern chipmunks (Gharnit *et al.* 2020). A larger sampling window could potentially provide more opportunities for capturing individuals, which would necessitate access to these hard-to-reach sites earlier in the active season. Going forward, researchers working across a diversity of taxa could employ standardized assays of exploration and boldness to assess inter and intraspecific variation in repeatability, as well as the incidence and prevalence of personality trait correlations and syndromes.

Table 1. Summary of individuals analyzed for this study and their capture history.

ID	*Locality*	*Species*	*Sex*	*Days Between Trials*
419	Arrowhead	s	m	1
435	Arrowhead	s	f	1
478	Arrowhead	s	m	2
497	Saddlebag	s	m	1
47511E6168	Arrowhead	s	f	1
475273455B	Arrowhead	s	m	1
47527A4D5E	Saddlebag	s	f	7
4754724B0C	Arrowhead	s	f	1
4753494663	Arrowhead	s	f	1

Figure Legends

Figure 1. A. Image of open field test arena deployed in the field. B. Diagram of open field test arena space.

Figure 2. Reaction norms of trait values of the first trial and second trial for A. Boldness, and B. Exploration.

Figure 1.

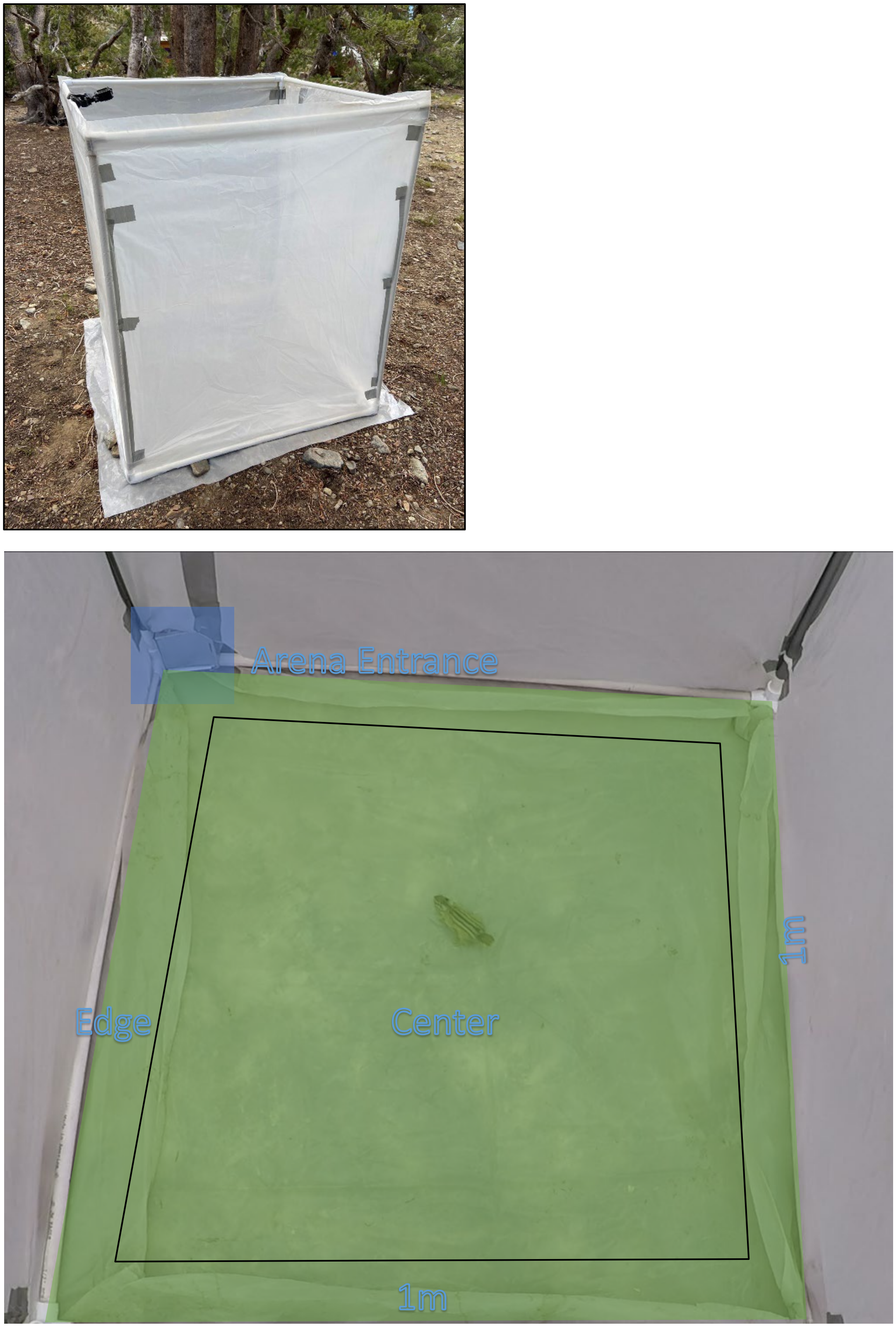
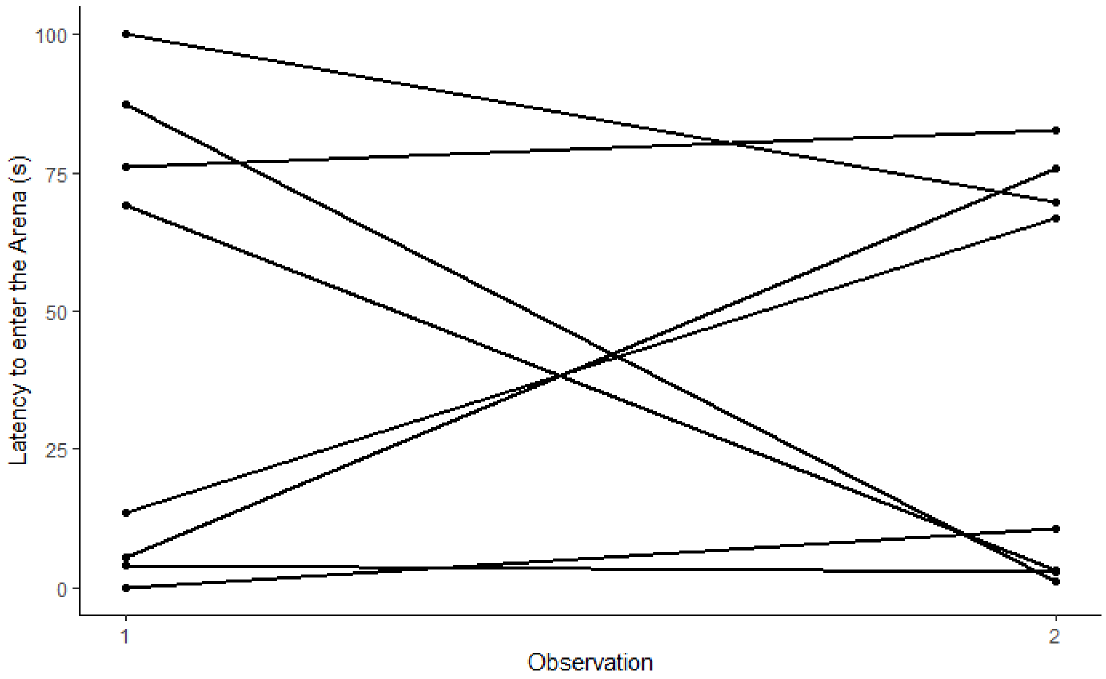


