TO BOLDLY GO: BOLDNESS PREDICTS BEHAVIOR AND SURVIVORSHIP OF A CRITICAL PREY SPECIES

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DEDICATION

I dedicate this thesis to my parents, Lauren and Tom, and my big brother, Billy Tinkle. Thank you for your belief and support, and for teaching me that the natural things of this world have immeasurable value. And to Daniel who makes me significantly happier every day ($F_{1, 364} = 20.81$; $p<0.0001$).

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AUTOBIOGRAPHICAL SKETCH OF THE AUTHOR

Zoe Tinkle was born in Dallas, Texas and raised in Boulder and Longmont, Colorado. She and her family went camping nearly every weekend of her childhood, which developed her interest and respect for wildlife and the space they occupy. Zoe attended Boise State University in Boise, Idaho and graduated with a Bachelor of Arts in Biology in May 2012. After earning her Bachelors, Zoe worked for the Idaho Army National Guard (IDARNG) Environmental Management Office (EMO). The primary goal of this office is to manage the natural and cultural resources on lands of military training across Idaho, particularly in the Birds of Prey National Conservation Area (BOPNCA) south of Boise, Idaho. Zoe continued to work for this office until January 2014, when she joined the Masters of Science program at Boise State University. Zoe also developed an education and outreach program during her time at Boise State called the Idaho Adopt a Scientist Program that aimed to increase the connectivity between local classrooms and the research and scientists in their area. Currently, Zoe is working as a Natural Resources Specialist at the IDARNG EMO. Her work focuses on habitat restoration for the management of critical botanical and wildlife species in the BOPNCA.

ABSTRACT

Understanding population dynamics is at the core of conservation biology. However, our understanding of the mechanisms driving population dynamics remains unclear in many cases. Animal behavior in response to biotic and abiotic stressors is an important driver of these population dynamics and varies both within- and among-individuals in a population. Consistent differences in behavior among individuals within a population are referred to as personality traits. Boldness, a personality trait representing the willingness of an individual to engage in risky behavior, may help predict individual and community-level consequences, such as survivorship. Here, we investigated the inter- and intra-individual variation in risk-taking behavior (i.e., boldness) and the ecological consequences of such variation in a wild population of Piute ground squirrels (*Urocitellus mollis*). Boldness was quantified using an in-field handling bag test. Response to the handling bag test varied among individuals by sex, age, time in trap before test, season, and year but was consistent within individuals, suggesting that the handling bag test was a reliable measurement of personality (i.e., boldness). We found that boldness had a positive relationship with trappability and a negative relationship with survivorship. Additionally, we found that the effect of boldness on survivorship was higher in females than males and higher for squirrels captured in a habitat with shrub cover than in a habitat with just grass and no shrub cover. Our results suggest that animal personality can predict important life-history consequences, such as survivorship, and could therefore be used to

better understand the mechanisms driving population dynamics patterns and better inform population conservation and management practices.

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GENERAL INTRODUCTION

The field of conservation biology was born from the need to conserve biodiversity in the face of widespread environmental impacts. Wildlife conservation and management practices have long been informed by the quantification of population demographics (i.e., survival, reproduction, and dispersal), and how demographics vary over time and space. Demographics are traditionally measured by birth, death, immigration, and emigration rates (Berger-Tal and Saltz, 2016; Cappuccino and Price, 1995). While directly measuring population dynamics is important in determining the current state of a population, a great deal of inference is required to model populations across different spatial and temporal scales and across varying contexts, resulting in error of input values and interpretation of the output (Thomas et al., 2005). Therefore, to make inferences about a population across contexts (e.g., response to anthropogenic disturbance, climate change, loss of habitat, etc.), it is not only important to quantify the current state of a population, but also to understand the underlying mechanisms that lead to variation in population demographics.

Demographic patterns arise as a result of the cumulative consequences of interactions between the behaviors individuals express and the environment where they exist (Berger-Tal and Saltz, 2016). Therefore, animal behavior is an important predictor of population-level demographics. Over the last two decades, there has been increasing attempts to use measures of animal behavior to inform conservation efforts (reviews: Angeloni et al., 2008; Berger-Tal et al., 2015). Animal behavior, itself, is a product of complicated interactions between internal and external factors and varies within and among individuals. Therefore, to understand the potential mechanisms resulting in larger-scale patterns in population dynamics, one must understand not only the behaviors an animal exhibits, but how variable the behavior is both within and among individuals, and the ecological consequences of this variation. Stable behavioral differences among individuals across time and contexts is referred to as animal personality (Dingemanse and Réale, 2005; Réale et al., 2007), and has been documented in a wide range of taxa (Bell et al., 2009; Michelena et al., 2009; Rodriguez-Prieto et al., 2009; Sih et al., 2004). Animal personality has been shown to influence significant life-history consequences, such as survivorship (Bergeron et al., 2013; Ciuti et al., 2012; Madden and Whiteside, 2014), reproduction (Both et al., 2005; Réale et al., 2000), and dispersal (Møller and Garamszegi, 2012; Smith and Blumstein, 2008). However, in a review of twenty years of published literature where animal behavior was linked to conservation, animal personality was the least represented behavioral theme (Berger-Tal et al., 2015). Therefore, there is a need to incorporate individual variation in behavior into population dynamics research and conservation actions. Investigating the interactions among variation in personality, behavior, and habitat structure could improve our understanding of individual, population, and community-level dynamics.

The overall objective of this study was to use an in-field behavioral test to examine inter- and intra-individual variation boldness (Réale et al., 2007; Wilson et al., 1994) and the ecological consequences (i.e., trappability and survivorship) of this variation in a wild population of Piute ground squirrels (*Urocitellus mollis*, hereafter Piutes). Boldness is a personality trait that reflects the willingness of an individual to take risks and is typically associated with increased trappability (Carter et al., 2012; Mella et al., 2016) and decreased survival (Bergeron et al., 2013; Ciuti et al., 2012; Madden and Whiteside, 2014; Smith and Blumstein, 2008). Therefore, we predicted that boldness in Piutes will be positively correlated with trappability and negatively correlated with survivorship. We also predicted that when modeling survivorship, models that included boldness as an individual covariate would predict survivorship better than those that did not include boldness. To test these predictions, we trapped and observed Piutes at two study sites located within the Morley Nelson Snake River Birds of Prey National Conservation Area (SRBPNCA) in southwestern Idaho, USA. Piutes are the major prey species for predators such as prairie falcons (*Falco mexicanus*; Steenhof and Kochert, 1988) and American badgers (*Taxidea taxus*; Messick and Hornocker, 1981) due to their relatively high densities (Antolin et al., 2001). This, coupled with their high probability of capture (Appendix A), important ecological role, and management priority, make Piutes the ideal study species to test our predictions.

In Chapter 1, we focused on quantifying the inter- and intra-individual variation in boldness of Piutes. First, we measured risky behavior among individuals and predicted that risky behavior would vary by sex, age, and the habitat type of the site where the individual was captured. Second, we predicted that we could detect consistent individual differences in risky behavior (i.e., boldness) using an in-field assay. Finally, we predicted that boldness of individuals would be positively correlated with movement and trappability, which have been shown to be behaviors associated with risk-taking. To test these predictions, we compared boldness of individuals over two years (2014 and 2015) in southwestern Idaho over two seasons (pre-juvenile emergence and post-juvenile emergence) in two habitats that varied in shrub cover. Individuals underwent a handling bag test where mobile time in the bag over one minute represented a measure of riskiness (i.e., boldness). First, we found that risky behavior during the handling bag test significantly varied with sex, age, time in trap before the test, season, and year. However, boldness did not vary by habitat type. Secondly, we found that individual identity explained risky behavior during the handling bag test more than sex, age, time in trap, season and year, which suggested that the in-field handling bag test was a reliable measurement of personality (i.e., boldness). Finally, we found that boldness was positively correlated with trappability, but not movement. Overall, this chapter revealed that Piutes differed consistently in their risk-taking behavior (i.e., boldness) within a population and that boldness is positively correlated with other risky behaviors, such as trappability.

In Chapter 2, we investigated the relationship between boldness and survivorship and how sex, year, and habitats that differ in cover influence this relationship. We predicted that the addition of boldness as an individual covariate in survivorship models would improve our models and that survivorship would be negatively correlated with boldness. In addition, we predicted that individuals from different sexes, in different years, and in different habitats would vary in survivorship and that boldness would affect survivorship in each group differently. Overall, boldness had a negative relationship with survivorship. The negative effect of boldness on survivorship was slightly stronger for females than for males, varied in effect size by year, and was stronger in the high cover habitat type than in low cover. This chapter outlines the important role personality (i.e., boldness) can play in our ability to estimate and understand survivorship of individuals within different demographic groups, over time, and in different habitat types.

This research contributes to the growing body of science aimed to connect the principles of individual variation in behavior and the ecological consequences of this variation. Wildlife managers can use a simple in-field test that predicts boldness to develop more predictive survivorship models and better understand the mechanisms behind large-scale population dynamics patterns.

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CHAPTER 1: INTER- AND INTRA-INDIVIDUAL VARIATION IN RISKINESS OF A CRITICAL PREY SPECIES

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Abstract

Consistent individual differences in behavior of animals (i.e., personality) have been shown in a variety of taxa. Moreover, understanding variation in personality within a population is of growing interest in the study of animal behavior due to the consistency in which personality-linked behaviors are expressed. Variation in personality can be mediated by external (e.g., habitat structure, predation pressure) and internal factors (e.g., nutritional state). Understanding boldness, a personality trait that reflects the willingness of an individual to engage in risky behaviors, can help predict important life-history characteristics, such as reproductive success, survivorship, and dispersal, which effect population-level patterns and potentially multi-trophic level interactions. Here, we focus on the inter- and intra-individual variation in risky behavior of a critical prey species: the Piute ground squirrel (*Urocitellus mollis*). First, we predicted that risky behavior would vary by sex, age, and habitat type. Second, we predicted that we could detect consistent individual differences in risky behavior (i.e., boldness) using an in-field assay. Finally, we predicted that boldness of individuals would be positively correlated with two other measures of risky behavior: movement and trappability. To test these predictions, we compared boldness of individuals over two years (2014 and 2015) in southwestern Idaho over two seasons (pre-juvenile emergence and post-juvenile emergence) in two habitats that varied in shrub cover (sagebrush and grass). Individuals underwent a handling bag test where mobile time in the bag over one minute represented a measure of boldness. Sex, age, time in trap before the test, season, and year were significant factors in predicting mobile time. Habitat type did not significantly contribute to differences in mobile time. In a mixed-model approach, individual identity explained mobile time in handling bag and mobile time was repeatable within individuals. These results suggest that the in-field test of mobile time was a reliable measurement of personality (i.e., boldness). Finally, we found that boldness was positively correlated with trappability, but not movement of Piutes. Overall, this study found that risky behavior varied by sex, age, testing conditions, and over time, but differed consistently among individuals, indicating the presence of a personality trait. Moreover, boldness was predictive of trappability, a measurement commonly used to describe the riskiness of an individual, validating our assumption that the handling bag test was measuring variation in boldness among individuals.

Introduction

Animal conservation and management relies on the ability to measure, predict, and, in some cases, alter population dynamics. These dynamics result from a combination of basic demographic processes such as survival, reproduction, and dispersal. Demographic patterns arise as a result of the cumulative consequences of interactions between the behaviors individuals express and the environment where they exist (Berger-Tal and Saltz, 2016). Animal behavior, itself, is a result of complicated interactions between internal and external factors and varies within and among individuals. Therefore, to understand how behavior of individuals influence larger-scale population dynamics patterns, one must understand not only the behaviors an animal exhibits, but also how variable the behavior is and the ecological consequences of this variation.

Documenting variation in behavior among individuals within the same population has a long history (Clark and Ehlinger, 1987; Huntingford, 1976). However, the source of this variation was largely left unexplained or attributed to statistical noise (Dall et al., 2004). Recently, research has suggested that this variation may be attributed to stable behavioral differences among individuals across time and contexts, which are referred to as personality traits (Dingemanse and Réale, 2005; Réale et al., 2007), and have been documented in a wide range of taxa (Bell et al., 2009; Michelena et al., 2009; Rodriguez-Prieto et al., 2009; Sih et al., 2004). Variation in behavior among individuals can also be attributable to differences in sex (Ball and Balthazart, 2008; Worthington and Swallow, 2010, Øverli et al., 2006), age (Desrochers, 1992), and environmental conditions, including habitat structure (Brown, 1992), and forage availability and quality (Mella et al., 2015), which can vary spatially and temporally (Camp et al., 2012). Differences in behavior among sexes can be attributable to differences in life history requirements, mating strategy, and hormonal differences. For example, in rainbow trout (*Oncorhynchus mykiss*), females are more likely to engage in risky behaviors than males due to differences in cortisol response to stimuli where males had higher levels of cortisol than females, causing males to exhibit anti-risk behaviors. Juveniles and adults typically face drastically different life history requirements, such as higher juvenile-than-adult dispersal, adult-only mating systems, and the learned experience adults have that juveniles lack. These differences lend themselves to differences in behavioral strategies among juveniles and adults. For example, in European blackbirds, juveniles had less foraging success than adults (Desrochers, 1992), but increased their foraging success as they gained experience. Individuals may also differ in their behaviors depending on the habitat characteristics. For example, brushtail possums (*Trichosurus vulpecula*) in relatively safe habitats are more likely to forego anti-predator behaviors and increase foraging behaviors.

In particular, prey behavior is largely mediated by risk avoidance. Prey forage to avoid the risk of starvation and express anti-predator behaviors to avoid the risk of predation (Lima and Dill, 1990; Llandres et al., 2012; Preisser et al., 2005). Among-individual variation in risk-taking behavior can have significant life-history consequences, such as survivorship, reproduction, and dispersal (Bergeron et al., 2013; Møller and Garamszegi, 2012; Réale et al., 2010; Smith and Blumstein, 2008). For example, consistent variation in movement has been shown to predict hunting season survival in elk (*Cervus canadensis*) where bold individuals, defined as those who exhibited higher rates of movement throughout the hunting season, were more likely to be harvested than those that moved less (Ciuti et al., 2012). Réale, et al. (2000) found that big horn sheep ewes (*Ovis canadensis*) exhibited consistent individual differences in their willingness to enter a baited trap (i.e., trappability), and that this variation in a risky behavior was predictive of reproductive success where riskier ewes had higher reproductive success than non-risky ewes.

Because personality traits can shape how an individual perceives and interacts with the environment (Sih et al., 2012), they can also be an important factor shaping the ecology and evolution of prey. At the community level, the variation in personality of one species is likely to impact the interactions with other species in other trophic levels. For instance, species with high behavioral variation could potentially withstand natural – and anthropogenic – environmental change (Sih et al., 2011) and therefore impact the longevity and context of species interactions and the overall food web structure (Moya-Laraño, 2011). Investigating the interactions among variation in personality, behavior, and habitat structure could improve our understanding of individual, population, and community-level dynamics in a changing landscape.

In this study, we quantified the inter- and intra-individual variation in risky behavior (i.e., boldness; Réale et al., 2007), using a wild population of Piute ground squirrels (*Urocitellus mollis*, hereafter Piutes) at two study sites with structurally distinct habitats representing relatively risky and relatively safe habitats. First, we predicted that risky behavior would vary by sex, age, and habitat type. Specifically, we predicted that female Piutes would exhibit more risky behavior than males. We also predicted that juvenile Piutes would exhibit more risky behavior than adults. Habitat structure has been shown to directly influence anti-predator behavior where individuals are less likely to engage in risky behaviors when the habitat is risky (Lima, 1998). For this study, we define habitat risk by the aerial cover at the site. Aerial cover is likely to influence actual and perceived predation risk for Piutes due to the presence of aerial predators. Therefore, we predict that Piutes captured at the native grass site, where there is no aerial cover, will exhibit less risky behavior than those captured at the sagebrush site, where there is aerial cover. Second, we predicted that we could detect consistent individual differences in risky behavior (i.e., boldness) using an in-field handing bag test. This technique has been used to assess consistent differences in behavior of Eastern chipmunks (*Tamias striatus*; Martin and Réale, 2008a, 2008b; Montiglio et al., 2012), brushtail possums (*Trichosurus vulpecula*; Mella et al., 2016), and North American red squirrels (*Tamiasciurus hudsonicus*; Boon et al., 2007). Finally, we predicted that boldness of individuals would be positively correlated with movement and trappability. Both movement and trappability can be considered as risky behaviors (Carter et al., 2012; Fraser et al., 2001; McLean, 2014) and can be used to validate the context of the handling bag test as a measure of boldness.

Overall, this study describes the consistent differences in risky behavior among individuals of the same population, the factors that contribute towards this variation, and the ecological consequence of this variation. Our study system is ideal to investigate these predictions due to the relatively high predation pressure Piutes experience across their range, ease of capture, and high probability of recapture.

Methods

Study system

Piutes are ideal subjects for the study of variation in behavior because they are important prey for a variety of predators (Hubbs and Boonstra, 1998; Schmutz and Hungle, 1989). Specifically, Piutes occur in relatively high densities (Antolin et al., 2001; Appendix A), they live in a variety of habitat types across their range (Yensen et al., 2003), and they are a major prey species of many aerial and terrestrial predators in the Morley Nelson Snake River Birds of Prey National Conservation Area (SRBPNCA; Steenhof and Kochert, 1988; Yensen et al., 1992) located in southwestern Idaho (Figure 1.1). This area is home to one of North America's most dense and diverse populations of breeding raptors and exhibits a range of vegetative structure, both of which combine to provide variable "fearscapes" for Piutes.

Study sites were randomly established in one of two structurally distinct habitat types that occur across the NCA, defined by the dominant-habitat type: (1) A sagebrush site dominated by Wyoming big sagebrush (*Artemisia tridentata wyo.*) with native perennial grass Sandberg's bluegrass (*Poa secunda*) understory, and (2) A native grass site dominated by Sandberg's bluegrass only with no shrub cover (Baun et al. 2013; Figure 1.2). These sites are involved in an ongoing mark-and-recapture trapping study of Piutes from 2013 to 2016 and are separated by 3.9km.

Live trapping

In 2014 and 2015, live trapping was used to assess basic population dynamics of Piutes at each study site (Anderson et al., 1983) and to perform in-field behavioral assays to measure boldness. Each trapping web consisted of 96 Tomahawk Live Traps (7x7x41cm; Tomahawk Live Trap Co., Tomahawk, WI) spaced evenly at every 20m along twelve radii measuring 160m in length (Figure 1.3). The total area of each trapping web was 80,425m^2 or 8.04ha.

Live trapping was conducted in two separate seasons throughout the active period of Piutes, once in late March/early April, before the emergence of juveniles (pre-juvenile season), and a second time in late April/early May, after the emergence of juveniles (post-juvenile season; Table 1.2). A robust sampling design was implemented to assess the consistency and potential habituation of individuals to the in-field behavioral assay (i.e., static handling bag test), as well as assess the impact of varying temporal scales on behavior. Each site was pre-baited for three days prior to live trapping to avoid confounding initial trap response (Gurnell, 1980). Upon capture, individuals were covered with burlap and the time of capture was recorded. Each animal was marked with a passive integrated transponder (PIT) tag (Biomark, Boise, ID) after the behavioral assay was conducted for individual identification.

Quantifying boldness

For each individual, we measured consistency in risky behavior of individuals using a static handling bag test (Martin and Réale, 2008a; Réale et al., 2000) in 2014 and 2015 (Table 1.2). Boldness, commonly used as a measure of an animal's willingness to engage in risky behavior (Petelle et al., 2013; Réale et al., 2007), is here defined as an individual's behavioral response to being trapped and handled. In similar studies on other species, animals with higher cortisol levels (i.e., more stressed) were less mobile (i.e., static) during human handling and consequently defined as docile (Koolhaas et al., 1999; Martin and Réale, 2008a). Therefore, we attributed higher mobile time during the handling bag test to be an expression of more risky behavior and therefore a measure of boldness.

During the handling bag test, ground squirrels were moved from their trap to a dark, cloth handling bag. We then suspended them in the handling bag for one minute and quantified the amount of time (sec) spent mobile (i.e., non-static). The wait time from collection of a trapped individual until the static handling bag test was recorded as well as the location of the trap. After the static handling bag test, individuals were handled to obtain demographic characteristics (i.e., sex, age, weight) and marked with a passive integrated transponder (PIT) tag if one was not already present.

Mean daily movement (MDM)

Mean daily movement (MDM) estimates were obtained using the software DENSITY version 5.0 (Efford, 2012). MDM values are calculated using trap-revealed movement from recaptured individuals. This value will give an average distance moved at each site. However, this is a coarse estimate of movement and does not take in to account path of travel, movements of those not recaptured, or potential differences in movement patterns of different demographic groups, which are likely to exist in this species. All MDM estimates are reported as average meters per day.

Trappability

Trappability was measured as the number of captures of an individual over the total number of encounter occasions the individual was available for capture (i.e., from the first capture to the last capture). For example, if an individual was trapped ten times but was available for capture over 20 days of trapping, that individual’s trappability score would be 0.5.

Data analysis

To explain inter- and intra-individual variation in test responses to the static handling bag test (i.e., boldness), we used a univariate linear mixed-effect model approach adapted from Dingemanse and Dochtermann (2013). First, we used model selection using AICc from a set of *a priori* candidate linear mixed models to investigate the effect of sex, age, body weight, wait time, test number, study site (i.e., sagebrush or native grass), trapping season (pre-juvenile season and post-juvenile season) and year (2014 and 2015) on time spent mobile during the handling bag test (log-transformed). In all models, individual identity was included as a categorical random effect. We tested whether individuals consistently differed in risky behavior by comparing two models using a log-likelihood ratio: one with only fixed effects and a second with fixed effects and individual identity as a random effect (Dingemanse and Dochtermann, 2013). Residuals were tested for normality visually. Individual boldness scores were obtained using best linear unbiased predictors (BLUPs), which provided estimates of individual boldness after accounting for other terms within the model.

Repeatability is a measure of the intra-individual variance compared with the inter-individual variance in mobile time during the handling bag test and gives the phenotypic variance in mobile time explained by the individual identity (Réale et al. 2000; Dingemanse et al. 2002). We calculated repeatability (r) as the proportion of variation attributed to individual identity (V_{ind}) over the total variation in the mixed-model (Dingemanse and Dochtermann, 2013):

$$r = \frac{V_{ind}}{V_{ind} + V_{e0}}$$

Where V_{ind} is the intra-individual variation in boldness and V_{e0} is the inter-individual variation in boldness. Consistent differences among individuals in behavior over repeated measures can be caused by individual differences in habituation rates across tests (i.e., some individuals decrease their response to the assay while others do not; Dingemanse et al., 2010). Thus, in addition to measuring the average habituation rate of the tested population, we also measured whether individuals differed in habituation rates. We thus tested for an interaction between test number and individual identity (i.e., random slopes as outlined in Dingemanse and Dochterman, 2013). We tested for the significance of this interaction term by running two models: one with the significant fixed effects (i.e., sex, age, wait time, test number, season and year) and individual identity as a random effect and a second with an additional random effect of test number (i.e., the successive order of administered test for each individual). These models were then compared using a log-likelihood ratio test (Dingemanse and Dochtermann, 2013).

To test whether consistent variation in time spent mobile during the handling bag test (i.e., boldness) could predict mean daily movement or trappability, we regressed these variables on individual BLUPs extracted from the best mixed model predicting time spent mobile during the handling bag test. All statistical analyses were conducted using R (version 3.2.4; Team, 2014) using the lme4 and lmtest packages. Model selection processes and full R code can be found in Appendix B.

Results

Inter- and intra-individual variation in boldness

Boldness scores were estimated from the amount of time spent mobile (s) during the handling bag test for a total of 372 individuals. Sex (p=0.0277), age (p<0.001), wait time (p=0.0078), season (p<0.001), year (p<0.001), and the interaction between sex and age (p=0.0117) all had a significant effect on time spent mobile during the handling bag test (see Table 1.1 for estimates). Test number was not significant (p=0.0513). However, test number was maintained in the final model to account for potential habituation to the test after repeated measures (see Appendix B for full model selection).

For juveniles, females were more mobile, though not significantly more, than males ($F_{1,115}$=2.5207, p=0.1151), and for adults, males were significantly more mobile than females ($F_{1,631}$=8.0450, p=0.0047). In addition, females were significantly more mobile as juveniles than as adults ($F_{1,409}$=22.6917, p<0.0001), but males did not differ significantly in mobility by age $F_{1,337}$=0.8365, p = 0.3611; Figure 1.4). Wait time had a significant positive effect on time spent mobile during the handling bag test ($F_{1,676}$=40.0361, p<0.0001, Figure 1.5). Individuals were more mobile during the pre-juvenile season than the post-juvenile season ($F_{1,748}$=6.5161, p<0.0109; Figure 1.6) and more mobile in 2014 than 2015 ($F_{1,748}$=55.5924, p<0.0001; Figure 1.7). As test number increased, time spent mobile significantly increased ($F_{1,748}$=8.7670, p=0.0032; Figure 1.8). We tested for the effect of habitat type on time spent mobile during the handling bag test by running our final model with and without study site as a fixed effect and found that it did not contribute to variation in mobile time (Figure 1.9). We also found that body weight did not have a significant effect on time spent mobile during the handling bag test and was therefore not included in the final mixed-effect model (for detailed modeling results, see Appendix B).

