To the University of Wyoming:

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Brito, Brittany T., Linking occupancy, rarity, and resource use in a pair of smooth-toothed pocket gophers, M.S., Department of Zoology and Physiology, December, 2020.

ABSTRACT

Members of the genus *Thomomys* (the smooth-toothed pocket gophers) are widely distributed across western North America, typically with geographic ranges that are almost entirely allopatric or parapatric. In Wyoming, the geographic range of the widespread northern pocket gopher (*Thomomys talpoides*) encompasses that of the Wyoming pocket gopher (*T. clusius*), one of the most geographically restricted mammals in North America. Overlap in geographic ranges and low capture success have limited the ability to monitor Wyoming pocket gophers. In chapter one, I evaluated the use of tunnel diameter as a noninvasive method to detect pocket gopher species occupancy. Tunnel diameter can be used to help distinguish between occupancy by the Wyoming pocket gopher and its more abundant, widespread congener, the northern pocket gopher. In addition to its restricted geographic range, the Wyoming pocket gopher is confined to areas containing Gardner's saltbush (*Atriplex gardneri*, Family Amaranthaceae) in Carbon and Sweetwater Counties, Wyoming. In chapter two, I tested whether and how consumer-resource relationships involving Gardner's saltbush were correlated with the commonness and rarity of northern pocket gophers and Wyoming pocket gophers, respectively. Through a combination of DNA metabarcoding and cafeteria-style feeding experiments, I demonstrated that Wyoming pocket gophers specialize on Gardner's saltbush, a food plant that is avoided by northern pocket gophers both in the field and in the lab. I suggest that Wyoming pocket gophers can persist within their small geographic range by capitalizing on Gardner's saltbush, a food plant that requires some combination of physiological, morphological, and behavioral adaptations to exploit.

LINKING OCCUPANCY, RARITY, AND RESOURCE USE IN A PAIR OF SMOOTH-TOOTHED POCKET GOPHERS

by

Brittany T. Brito

A thesis submitted to the Department of Zoology and Physiology

and the University of Wyoming

in partial fulfillment of the requirements

for the degree of

MASTER OF SCIENCE

in

ZOOLOGY AND PHYSIOLOGY

Laramie, Wyoming

December 2020

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DEDICATION PAGE

To Murphy

Until we meet again.

ACKNOWLEDGMENTS

This study was made possible by generous contributions from the Wyoming Governor’s Endangered Species Account Funds, the University of Wyoming’s Department of Zoology and Physiology, and the American Society of Mammalogists Grants in Aid of Research. I would like to give a special thanks to Z. Walker and N. Bjornlie of the Wyoming Game and Fish Department, without whom this project would have never commenced.

I would like to express my deepest gratitude to my advisor, Dr. Jacob Goheen, for granting me the opportunity to conduct research on one of Wyoming’s rarest mammals. His unwavering support and expertise were instrumental to the success of my research. I thank my committee members, Dr. Matthew Carling and Dr. Kevin Wilcox, for their feedback and support during my project. I am deeply indebted to the brilliant members of the Goheen Lab, whose support, encouragement and friendship guided me throughout this process. Furthermore, I am grateful to the many professors, post-docs, and fellow graduate students who provided insight, feedback, encouragement, and friendship during my time at the University of Wyoming. I am especially grateful to my field technicians, J. Sanchez, T. Thorvaldson, F. Ngo, T. Park, S. Kemp, T. Cooke, C. Burdett, B. Flickinger, and J. Boulerice for their hard work and dedication to my research.

I thank my best friend, Andrea Lien, who has been by my side for nearly 20 years. She has believed in me throughout all my life endeavors and I am forever grateful to have her in my life. I thank my fiancé, Cody Burdett, for his unending patience and love throughout this process. Finally, I thank my family for encouraging me to further my education and pursue my dreams. I am especially grateful to parents, who instilled in me the virtues of perseverance and commitment.

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CHAPTER ONE

Tunnel diameter as a noninvasive method of detecting pocket gopher (Geomyidae) occupancy

Accepted by the Wildlife Society Bulletin *in press*

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ABSTRACT

Challenges in monitoring rare and elusive species often involve low detection and sampling success. Noninvasive methods have allowed researchers to more efficiently monitor rare and elusive species while reducing costs of more invasive, traditional techniques. We evaluated the use of a noninvasive method as an alternative to live-trapping pocket gophers. We found that tunnel diameter can be used to help distinguish between occupancy by the Wyoming pocket gopher (*Thomomys clusius*; a species of conservation concern) and its more abundant and widespread congener, the northern pocket gopher (*T. talpoides*). Our method reduces reliance on more invasive methods of monitoring occupancy (i.e., live- or kill-trapping) for co-occurring pocket gopher species, and likely can be extended to survey for other species of fossorial mammals.

KEY WORDS fossorial, noninvasive methods, northern pocket gopher, occupancy, *Thomomys clusius*, *Thomomys talpoides*, tunnel diameter, Wyoming, Wyoming pocket gopher.

INTRODUCTION

Traditional methods of monitoring species occupancy and distribution (e.g., live-trapping, kill-trapping) are invasive and often time-consuming and expensive. Noninvasive methods (e.g., camera traps, track and scat surveys, hair snares, eDNA, etc.) are viable alternatives, many of which reduce the stress, injury, and mortality associated with traditional methods (Pauli et al. 2010). Further, such noninvasive sampling methods are commonly used to study rare or elusive species because they can increase detection and sampling success (García-Alaníz et al. 2010, Mills et al. 2015, Diggins et al. 2016, Alibhai et al. 2017).

Noninvasive techniques could improve management efforts for rare and elusive species that exhibit fossorial lifestyles. Fossorial animals can be categorized as semi-fossorial or subterranean (Shimer 1903). Semi-fossorial rodents, such as ground squirrels (e.g., *Ictidomys* spp., *Urocitellus* spp.) and prairie dogs (*Cynomys* spp.), are regularly seen aboveground and use burrows principally for rearing young and protection from predators and weather (Murie and Michener 1984, Hoogland 1995). Their conspicuousness aboveground facilitates species identification and field observation, without needing to trap individuals (Slade and Balph 1974, Fagerstone and Biggins 1986, Menkens et al. 1990, Proulx et al. 2012, Boulerice et al. 2019). In contrast, subterranean species spend their lives almost entirely underground and, as a result, are often poorly understood and difficult to detect.

Subterranean species, such as pocket gophers (Family Geomyidae), excavate extensive tunnels below the surface for foraging and nesting and are rarely active on the surface (Huntly and Inouye 1988, Reichman and Seabloom 2002, Romañach et al. 2007). Pocket gophers are typically solitary animals that rarely interact with conspecifics outside of the breeding season (Hansen and Miller 1959, Howard and Childs 1959). Geomyids are widely distributed across

North America, with geographic ranges of species that are frequently non-overlapping (i.e., allopatric or parapatric; Vaughan 1967, Hoffman and Choate 2008). Where there is no overlap in geographic ranges, conspicuous mounds can be used to document pocket gopher presence. However, at interspecific contact zones, different species can be found in close proximity to each other (Kennerly 1959, Vaughan 1967, Thaeler 1968, Reichman and Baker 1972, Patton et al. 1984). In such cases, researchers have historically resorted to live- or kill-trapping to identify species (Vaughan 1967, Hoffman and Choate 2008, Keinath et al. 2014).

The geographic range of the widespread and abundant northern pocket gopher (*Thomomys talpoides*) encompasses that of the Wyoming pocket gopher (*T. clusius*), one of the most geographically-restricted mammals in North America. Due to this restricted geographic range and increasing energy development (e.g., natural gas, wind power) throughout its range, the Wyoming pocket gopher has been categorized as a Tier 1 Species of Greatest Conservation Need in Wyoming (Wyoming Game and Fish Department 2017). Multiple petitions for listing have been submitted to the United States Fish and Wildlife Service (USFWS); however, USFWS was limited by the data required to initiate a status review (United States Fish and Wildlife Service 2016). Additionally, overlap in geographic ranges and low capture success have limited the ability of managers to monitor the Wyoming pocket gopher. An alternative method of assessing pocket gopher occupancy would, therefore, improve management strategies by increasing detection, while simultaneously reducing costs associated with time- and labor-intensive trapping methods.

Previous research has established a relationship between pocket gopher body mass and tunnel diameter (Vleck 1979, 1981; Roberts et al. 1997; Wilkins and Roberts 2007; Griscom et al. 2010; Keinath et al. 2014). However, this relationship has not yet been tested as a means of determining pocket gopher species occupancy. We tested tunnel diameter as a predictor of occupancy for 2 species of pocket gopher: the Wyoming and northern pocket gopher, averaging 60 and 100 g, respectively. Further, because pocket gopher species typically and markedly vary in size (e.g., *T. bottae* [ca. 109 g], *Geomys breviceps* [ca. 120 g], *G. bursarius* [ca. 148 g], *G. personatus* [ca. 274 g]; Miller 1964, Wilkins and Roberts 2007), and tunnel diameters are proportional to the relative body mass of gophers (Vleck 1979, 1981; Wilkins and Roberts 2007; Keinath et al. 2014), we expect that our methods can be extended to other contact zones or areas in which ≥2 species of pocket gopher co-occur.

STUDY AREA

We studied pocket gophers in ca. 2,000 km² across Carbon and Sweetwater counties in south-central Wyoming, USA. Our study area ranged from 1,980 to 2,440 m in elevation and was characterized by an average winter temperature of −4˚ C, average summer temperature of 20˚ C, and average annual precipitation of 27 cm (range of 13–50 cm; Wiken et al. 2011, Keinath et al. 2014). The topography of the area featured hills, plateaus, and ephemeral water features. Shrubs dominated our study area, including big sagebrush (*Artemisia tridentata*), birdfoot sage (*A. pedatifida*), Gardner's saltbush (*Atriplex gardneri*), and winterfat (*Krascheninnikovia lanata*). Sandberg bluegrass (*Poa secunda*), Indian ricegrass (*Achnatherum hymenoides*), western wheatgrass (*Pascopyrum smithii*), and needle-and-thread grass (*Hesperostipa comata*) were common grasses. The land was predominately owned and managed by the Bureau of Land Management (BLM) and private landowners. Oil and gas development, including roads, pipelines, and other associated buildings, occurred throughout the study area.

METHODS

We selected sites for live-trapping using a combination of previous capture locations and randomly generated points (ArcMap v. 10.1, Esri, Redlands, California, USA) for predicted Wyoming pocket gopher occurrence (Keinath et al. 2014). Trap sites were 640-km^2 quarter sections located on BLM land. At each site, we conducted surveys for the presence of gopher mounds (Griscom et al. 2010). Surveyors walked 16 linear north-south transects within each site, spread 50 m apart, and searched within a 20-m buffer on either side of the transect. When mounds were found, the surveyor counted the number of fresh and old mounds within a 20-m search radius and marked the location of the freshest mounds with a handheld GPS (GPSMAP 64S, Garmin Ltd., Olathe, KS, USA). The surveyor then continued to search the transect for additional mounds.

