

**Foraging Activity and Survival of the Northern Idaho Ground
Squirrel are Influenced by Climate, Hibernation, Endogenous
State, and Competition with a Coexisting Congener**

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Abstract

Understanding the ultimate drivers of evolution and population regulation are core goals of ecology. Climate change can affect the evolution and persistence of free-ranging animals via myriad mechanistic pathways, and so is of particular interest to researchers, policy makers, and the public. Negative changes in abundance and demographic vital rates in response to climate change have been documented in some animals, but the mechanisms underpinning these relationships are often not well understood such that we lack the ability to make generalized predictions about the effects of future climate change on animal behavior, abundance, and evolution. Furthermore, species and individual level traits likely mediate the effects of climate on animals. For example, species with strongly seasonal annual cycles – like obligate hibernators – may be particularly sensitive to climate change. A better understanding of how climate interacts with and influences variation in behavior and life-history is needed to explain patterns observed in nature and inform the conservation of species, biological communities, and ecological processes.

We investigated mechanisms shaping behavior and demography of the northern Idaho ground squirrel (*Urocitellus brunneus*), a federally threatened species endemic to a small portion of west-central Idaho, USA. The squirrels suffered population declines in the late 20th century and now persist in a fragmented metapopulation consisting of <3000 individuals. These small herbivores hibernate for 8.0-9.5 months per year, leaving just few months during which they must reproduce and attain sufficient fat reserves to survive their long hibernation period and reproduce in future years. Food limitation resulting from anthropogenic fire suppression and/or competition with the larger, co-occurring Columbian ground squirrel may constrain northern Idaho ground squirrel populations. Climate, therefore, potentially influences northern Idaho ground squirrels in at least 3 ways: by 1) altering time and energy allocated to thermoregulatory behavior, 2) influencing forage availability directly, and 3) modulating competitive interactions with Columbian ground squirrels. We sought to test predictions regarding the effects of climate, hibernation, competition, and endogenous state on northern Idaho ground squirrel foraging activity and survival based on these hypothesized mechanistic pathways.

Chapter 1 tests predictions of Optimal Foraging Theory to explain variation in the amount of time northern Idaho ground squirrels allocate to aboveground foraging activity. Specifically, we sought to elucidate the effects of thermal environment, predation risk, and endogenous state on squirrel foraging activity. We also considered the effects of hibernation behavior and the squirrel's strongly seasonal annual cycle on their foraging behavior – a novel aspect of this study. Foraging time increased as the aboveground active season progressed and hibernation approached, suggesting

energetic thresholds imposed by that extreme adaptation to seasonally unsuitable conditions drive foraging behavior during the active season. Furthermore, heavy squirrels foraged less relative to lean squirrels as hibernation approached, indicating that squirrels in poor body condition accepted increasingly greater predation risk compared to their heavier counterparts as residual foraging opportunities diminished. Extreme temperatures also negatively influenced time spent foraging, meaning that an increase in overall temperature as well as increases in extreme weather events expected as a result of climate change may constrain foraging opportunities for these threatened squirrels. Management actions that improve forage abundance and quality, therefore, are likely to increase squirrel fitness and so populations by allowing squirrels to better avoid aboveground risks posed by extreme thermal conditions and predation while still attaining the necessary fat reserves to survive their long hibernation period and reproduce in the future.

Chapter 2 considers the effects of seasonal temperature and precipitation metrics on survival of northern Idaho ground squirrels as well as two coexisting species – Columbian ground squirrels (*Uroditellus columbianus*) and yellow-pine chipmunks (*Tamias amoenus*) – with an eye toward predicting the effects of climate change on populations of these imperiled squirrels and herbivorous and hibernating animals more broadly. We also tested for hypothesized negative effects of competition with the larger, socially dominant Columbian ground squirrel on northern Idaho ground squirrels and whether changes in climate have implications for competitive interactions between the species. Northern Idaho ground squirrel survival was negatively density dependent, suggesting the squirrels are, in fact, food or space limited. Moreover, Columbian ground squirrel density had a sharp negative effect on northern Idaho ground squirrel survival during the active season, compelling evidence of competition between the two ground squirrel species. Winter snowfall negatively influenced northern Idaho ground squirrel survival, but positively and strongly influenced Columbian ground squirrel survival, suggesting that climate modulates competition between the congeners by influencing Columbian ground squirrel survival and so abundance and distribution. Changes in forage availability related to winter snowpack likely underpin these patterns, and this is one of the first studies to demonstrate such a mechanistic pathway by which climate can influence the demography of coexisting species. The apparent negative effects of competition on northern Idaho ground squirrel survival suggest that management actions aimed at benefiting the threatened squirrels are most likely to be successful in areas where they will not be subsequently outcompeted by Columbian ground squirrels or when coupled with control of the larger squirrels.

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Dedication

To my parents, Sylvia Titgemeyer and Michael Allison, who instilled in me a love for and curiosity about the natural world; my best friend and partner, Alice Morris, who is always ready for an adventure; and the squirrels – they challenge and inspire me daily.

Table of Contents

Abstract	ii
Acknowledgments	iv
Dedication	v
Table of Contents	vi
List of Tables	vii
List of Figures	viii
Statement of Contribution	ix
Chapter 1: Daily Foraging Activity of an Imperiled Ground Squirrel: Effects of Hibernation, Thermal Environment, Body Condition, and Conspecific Density	1
ABSTRACT	1
INTRODUCTION	1
STUDY SPECIES AND SYSTEM	4
METHODS	6
Data Collection	6
Statistical Analyses	8
RESULTS	11
DISCUSSION	13
LITERATURE CITED	17
Chapter 2: Climate Influences Survival of Coexisting Species Directly and by Modulating Interspecific Competition	31
ABSTRACT	31
INTRODUCTION	31
STUDY SPECIES AND SYSTEM	34
METHODS	35
Data Collection	35
Statistical Analyses	37
RESULTS	39
Northern Idaho Ground Squirrels	39
Columbian Ground Squirrels	40
Yellow-pine Chipmunks	40
DISCUSSION	41
LITERATURE CITED	45

List of Tables

Table 1.1. Predicted relationships between a suite of intrinsic and extrinsic predictor variables and daily foraging activity of northern Idaho ground squirrels.....	26
Table 1.2. Top models designed to explain variation in foraging activity of northern Idaho ground squirrels	27
Table 1.3. Model-averaged parameter estimates for all predictor variables based on a model selection effort that compared a suite of generalized linear mixed-effects models designed to explain variation in foraging activity of northern Idaho ground squirrels	28
Table 2.1. Covariates predicted to influence survival of northern Idaho ground squirrels, Columbian ground squirrels, and yellow-pine chipmunks.....	55
Table 2.2. Top stage-one Cormack-Jolly-Seber models designed to explain variation in survival of northern Idaho ground squirrels, Columbian ground squirrels, and yellow-pine chipmunks	56
Table 2.3. Top stage-three Cormack-Jolly-Seber models designed to explain variation in survival of northern Idaho ground squirrels, Columbian ground squirrels, and yellow-pine chipmunks	58

List of Figures

- Figure 1.1.** We placed radio-collars equipped with geolocators in different positions relative to the entrance of a northern Idaho ground squirrel nest burrow to determine the threshold for classifying a squirrel as above or below ground during a given sampling interval..... 29
- Figure 1.2.** Model-averaged marginal effects on aboveground foraging activity of northern Idaho ground squirrels based on a model selection effort that compared a suite of generalized linear mixed-effects models designed to explain variation in foraging activity 30
- Figure 2.1.** Model-averaged marginal effects of sex, age class, and season on monthly survival of northern Idaho ground squirrels, Columbian ground squirrels, and yellow-pine chipmunks based on the top Cormack-Jolly-Seber models designed to explain variation in survival 60
- Figure 2.2.** Model-averaged marginal effects of climate and competition on monthly survival of northern Idaho ground squirrels based on the top stage-three Cormack-Jolly-Seber models designed to explain variation in survival 61
- Figure 2.3.** Model-averaged marginal effects of climate on monthly survival of Columbian ground squirrels based on the top Cormack-Jolly-Seber models designed to explain variation in survival 62
- Figure 2.4.** Model-averaged marginal effects of climate on monthly survival of yellow-pine chipmunks based on the top Cormack-Jolly-Seber models designed to explain variation in survival. 63

Statement of Contribution

AZTA and CJC contributed to the study conceptualization, methodology, and formal analyses. AZTA oversaw data collection and curation, wrote the first manuscript draft, and prepared data visualization for the manuscript. CJC acquired funding for the study and provided revisions of all manuscript drafts.

Chapter 1: Daily Foraging Activity of an Imperiled Ground Squirrel: Effects of Hibernation, Thermal Environment, Body Condition, and Conspecific Density

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ABSTRACT

Food acquisition is among the most important tasks faced by free-ranging animals. Predation and thermal risks, however, can make foraging a costly endeavor and foraging can preclude other important activities. Moreover, seasonal life-cycle events such as hibernation impose energetic thresholds and time constraints on foraging. These factors interact with an animal's endogenous state to influence foraging behavior. We tested a suite of predictions based on foraging theory to explore the effects of thermal environment, body condition, and conspecific density on aboveground activity (which is primarily foraging activity) of the northern Idaho ground squirrel (*Uroditellus brunneus*), an imperiled rodent that hibernates for 9 months each year. We took advantage of the squirrels' semi-fossorial lifestyle to document daily aboveground activity by attaching geolocators to squirrels. We modeled squirrel activity with generalized linear mixed-effects models to document the relative importance of thermal environment, body condition, and conspecific density for daily aboveground activity. Aboveground activity by northern Idaho ground squirrels increased throughout their active season and leaner squirrels increased their activity more than heavier squirrels as residual foraging opportunities diminished. Thermal conditions also influenced squirrel activity: squirrels spent less time aboveground during extreme temperatures and on days with significant precipitation. Aboveground activity of northern Idaho ground squirrels largely adhered to predictions of risk-sensitive and state-dependent foraging theory. Management actions that enhance forage will likely improve the probability of recovery for this federally threatened species by minimizing tradeoffs squirrels need to make to acquire sufficient food to survive hibernation and reproduce in subsequent years.

INTRODUCTION

Obtaining sufficient food is arguably the most important task free-ranging animals confront each day. Foraging decisions are, however, more nuanced than merely maximizing food intake, and herbivorous animals face tradeoffs regarding when, where, and what to eat (Caraco et al. 1980;

Stephens 1981; McNamara and Houston 1992). Tradeoffs involve balancing foraging with other activities and are defined by costs incurred by foraging. The costs associated with foraging in free-ranging animals fall broadly into 3 categories: 1) direct risk of mortality, 2) energetic costs, and 3) opportunity costs. Foraging often increases predation risk for animals (Sih 1982; Lima 1998; Brown and Kotler 2004; Preisser et al. 2005), and herbivores weigh predation risks when making foraging decisions (Lima and Dill 1990; Houston et al. 1993; Verdolin 2006). Thermal conditions also influence foraging decisions by delineating tradeoffs between foraging and self-maintenance (Kenagy 1973; Caraco et al. 1990; Cerdá et al. 1998). Moreover, foraging can preclude investment in other activities, such as mating (Mitchell et al. 1990; Wolff and Horn 2003; Pelletier et al. 2009) and caring for young (Rangely and Godin 1992; Komdeur and Kats 1999; Williams et al. 2016). Identifying factors that explain variation in foraging activity can elucidate important selection pressures animals face and thereby help determine the fitness landscape driving the evolution of an animal's life-history strategy.

Costs of foraging can interact with an animal's endogenous state to influence foraging choices: animals in poor nutritional or energetic condition are more likely to forage despite predation and thermal risks (McNamara and Houston 1996; Nonacs 2001; Rands 2004). Energetic state is particularly likely to influence foraging choices in obligate hibernators because these animals have a limited annual period – only a few months per year in some cases – during which food acquisition is possible and individuals must attain sufficient resources to survive hibernation. Past studies of foraging in hibernators focused on diet (Ritchie 1988; Frank et al. 1998; Lehmer et al. 2006), but the reduction in annual residual foraging time as the active season progresses may also influence daily time spent foraging (Davis 1976; Kenagy et al. 1989; Williams et al. 2016). Furthermore, risk-tolerance by animals in poor energetic condition should increase as residual foraging time decreases (i.e., as hibernation approaches) and the relative importance of acquiring sufficient energetic reserves for hibernation increases compared to other activities. However, previous studies have not linked hibernation to state-dependent foraging decisions or explicitly dealt with the concept of residual foraging time as hibernation approaches. We sought to test predictions based on foraging theory regarding the influence of endogenous state, mortality risk, and energetic costs on daily foraging activity in a small, herbivorous hibernator.

The northern Idaho ground squirrel (*Urocitellus brunneus*) is a semi-fossorial, obligate hibernator endemic to a 1600-km² area in west-central Idaho, USA. The squirrels are semi-colonial and inhabit xeric, rocky meadows interspersed among coniferous forest during their active season (Goldberg et al. 2020a; Helmstetter et al. 2021). The U.S. Fish and Wildlife Service listed the species as federally threatened under the Endangered Species Act in 2000 due to declines in abundance and

distribution attributed to habitat loss that resulted in small, fragmented populations (U.S. Fish and Wildlife Service 2000). Adult northern Idaho ground squirrels hibernate 8.0-9.5 months per year (mid-July through early April on average; Goldberg and Conway 2021), leaving just a few months for each squirrel to reproduce and forage. Northern Idaho ground squirrels eat a wide variety of forbs and grasses (Dyner and Yensen 1996; Yensen et al. 2018; Goldberg et al. 2020b) and adult squirrels increase their body mass by 25%-150% during the short active season (mean post-hibernation body mass = ~125 g for males and females and mean pre-hibernation body mass = ~250 g for males and ~180 g for females) to provide sufficient fat reserves to endure their long hibernation period (Allison et al. 2020). Squirrel foraging consists of search forays, which take squirrels up to 100 m from nest burrows (Dyner and Yensen 1996), and consumption of forage, with these foraging bouts frequently punctuated by bouts of stationary vigilance lasting a few seconds to a few minutes.

Optimal foraging theory posits that animals can maximize future reproduction by optimizing foraging time (Werner and Anholt 1993; Steiner and Pfeiffer 2007). For northern Idaho ground squirrels, that means retreating to burrow refugia when foraging costs outweigh benefits because predation risk is lower (Holmes 1984; Karels and Boonstra 1999; Camp et al. 2012) and thermal conditions are consistently suitable within burrows (Chappell and Bartholomew 1981a; Vispo and Bakken 1993; Long et al. 2005; Milling et al. 2017). However, squirrels must emerge above ground to forage, and forage availability and body mass are positively correlated with survival and fecundity in sister taxa (Murie and Boag 1984; Dobson and Kjelgaard 1985a, b; Ritchie and Belovsky 1990; Van Horne et al. 1997; Bennett 1999; Karels et al. 2000). We sought to document how northern Idaho ground squirrels resolve foraging tradeoffs by examining intrinsic and extrinsic factors that influence aboveground (i.e., foraging) activity. Three selection pressures that potentially explain variation in daily foraging activity of these threatened squirrels are: 1) energetic requirements of hibernation, 2) thermal intolerance, and 3) predation risk. We used risk-sensitive and state-dependent foraging theory to elucidate the following explicit and testable predictions of the 3 agents of natural selection (Table 1).