Individual identity had a significant effect on the handling bag test (p=0.0179, Table 1.1) indicating that the handling bag test was a measurement of individual differences in behavior not explained by the previously described fixed effects. Repeatability for boldness was 0.30, which falls within the 95% confidence interval of average reported repeatability of endotherm behavior ($0.28 \leq 0.33 \leq 0.36$, Bell et al., 2009). We found no evidence of individual variation in habituation rate to the handling bag test (for detailed results, see Appendix B).

Mean daily movement (MDM)

Linear regression revealed no significant relationship between boldness score (i.e., BLUP) and mean daily movement (MDM; $F_{1,290}$=3.501, p=0.0623, Y=3.152*BLUP +16.75; Figure 1.9).

Trappability

Linear regression revealed a significant, positive relationship between boldness score (i.e., BLUP) and trappability ($F_{1,369}$=3.891, p=0.0493, Y=0.06473*BLUP + 0.7109; Figure 1.9).

Discussion

Inter- and intra- individual variation in boldness

Variation in time spent mobile during the handling bag test (i.e., boldness) was affected by sex, age, wait time, season, and year. The effect of sex alone was relatively weak, however the interaction between sex and age was significant. Females were the most variable in their boldness between to the age classes, being significantly more mobile as juveniles than as adults, while males did not differ significantly between life stages. In a meta-analysis of the consistency of behaviors across 789 studies, Dall et al. (2004) found that, overall, males exhibited more consistency in behavior than females across taxa. This review also found that this sex difference was observed in adults, but not in juveniles, which is consistent with our finding that juvenile mobility time did not vary significantly by sex.

Wait time (time from when the individual was picked up from the trapping grid to when they underwent the handling bag test) was positively correlated with mobility time. The positive relationship between wait time and time spent mobile may be due to individuals habituating to the novelty of the trapping process and a reduction in their "freeze" response in the handling bag. We recognize that the wait time defined here is likely an underestimation of the actual time an individual has spent in a trap (i.e., from the moment of capture to handling bag test). The order by which traps were collected and individuals were processed was random, therefore we cannot conclude whether a more accurate estimation of wait time would change our results.

Season and year both had significant effects on time spent mobile during the handling bag test. In general, the time spent mobile decreased as the time during the study went on. This is inconsistent with our finding of test habituation (i.e., test number) which had a positive effect on time spent mobile. Therefore, it is unlikely that the effect of season and year is an indication of long-term habituation to the handling bag test. Other explanations may include external factors that vary temporally, such as population demographics or changes in trapping effort. If tchanges in demographics explained our results, we would expect that the proportion of individuals with demographic characteristics that were consistent with lower mobility time (i.e., adult females) would increase from pre- to post-juvenile seasons and from 2014 to 2015, thus negatively biasing the mobility times. However, this was not consistent with ratios observed in this study where proportion of adult females to all squirrels (pre-juvenile 2014=0.64, post-juvenile 2014=0.37, pre-juvenile 2015=0.56, post-juvenile 2015=0.65; see Appendix A). There were far more juveniles during the post-juvenile seasons than during the pre-juvenile seasons. However, given that juveniles had higher mobility times than adults, we would expect to see higher mobility times during the post-juvenile seasons, the opposite pattern than what was observed. Another potential explanation is a difference in wait time during trapping seasons and years. As trapping continued, an effort was made to decrease the amount of time an individual spent in the trap, which decreased the average wait time by 73 minutes from 2014 to 2015. Given that wait time increases mobility time, we would predict that mobility time would increase from 2014 to 2015, which was consistent with the pattern observed (Figure 1.7).

Contrary to our predictions, we did not find effect an of habitat type on the variation in the observed mobile time during the handling bag test. For this study, we assumed that the level of risk in the habitat depended on that amount of physical cover. However, cover may not be the only level of risk in a habitat. For Piutes, it is possible that the density of subterranean burrows could vary by habitat type resulting in a difference in overall refuge. In 2013, a burrow-count study was conducted on these sites to as a part of a method validation study and it found that burrows existed in higher densities at the native grass site (133 burrows/ha) than at the sagebrush site (49 burrows/ha; Yensen, et al., 2014 *unpub*). Potentially, the lack of shrub cover at the native grass site is off-set by the increase in burrows, therefore eliminating an uneven selective pressure on risky behavior. Another possible explanation is that the actual predation pressure (i.e., resulting in death) is the same at both sites. If boldness is associated with genetic variation, the high gene flow between the sites could also prevent the emergence of differences in boldness between habitats. Antolin et al. (2001) found relatively low levels of genetic differentiation among, and no evidence of inbreeding within, three populations of Piutes separated by a minimum of 8km, which is over twice the distance apart than the sites used in this study. Therefore, it is possible that the external selection pressures of low cover versus high cover have been washed out by a high degree of movement among populations. Another possible explanation is that the amount of time since the cover was removed (due to fire) from the native grass site has been too short to allow any significant phenotypic differences between sites to emerge.

We observed important consistent individual differences in boldness among individuals. As in other species (i.e., eastern chipmunks, *Tamias striatus*; Montiglio et al., 2012, and brushtail possums, *Trichosurus vulpecula*; Mella et al., 2015), the handling bag test is a measure of an individual's willingness to engage in risky behaviors. It is likely that this technique can be used for many other prey species with similar life history characteristics as Piutes.

Mobility during the handling bag test was a predictive personality trait of individual Piutes and was found to be repeatable (30%). In other words, of the variation observed in time spent mobile during the handling bag test, 30% is due to differences among individuals not explained by significant fixed effects (i.e., sex, age, wait time, test number, season, and year). A behavior is repeatable when individuals behave consistently through time and differently from each other. Repeatability of behaviors has been used as the first step to determining a genetic basis for a behavior (Boake, 1989). Boldness has been shown to significantly affect life-history characteristics (reviewed in Biro and Stamps, 2008) such as survivorship (Ciuti et al., 2012; Chapter 2), fecundity (Bridger et al., 2015; Wilson et al., 2010), and growth (Réale et al., 2000). Thus, boldness can be a powerful predictor of individual and population-level success. Individually, boldness can predict important behaviors that effect energy expenditure through movement (Fraser et al., 2001), foraging decisions (Mella et al., 2015), and reproductive success (Réale et al., 2000), and the effects of these individual behaviors are cumulative and can drive population-level patterns. For populations, differences in behavior strategies among individuals generally promotes population stability, resilience and persistence (McCann, 2000; Oldroyd and Fewell, 2007; Wolf and Weissing, 2012). Therefore, consistent differences in behavior can predict significant life-history consequences for individuals, these consequences accumulate to influence population-level patterns, and the variation in behavioral types within a population can influence the persistence of that population.

Boldness, movement, and trappability

Boldness was found to predict trappability, but not mean daily movement. Movement has been found to be positively correlated with boldness as it is a form of risk-taking behavior (Fraser et al., 2001). Contrary to our predictions, movement of ground squirrels was not predicted by their boldness. However, there is a positive trend between boldness and movement. One potential reason for this may be that our estimation of movement, based on straight-line distance between recapture locations, was not representative of actual daily movement. Finer-scale movement data would likely improve our understanding of the relationship between boldness and movement. Movement has been shown to affect survivorship (Ciuti et al., 2012), reproduction (Morales et al., 2010), and dispersal (Travis et al., 2012), and therefore is still an important risk-taking behavior to consider.

The willingness of an individual to enter a baited trap reflects its willingness to engage in a risky behavior, therefore bolder individuals are expected to have higher trappability. This is consistent with our results where individuals that were more mobile during the handling bag test (i.e., more bold) were also more likely to have a higher trappability. Boon et al. (2008) also found that trappability in North American red squirrels (*Tamiasciurus hudsonicus*) was predicted by boldness and that boldness was negatively correlated with over-winter survival of females and positively correlated with the probability of offspring overwinter survival. Therefore, the variation in boldness associated with trappability could contribute significantly to predicting fitness tradeoffs and, therefore, the maintenance of variation in behavior that we observe.

Conclusion

Overall, we found that mobility time was a reliable way to estimate boldness of a wild population of Piute ground squirrels and that boldness was repeatable and predictive of trappability. We can use this in-field test to investigate how other internal (e.g., physiological stress, nutritional state) and external factors (e.g., predation and parasitism pressure, quantity and quality of forage, climatic conditions) may interact with boldness to influence behaviors at varying spatial and temporal scales. In the future, we should assess the relationship between boldness and significant life-history consequences such as reproductive success, survivorship (Chapter 2), and dispersal, which interact to predict population-level patterns important for informing management and conservation of wildlife across varying scales.

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Table 1.1. Estimates and significance of fixed effects on time spent mobile during the handling bag test. Results from the linear mixed model where ground squirrel PIT tag ID was included as a random effect (i.e., model to detect personality effect, V_{ind}).

Random Variables	Components	Variance	r	LRT (Chisq)	*P*
ID	V_{ind}	0.5492	29.9%	5.6082	**0.0179**
	V_{e0}	1.2880			

Terms	**Coefficient±SE**	***df***	***t***	***P***
Intercept	1.7466±0.1452	531.9	12.028	**<0.001**
Sex (Male)	0.2946±0.1332	337.1	2.212	**0.0277**
Age (Juvenile)	0.8422±0.1977	605.8	4.261	**<0.001**
Wait Time	0.0027±0.001	658.5	2.667	**0.0078**
Test number	0.1131±0.0579	664.6	1.953	0.0513
Season (PreJuv)	0.7941±0.185	652.9	4.293	**<0.001**
Year (2015)	-0.5824±0.1428	668.8	-4.078	**<0.001**
Sex*Age(Male*Juvenile)	-0.7345±0.2903	622.3	-2.53	**0.0117**

ID = individual PIT tag ID; V_{ind} = intra-individual variation in mobile time; V_{e0} = inter-individual variation in mobile time; r = repeatability of static handling bag test [$V_{ind}/(V_{ind}+V_{e0})$]; LRT: log-likelihood ratio test chi square value. Ground squirrel PIT tag ID was included as a random effect (V_{ind}, $N = 373$ individuals, 678 samples). Significant *P* values are depicted in bold.

Table 1.2 Schedule of events from 2013-2016 during the pre-juvenile (PreJuv) and post-juvenile (PostJuv) seasons. "X" denotes that the activity was performed during the corresponding timeframe.

Activity								
Handling bag test			X	X	X	X		
Trapping	X	X	X	X	X	X	X	X
	PreJuv	PostJuv	PreJuv	PostJuv	PreJuv	PostJuv	PreJuv	PostJuv
	2013		2014		2015		2016	

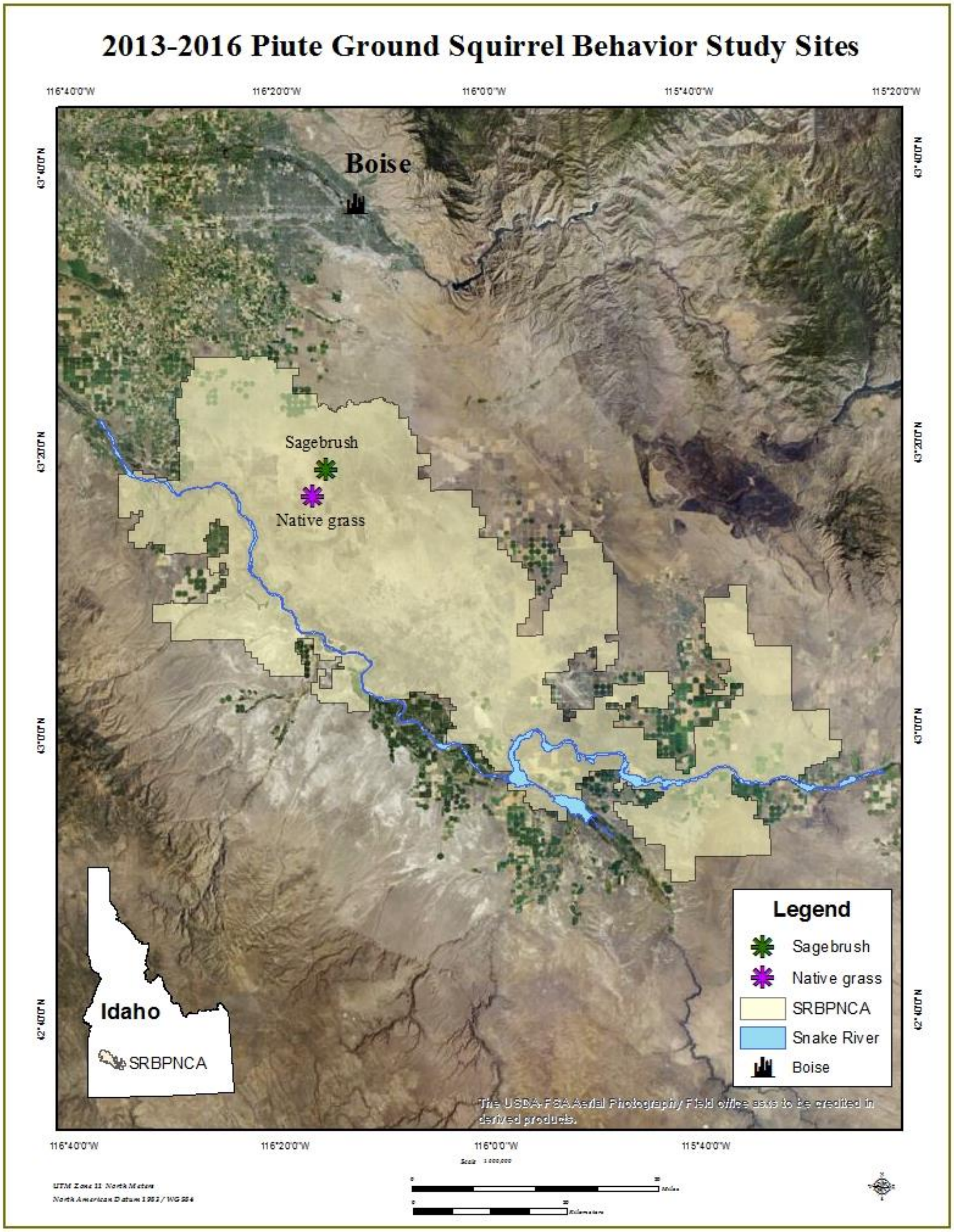

Figure 1.1. Map of study sites dominated by sagebrush (*Artemisia tridentata wyomingensis*) and native grass (*Poa secunda*) where behavior was measured for Piute ground squirrels (*Urocitellus mollis*). The sites are located south of Boise, Idaho within the Snake River Birds of Prey National Conservation Area. UTMs of grid center points- sagebrush: 11T E560018, N4795703; native grass: 11T E558430, N4792390.

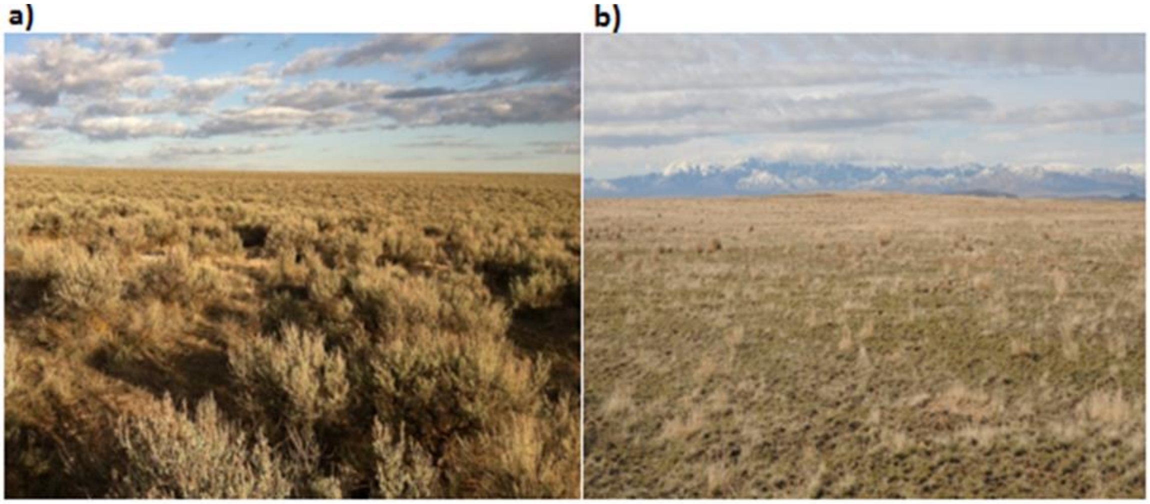

**Figure 1.2	2013-2015 study sites: (a) site dominated by sagebrush (*Artemisia tridentata wyomingensis*) and (b) site dominated by native grass (*Poa secunda*). Photos taken by Zoe Tinkle, 2013.**

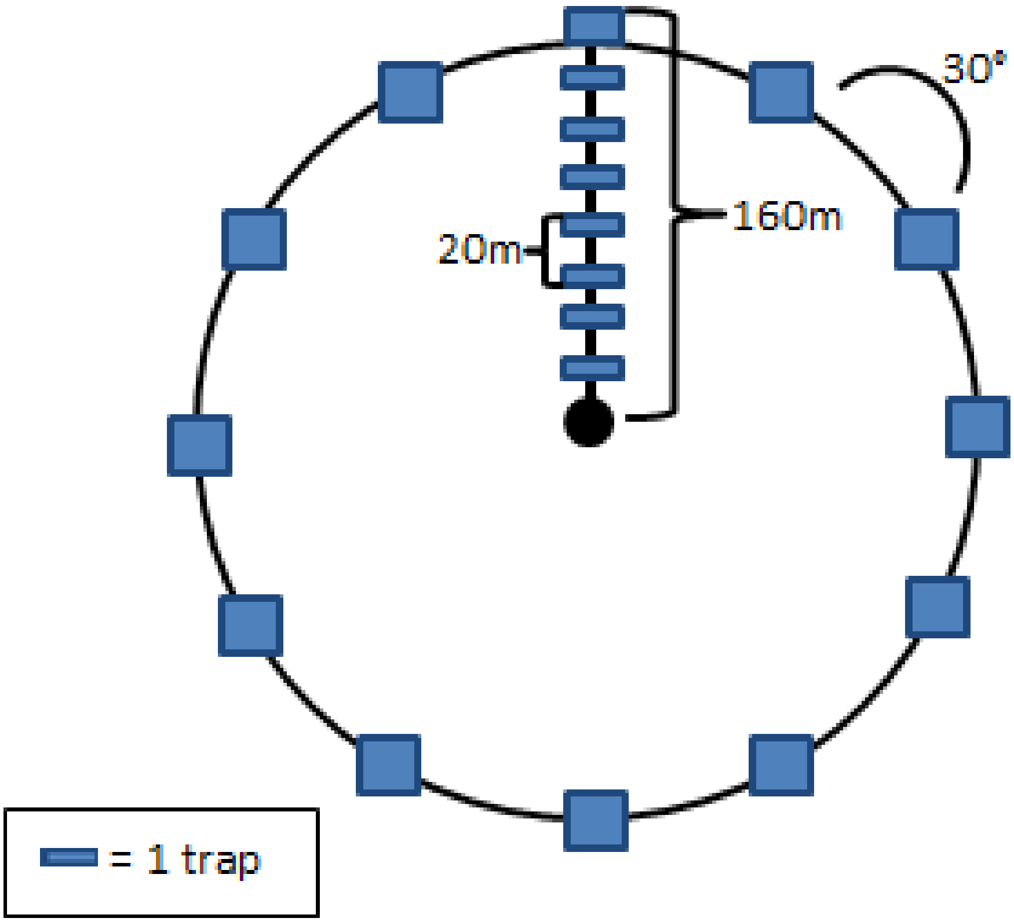

Figure 1.3. **Graphical representation of live trapping web layout. Each web consists of twelve radii spaced by 30 degrees and 96 traps evenly spaced at every 20m along each radius.**

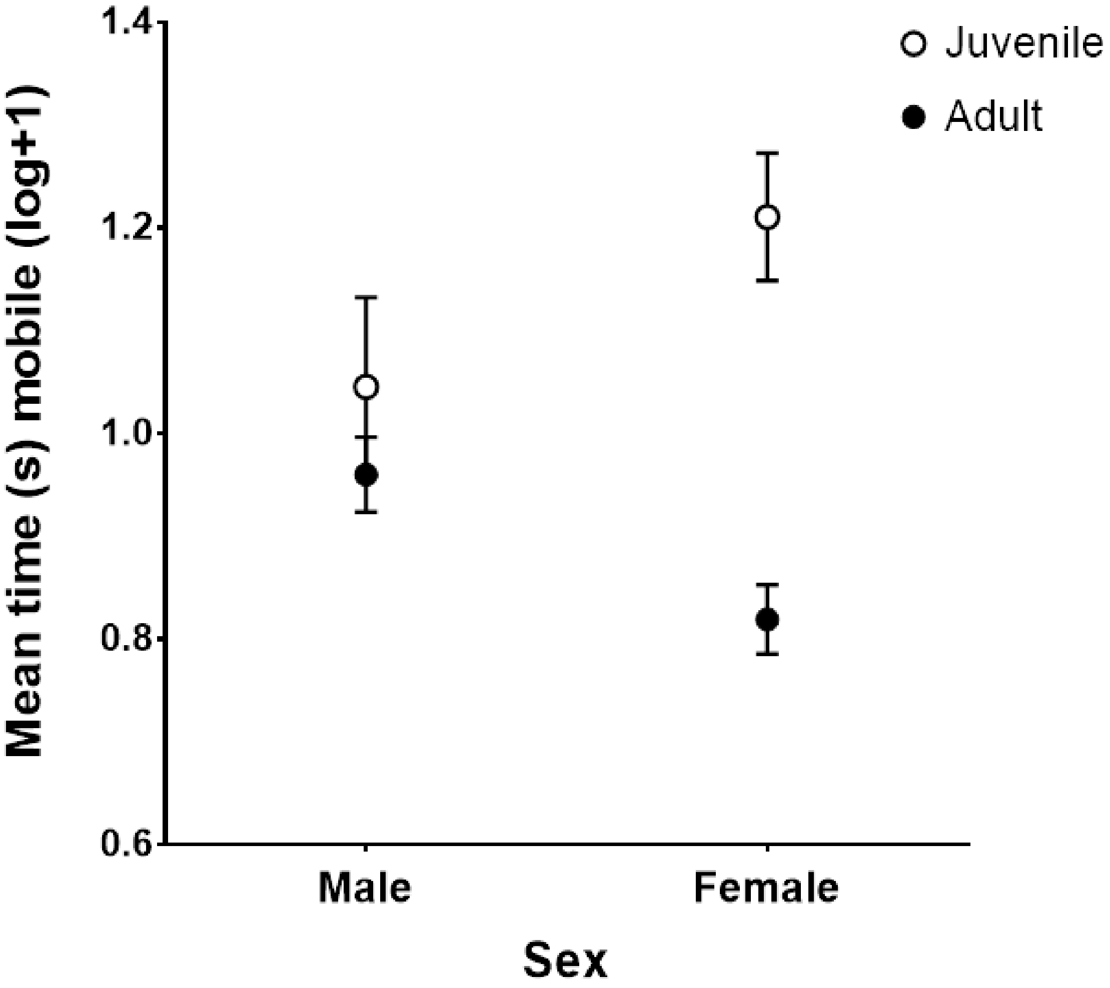

Figure 1.4. Effect of sex and age on mean time (in seconds) spent mobile during handling bag test for male (N=52) and female juveniles (N=65, open circles) and male (N=287) and female adults (N=346, closed circles). Bars represent standard error of the mean (SEM).

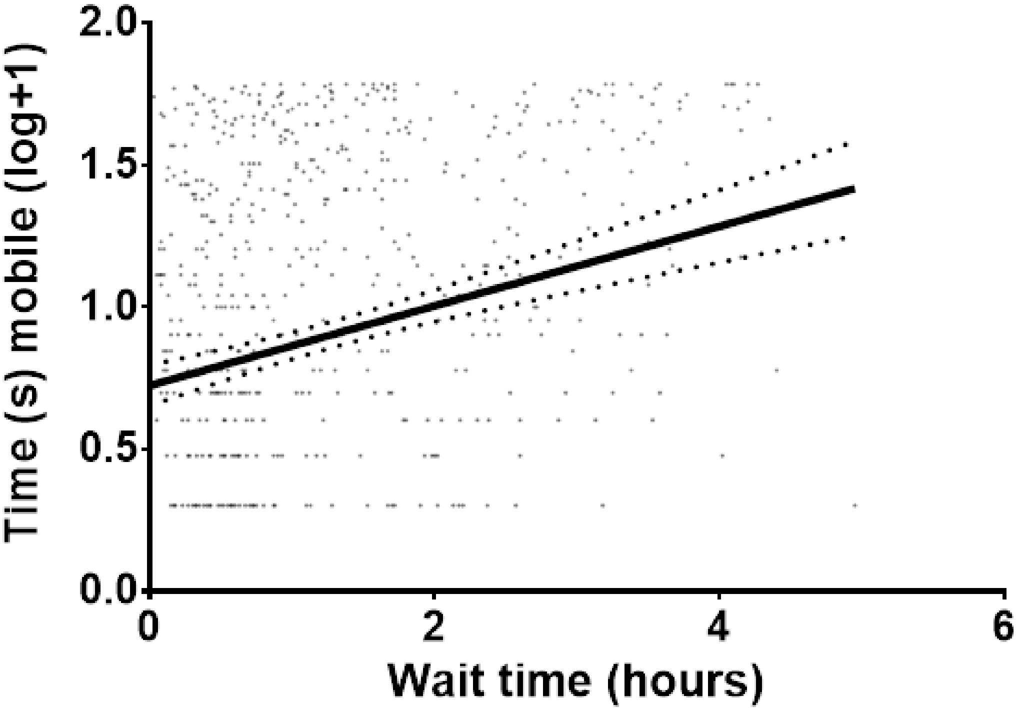

Figure 1.5. The effect of wait time (time spent in trap from pick-up to handling bag test, in hours) on the time spent mobile in handling bag test ($F_{1,676}$=40.0361, p<0.0001, Y=0.1402239*WaitTime+0.723995, N=750). Solid line represents line of best fit with 95% confidence intervals (dotted lines).