We live-trapped pocket gophers from June to October, 2017–2019. We dug from the center of fresh mounds until a tunnel was located, then set one trap per tunnel opening. We used Sherman live traps (Model SFG, H.B. Sherman Traps, Inc., Tallahassee, FL, USA) and custom-built Harmony traps (Harmony Metalworks, Laramie, WY, USA) baited with sweet potato. To mimic the continuation of gopher tunnels and provide insulation from weather, we placed traps level with the tunnel opening, placed a black trash bag over the trap, and buried them with soil. We checked traps hourly throughout the day and left them open overnight for 3 consecutive days. Upon capture of a gopher, we recorded body mass, sex, and diameter of the tunnel. We did not record individual age class because accurate classification is difficult to determine without euthanasia (Howard and Childs 1959, Hansen 1960). To measure the widest part of the tunnel to the nearest millimeter, we used a shovel to cut a vertical cross-section. All procedures adhered to the guidelines for use of wild mammals in research recommended by the American Society of

Mammalogists (Sikes et al. 2016) and met the requirements of the University of Wyoming Animal Care and Use Committee (Protocol: 20170410JG00273-02).

To determine if either species displayed sexual dimorphism, we conducted a t-test to compare mean body mass between species. We quantified the relationship between tunnel diameter and occupancy of both Wyoming pocket gopher and northern pocket gopher with logistic regression ($\alpha = 0.05$) using occupancy (presence-absence) data. We modeled pocket gopher species as the response variable (0 = northern pocket gopher; 1 = Wyoming pocket gopher) and tunnel diameter as a predictor variable. To evaluate the goodness of fit of the model, we used Nagelkerke's pseudo-R^2 (Nagelkerke 1991). We validated the model using area under the receiver operating characteristic curve (AUC; Swets 1988, Manel et al. 2001). All analyses were conducted in Program R, Version 3.4.3.

RESULTS

We captured a total of 64 northern pocket gophers and 50 Wyoming pocket gophers from June 2017 to October 2019. There was no difference in mean body mass between northern pocket gopher males and females ($\overline{x}$ = 80.85 g, SE = 4.81; $\overline{x}$ = 80.72 g, SE = 5.09 respectively, P = 0.98). Similarly, there was no difference in mean body mass between male and female Wyoming pocket gophers ($\overline{x}$ = 53.87 g, SE = 1.68; $\overline{x}$ = 50.0 g, SE = 2.29 respectively, P = 0.19). Tunnel diameter measurements were collected for 110 pocket gophers (n = 63 northern pocket gophers; n = 47 Wyoming pocket gophers). Mean tunnel diameter was 47.38 mm (range = 34–66 mm, SE = 1.04) and 61.95 mm (range = 44–78 mm, SE = 1.10) for Wyoming pocket gophers and northern pocket gophers, respectively. The probability of occupancy by Wyoming pocket gophers was related to lower values of tunnel diameter ($\beta = -0.22$, Nagelkerke's R^2 =

0.59, $P \leq 0.001$; Fig. 1). The overall model accuracy was high (AUC = 0.90). The logistic output equation for pocket gopher species occupancy was $\ln(p/1-p) = (-0.22*\text{diameter}) + 11.78$.

DISCUSSION

We implemented a noninvasive sampling method to quantify occupancy of a rare fossorial species. The probability of Wyoming pocket gopher occupancy can be determined from tunnel diameter measurements, with probability increasing in tunnels <53 mm in diameter. In contrast, the probability of northern pocket gopher occupancy increases in tunnels >53 mm in diameter. We recommend the following classification percentages at various tunnel diameter categories: <40 mm= > 95.2% chance of Wyoming pocket gopher occupancy; 40–50 mm= 95.2–68.2% chance of occupancy; 50–60 mm 68.2–19.5% chance of occupancy; 60–70 mm= 19.5–2.6% chance of occupancy; >70 mm= <2.6% chance of occupancy. The use of this method can reduce financial costs, time, tunnel disturbance, and negative factors associated with live-trapping (e.g., stress, injury, mortality). As energy development continues to expand throughout their restricted geographic range, tunnel-diameter measurements serve as an effective means of predicting Wyoming pocket gopher occupancy that can allow managers to more efficiently designate conservation interventions.

Variation in body mass between species of pocket gopher influences tunnel shape (Vleck 1979, Wilkins and Roberts 2007); therefore, our method requires an initial validation of species-specific tunnel metrics through live trapping before implementing with additional species or in other locations not evaluated here. In some cases, sexual dimorphism (e.g., a female of species *A* and a male of species *B*) may result in overlap of tunnel diameters and increase the possibility of species misidentification, although the potential for such overlap was minimal in the current study. Similar body mass at different life stages (e.g., an adult of species *A* and a juvenile of species *B*) may also result in overlap of tunnel diameters. Under both scenarios, it would be necessary to collect repeated tunnel measurements within a trapping area to determine a range of tunnel diameters. If the range of measurements coincides with intermediate values of the species-specific tunnel measurements, then data on habitat characteristics can further improve our overall ability to determine species occupancy. For example, vegetation and soil composition at sites occupied by Wyoming pocket gophers differ from sites occupied by northern pocket gophers, with Wyoming pocket gopher sites containing more Gardner's saltbush (*Atriplex gardneri*) and soil with greater clay content (Keinath et al. 2014). It is important to note that additional survey techniques should be used when the consequences of misidentification are high.

The use of tunnel-diameter measurements to determine occupancy could be extended to other fossorial mammals, such as other species of pocket gophers and tuco-tucos (*Ctenomys* spp.). For example, the geographic range of the widespread northern pocket gopher in Wyoming not only encompasses that of the Wyoming pocket gopher, but also encompasses those of the Idaho pocket gopher (*T. idahoensis*) and Sand Hills pocket gopher (*Geomys lutescens*, formerly *G. bursarius lutescens*; Genoways et al. 2008, Chambers et al. 2009). The ca. 50 g Idaho pocket gopher should occupy tunnels with smaller average diameters than that of the ca. 100 g northern pocket gopher. In contrast, the ca. 190 g Sand Hills pocket gopher should occupy tunnels of larger average diameters than northern pocket gopher . Our noninvasive sampling method could also be applied to tuco-tucos, a South American rodent with ecological roles comparable to that of North American pocket gophers. Some species of tuco-tuco are solitary (Lacey et al. 1998) and spend large quantities of time in underground tunnels. Because most species of tuco-tuco exhibit allopatric or parapatric distributions (Kubiak et al. 2015), tunnel diameter measurements could improve occupancy estimates in areas of interspecific contact zones.

In sum, we have developed a noninvasive and quantitative method to predict occupancy of pocket gophers within interspecific contact zones. Our intent is not to replace comprehensive habitat and observational approaches, but rather to provide a low-cost, readily implemented assessment of pocket gopher occupancy. Our method can reduce reliance on more invasive methods of monitoring occupancy (i.e., live- or kill-trapping) and could be applied to other subterranean mammals where detection estimates are low and species' ranges come into contact.

ACKNOWLEDGMENTS

A special thanks to Z. Walker and N. Bjornlie with the Nongame Program of the Wyoming Game and Fish Department. We would like to thank field technicians J. Boulerice, C. Burdett, T. Cooke, B. Flickinger, S. Kemp, F. Ngo, T. Park, and T. Thorvaldson for their contribution to the project. We thank the J. Goheen Lab, R. Applegate (Associate Editor), J. Wallace (Editorial Assistant), and 2 anonymous reviewers for their helpful comments on this manuscript. Funding from the Wyoming Governor's Endangered Species Account Funds and the University of Wyoming's Department of Zoology and Physiology made this project possible.

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FIGURES

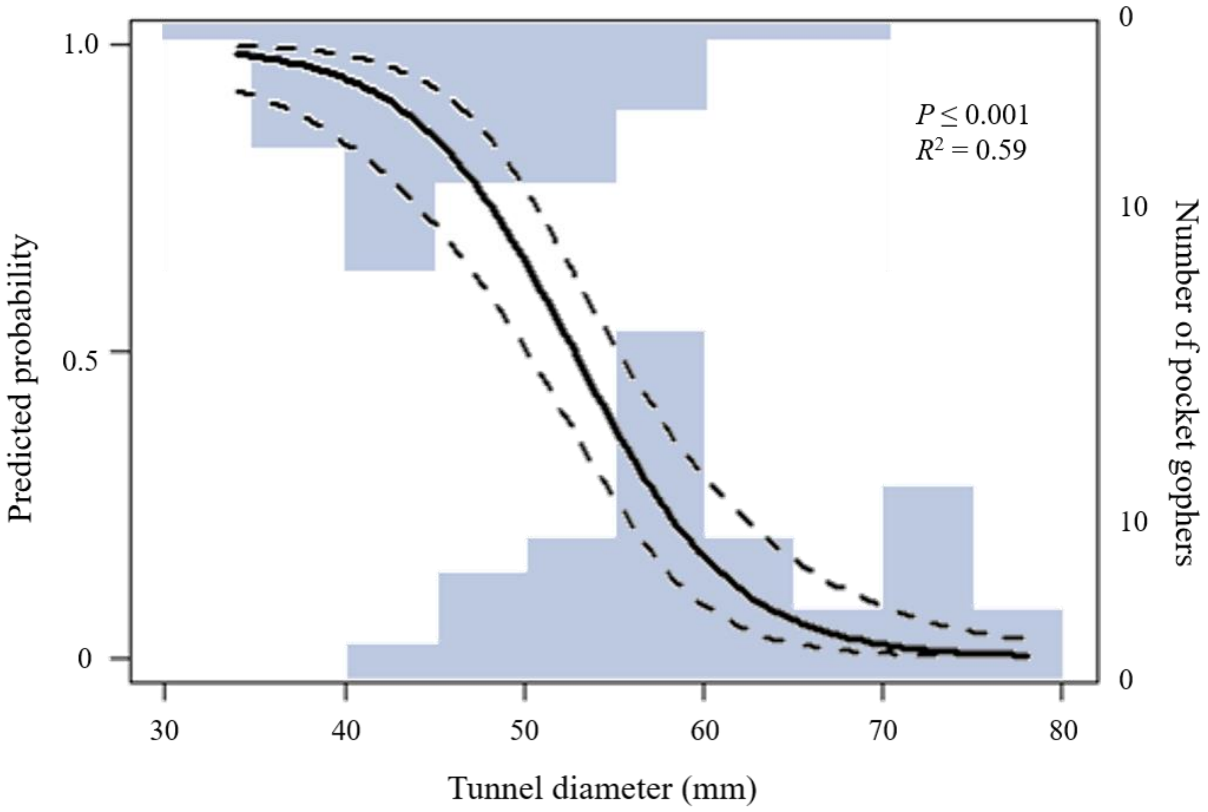

Figure 1. Fitted logistic regression curve displaying the probability of Wyoming pocket gopher occupancy based on tunnel diameter measurements collected in south-central Wyoming, USA, from 2017 to 2019 (*n* = 110, Nagelkerke's $R^2 = 0.59$, $P \leq 0.001$). Histograms represent the number of tunnel diameter measurements collected for Wyoming pocket gopher (top) and northern pocket gopher (bottom) at a given tunnel diameter.