1. To evaluate the extent to which energetic and nutritional thresholds imposed by hibernation affect foraging activity, we tested the prediction that foraging activity increases throughout the active season as residual foraging time decreases and the relative importance of acquiring the necessary energetic reserves to survive hibernation increases.
2. To evaluate the extent to which thermal intolerance affects foraging activity, we tested the prediction that squirrels spend less time foraging above ground at extreme ambient temperatures (highs and lows) accounting for effects of solar radiation and precipitation,

given that temperatures outside the thermoneutral zone of northern Idaho ground squirrels pose energetic costs and mortality risks for squirrels.

3. To evaluate the extent to which predation risk affects foraging activity, we tested 3 predictions:
 - a) leaner squirrels spend more time foraging than their heavier counterparts, indicating an increased tolerance for predation risk by squirrels with greater energetic and nutritional needs;
 - b) foraging activity by leaner squirrels increases relative to heavier squirrels throughout the active season as the energy deficit to residual-foraging-time ratio disparity between the two increases;
 - c) foraging activity is positively associated with conspecific density, resulting from increased group vigilance and diluted predation risk allowing squirrels to forage more without increasing mortality risk.

STUDY SPECIES AND SYSTEM

Northern Idaho ground squirrels have one of the smallest distributions of any mammal in North America (Helmstetter et al. 2021). The adult population is currently estimated at 2500-3000 individuals within a fragmented metapopulation wherein ~70 extant sites support squirrels and most sites contain <25 individuals (Wagner and Evans Mack 2021). Male squirrels emerge from hibernation in late March or early April (mean = 1 April), ~2 weeks before females on average (mean = 16 April; Goldberg and Conway 2021). Female northern Idaho ground squirrels mate within a few days of emergence and produce a litter of 2-7 pups ~23 days after copulation (Michener 1985; Sherman 1989; Sherman and Runge 2002). Pups are cared for and nursed entirely underground, only emerging from natal burrows in June, ~30 days after parturition; juveniles become independent of their mother a few days after initial emergence from natal burrows (Sherman 1989; Yensen and Sherman 1997). Adult squirrels at most sites immerse into hibernation in July (mean = 14 July) with juveniles immersing almost a month later on average (mean = 10 August). While individual squirrels may be active for as little as 2.5 months, intraspecific variation in annual phenology results in a 4-month active season for adults at the species level, lasting from late March to late July. Furthermore, annual phenology varies by elevation – squirrels at higher elevations immerse into and emerge from hibernation later and have shorter active seasons than squirrels at lower elevation sites – likely due to differences in overwinter snowpack and phenology of forage plants (Goldberg and Conway 2021). High juvenile mortality means most northern Idaho ground squirrels do not survive their first year (Sherman and Runge 2002; Allison et al. 2020). Female northern Idaho ground squirrels that do

survive their first winter typically live 3-5 years, though individuals can reach 7 years of age; adult male squirrels have shorter lifespans, typically living 1-3 years, though they can live to 5 years of age. Woody vegetation encroachment into meadow habitat caused by anthropogenic fire suppression is thought to be the primary driver of past population declines and range contraction, which led to the species' listing under the Endangered Species Act (Sherman and Runge 2002; Suronen and Newingham 2013; Allison et al. 2020). However, the fire suppression hypothesis has not been tested or verified, and other potential threats to the northern Idaho ground squirrel include competition for food and burrowing space with the larger, sympatric Columbian ground squirrel (*Urocitellus columbianus*; Dyni and Yensen 1996; Yensen and Dyni 2020), novel/invasive pathogens (e.g., sylvatic plague; Goldberg et al. 2021), reduction in dispersal corridors among sites (Gavin et al. 1999; Garner et al. 2005; Barbosa et al. 2021), and negative effects of climate change (Goldberg and Conway 2021).

Our 7 study sites were in Adams County, Idaho, USA, and spanned most of the extant range of the northern Idaho ground squirrel. The study site elevations ranged from 1275-1700 m. The mean daily high/low temperature, measured by the West Branch SNOTEL station (~10 km from our nearest study site and 1695 m in elevation), during the squirrels' aboveground active season ranged from 10 °C/-1 °C in April to 26 °C/11 °C in July during the study (2017-2020). The mean daily high/low temperature during the squirrels' hibernation season ranged from 26 °C/12 °C in August to 1 °C/-6 °C in December. The mean annual precipitation during the study was 107 cm, most of which fell as winter snow (mean maximum snow depth at study sites = 107 cm, mean number of days with ≥ 2 cm of snow cover at study sites = 144). Spring meltwater from the winter snowpack (mean final day of ≥ 2 cm snow cover = 14 April) provides lush green grasses and forbs for the squirrels to eat in late spring and early summer each year, but grasses and forbs desiccate as the summer progresses and the sites are arid by mid-July.

Our study sites were imbedded in a montane matrix of coniferous forest, riparian corridors, and meadows. Shallow, rocky soils characterized most meadows, while forested areas had deeper soils. Northern Idaho ground squirrels spend the active season burrowing and foraging in meadows and often move into adjacent forest to hibernate (Goldberg et al. 2020a). Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) dominated the overstory in forested areas at our study sites. Common forest understory plants included snowberry (*Symphoricarpos* spp.), spiraea (*Spiraea* spp.), pine grass (*Calamagrostis rubescens*), elk sedge (*Carex geyeri*), heart-leaf arnica (*Arnica cordifolia*), and wild strawberry (*Fragaria* spp.). Common plants in meadows included big sagebrush (*Artemisia tridentata*), bluegrass (*Poa* spp.), brome (*Bromus* spp.), buckwheat (*Eriogonum* spp.), wild onion (*Allium* spp.), and biscuitroot (*Lomatium* spp.). Northern Idaho ground squirrels co-

occurred with a suite of other small mammals, including Columbian ground squirrels, yellow-pine chipmunks (*Tamias amoenus*), American red squirrels (*Tamiasciurus hudsonicus*), mountain cottontails (*Sylvilagus nuttallii*), snowshoe hares (*Lepus americanus*), northern pocket gophers (*Thomomys talpoides*), deer mice (*Peromyscus maniculatus*), and montane voles (*Microtus montanus*). Predators of ground squirrels in our study system included badgers (*Taxidea taxus*), martens (*Martes americana*), long-tailed weasels (*Neogale frenata*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), red-tailed hawks (*Buteo jamaicensis*), goshawks (*Accipiter gentilis*), prairie falcons (*Falco mexicanus*), and western rattlesnakes (*Crotalus oregonus*). Cattle grazing, hunting, ATV operation, hiking, and camping were common human land uses within the study area throughout the year, but our study sites were remote and human activity was uncommon within squirrel colonies during the northern Idaho ground squirrel active season.

METHODS

Data Collection

Our work was part of an ongoing habitat restoration study (see Allison et al. 2020 for details) for which we attached VHF radio-collars (Holohil Systems, Ottawa, Ontario; BD-2C; Lotek, Newmarket, Ontario; CTx Ag392) to northern Idaho ground squirrels at 7 study sites from 2017-2020. We captured squirrels in Tomahawk live traps (Tomahawk Live Trap, Hazelhurst, WI; 13 x 13 x 41 cm and 15 x 15 x 50 cm) placed at burrow entrances and baited with a mixture of peanut butter, oats, and imitation vanilla. We also captured squirrels with “focal traps” inserted directly into burrow openings into which sighted squirrels immersed; we temporarily blocked nearby burrow openings to ensure squirrels emerged from the opening covered by our trap. We captured squirrels later in their active season (mid-June to mid-July) and collared squirrels with body masses ≥ 140 g to minimize the likelihood of a squirrel growing too large for its collar before hibernation. We collared $\leq 33\%$ of squirrels at a site to minimize our impact on a given population. We marked each squirrel with 2 metal ear tags (National Band & Tag Co., Newport, KY; 1005-1) and/or a passive integrated transponder tag (Biomark, Boise, ID; HDX12) for individual identification when squirrels were not radio-marked. We attempted to distribute collars equitably between males and females within and among study sites each year. We released all captured animals at their capture locations after a brief post-processing monitoring period. We deployed 92 collars (33 in 2017, 29 in 2018, and 30 in 2019) on 83 northern Idaho ground squirrels (43 females and 40 males); we attached a new collar in a subsequent year to 9 squirrels collared previously during the study. Because our study relied on focal, radio-collared squirrels, we were unable to blindly record or analyze data.

We attached geolocators (Migrate Technology, Cambridge, United Kingdom; Intigeo-C65) to radio-collars with a combination of glue, epoxy, and nylon wrapping. The collars with transmitters and geolocators weighed 3.5 g (1.3-2.5% of squirrel body mass). Geolocators sampled light intensity every minute and recorded the maximum of those measurements across 5-min sampling intervals (0:01-0:05, 0:06-0:10, etc.), allowing us to determine when a squirrel was above or below ground (Long et al. 2005; Williams et al. 2014). We placed a string of 5 collars equipped with geolocators in different positions relative to the entrance of a northern Idaho ground squirrel nest burrow for 24 hours on a cloudless day in summer 2020 to determine the best light intensity threshold for determining when a squirrel was above or below ground. We placed the string of 5 geolocators in the following positions in relation to the mouth of the burrow: outside the burrow without overhead obstruction, in the burrow mouth, and 5 cm, 15 cm, and 25 cm into the burrow (Fig. 1a). We placed a 6th geocator outside the burrow in full shade ~100 m from the burrow mouth to account for cloudy days or squirrels foraging in shade. The geolocators in the burrow mouth and 5 cm below the burrow entrance recorded values ≥ 1000 lux during 22% and 7% of sampling intervals from 8:00-20:00 MDT and the 2 geolocators > 5 cm below the entrance never recorded values ≥ 1000 lux (Fig. 1b). Conversely, the shaded and non-shaded aboveground geolocators recorded values ≥ 1000 lux on 97% and 100% of sampling intervals from 8:00-20:00 MDT. We therefore used 1000 lux as the threshold value to classify squirrels as above (≥ 1000 lux) or below (< 1000 lux) ground.

We observed focal squirrels during 24 observation sessions of 40-120 min duration (31.3 hrs total time at observation posts, all between 8:00 and 21:00 MDT) from late April to mid-July in 2021 to construct an aboveground time budget for northern Idaho ground squirrels. Late April to mid-July covered the time of year when nearly all adult northern Idaho ground squirrels were active. We conducted observation sessions at 4 study sites chosen to include the range of variation in elevation and habitat characteristics (e.g., xeric, rocky meadows vs. mesic meadows with deeper soil) encompassed by our study sites. At each observation site, we selected a vantage point that best allowed us to observe squirrel behavior within the site (e.g., little obstruction from shrubs or terrain). We observed squirrels through binoculars from the tops of vehicles or ladders from a distance > 15 m to ensure squirrel behavior was not influenced by our presence. Once we detected an aboveground squirrel, we recorded the amount of time engaged in the following behaviors: foraging (searching for, collecting, and ingesting food), vigilance (standing motionless, bipedally or quadrupedally, with head up and not foraging), locomotion (walking or running and not foraging), self-grooming (scratching, preening, or cleaning face), intraspecific interactions (chasing, chased by, or fighting with another northern Idaho ground squirrel), and collecting nest material (searching for and collecting nest material). We spoke into audio-recorders while observing squirrels to mark the beginning of each

observed behavior and played back the recordings with a timestamp to measure time spent on each behavior to the nearest second (the elapsed time between when a given behavior was noted and the subsequent behavior was noted in the recording). During the 31.3 hrs at observation posts, we accumulated 14.9 hrs of observed squirrel time (i.e., time with eyes on a focal squirrel, recording time budget data) from 116 observed squirrels.

We recaptured radio-collared squirrels 0-3 times between collaring and hibernation emergence to measure body mass. We also attempted to recapture radio-collared squirrels the following spring to measure body mass, recover geolocator data, and remove collars from squirrels which had not already shed them. Geolocators, therefore, recorded data for individual squirrels in the summer they were collared and the following spring (we obtained spring data only for squirrels that did not shed their collar before then). We recovered 69 geolocators (75% of the 92 deployed) from 62 individual northern Idaho ground squirrels. We were unable to locate and recover the remaining 23 geolocators, presumably because the squirrels were depredated/scavenged, immigrated, or the collars failed. The 69 recovered geolocators recorded 477,504 records of activity across 1,659 complete squirrel-days from summer 2017 through spring 2020.

Capture efforts from the larger restoration project (Allison et al. 2020) provided an index of northern Idaho ground squirrel density (# captured squirrels/ha within the trapping plot) at each study site each year. We measured ambient aboveground temperature and light intensity (as an index of solar radiation) with 2 data loggers (Onset, Bourne, MA; HOBO pendant temp/light, 64k) at each study site: one logger placed without overhead obstruction to measure light intensity and a second logger placed in a shaded position to measure temperature. The loggers recorded light intensity and temperature synchronously every 30-60 min (variable by site) in summer 2017 and spring 2018 and every 15 min for the remainder of the study. We obtained daily precipitation data for the study area from the nearest SNOTEL station (West Branch) because precipitation strongly affects the thermal environment experienced by mammals (Gebremedhin and Wu 2001).

Statistical Analyses

We separately tested for seasonal and sex differences in northern Idaho ground squirrel foraging activity with two-way, independent-sample Welch's *t*-tests in R (V 4.0.2; R Core Team 2020). Our sample sizes for each group were sufficiently large ($n > 400$ in all cases) to meet the normality assumption under the Central Limit Theorem and Welch's *t*-tests do not require equal variance. We checked for outliers before conducting *t*-tests.

We modeled northern Idaho ground squirrel body mass to predict daily expected mass values for squirrels across the active season, which we used to generate a metric of individual body condition

by comparing the predicted masses to actual masses of radio-collared squirrels. We modeled ground squirrel body mass as a normal distribution with linear mixed-effects models in the lme4 package in R (Bates et al. 2020). We used 1863 adult male body mass records from 737 individuals and 3277 adult female body mass records from 936 individuals collected as part of the larger restoration study from 2013-2020 (Allison et al. 2020). By modeling body mass as a function of day of year, we accounted for the significant seasonal changes in body mass that characterize ground squirrel annual cycles. We modeled male and female body mass separately due to sex-specific differences in seasonal changes in body mass caused by differential reproductive cycles. The global model for both sexes included crossed random intercepts for squirrel ID and year, and fixed effects for: 1) age class, 2) study site, and 3) Julian day (4th degree polynomial). We compared all subsets of the global model and determined the top model based on Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002) by using the MuMIn package in R (Bartoń 2020). We used the top model for each sex to predict expected squirrel body masses by study site for each day from mid-April to early August. We then calculated the ratio of each radio-collared squirrel's actual mass on each day it was captured and weighed to the predicted body masses for the squirrels on those days. We used this ratio (actual mass/expected mass) as a metric of squirrel body condition, where values <1 represented squirrels in relatively poor body condition, 1 represented squirrels of average body condition, and values >1 represented squirrels in relatively good body condition. To model aboveground activity, we paired all 5-min sampling intervals from a given squirrel-day of geolocator data with the body condition value derived from the most temporally proximate body mass record for that squirrel within that year (i.e., we never matched body condition values with activity records from a different year). The time between a body mass record used to estimate body condition and a paired sampling interval ranged from 0 to 62 days (though most were within 10 days; median = 6 days) due to unequal intervals between capture events within and among individual squirrels. Because error in our body condition metric may increase as the time between a body mass record and a paired activity measurement grows, we conducted analyses of 5 data sets, including our full dataset and 4 subsets thereof. The 4 subsets included only sampling dates where the geolocator-derived activity samples were within 40, 30, 20, and 10 days of the nearest body mass record. The results from these 4 data subsets were quantitatively and qualitatively similar to the results produced from our full dataset, so we present only the results of the full dataset.