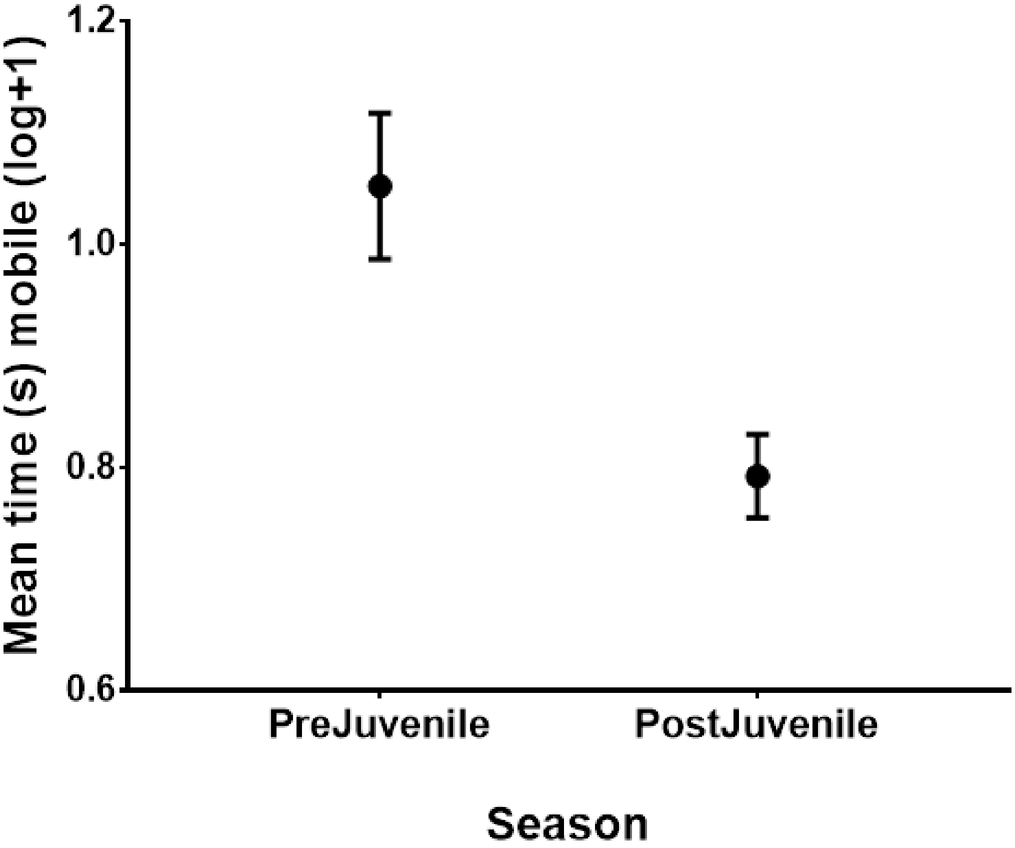

Figure 1.6. The effect of the prejuvenile (N=136) and postjuvenile (N=624) seasons on average time spent mobile (s) during the handling bag test (t=3.029, df=758, p=0.0025). Bars represent standard error of the mean (SEM).

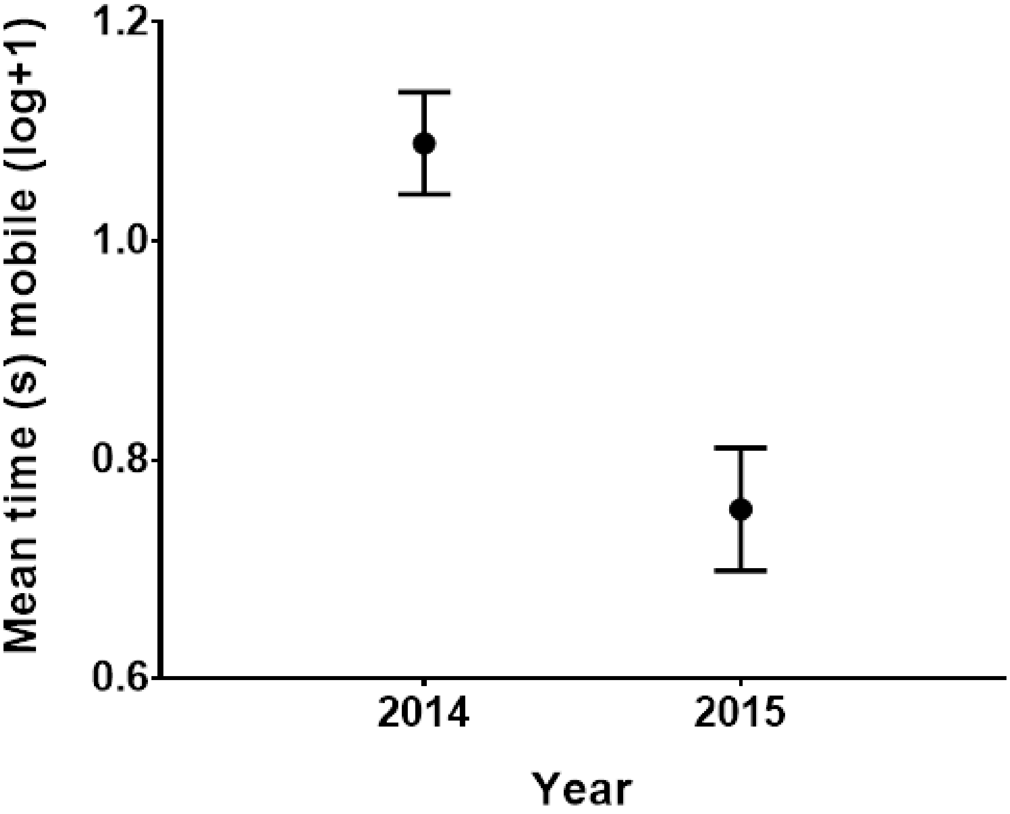

Figure 1.7. The effect of year on average time spent mobile (s) during the handling bag test during 2014 (N=513) and 2015 (N=237; t=4.257, df=748, p<0.0001). Bars represent standard error of the mean (SEM).

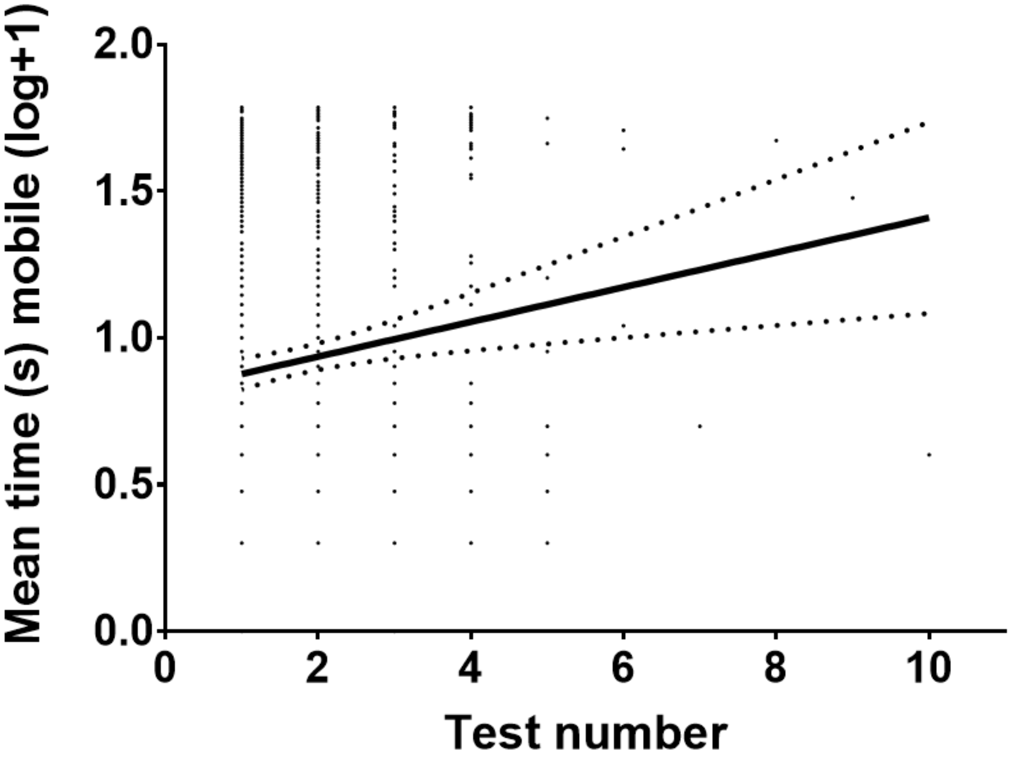

Figure 1.8. **The effect of test number on the time spent mobile in handling bag test ($F_{1,748}$=8.767, p=0.0032, Y=0.05912*TestNumber+0.8183, N=750). Solid line represents line of best fit with 95% confidence intervals (dotted lines).**

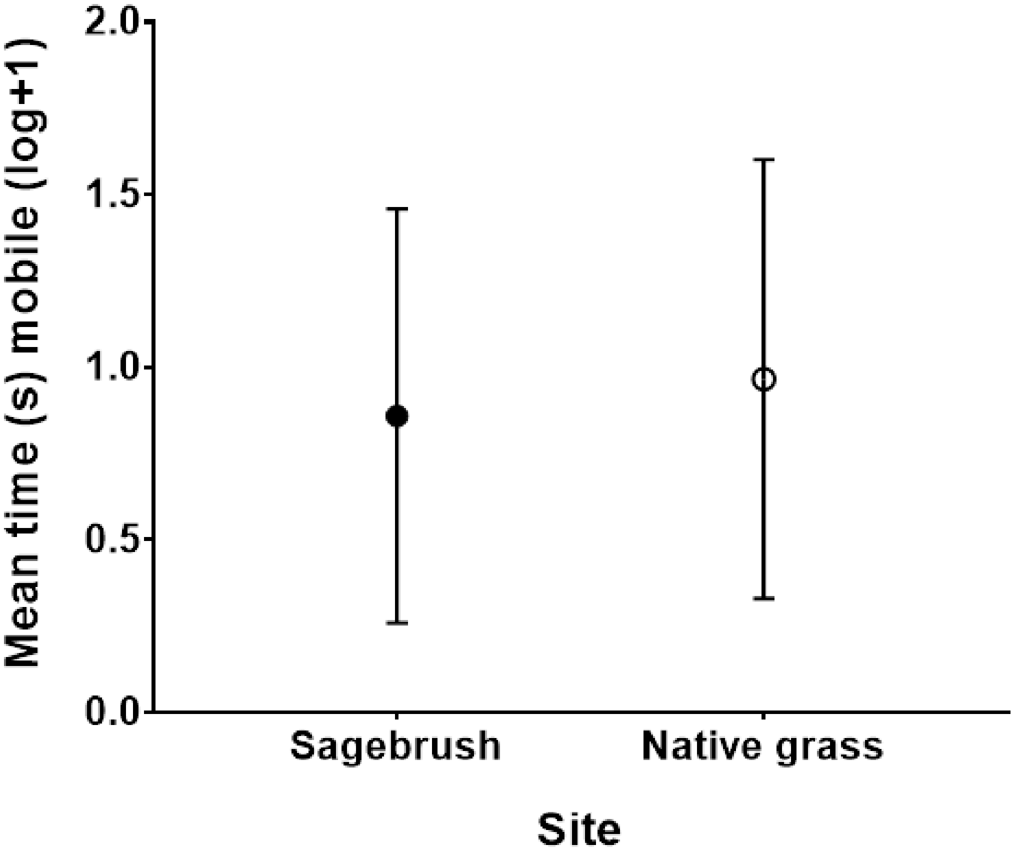

Figure 1.9. The effect of site (i.e., habitat type) on average time spent mobile (s) during the handling bag test at the sagebrush site (N=157) and in the native grass habitat (N=215). Bars represent standard error of the mean (SEM).

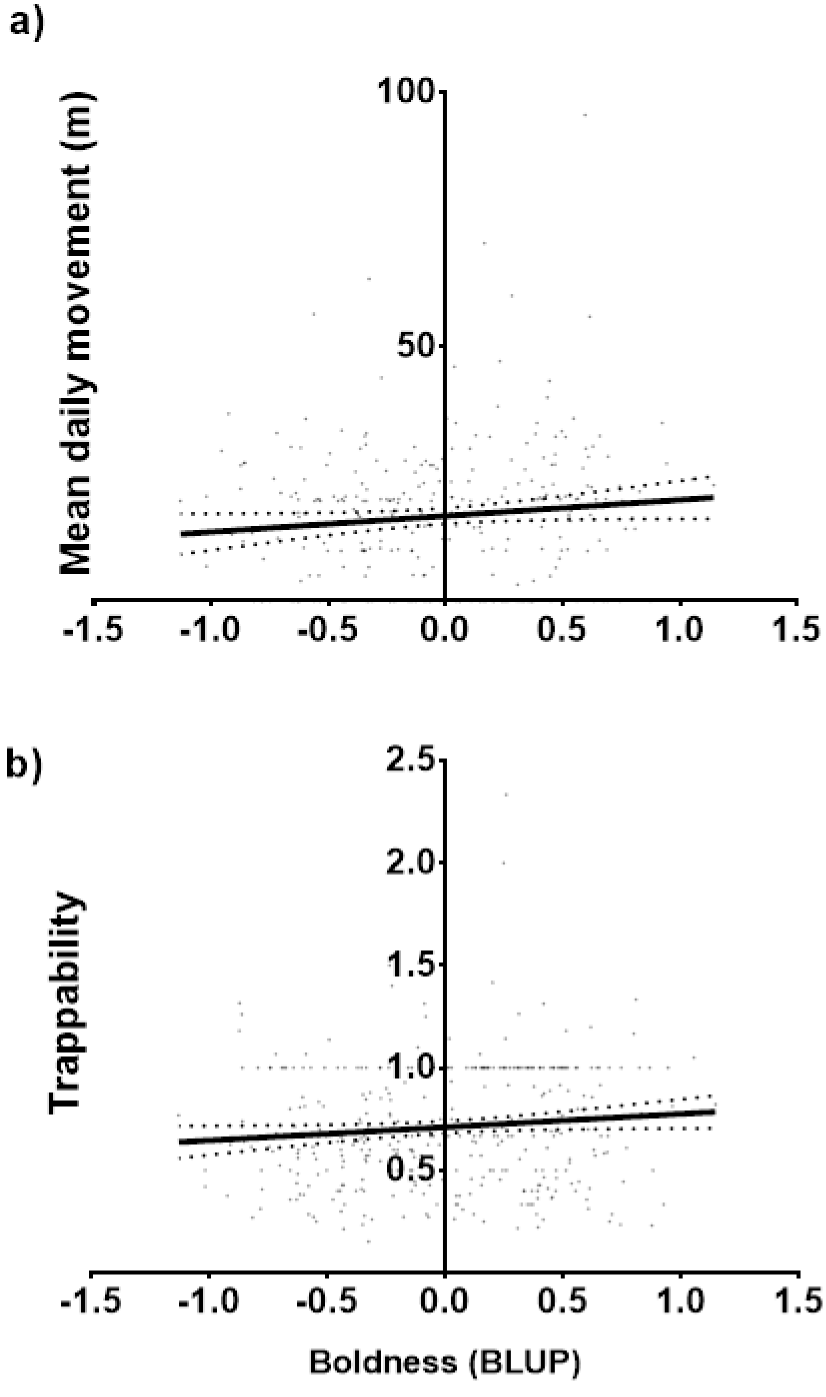

Figure 1.10. Effect of boldness (quantified by best linear unbiased predictors, BLUP) on (a) mean daily movement (in meters; $F_{1,290}$=3.501, p=0.0623, Y=3.152*BLUP +16.75) and (b) trappability ($F_{1,369}$=3.891, p=0.0493, Y=0.06473*BLUP + 0.7109). Solid lines represent lines of best fit with 95% confidence intervals (dotted lines).

CHAPTER 2: VARIATION IN BOLDNESS PREDICTS SURVIVORSHIP OF A CRITICAL PREY SPECIES IN STRUCTURALLY VARIABLE HABITATS

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Abstract

Animal behavior, which can vary spatially, temporally, and across contexts, has been shown to influence significant life history characteristics, such as survivorship. Variation in behavior can be attributed to difference in sex, age, and environmental conditions, among others. However, behavioral differences among individuals within a population that are consistent across time and contexts (i.e., personality traits) exist and create a heterogeneous behavioral landscape. Personality traits such as boldness, a personality trait representing the willingness of an individual to engage in risky behavior, may help predict individual and community-level consequences, such as survivorship. We investigated the relationship between boldness and survivorship overall and how that relationship is influenced by sex, year, and habitats that differ in cover. Specifically, we estimated daily survivorship of a wild population of Piute ground squirrels (*Urocitellus mollis*) in yearly intervals from 2013-2016 using live mark-recapture trapping. We estimated boldness using an in-field behavioral assay and linear mixed models. We found that the addition of boldness in survivorship models significantly increased our power to predict survival. Boldness had a negative relationship with survivorship. The negative effect of boldness on survivorship was slightly stronger for females than for males, did not vary in effect size by year, and was stronger in the high cover habitat type than the low cover. These results outline the importance of behavioral variation as a driver of important life history consequences, such as survivorship. Animal personality is an emerging and important tool to predict life-history consequences of individuals and therefore improve our understanding of how populations change over time and across space.

Introduction

The primary objective in conservation biology and wildlife management is to conserve species and their habitats over time, across space, and in the face of environmental change. To do so, information about how populations vary over time and across space is needed. The process of population fluctuation due to the addition of individuals from birth and immigration and the removal of individuals from death and emigration is referred to as population dynamics. Therefore, population dynamics are a net result of the collective fates of individuals within a population. Traditionally, population dynamics have been quantified as the number of individuals experiencing each life history characteristic (i.e., birth, immigration, death, or emigration). However, by simply identifying the fates of individuals, there is very little predictive power, and projecting how populations will fluctuate in the future is difficult.

To better understand the mechanisms that lead to the fates of individuals, research has turned to animal behavior. Animal behavior has long been shown to influence significant life history characteristics (Berger-Tal and Saltz, 2016). Additionally, behavioral strategies will vary among individuals, which will therefore lead to differences in life history characteristics among individuals within a population (Lima and Zollner, 1996). For instance, variation in behaviors among individuals that influence probability of predation or starvation interact with external factors, such as predator density or food availability, to give rise to differential rates of survival among individuals. While understanding the behaviors that lead to life history consequences of individuals is important for understanding the current state of a population, researchers still lack the ability to predict how animals will behave in the future and, therefore, lack the ability to predict how populations will fluctuate in the future. Therefore, it is not only important to understand behaviors and the consequences of those behaviors given different environmental contexts, but also the consistency in which individuals express these behaviors. By focusing on consistent behaviors, we can predict the behavior an individual will express and the consequence of that behavior before specific events occur.

While variation in behavior among individuals within the same population has been well-documented (Clark and Ehlinger, 1987; Huntingford, 1976), the source of this variation was largely left unexplained or attributed to statistical noise (Dall et al., 2004). Recently, research has suggested that behavioral variation may be attributed to consistent behavioral differences among individuals across time and contexts, which are referred to as personality traits (Dingemanse and Réale, 2005; Réale et al., 2007). Personality traits have been documented in a wide range of taxa (Bell et al., 2009; Michelena et al., 2009;

Rodriguez-Prieto et al., 2009; Sih et al., 2004). Boldness, for example, is a personality trait that reflects the willingness of an individual to engage in risky behaviors. Boldness may be a particularly important personality trait for understanding prey population dynamics because prey behavior is largely characterized by risk avoidance (Lima and Dill, 1990). Among-individual variation in risk-taking behavior can have significant life-history consequences, such as survivorship, reproduction, and dispersal (Bergeron et al., 2013; Møller and Garamszegi, 2012; Réale et al., 2010). For example, boldness has been shown to predict hunting season survival in elk (*Cervus canadensis*) where bold individuals, defined as those who exhibited higher rates of movement throughout the hunting season, were more likely to be harvested than those that moved less (Ciuti et al., 2012). The close relationship between risky behaviors and survivorship coupled with the evidence that the expression of risky behaviors varies consistently among individuals within the same population points to the importance of knowing not only how individuals within a population vary in risk-taking behavior but how that variation (i.e., boldness) influences survivorship (Bergeron et al., 2013; Réale et al., 2010; Smith and Blumstein, 2008).

Overall, boldness has a negative effect on survivorship. However, the effect size of boldness on survivorship can vary due to differences between sexes, among years, among habitat types. For systems where males and females have significantly different life histories, the effect of boldness on survivorship may vary by sex. For instance, boldness has been shown to be positively correlated with movement. Therefore, in populations with male-biased dispersal or where females are more likely to have small natal home ranges, boldness would have a greater effect of the survivorship of males than females. Conversely, in many systems, including bighorn sheep (Réale et al., 2000) and eastern mosquitofish (Wilson et al., 2010), female boldness is positively correlated with reproductive success. The consequence of bold behavior is dependent on the environmental context in which the behavior is being expresses. Environmental characteristics vary over time due to differences in primary productivity, predator densities, population densities, and cover availability. Therefore, the effect of boldness on survivorship may vary temporally, where bold behavior may be more advantageous in a year with very few predators and high cover, but less advantageous in a year with high predators and low cover. Additionally, the environmental riskiness individuals experience can vary spatially, and therefore the negative effect of boldness on survivorship may be higher in a relatively risky habitat and lower in a relatively safe habitat. In Eurasian minnows, boldness had a greater negative effect on survivorship in minnows that lived in a stream with high predator and parasite risk than those that lived in a relatively safe stream with low predator and parasite risk (Kortet et al., 2015). Therefore, while individuals express consistent risky behaviors over time and across contexts (i.e. boldness), the life history consequences of those behaviors are context-specific and may vary by sex, year, and habitat type. Understanding the interplay between boldness and survivorship given different contexts will help us understand current population states and predict population fluctuations in to the future.

In this study, we quantify the relationship between boldness and survivorship of a wild population of Piute ground squirrels (*Urocitellus mollis,* hereafter Piutes) from 2013-2016. First, we predicted that the addition of boldness to survivorship models would improve our estimation of survivorship. Secondly, we predicted that boldness would have an overall negative effect on survivorship. Finally, we predicted that the effect of boldness on survivorship would vary by sex, year, and habitat type. Specifically, we predicted that due to high dispersal rates of male Piutes, the effect of boldness on survivorship would be greater for males than females. There were no notable differences in environmental conditions at our study locations over the four years of the study, so we predicted that the effect of boldness on survivorship would be equal among years. Finally, we predicted that a habitat with no aerial cover would be riskier than a habitat with aerial cover and therefore that the effect of boldness on survivorship would be greater at the riskier habitat. This study is the first step in applying personality of individuals to better estimate survival and, therefore, our ability to understand current and predict future population dynamics.

Methods

Study system

Boldness and survivorship of Piutes were estimated at two study sites located in two structurally distinct habitats. Piutes are ideal subjects for the study of variation in behavior because they are important prey for a variety of predators (Hubbs and Boonstra, 1998; Schmutz and Hungle, 1989). Specific to our system, they occur in relatively high densities (Antolin et al., 2001; Appendix A), they live in a variety of habitat types across their range (Yensen et al., 2003), and they are a major prey species of many aerial and terrestrial predators in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA; Steenhof and Kochert, 1988; Yensen et al., 1992) located in southwestern Idaho (Figure 2.1). This area is home to one of North America's most diverse and dense populations of breeding raptors and exhibits a range of vegetative structure, both of which combine to provide variable fearscapes for Piutes, highlighting the potential importance of understanding the consequences of risky behaviors for Piutes.

Two study sites were randomly established in one of two structurally distinct habitat types that occur across the NCA, defined by the dominant-habitat type: (1) A sagebrush site dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with a native grass understory, and (2) A native grass site dominated by Sandberg's bluegrass (*Poa secunda*) with no shrub cover (Baun et al. 2013; Figure 2.1 and Figure 2.2). These sites were used as part of an ongoing mark-and-recapture trapping study of Piutes from 2013 to 2016 (Appendix A). The study sites are separated by 3.9km.

Live trapping

From 2013-2016, live mark-and-recapture trapping was used to assess basic population dynamics of Piutes at each study site (Anderson et al., 1983) and to perform in-field personality assays. Each trapping web consisted of 96 Tomahawk Live Traps (7x7x41cm; Tomahawk Live Trap Co., Tomahawk, WI) spaced evenly at every 20m along twelve radii measuring 160m in length (Figure 2.3). The total area of each trapping web was 80,425m² or 8.04ha.