CHAPTER TWO

Resolving circularity between rarity and resource specialization in a pair of smooth-toothed pocket gophers

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ABSTRACT

Understanding the determinants of species rarity is a perennial challenge for ecologists and conservation biologists. In addition to resource specialization, competitive interactions may limit species' abundance and distribution, thereby accentuating rarity. However, resource partitioning can reduce or altogether offset such competitive effects, and thus permit species to thrive alongside more common, widespread competitors within a narrow range of environmental conditions. In south-central Wyoming, the Wyoming pocket gopher (*Thomomys clusius*) (1) is restricted to areas dominated by Gardner's saltbush (*Atriplex gardneri*, Family Amaranthaceae); and (2) inhabits a geographic range that is entirely encompassed by a relatively abundant and widespread congener (*T. talpoides*, the northern pocket gopher). However, the consumer-resource dynamics underlying the relationships among Wyoming pocket gophers, northern pocket gophers, and Gardner's saltbush are poorly understood. I used a path analysis model to reject the null hypothesis that Wyoming pocket gophers and Gardner's saltbush co-occur solely because they require similar soil conditions. Through a combination of DNA metabarcoding and cafeteria-style feeding experiments, I demonstrated that Wyoming pocket gophers specialize on Gardner's saltbush, a food plant that is avoided by northern pocket gophers both in the field and in the lab. Although I could not distinguish between obligate and facultative specialization by Wyoming pocket gophers, the checkerboard-like distributions of these two *Thomomys* likely reflect the outcome of a consumer-resource dynamic, mediated through Gardner's saltbush. I suggest that Wyoming pocket gophers can persist within their small geographic range by capitalizing on Gardner's saltbush, a food plant that requires some combination of physiological, morphological, and behavioral adaptations to exploit. Quantifying consumer-resource interactions reveals correlates of species rarity and can therefore provide a mechanistic basis for the further refinement and testing of hypotheses on the abundance and distribution of closely related species.

KEY WORDS commonness, interspecific competition, resource partitioning, rodent, *Thomomys*, Wyoming

INTRODUCTION

Nearly 40 years ago, Rabinowitz (1981) detailed pathways to species rarity derived from combinations of habitat specificity, abundance, and geographic range size. The most restrictive characteristics of these ‘7 forms of rarity’—narrow habitat specificity and low abundance within a restricted geographic range—are regarded as hallmarks of ecological specialists, with ecologists commonly interpreting the latter two characteristics as outcomes of habitat specificity (or resource breadth more broadly; e.g., MacArthur 1972; Brown 1984; Gaston et al. 1997; Devictor et al. 2010; Botts et al. 2013). However, there is potential for circularity in objectively identifying “specialists” (or “generalists”, conversely) based solely on their abundance and geographic range size: specialists are thought to occur at low abundances over restricted geographic ranges because they cannot exploit a wide diversity of resources (i.e., specialists are uncommon within their narrow distributions because they specialize; Futuyma and Moreno 1988; Ferry-Graham et al. 2002). Consequently, and by themselves, data on species abundance and distributions may not permit discrimination among resources that are required, preferred, or avoided altogether.

In addition to consumer-resource interactions, interspecific competition can limit the abundance and distribution of subordinate competitors, thereby resulting in their rarity (e.g., Bull 1991; Pasch et al. 2013; Yackulic 2017). Competitive interactions are often asymmetric, in which a dominant competitor reduces the abundance and potentially excludes one or more subordinate species. Alternatively, resource partitioning can relax interspecific competition and maintain subordinate species alongside ecologically similar, dominant competitors from local to continental scales (i.e., MacArthur 1958; Grant 1972; Schoener 1974; Brown et al 2000; Stuart and Losos 2013). For example, and over evolutionary time, competition between the greater white-toothed shew (*Crocidura russula*) and the lesser white-toothed shrew (*C. suaveolens*) has confined the latter to a subset of habitats on the Iberian Peninsula (Biedma et al. 2020). *Crocidura suaveolens* outcompetes *C. russula* in a single habitat—tidal marshes—thus reversing the typical dominance by *C. russula* in other habitats (Biedma et al. 2020). Consequently, subordinate species can persist by capitalizing on foods or habitats that are unavailable or inefficiently used by otherwise dominant competitors.

In short, Rabinowitz's most restrictive form of rarity may reflect two distinct, resource-based processes: (1) through adaptation, in which rare species *require* resources that themselves are rare, restricted, or both (hereafter 'obligate specialists'; Shipley et al. 2009, Stephens et al. 2019); or (2) through rare species' tolerance of resources that are avoided by their more common, widespread counterparts (hereafter 'facultative specialists'; Shipley et al. 2009, Stephens et al. 2019). While both obligate and facultative specialization can result in low abundance within a restricted geographic range, the third dimension of Rabinowitz's classification—resource breadth—is key to understanding the pathway by which rarity occurs. Specifically, obligate specialization stems from fixed requirements on one or more particular resources to persist, while facultative specialization simply requires a tolerance for one or more resources that are avoided by common, widespread counterparts. Quantifying any flexibility (or lack thereof) surrounding consumer-resource interactions should therefore illuminate the mechanisms underlying apparent ecological specialization, and their relationship with abundance and geographic range size (see also Verberk et al. 2010).

Members of the genus *Thomomys* (the smooth-toothed pocket gophers) are widely distributed across western North America, typically with geographic ranges that are almost entirely allopatric or parapatric (Kennerly 1959; Vaughan 1967; Hoffman and Choate 2008).

This genus consists of a few species (*T. bottae*, *T. talpoides*, *T. umbrinus*) that are common within expansive geographic ranges and several others that exhibit comparatively restricted geographic ranges; therefore, members of this genus present an opportunity to test resource-based correlates of commonness and rarity, *sensu* Rabinowitz (1981). In Wyoming, USA, the geographic range of the widespread northern pocket gopher (*Thomomys talpoides*) encompasses that of the Wyoming pocket gopher (*T. clusius*), one of the most geographically restricted mammals in North America (Fig. 1). Although hybridization is relatively common in *Thomomys* and in pocket gophers more generally (Thaeler 1968; Patton et al. 1972, 1979, 1984; Genoways et al. 2008), these species do not hybridize (McDonald and Parchman 2010; this study [Supplemental Data SD_1]). These congeners differ widely in abundance and the size of their geographic ranges. The Wyoming pocket gopher is uncommon throughout a restricted geographic range and is confined to areas containing Gardner's saltbush (*Atriplex gardneri*, Family Amaranthaceae) in Carbon and Sweetwater Counties, Wyoming (Thaeler and Hinesley 1979; Keinath et al. 2014). In contrast, the northern pocket gopher is common throughout an expansive distribution from southern Canada through the Sierra Nevada range and New Mexico and is roughly 5x as abundant as the Wyoming pocket gopher in Carbon and Sweetwater Counties (Thaeler and Hinesley 1979). With respect to the rarity of Wyoming pocket gophers, it remains unclear whether Gardner's saltbush represents (1) a shrub with overlapping environmental requirements (e.g., soil pH, salinity, and texture) as Wyoming pocket gophers, but that is neither avoided nor preferred by either species of pocket gopher; (2) a food that Wyoming pocket gophers require, and on which they therefore specialize obligately; or (3) a food that is tolerated by Wyoming pocket gophers, but which northern pocket gophers do not consume.

I tested whether and how consumer-resource relationships involving Gardner's saltbush were correlated with the commonness and rarity of northern pocket gophers and Wyoming pocket gophers, respectively (Table 1). First, using a path analysis model, I tested the hypothesis that Wyoming pocket gophers co-occur with Gardner's saltbush not because of any resource-based mechanism, but rather because both simply require the same soil characteristics. Given rejection of this null hypothesis, I then combined DNA metabarcoding and cafeteria-style feeding experiments to evaluate whether Wyoming pocket gophers selected or simply tolerated Gardner's saltbush (the '*Obligate specialization*' hypothesis and the '*Facultative specialization*' hypothesis, respectively), and whether northern pocket gophers tolerated or avoided this particular shrub (the '*Diet generalism*' hypothesis and the '*Resource partitioning*' hypothesis, respectively; Table 1).

MATERIALS AND METHODS

Study Area

I conducted my work across Carbon and Sweetwater Counties in south-central Wyoming, USA. My study area (approximately 2,000 km^2) consisted mostly of public land managed by the Bureau of Land Management and land managed by private landowners. The study area ranged from 1,950-2,200 m and was characterized by an average winter temperature of -4˚ C, an average summer temperature of 20˚ C, and average annual precipitation of 27 cm (Wiken et al. 2011; Keinath et al. 2014). Big sagebrush (*Artemisia tridentata*) was the most abundant shrub, with some areas dominated by Gardner's saltbush, birdfoot sagebrush (*Artemisia pedatifida*), and winterfat (*Krascheninnikovia lanata*). Sandberg bluegrass (*Poa secunda*), Indian ricegrass (*Achnatherum hymenoides*), western wheatgrass (*Pascopyrum smithii*), and needle-and-thread grass (*Hesperostipa comata*) were common grasses. Oil and natural gas extraction, including its associated infrastructure (e.g., roads, well pads), occurred throughout the study area.

In June of 2017 – 2019, I surveyed for the presence of pocket gophers at eighteen 640 km^2 (quarter section) sites. Members of the genus *Thomomys* excavate chambers at the terminus of tunnels, creating diagnostic mounds that are conspicuous aboveground (Brown and Hickman 1973; Huntly and Reichman 1994; Brito and Sanchez *in press*). Upon identifying active mounds at 15 sites, I live-trapped pocket gophers from June to October 2017 - 2019. All sites were sampled at least once in each of the 3 years; 2 sites were sampled twice in each of the 3 years. Sherman live traps (Model SFG, H.B. Sherman Traps, Inc., Tallahassee, Florida) and locally constructed Howard traps (1952) were positioned at tunnel openings. Traps were baited with sweet potato, covered with black trash bags (pocket gophers respond to light by back-filling traps with soil), and buried with soil. I checked traps hourly from 800-1800, and left traps open overnight for 3 consecutive days, after which the number of unique individuals captured did not increase (Supplemental Data SD_2).

At each site, I randomly collected three soil samples within 20 m^2 of a focal (live-trapped) gopher mound. I collected samples using a 17.78 cm tubular soil sampler with a 1.27cm diameter. Soil samples were analyzed at the Environmental Analytical Laboratory (Brigham Young University, Provo, UT) for pH, salinity (EC dS/m), and soil texture. I calculated the average of each soil characteristic from each site (mean # of soil samples +/- SE) for use in path analysis modeling (see below). I quantified distance to the nearest natural gas infrastructure (e.g., roads, two-tracks, well pads; hereafter 'human disturbance') using a handheld range finder.