We restricted our aboveground activity analysis to include only daylight hours because ground squirrels are not known to forage at night and our geolocators could not detect aboveground activity in darkness. We paired each 5-min sampling interval from the geolocator data with the most temporally proximate site-specific ambient light intensity and temperature records (range = 0-30 min

distant, median = 5 min distant). We excluded data from the day we initially collared each squirrel, the 3 days prior to hibernation emergence for individual squirrels when known, the day after each squirrel emerged from hibernation, and the day a squirrel lost its collar. We also excluded any additional post-hibernation days before a squirrel first spent 100 minutes above ground in a single day and days we trapped at a given site to ensure we modeled activity of fully active squirrels that were not disturbed by our trapping activities. Finally, we excluded days for which we did not have temporally appropriate body mass data for individual squirrels (i.e., when a squirrel was not recaptured following hibernation) and days without site-specific light intensity and temperature data. We designated 9 squirrels whose age class was unknown (we cannot distinguish yearlings from ≥ 2 -year-olds unless a squirrel was initially captured as a juvenile) as yearlings due to their low body masses at initial capture (< 130 g; Sherman and Runge 2002). We used 211,128 sampling intervals from 1142 active squirrel-days spread across 59 individual squirrels in our modeling effort, including data from summer 2017 through spring 2020.

We built generalized linear mixed-effects models in the lme4 package in R to model the probability of a squirrel being above ground during a given 5-min sampling interval as a binomial distribution with a logit link function. Our global model included nested random intercepts for squirrel ID and study site and a crossed random intercept for year. We considered 9 predictor variables in our global model: 1) squirrel age class, 2) squirrel sex, 3) conspecific density, 4) body condition, 5) Julian day (quadratic), 6) proportional time of day (i.e., daylight hours scaled from 0 to 1; 4th degree polynomial), 7) ambient aboveground light intensity (quadratic), 8) ambient aboveground temperature (quadratic), and 9) daily precipitation. We considered the two-way interaction between body condition and Julian day to test for changes in state-dependent behavior as residual foraging time decreases (i.e., as hibernation approached). We also considered the two-way interaction between ambient aboveground temperature and light intensity to test for a “heat index” effect. We considered effects of squirrel age class and sex to improve model accuracy because we assumed *a priori* that tradeoffs regarding foraging activity might vary among age and sex classes. We tested our predictor variables for collinearity with a correlation matrix before we modeled aboveground activity. We only considered models that included variables with $|r| < 0.6$ correlations with all other variables in the model. We standardized continuous variables and centered them on 0 before inclusion in modeling to promote model convergence and allow model-averaging (Bolker et al. 2009). We checked for uninformative predictor variables (85% confidence interval overlaps zero; Arnold 2010). We compared all subsets of the global model based on AIC_c using the MuMIn package in R and we model-averaged among models receiving at least 0.05 Akaike importance weight (w_i) to produce final parameter estimates. We used the marginal coefficient of determination for our top

model to assess absolute model fit because AIC_c only provides information about relative model fit (Burnham et al. 2011).

RESULTS

Daytime aboveground activity of northern Idaho ground squirrels primarily occurred between 7:00 and 21:30 MDT with small shifts in active hours as the active season progressed. Within that time window, aboveground activity followed a bimodal pattern during summer months (June-August), with peaks in the morning and evening. Female squirrels also had a bimodal activity pattern during March-May, again with peaks in the morning and the evening, but males had a unimodal activity pattern during March-May, with a single peak in the afternoon. Squirrels spent an average of 487 min/day (SD = 220 min) above ground, which equated to an average of 52% of daylight sampling intervals above ground per day (range = 0-84%). We detected differences in time spent above ground between summer (June-August) and spring (March-May; $t = 33.4$, $df = 747$, $p < 0.0001$). Squirrels spent 126% more time above ground per day in summer (mean = 583 min, SD = 149 min) than after emerging from hibernation in spring (mean = 258 min, SD = 192 min). Males spent 6% more time above ground per day (596 min/day, SD = 142 min) than females (564 min/day, SD = 157 min) during summer ($t = 3.6$, $df = 998$, $p < 0.001$) and 42% less time above ground per day (224.8 min/day, SD = 199 min) than females (319 min/day, SD = 162 min) during spring ($t = 5.6$, $df = 415$, $p < 0.0001$).

Squirrels spent 63% of their aboveground time foraging, 28% vigilant, 5% locomoting, and 4% on other activities. Additionally, 38% of time spent vigilant and 26% of time spent locomoting were immediately preceded and followed by a bout of foraging, suggesting a substantial amount of vigilance and locomotion were extensions of the need to forage rather than important aboveground activities per se. Aboveground foraging time increased throughout the active season (47% in April/May, 63% in June, 81% in July), and varied a bit with time of day (67% from 8:00-12:00, 46% from 12:00-16:00, 58% from 16:00-21:00). Foraging was always the most common behavior during observation sessions, except during the afternoon, when squirrels spent 53% of their time vigilant. We were unable to determine the sex of focal squirrels during observation sessions (sex is not obvious unless a squirrel is lactating or in-hand, where genitalia can be inspected). Two other observational studies of congeners (*Uroditellus*) found no sex differences in aboveground behavior (Zegers 1981; Sharpe and Van Horne 1998) and northern Idaho ground squirrel diet does not differ between the sexes (Goldberg et al. 2020b). We, therefore, feel confident we did not miss any sex differences in foraging behavior that would undermine our interpretations, especially as the predictions of foraging theory we tested are not sex-specific.

The global model designed to explain variation in northern Idaho ground squirrel aboveground activity was the top model and included fixed effects for: 1) squirrel sex, 2) squirrel age class, 3) conspecific density, 4) a two-way interaction between body condition and Julian day (quadratic), 5) proportional time of day (4th degree polynomial), 6) a two-way interaction between ambient temperature (quadratic) and ambient light intensity (quadratic), and 7) daily precipitation (Table 2). The top model had 70% of model weight, explained 78% of the variation in northern Idaho ground squirrel aboveground activity, and performed much better than the null model ($\Delta AIC_c = 111816.81$, $w_i = 0.00$). We model-averaged the top model with 1 additional model ($w_i = 0.30$) and present model-averaged parameter estimates from these 2 models (Table 3).

The bimodal activity pattern of northern Idaho ground squirrels seen in the raw geolocator data was largely flattened once we accounted for individual ID, spatiotemporal effects, body condition, conspecific density, and thermal conditions (Fig. 2a). That is, squirrels were highly likely (>80% probability) to be above ground throughout the day with the other predictor variables in the model held constant at their means. Body condition and day of year affected aboveground activity of northern Idaho ground squirrels: activity increased throughout the active season, peaking on 12 July and remaining high through the end of the active season (Fig. 2b). The probability of a squirrel being above ground during a given 5-min interval on 12 July (90.9%) was 13.9% greater than during a given 5-min interval on 1 May (77.0%). Heavier squirrels were more likely to be above ground during daylight hours early in the year (82.5% probability for “heavy” squirrels and 70.4% probability for “lean” squirrels during a given 5-min interval on 1 May), whereas leaner squirrels spent more time above ground during late summer (78.2% probability for “heavy” squirrels and 87.8% probability for “lean” squirrels during a given 5-min interval on 15 July), as hibernation approached. Aboveground squirrel activity was positively associated with conspecific density such that the probability of a squirrel being above ground during a given 5-min interval was 8.5% greater at a density of 12 squirrels/ha (94.5%) than at 2 squirrels/ha (86.0%; Fig. 2c). Ambient aboveground temperature and light intensity influenced above ground activity: squirrels were more likely to be above ground at low temperature extremes when solar radiation was high (85.6% probability at “high” solar radiation and 37.8% probability at “low” solar radiation during a given 5-min interval at 5 °C) and at high temperature extremes when solar radiation was low (76.7% probability at “high” solar radiation and 95.1% probability at “low” solar radiation during a given 5-min interval at 35 °C), indicating a heat index effect (Fig. 2d). Time spent aboveground was low at very cold temperatures regardless of solar radiation (30.4% probability at “high” solar radiation and 2.6% probability at “low” solar radiation during a given 5-min interval at -10 °C). Aboveground activity was also negatively associated with daily precipitation such that the probability of a squirrel being above

ground during a given 5-min interval was 17.6% lower with 5 cm daily precipitation (73.8%) than 0 cm daily precipitation (91.4%; Fig. 2e). Importantly, the temporally near-instantaneous effect sizes presented here are likely compounded through time for individual squirrels, yielding ecologically significant differences among individuals on which natural selection can act.

DISCUSSION

Our focal behavioral watches confirmed what we have observed informally for northern Idaho ground squirrels across 9 years of intensive study: squirrels spent a majority of aboveground time foraging (63%) and performing behaviors – vigilance (28%) and locomotion (5%) – that facilitate foraging. There was, however, some variation in these percentages by month and time of day and squirrels likely alter the ratio of time spent foraging compared to time spent vigilant in response to changes in predation risk, forage availability, and endogenous state (Arenz and Leger 1999; Unck et al. 2009; van der Marel 2019), resulting in a dynamic relationship between time spent above ground and time spent actively acquiring and ingesting food. Non-foraging above ground activities, especially those related to breeding (e.g., searching for mates) and burrow maintenance (e.g., collecting nest material), may take up more time early in the active season, though foraging remains an imperative. Other studies that documented aboveground time budgets of ground squirrels (*Marmotini*) also reported that foraging, vigilance, and, to a lesser extent, locomotion comprised the vast majority of aboveground activity (Shaw 1945; Streubel 1975; Betts 1976; Zegers 1981; Leger et al. 1983; Kenagy et al. 1989; MacWhirter 1991; Loughry 1993; Sharpe and Van Horne 1998; Everts et al. 2003; Hannon et al. 2006). Therefore, we believe our model of aboveground activity provides a useful test of the predictions of optimal foraging theory for northern Idaho ground squirrels.

Aboveground activity of northern Idaho ground squirrels largely adhered to predictions of optimal foraging theory: day of year, body condition, conspecific density, and thermal conditions influenced the amount of time squirrels spent above ground. The bimodal pattern in aboveground activity became nearly unimodal once we accounted for those factors, suggesting aboveground thermal conditions explain most of the afternoon lull in aboveground activity. Activity patterns of Arctic ground squirrels (*Urocitellus parryii*; Williams et al. 2014), American red tree squirrels (Pauls 1978; Williams et al. 2014), European red tree squirrels (*Sciurus vulgaris*; Wauters et al. 1992), common degus (*Octodon degus*; Bacigalupe et al. 2003), and coruros (*Spalacopus cyanus*; Rezende et al. 2003) also changed seasonally from a bimodal pattern during the summer to unimodal during the winter or when activity was modeled as a function of thermal conditions. This suggests thermal conditions shape foraging activity in many rodents, including arboreal and semi-fossorial taxa. An alternative explanation of the bimodal activity pattern we observed in the raw data is use of burrows

by satiated squirrels, which can fill their relatively short hindguts when food is abundant (Hume et al. 1993). Satiation, however, did not appear to be a major constraint on daily foraging activity of northern Idaho ground squirrels as the bimodal activity pattern in the raw data was largely flattened by our model despite the fact that we did not include any metric of satiation as a predictor variable.

Northern Idaho ground squirrels are likely a primary prey item for badgers and red-tailed hawks and a supplemental food source for several other predators (Yensen and Sherman 1997). Squirrels forage above ground, but quickly retreat to burrows in response to acute predation risk (Yensen et al. 1991). Badgers often excavate burrow systems to capture ground squirrels, though primarily at night rather than during the daylight hours included in our analyses (Murie 1992; Michener 2004). The perceived threat of predation may also influence squirrel foraging behavior given that aboveground activity was positively correlated with conspecific density. This suggests squirrels increase foraging time when vigilance for potential predators is highest and predation risk is diluted. The benefits of group-living and sociality for vertebrates in the face of predation are well documented (Alexander 1974; Foster and Treherne 1981; Clark and Dukas 1994; Janson 1998; Sorato et al. 2012), including in sister taxa to northern Idaho ground squirrels (Sherman 1985; van der Marel 2019). The reduced predation risk attained by foraging in groups could enhance energetic intake (Caraco 1980) and access to high-quality foraging patches for northern Idaho ground squirrels as it does for other rodents (Brown 1988; Thorson et al. 1998). Alternatively, increased aboveground activity at sites with high squirrel densities could reflect intraspecific scramble competition for limited food resources (Lima et al. 1999; Beauchamp and Ruxton 2003). Emergence of juvenile squirrels from natal burrows likely had little effect on adult foraging behavior because juveniles emerge from natal burrows and begin feeding themselves in June, overlapping with adults for only 2-6 weeks each summer. Additionally, juveniles are substantially smaller than and behaviorally subordinate to adults during that 2-6-week period, meaning they require less food and are relatively poor competitors. Competition for food with the larger, physically dominant Columbian ground squirrel, however, could increase foraging time for northern Idaho ground squirrels (Dyini and Yensen 1996). Future studies should measure or manipulate forage availability to disentangle these alternative hypotheses.

Northern Idaho ground squirrels can further mitigate predation risk by spending more time in burrows. However, the energetic and nutritional requirements of spending 8.0-9.5 months hibernating each year place limits on the amount of time a squirrel can spend underground during the active season. Risk-sensitive and state-dependent foraging therefore predict: 1) daily foraging time increases as time to hibernation decreases, 2) squirrels in poor condition spend more time foraging than those in good condition, and 3) the disparity between these groups increases as residual foraging time

decreases. Northern Idaho ground squirrel aboveground activity partially supported these predictions. Daily time spent above ground increased throughout the active season. Though this result fits the first prediction, some other hibernating squirrel species apparently reduce foraging time as the season progresses while still gaining mass (Zegers 1981). Lower predation risk during the summer would explain the seasonal pattern in time spent above ground. Though we have no explicit measure of predation risk for northern Idaho ground squirrels, we documented depredations by multiple predators throughout the active season and have not noticed any obvious consistent changes in predation risk across the active season. A seasonal increase in foraging time could also reflect waning forage abundance and nutritional quality as plants senesce in the summer, especially because northern Idaho ground squirrels are thought to be food limited due to woody vegetation encroachment into occupied meadows (Sherman and Runge 2002). Vegetation sampling data from our larger restoration study showed no decrease in forb cover from spring to summer across the 7 study sites (0.03% increase) and only a small decrease in grass cover (0.9%; Allison et al. 2020). The wide variety of plants consumed by northern Idaho ground squirrels (>120 genera) and seasonally flexible diets that incorporate more seeds and roots later in the active season may mitigate the effects of any seasonal declines in nutritious green forb and grass availability on squirrel foraging activity (Yensen et al. 2018; Goldberg et al. 2020b).