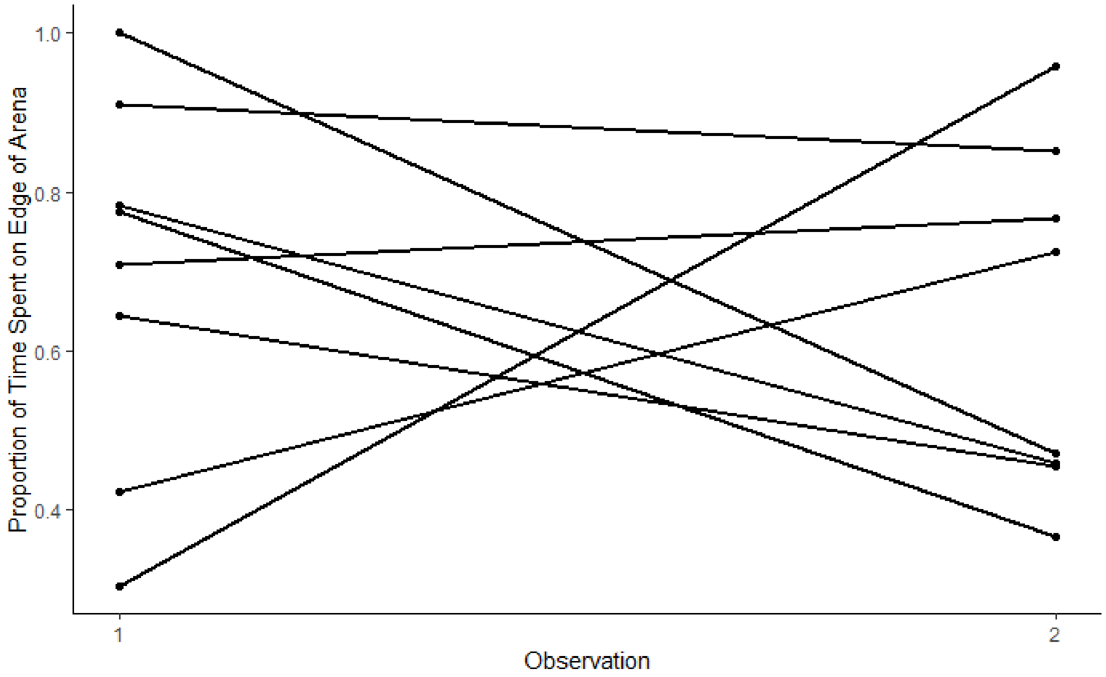
Figure 2.

A.



Latency to enter the Arena (s)
100
75
50
25
0
1
2
Observation

B.



Proportion of Time Spent on Edge of Arena
1.0
0.8
0.6
0.4
1
2
Observation

Conclusions

Lodgepole (*Tamias speciosus*) and alpine (*Tamias alpinus*) chipmunks from the Central Sierra Nevada Region of California exhibit significant differences in their exploration and boldness behavior. Individual repeatability of these behaviors was not statistically significant, most likely due to the limited number of individuals that could be tested more than once during this study. Expression of boldness and exploration was not correlated. Accordingly, in my study species, these behavioral traits do not appear to form a behavioral syndrome. Demographically, I found little difference between the study species with regard to key traits such as reproductive output and survival. Thus, despite clear species-level differences in response to climate change, this variation was not clearly associated with demographic patterns indicating population decline versus persistence.

When tested for the first time, individual *T. speciosus* tended to be more bold, more exploratory, and more active than individual *T. alpinus*. This outcome supports the hypothesis that the more generalist *T. speciosus* will more readily interact with novel stimuli than the specialist *T. alpinus*. These responses, however, were not significantly repeatable in the subset of *T. speciosus* that were tested more than once, raising important questions regarding the nature and necessity of demonstrating repeatability when working with free-living animals. It is likely that the lack of repeatability reflects the small sample size for these analyses, which was due to low rates of the recaptures necessary to conduct multiple behavioral assays on the same individual. If taken at face value, this lack of repeatability casts doubt on the ability of selection to act on the measures of boldness and exploration examined, in which case the clear and consistent interspecific differences in these behaviors detected are puzzling. Future studies of response to novelty response should vary the temporal window over which multiple behavioral tests are conducted as well as control for habituation and sampling bias.

The relationship between body length and body mass varied significantly between the study species, with *T. speciosus* tending to have a steeper positive slope to this relationship than *T. alpinus*. Scaled mass index body condition scores revealed that there was extensive local variation in body condition, as well as temporal variation from year to year. Reproductive output, calculated from museum specimens and estimated from population age structure, did not vary between species. While individual *T. speciosus* were on average more likely to be recaptured year-to-year than individual *T. alpinus*, these interspecific differences were not significant when study site was taken into account. These demographic traits, while fundamental to population dynamics that drive species distribution on the landscape, varied little between species undergoing markedly different changes in distribution in our study area, providing no clear indication of different demographic trajectories (e.g., decline versus persistence) between they study species. Future studies with longer term mark-recapture datasets can further elucidate these demographic patterns and thus provide better insights into the role of stochasticity in yielding large-scale population changes given minimal variation in key demographic parameters.