Live trapping was conducted in two separate seasons throughout the active season of Piutes, once in late March/early April, before the emergence of juveniles (pre-juvenile season), and a second time in late April/early May, after the emergence of juveniles (post-juvenile season; Table 2.2). A robust sampling design was implemented to assess the individuals' repeatability of behavior to the in-field personality assay (i.e., static handling bag test), as well as assess the impact of varying temporal scales on behavior and survivorship. Each site was pre-baited for three days prior to live trapping to avoid confounding initial trap response (Gurnell, 1980). Upon capture, individuals were covered with burlap and the time of capture, sex, age, weight, and trap location was recorded. Each animal was marked with a passive integrated transponder (PIT) tag (Biomark, Boise, ID) for individual identification.

Quantifying boldness

For each ground squirrel, we measured consistency in individual behavioral traits relating to boldness using a static handling bag test (Martin and Réale, 2008; Réale et al., 2000). Boldness, commonly used as a measure of risky behavior (Petelle et al., 2013; Réale et al., 2007), is here defined as an individual's behavioral response to being trapped and handled. In similar studies on other species, animal with higher cortisol levels (i.e., more stressed) were less mobile (i.e., static) during human handling and consequently defined as docile, or less risky (Koolhaas et al., 1999; Martin and Réale, 2008). Therefore, we attributed higher mobile time during the handling bag test to be an expression of more risky behavior and therefore a measure of boldness.

To measure mobility, ground squirrels were moved from their trap to a dark, cloth handling bag. We then suspended them in the handling bag for one minute and quantified the amount of time (sec) spent mobile (i.e., non-static). The time from collection of a trapped from the trapping the trapping grid until the start of the static handling bag test was recorded and defined as "wait time". Individuals underwent the handling bag test upon each recapture and the test number was recorded as the successive number of times an individual had experienced the test. Test number among individuals ranged from one encounter to 10 with an average of two.

Statistical analyses

A univariate mixed-modeling approach was used to generate boldness scores for individuals using their time spent mobile during repeated handling bag tests (Dingemanse and Dochtermann, 2013). Fixed effects included in the final mixed model included sex, age, wait time, test number, season and year. Individual boldness scores were obtained using best linear unbiased predictors (BLUPs), which provided estimates of random effects independent of other terms within the model, standardized to a mean of zero. For a full description of model construction and selection, see Chapter 1 and Appendix B.

Daily survivorship (s) was estimated using the Huggins p and c "robust" mark-recapture design in Program MARK version 6.2 (Cooch and White, 2001). Model selection using AICc model selection criterion (Hurvich and Tsai, 1989) from a set of *a priori* candidate models. For simplicity, we assumed that immigration (g') and emigration (g") were constant (did not vary by time) and equal to each other. To determine the best model for estimating survivorship, we first ran a set of candidate models (n=6) without boldness as a covariate where probability of capture (p) and probability of recapture (c) were either constant, time-dependent, or equal to each other. Next, we chose the top model from this selection using AICc and used that as the base model structure for all other analyses (Appendix B). To test for the effect of boldness on our ability to estimate survivorship, we used individual boldness scores (i.e., BLUPs) as a covariate of survivorship. This was used when estimating the effect of boldness on survivorship overall, by sex, by year, and by habitat. For effect of year, daily survivorship was estimated for the yearly intervals from 2013 to 2014, 2014 to 2015, and 2015 to 2016.

Linear regressions were used to determine if slopes of relationship between boldness and survivorship varied significantly from zero and, when appropriate, if slopes varied significantly from each other. Regressions were run in R (version 3.2.4; Team, 2014) using the lm package.

Results

Boldness scores were estimated for a total of 372 individuals in 2014 and 2015. Survivorship was estimated using encounter histories from all individuals trapped at both sites from 2013-2016 (N=1,826). For individuals without a boldness score, the population mean was used (i.e., BLUP=0). Of the total individuals caught, 859 were males and 967 were females, 873 were captured at the sagebrush site and 953 were captured at the native grass site.

Survivorship with no behavior

The best model when boldness was not included as a covariate was where probability of capture (p) and probability of recapture (c) were time dependent, but not equal to each other (Table 2.1). Therefore, this structure was used as the base model for all of the following analyses. For model selection results and estimates from the top model, see Appendix B.

Survivorship and boldness overall

Overall, the addition of boldness (BLUP) as a covariate in predicting survivorship greatly improved our model, with the boldness model have an AICc weight of 0.95293 (Table 2.1). There was a negative relationship between boldness and survivorship ($F_{1,99}$=15586, $p<0.0001$, $Y=-0.0008011*BLUP+0.9969$; Figure 2.4). Survivorship estimates were estimated as daily survivorship (i.e., the probability of surviving each day), so while the difference between the minimum (0.99574) and maximum (0.99769) daily survival seems small, the minimum annual survivorship (0.21051) is more than half that of the maximum annual survivorship (0.42993) where the annual interval is 365 days.

Survivorship and sex

When compared to the "no behavior" model, estimating survivorship for sexes separately greatly improved the model with an AICc weight of 0.99992 (Table 2.1). Overall, males had a lower daily survivorship (0.996494) than females (0.997390). When compared to the sex-dependent model, the addition of boldness (BLUP) as a covariate when estimating survivorship of the sexes separately improved the model with a combined AICc weight of 0.95675 (Table 2.1). Testing whether the effect of boldness on survivorship was equal among sexes (sex + BLUP) or varied by sex (sex * BLUP) showed that both models were competing (within 2 delta AICc) and were therefore model-averaged. Again, boldness had an overall negative effect on daily survivorship of both males ($F_{1,99}$=21475, p<0.0001, Y=-0.0007779*BLUP+0.9964) and females ($F_{1,99}$=11359, p<0.0001, Y=-0.0008062*BLUP+0.997) and effected females slightly more than males ($F_{1,198}$=9.394, p=0.0025; Figure 2.5).

Survivorship and year

When compared to the "no behavior" model, estimating survivorship separately each year greatly improved the model with an AICc of 0.82788 (Table 2.1). Daily survivorship was highest during the 2014-2015 interval (0.9983074) and lowest during the 2015-2016 interval (0.9967049). Refer to Appendix A for more details. When compared to the year-dependent model, the addition of boldness (BLUP) as a covariate of survivorship of the years separately improved the model with an AICc weight of 0.95288 (Table 2.1). Testing whether the effect of boldness on survivorship was equal among years (year + BLUP) or varied by year (year * BLUP) showed that the effect of boldness on survivorship was equal among years (Table 2.1). Overall, boldness had a negative effect on daily survivorship in all years (2013-2014: $F_{1,99}$=16376, p<0.0001, Y=-0.004949*BLUP+0.9976; 2014-2015: $F_{1,99}$=24847, p<0.0001, Y=-0.004949*BLUP+0.998; 2015-2016: $F_{1,99}$=11869, p<0.0001, Y=-0.001767*BLUP+0.994; Figure 2.6).

Survivorship and habitat

When compared to the "no behavior" model, estimating survivorship separately by habitat greatly improved the model with an AICc of 0.99999 (Table 2.1). Daily survivorship was higher at the sagebrush site (0.9974728) than at the native grass site (0.9965094). When compared to the habitat-dependent model, the addition of boldness (BLUP) as a covariate of survivorship greatly improved the model with an AICc of 0.72835 (Table 2.1). Testing whether the effect of boldness on survivorship was equal among sites (site + BLUP) or varied by site (site * BLUP) showed that the effect of boldness on survivorship varied by site (Table 2.1). Overall, boldness had a negative effect on daily survivorship at the sagebrush ($F_{1,99}$=3762, p<0.0001, Y=-0.001448*BLUP+0.9972) and the native grass site ($F_{1,99}$=587964, p<0.0001, Y=-0.0001413*BLUP+0.9965) and effected daily survivorship at the sagebrush site more than the native grass site ($F_{1,198}$=3064, p<0.0001; Figure 2.7).

Discussion

In this study, boldness had a negative effect on survivorship overall, by sexes, by year, and by habitat and the addition of boldness as a covariate of survivorship greatly improved model likelihood in all cases. With such strong evidence for the negative relationship between boldness and survivorship, one might expect that over time, bold individuals would be removed from the population and only less bold, or shy, individuals would remain. However, recent work suggests that variation in boldness within populations may be maintained due to fitness trade-offs (i.e., the trade-off hypothesis; Sih et al., 2004) where the fitness consequence of boldness may vary depending on context. In a meta-analysis by (Smith and Blumstein, 2008), bolder individuals generally have greater reproductive success but lower survivorship. Therefore, the bold phenotype may be maintained over time despite lower survivorship through greater fecundity (Dugatkin and Alfieri, 2003; Wolf et al., 2007). At the time of the Smith and Blumstein review, the relationship between personality traits and survivorship had only been described in captive and managed populations. However, recent work has demonstrated that personality can predict survivorship of individuals in wild populations, such as in Eastern chipmunks (Bergeron et al., 2013), and Piutes in our study, though studies of this nature are still relatively uncommon (Berger-Tal et al., 2015).

In this study, we measured fitness by survivorship. However, fitness can be measured in many other ways, particularly in regards to reproductive success. As stated earlier, the offset of boldness evolutionarily may be the benefit of increased fecundity for bold individuals. In the future, we suggest the relationship between boldness and reproductive success and the heritability of boldness in this species should be investigated to understand the long-term effects of boldness on overall fitness.

Survivorship, boldness, and sex

In the Smith and Blumstein (2008) meta-analysis, they found that aggression, which has been shown to correlate with boldness (Huntingford, 1976; Riechert and Hedrick, 1993; Wolf et al., 2007), has a positive effect on survival and that the positive effect was larger in females than in males. This observation is inconsistent with our results where the negative effect of boldness on female survivorship was greater than that of males. There has been evidence to suggest a positive relationship between boldness and reproductive success in female mink (*Mustela vison*; Korhonen et al., 2002) and big horn sheep (*Ovis canadensis*; Réale et al., 2000). For mink, boldness was positively correlated with litter size and for big horn sheep, boldness was correlated with increased weaning success and a younger age of sexual maturity. While more bold females may produce more young and have more successful reproduction, there may be a trade-off between reproductive success and female survivorship, as outlined in Williams (1966). Reproduction is energetically costly, so an increase in litter size or reproductive effort may increase the energy requirements for a female and decrease survivorship. This theory also supports the evolutionary basis of why personality types are maintained, outlined in Wolf et al. (2007), where they propose that the fitness benefits of investing in reproduction early (i.e., bold females) may be balanced by the risk of not investing in other behaviors such as predation avoidance, foraging, etc.

Survivorship, boldness, and year

In this study, we found that survivorship varied by year and that the effect of boldness on survivorship was equal among years. This study focused on a four-year span with three yearly intervals, so our conclusions on these results are limited to this temporal scale. However, if this pattern were to hold and we had knowledge of the heritability of boldness behavioral phenotype, it could have implications for predictability of negative selection on boldness over time.

Survivorship, boldness, and habitat

In this study, we found that the effect of boldness on survivorship varied significantly by habitat type. It should be noted that these results are limited due to our sampling of one site per habitat type, therefore conclusions based on these results may be limited to this spatial scale. However, our results do suggest that the effect of boldness on survivorship may be spatially explicit. The biotic and abiotic components of an animal's environment which contribute to its relative riskiness (i.e., "fearscape") has been shown to affect behavior and survivorship in significant ways (Brown, 1999; Camp et al., 2012; Urban, 2007). Difference in mean boldness due to relative habitat risk has been noted in other taxa. For example, Eurasian minnows (*Phoxinus phoxinus*) that lived in a relatively risky tributary (i.e., high predation and parasitism) exhibited higher mean boldness than minnows in a less risky tributary of the same river system (Kortet et al., 2015). In Chapter 1, we found that mean boldness did not differ by habitat type. Therefore, it is likely that habitat type is not shaping how bold individuals are, but rather differentially influencing the consequence of boldness (e.g., survivorship) within populations. We predicted that boldness would have a larger effect on individuals from the native grass habitat type than the sagebrush due to the lack of vegetative structure and the negative relationship between riskiness and survivorship. However, this prediction was not consistent with our results where the effect of boldness on survival was higher at the sagebrush site where there was more cover compared to the native grass site. For this study, we defined the riskiness of the habitat by the relative risk attributable to the level of physical cover, however cover may not be the only contributor to the riskiness of a habitat.

For Piutes, it is possible that the density of subterranean burrows could vary by habitat type resulting in a difference in overall refuge. In 2013, a burrow-count study was conducted on these sites as part of a method validation study. The study found that burrows existed in higher densities at the native grass site (133 burrows/ha) than at the sagebrush site (49 burrows/ha; Yensen, et al., 2014 *unpub*). Potentially, the lack of shrub cover at the native grass site is off-set by the increase in burrows and therefore eliminating an uneven selective pressure on risky behavior. The relative quality of differing refuge types may depend on the diversity and type of predators present. For instance, at the native grass site, the most commonly encountered predator type may encounter may be aerial due to the lack of aerial prey cover and lack of terrestrial predator concealment. Additionally, at the sagebrush site, the most commonly encountered predator type may be terrestrial because aerial predators are deterred by the aerial cover and terrestrial predators are able to approach more readily due to increased terrestrial concealment (Camp et al., 2012). As such, there may be balanced trade-offs between visibility to detect specific predators that is afforded by low over and concealment to prevent detection by predators that is afforded by high cover (Crowell et al., 2016).

An additional explanation for a higher effect of boldness on survivorship at the sagebrush site could be the interference of vegetative structure on how alarm calls propagate through the immediate population. Ground squirrels (*Urocitellus sp.*) emit and react to a variety of alarm calls in response to the danger of predators (Sherman, 1985). Alarm calls of Gunnison's prairie dogs (*Cynomys gunnisoni*) are transmitted differently in habitats the differ in habitat structure where maximum distance travelled by the call was lower and frequency of the call was higher in habitats where vegetative cover was highest (Perla and Slobodchikoff, 2002). It is possible that alarm calls are overall less likely or more difficult to be heard at the sagebrush site due to the dense vegetation resulting in a higher overall predation pressure.

Conclusion

Overall, we have demonstrated the strong relationship between animal personality and survivorship which can have far-reaching impacts on conservation and management of captive and wild animals. This study provides evidence that boldness has a significant effect on survivorship of a critical prey species in the wild and that the addition of boldness as a predictor when modeling greatly increases our ability to estimate survivorship. Population dynamics has been studied for decades, however wildlife managers continue to struggle with predicting population cycles and how populations will respond to increasing anthropogenic impacts. By providing one possible mechanism predicting survivorship, we can improve our predictive models of population dynamics and improve our understanding of how populations vary temporally, spatially, and across contexts. In doing so, we may better inform conservation and management strategies including population management plans, reintroduction and translocation efforts, captive breeding programs, and predictive population modeling. Additionally, our data suggest that the effect of boldness on survivorship varies by sex and habitat, but not by year. Therefore, while it is important to understand the overall effect of personality on life-history traits, it is likely that these effects differ by demographic groups and across habitat types. In the face of increasing habitat fragmentation due to habitat loss, degradation, and conversion, understanding the impact of personality on significant life-history consequences can help us to understand how populations within those varying habitats can respond to environmental change. The next step for this research is to model these factors (i.e., sex, year, and habitat) together and describe their interactions with boldness.

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Table 2.1. Models evaluating the effects of sex, year, habitat, and boldness (represented by best linear unbiased predictors; BLUP) on estimating daily survivorship (s). For the “no behavior” model results, the top two models from a set of six candidate models were used to determine the best survivorship model without the inclusion of sex, year, habitat, or boldness. Model parameters were probability of capture (p), probability of recapture (c), immigration (g’) and emigration (g”) and were either constant (.) or varied by time (t). The conditions of p and c from the top model from this initial analysis were used in all remaining models (i.e., p(t)c(t)g’=g”(.)). For sex, year, and habitat, we also tested whether the effect of boldness (BLUP) on daily survivorship was equal over each level of the parameter (+; e.g. for males and females) or varied by level (*). Number of parameters (K), AICc, delta AICc, AICc weights, and model likelihood values are presented for all models. Models in bold were the top models used in analysis and represented in Figures 2.4 - 2.7.

Effect	Model	K	AICc	Delta AICc	AICc Wt	Model Likelihood
No behavior						
	s(.)p(t)c(t) g'=g"(.)	**18**	**20925.83**	**0**	**1**	**1**
	s(.)p(t)c(.)g'=g"(.)	11	21138.12	212.2887	0	0
Overall						
	s(BLUP)	**12**	**24233.96**	**0**	**0.95293**	**1**
	s(.)	12	24239.97	6.016	0.04707	0.0494
Sex						
	s(sex)	**19**	**20896.91**	**0**	**0.99992**	**1**
	s(.)	18	20915.85	18.9351	0.00008	0.0001
Sex and Behavior						
	s(sex + BLUP)	**20**	**20891.4**	**0**	**0.68278**	**1**
	s(sex * BLUP)	**21**	**20893.23**	**1.8263**	**0.27397**	**0.4013**
	s(sex)	19	20896.92	5.5184	0.04325	0.0633
Year						
	s(year)	**12**	**24239.97**	**0**	**0.82788**	**1**
	s(.)	10	24243.12	3.1414	0.17212	0.2079

Year and Behavior						
	s(year + BLUP)	**12**	**24233.96**	**0**	**0.95288**	**1**
	s(year)	12	24239.97	6.016	0.04706	0.0494
	s(year * BLUP)	14	24253.39	19.4283	0.00006	0.0001
Habitat						
	s(habitat)	**19**	**20909.07**	**0**	**0.99999**	**1**
	s(.)	18	20932.07	23.0021	0.00001	0
Habitat and Behavior						
	s(habitat * BLUP)	**21**	**20901.96**	**0**	**0.72835**	**1**
	s(habitat + BLUP)	19	20904.09	2.1321	0.25082	0.3444
	s(habitat)	19	20909.07	7.1091	0.02083	0.0286

Table 2.2. Schedule of events from 2013-2016 during the pre-juvenile (PreJuv) and post-juvenile (PostJuv) seasons. "X" denotes that the activity was performed during the corresponding timeframe.

Activity								
Handling bag test			X	X	X	X		
Trapping	X	X	X	X	X	X	X	X
	PreJuv	PostJuv	PreJuv	PostJuv	PreJuv	PostJuv	PreJuv	PostJuv
	2013		2014		2015		2016	

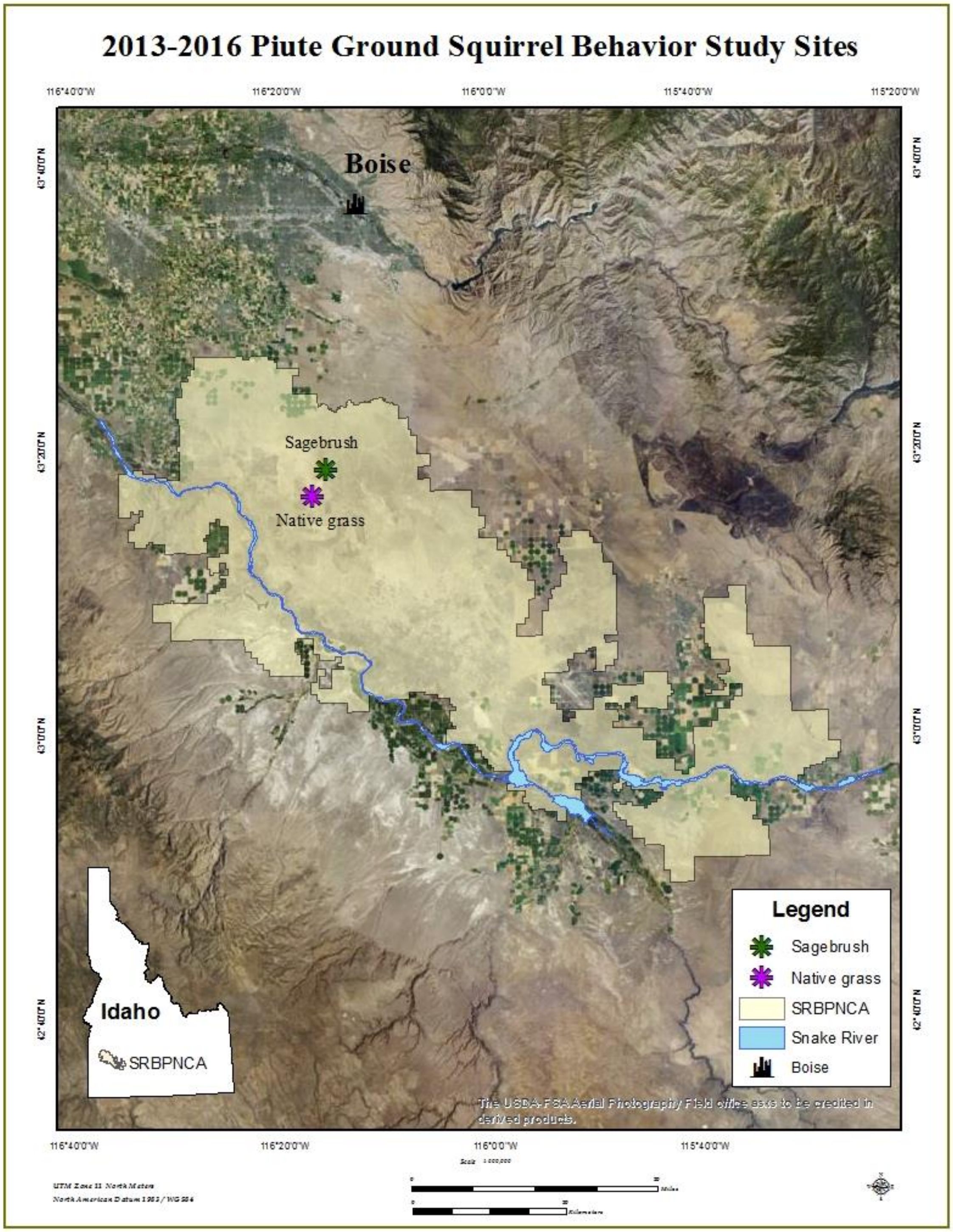

Figure 2.1. Map of study sites dominated by sagebrush (*Artemisia tridentata wyomingensis*) and native grass (*Poa secunda*) where behavior and survivorship was measured for Piute ground squirrels (*Urocitellus mollis*). The sites are located south of Boise, Idaho within the Snake River Birds of Prey National Conservation Area. UTMs of grid center points- sagebrush: 11T E560018, N4795703; native grass: 11T E558430, N4792390.

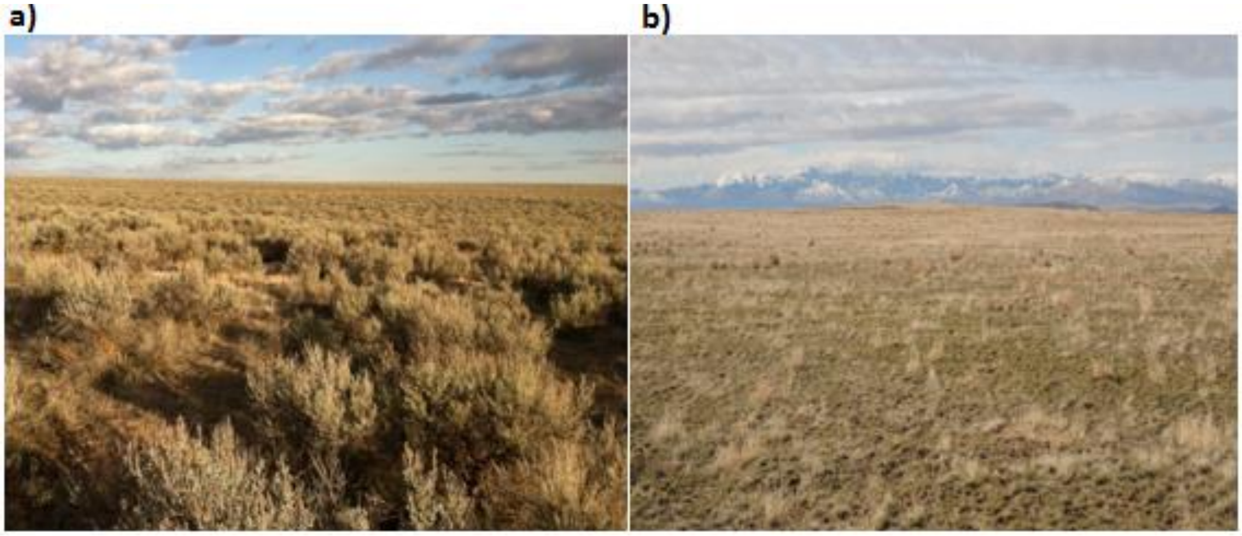

Figure 2.2. 2013-2015 study sites: (a) site dominated by sagebrush (*Artemisia tridentata wyomingensis*) and (b) site dominated by native grass (*Poa secunda*). Photos taken by Zoe Tinkle, 2013.