Squirrels in poor body condition spent less time above ground during spring months, but increased their activity more so than squirrels in good condition as the active season progressed. By summer – when residual foraging opportunities were few – aboveground activity by leaner squirrels exceeded that of heavier individuals. This result corroborates many past studies across a wide array of taxa implicating energetic state as a factor influencing daily foraging behavior (McNamara and Houston 1996; Olsson et al. 2002; Kotler et al. 2004; Balaban-Feld et al. 2019; Denryter et al. 2020) and suggests northern Idaho ground squirrels modulate foraging activity at 2 temporal scales – 1) daily during the active season, and 2) annually via hibernation immergence date (Goldberg and Conway 2021) – to balance energetic needs and predation risk. Incorporating the energetic thresholds and time constraints imposed upon foraging animals by obligate hibernation is a novel aspect of this study. Future studies of hibernating herbivores should incorporate this latent variable to better explain the complexity of daily foraging decisions as free-ranging animals navigate tradeoffs between foraging and predation risk and how the optimal strategy to resolve those tradeoffs changes as hibernation approaches.

Aboveground activity of northern Idaho ground squirrels is further influenced by aboveground thermal conditions. Northern Idaho ground squirrels were less likely to be above ground at cold (<15 °C) and hot (>30 °C) ambient temperatures, which suggests foraging is not energetically

profitable at such extremes. Solar radiation mitigated or exacerbated the effect of ambient temperature: squirrels were more likely to be above ground in cold weather when solar radiation was high and in hot weather coupled with low solar radiation. This is not surprising as solar radiation can greatly affect the operative temperature of small mammals, adding up to 10 °C in some cases (Chappell and Bartholomew 1981b; Walsberg and Wolf 1995). Squirrels were also less active on days with more precipitation, presumably to avoid increased evaporative heat loss from wet fur (Gebremedhin and Wu 2001). If we had recorded locally derived precipitation data for each study site, the relationship with precipitation would likely have been even stronger (see Williams et al. 2016). Northern Idaho ground squirrels likely use burrows as thermal refugia, where insulative nests provide warmth (Gedeon et al. 2010) and stable burrow temperatures allow squirrels to offload heat accumulated in hot weather (Milling et al. 2017). Temperature-dependent foraging activity of northern Idaho ground squirrels corroborates results from studies of sister taxa (Chappell and Bartholomew 1981a; Vispo and Bakken 1991; Sharpe and Van Horne 1999; Long et al. 2005; Váczi et al. 2006; Williams et al. 2014, 2016) and suggests that regionally-projected increases in extreme thermal conditions and precipitation resulting from climate change (Littell et al. 2011) could degrade foraging conditions for these threatened squirrels.

Behaviors associated with reproduction may put some additional constraints on aboveground activity by northern Idaho ground squirrels. However, the breeding season for males lasts only ~2 weeks in early spring, when females emerge from hibernation, and individual females are receptive to males for a single afternoon shortly after emerging from hibernation (Sherman 1989). Thus, we do not believe these breeding behaviors confounded our results. Copulation takes place below ground, but generally lasts only minutes (Sherman 1989), making it unlikely this behavior would explain much variation in aboveground activity had we measured it. Natal care by females likely influences time spent above ground, though the strength and directionality of the relationship may depend on forage availability (MacWhirter 1991; Williams et al. 2016). Males in our study spent slightly more time above ground than females, which could reflect the need for females to care for young below ground. If so, effective habitat management for northern Idaho ground squirrels may increase both survival and recruitment by allowing females to spend more time and energy raising offspring.

We tested a suite of predictions based on risk-sensitive and state-dependent optimal foraging theory and demonstrated that a small obligate hibernator modulates activity in response to thermal conditions, residual foraging time, and endogenous state. Northern Idaho ground squirrels are imperiled: the species is endemic to just 2 counties in west-central Idaho and <3000 squirrels persist (Wagner and Evans Mack 2021). Habitat improvement and expansion via forest thinning and prescribed burning has been the primary management tool applied to promote northern Idaho ground

squirrel recovery (Suronen and Newingham 2013; Allison et al. 2020). These efforts will likely be most effective when availability of preferred forage plants is increased, due to the tradeoffs between foraging and aboveground threats. Squirrels can more quickly attain the energy and nutrients required for hibernation if forage quality and quantity improve, allowing squirrels to reduce predation and thermal risks by spending more time in burrows. Higher population densities may further benefit squirrels by increasing predator detection and diluting predation risk (Allee effects), allowing individual squirrels to increase foraging time without decreasing survival probability. That is, the decreased risk of predation associated with sociality may promote foraging activity, allowing squirrels to attain better energetic states to survive hibernation and reproduce in future years. If, however, intraspecific scramble competition decreases foraging efficiency at high densities of northern Idaho ground squirrels, squirrels will need to navigate tradeoffs among foraging, predation risk, and thermal intolerance as populations increase. Additional studies that integrate the synergistic relationships among foraging opportunities, predation risk, and thermal conditions are needed so that scientists can work with managers to better plan and implement effective and cost-efficient recovery strategies for rare, endemic animals like the northern Idaho ground squirrel.

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Table 1.1. Predicted relationships (+ = positive, - = negative, +/- = quadratic, x = interaction) between a suite of intrinsic and extrinsic predictor variables and daily foraging activity of northern Idaho ground squirrels during the April-July active season. Predictions are based on 3 potential selection pressures from optimal foraging theory to explain northern Idaho ground squirrel foraging activity: 1) the energetic requirements of hibernation, 2) predation risk, and 3) thermal risk.

	Hibernation Requirements	Predation Risk			Thermal Risk			
		Body Condition			Temperature			
	Residual Foraging Opportunities	Body Condition	Residual Foraging Opportunities	Conspecific Density	Temperature	Solar Radiation	Solar Radiation	Precipitation
Foraging Activity	-	-	x ¹	+	+/-	+/-	x ²	-

¹ The magnitude of the negative relationship between foraging activity and body condition is predicted to increase as residual foraging opportunities decrease (i.e., as hibernation approaches).

²Foraging activity at low solar radiation is predicted to increase as temperature increases and foraging activity at high solar radiation is predicted to decrease as temperature increases due to a “heat index” effect.

Table 1.2. Top models designed to explain variation in aboveground (i.e., foraging) activity of northern Idaho ground squirrels. All models included data from 1142 squirrel-days and 211,128 sampling intervals derived from 59 geolocator-equipped, free-ranging adult squirrels during summer 2017 through spring 2020. The table includes all models with >0.01 Akaike model weight (w_i), the global model (which was also the top model), and the null (random intercept only) model. Random intercepts are included in parentheses. Variable notation is as follows: Sex = squirrel sex, Age = squirrel age class, Sq. Dens = conspecific density, Mass = body condition, J. Day = Julian day, Time = proportional time of day, Light = aboveground ambient light intensity, Temp = aboveground ambient temperature, Precip = daily precipitation, Sq. ID = squirrel ID, Site = study site, and Year = year.

Model	ΔAIC_c	w_i
Sex + Age + Sq. Dens + Mass*J. Day ² + Time ⁴ + Light ² *Temp ² + Precip + (Sq. ID) + (Site) + (Year)	0.00	0.70
Age + Sq. Dens + Mass*J. Day ² + Time ⁴ + Light ² *Temp ² + Precip + (Sq. ID) + (Site) + (Year)	1.67	0.30
(Sq. ID) + (Site) + (Year)	111752.30	0.00

Table 1.3. Model-averaged parameter estimates, 95% confidence intervals, and p-values for all predictor variables included in models receiving ≥ 0.05 Akaike model weight (w_i) based on a model selection effort that compared a suite of generalized linear mixed-effects models designed to explain variation in aboveground (i.e., foraging) activity of northern Idaho ground squirrels. All models included data from 1142 squirrel-days and 211,128 sampling intervals derived from 59 geolocator-equipped, free-ranging adult squirrels during summer 2017 through spring 2020.

Parameter		Estimate	Lower 95% CI	Upper 95% CI	p
Sex	Female				
	Male	0.24	-0.18	0.67	0.27
Age Class	≥ 2 -years-old				
	1-year-old	-0.22	-0.30	-0.14	0.00
NIDGS Density		0.10	0.07	0.14	0.00
Relative Time of Day ⁴		577.26	561.71	592.82	0.00
		-999.06	-1015.96	-982.17	0.00
		517.80	504.51	531.10	0.00
		-403.19	-413.48	-392.90	0.00
Daily Precipitation		-0.26	-0.31	-0.21	0.00
Julian Day ² * Body Condition		-645.88	-727.95	-563.81	0.00
		-371.04	-422.45	-319.63	0.00
Temperature ² * Light Intensity ²		-100401.22	-106331.98	-94470.46	0.00
		54623.51	50259.57	58987.44	0.00
		-13228.41	-17365.10	-9091.72	0.00
		12436.30	8961.60	15911.01	0.00

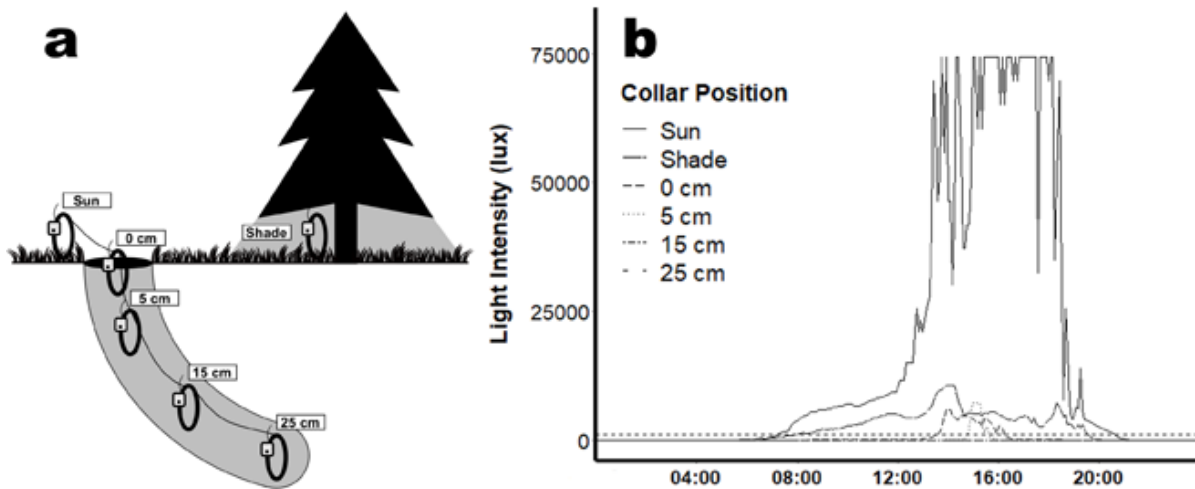


Figure 1.1. We placed 5 radio-collars equipped with geolocators in different positions relative to the entrance of a northern Idaho ground squirrel nest burrow (a) for 24 hours on a cloudless day in summer 2020 to determine the threshold for classifying a squirrel as above or below ground during a given sampling interval. We placed a 6th geolocator ~100 m away in full shade to account for cloudy days and squirrels foraging in shade. The geolocators at 0 cm (burrow mouth) and 5 cm below the nest burrow entrance recorded values ≥ 1000 lux (horizontal dashed line) on 22% and 7% of sampling intervals from 8:00-20:00 MDT and the 2 geolocators >5 cm below the entrance never recorded values ≥ 1000 lux (b). Conversely, the shaded and non-shaded aboveground geolocators recorded values ≥ 1000 lux on 97% and 100% of sampling intervals from 8:00-20:00 MDT. We therefore used 1000 lux as the threshold to determine whether a squirrel was above (≥ 1000 lux) or below (< 1000 lux) ground for geolocator readings we obtained from free-ranging squirrels.

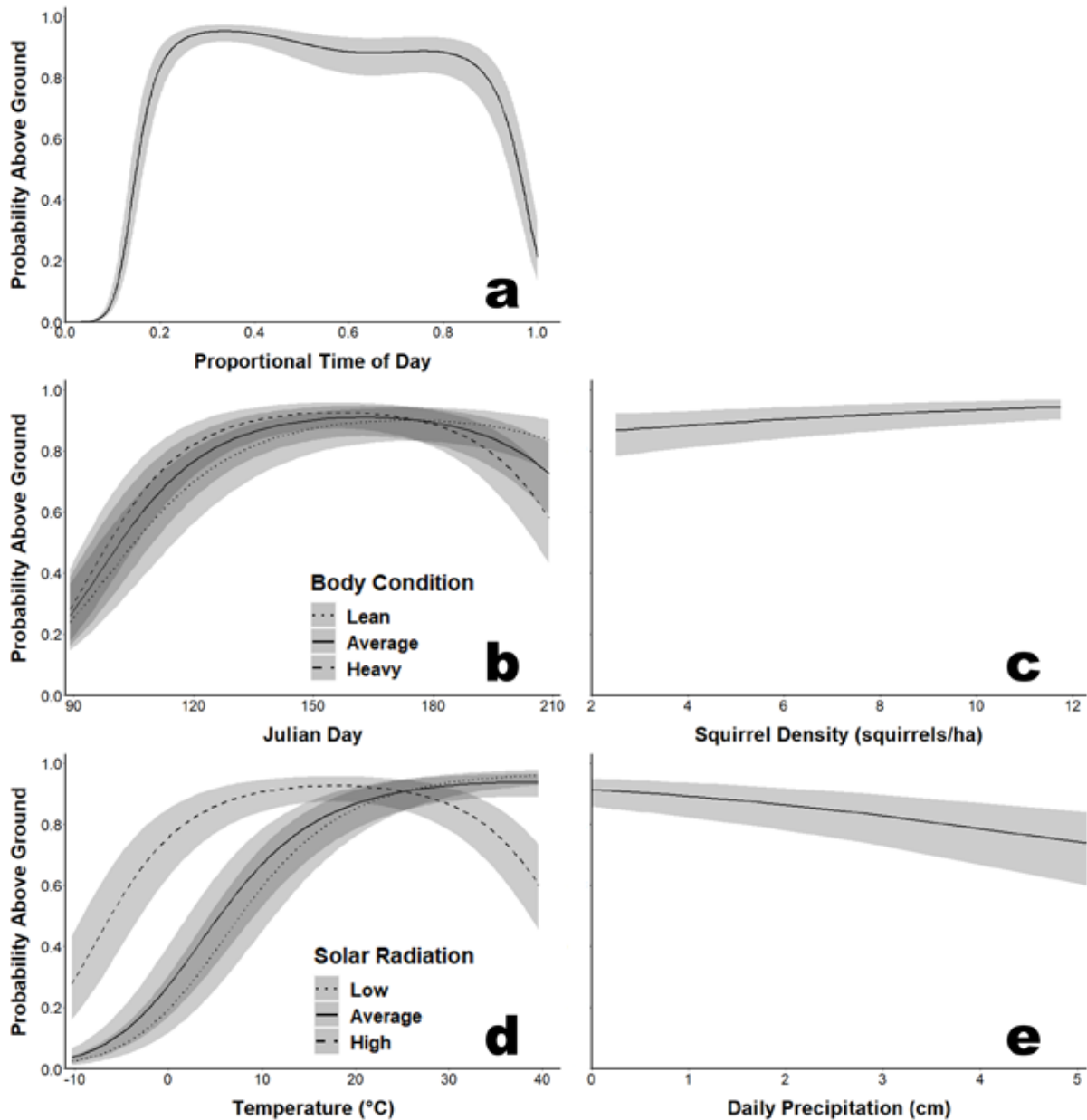


Figure 1.2. Aboveground (i.e., foraging) activity ($\pm 95\%$ CI) of northern Idaho ground squirrels was highest during mid-morning hours and lowest in the hours immediately after sunrise and before sunset (a); x-axis is proportional time of day for daylight hours, which accounts for changes in daylength across the active season (i.e., 0.5 = solar noon). Julian day (b), body condition (b), and conspecific density (c) influenced aboveground activity ($\pm 95\%$ CI) of northern Idaho grounds during daylight hours. Thermal conditions – ambient aboveground temperature, ambient aboveground solar radiation (d), and daily precipitation (e) – also influenced aboveground activity ($\pm 95\%$ CI) of northern Idaho ground squirrels during daylight hours. We generated these partial effects plots from model-averaged parameter estimates from the top generalized linear mixed-effects models designed to explain variation in northern Idaho ground squirrel aboveground activity. All models included data from 1142 squirrel-days and 211,128 sampling intervals derived from 59 geolocator-equipped, free-ranging adult squirrels during summer 2017 through spring 2020.