Diet and Food Availability

To quantify diets (food use) of individuals, I collected fecal pellets directly from pocket gophers during processing. Plant DNA was extracted, amplified using *trn*L primers via PCR, and then sequenced (Jonah Ventures, Boulder, CO, USA). Using a taxonomic reference library, I identified Operational Taxonomic Units (OTUs) to the lowest taxonomic resolution possible. I adjusted taxonomic identities when the plant species (diagnosed by the reference library) was absent from my study area, but a closely related species (i.e., in the same genus) occurred in my study area (Soininen et al. 2013). I quantified relative read abundance (RRA, defined as the proportion of sequence reads in a sample divided by the total number of sequence reads in that sample; Kartzinel et al. 2015) for each fecal sample, excluding species with RRA <1% (Kartzinel et al. 2015; Iwanowicz et al. 2016).

To assess food availability, I recorded the percent cover of shrubs, forbs, and grasses using line-intercept transect methods (Canfield 1941). I centered four 10 m transects at cardinal and intercardinal directions on each mound at which a gopher was captured. Each set of 4 transects was paired with a set of 4 predetermined transects, centered on a point generated randomly within sites (ArcMap v. 10.1). Each plant was identified to the lowest taxonomic resolution possible (I was not able to identify past genus for most plants in Poaceae). To quantify site-specific food availability, I combined all line-intercept data (both from capture points and associated random points).

Feeding Trials

I conducted cafeteria-style feeding trials to test whether Wyoming pocket gophers and northern pocket gophers exhibited different preferences (i.e., food use, holding availability constant) for 4 species of plants. Feeding trials were conducted simultaneously with trapping efforts from June – October in 2019. Individual gophers (n = 6 per species) were held separately for 24 hours in plastic enclosures (61 x 46 x 48 cm) containing ca. 20 cm of locally collected soil. To mimic natural tunnels, I constructed artificial tunnels out of 7.62 cm PVC pipe and a tee connector to allow gopher entry. Each artificial tunnel had two 1.3 cm holes drilled in the top to allow plant roots to be inserted inside artificial tunnels while the stems and leaves remained above the surface. I buried the two artificial tunnels at opposite ends of the enclosure with the exposed tee joint openings facing the center of the enclosure. Gophers were simultaneously presented with 20.0 g ± 1.0 g of Gardner's saltbush, Indian ricegrass, fringed sagebrush (*Artemisia frigida*), and spiny phlox (*Phlox hoodii*), all of which were relatively common across my study sites. I selected these four species of potential food plants to represent three functional groups (shrubs [fringed sagebrush, Gardner's saltbush], forbs [spiny phlox], and grasses [Indian ricegrass]). Because Gardner's saltbush was rarely available to northern pocket gophers (i.e., northern pocket gophers were rarely sampled at sites dominated by Gardner's saltbush; see Results), I was particularly interested in whether northern pocket gophers would proportionally consume or avoid Gardner's saltbush in feeding trials, per the *Diet Generalism* and *Resource partitioning* hypotheses, respectively (Table 1). Additionally, preliminary results from DNA metabarcoding of diets indicated that, on average, ca. 60% of Wyoming pocket gophers diets were comprised of Gardner's saltbush, and ca. 50% of northern pocket gopher diets were comprised of members of the family Asteraceae. For each individual gopher, I conducted two 12-hour feeding trials. After the first trial, I removed gophers from enclosures to collect, sort, and weigh the remaining biomass for each potential food plant. Once all remaining plant biomass was removed, gophers were returned to enclosures to commence the second 12-hour trial. All procedures adhered to the guidelines for use of wild mammals in research recommended by the American Society of Mammalogists (Sikes et al. 2016) and met the requirements of the

University of Wyoming Institutional Animal Care and Use Committee (Protocol: 20170410JG00273-02).

Statistical Analysis

I used path analysis modeling to quantify the effects of site-specific predictors (pH, salinity, soil texture, the occurrence of Gardner's saltbush, and distance to natural gas infrastructure) on the presence of Wyoming pocket gophers, based on my live-trapping efforts. I developed an *a priori* path analysis model (Fig. 2A) based on research by Keinath et al. (2014) using the *piecewiseSEM* package (Lefcheck 2016) in Program R. I inspected Variance Inflation Factors (VIFs) of covariates to check for collinearity. Covariates with VIFs <3.0 were retained in the model. I modeled Gardner's saltbush and Wyoming pocket gophers as binary responses (i.e., presence/absence) using logistic regression, and I tested model fit using Fisher's *C* (Shipley 2000). A Fisher's *C* test statistic indicates good model fit if it produces a *P* value greater than the significance threshold ($\alpha = 0.05$), indicating that the hypothesized model would not benefit from additional pathways (Lefcheck 2016). I report relative effect sizes using the latent theoretic approach for standardizing estimates (Lefcheck 2016; Grace et al. 2018).

To test the null hypothesis that diet was proportional to food availability, I calculated Jacobs' *D* index: $D_i = (r_i - p_i) / r_i + p_i - 2r_ip_i$, where r_i is the proportion of food plant *i* consumed and p_i is the proportion of food plant *i* available (Jacobs 1974). Jacobs' *D* ranges from -1 to 1, where negative values indicate avoidance and positive values indicate selection. Values close to 0 indicate use in proportion to availability. I calculated Jacob's *D* when both use and availability were sampled (Soininen et al. 2015). A negative mean Jacobs' *D* index can occur when a specific food plant is unavailable to most individuals, or has low availability for most individuals. I excluded 6 gophers (2 Wyoming pocket gophers, 4 northern pocket gophers) with sequence reads of plant species that did not occur (i.e., were not available) at my study site (Soininen et al. 2015). To compare the degree of diet selection between species for different food plants, I computed Jacobs' *D* using the *dietr* package (Borstein 2019). Because of the unequal number of fecal samples between species, I randomly sampled Jacobs' *D* indices associated with each food from 12 Wyoming pocket gophers, without replacement, 1000 times. For each food plant, I compared the mean observed Jacobs' *D* index of northern pocket gophers to this distribution of resampled Jacobs' *D* indices. To compare diet breadth of Wyoming pocket gophers and northern pocket gophers, I calculated total niche width using the *RInSp* package in Program R (Zaccarelli et al. 2013). Total niche width (TNW) is the summation of the within-individual component (WIC) and the between-individual component (BIC) of niche width and is synonymous with diet breadth in this study (Roughgarden 1972; Bolnick et al. 2002).

Following cafeteria-style feeding trials, I used a linear mixed effect model to first explore if trial and individual had a significant effect on feeding preferences. Food plant species, gopher species, and initial plant biomass were treated as fixed effects, with a food plant x gopher species interaction. Trial and individual were treated as random effects. Since I found no evidence that trial or individual influenced diet preference, I used Jacobs' *D* index to calculate selection of food plants (Jacobs 1974). All statistical analyses were conducted in Program R (version 3.6.3, R Core Team 2020).

RESULTS

I captured 64 northern pocket gophers (at 10 out of 15 sites) and 50 Wyoming pocket gophers (at 10 out of 15 sites) from June 2017 to October 2019. Both species were captured at 4 out of 15 sites. I fit a path analysis model to quantify the effects of pH, salinity, clay content, distance to human disturbance, and Gardner's saltbush occurrence on that of Wyoming pocket gophers. The occurrence of Gardner's saltbush was the sole predictor of Wyoming pocket gopher occurrence ($\beta = 0.83$, $P < 0.0001$). The occurrence of Gardner's saltbush increased with clay content ($\beta = 0.22$, $P = 0.034$) and pH ($\beta = 0.33$, $P = 0.023$) in the soil, and decreased with salinity ($\beta = -0.41$, $P = 0.008$). Beyond their effects on Gardner's saltbush, neither soil salinity nor clay content directly affected the occurrence of Wyoming pocket gophers. Proximity to infrastructure associated with oil and natural gas development did not affect the occurrence of Wyoming pocket gophers or Gardner's saltbush. The path analysis model represented the data adequately, suggesting no important paths were excluded (Fisher's $C = 4.09$, *d.f.* = 6, $P = 0.67$; Fig. 2B). The final model explained the majority of total variance in Wyoming pocket gopher occurrence (Nagelkerke's $R^2 = 0.80$) but explained less of the total variance of Gardner's saltbush occurrence (Nagelkerke's $R^2 = 0.51$).

Sites occupied by northern pocket gophers were primarily dominated by grasses (Poaceae) and *Artemisia* spp. (Table 2, Fig.3A). Big sagebrush (*A. tridentata*) was the most common *Artemisia* spp. found at sites occupied by northern pocket gophers, with most sites containing some fringed sagebrush (*A. frigida*) and birdfoot sagebrush (*A. pedatifida*). Wyoming pocket gophers occupied sites that were dominated by *Artemisia* spp. (Fig. 3A); however, these sites were dominated by birdfoot sagebrush, with scattered fringed sagebrush and big sagebrush. All Wyoming pocket gophers were sampled at sites in which Gardner's saltbush occurred; Gardner's saltbush was the second most abundant species of plant at sites occupied by Wyoming pocket gophers. The diets of northern pocket gophers contained 16 plant taxa and the diets of Wyoming pocket gophers contained 14 plant taxa; 9 plant taxa were present in the diets of both pocket gopher species (Table 2, Fig. 3B,C). All Wyoming pocket gophers consumed Gardner's saltbush (mean RRA = 56.94% ± *SE* 5.83). A single northern pocket gopher consumed Gardner's saltbush (mean RRA = 2.82%). Jacob's *D* indices are presented in Table 2 (Fig. 3C). Diet breadth (TNW) was higher for northern pocket gophers (2.07) than Wyoming pocket gophers (1.58, Fig. 4).

Wyoming pocket gophers consumed less plant biomass during the cafeteria-style feeding trials than northern pocket gophers (8.51g ± *SE* 0.55, 11.08g ± *SE* 0.82, respectively). Northern pocket gophers showed no preference for fringed sagebrush (*D* = 0.02 ± *SE* 0.07) or Indian ricegrass (*D* = 0.04 ± *SE* 0.04), preferred spiny phlox (*D* = 0.19 ± *SE* 0.06), and avoided Gardner's saltbush (*D* = -0.46 ± *SE* 0.1; Fig. 5). In contrast, Wyoming pocket gophers neither preferred nor avoided any food plants during feeding trials (Fig. 5).

DISCUSSION

Beyond their effect on occurrence of Gardner's saltbush, soil properties (clay content, pH, and salinity) did not directly affect the occurrence of Wyoming pocket gophers. Because the sole predictor of Wyoming pocket gopher occurrence was the occurrence of Gardner's saltbush, I rejected the null hypothesis that associations between Wyoming pocket gophers and Gardner's saltbush arose from overlapping environmental (soil) requirements. Instead, the strong affiliation for Gardner's saltbush by Wyoming pocket gophers likely reflects a combination of a consumer-resource dynamic between these two species, and a congeneric pocket gopher (northern pocket gophers). All Wyoming pocket gophers sampled during my study utilized Gardner's saltbush, supporting the *Obligate specialization* hypothesis. However, Wyoming pocket gophers exhibited no preference for Gardner's saltbush during feeding trials, supporting the *Facultative specialization* hypothesis. In contrast, Gardner's saltbush was avoided in feeding trials by northern pocket gophers and was unavailable to northern pocket gophers in the field (with the exception of two individuals), lending support for the *Resource partitioning* hypothesis. In sum, and irrespective of whether they are obligate or facultative specialists, my results indicate that Wyoming pocket gophers persist within a small geographic range by capitalizing on a resource that is neither consumed by nor available to northern pocket gophers.