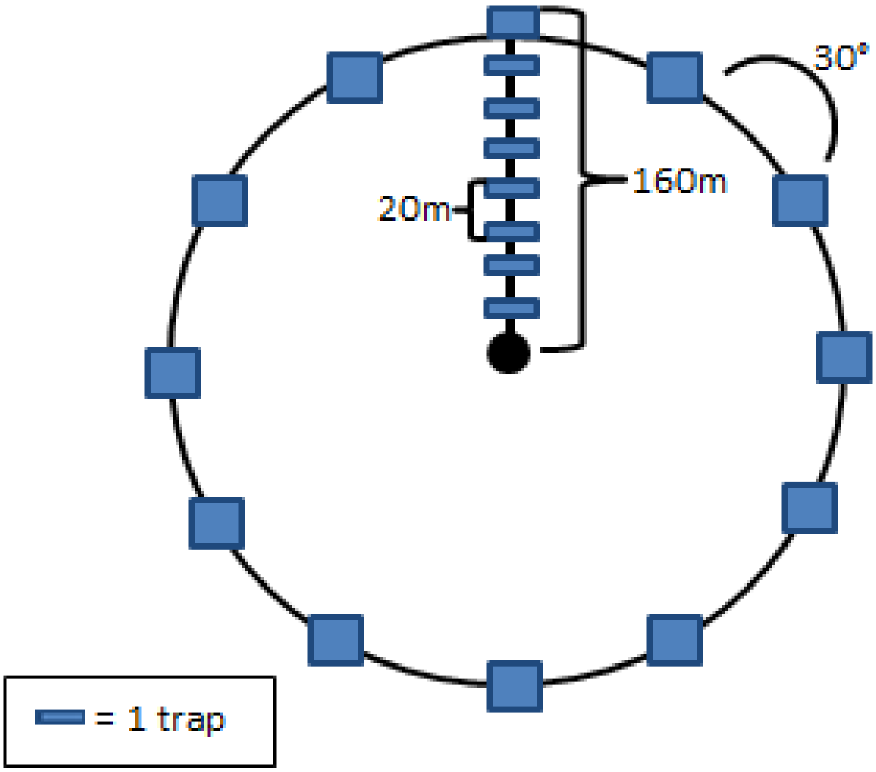

Figure 2.3. Graphical representation of live trapping web lay-out. Each web consists of twelve radii spaced by 30 degrees and 96 traps evenly spaced at every 20m along each radius.

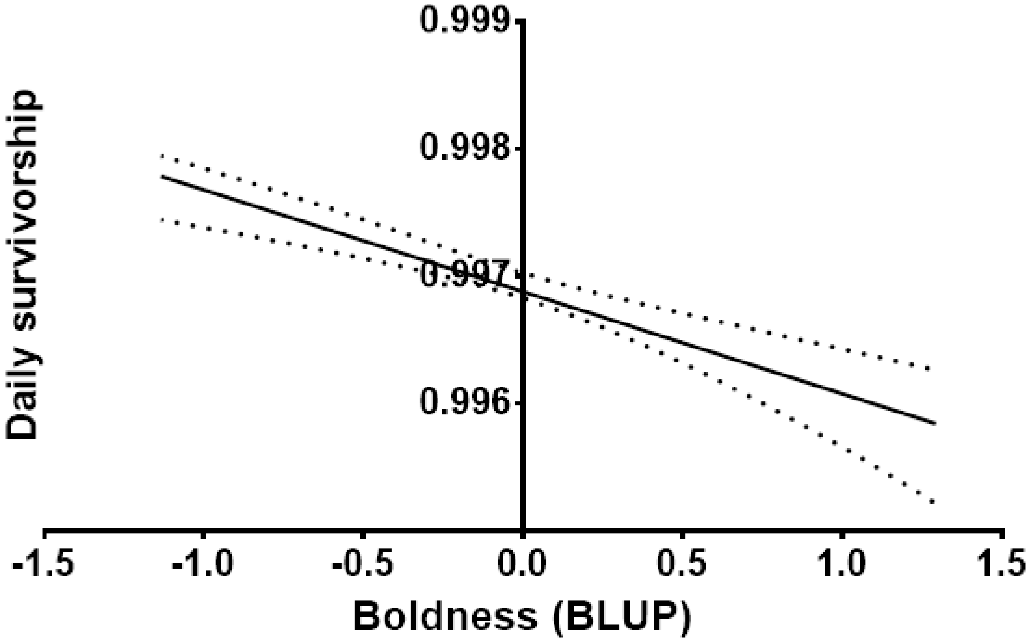

Figure 2.4. The overall relationship between boldness (quantified by best linear unbiased predictors; BLUP) and daily survivorship ($F_{1,99}$=15586, p<0.0001, Y=-0.0008011*BLUP + 0.9969) for all individuals trapped at the sagebrush and native grass site 2013-2016. Dotted lines represent standard error of the mean (SEM).

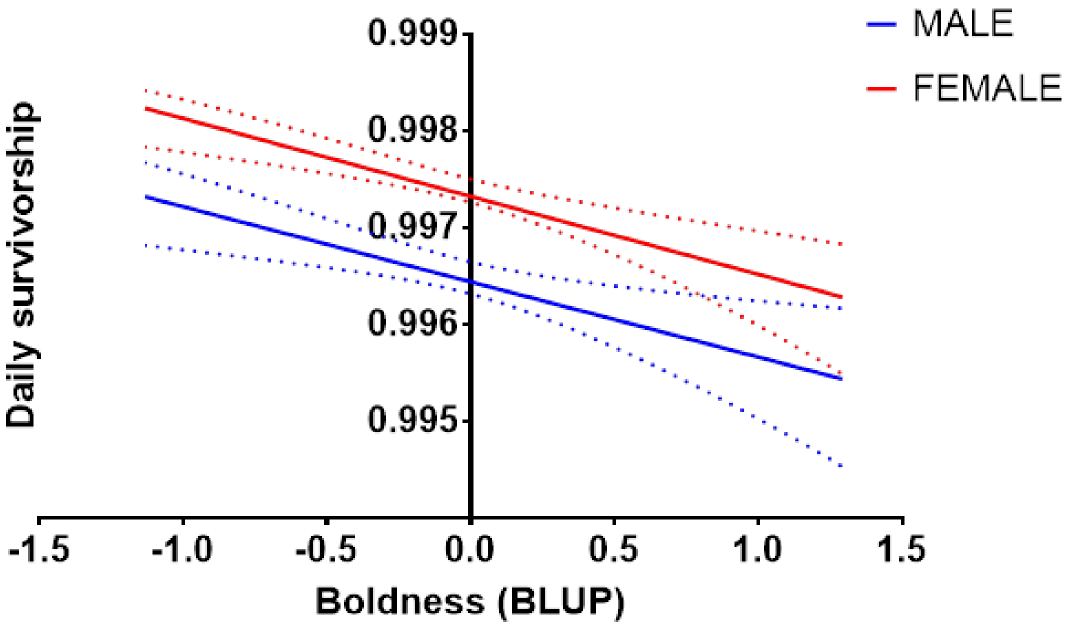

Figure 2.5. The overall relationship between boldness (quantified by best linear unbiased predictors, BLUP) and daily on survivorship in males ($F_{1,99}$=21475, p<0.0001, Y=-0.0007779*BLUP+0.9964) and females ($F_{1,99}$=11359, p<0.0001, Y=-0.0008062*BLUP+0.997). The effect of boldness on daily survivorship was greater in females than males ($F_{1,198}$=9.394, p=0.0025). Dotted lines represent standard error of the mean (SEM).

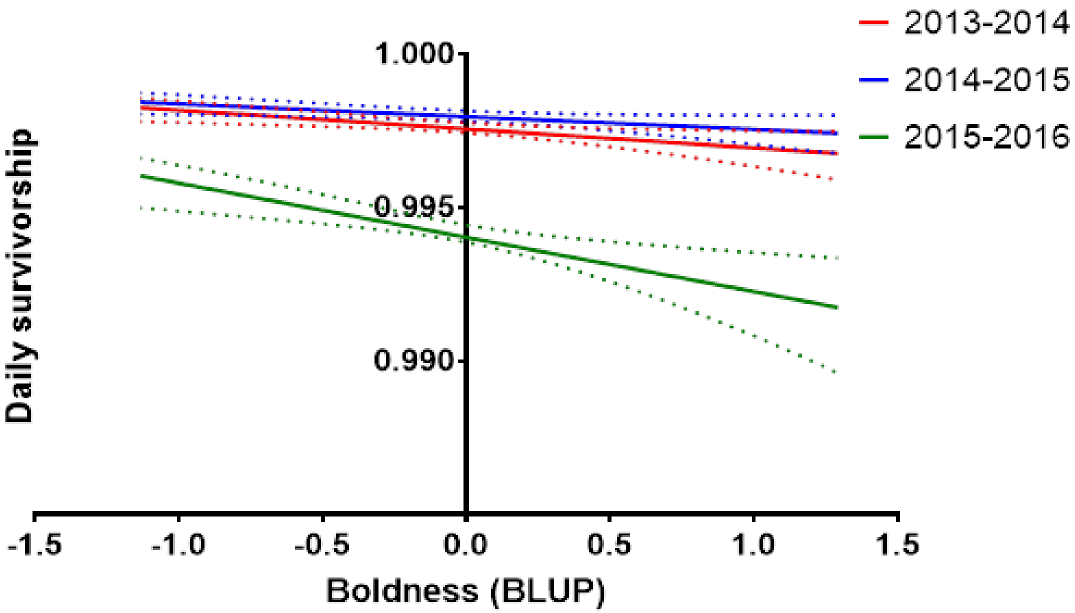

Figure 2.6. The effect of boldness (quantified by best linear unbiased predictors, BLUP) on daily survivorship over all years (2013-2014: $F_{1,99}$=16376, p<0.0001, Y=-0.004949*BLUP+0.9976; 2014-2015: $F_{1,99}$=24847, p<0.0001, Y=-0.004949*BLUP+0.998; 2015-2016: $F_{1,99}$=11869, p<0.0001, Y=-0.004949*BLUP+0.994). Dotted lines represent standard error of the mean (SEM).

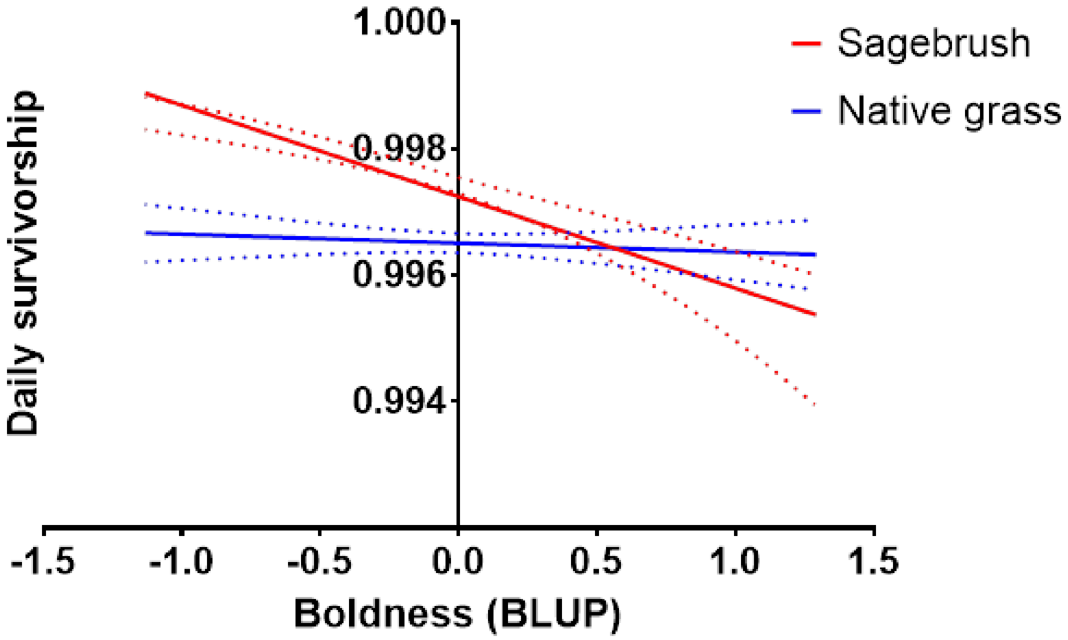

Figure 2.7. The effect of boldness (quantified by best linear unbiased predictors, BLUP) on daily survivorship at the sagebrush site ($F_{1,99}$=3762, p<0.0001, Y=-0.001448*BLUP+0.9972) and the native grass site ($F_{1,99}$=587964, p<0.0001, Y=-0.0001413*BLUP+0.9965). Boldness had a greater effect on survivorship at the sagebrush site than the native grass site ($F_{1,198}$=3064, p<0.0001). Dotted lines represent standard error of the mean (SEM).

GENERAL DISCUSSION

Overall, this study assessed the variation in risky behavior within and among individuals and the ecological importance of this variation in its power to predict behaviors associated with risk (i.e., trappability; Chapter 1) and survivorship (Chapter 2). In Chapter 1, we first found that risky behavior (i.e., time spent mobile during the handling bag test) varied by sex, age, wait time in trap, test number, season, and year, but not by habitat type. We then found that risky behavior was repeatable (30%) within individuals. In other words, of the variation observed in time spent mobile during the handling bag test, 30% is due to differences among individuals not explained by significant fixed effects (i.e., sex, age, wait time, test number, season, and year). This suggests that the handling bag test is a valid test for detecting a personality trait (i.e., boldness) in a wild population of prey. As in other species (i.e., eastern chipmunks, *Tamias striatus*; Montiglio et al., 2012, and brushtail possums, *Trichosurus vulpecula*; Mella et al., 2015), the handling bag test is a predictive measure of the personality trait boldness and therefore a reflection of an individual's willingness to engage in risky behaviors. It is likely that this technique can be used for many other species, particularly for prey where behavior is largely driven by the need to avoid predation risk. The handling bag test is a relatively inexpensive, non-invasive technique that, coupled with significant fixed effects, has the potential to uncover the underlying behavioral traits that can significantly influence life-history consequences and decision-making.

In the first chapter, we also investigated the ecological significance of this consistent variation in risky behavior (i.e., boldness) and found that boldness was positively correlated with trappability. The willingness of an individual to enter a baited trap reflects its willingness to engage in a risky behavior, therefore individuals with greater trappability are expected to be more risky (i.e., more bold). In North American red squirrels (*Tamiasciurus hudsonicus*), trappability was negatively correlated with over-winter survival of females and positively correlated with the probability of offspring overwinter survival (Boon et al., 2008). Therefore, the variation in riskiness associated with trappability could contribute significantly to predicting fitness tradeoffs and, therefore, our ability to predict population dynamics patterns over time.

In Chapter 2, we found that boldness, overall, greatly improved our models estimating daily survivorship. The failure to acknowledge consistent intra-individual differences in behavior could lead to less accurate survivorship estimates. In fact, DiRienzo et al. (2013) found that in predator-prey models using crickets and black widow spiders, taking in to account not only the personality traits of the prey (syntopic field cricket, *Gryllus integer*), but also of the predator (black widow spider, *Latrodectus hesperus*) and the combination during predator-prey encounters greatly increased (3-10 times) their understanding and predictability of prey survivorship and predator success. Secondly, we found that overall, boldness was negatively correlated with daily survivorship. Survivorship, along with reproductive success and dispersal, contributes to the overall population dynamics patterns we measure in wildlife conservation and management. Our ability to not only obtain more accurate estimates of survivorship with known variation in personality, but to describe the underlying mechanisms that contribute to variable survivorship is crucial in predicting individual and population-level patterns over time, space, and contexts. Decreased survivorship for bold individuals has been shown in other taxa in response to predation by both non-human (meta-analysis: Smith and Blumstein, 2008) and human predators (Ciuti et al., 2012; Madden and Whiteside, 2014). If human hunters and natural predators are targeting prey with the same personality type, it is possible that selection pressures on bold personality types may overcome the trade-offs of increased fecundity and narrow the variation in behavioral types within a population.

The results from this study could also be used to inform management decisions where the reintroduction or translocation of a species is necessary. For example, swift foxes (*Vulpes velox*) that were more bold were less likely to survive reintroduction (Bremner-Harrison et al., 2004) and, conversely, Tasmanian devils that survived translocation were 3.5 times more bold than those that did not survive (Sinn et al., 2014). Results suggest that the relationship between boldness and survivorship is species or context specific, and understanding the personality traits and individual expressed could greatly increase the success of reintroduction and translocation projects.

With this well-documented relationship between boldness and decreased survivorship, one may expect that selection would favor shy (i.e., less bold) individuals and that the bold phenotype would be removed from populations. However, the bold phenotype is maintained, and, in fact, populations typically exhibit a large amount of variation in behavioral phenotypes. One possible explanation for this is the fitness trade-offs, where the fitness consequence of boldness may vary depending on context (i.e., the trade-off hypothesis; Sih et al., 2004). For example, a bolder individual could benefit in certain habitats or situations, such as when boldness allows for increased foraging time, but in other situations it might be less advantageous, such as in the presence of predators (Smith and Blumstein, 2008).

Therefore, to understand the context-specific consequences of boldness, we investigated the interaction between boldness and sex, year, and habitat in predicting survivorship. We found that the effect of boldness of survivorship varied significantly by sex, year, and habitat, suggesting that, while the overall effect of boldness on survivorship is negative, the effect size depends on context. There are likely interactive effects among these three factors that should be explored in future analyses.

Understanding the predictors and consistency of behavioral variation within and among individuals greatly increased our ability to predict survivorship overall and under specific contexts. The results from this study suggest that the inclusion of such variation is vital to predictive population dynamics models. In the future, the relationship between behavioral variation and reproductive success and dispersal, vital contributors to population dynamics models, should also be investigated for this species.

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APPENDIX A

2013-2016 Piute ground squirrel population densities in the Orchard Combat Training Center, Southwestern Idaho

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Introduction

Demographic characteristics of a population estimated from field studies serve to inform the basis of wildlife population biology and, ultimately, the development of effective population management strategies. For most populations, these demographic characteristics can be summarized by the widely-used “BIDE” equation (Mills, 2012):

$$N_{t+1} = N_t + B + I - D - E$$

This equation is used to determine the abundance (N) at a given time ($t + 1$) by taking the abundance at the previous time step (t) and adding the number of individuals entering the population through birth (B) or immigration (I) and then subtracting the number of individuals leaving the population through death (D) or emigration (E). This simplified summary of demographic characteristics can be applied at finer scales within a population (i.e., males vs. females or separate age classes) to better estimate the state of the population where these groups experience differences in birth, immigration, death, and emigration rates. However, the measurement of these parameters is complicated by uncertainty and often requires a great deal of effort and time to obtain. Capture-mark-recapture (CMR) sampling methods can be used to obtain estimates of abundance, density, and survivorship of a subsample within a population of interest, which can then be applied to larger population scales. Computer programs such as MARK (White and Burnham, 2010) and DENSITY (Efford, 2012) have been developed to allow researchers to obtain these population parameter estimates from CMR datasets.

Often, the development of research projects on population demographics is prompted by the need to monitor, protect, or restore a species or population of concern. The Great Basin of the western United States is home to many species of conservation interest for land managers, including the Piute ground squirrel (*Urocitellus mollis*, hereafter Piutes). Piutes are small, ground-dwelling squirrels that serve as a critical prey species for many aerial and terrestrial predators in the Morley Nelson Snake River Birds of Prey National Conservation Area (hereafter SRBPNCA (Steenhof and Kochert, 1988; Yensen et al., 1992) including prairie falcons (*Falco mexicanus*; Steenhof and Kochert, 1988) and American badgers (*Taxidea taxus*; Messick and Hornocker, 1981). Established in 1993, the SRBPNCA's 600,000 acres in southwestern Idaho (www.blm.gov) is host to one of North America's highest diversities and largest densities of breeding raptors. As such, Piutes are considered a critically important prey species to monitor over time and across variable habitats.

Here, we provide a brief summary of (1) population density and (2) survivorship of Piutes in four habitat types within and among years.

Methods

Study sites

The study area falls within the boundaries of the Morley Nelson Snake River Birds of Prey National Conservation Area (hereafter, SRBPNCA) in southwestern Idaho, specifically the area within and immediately surrounding the boundaries of the Orchard Combat Training Center (OCTC). In 2013, three live trapping sites were established and located in a habitat dominated by vegetation types found commonly throughout the SRBPNCA. One site was located in habitat dominated by native shrub Wyoming big sagebrush (*Artemisia tridentata wyomingensis*, ARTR), a second site was located in habitat dominated by a native bunchgrass, Sandberg's bluegrass (*Poa secunda*, POSE) with no shrub cover, and a third site was located in habitat dominated by exotic annual species, mostly cheatgrass (*Bromus tectorum*), bur buttercup (*Ceratocephalus testiculata*), and some exotic mustard species (EXAN, Figure A.1).

In 2014, these three site locations were used again as well as the addition of three paired sites in the same habitat types. Also in 2014, two additional sites were established in a fourth habitat type dominated by forage kochia (*Bassia prostrata*, BAPR) for a total of eight study sites in 2014 (Figure A.1, Figure A.2). The study sites trapped in 2014 were trapped again in 2015. For all habitat types surveyed, sites located outside the OCTC were located no more than 5km from their paired site inside the OCTC (Figure A.1 and Table A.1). Naming conventions for sites included their four-letter site acronym and a number depicting whether the site was located inside (1) or outside (2) the Orchard Combat Training Center (Table A.1).

Study species

Piute ground squirrels, previously known as Townsend's ground squirrels (*Spermophilus townsendii*), are relatively small ground squirrels distinguished by their small external ears, light ventral and darker dorsal sides, and short tail (Yensen et al., 2003b). The largest populations of Piutes are found in the BOPNCA, and they are the only ground squirrel species found within the boundaries of the OCTC (Yensen, 2000; Yensen et al., 2003b).

Piutes are obligate hibernators and they are only active from late January/early February to late May/June. When summer temperatures increase to more than 40°C and resources become limited, Piutes will go below ground and spend the next eight months in torpor (Sharpe and Van Horne, 1999; Smith and Johnson, 1985). Piute diets consist mostly of grass seeds and leaves, forb seeds and leaves, roots and sometimes shrubs, including sagebrush and winterfat (*Krascheninnkovia lanata*), when resources are limited (Van Horne et al., 1998; Yensen and Quinney, 1992).

Live trapping

At each study site, a circular trapping web was established for live capture-mark-recapture trapping. The center of each web was located semi-randomly to ensure the edge of the trapping web did not overlap any roads and that the trapping web stayed within the intended vegetation type with a minimum 100m-buffer around the web. From the center point, 12 radii spaced 30° apart extended out a distance of 160m each (320m diameter). Trap locations were spaced by 20m along each radius and marked with pin flags. Eight trap locations were marked per radius for a total of 96 trap locations per trapping web (Figure A.3).

At each study site, Piutes were live-trapped, processes, marked, and released at the point of capture. Two trapping seasons were established during the Piute active seasons from 2013-2015, one to trap adults prior to juvenile emergence and a second to trap adults and juveniles after the juveniles have emerged (Table A.1). Trapping seasons were no more than six days long and were separated by at least two weeks in all cases. For analysis, a robust design method was used which makes the assumption that the population is closed during trapping seasons (no birth, death, immigration or emigration), but open between seasons and among years.

For live trapping, one Tomahawk live trap (7x7x41 cm; Tomahawk Live Trap Co., Tomahawk, WI) was placed at each trap location along the trapping web radii. Each trapping web was pre-baited for three or four days prior to trapping. Pre-baiting is used to enhance trap response by effectively habituating the squirrels to the traps and allowing squirrels to come in contact with bait before live trapping occurs (Gurnell, 1980).

During trapping days, all traps were opened shortly after sunrise and baited with peanut butter and oats. Once a ground squirrel was captured, the trap was carried to a processing station located off the trapping web. For processing, squirrels were moved from the trap to a pre-weighed cloth handling bag. Once in the handling bag, squirrels were weighed to the nearest 5g using a Pesola^{TM} hand-held balance and the sex and age was recorded. Sex was determined by urogenital distance and age was determined by body size and mass as either juvenile or adult. In 2013, the age class "yearling" was included but was subsequently removed as an option in 2014 due to inconsistency in the differentiation between yearling and adult ground squirrels in the field.

Each ground squirrel was scanned during processing for the presence of a passive integrated transponder (PIT) tag. If one was detected, the unique alpha-numeric identification code and the label of the trap in which the individual was captured was recorded. If no PIT tag was detected, a 12mm 125 kHz or an 8.4mm 134.2 kHz PIT tag (BioMark, Boise, Idaho) was inserted subcutaneously above the shoulder blades. In accordance with tag weight recommendations, the 8.4mm PIT tags were used to tag ground squirrels weighing less than 80g. After processing, squirrels were put back in to their traps, returned to their point of capture and released.

Density estimates were derived from capture-mark-recapture abundance estimates and has been an *ad hoc* process where the effective trapping area (ETA) was estimated as it was in Yensen et al. (2014) as the area of the circular trapping web with a 10m buffer, making the radii 170m in length and thus making the ETA of each grid equal to 9.08ha.

Analysis of trapping data

Trapping data was inputted into a Microsoft Access database and underwent extensive quality assurance and control (QA/QC) to correct for inconsistent or missing data, when possible. Population estimates were calculated for pre- and post-juvenile trapping seasons separately to account for the increase in population size attributed to the emergence of juveniles, which has been documented to increase by 250% (Yensen et al., 2003a). The robust CMR study design allows for the estimation of survivorship both between trapping seasons and among trapping years.