Chapter 2: Climate Influences Survival of Coexisting Species Directly and by Modulating Interspecific Competition

ABSTRACT

Understanding human impacts on free-ranging animals is a core objective of contemporary ecology and of primary interest to policy makers and the public. Despite this, relatively little is known about the mechanisms by which climate shapes the demography of animal populations, making it difficult to predict the explicit effects of future climate change on population dynamics, species persistence, and biodiversity. Climate change can reorganize biological communities, potentially altering competitive interactions among coexisting species. We investigated the synergistic effects of climate, interspecific competition, and hibernation on survival of 3 sympatric sciurids – the federally threatened northern Idaho ground squirrel (*Urocitellus brunneus*), the larger Columbian ground squirrel (*Urocitellus columbianus*), and the smaller yellow-pine chipmunk (*Tamias amoenus*) – to provide a basis for understanding how climate interacts with fundamental ecological processes to inform population viability and the coexistence of species. All 3 squirrels had higher survival during hibernation than the active season, though climate variables associated with the duration of hibernation affected overwinter survival of the 3 species differently. Northern Idaho ground squirrels displayed density-dependent survival, and Columbian ground squirrel density negatively influenced survival of the smaller, socially subordinate species. Winter snowfall positively influenced survival of Columbian ground squirrels, but the opposite was true of northern Idaho ground squirrels, suggesting climate-driven changes in forage availability modulate competitive interactions between these species. Our results are novel in elucidating multiple mechanistic pathways by which climate change is likely to affect survival of a rare, endemic animal: directly via thermal tolerance and via changes in the synergistic effects of forage availability and interspecific competition.

INTRODUCTION

Understanding how human actions impact free-ranging animals is a central goal of modern ecology, and the impacts of climate change on animal populations are of particular interest to researchers, policy makers, and the public. Many studies have explored relationships between climate change and phenological or range shifts of animals (Inouye et al. 2000; Thuiller 2004; Parmesan 2006), but comparatively few studies have investigated climate effects on the demography of animal populations (Selwood et al. 2015; Paniw et al. 2021) or the mechanisms underlying such relationships (Tylianakis et al. 2008). For example, survival is a primary demographic trait that directly influences the abundance and distribution of species (Cole 1954; Gaillard et al. 1998; Oli and Dobson 2003;

Ozgul et al. 2006), but we know surprisingly little about explicit mechanisms by which climate influences survival of free-ranging animals. The dearth of information about climate effects on survival stems from the requirements of high-quality, long-term, individual-level data for mechanistic studies of survival (Miller-Rushing et al. 2010). However, documenting the processes by which climate affects survival will generate explicit predictions regarding the effects of future climate change on population dynamics, species persistence, and the composition of biological communities, and hence, will aid development of effective management strategies for species and ecosystems of conservation concern.

Climate can affect animal survival directly via thermal tolerance (Pörtner and Farrell 2008), but also via numerous indirect and often synergistic mechanistic pathways (Gilman et al. 2010; Walther 2010; Blois et al. 2013). For instance, climate influences forage availability for herbivores (Mysterud et al. 2001; Forchhammer et al. 2005; Doiron et al. 2013), and many herbivores are food limited (Lack 1954; Sinclair 2003; White 2008). Moreover, survival is density-dependent in many animal taxa (Skogland 1985; Van Buskirk and Smith 1991; Forrester 1995; Jonsson et al. 1998; Karels and Boonstra 2000; Fay et al. 2015), indicating that intraspecific competition for limited resources constrains survival in many species. The relationship between competition and survival is likely influenced by environmental conditions (e.g., climate and forage availability) in conjunction with population density (Fowler 1981; Wauters and Lens 1995), but the interactions among these factors are difficult to document and are rarely explored in free-ranging animal populations. Furthermore, climate-mediated changes in forage availability likely underpin many of the observed shifts in species' ranges associated with climate change (Van der Putten et al. 2010), shuffling biological communities and potentially altering competitive interactions within and among species (Tylianakis et al. 2008; Milazzo et al. 2013; Alexander et al. 2015).

Documenting effects of interspecific competition on survival among coexisting species is difficult, and consequently, studies doing so are exceedingly rare (Eccard and Ylönen 2003; Liesenjohann et al. 2011; Sozio and Mortelliti 2016). Such studies, however, help elucidate the demographic consequences of shifting community assemblages resulting from climate change and other anthropogenic actions. Inferring evidence of competition from niche partitioning is a common research approach (MacArthur 1958; Schoener 1974; Jenkins and Wright 1988; Wauters et al. 2002; Glen and Dickman 2008; Kartzinel et al. 2015), but patterns of niche partitioning among coexisting species are insufficient to form strong conclusions regarding interspecific competitive interactions. Dominant species in a community may relegate subordinate species to suboptimal habitat patches (Rosenzweig 1981, 1991), potentially curtailing survival of the subordinate. Alternatively, observed niche partitioning may reflect differential competitive (i.e., performance) abilities, whereby a socially

subordinate species prevails in patches where it is competitively superior with no effect (or even a positive effect) on survival (Brown 1989). Explicitly testing for contemporaneous effects of competitor density on fecundity or survival is a more direct and convincing approach to elucidating competitive interactions between coexisting species and provides insight into the explicit mechanism(s) that underly population dynamics and the evolution of life-history strategies. Moreover, climate often directly influences animals and/or modulates forage availability and, hence, likely alters competitive interactions among coexisting herbivores such that spatiotemporal climate variation provides an opportunity to assess how climate change will exacerbate or mitigate interspecific competition in the future. We used a 9-year dataset of marked animals to explore the effects of mechanistic interactions between climate and interspecific competition on survival of 3 coexisting herbivorous mammals, including an imperiled species of high conservation concern.

The northern Idaho ground squirrel (*Uroditellus brunneus*) is a small, semi-fossorial rodent endemic to a 1600-km² area in western Idaho, USA (Burak et al. 2018). Population declines in the 20th century resulted in a fragmented metapopulation in which <3000 individuals persist (Barbosa et al. 2021; Wagner and Evans Mack 2021), and the U.S. Fish and Wildlife Service listed the species as federally threatened under the Endangered Species Act in 2000 (U.S. Fish and Wildlife Service 2000). Northern Idaho ground squirrels are obligate hibernators, spending 8.0-9.5 months hibernating each year (mid-July to early April on average for adults) to avoid seasonal famine and unsuitable thermal conditions (Goldberg and Conway 2021; Morris et al. 2021). The squirrels live in social groups during the active season, inhabiting xeric, rocky openings embedded within an otherwise forested landscape (Goldberg et al. 2020a; Helmstetter et al. 2021), where they often co-occur with or live adjacent to 2 additional sciurid obligate hibernators: the larger, more common Columbian ground squirrel (*Uroditellus columbianus*) and the smaller, ubiquitous yellow-pine chipmunk (*Tamias amoenus*; Morris et al. 2021).

These 3 species may be particularly sensitive to climate change due to their highly seasonal annual cycles (Paniw et al. 2020). Though behavioral plasticity and energetic state can buffer animals against otherwise negative effects of climate change on demography (Long et al. 2014), obligate hibernation imposes annual energetic thresholds on animals, constraining foraging responses to climate change (Allison and Conway 2022). Unsurprisingly, then, fitness consequences of climate change have been documented in other obligate hibernators, including ground squirrels (Ozgul et al. 2010; Lane et al. 2012; Turbill and Prior 2016; Falvo et al. 2019; Cordes et al. 2020). Specifically, climate variables regulating the timing and duration of hibernation may affect survival by altering the relative importance of seasonal selection pressures (Turbill et al. 2011; Cordes et al. 2020). Moreover, competition with Columbian ground squirrels influences northern Idaho ground squirrel behavior

(Dyner and Yensen 1996; Yensen and Dyner 2020), potentially limiting the smaller squirrel's plasticity (particularly as it pertains to foraging habitat selection) in response to climate change, and hence, negatively impacting survival, though tests of the demographic consequences of interspecific competition between the ground squirrels are lacking. Consequently, this system provided an ideal chance to evaluate the interactive effects of climate and competition on survival of coexisting species with conservation implications for a rare, endemic animal.

STUDY SPECIES AND SYSTEM

Northern Idaho ground squirrels, Columbian ground squirrels, and yellow-pine chipmunks are generalist herbivores, consuming a wide variety of plant parts and taxa (Tevis Jr. 1953; Kuhn and Vander Wall 2009; Harestad 1986; Dyner and Yensen 1996; Yensen et al. 2018; Goldberg et al. 2020b), and the 2 ground squirrel species are known to have substantial diet overlap (Dyner and Yensen 1996). All 3 species are obligate hibernators, though the ground squirrels and chipmunk differ in hibernation strategy. The two ground squirrel species are fat-storing hibernators and have a similar 8.0-9.5-month hibernation period (Young 1990a; Dyner and Yensen 2020; Goldberg and Conway 2021; Morris et al. 2021), whereas chipmunks are food-storing hibernators (i.e., they cache food for use during hibernation) and hibernate for 4.0-4.5 months annually (~mid-November to mid-March; Kenagy and Barnes 1988; Vander Wall 2019). As such, chipmunks have a longer active foraging season and need not accumulate as much pre-hibernation fat as ground squirrels (i.e., chipmunks are more income foragers by comparison). Ground squirrels and chipmunks hibernate in specially excavated burrow systems, which are plugged during heterothermy, providing refuge from harsh aboveground thermal conditions and predation (Kuhn and Vander Wall 2009; Young 1990b; Goldberg and Conway 2021). Diet, habitat, and behavioral similarities between the northern Idaho ground squirrel and Columbian ground squirrel imply a high potential for competitive interactions between them, with the ~3x larger Columbian ground squirrels presumably socially dominant over northern Idaho ground squirrels (Dyner and Yensen 1996; Yensen and Dyner 2020).

We collected detailed data for 9 years at 10 study sites within the extant range of the northern Idaho ground squirrel in western Idaho, USA. The 10 study sites represented much of the elevational gradient occupied by this rare squirrel, ranging from 1275 m to 1700 m above sea level. Mean daily temperature, derived from gridMET weather models (Abatzoglou 2013), ranged from -4.6 °C in December at the coldest site to 20.2 °C in July at the warmest site during the study (2013-2021). Mean annual precipitation at study sites was 831 mm (range among sites and years = 461-1259 mm), which primarily fell as snow during the winter months, when squirrels were hibernating. Snowmelt date (final day >10 cm residual winter snowpack) is positively correlated with squirrel emergence

from hibernation (Sheriff et al. 2011; Lane et al. 2012; Williams et al. 2017; Goldberg and Conway 2021; Morris et al. 2021) and varied among study sites and years, ranging from 7 February at the least snowy site in 2015 to 7 May at the snowiest site in 2019. Spatiotemporal variation in weather across 9 years at the 10 study sites provided an excellent opportunity to investigate the effects of climate on survival of the 3 sciurids.

Northern Idaho ground squirrels primarily occupied sparsely vegetated patches with shallow, rocky soil and little overhead canopy cover during their 2.5-4.0 month active season, and moved to areas with deeper soil to hibernate. Columbian ground squirrels inhabited more productive areas – mesic meadows, forest-meadow ecotones, and woodlands – often adjacent to northern Idaho ground squirrels. The 2 ground squirrels used different microhabitats at a fine spatial scale, but still frequently overlapped in space and time along boundaries and during foraging ventures. Yellow-pine chipmunks were most common in areas with some vertical habitat structure, including shrubs, boulders, logs, and small trees, with local distributions broadly overlapping those of both ground squirrel species. Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) predominated in forest overstories at the study sites. Common plants in northern Idaho ground squirrel active-season use areas included big sagebrush (*Artemisia tridentata*), buckwheat (*Eriogonum* spp.), bluegrass (*Poa* spp.), wild onion (*Allium* spp.), and biscuitroot (*Lomatium* spp.). Common plants in Columbian ground squirrel active-season use areas included elk sedge (*Carex geyeri*), pine grass (*Calamagrostis rubescens*), heart-leaf arnica (*Arnica cordifolia*), cinquefoil (*Potentilla* spp.), and common yarrow (*Achillea millefolium*). Chipmunks frequented patches with high volumes of snowberry (*Symphoricarpos* spp.), wax currant (*Ribes cereum*), antelope bitterbrush (*Purshia tridentata*), and snowbrush ceanothus (*Ceanothus velutinus*) in addition to big sagebrush. Squirrel predators most prevalent at study sites were American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), and red-tailed hawks (*Buteo jamaicensis*). Hunting, livestock grazing, and harvesting timber were the primary human activities in the study area, though humans rarely visited our remote study sites.

METHODS

Data Collection

We captured and marked northern Idaho ground squirrels, Columbian ground squirrels and yellow-pine chipmunks annually at the 10 study sites for 9 years (2013-2021; see Morris et al. 2021 for additional details). Nine of the 10 study sites were rectangular, 8-ha trapping plots and 1 study site was a non-regular, 4-ha polygon. Half of each 8-ha trapping plot was centered on a patch occupied by

northern Idaho ground squirrels and the other half was immediately adjacent, seldom occupied habitat. We captured ≥ 2 individuals of each squirrel species at each study site during the study. We trapped each site 8 days per year, split equally between a spring trapping session (Late April through early June, depending on elevation and access) and a summer trapping session (mid-June to late July), with each session spanning ~ 3 weeks at a given site. Trapping dates varied slightly year-to-year due to annual variation in snowpack (and accessibility in spring) and other logistical considerations. We allowed ≥ 2 full days between trapping days at each study site to minimize disturbance of foraging activity of the federally threatened northern Idaho ground squirrel. We trapped 9 of 10 study sites for 10 h per trapping day ($\sim 7:30$ - $17:30$ MDT) during spring and 6 h per trapping day ($\sim 7:00$ - $13:00$ MDT) during summer; we trapped the 10th study site 6 h per trapping day during spring and summer sessions. The shorter summer trapping days allowed us to avoid capturing animals during the hottest time of day, when squirrels are less active and heat stress poses mortality risk to captured animals. Similarly, we ceased trapping at ambient temperatures ≥ 25 °C or during bouts of heavy precipitation.