Regardless of whether they do so obligately or facultatively, dietary specialists often possess physiological, morphological, or behavioral adaptations, which permit them to handle the resources on which they specialize more efficiently than dietary generalists (Drummond 1983; Crowell et al. 2018). Within mammals, herbivorous specialists tend to consume plants that are available year-round, have relatively low nutritional content, and possess chemical or mechanical defenses (Dearing et al. 2000; Shipley et al. 2009; Crowell et al. 2018; Stephens et al. 2019). *Atriplex* is a low-growing shrub well adapted to saline, alkaline, and clay soils (Ansley and Abernethy 1984), occurring in harsh, arid areas with extreme temperatures fluctuations and high winds (Stubbendieck et al. 1981; Ansley and Abernethy 1984). *Atriplex* concentrates salt from the soil into the outer leaf cells (Mares et al. 1997); eventually, cells burst and deposit salt crystals on the outer surface of the leaves, providing protection from UV radiation and deterring potential herbivory (Mares et al. 1997). While *Atriplex* is available year-round, the high concentrations of salt in its leaves safeguard against high consumption, unless fresh water is readily available or its consumers are equipped with behavioral, physiological, or morphological adaptations (Kenagy 1973). Unlike its granivorous congeners, the chisel-toothed kangaroo rat (*Dipodomys microps*) forages almost exclusively on *Atriplex* leaves, and possess highly specialized kidneys to concentrate urine, permitting them to persist in arid environments (Kenagy 1972; Kennagy 1973; Mares et al. 1997). Additionally, chisel-toothed kangaroo rats have broad, chisel-shaped lower incisors, which allow them to shave off the hypersaline surface layers of *Atriplex* leaves and minimize salt intake before consuming the inner leaf (Kenagy 1972;

Kenagy 1973). These adaptations allow chisel-toothed kangaroo rats to capitalize on *Atriplex* leaves and may be an evolutionary outcome to minimize interspecific competition and facilitate coexistence with its granivorous congeners and other granivorous rodents (Kenagy 1972).

The ability to consume *Atriplex* and other halophytic plants has been documented in other species of rodents. Similar to chisel-toothed kangaroo rats, the fat sand rat (*Psammomys obesus*) of North Africa removes the outer, salty tissues from *Atriplex* and other halophytic plants before consumption (Degen 1988). Fat sand rats also possesses highly specialized kidneys to excrete extremely concentrated urine (Schmidt-Nielsen 1964; Abdallah and Tawfik 1969). In Argentina, the red vizcacha rat (*Tympanoctomys barrerae*) inhabits the halophytic vegetation surrounding salt flats in the Monte Desert, and uses chisel-shaped lower incisors paired with two "bristle brushes" of stiff hairs located posterior to the upper incisors to remove the hypersaline outer surface of *Atriplex* leaves (Mares et al. 1997). Additionally, red vizcacha rats have specialized kidneys with an elongated renal papilla to remove salt via countercurrent filtration (Abdallah and Tawfik 1969). I hypothesize that Wyoming pocket gophers may exhibit similar adaptations to consume high quantities of Gardner's saltbush. Given that its widespread, common congener is uncommon where Gardner's saltbush occurs in the field, and avoids Gardner's saltbush in feeding trials, I suspect that such high quantities of consumption by Wyoming pocket gophers on Gardner's saltbush represents a strategy by which to minimize competition and partition resources with northern pocket gophers.

Typically, pocket gophers are solitary animals that vigorously defend their territories (Hansen and Miller 1959; Howard and Childs 1959). While most geographic ranges of pocket gophers are allopatric, areas of parapatry may occur where the ranges of two species abut; such parapatry has been interpreted as the outcome of competitive exclusion (Kennerly 1959; Miller

1964; Vaughan 1967; Hoffman and Choate 2008). While the mechanisms promoting competitive exclusion are poorly understood, Howard and Childs (1959) suggested a correlation between body size, competitive dominance, and resource requirements, such that individuals of larger species tended to outcompete those of smaller species. For four species of pocket gophers in Colorado, the species with the strictest requirements (*Geomys bursarius*) was both one of the largest species and the superior competitor, confining the (smaller) subordinate competitors (*T. bottae* and *T. talpoides*) to less favorable habitats (Miller 1964). This relationship between body size, competitive dominance, and restricted resource requirements have held elsewhere, resulting in smaller species being restricted to less favorable habitats (Kennerly 1959; Best 1973). Wyoming pocket gophers are smaller than northern pocket gophers in both body length and weight (Thaeler and Hinesley 1979; Keinath et al. 2014; Brito and Sanchez *in press*), suggesting that they are confined to areas unusable by the competitively superior northern pocket gopher.

Exclusion and removal experiments provide some of the best evidence for the effect of competition in restricting the local abundance and distribution of species (Hairston 1980; Neet and Hausser 1990; Hamel et al. 2012; Pasch et al. 2013; Eurich et al. 2018). While results of this study suggest that competitive exclusion by northern pocket gophers may delineate the geographic range of Wyoming pocket gophers, manipulative exclusions and removals are not feasible in this study system for several reasons. Pocket gophers excavate extensive tunnels belowground, are rarely active on the surface, and are challenging to live trap relative to other small mammals (Huntly and Inouye 1988; Reichman and Seabloom 2002; Romañach et al. 2007). Given their subterranean lifestyle, it would be difficult to determine if all northern pocket gophers were removed from the area and to monitor if Wyoming pocket gophers – which occur at low densities – respond numerically, expand their distribution, or both in the absence of northern pocket gophers.

Understanding species rarity presents many challenges, as definitions of ‘rarity’ vary (Rabinowitz 1981, Violle et al. 2017). Rarity may arise from two distinct resource-based processes: (1) a species requires a resource that is itself rare; or (2) a species can capitalize on a resource that is unavailable or avoided by otherwise-dominant competitors. Quantifying resource breadth provides a means to understand the pathway by which rarity occurs. Resource partitioning likely allows Wyoming pocket gophers to persist by capitalizing on a resource that is unavailable to and unused by northern pocket gophers, a more common, more generalized, and more widespread congener. I hypothesize that interspecific competition has led to some combination of physiological, morphological, and behavioral adaptations by which Wyoming pocket gophers can persist within the geographic range of an otherwise-dominant competitor, thereby highlighting the central role of resource specificity as a the mechanistic basis for commonness and rarity.

ACKNOWLEDGMENTS

A special thanks to Z. Walker with the Nongame Program of the Wyoming Game and Fish Department for his support throughout this research. D. Keinath, G. Beauvais, K. Wilcox, J. Beck, and D. McDonald provided helpful conversation or manuscript comments. B. Jesmer and J. Pansu provided R code to create figures 3 and 4. I would like to thank field technicians J. Sanchez, T. Thorvaldson, F. Ngo, T. Park, S. Kemp, T. Cooke, C. Burdett, B. Flickinger, and J. Boulerice for their contribution to the project. Funding from the Wyoming Governor’s Endangered Species Account Funds, the University of Wyoming’s Department of Zoology and

Physiology, and the American Society of Mammalogists Grants in Aid of Research has made this project possible.

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TABLES

Table 1. Hypotheses and associated predictions regarding consumer-resource interactions among Gardner's saltbush, Wyoming pocket gophers, and northern pocket gophers. The '*Obligate specialization*' and '*Facultative specialization*' hypotheses apply to Wyoming pocket gophers and are exclusive from each other but not from the '*Diet generalism*' or '*Resource partitioning*' hypotheses. The '*Diet generalism*' and '*Resource partitioning*' hypotheses apply to northern pocket gophers and are exclusive from each other.

	Hypothesis	Predictions
Wyoming pocket gopher		
• *Obligate specialization hypothesis*	The Wyoming pocket gopher requires Gardner's saltbush to persist.	a. Path Analysis Model: Wyoming pocket gophers co-occur with Gardner's saltbush because they consume it, and not simply because of overlapping soil requirements of Wyoming pocket gophers and Gardner's saltbush. b. Total niche width: Wyoming pocket gophers exhibit narrower diet breadth relative to northern pocket gophers. c. Selection ratios: Wyoming pocket gophers select Gardner's saltbush more than expected based on its availability, with all individuals consuming Gardner's saltbush. d. Feeding trials: Wyoming pocket gophers prefer Gardner's saltbush to other food plants.

- *Facultative specialization hypothesis*	The Wyoming pocket gopher tolerates Gardner's saltbush but do not require it to persist.	a. Path Analysis Model: Wyoming pocket gophers co-occur with Gardner's saltbush because they consume it, and not simply because of overlapping soil requirements of Wyoming pocket gophers and Gardner's saltbush. b. Total niche width: Diet breadth either does not differ appreciably from northern pocket gophers, or it is slightly broader (from consumption of Gardner's saltbush). c. Selection ratios: Wyoming pocket gophers consume Gardner's saltbush and other food plants in proportion to their availability. d. Feeding trials: Wyoming pocket gophers exhibit no preference for any food plant, consuming plants in proportion to their availability.
Northern pocket gopher		
- *Diet generalism hypothesis*	The northern pocket gopher is a dietary generalist and can tolerate Gardner's saltbush.	a. Total niche width: northern pocket gophers exhibit wider diet breadth than Wyoming pocket gophers. b. Selection ratios: northern pocket gophers consume plants in proportion to their availability. Northern pocket gophers are found in some sites containing Gardner's saltbush. c. Feeding trials: northern pocket gophers exhibit no preference for any food plant, consuming plants in proportion to their availability.

• *Resource partitioning hypothesis*	The northern pocket gopher avoids Gardner’s saltbush.	a. Total niche width: northern pocket gophers diet breadth does not differ appreciably from Wyoming pocket gophers, or it is slightly narrower (from avoidance of Gardner’s saltbush). b. Selection ratios: northern pocket gophers consume plants in proportion to their availability. c. Feeding trials: northern pocket gophers avoid Gardner’s saltbush.

Table 2. Mean availability, use, and selection (Jacob's *D*) of food plants comprising >1% of the diet consumed by ≥1 northern pocket gopher (*Thomomys talpoides*, n = 12) and ≥1 Wyoming pocket gopher (*T. clusius*, n = 24). A negative Jacobs' *D* index indicates avoidance, positive values indicate selection, and values approaching zero indicate use in proportion to availability. Dashes indicate plant species that were not available. A negative mean Jacob's *D* index can occur when a food plant is unavailable to most individuals or it is available in low amounts to most individuals.