Daily survivorship, probability of capture, probability of recapture, immigration and emigration rates within and among trapping years was estimated using the software package MARK 6.0 (White and Burnham, 2010). Estimates were calculated using a Huggins' p and c robust design (Huggins, 1989; Pollock et al., 1990) and the Aikaike's Information Criterion corrected for sample size (AICc) weights were used to evaluate the relative support for all candidate models *a posteriori*. For simplicity and based on model selection in previous years, immigration and emigration were for all candidate models were set to be constant and equal to each other. This robust design assumes that the population is closed during trapping seasons and open between trapping seasons. Because trapping seasons take place over a two- to six-day span, it is safe to assume that negligible movement in or out of the population is occurring during this time. Models were built to evaluate the effect of time (i.e., trapping occasion) on survivorship, probability of capture, and probability of recapture. Survivorship estimates were given as daily survivorship (i.e., the probability of survival each day) to enable us to compare sites trapped at different time interval lengths. To calculate the interval survivorship, take the daily survivorship estimate and raise it to the power of the number of days in that interval. For example, if a daily survivorship estimate is equal to 0.9987 over an interval of 365 days, the interval (in this case, yearly) survivorship would be equal to 0.9987^{365} = 0.62204.

All other statistical analyses were conducted using JMP 10.0 (Institute, 2000) and R version 3.2.4 (Team, 2014).

Results

Captures

During this study, we captured 14,352 ground squirrels, 4,326 of which were unique individuals (Table A.2) over four years at eight trapping locations. The overall recapture rate (number of recaptures/total number of captures) was 0.70.

Population Density

Density was highly variable within and among trapping sites. Here, we discuss the overall differences among habitat type and years. Overall, the habitat type (two sites per habitat type, inside and outside the OCTC) with the highest average density of ground squirrels (mean±SEM individuals/ha) was the native grass (31.916±3.582) followed by sagebrush (23.713±2.651), then exotic annuals (20.570±5.337), and the habitat type with the lowest average density was the forage kochia habitat type (14.022±6.470; Figure A.4).

For sagebrush and native grass, average population density was highest in 2013 and 2015 and lowest in 2014 and 2016. For exotic annuals, average densities decreased from 2013 to 2014, but increased every year after (2015 and 2016). Similarly, in forage kochia, average densities increased from 2014-2016 (not trapped in 2013; Figure A.5).

For all habitat types, densities were highly variable by site and an increase in sample size is needed to draw any meaningful conclusions from these data.

Survivorship

Survivorship was relatively steady during the 2013-2014 and 2014-2015 intervals, however for a portion of the sites there was a decline in survivorship from 2015-2016 (Figure A.6). Particularly, at the native grass and sagebrush sites inside the OCTC (these sites were used for Chapter 1 and Chapter 2), survivorship was much lower from 2015-2016 than in previous years. At the sagebrush site, survivorship from 2014-2015 was 0.612 and decreased to 0.209 during the 2015-2016 interval. At the native grass site, survivorship from 2014-2015 was 0.626 and decreased to just 0.127 during the 2015-2016 interval. In 2015-2016, we sent ground squirrel carcasses for testing to the CDC and found the presence of the bacteria *Yersinia pestis* which is responsible for the plague. We believe this year, at these sites, there was an epizootic plague event.

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Table A.1. Dates of Piute ground squirrel live trapping during pre- and post-juvenile emergence seasons in 2013-2016.

	2013		2014		2015		2016	
Site*	PreJuv	PostJuv	PreJuv	PostJuv	PreJuv	PostJuv	PreJuv	PostJuv
ARTR1	March 24, 25, 28, 29, April 2	May 1, 2, 5, 6	March 14-16	April 18-20	February 27, March 3-5, 8, 13	April 3, 7, 9, 12, 25	March 8, 9, 10	April 5, 6, 7
ARTR2	--	--	March 21-23	April 25-27	March 3-5	April 7, 9	March 8, 9, 10	April 5, 6, 7
BAPR1	--	--	March 10-12	April 14-16	March 24-26	April 27-29	February 23, 24, 25	Aril 12, 13, 14
BAPR2	--	--	March 17-19	April 21-23	March 24-26	April 27-29	February 23, 24, 25	Aril 12, 13, 14
EXAN1	March 18, 19, 22, 23	April 25, 26, 29, 30	March 14-16	April 18-20	March 17-19	April 21-23	March 1, 2, 3	April 26, 27, 28
EXAN2	--	--	March 21-23	April 25-27	March 17-19	April 21-23	March 1, 2, 3	April 26, 27, 28
POSE1	March 16, 17, 20, 21	May 2, 3, 7, 8	March 14-16	April 18-20	March 10-12, 14, 20	April 10, 11, 15, 16	March 15, 16, 17	April 19, 20, 21
POSE2	--	--	March 21-23	April 25-27	March 10-12	April 15, 16	March 15, 16, 17	April 19, 20, 21

*Site acronyms: ARTR = Wyoming big sagebrush (*Artemisia tridentata wyomingensis*); BAPR = Forage kochia (*Bassia prostrata*); EXAN = exotic annuals, mostly cheatgrass (*Bromus tectorum*), bur buttercup (*Ceratocephalus testiculata*) and small pockets of exotic mustard species; POSE = Sandberg's bluegrass (*Poa secunda*). Site acronyms ending in the number "1" indicate sites located within the OCTC and those with the number "2" are sites located outside the OCTC.

Table A.2. Number of days trapped, captures, recaptures, unique individuals, and recapture rate of ground squirrels trapped from 2013-2016.

Site	Year	Days trapped	Total captures	Unique individuals*	Recaptures	RecapRate
ARTR1*	2013	9	845	247	598	0.70769231
	2014	6	568	84	484	0.85211268
	2015	11	1133	203	930	0.82082966
	2016	6	1214	315	899	0.74052718
ARTR2	2014	6	99	69	30	0.3030303
	2015	6	203	115	88	0.43349754
	2016	6	249	72	177	0.71084337
BAPR1	2014	6	99	45	54	0.54545455
	2015	6	573	216	357	0.62303665
	2016	6	952	180	772	0.81092437
BAPR2	2014	6	4	3	1	0.25
	2015	6	52	22	30	0.57692308
	2016	6	591	213	378	0.63959391
EXAN1	2013	8	478	182	296	0.61924686
	2014	6	222	29	193	0.86936937
	2015	6	344	103	241	0.7005814
	2016	6	525	219	306	0.5828571
EXAN2	2014	6	122	88	34	0.27868852
	2015	6	587	158	429	0.73083475
	2016	6	603	178	425	0.70480929
POSE1	2013	8	924	345	579	0.62662338
	2014	6	486	70	416	0.85596708
	2015	9	926	239	687	0.74190065
	2016	6	769	273	496	0.6449935
POSE2	2014	6	402	200	202	0.50248756
	2015	5	507	168	339	0.66863905
	2016	6	676	250	426	0.63017751

*Site acronyms: ARTR = Wyoming big sagebrush (*Artemisia tridentata wyomingensis*); BAPR = Forage kochia (*Bassia prostrata*); EXAN = exotic annuals, mostly cheatgrass (*Bromus tectorum*), bur buttercup (*Ceratocephalus testiculata*) and small pockets of exotic mustard species; POSE = Sandberg's bluegrass (*Poa secunda*). Site acronyms ending in the number "1" indicate sites located within the OCTC and those with the number "2" are sites located outside the OCTC.

Table A.3. Piute ground squirrel population structure: gender and age class structure of unique individuals on eight trapping sites within and outside the Orchard Combat Training Center (OCTC) from 2013-2016. Individuals that did not have a sex or age recorded were not included in this analysis. The percentage of adult females in the adult population are compared to values indicated in Antolin et al. 2001.

		Sex			**Age**			**Gender and Age**							
Site	Year	Male	Female	Sex ratio (M:F)	Adult	Juv	Age ratio (J:A)	Adult male	Adult female	Adult sex ratio (M:F)	% Adult female	Juv male	Juv female	Juv sex ratio (M:F)	**TOTAL**
Sage-brush	2013	121	126	0.96:1	210	37	0.18:1	108	102	1.06:1	48.6	12	25	0.48:1	**247**
	2014	94	152	0.62:1	170	76	0.45:1	65	105	0.62:1	61.8	29	47	0.62:1	**246**
	2015	129	199	0.65:1	297	32	0.11:1	115	182	0.63:1	61.3	14	17	0.82:1	**330**
	2016	166	230	0.72:1	277	119	0.43:1	118	159	0.74:1	57.4	48	71	0.68:1	**396**
Native grass	2013	187	156	1.2:1	232	113	0.49:1	143	88	1.63:1	37.9	44	68	0.65:1	**345**
	2014	96	121	0.72:1	175	42	0.24:1	75	100	0.65:1	57.1	21	21	1.0:1	**217**
	2015	132	199	0.66:1	300	31	0.10:1	120	180	0.67:1	60.0	12	19	0.63:1	**331**
	2016	157	169	0.93:1	235	91	0.39:1	109	126	0.87:1	53.6	48	43	1.1:1	**326**

	% Adult Females	
Antolin et al. 2001*		71.3
This study:	2013	43.3
	2014	59.5
	2015	60.7
	2016	55.5

* Percentage of adult females in the adult population compared to values in the Antolin et al. 2001 study.

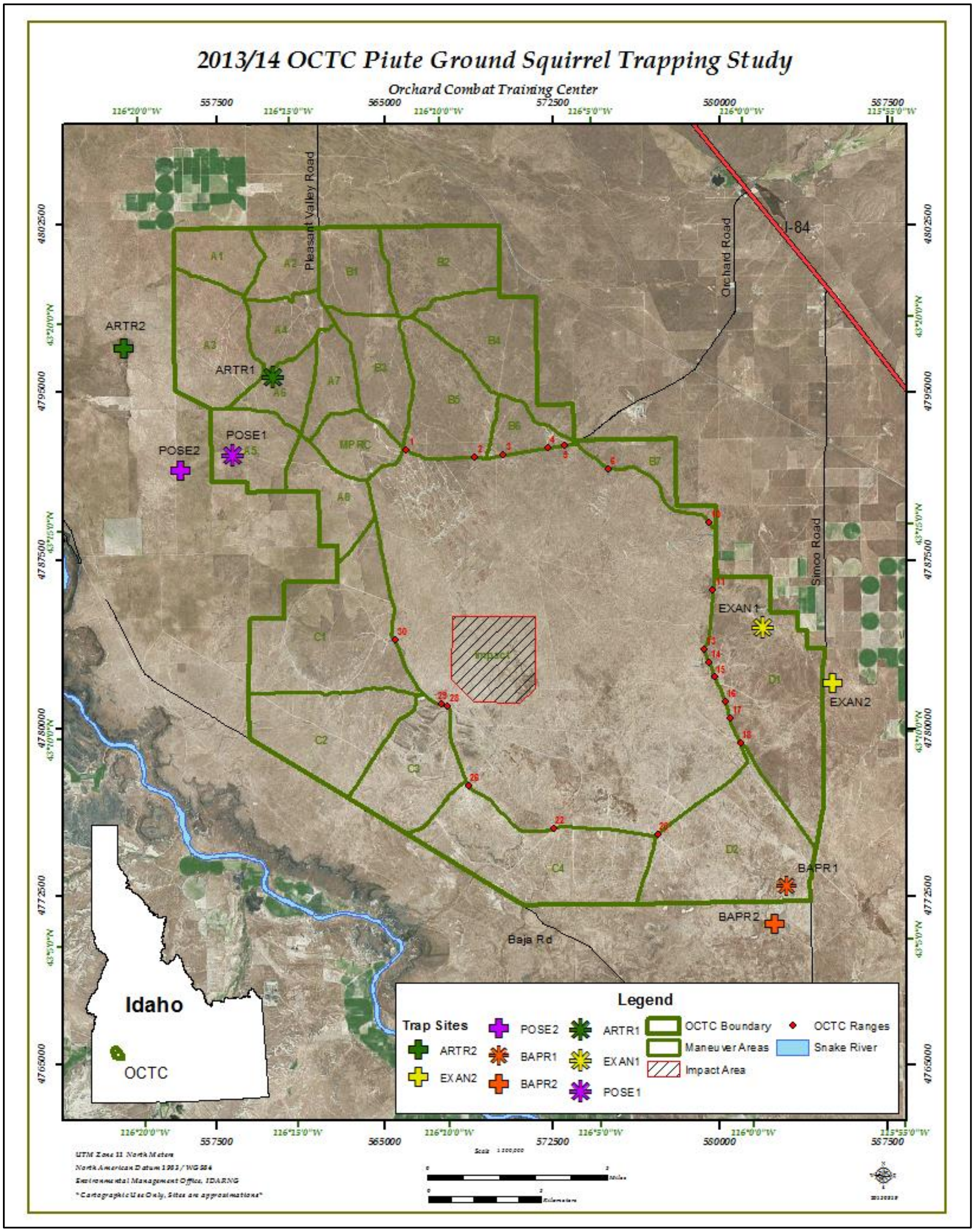


Figure A.1. Map of trapping locations inside and outside the Orchard Combat Training Center (green boundary). ARTR = sagebrush, BAPR = forage kochia, EXAN = exotic annuals, POSE = native grass.

Figure A.2. 2013-2016 Study sites. Top left: dominated by Wyoming big sagebrush (Artemisia tridentata wyo.; ARTR). Top right: dominated by exotic annuals (mostly Bromus tectorum; EXAN). Bottom left: site dominated by Sandberg's blue grass (Poa secunda; POSE) which is a native perennial grass. Bottom right: site dominated forage kochia (Bassia prostrata).

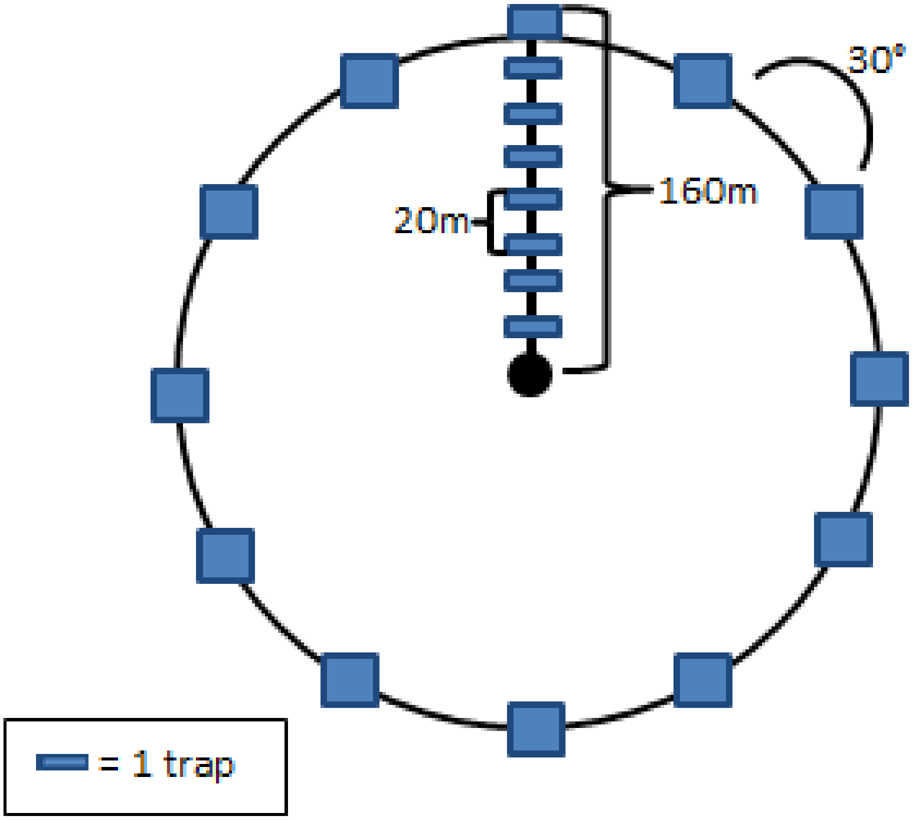


Figure A.3. Graphical representation of live trapping web lay-out. Each web consists of twelve radii spaced by 30 degrees and 96 traps evenly spaced at every 20m along each radius.

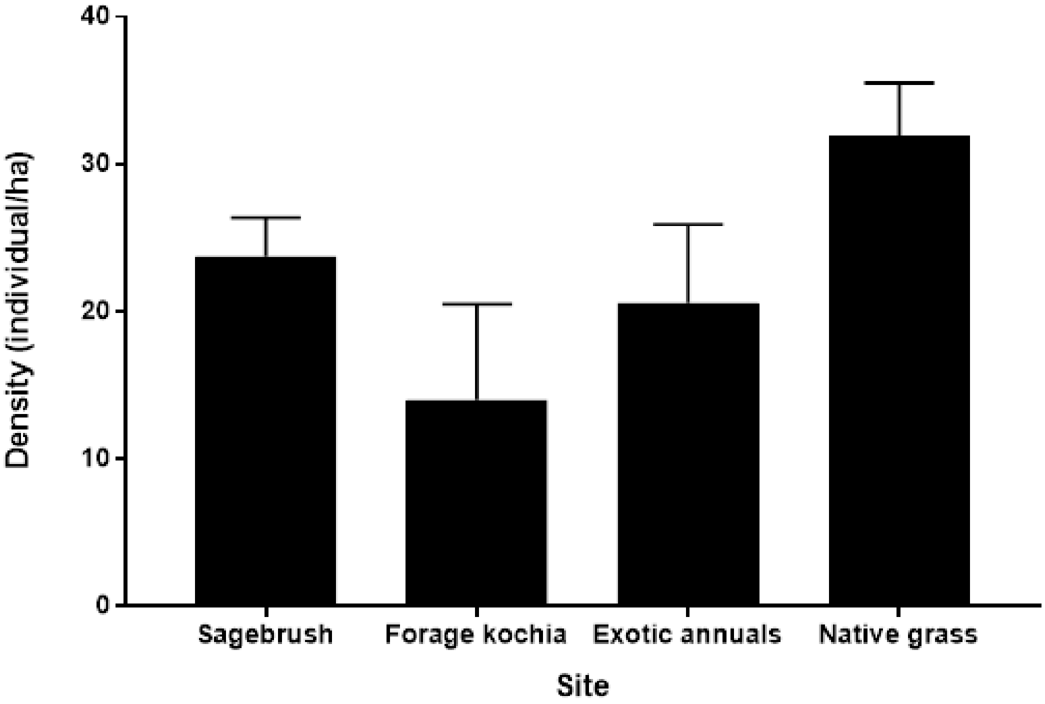


Figure A.4. Average density (individuals/ha) for all sites (inside and outside), all years (2013-2016), all seasons (pre and postjuvenile) by habitat type. Bars represent standard error of the mean (SEM).

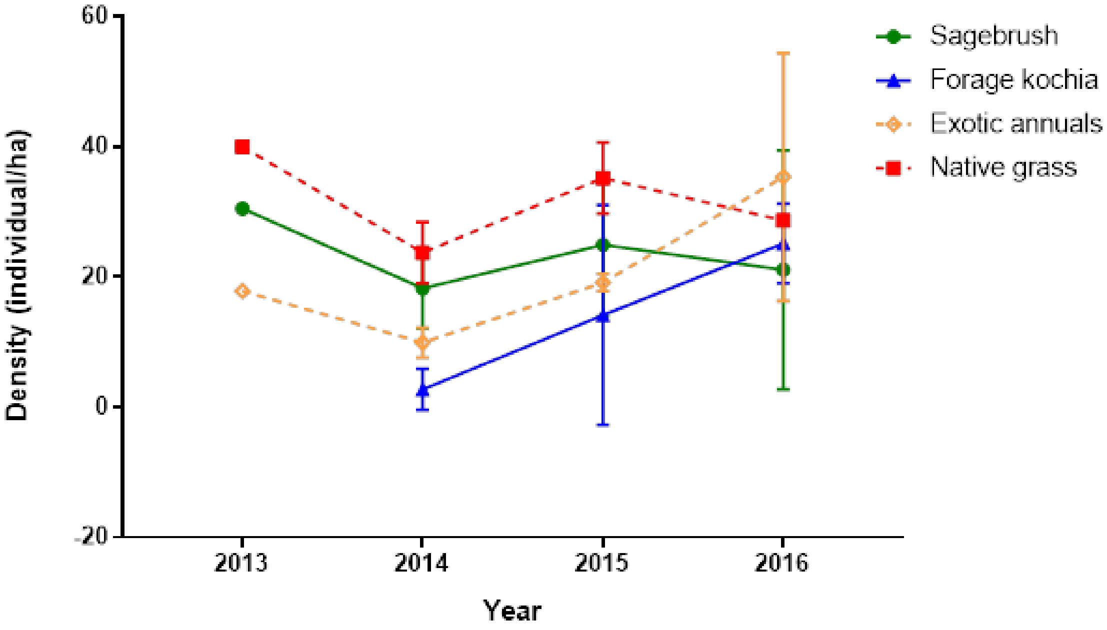


Figure A.5. Average density (individuals/ha) for all sites (inside and outside) and seasons (pre and postjuvenile) over time (2013-2016). Bars represent standard error of the mean (SEM).

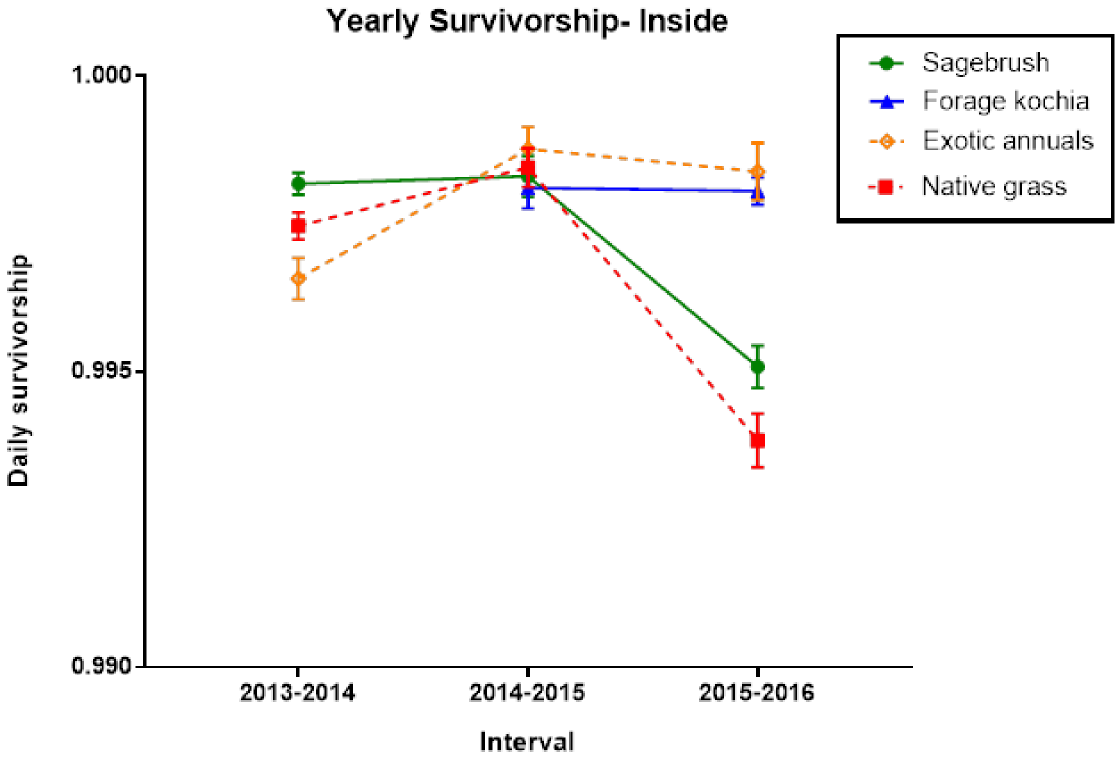


Figure A.6. Daily survivorship for yearly intervals from 2013-2016 at sites located inside (top) and outside (bottom) the Orchard Combat Training Center (OCTC). Bars represent standard error of the mean (SEM).