We captured squirrels in Tomahawk live traps (Tomahawk Live Trap, Hazelhurst, WI, 13 x 13 x 41 cm and 15 x 15 x 50 cm) baited with a mixture of peanut butter, oats, and imitation vanilla. We set 30 traps approximately in a 6 x 5 trap grid at each study site each trapping day, with traps placed at burrow entrances and other areas likely to be frequented by squirrels to maximize trap success. We shifted the trap grid each trapping day during a given session, placing traps in new locations within the grid, to capture as many individuals of each species as possible during a session and to ensure equal capture probability among individuals during a session. We also captured northern Idaho ground squirrels in non-baited, “focal traps” to increase capture numbers of these rare squirrels (Morris et al. 2021). We placed focal traps at burrows into which we saw a northern Idaho ground squirrel retreat such that the trap covered the burrow entrance; we temporarily blocked nearby burrow openings to prevent squirrels that had retreated from escaping and to funnel squirrels into the focal trap. We checked all traps for captured squirrels every 30-60 minutes throughout the day and brought captured squirrels to a shaded area for processing. We released squirrels at their capture locations during the trap check following processing and reset Tomahawk traps to capture additional individuals.

We recorded the sex (male or female) and age class (juvenile or adult) of each captured squirrel and marked all individuals for capture-mark-recapture survival analyses. We marked northern Idaho ground squirrels and Columbian ground squirrels with a metal ear tag (National Band & Tag Co., Newport, KY, 1005-1) in each ear and chipmunks with a passive integrated transponder tag (PIT; Biomark, Boise, ID, HDX12) for individual identification. We also marked ground squirrels that lost an ear tag or had ripped ears with a PIT tag to prevent data loss. Overall, we captured 1689 northern

Idaho ground squirrels (821 males and 868 females, 469 and 537 of which were captured as juveniles), 1291 Columbian ground squirrels (691 males and 600 females, 191 and 188 of which were captured as juveniles), and 2590 yellow-pine chipmunks (1327 males and 1263 females, 469 and 399 of which were captured as juveniles) for inclusion in survival analyses. Our capture efforts also provided an annual index of population density for each species at each study site (# of squirrels captured/trapping plot area), which allowed us to test whether intra- and/or interspecific competition affected survival.

We downloaded gridMET daily, 4-km resolution temperature and precipitation data (Abatzoglou 2013) and SNODAS daily, 1-km resolution snowpack data (National Operational Hydrologic Remote Sensing Center 2004). We used these data to generate 6 annual climate variables at each study site for inclusion as covariates in survival models: 1) total precipitation (mm) during the active season (1 April – 31 July), 2) mean summer active-season (1 June – 31 July) daily high temperature (°C), 3) mean hibernation season (1 August – 31 March) daily mean temperature (°C), 4) snowmelt date (last Julian day ≥ 10 cm residual winter snowpack), 5) number of hibernation days (1 August – 31 March) with snow cover present (≥ 10 cm in depth), and 6) total winter snowfall (in mm; 1 December – 31 March). We selected these climate variables to allow comparison to other studies of ground squirrel survival that considered effects of similar variables (Falvo et al. 2019; Cordes et al. 2020).

Statistical Analyses

We constructed individual capture histories across the 18 capture occasions (trapping sessions) for all marked squirrels, which we used to model monthly (30-day timestep) survival by species with Cormack-Jolly-Seber models (Cormack 1964; Jolly 1965; Seber 1965; Lebreton et al. 1992) in Program MARK (White and Burnham 1999) via the RMARK package (Laake 2019) in R (V 4.1.3; R Core Team 2020). We took a three-stage model selection approach to ensure we correctly fit demographic, season, and density variables explicitly predicted to influence squirrel survival (Table 1) to the data before layering effects of climate onto those underlying covariates. In this way, we also reduced the total number of models under consideration.

The global stage-one survival sub-model for each species included covariates of squirrel sex (male or female), squirrel age class (juvenile or adult), season (active season or hibernation season), and conspecific density. We delineated the ~1.5-month interval between spring and summer trapping sessions, during which all individuals of each species were not hibernating, as the active season. We defined the hibernation season as the ~10.5-month interval between the summer and spring trapping sessions, a period that encompassed the hibernation extent of all 3 species but also included 2-4

weeks of aboveground activity of ground squirrels and ~20 weeks of aboveground activity of chipmunks. We considered squirrels to be juveniles through their first winter, and we accounted for variation in the timing of trapping sessions by manually programming intersession time intervals as the average mid-session to mid-session period among all sites for a given interval. The global stage-one survival sub-models for northern Idaho ground squirrels and Columbian ground squirrels also contained covariates for the density of the other ground squirrel species to test for predicted effects of interspecific competition on survival. The detection sub-model of the global stage-one model included 3 of the same covariates as the survival sub-model: squirrel sex, squirrel age class, and season or capture occasion (we never included season and capture occasion in the same model because they were confounded). We used Program RELEASE (Burnham et al. 1987) within the RMARK package in R to estimate the variance inflation factor (\hat{c}) for each species before conducting model selection and used the resulting \hat{c} values (northern Idaho ground squirrels = 1.39, Columbian ground squirrels = 2.72, yellow-pine chipmunks = 1.61) to correct for mild overdispersion in the data. We used Akaike's Information Criterion corrected for overdispersion (QAIC; Burnham and Anderson 2002) to compare all subsets of the global models, including all possible full interaction structures among the survival covariates but no interactions among the detection covariates. We used the top stage-one model as the informed null model for stages two and three.

The stage-two survival models considered univariate effects of the 6 climate covariates layered onto the top stage-one model to narrow down the candidate variables for inclusion in stage-three models for each species. This was necessary because many of the climate covariates were collinear ($|r| > 0.6$). We applied climate variables to the season (hibernation or active) during which they were recorded and the subsequent season to account for short-term lag effects and accumulation effects of precipitation. We tested additive effects of each climate variable as well as all two-way interactions that included a climate variable that did not alter the structure of the informed null survival sub-model (i.e., we considered no additional interactions among the stage-one covariates or between climate covariates). We did not consider climate effects in the detection sub-models to limit the number of candidate models; the effect of capture occasion considered in stage-one implicitly accounted for temporal variation in climatic conditions. We compared all stage-two models by QAIC and selected which non-collinear climate covariates to include in the stage-three survival sub-models by total Akaike model weight (w_i) of the models including each climate variable.

Stage-three survival sub-models for each species included the non-collinear climate covariates from stage-two layered onto the informed null model derived in stage-one. We used QAIC to compare all subsets of the climate covariates layered onto the informed null survival sub-model, including all possible two-way interactions between each climate covariate and the stage-one

covariates that did not alter the structure of the informed null model (i.e., we considered no additional interactions among the stage-one covariates or between climate covariates). We model-averaged all candidate models to produce model-based predictions of marginal effects for all covariates.

RESULTS

Temperature and precipitation directly influenced survival of northern Idaho ground squirrels, Columbian ground squirrels, and yellow-pine chipmunks, though the directional effects varied among species, sex, age, and season. Thermal conditions during hibernation were especially important for survival of Columbian ground squirrels and yellow-pine chipmunks, while active-season precipitation influenced survival of northern Idaho ground squirrels and chipmunks. Winter snowpack was associated with survival of all 3 squirrels, most likely via the synergistic effects of forage availability, hibernation, and competition. Northern Idaho ground squirrel survival was apparently regulated by intra- and interspecific competition, evidenced by negative effects of conspecific and competitor densities. Winter snowfall increased Columbian ground squirrel survival during the subsequent active season, but the opposite was true for northern Idaho ground squirrels, suggestive of the premise that climate interacts with forage availability and competition to shape survival of the smaller, imperiled northern Idaho ground squirrel. Detailed, species-specific results are below.

Northern Idaho Ground Squirrels

Northern Idaho ground squirrel survival differed by squirrel sex, squirrel age class, and season (Table 2). Female northern Idaho ground squirrels of both age classes had higher survival rates than their male counterparts during the active and hibernation seasons, and adults of both sexes had higher survival rates than juveniles of the same sex during both seasons (Figure 1a). Survival was higher during hibernation than the active season for all age-sex classes. Conspecific density was negatively associated with northern Idaho ground squirrel survival across all combinations of age class, sex, and season (Figure 2a). Columbian ground squirrel density interacted with season such that density negatively influenced northern Idaho ground squirrel survival across all age-sex classes during the active season, but had a negligible effect during hibernation (Figure 2b).

The top, non-colinear climate covariates influencing northern Idaho ground squirrel survival were total winter snowfall, active-season precipitation, and hibernation season temperature, though there was a high degree of model uncertainty regarding the manner in which the climate covariates (especially winter snowfall) interacted with the other covariates (Table 3). The effect of total winter snowfall on survival varied by age and season (Figure 2c). Adult survival was negatively associated with total winter snowfall, with a stronger effect during the subsequent active season than during

hibernation. Interestingly, there was some support for an interaction between the effects of Columbian ground squirrel density and total winter snowfall on the survival of these rare squirrels, implying that competition may mediate the impact of winter snow or vice versa. Total winter snowfall mildly and negatively influenced juvenile active-season survival, though less so than it did for adults; the effect during hibernation was slightly positive. Active season precipitation negatively influenced survival, more so during the active season than hibernation. While hibernation season temperature was included in 1 model within 2.00 QAIC of the top stage-three model, the covariate did not have a large directional influence on northern Idaho ground squirrel survival.

Columbian Ground Squirrels

Columbian ground squirrel survival differed by squirrel sex, squirrel age class, and season (Table 2). Female Columbian ground squirrels of both age classes had higher survival rates than their male counterparts during the active and hibernation seasons, and adults of both sexes had higher survival rates than juveniles of the same sex during both seasons (Figure 1b). Survival was higher during hibernation than the active season for all age class-sex combinations. Survival was not significantly influenced by conspecific density or northern Idaho ground squirrel density (Table 2), meaning the effects of interspecific competition were unidirectional between the 2 ground squirrel species.

The top, non-colinear climate covariates influencing Columbian ground squirrel survival were total winter snowfall, active-season temperature, and hibernation season temperature, though there was a high degree of model uncertainty regarding the manner in which the climate covariates (especially winter snowfall and hibernation season temperature) interacted with the other covariates (Table 3). Total winter snowfall was positively associated with Columbian ground squirrel active-season survival for all age class-sex combinations, but had little influence on survival during hibernation (Figure 3a). Temperature during the hibernation season was positively associated with active-season and overwinter survival (Figure 3b). While active-season summer temperature was included in 1 model within 2.00 QAIC of the top stage-three model, the covariate did not have a large directional influence on Columbian ground squirrel survival.

Yellow-pine Chipmunks

Yellow-pine chipmunk survival differed by squirrel sex, squirrel age class, and season, but was not significantly influenced by conspecific density (Table 2). Female yellow-pine chipmunks of both age classes had higher survival rates than their male counterparts during the hibernation season, but females had similar survival to males during the active season (Figure 1c). Adults of both sexes

had higher survival rates than juveniles of the same sex during both seasons and survival was higher during hibernation than the active season for all age class-sex combinations.

The top, non-colinear climate covariates influencing yellow-pine chipmunk survival were hibernation season snow cover, active-season precipitation, and hibernation season temperature, though there was a high degree of model uncertainty regarding the manner in which the climate covariates (especially hibernation season temperature) interacted with the other covariates (Table 3). Number of days with snow cover was mildly and negatively associated with active-season and overwinter survival for all age-sex classes, though the effect during the active season was stronger for males than females (Figure 4a). Hibernation season temperature interacted with season such that temperature positively influenced hibernation season survival for all age-sex classes, but had a slight negative effect on active season survival. Active-season precipitation also influenced survival of yellow-pine chipmunks, with opposite directional effects for adults (positive) and juveniles (negative; Figure 4b).

DISCUSSION

Climate directly influenced survival of 3 sciurid obligate hibernators and also affected survival and of the federally threatened northern Idaho ground squirrel via a synergistic mechanistic pathway: by influencing survival (and so density) of the larger, socially dominant Columbian ground squirrel. Overall, our seasonal survival estimates for Columbian ground squirrels and yellow-pine chipmunks were consistent with estimates from previous studies (Broadbooks 1970; Neuhaus and Pelletier 2001). Our estimates of seasonal survival for the federally threatened northern Idaho ground squirrel are the first such estimates available. The only prior study to estimate survival of these rare squirrels estimated annual survival but not seasonal survival (Sherman and Runge 2002). Our northern Idaho ground squirrel survival estimates, when converted to annual survival estimates, are comparable to those of Sherman and Runge (2002), which is concerning because those estimates were derived from a single, rapidly declining population. Moreover, conspecific density was negatively associated with northern Idaho ground squirrel survival, suggesting these rare squirrels are food- or space-limited, which may help explain the species' rarity. Density-dependence resulting from food limitation has been observed in sister taxa (Karels and Boonstra 2000; Dobson and Oli 2001), and northern Idaho ground squirrels are thought to be similarly food-limited (Dyni and Yensen 1996; Sherman and Runge 2002).

Northern Idaho ground squirrels, Columbian ground squirrels, and yellow-pine chipmunks all had higher hibernation season survival than active-season survival, which corroborates a growing body of literature suggesting increased survival is a major benefit associated with mammalian

hibernation such that hibernators generally have slow body size-adjusted life histories (Turbill et al. 2011 and citations therein; Bieber et al. 2012; Le Cœur et al. 2016; Reusch et al. 2018; Cordes et al. 2020). Higher survival during hibernation is thought to result from decreased predation and reduced costs of predator avoidance during inactivity (Turbill et al. 2011; Turbill and Stojanovski 2018). Survival during hibernation per se may be even higher than our “hibernation season” estimates because the period we used for hibernation encompassed parts of the active season, including the mating season, for all 3 species (due to unavoidable logistical constraints of trapping). Furthermore, climate is associated with annual survival of hibernating species – species in warmer climates have lower survival on average (Turbill and Prior 2016) – and unsuitable thermal conditions for hibernation constrain their distributions (Humphries et al. 2002). Climate change may, therefore, have particularly strong effects on survival of obligate hibernators, including the 3 squirrels we studied.

Climate events that cause animals to shorten the duration of hibernation, like earlier spring snowmelt associated with long-term projections of warming temperatures and reduced winter snowpack in the American West (Gutzler and Robbins 2011; IPCC 2021), may reduce survival by increasing annual exposure to predation risk (Turbill et al. 2011; Turbill and Prior 2016). Snowpack is positively associated with plant productivity and so likely also with forage availability for herbivores (Barichivich et al. 2014; Harpold 2016), which is often positively associated with survival in sciurids (Murie and Boag 1984; Dobson and Kjelgaard 1985a, b; Van Horne et al. 1997; Bennett 1999; Karels et al. 2000). While changes in enforced hibernation period should impact all hibernating species, variation in forage availability is predicted to disproportionately affect larger animals that require more food (Lindstedt and Boyce 1985; Gardner et al. 2011; Brown et al. 2017). Winter snow conditions influenced survival of all 3 squirrel species we investigated, but we found mixed evidence in support of the prediction that winter snowpack is positively associated with survival of hibernating species: snow only positively influenced survival of juvenile northern Idaho ground squirrels during hibernation (slightly) and Columbian ground squirrels during the subsequent active season.