		Thomomys talpoides			*Thomomys clusius*		
Family	Species	Availability	Use	Jacobs' *D* ± *SE*	Availability	Use	Jacobs' *D* ± *SE*
Amaranthaceae	*Atriplex gardneri*	2.65	2.82	-0.45 ± 0.55	26.35	56.94	0.46 ± 0.10
	Kochia americana	0.06	0.00	-1.00 ± 0.00	1.31	0.57	-0.71 ± 0.20
	Krascheninnikovia lanata	0.90	3.82	-0.74 ± 0.18	2.41	5.54	-0.65 ± 0.15
	Salsola kali	—	—	—	0.11	1.63	-0.51 ± 0.49
Asteraceae	*Artemisia* spp.	33.02	0.90	-0.95 ± 0.03	37.26	11.88	-0.74 ± 0.07
	Other Asteraceae	11.76	32.72	0.20 ± 0.19	5.73	0.39	-0.90 ± 0.05
Brassicaceae	*Descurainia*	0.05	0.00	-1.00 ± 0.00	0.79	1.19	-0.57 ± 0.23
Caryophyllaceae	*Arenaria hookeri*	1.42	2.96	-0.51 ± 0.25	0.55	0.00	-1.00 ± 0.00
Fabaceae	*Lupinus* spp.	0.70	0.55	-0.38 ± 0.62	—	—	—
	Other Fabaceae	1.01	8.90	-0.20 ± 0.32	—	—	—
Malvaceae	*Sphaeralcea coccinea*	—	—	—	0.01	3.13	-0.50 ± 0.33
Orobanchaceae	*Cordylanthus ramosus*	0.77	0.37	-0.67 ± 0.33	0.99	0.00	-1.00 ± 0.00
Poaceae	*Achnatherum hymenoides*	2.20	0.95	-0.68 ± 0.19	3.48	0.48	-0.92 ± 0.06
	Hesperostipa comata	1.49	14.97	-0.08 ± 0.31	0.17	0.00	-1.00 ± 0.00
	Poa spp.	5.73	0.82	-0.82 ± 0.13	2.43	0.26	-0.96 ± 0.04
	Triticeae	13.61	6.88	-0.50 ± 0.18	7.79	6.31	-0.54 ± 0.14
	Other Poaceae	21.14	19.48	-0.27 ± 0.19	9.20	6.88	-0.34 ± 0.13
Polemoniaceae	*Linanthus pungens*	0.19	0.15	-0.77 ± 0.23	0.29	0.00	-1.00 ± 0.00
	Phlox hoodii	2.77	0.82	-0.66 ± 0.21	0.87	0.32	-0.89 ± 0.08
Polygonaceae	*Eriogonum* spp.	0.20	0.00	-1.00 ± 0.00	0.27	4.48	-0.63 ± 0.17
Santalaceae	*Comandra umbellata*	0.32	2.89	0.50 ± 0.21	—	—	—

FIGURES

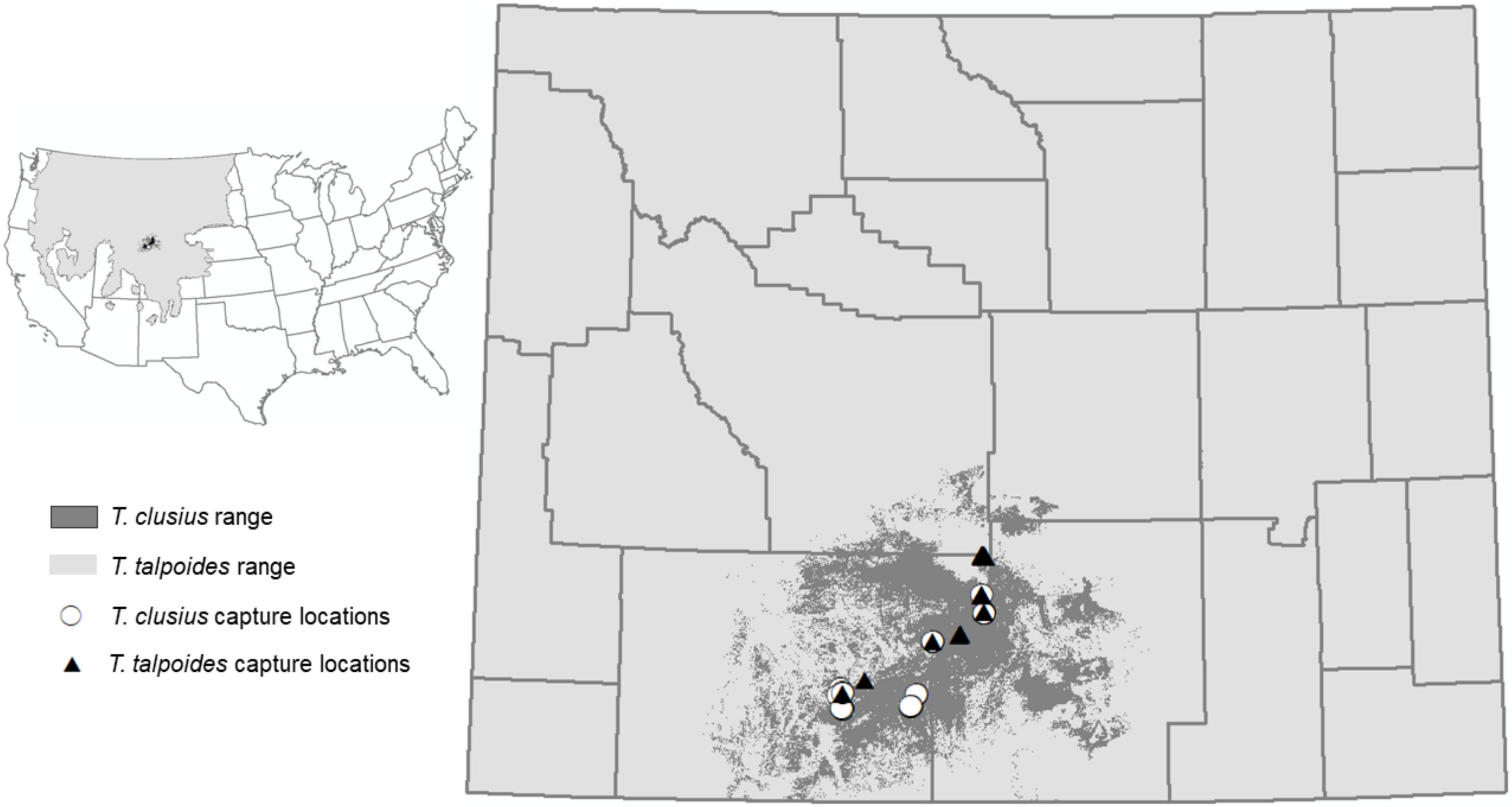

Figure 1. Map depicting Wyoming pocket gopher (*Thomomys clusius*) and northern pocket gopher (*T. talpoides*) geographic ranges within the continuous United States (Keinath et al. 2014, U.S. Geological Survey – Gap Analysis Project 2017). White circles outlined in black indicate confirmed Wyoming pocket gopher capture locations and black triangles indicate confirmed northern pocket gopher capture locations. Multiple captures may occur at a single capture location.

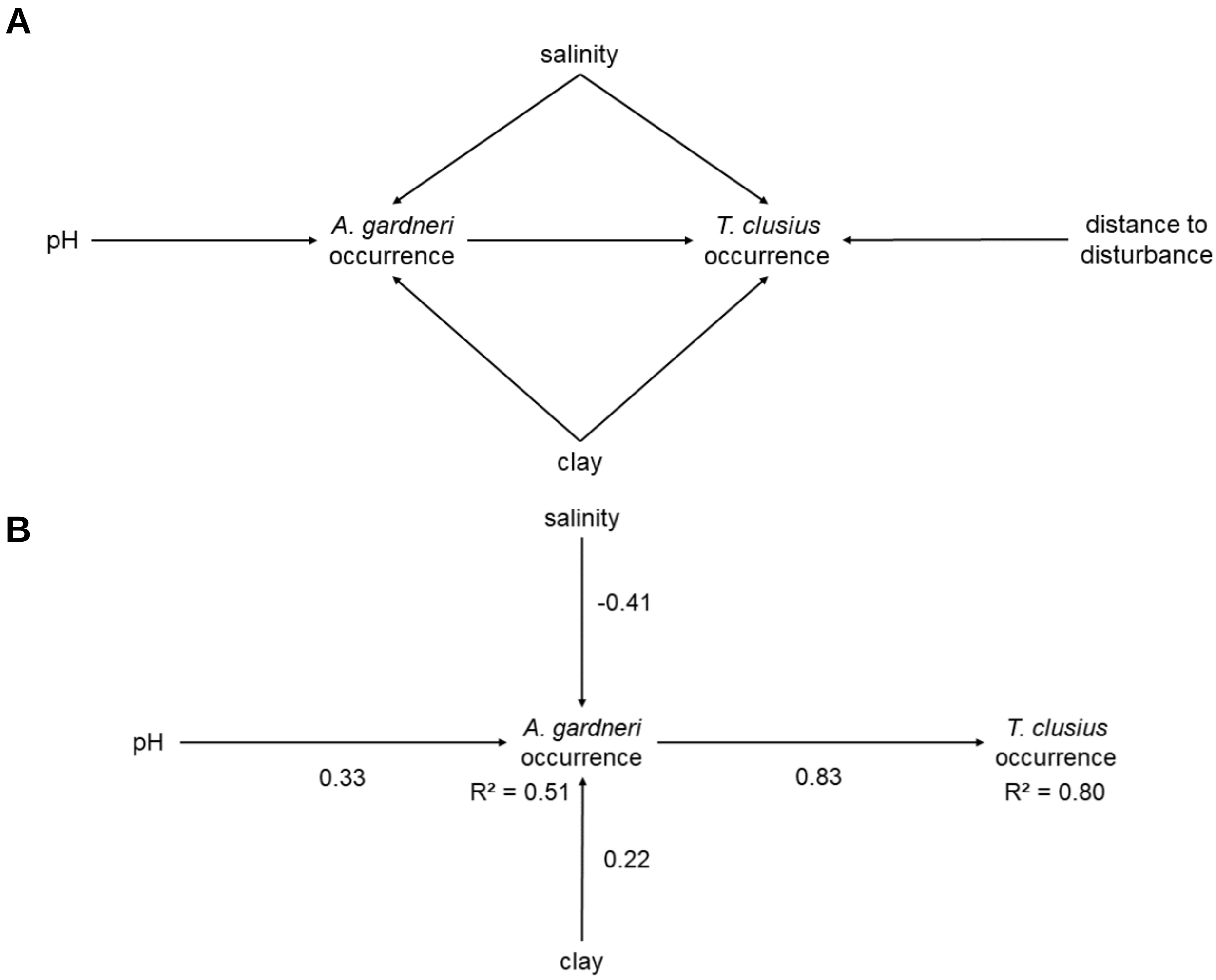

Figure 2. (A) Conceptual *a priori* path analysis model illustrating the hypothesized influences of pH, salinity, clay content, distance to human disturbance and Gardner's saltbush (*Atriplex gardneri*) occurrence on Wyoming pocket gopher (*Thomomys clusius*) occurrence. (B) Path analysis model quantifying the effects of pH, salinity, clay content, and Gardner's saltbush occurrence on Wyoming pocket gopher occurrence. Standardized estimates are reported. All arrows represent significant paths (*P* < 0.05). Occurrence of Wyoming pocket gophers was driven largely by that of Gardner's saltbush, which in turn was driven by a combination of pH, salinity, and clay content of soil.