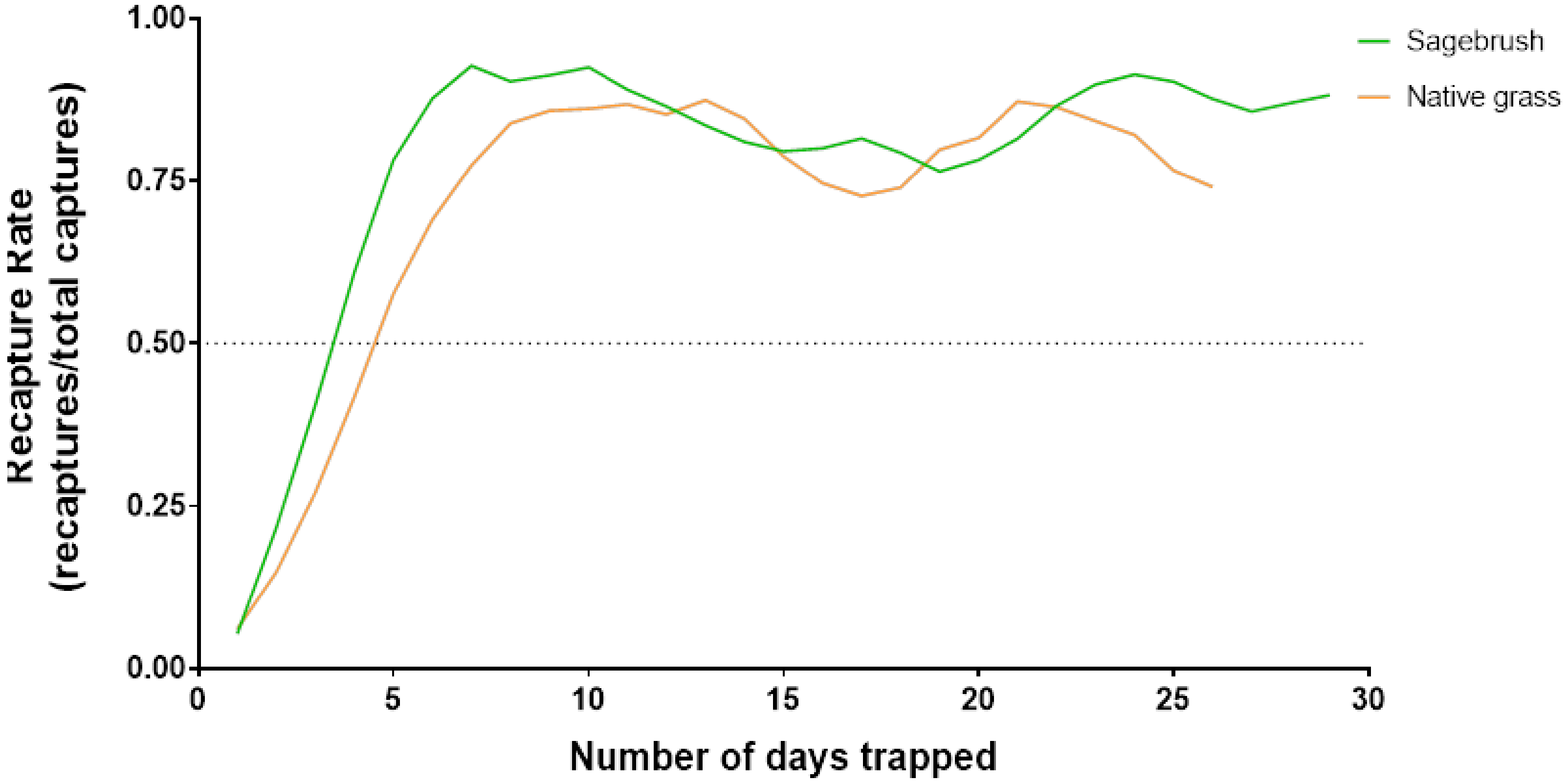


Figure A.7. Recapture rate (number of recaptures/total number of captures) as the number of days trapped increases at the sagebrush (green line) and native grass sites (orange line). The black dashed line is a reference line representing where the recapture rate is 50%.

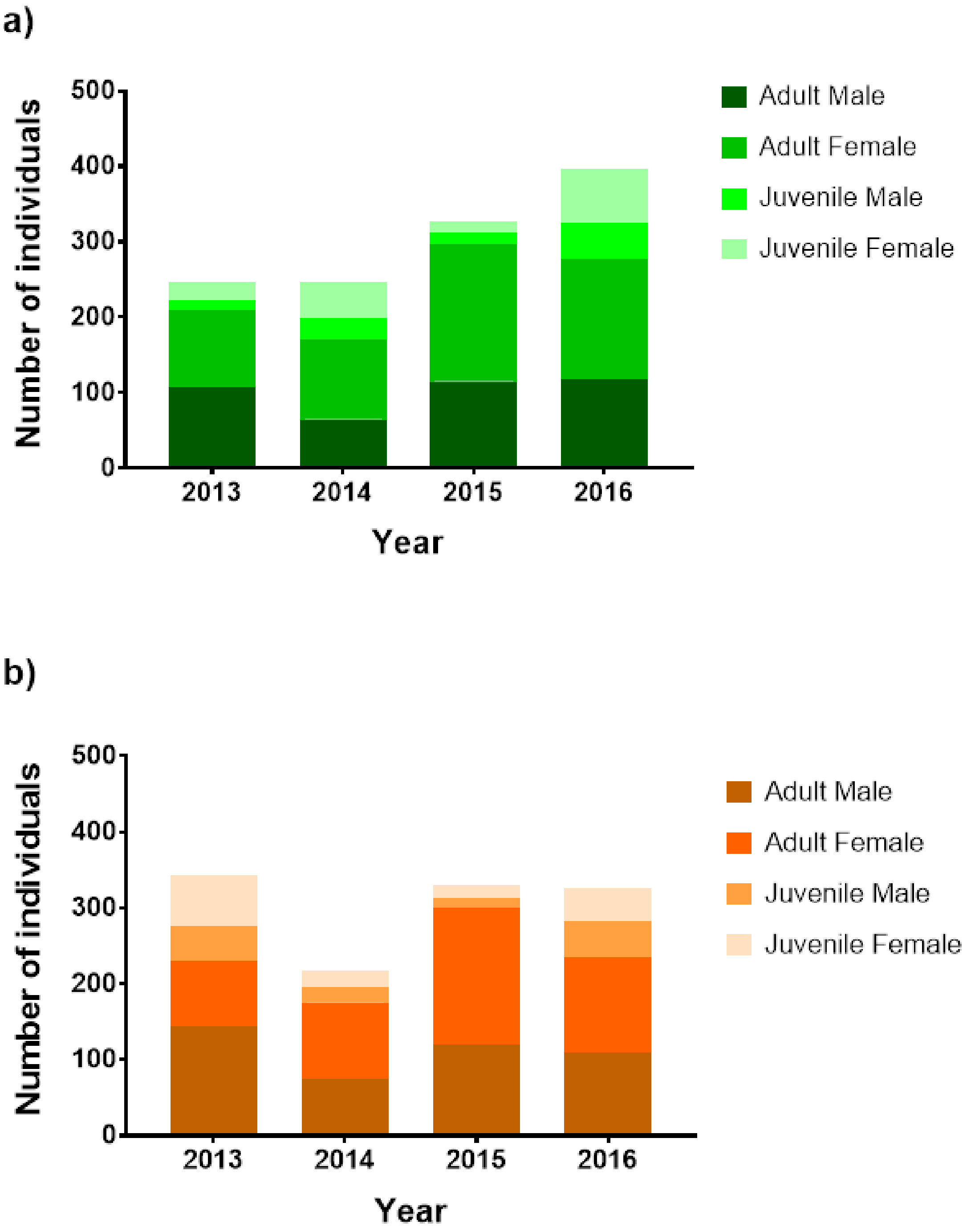


Figure A.8. **Demographics of individuals trapped at the a) sagebrush (green) and b) native grass (orange) sites. Bars represent total number of individuals caught.**

APPENDIX B

MODEL SELECTION AND R CODE

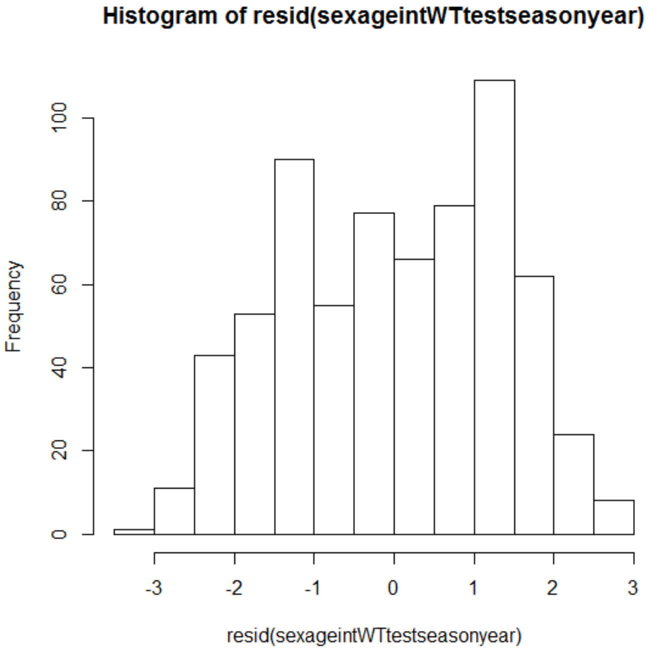
Chapter 1: Mixed Model Results

Fixed-effect model

Model selection based on AICc:

Model	K	AICc	Delta AICc	AICc wt	LL
sex*age+ wait time + test number + season + year	**9**	**2342.01**	**0.00**	**0.93**	**-1161.87**
sex + age + wait time + test number + season + year	8	2347.05	5.03	0.07	-1165.42
weight + wait time + test number + season + year	7	2360.67	18.66	0.00	-1173.25

Test residuals for normality



Top fixed-effect model summary

Terms	Coefficient	SE	t	p
Intercept	1.728221	0.135569	12.748	<0.001
Sex (male)	0.34192	0.114772	2.979	0.003
Age (juvenile)	0.857481	0.191909	4.468	<0.001
Wait time	0.002725	0.001003	2.718	0.00674
Test number	0.131235	0.05418	2.422	0.01569
Season (prejuv)	0.786707	0.191475	4.109	<0.001
Year (2015)	-0.574278	0.142919	-4.018	<0.001
Sex*Age (Male*Juv)	-0.747313	0.281659	-2.653	0.00816

Residual standard error: 1.351 on 670 degrees of freedom
Multiple R-squared: 0.1366, Adjusted R-squared: 0.1275

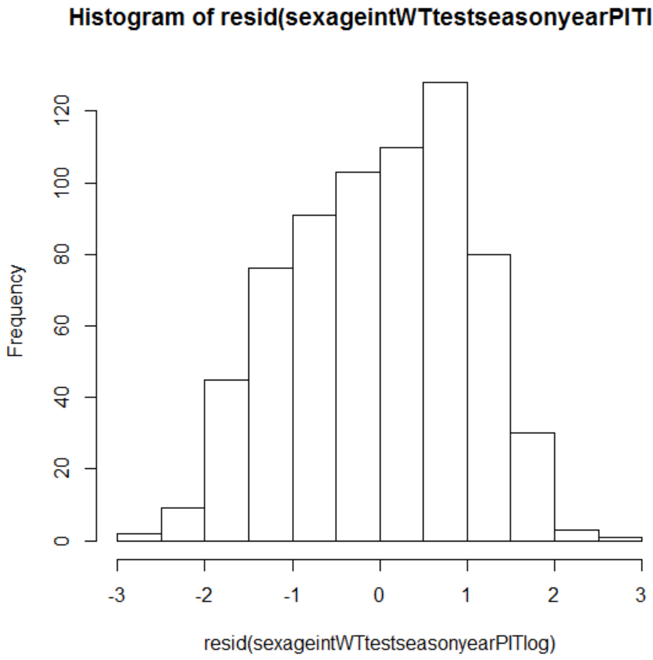
F-statistic: 15.14 on 7 and 670 DF, p-value: < 2.2e-16

Mixed model

Log-likelihood ratio test (fixed effect vs. fixed effect + random effect)
Model 1: log(WIGS + 1) ~ Sex * Age + WaitTime + WIGNUMTOT + Season + Year
Model 2: log(WIGS + 1) ~ Sex * Age + WaitTime + WIGNUMTOT + Season + Year + (1 | PitTagID.)

Model	#Df	LogLik	Df	Chisq	p
1	9	-1161.9			
2	10	-1159.1	1	5.6082	0.01788

Test for normality



Mixed model summary
Random effects:

Groups	Name	Variance	Std.Dev
PitTagID	Intercept	0.5492	0.7411
Residual		1.2880	1.1349

Terms	Estimate	SE	df	t	p
Intercept	1.746586	0.145211	531.9	12.028	<0.001
Sex (male)	0.294607	0.133202	337.1	2.212	0.02766
Age (juvenile)	0.842201	0.197656	605.8	4.261	<0.001
Wait time	0.002699	0.001012	658.5	2.667	0.00784
Test number	0.113063	0.057899	664.6	1.953	0.05127
Season (prejuv)	0.794054	0.184981	652.9	4.293	<0.001

Year (2015)	-0.582418	0.142814	668.8	-4.078	<0.001
Sex*Age (Male*Juv)	-0.734454	0.290286	622.3	-2.53	0.01165

Site effect?

Model 1: log(WIGS + 1) ~ Sex * Age + WaitTime + WIGNUMTOT + Season + Year + (1 | PitTagID.)
Model 2: log(WIGS + 1) ~ Sex * Age + WaitTime + WIGNUMTOT + Season + Year + Site + (1 | PitTagID.)

Model	Df	AIC	BIC	logLik	deviance	Chisq	Chi df	p
1	10	2309.3	2354.5	-1144.7	2289.3			
2	11	2310.0	2359.7	-1144.0	2288.0	1.3105	1	0.2523

Habituation test

Model 1: log(WIGS + 1) ~ Sex * Age + WaitTime + WIGNUMTOT + Season + Year + (1 | PitTagID.)
Model 2: log(WIGS + 1) ~ Sex * Age + WaitTime + WIGNUMTOT + Season + Year + (WIGNUMTOT | PitTagID.)

Model	#Df	LogLik	Df	Chisq	p
1	10	-787.27			
2	12	-787.07	2	0.4043	0.817

Code

```
###################### VAR IN WIGGLE TIME- model selection
#######################
filename = "D:/GroundSquirrels/Data/R/Personality/WiggleModels_AllWigglesAll.csv"
AWA <- read.csv(filename)
str(AWA)
AWA$WIGS <- as.numeric(AWA$WIGS)
AWA$NetWeight <- AWA$NetWeight.g.
AWA$NetWeight <- as.numeric(AWA$NetWeight)
AWA$Observer <- AWA$Observer.s.
AWA$Year <- as.factor(AWA$Year)
AWA$Sex <- AWA$Sexx
AWA$WaitTime < as.numeric(AWA$WaitTime)
AWA$WaitTime
str(AWA)
maxcap = as.data.frame(with(AWA,aggregate(WIGNUMTOT, by = list(PitTagID.),
FUN=max)))
AWA = merge(AWA, maxcap, by.x = "PitTagID.", by.y = "Group.1")
str(AWA)
names(AWA)[38] <- "testnumber"
AWA$WIGNUMTOT <- scale(AWA$WIGNUMTOT)
AWA$WIGNUMTOT
str(AWA)

######Libraries#######
library(AICcmodavg)
```

```
library(lmtest)
library(lme4)

#######Candidate models#########
##Fixed Effects: sex, age, wait time, test number and ##
##net weight (not included in models where age and ##
##sex is present)##
######################################################

##Fixed-effect-only Models##

sexageintWTtestseasonyear = lm(log(WIGS+1) ~ Sex * Age + WaitTime + WIGNUMTOT +
Season + Year, data = AWA)
sexageWTtestseasonyear = lm(log(WIGS+1) ~ Sex + Age + WaitTime + WIGNUMTOT +
Season + Year, data = AWA)
NWWTtestseasonyear = lm(log(WIGS+1) ~ NetWeight + WaitTime + WIGNUMTOT + Season
+ Year, data = AWA)

##Best Fixed-effect Model##
aictab(cand.set=list(sexageintWTtestseasonyear,sexageWTtestseasonyear,NWWTtestseasonyear)
,modnames=c('sexageintWTtestseasonyear','sexageWTtestseasonyear','NWWTtestseasonyear')
,sort=TRUE, c.hat=1, second.ord=TRUE)

##TOP FIXED-EFFECT MODEL = sexageintWTtestseasonyear##
summary(sexageintWTtestseasonyear)
##Visualize resids for normality##
hist(resid(sexageintWTtestseasonyear))

#####################################################
##Mixed Model##
sexageintWTtestseasonyearPIT = lmer(log(WIGS+1) ~ Sex * Age + WaitTime + WIGNUMTOT
+ Season + Year + (1|PitTagID.), data = AWA)
##Visualize resids for normality
hist(resid(sexageintWTtestseasonyearPIT))

##LL Ratio Test##
lrtest(sexageintWTtestseasonyear, sexageintWTtestseasonyearPIT)

##Performs better when random effect is included##
summary(sexageintWTtestseasonyearPIT)

#####################################################
##Site effect?##
sexageintWTtestseasonyearSITEPIT= lmer(log(WIGS + 1) ~ Sex * Age + WaitTime +
WIGNUMTOT + Season + Year + Site + (1|PitTagID.), data = AWA)

anova(sexageintWTtestseasonyearPIT, sexageintWTtestseasonyearSITEPIT)

##No site effect##

#####################################################
```

```
##Habituation effect?##
sexageintWTtestseasonyearPIT1 = lmer(log(WIGS+1) ~ Sex * Age + WaitTime +
WIGNUMTOT + Season + Year + (1|PitTagID.), data = AWA[AWA$testnumber > 1,])
sexageintWTtestseasonyearPITtestnumber = lmer(log(WIGS+1) ~ Sex * Age + WaitTime +
WIGNUMTOT + Season + Year + (1|PitTagID.) * (1|WIGNUMTOT), data =
AWA[AWA$testnumber > 1,])
lrtest(sexageintWTtestseasonyearPIT1, sexageintWTtestseasonyearPITtestnumber)

##No habituation effect##

########################################################
##BLUPs##
ranef(sexageintWTtestseasonyearPIT)

########################################################
##Plots##
AWA$WIGSlog <- (log((AWA$WIGS)+1))
plot(AWA$Sex:AWA$Age, AWA$WIGSlog)
plot(AWA$WaitTime, AWA$WIGSlog)
```

Chapter 2: Model selection

No behavior model:

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{p(t)c(t)s(.)g'g"(.)}	**20925.83**	**0**	**1**	**1**	**18**	**20889.71**
{p(t)c(.)s(.)g'g"(.)}	21138.12	212.2887	0	0	11	21116.07
{p(.)c(t)s(.)g'g"(.)}	21212.07	286.2367	0	0	11	21190.02
{p(t)=c(t)s(.)g'g"(.)}	21342.31	416.4813	0	0	10	21322.27
{p(.)c(.)s(.)g'g"(.)}	21429.46	503.6288	0	0	4	21421.45
{p(.)=c(.)s(.)g'g"(.)}	21608.83	683.0011	0	0	3	21602.83

Model output:

{p(t)c(t)s(.)g'g"(.)}

Parameter	Year	Season	Estimate	Standard error	Lower (95%CI)	Upper (95%CI)
g'=g"			0.0033479	0	0.0033479	0.0033479
p	2013	PreJuv	4.75E-08	2.27E-07	4.03E-12	5.60E-04
p	2013	PostJuv	0.1675746	0.0120377	0.145287	0.192511
p	2014	PreJuv	0.4157603	0.0213783	0.3745597	0.4581729
p	2014	PostJuv	0.2827092	0.0162982	0.2518836	0.3157152

p	2015	PreJuv	0.3219015	0.0170316	0.2894662	0.3561494
p	2015	PostJuv	0.2200388	0.0110109	0.1992179	0.2423771
p	2016	PreJuv	0.4269466	0.0351485	0.3598777	0.4968139
p	2016	PostJuv	0.3877881	0.0207729	0.3479377	0.4291985
c	2013	PreJuv	0.4930045	0.0243952	0.4453987	0.5407375
c	2013	PostJuv	0.5602467	0.0171361	0.5264346	0.5935088
c	2014	PreJuv	0.5216916	0.0256591	0.47135	0.5715965
c	2014	PostJuv	0.2845252	0.0134399	0.2589323	0.3115841
c	2015	PreJuv	0.3821864	0.0139693	0.3552054	0.4099139
c	2015	PostJuv	0.4179612	0.0189982	0.3812572	0.4555969
c	2016	PreJuv	0.4957831	0.0228687	0.4511138	0.5405198
c	2016	PostJuv	0.5328777	0.0176835	0.4981149	0.567324
Survivorship		Overall	0.9969443	9.94E-05	0.9967431	0.9971331

APPENDIX C

Foraging And Behavior Of Piute Ground Squirrels (Urocitellus Mollis) At Artificial Feeding Stations

Introduction and purpose

In 2014 and 2015, feeding trials were conducted at the sagebrush-dominant (ARTR1) and native grass-dominant (POSE1) study sites inside the Orchard Combat Training Center (OCTC; Figure C.1 and Figure C.2). Artificial feeding stations, such as the ones used in this study, are used to determine the relative value of patches by measuring the "giving up densities" (GUDs) of these patches which reflect when an animal is willing to give up a depletable food resource (Brown, 1988; Brown and Kotler, 2004). An animal is more likely to give up a food resource at the feeding station when higher quality food is available elsewhere or when there are safer foraging areas available elsewhere. Therefore, higher GUDs (i.e., greater density of seeds remaining) in one study site or time period relative to another may indicate that the surrounding habitat has higher quality of food relative to the food resource provided at the feeding station or that the feeding station is a riskier foraging location (i.e., high predation risk) than elsewhere.

Methods

At each site, artificial feeding stations were placed at 40m or 80m from the center of the trapping web on every other trap radius (Figure C.2) for a total of six feeding patches per site. Two artificial feeding stations were located within each foraging patch 1m apart in a paired design. The paired design was used to assess the effect of within-habitat differences in refuge on foraging behavior. At the ARTR1 trapping site, each foraging patch included one feeding station placed under cover of a shrub and the other in the open 1m away from the covered station (Figure C.3). At the POSE1 site, each foraging patch included two feeding stations located 1m away from each other and the distance to the nearest burrow was recorded for each feeding station.

Each foraging patch had an infrared video camera to record behavior of Piutes at the paired feeding stations, a PIT tag reader antenna around the edge of the station, and a datalogger to record the unique PIT tag ID of any animals that visit the feeding station and the time stamp of that visit to record the length of time each animal spent at the feeding station (Figure C.3). Feeding trays were constructed from 3L plastic cylindrical containers (6.4 x 6.4 x 10.7 inches) filled with 2L of sand and mixed with 250 (approximately 0.6L or 25.0g) commercially available pumpkin seeds resulting in a starting density of approximately 12.5g/L (or 125 seeds/L) of food. Pumpkin seeds were selected over other food types tested (i.e., peanuts, sunflower seed, corn nuts, hazelnuts, and edamame) because they were consumed by Piutes but not depleted during the assay and allowed for relatively fast and accurate quantification of food remaining.

The seed mixture was offered to animals during periods when trapping was not occurring, but feeding stations occurred at the same locations of trapping. The feeding trays were open from approximately 0700-1900hr for two to three days in a row throughout the ground squirrel active season in 2014 and 2015. At the end of each trail (i.e., end of each day) the sand and seeds are removed from the plastic container, seeds were separated from the sand and counted.

The identity of the animal foraging at the feeding tray was determined by aligning the time stamp of the PIT tag reader and the time stamp of the recorded video. This enabled us to know the sex, age, and approximate mass (based on most recent trapping event) of the individual foraging at the feeding tray and correlate these aspects to the behavior observed in the videos. In addition, videos allowed us to monitor behavioral interactions among squirrels (e.g., social or aggressive), anti-risk behaviors (e.g., vigilance, alarm calls), as well as foraging behavior (e.g., time spent foraging, giving up density). The behaviors we focused on for this report are aggression (i.e., aggressive, non-social interaction with a conspecific), exploration (i.e., head down exploring environment, not foraging), foraging (i.e., actively feeding with head up or head down), and vigilance (i.e., quadrupedal or bipedal alertness). Piutes can forage and be vigilant in the bipedal position simultaneously (i.e., head up foraging), but these behaviors were analyzed separately.

Preliminary analysis of behavioral observation data collected during feeding trials investigated the variation in giving up density (GUD) and time budgets from videos taken at the sagebrush-dominant (ARTR1) and native grass-dominant (POSE1) sites inside the OCTC. The GUD measurement is defined as the amount of pumpkin seeds left in a feeding tray at the end of a trail (i.e., at the end of the day). All statistical analyses were conducted using JMP 10.0 (SAS Institute, 2000) and video recordings were analyzed using the software BORIS v2.1 (Friard and Gamba, 2016).

Results and Discussion

Giving Up Densities (GUDs)

The giving up density (GUD), represented as the density of pumpkin seeds left in a tray after a trail day (seeds/liter of sand), was significantly higher at the native grass-dominated site (POSE1, mean=88.0 seeds/L) than at the sagebrush-dominated site (ARTR1, mean=41.7; X^2=5.4857, df=1, p=0.0192; Figure C.4). There was no difference in consumption at GUDs situated under sagebrush or 1m away in the open (p=0.7558; Figure C.5) and no significant relationship between giving up density and distance to nearest burrow (p=0.0836; Figure C.6).

The interpretation of GUDs can be complex, but in general, high GUD values have been associated with a relatively high perceived cost of foraging at that feeding tray (Bedoya-Perez et al., 2013). Therefore, higher GUDs at the native grass site than at the sagebrush site could be interpreted in many ways, two of which are: the forage availability and/or quality around the feeding tray (i.e., the surrounding vegetation) is greater at the native grass site than at the sagebrush site, or that the immediate risk of foraging at the feeding tray (i.e., predation risk) is greater at the native grass site than at the sagebrush site. To test these hypotheses, we suggest quantifying the forage availability and quality and the predation risk, both direct (i.e., predation pressure) and indirect (i.e., percent canopy cover and refuge density) at both sites. GUDs have been used in management settings as an indicator of habitat preference, predation risk, and inter- and intra-specific competition (Brown, 1988), and may be used to monitor responses of Piutes to climate, changes in disturbance, and forage quality and availability.

Time budgets

Overall, individuals were more alert in the native grass habitat than the sagebrush, spent more time exploring in the sagebrush habitat that in native grass, and did not differ in amount of time spent exploring (Figure C.7). Exploration is more often linked to risky-taking behavior and vigilance is anti-risk, therefore we would expect that individuals in the relatively risky habitat type (native grass) would increase vigilance and decrease exploration. Another explanation could be that resources are more densely assembled in the native grass site, so exploration is not as necessary as it is in the sagebrush habitat. Additionally, the predator densities may be higher at the native grass site than the sagebrush resulting in an increase in time spent vigilant.