The findings in this dissertation serve as the first characterization of exploration and boldness behavior in the two species of chipmunks that are the focus of this work. They also provide the first characterization of the demographics of these species. Accordingly, these data raise important questions regarding the importance of individual behavioral variation and population-level demographic processes that should be explored in greater detail as part of future studies of these animals. Individual-, population-, and species-level responses to changing environmental conditions are complex and the results of my dissertation research underscore the likelihood that analyses of no one type of response will be sufficient to understand the large-scale changes in elevational distribution that initiated this line of inquiry.

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Appendices

Chapter 2 Appendix

Supplementary Table 1. A data table of the museum individuals included in the analysis of female reproductive output. All specimens are housed in UC Berkeley's Museum of Vertebrate Zoology. Identifying information for each specimen was collected from online specimen database Arctos, and reproductive information was then collected from physical specimen tags.

GUID	SCIENTIFIC_NAME	COUNTRY	STATE_PROV	SPEC_LOCALITY	VERBATIM_DATE	DEC_LAT	DEC_LONG	REPRODUCTIVE_DATA
MVZ:Mamm:201430	Tamias alpinus	United States	California	upper Lyell Canyon, Yosemite National Park	29-Jul-03	37.76807	-119.255	scars 1R-2L
MVZ:Mamm:207199	Tamias alpinus	United States	California	E end Fletcher Lake, Yosemite National Park	13-Jul-04	37.79778	-119.336	scars R1m K3
MVZ:Mamm:207203	Tamias alpinus	United States	California	Evelyn Lake, Yosemite National Park	16-Jul-04	37.80485	-119.328	scars R3, 1L
MVZ:Mamm:207204	Tamias alpinus	United States	California	Evelyn Lake, Yosemite National Park	16-Jul-04	37.80485	-119.328	scars R3, L3
MVZ:Mamm:207205	Tamias alpinus	United States	California	Evelyn Lake, Yosemite National Park	17-Jul-04	37.80485	-119.328	scars R3, L3
MVZ:Mamm:207206	Tamias alpinus	United States	California	Evelyn Lake, Yosemite National Park	18-Jul-04	37.80485	-119.328	scars R1, L2
MVZ:Mamm:207207	Tamias alpinus	United States	California	Evelyn Lake, Yosemite National Park	18-Jul-04	37.80485	-119.328	scars R2, L3
MVZ:Mamm:207208	Tamias alpinus	United States	California	Vogelsang Lake, Yosemite National Park	18-Jul-04	37.78769	-119.347	scars R2, L2

MVZ:Mamm:207209	Tamias alpinus	United States	California	Vogelsang Lake, Yosemite National Park	18-Jul-04	37.78769	-119.347	scars
MVZ:Mamm:207210	Tamias alpinus	United States	California	Vogelsang Lake, Yosemite National Park	18-Jul-04	37.78769	-119.347	scars
MVZ:Mamm:207211	Tamias alpinus	United States	California	Vogelsang Lake, Yosemite National Park	18-Jul-04	37.78769	-119.347	scars
MVZ:Mamm:216270	Tamias alpinus	United States	California	Upper Lyell Canyon, Yosemite National Park	########	37.76807	-119.255	scars 2R, 2L
MVZ:Mamm:216271	Tamias alpinus	United States	California	Upper Return Creek, Virginia Canyon, Yosemite National Park	24-Jul-05	38.06129	-119.339	parais
MVZ:Mamm:217185	Tamias alpinus	United States	California	upper Lyell Canyon, Yosemite National Park	########	37.76458	-119.252	nulliparous
MVZ:Mamm:217186	Tamias alpinus	United States	California	upper Lyell Canyon, Yosemite National Park	########	37.76807	-119.255	nulliparous
MVZ:Mamm:217187	Tamias alpinus	United States	California	upper Lyell Canyon, Yosemite National Park	########	37.75675	-119.259	
MVZ:Mamm:217188	Tamias alpinus	United States	California	upper Lyell Canyon, Yosemite National Park	########	37.75675	-119.259	