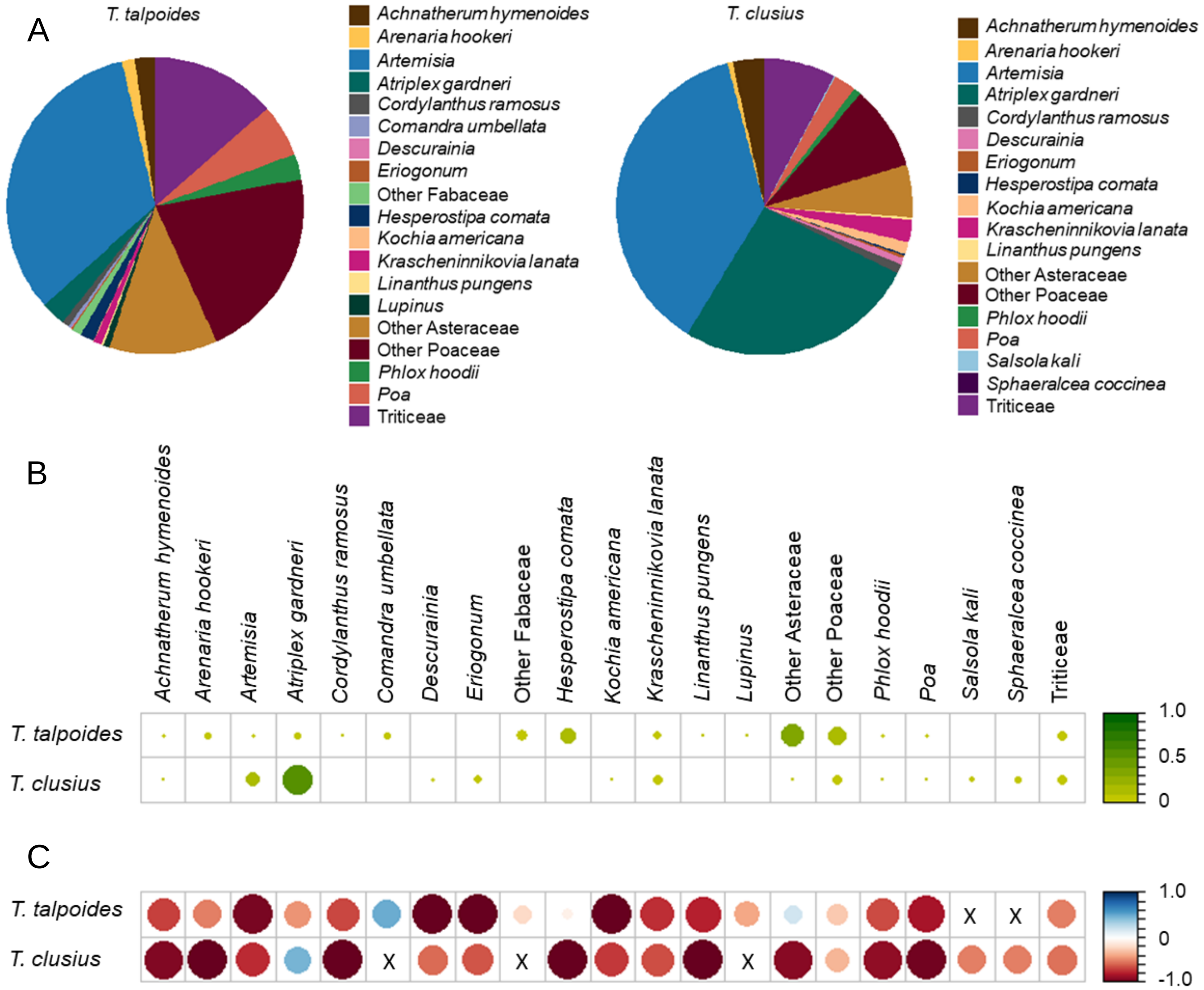

Figure 3. Mean food availability, utilization, and selection for northern pocket gophers (*Thomomys talpoides*) and Wyoming pocket gophers (*T. clusius*) across 15 sites in southcentral Wyoming. (A) Relative availability of plant taxa for each pocket gopher species that were consumed by at least one species of gopher. (B) The average proportional contribution of plant taxa in the diets of all gophers based on average relative read abundance (RRA). Darker shading and larger size reflect higher RRA across all individuals within a population. (C) Jacobs' *D* index for each plant taxa. Values range from -1 (strongest avoidance) to 1 (strongest selection). Color

and size reflect avoidance (red) or selection (blue). X’s indicate a food plant that was not available to a particular pocket gopher species.

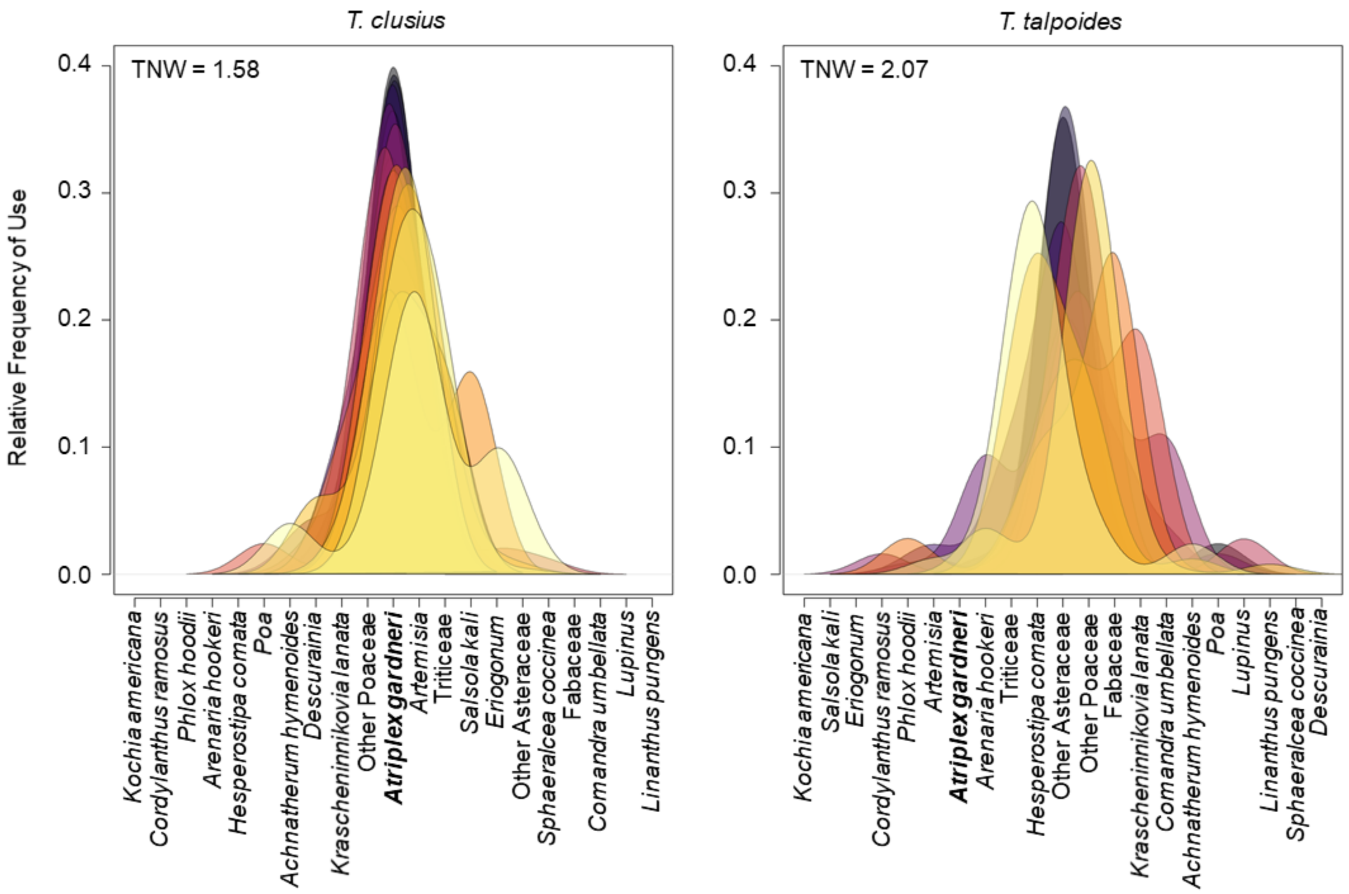

Figure 4. Density plot depicting the most frequently used food plants for Wyoming pocket gophers (*Thomomys clusius*, n = 21) and northern pocket gophers (*T. talpoides*, n = 12). Food plants were ranked from the most frequently used items (center of x-axis) to the least used items (left and right sides of the x-axis). Density (y-axis) reflects relative frequency of use in diets. Individual density plots were set to 50% transparency, so more saturated colors indicate greater overlap among individuals. Diet breadth (total niche width, TNW) was calculated using all individuals of each species (*Thomomys clusius*, n = 24, *T. talpoides*, n = 12). The diets of three individual Wyoming pocket gophers who were outliers were removed from the figure. Wyoming pocket gophers were characterized by a narrower population-level diet breadth (TNW) than northern pocket gophers.