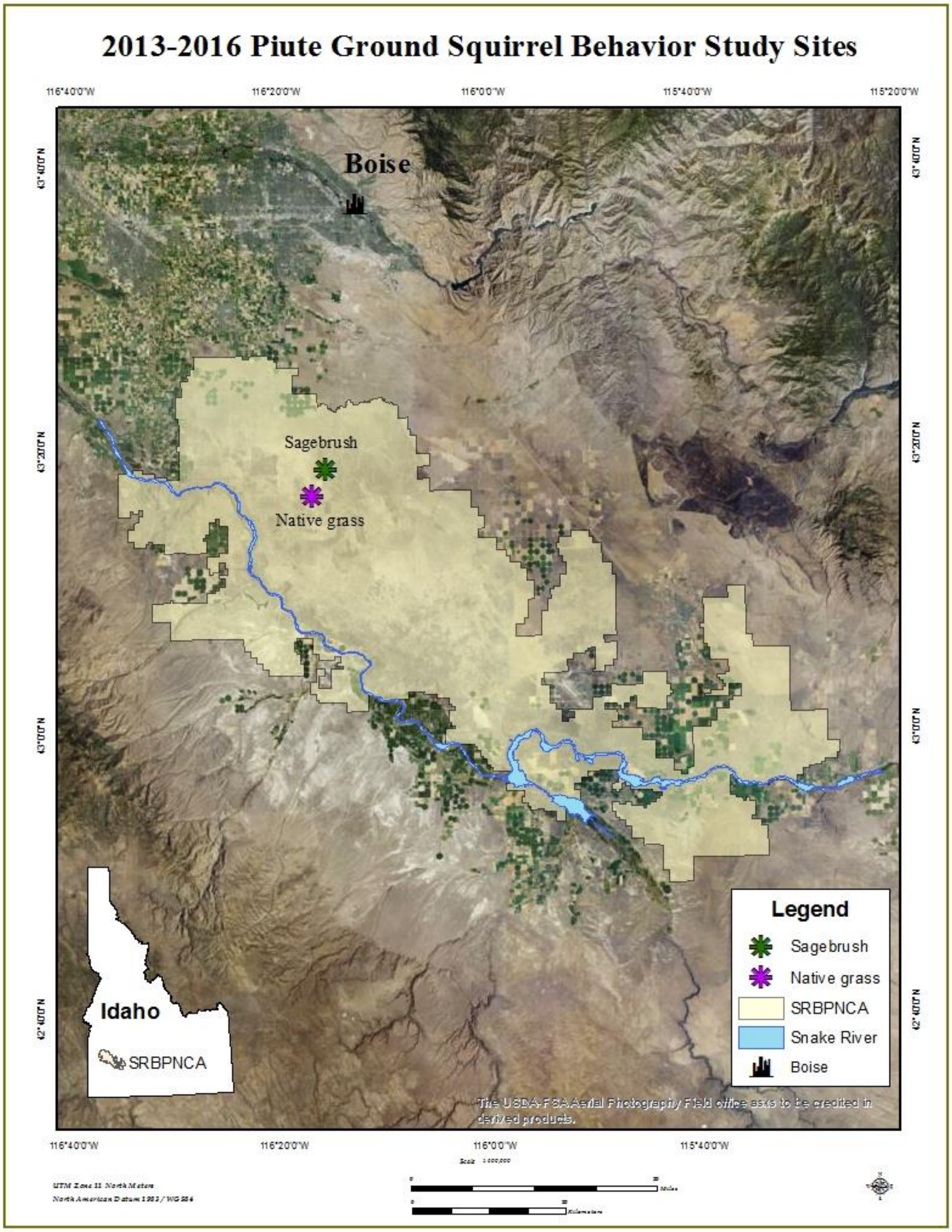


Figure C.1. **Map of study sites dominated by sagebrush (*Artemisia tridentata wyomingensis*) and native grass (*Poa secunda*) where behavior was measured for Piute ground squirrels (*Urocitellus mollis*). The sites are located south of Boise, Idaho within the Snake River Birds of Prey National Conservation Area. UTMs of grid center points- sagebrush: 11T E560018, N4795703; native grass: 11T E558430, N4792390.**

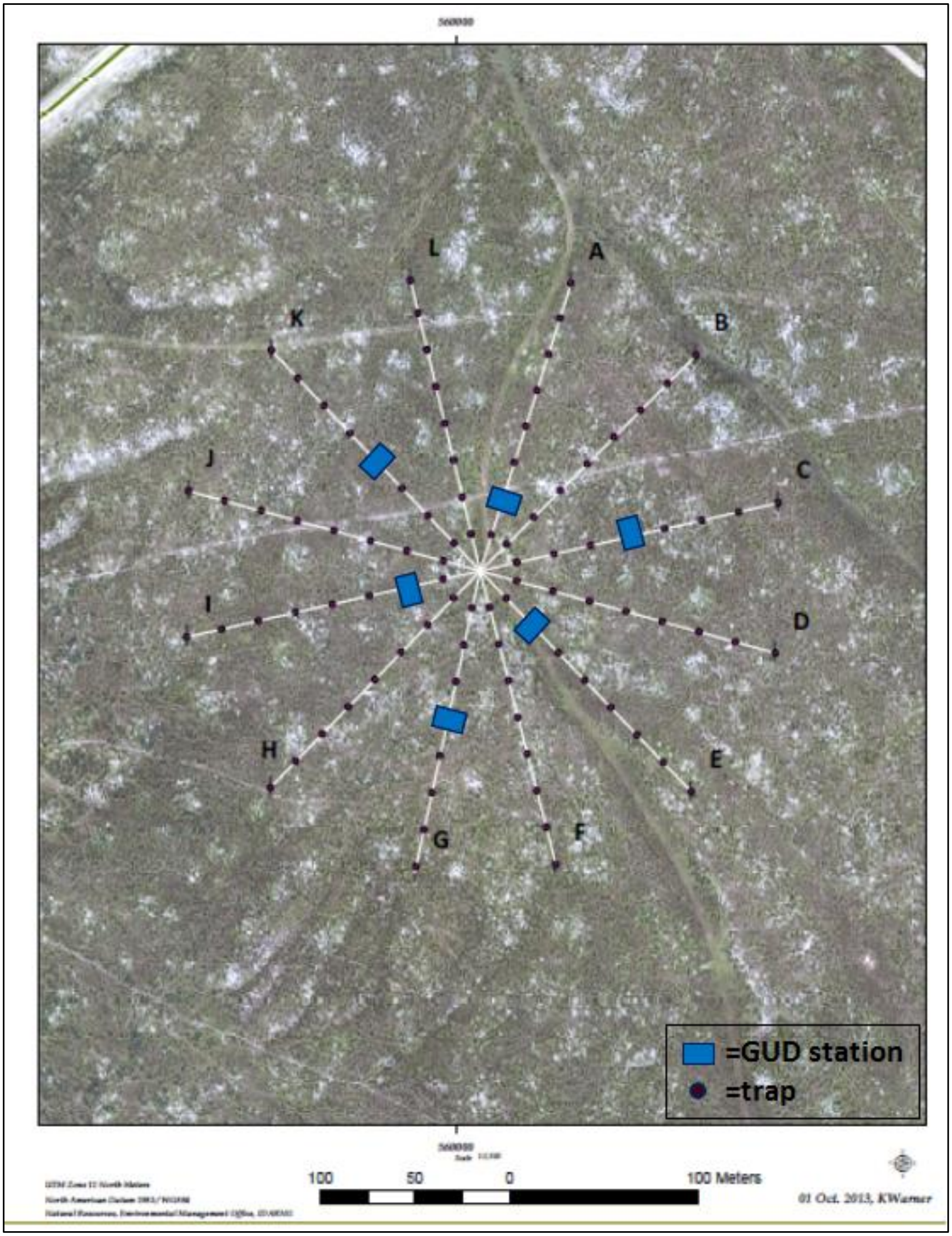


Figure C.2. Location of feeding stations (GUDs) in relation to the trapping web configuration. Circles represent locations of traps and blue boxes represent the feeding station location.

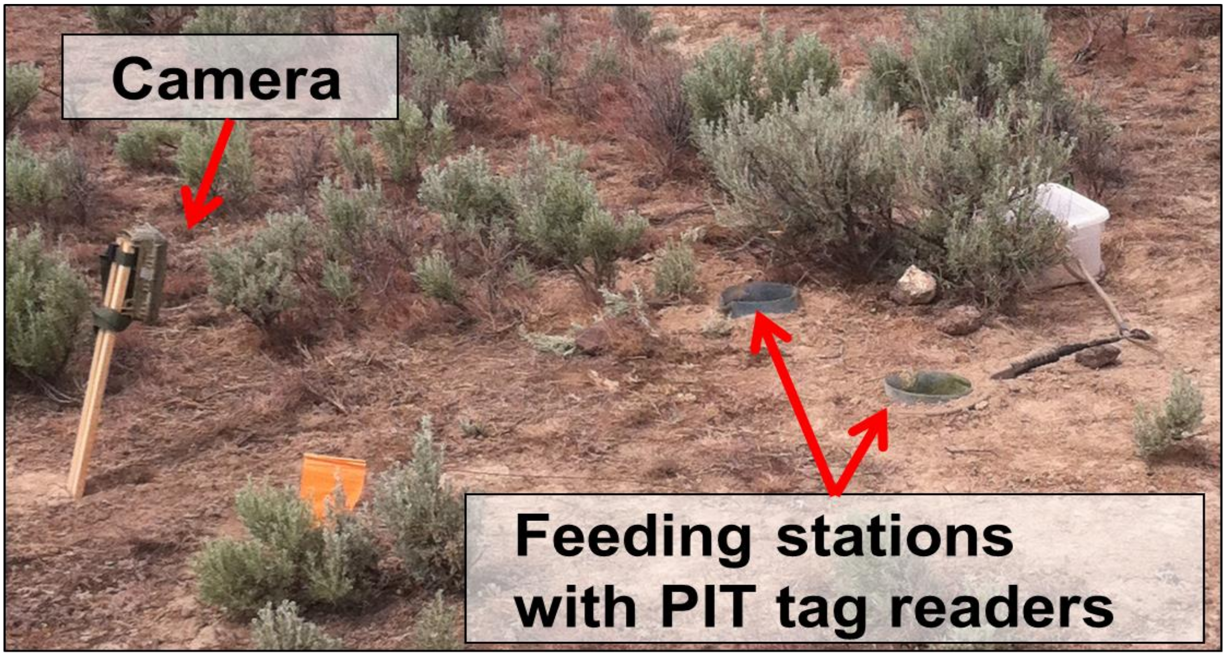


Figure C.3. **Photo of one feeding station location at the sagebrush site. Each location included two feeding stations (GUDs; one under cover and one 1 meter away in the open), one trail camera to take video, and one passive PIT tag reader.**

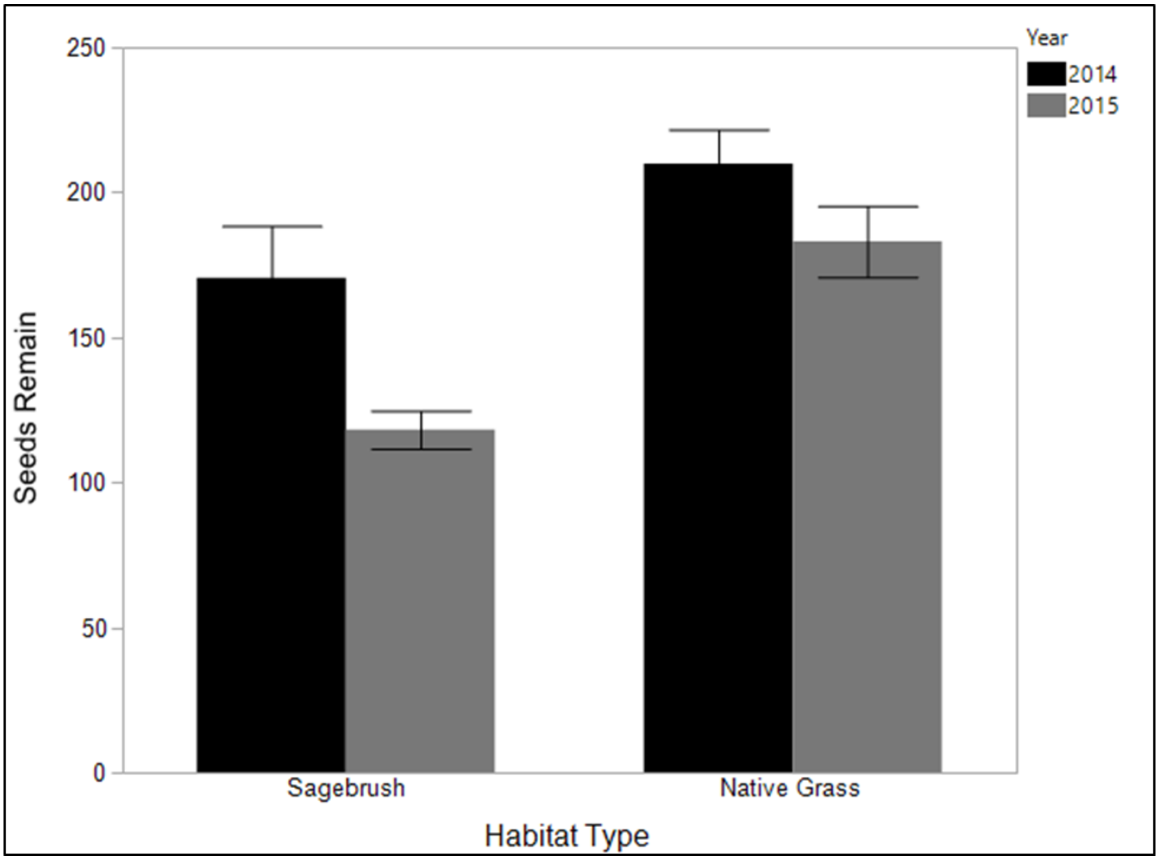


Figure C.4. **The average number of seeds that remained after each feeding trail by habitat type and year (black bars- 2014, grey bars- 2015). Overall, more seeds remained at the native grass site than at the sagebrush site (X^2=5.4857, df=1, $p<0.05$).**

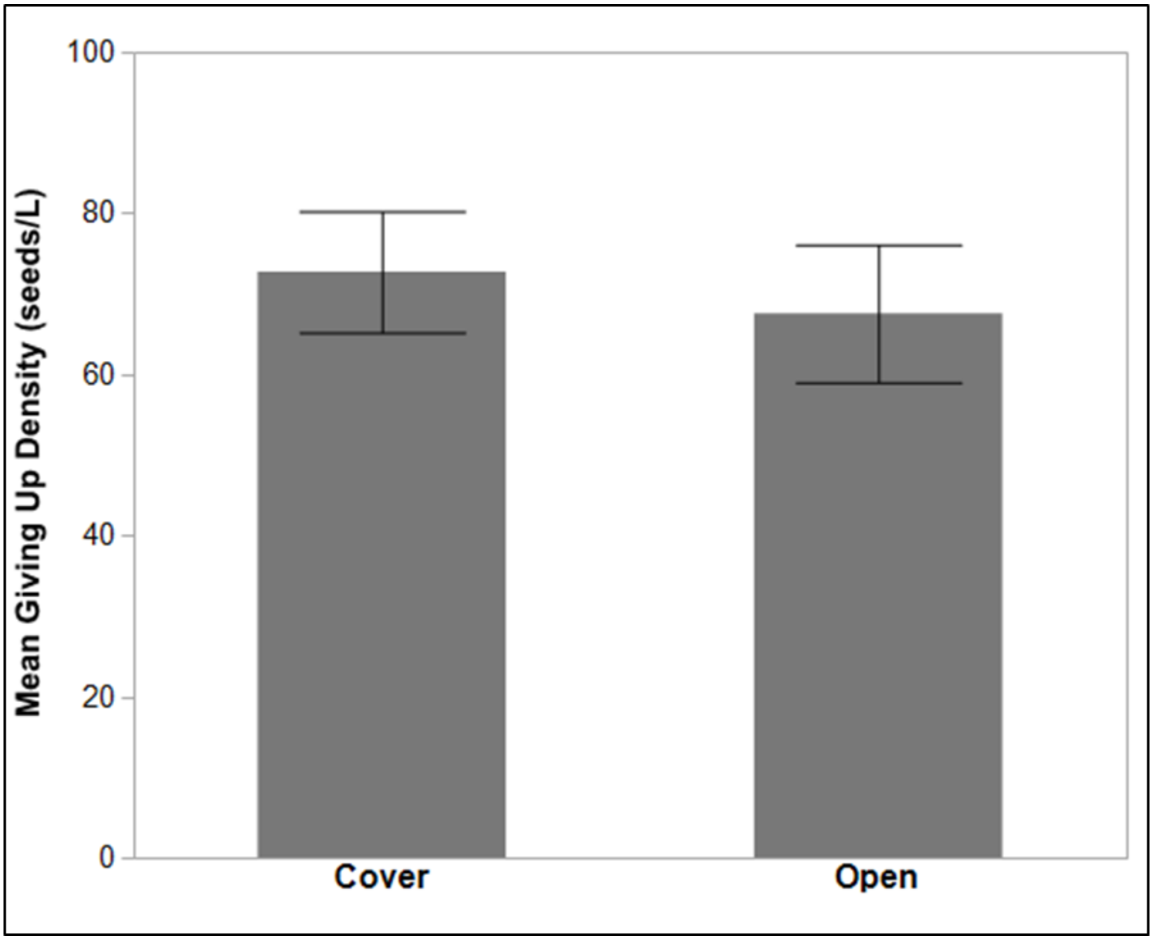


Figure C.5. **The effect of cover (in the sagebrush site) and the average density of seeds (seeds/L sand) that remained after each feeding trail (t=1.037 df=1, p=0.7558).**

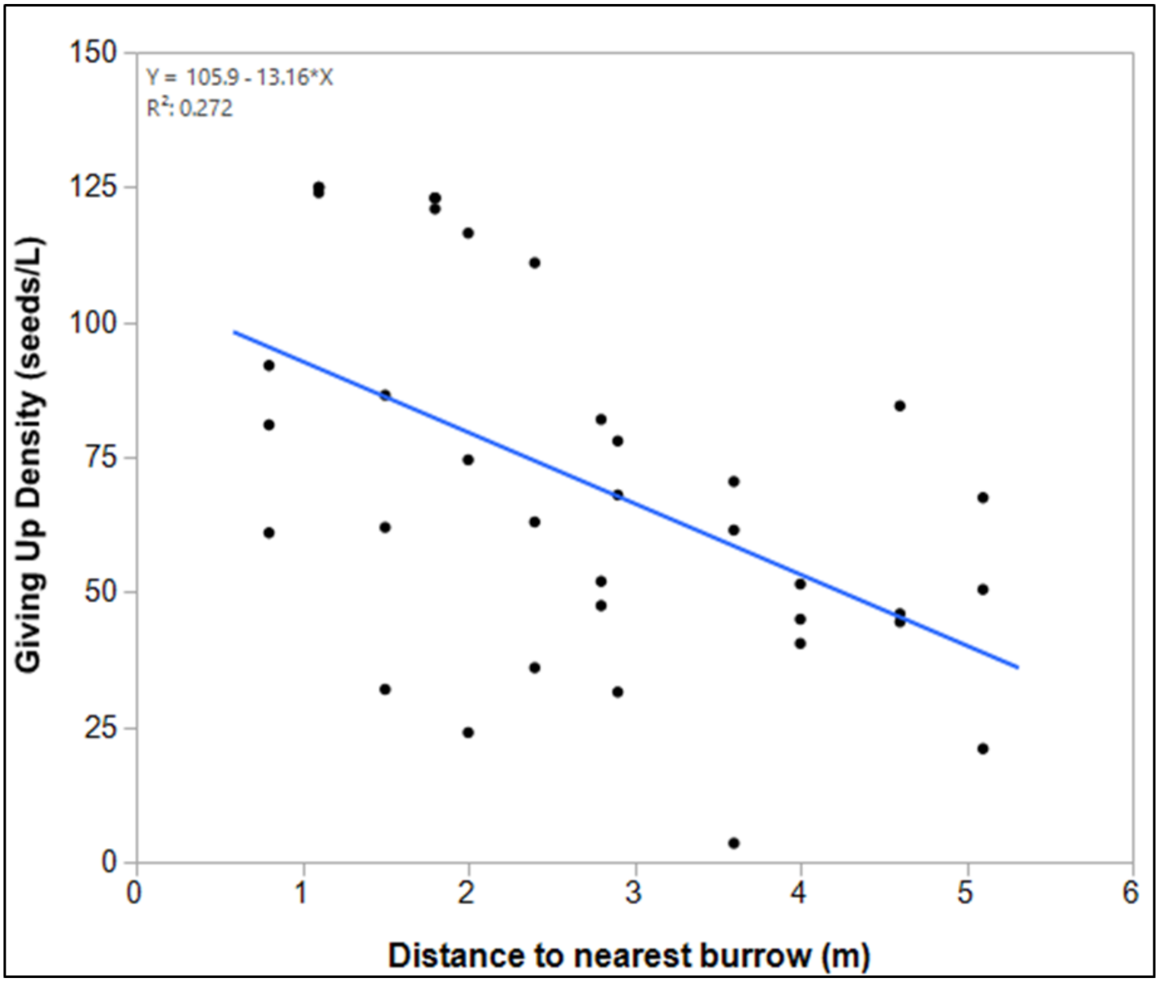


Figure C.6. **Relationship between distance to nearest burrow (meters) and the average density of seeds left (seeds/L sand) after each feeding trail (R^2=0.272, p=0.0836).**

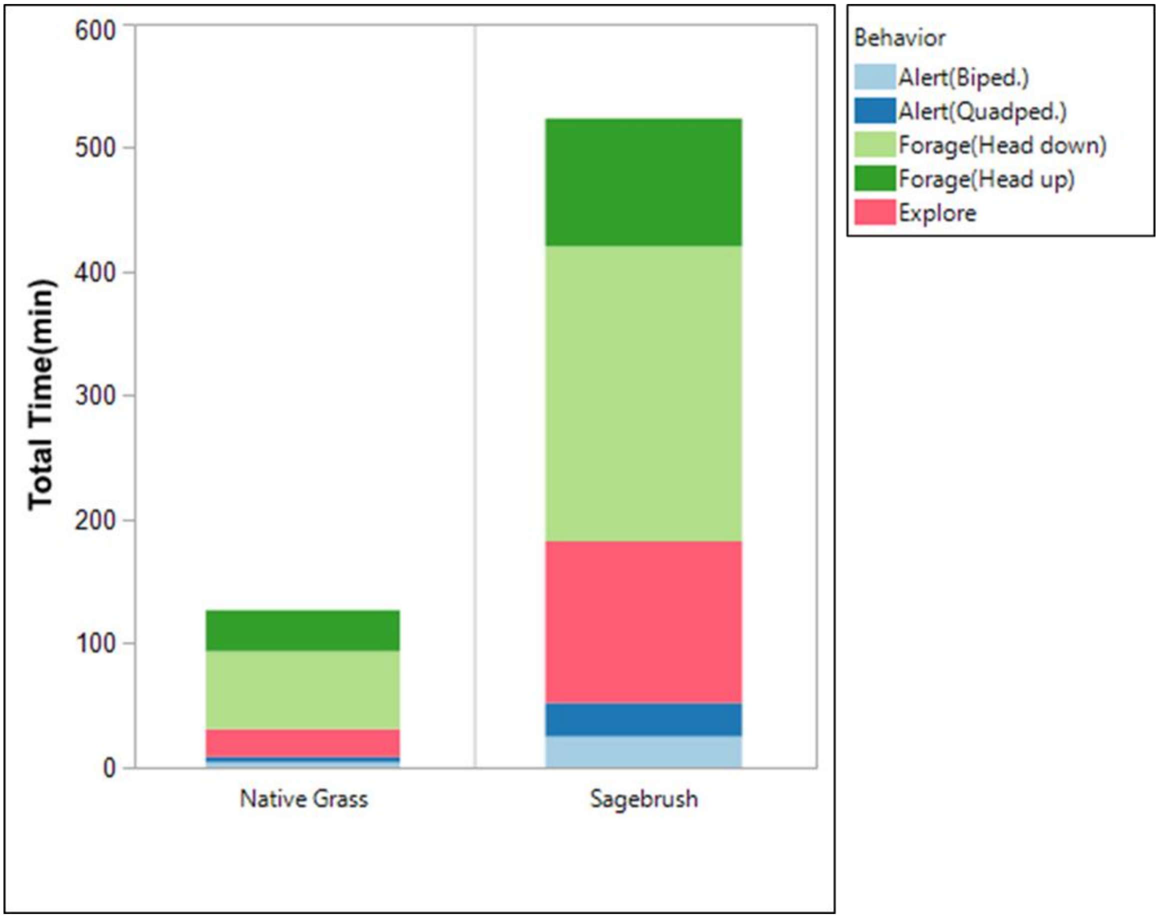


Figure C.7. Total amount of time spent being alert while bipedal (light blue), quadrupedal (dark blue), foraging with the head down (light green), head up (dark green), and exploring with the head down (pink) of Piute ground squirrels at the feeding stations.

Literature cited

Bedoya-Perez, M.A., Carthey, A.J.R., Mella, V.S.A., McArthur, C., and Banks, P.B. (2013). A practical guide to avoid giving up on giving-up densities. Behavioral Ecology Sociobiology 67, 1541–1553.

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