MVZ:Mamm:217180	Tamias alpinus	United States	California	upper Lyell Canyon, Yosemite National Park	########	37.76458	-119.252	nulliparous
MVZ:Mamm:217181	Tamias alpinus	United States	California	upper Lyell Canyon, Yosemite National Park	########	37.76458	-119.252	scars 2R-3L
MVZ:Mamm:217183	Tamias alpinus	United States	California	upper Lyell Canyon, Yosemite National Park	########	37.76458	-119.252	nulliparous
MVZ:Mamm:219990	Tamias alpinus	United States	California	Upper Cathedral Lake, Yosemite National Park	21-Jul-07	37.84117	-119.412	
MVZ:Mamm:219991	Tamias alpinus	United States	California	Upper Cathedral Lake, Yosemite National Park	21-Jul-07	37.84117	-119.412	scars 3R-0L; post lact
MVZ:Mamm:219993	Tamias alpinus	United States	California	Upper Cathedral Lake, Yosemite National Park	21-Jul-07	37.84117	-119.412	nulliparous
MVZ:Mamm:219996	Tamias alpinus	United States	California	Upper Cathedral Lake, Yosemite National Park	23-Jul-07	37.84117	-119.412	nulliparous
MVZ:Mamm:219997	Tamias alpinus	United States	California	Upper Cathedral Lake, Yosemite National Park	24-Jul-07	37.84117	-119.412	post lact
MVZ:Mamm:219989	Tamias alpinus	United States	California	Upper Cathedral Lake, Yosemite National Park	21-Jul-07	37.84117	-119.412	post lact

MVZ:Mamm:220005	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	3-Aug-07	37.64537	-119.42	
MVZ:Mamm:220021	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	8-Aug-07	37.64537	-119.42	
MVZ:Mamm:219987	Tamias alpinus	United States	California	Upper Cathedral Lake, Yosemite National Park	21-Jul-07	37.84117	-119.412	scars 2R, 0L
MVZ:Mamm:220006	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	3-Aug-07	37.64537	-119.42	
MVZ:Mamm:220007	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	3-Aug-07	37.64537	-119.42	
MVZ:Mamm:219988	Tamias alpinus	United States	California	Upper Cathedral Lake, Yosemite National Park	21-Jul-07	37.84117	-119.412	nulliparous
MVZ:Mamm:220003	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	3-Aug-07	37.64537	-119.42	
MVZ:Mamm:220004	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	3-Aug-07	37.64537	-119.42	
MVZ:Mamm:220008	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	3-Aug-07	37.64537	-119.42	

MVZ:Mamm:220010	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	3-Aug-07	37.64537	-119.42	post lact
MVZ:Mamm:220011	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	4-Aug-07	37.64537	-119.42	
MVZ:Mamm:220013	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	4-Aug-07	37.64537	-119.42	
MVZ:Mamm:220016	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	4-Aug-07	37.64537	-119.42	
MVZ:Mamm:220018	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	8-Aug-07	37.64537	-119.42	
MVZ:Mamm:220020	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	8-Aug-07	37.64537	-119.42	
MVZ:Mamm:220023	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	9-Aug-07	37.64537	-119.42	
MVZ:Mamm:219998	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	2-Aug-07	37.64537	-119.42	scars 1R-2L; post lact
MVZ:Mamm:219999	Tamias alpinus	United States	California	Lower Ottaway Lake, Yosemite National Park	2-Aug-07	37.64537	-119.42	nulliparous

MVZ:Mamm:219995	Tamias alpinus	United States	California	Upper Cathedral Lake, Yosemite National Park	22-Jul-07	37.84117	-119.412	
MVZ:Mamm:222200	Tamias alpinus	United States	California	Mono Pass	23-Jul-08	37.85461	-119.214	scars 2R-2L
MVZ:Mamm:222201	Tamias alpinus	United States	California	Middle Young Lake, Yosemite National Park	5-Aug-08	37.93876	-119.34	scars 2R, 1L
MVZ:Mamm:222202	Tamias alpinus	United States	California	Middle Young Lake, Yosemite National Park	5-Aug-08	37.93876	-119.34	scars 1R, 0L
MVZ:Mamm:227067	Tamias minimus scrutator	United States	California	1.1 mi W Sanger Meadow, Sierra Nevada	########	37.17588	-118.467	nulliparous