The number of days of snow cover at study sites was negatively associated with survival of yellow-pine chipmunks. Food-storing hibernators, like yellow-pine chipmunks, may be negatively impacted by additional days of snow cover if perishable food caches are degraded by moisture or are exhausted before spring snowmelt (Vander Wall 1990). Alternatively, early autumn snowfall may diminish foraging opportunities as chipmunks compile their winter larders. The effects of total winter snowfall on northern Idaho ground squirrel survival varied among age classes and seasons. Snowfall had little effect on hibernation-season survival and had a stronger (negative) effect on active-season survival of adults than juveniles. Good forage years may prompt adult squirrels to invest more heavily in reproduction, resulting in a decrease in survival during the active season due to the cost of

reproduction (Ruf et al. 2006). However, late snowmelt associated with high winter snowfall may reduce juvenile survival by delaying reproduction and so juvenile emergence from natal burrows, leading to lower body masses and less time during which to attain sufficient mass to survive hibernation (Williams et al. 2017; Morris et al. 2021). Total winter snowfall also had a negative effect on active-season juvenile survival in the yellow-bellied marmot (*Marmota flaviventer*), a closely related obligate hibernator (Cordes et al. 2020).

An alternative explanation for the negative effect of snowfall on survival involves competition for food and burrowing space with the ~3x larger Columbian ground squirrel (Dyner and Yensen 1996; Yensen and Dyner 2020). Total winter snowfall strongly and positively influenced survival of Columbian ground squirrels, the largest of the 3 species, which corroborates a pattern across mammalian taxa – larger species are more responsive to climate change (McCain and King 2014) – perhaps because subsequent changes in forage availability have the greatest effect on species that require more food (Lindstedt and Boyce 1985; Gardner et al. 2011; Brown et al. 2017). More importantly, Columbian ground squirrel density strongly and negatively influenced active-season survival of northern Idaho ground squirrels. If winter snowfall promotes forage availability for ground squirrels and consequently Columbian ground squirrel survival, it may result in population expansion and/or altered habitat selection (i.e., a functional response) such that the larger squirrel invades patches that were previously most efficiently exploited, and only occupied by the smaller northern Idaho ground squirrels. We observed some anecdotal evidence supporting this idea: Columbian ground squirrel populations increased and expanded into areas previously occupied by northern Idaho ground squirrels at several study sites following a series of high-snowpack years between 2017 and 2021. This would explain why northern Idaho ground squirrels are often apparently relegated to xeric, rocky, sparsely vegetated patches, and for this reason, it also makes sense that northern Idaho ground squirrel density did not significantly influence survival of Columbian ground squirrels (i.e., the effects of heterospecific density on survival was unidirectional). These results are particularly important due to the conservation status of the northern Idaho ground squirrel. Negative density-dependent survival coupled with negative effects of competitor densities on survival suggest that current management actions (forest thinning and prescribed burning) designed to benefit this rare species by expanding and improving active-season foraging habitat may increase survival by releasing squirrels from intraspecific competition, but only so long as Columbian ground squirrels don't exclude northern Idaho ground squirrels from treated areas. This also suggests northern Idaho ground squirrels might have a competitive advantage over Columbian ground squirrels when conditions are warmer and drier, as is projected under long-term climate change in the region (Gutzler

and Robbins 2011; IPCC 2021). Non-snowpack climate variables can also influence animal survival by altering thermal conditions and forage availability.

Hibernation season temperature was positively associated with Columbian ground squirrel survival during hibernation and the following active season. Ambient temperature during the hibernation season also positively influenced yellow-pine chipmunk overwinter survival, though it had little effect on active season survival. Warmer temperatures during hibernation may reduce the somatic costs of hibernation by reducing torpor expression, though at the cost of increased energetic expenditure (Humphries et al. 2003; Boyles et al. 2020). Temperature during hibernation may also directly, or via more complex relationships with climate patterns than those we tested, positively correlate with foraging conditions or availability. The effects of winter temperature on annual survival in Uinta ground squirrels (*Urocitellus armatus*) was age-dependent (Falvo et al. 2019), which supports the notion that ambient temperature during hibernation influences survival of obligate hibernators, but suggests that it does so through multiple mechanistic pathways that vary among species, space, and time.

Interestingly, all age and sex classes of northern Idaho ground squirrels suffered reduced active-season survival as a result of increased active-season precipitation. This may, again, reflect increased competition from Columbian ground squirrels mediated by climate-driven changes in forage availability. Significant precipitation also degrades foraging conditions (Williams et al. 2016; Allison and Conway 2022) and can even lead to flooding of burrows in shallow, rocky soils (personal observation), possibly decreasing survival. Active-season precipitation also influenced survival of yellow-pine chipmunks, but the relationship differed between adults (positive) and juveniles (slightly negative). The mechanisms underpinning this difference between age classes are unclear, though adults may benefit from increased forage availability associated with high levels of precipitation and low levels of drought (Smith and Johnson 1985; Van Horne et al. 1997; Cordes et al. 2020), and age classes often differ in hibernation immergence and emergence dates. The effects of snowpack, precipitation, and temperature on survival of other mammalian obligate hibernators also varied among sex and age classes (Smith et al. 1985; Van Horne et al. 1997; Patil et al. 2013; Falvo et al. 2019; Cordes et al. 2020). Taken together, our results demonstrate that animal responses to climate change are nuanced and vary among species as well as among age and sex classes within species, likely in relation to differences in life history strategies and the multiple mechanistic pathways by which climate can influence animals. The effects of temperature and precipitation on survival of these squirrels is also compelling in light of the fact that elevation, which is closely tied to climatic conditions, is the biggest driver of adaptive differentiation among northern Idaho ground squirrel

populations (Barbosa et al. 2021), indicating that climate is a significant evolutionary pressure acting on species living in highly seasonal environments.

Survival is a vital demographic trait that directly influences population growth and the evolution of life history strategies via resource allocation-based tradeoffs with other demographic traits. We demonstrated that climate, competition, and hibernation are important mechanisms shaping survival rates of 3 coexisting, herbivorous small mammals, and that these processes interact via numerous synergistic pathways. Previous studies only rarely considered the explicit effects of competitor density, hibernation, or climate on the survival of free-ranging animals, which can only be accomplished through detailed, long-term data collection from sympatric populations of multiple species within a community. Hibernation is an important, but often overlooked, behavior and a key life history element that determines how climate change is likely to affect species persistence and population dynamics. Hibernation is a widespread trait in mammals and many other animal taxa undergo similar seasonal dormancy (e.g., brumation in herptiles). The stark differences in daily survival between hibernation and active seasons, presumably due to differences in predation, are an important aspect of life history for such species, and the seasonality of these annual cycle events may leave these species particularly vulnerable to climate change unless they can alter their life history strategies to increase recruitment, balancing the expected decrease in survival resulting from shorter and less severe winters (Inouye et al. 2000; Ozgul et al. 2010; Turbill and Prior 2016; Cordes et al. 2020; Paniw et al. 2020; though see Lane 2012).

Human actions are changing climates and the composition of biological communities across Earth, often with negative consequences for free-ranging animal populations, and hence, biodiversity. Accordingly, understanding these impacts is an urgent conservation need. Yet, progress toward such understanding remains stunted despite a vast expansion of climate-effects research in recent decades, perhaps due to the myriad pathways through which environmental change affects animals (Berteaux et al. 2006; Paniw et al. 2021). The effects of climate on survival of the 3 hibernating sciurids we studied suggest the impact of future climate change on animal populations may be pronounced and highly context-dependent. For instance, climate influenced survival of a species threatened with extinction by altering competitive interactions with a native, socially dominant species – a novel finding. Additional studies considering the interactive effects of climate and fundamental ecological processes are required to better understand the ultimate mechanisms underlying relationships between climate and demographic processes, which is needed for the conservation of rare and threatened species like the northern Idaho ground squirrel.

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Table 2.1. Covariates (proximate mechanisms) predicted to influence survival of northern Idaho ground squirrels, Columbian ground squirrels, and yellow-pine chipmunks and the ultimate mechanisms assumed to underly the predicted relationships.

Proximate Mechanism	Northern			Ultimate Mechanism(s)
	Columbian Ground Squirrel	Idaho Ground Squirrel	Yellow- pine Chipmunk	
Sex	F > M	F > M	F > M	Sexual selection
Age	A > J	A > J	A > J	Predation, food limitation, thermal intolerance
Season	Hib. > Act.	Hib. > Act.	Hib. > Act.	Predation
Conspecific Density	-	-	-	Competition, food limitation
Interspecific Competitor Density	=	- ¹		Competition, food limitation
Climate ²	+ or -	+ or -	+ or -	Thermal intolerance, food limitation, competition, predation

¹ Northern Idaho ground squirrel survival is predicted to be negatively associated with Columbian ground squirrel density due to interference competition.

² The effects of climate are predicted to be variable depending on the climate variable and the underlying factors limiting survival of a given species or demographic group.

Table 2.2. Top stage-one Cormack-Jolly-Seber models designed to explain variation in survival of northern Idaho ground squirrels (n = 1689), Columbian ground squirrels (n = 1291), and yellow-pine chipmunks (n = 2590) at 10 study sites from 2013 to 2021. The table includes all models with a ΔQAIC score < 2.00 , the global model (bold), and the null model.

Variable notation is as follows: sex = squirrel sex (male or female), age = squirrel age class (juvenile or adult), season = survival interval season (active or hibernation), nids = northern Idaho ground squirrel density, cogs = Columbian ground squirrel density, ypc = yellow-pine chipmunk density, and occasion = capture occasion.

Survival Sub-model	Detection Sub-model	ΔQAIC	w_i
<i>Northern Idaho Ground Squirrels</i>			
sex + age + season * cogs + nids	occasion	0.00	0.11
sex + age * cogs + season + nids	occasion	0.23	0.10
sex + age + season * cogs + nids	occasion + age	1.57	0.05
sex + age + season * cogs + nids	sex + occasion	1.74	0.04
sex + age * cogs + season + nids	occasion + age	1.75	0.04
sex + age * cogs + season + nids	sex + occasion	1.94	0.04
sex * age * season * nids * cogs	sex + occasion + age	35.90	0.00
Null	Null	354.31	0.00
<i>Columbian Ground Squirrels</i>			
sex + age + season	occasion	0.00	0.06
sex + age + season + cogs	occasion	0.66	0.04
sex + age * cogs + season	occasion	1.17	0.03
sex * season + age	occasion	1.66	0.03
sex + age * season	occasion	1.67	0.03
sex + age + season * nids	occasion	1.76	0.02
sex + age + season	occasion + age	1.99	0.02
sex * age + season	occasion	2.00	0.02
sex * age * season * nids * cogs	sex + time + age	44.53	0.00
Null	Null	189.48	0.00
<i>Yellow-pine Chipmunks</i>			
sex * season + age	sex + season	0.00	0.11
sex + age + season	sex + season	0.59	0.08
sex * season + age + ypc	sex + season	1.18	0.06
sex * season + age	sex + season + age	1.54	0.05

sex + age + season + ypc	sex + season	1.80	0.04
sex + age + season	season	1.95	0.04
sex * age * season * ypc	sex + season + age	10.96	0.00
Null	Null	226.39	0.00

Table 2.3. Top stage-three Cormack-Jolly-Seber models designed to explain variation in survival of northern Idaho ground squirrels (n = 1689), Columbian ground squirrels (n = 1291), and yellow-pine chipmunks (n = 2590) at 10 study sites from 2013 to 2021. The table includes all models with a Δ QAIC score <2.00 and the informed null model from stage one (which always had a Δ QAIC score <2.00). Variable notation is as follows: sex = squirrel sex (male or female), age = squirrel age class (juvenile or adult), season = survival interval season (active or hibernation), nids = northern Idaho ground squirrel density, cogs = Columbian ground squirrel density, sf = total winter snowfall (1 Dec – 31 Mar), sc = number of days hibernation season snow cover (1 Aug – 31 Mar), ht = mean daily mean hibernation season (1 Aug – 31 Mar) temperature, at = mean daily high active-season summer (1 Jun – 31 Jul) temperature, ap = total active season (1 Apr – 31 Jul) precipitation, and occasion = capture occasion.

Survival Submodel	Detection		
	Submodel	Δ QAIC	w_i
<i>Northern Idaho Ground Squirrels</i>			
sex + season * cogs + age * sf + nids	occasion	0.00	0.06
sex + season * cogs + age + nids	occasion	0.86	0.04
sex + season * cogs + age + nids + ap	occasion	1.34	0.03
sex + season * cogs + age * ap + nids	occasion	1.63	0.03
sex + season * cogs + age * sf + nids + ap	occasion	1.65	0.03
sex + season * cogs + age + nids + sf	occasion	1.84	0.02
sex + season * cogs + age * sf + nids + ht	occasion	1.91	0.02
sex + season * cogs * sf + age + nids	occasion	1.99	0.02
<i>Columbian Ground Squirrels</i>			
sex + season + age	occasion	0.00	0.06
sex + season + age + ht	occasion	0.19	0.06
sex + season * sf + age + ht	occasion	0.54	0.05
sex + season + age * ht	occasion	0.97	0.04
sex + season * sf + age	occasion	1.32	0.03
sex + season * ht + age	occasion	1.47	0.03
sex + season + age + at	occasion	1.63	0.03
sex * ht + season + age	occasion	1.65	0.03
sex + season + age + sf + ht	occasion	1.68	0.03
sex * ht + season * sf + age	occasion	1.94	0.02
sex + season + age + at + ht	occasion	1.98	0.02

Yellow-pine Chipmunks

sex * season + age + ht	sex + season	0.00	0.07
sex * season + age + sc	sex + season	0.10	0.07
sex * season + age	sex + season	0.28	0.06
sex * season + age * ap + sc	sex + season	0.43	0.06
sex * season + age * ap + ht	sex + season	0.65	0.05
sex * season + age + ap + ht	sex + season	0.92	0.04
sex * season + age + sc + ap	sex + season	1.05	0.04
sex * season + age * ap	sex + season	1.28	0.04
sex * season * ht + age	sex + season	1.42	0.03
sex * season + age * ap + sc + ht	sex + season	1.50	0.03
sex * season + age + sc + ht	sex + season	1.59	0.03
sex * season + age + sc + ap + ht	sex + season	1.73	0.03
sex * season + age * sc + age * ap	sex + season	1.84	0.03
sex * season + age * ap + age * ht	sex + season	1.89	0.03
sex * season + age * ht	sex + season	1.90	0.03

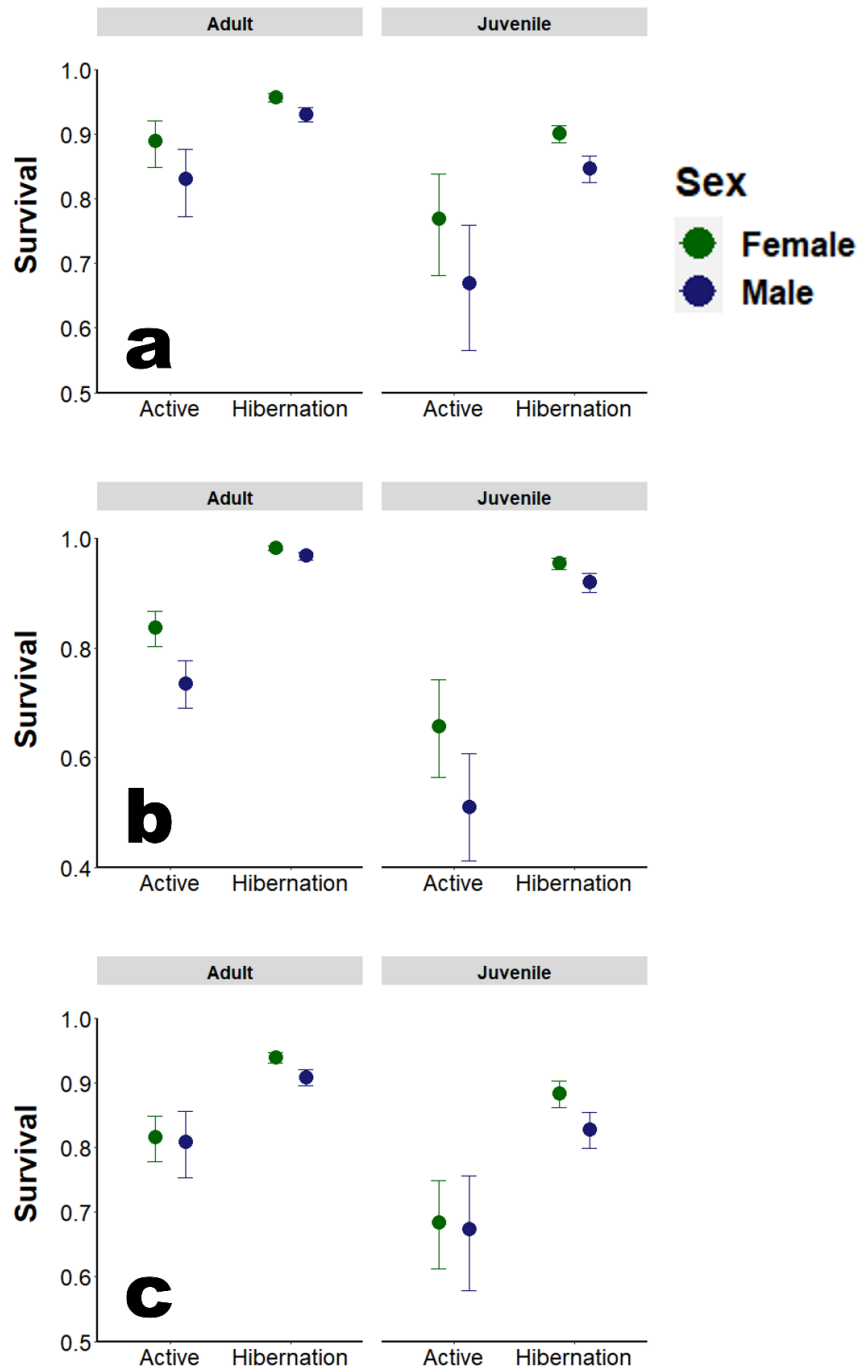


Figure 2.1. Model-averaged monthly (30-day time step) survival estimates ($\pm 95\%$ CI) for (a) northern Idaho ground squirrels ($n = 1689$), (b) Columbian ground squirrels ($n = 1291$), and (c) yellow-pine chipmunks ($n = 2590$) based on the top stage-three Cormack-Jolly-Seber models designed to explain variation in survival at 10 study sites from 2013 to 2021. Adult survival was higher than juvenile survival for both sexes during both seasons for each species. Female survival was higher than male survival for both age classes during both seasons for ground squirrels, but female chipmunks had similar survival to males during the active season. Survival was higher during hibernation than the active season for all age and sex classes of each species.

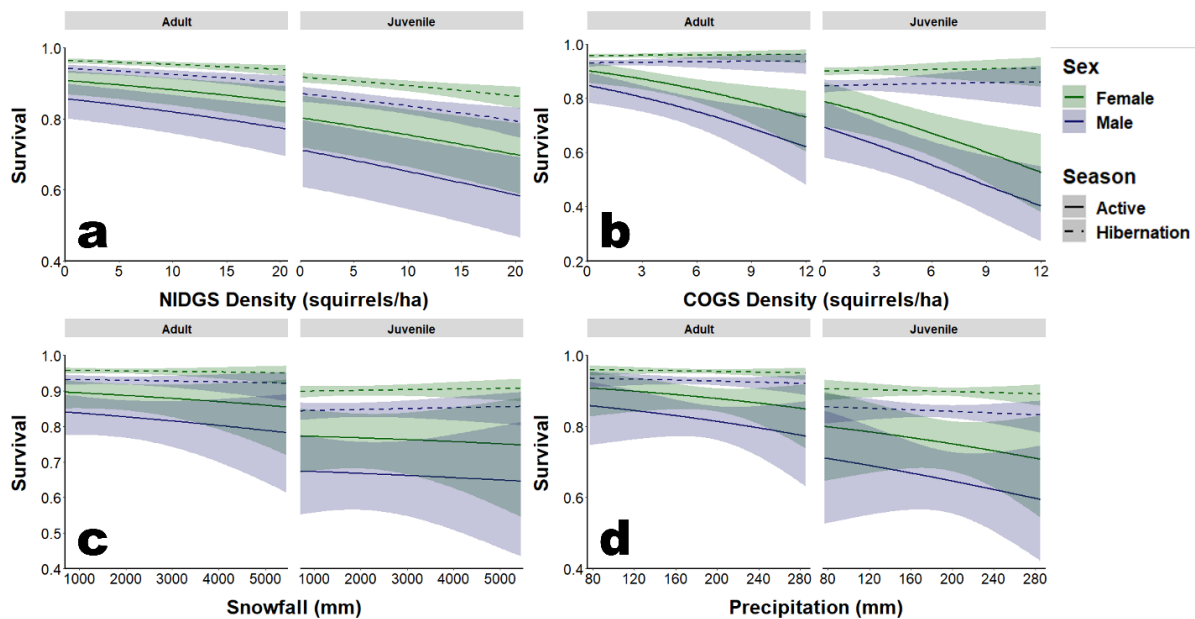


Figure 2.2. Model-averaged monthly (30-day time step) survival estimates ($\pm 95\%$ CI) for northern Idaho ground squirrels ($n = 1689$) based on the top stage-three Cormack-Jolly-Seber models designed to explain variation in survival at 10 study sites from 2013 to 2021. Survival was influenced by (a) conspecific density, (b) Columbian ground squirrel density, (c) total winter snowfall (1 Dec – 31 Mar), and (d) total active season (1 Apr – 31 Jul) precipitation.

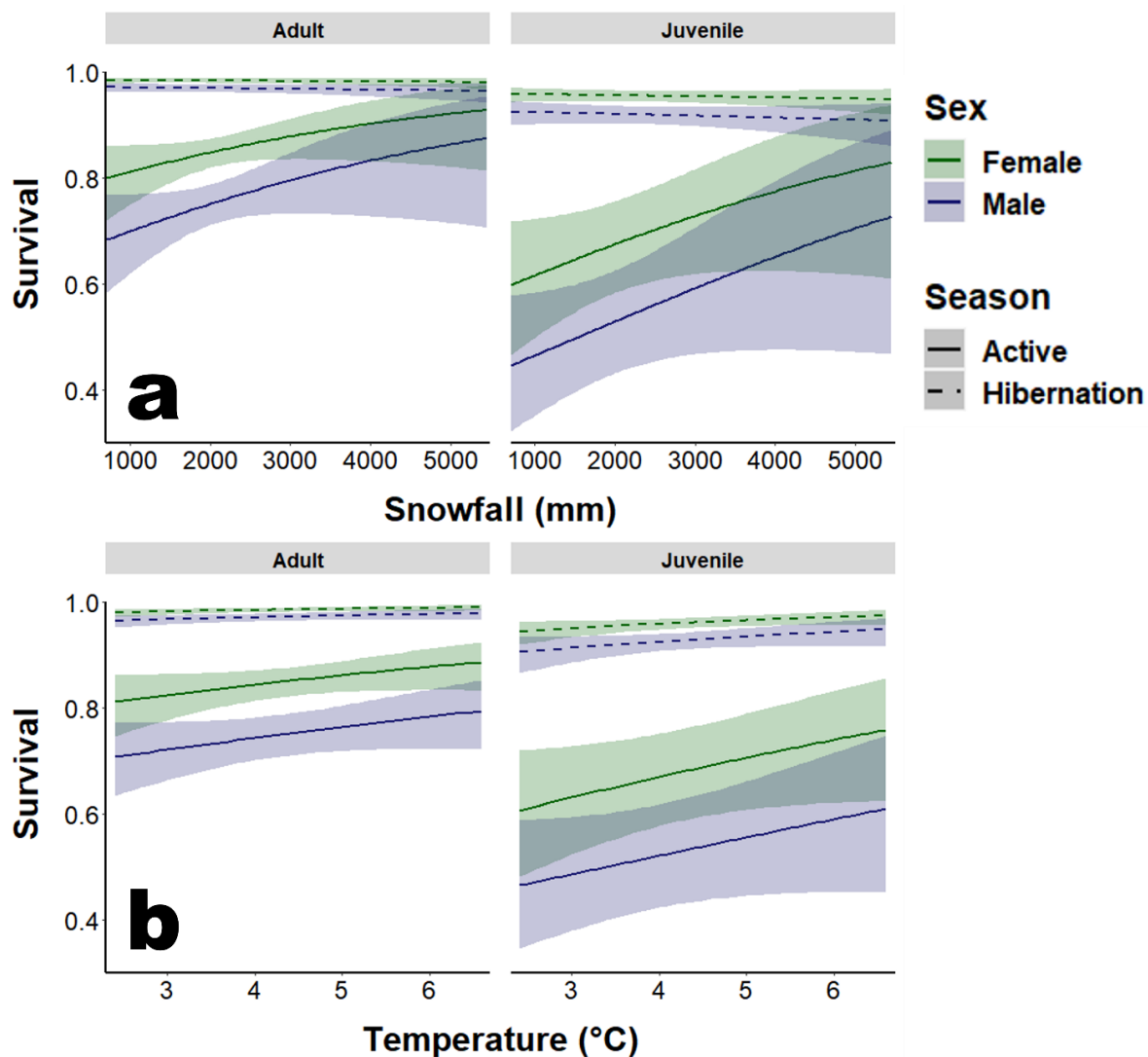


Figure 2.3. Model-averaged monthly (30-day time step) survival estimates ($\pm 95\%$ CI) for Columbian ground squirrels ($n = 1291$) based on the top stage-three Cormack-Jolly-Seber models designed to explain variation in survival at 10 study sites from 2013 to 2021. Survival was influenced by (a) total winter snowfall (1 Dec – 31 Mar) and (b) mean daily mean hibernation season (1 Aug – 31 Mar) temperature.

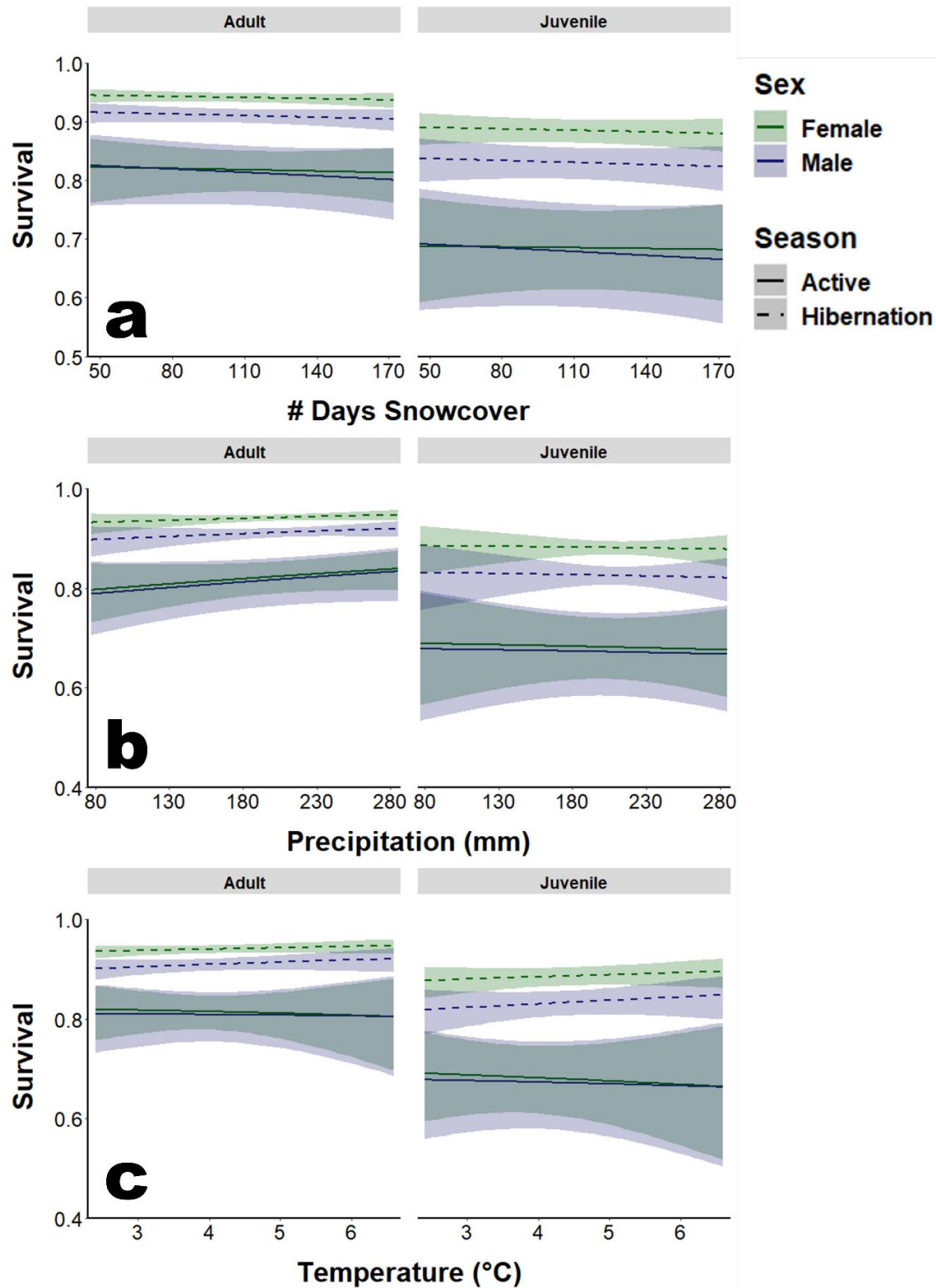


Figure 2.4. Model-averaged monthly (30-day time step) survival estimates ($\pm 95\%$ CI) for yellow-pine chipmunks ($n = 2590$) based on the top stage-three Cormack-Jolly-Seber models designed to explain variation in survival at 10 study sites from 2013 to 2021. Survival was influenced by (a) number of days hibernation season (1 Aug – 31 Mar) snow cover, (b) total active season (1 Apr – 31 Jul) precipitation, and (c) mean daily mean hibernation season (1 Aug – 31 Mar) temperature.