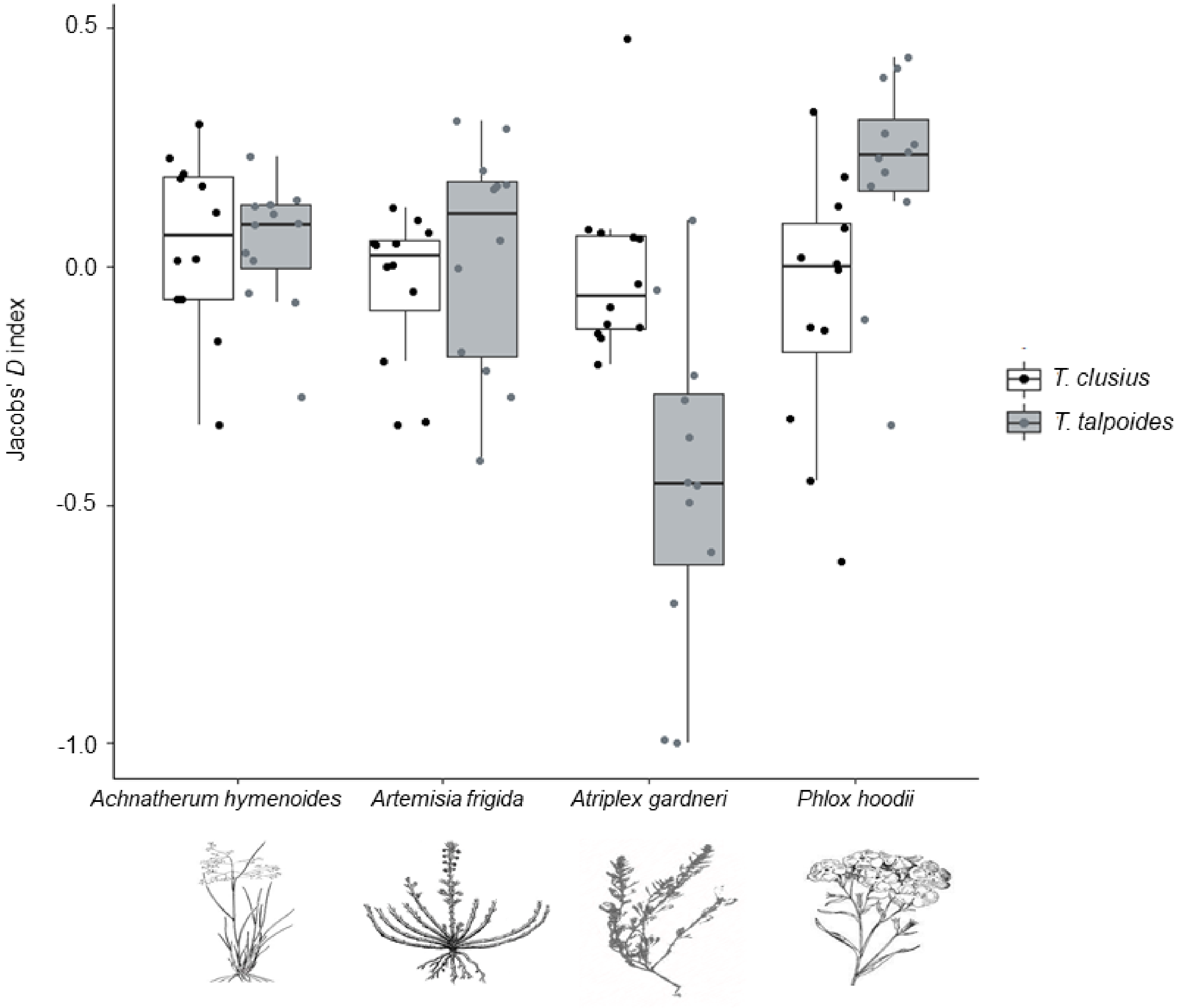

Figure 5. Food preferences of Wyoming pocket gophers (*Thomomys clusius*) and northern pocket gophers (*T. talpoides*) in multiple-choice cafeteria-style feeding trials. Jacob's *D* indices <1 indicate avoidance, >1 indicate preference, and values indistinguishable from 0 indicate no preference.

SUPPLEMENTARY DATA

Supplementary Data SD_{1}. — Assessment of hybridization frequency

Sampling

As described in the main text, gophers were trapped in south-central Wyoming. At the time of capture, a 3-4mm tail clip was taken from each gopher and stored in LN2 while in the field. Samples from 60 individuals were collected; 27 were identified as *T. talpoides* and 33 were identified as *T. clusius*.

DNA extraction and sequencing

I extracted genomic DNA from the 60 tail clips using DNeasy Tissue Kits (Qiagen Inc., Valencia, CA) using the manufacturer's recommended protocol. Following extraction, I assessed the quantity the DNA using Qubit Fluorometric Calibration (QFC; Invitrogen, Carlsbad, CA), following the manufacturer's recommended protocol. Of the 60 samples, 55 had concentrations of at least 25ng/ul. Five samples had concentrations less than 10ng/ul. I sent 25ul ul of DNA, regardless of concentration, to the Genomics Center at the University of Minnesota for Standard Genotyping-by-Sequencing (https://genomics.umn.edu/services/gbs). The University of Minnesota Genomics Core assessed the quality and quantity of all submitted samples using a PicoGreen assay. Based on their recommendations, all 60 samples were submitted for Genotyping-by-Sequencing. Briefly, the DNA extractions were digested with SbfI, prior to being individually barcoded during PCR and then pooled to sequence using the Illumina NextSeq 1 x 150bp Single-read platform.

Analyses

Following sequencing, the University of Minnesota Genomics Center provided their standard variant calling informatic service for all samples. This included demultiplexing the sequence files using the Illumina bcl2fastq package; individual samples with more than 2,000,000 raw reads were then subsampled down so that no sample had more than 2,000,000 reads in all subsequent analyses. After subsampling, the adapter sequences were removed using cutadapt (Martin 2011) and then Stacks 2.0 (Catchen et al. 2011) was used to generate the initial raw VCF files. The initial VCF output was then filtered using VCFTools (Danecek et al. 2011) to remove variants with a minor allele frequency of < 1%. Variants with genotype rates of <80% and samples with genotype rates of <50% were also removed. After this initial filtering, I retained all 60 samples and the final filtered SNP dataset had 5519 markers on 2502 loci.

From this filtered VCF file, I used VCFTools (Danecek et al. 2011) to winnow SNPs to one per locus by setting the ‘thin’ parameter to 200, which resulted in the retention of 2501 SNPs. I then generated a STRUCTURE (Pritchard et al. 2000) input file using PGDSpider (Lischer and Excoffier 2012). I ran three independent STRUCTURE runs with the following run parameters: MAXPOPS = 2; BURNIN = 50,000; NUMREPS = 1,500,000. Both the mainparams and extraparams files for these analyses can be found on our github repository for this project.

Results

All 60 samples (27 *T. talpoides* and 33 *T. clusius*) produced usable sequence data (Supplementary Table 1). With the exception of one sample, BE739AE (Supplementary Table 1), the minimum number of raw reads for any given sample was 1,482,022. The maximum was 4,433,773 and the mean number of raw reads across all 60 individuals was 2,032,521. Twenty-three samples were subsampled to retain 2,000,000 reads and for the other 37 samples, I retained all raw reads.

Based on the dataset of 60 gophers, I found no evidence of hybridization between the species. In all three STRUCTURE runs, every individual was assigned to one cluster or another with a probability of 1 (Supplementary Table 2). These assignments were made agnostic of the field-based species identity and in every analysis, individuals identified as *T. talpoides* in the field clustered with all other *T. talpoides* individuals (and vice-versa for T. *clusius*). There was never an instance in which an individual identified as one species in the field clustered with individuals of the other species.

Supplementary Table 1. Sample information for genetic analyses of hybridization between northern pocket gophers (*Thomomys talpoides*) and Wyoming pocket gophers (*T. clusius*).

Individual ID	Field species ID	STRUCTURE ID	# raw reads	# reads used in analyses
BE73955	*T. clusius*	73955	1718185	1718185
BE73956	*T. clusius*	73956	2343584	2000000
BE7395A	*T. clusius*	73951	1616387	1616387
BE7395F	*T. clusius*	73956	2056065	2000000
BE73963	*T. clusius*	73963	1606289	1606289
BE73964	*T. clusius*	73964	4433773	2000000
BE7396C	*T. clusius*	73963	1840864	1840864
BE7396E	*T. clusius*	73965	1743115	1743115
BE7396F	*T. clusius*	73966	1737752	1737752
BE73971	*T. clusius*	73971	1949309	1949309
BE73973	*T. clusius*	73973	2071942	2000000
BE73974	*T. clusius*	73974	1918646	1918646

BE73978	*T. clusius*	73978	1964396	1964396
BE7397A	*T. clusius*	73971	1957418	1957418
BE7397E	*T. clusius*	73975	1887303	1887303
BE73982	*T. clusius*	73982	3658589	2000000
BE73984	*T. clusius*	73984	2074131	2000000
BE73985	*T. clusius*	73985	2206208	2000000
BE73988	*T. clusius*	73988	3745968	2000000
BE73989	*T. clusius*	73989	2010474	2000000
BE73992	*T. clusius*	73992	2077912	2000000
BE73993	*T. clusius*	73993	1704913	1704913
BE73997	*T. clusius*	73997	1718009	1718009
BE739A1	*T. clusius*	73911	1538381	1538381
BE739A5	*T. clusius*	73915	2079364	2000000
BE739A7	*T. clusius*	73917	1793299	1793299
BE739AB	*T. clusius*	73912	1747771	1747771
BE739AC	*T. clusius*	73913	1899989	1899989
BE739AF	*T. clusius*	73916	1591126	1591126
BE739B0	*T. clusius*	73920	2707797	2000000
BE739B6	*T. clusius*	73926	1945408	1945408
NT1	*T. clusius*	111	1624681	1624681
NT2	*T. clusius*	112	1869445	1869445
BE7395C	*T. talpoides*	73953	1820561	1820561
BE7395D	*T. talpoides*	73954	1674804	1674804

BE73960	*T. talpoides*	73960	1629957	1629957
BE73961	*T. talpoides*	73961	1482022	1482022
BE73968	*T. talpoides*	73968	1894032	1894032
BE7396A	*T. talpoides*	73961	2044933	2000000
BE7396B	*T. talpoides*	73962	3534834	2000000
BE73976/BE73979	*T. talpoides*	73976	2175432	2000000
BE7397D	*T. talpoides*	73974	1876525	1876525
BE73981	*T. talpoides*	73981	2547898	2000000
BE73983	*T. talpoides*	73983	2174477	2000000
BE7398C	*T. talpoides*	73983	2158449	2000000
BE7398D	*T. talpoides*	73984	1597645	1597645
BE7398F	*T. talpoides*	73986	1731430	1731430
BE73990	*T. talpoides*	73990	1577805	1577805
BE73992	*T. talpoides*	73992	1780492	1780492
BE73995	*T. talpoides*	73995	2108920	2000000
BE73996	*T. talpoides*	73996	1777883	1777883
BE73998	*T. talpoides*	73998	1502989	1502989
BE7399A	*T. talpoides*	73991	1556578	1556578
BE7399D	*T. talpoides*	73994	2176304	2000000
BE739A0	*T. talpoides*	73910	1708064	1708064
BE739A3	*T. talpoides*	73913	2041718	2000000
BE739AE	*T. talpoides*	73915	870928	870928
BE739B4	*T. talpoides*	73924	2630628	2000000

BE739B7	*T. talpoides*	73927	3431530	2000000
NT3	*T. talpoides*	113	1605922	1605922

Supplementary Table 2. Inferred ancestry of 60 pocket gophers (27 *T. talpoides*, 33 *T. clusius*) based on three STRUCTURE runs. All individual gophers were assigned to one cluster or another with a probability of 1.

				1500k reps, run 1		1500k reps, run 2		1500k reps, run 3	
	Label	% missing	Pop	Inferred clusters		Inferred clusters		Inferred clusters	
1	73955	(4)	1	1.000	0.000	1.000	0.000	0.000	1.000
2	73956	(2)	1	1.000	0.000	1.000	0.000	0.000	1.000
3	73951	(1)	1	1.000	0.000	1.000	0.000	0.000	1.000
4	73953	(2)	1	0.000	1.000	0.000	1.000	1.000	0.000
5	73954	(13)	1	0.000	1.000	0.000	1.000	1.000	0.000
6	73956	(3)	1	1.000	0.000	1.000	0.000	0.000	1.000
7	73960	(13)	1	0.000	1.000	0.000	1.000	1.000	0.000
8	73961	(20)	1	0.000	1.000	0.000	1.000	1.000	0.000
9	73963	(3)	1	1.000	0.000	1.000	0.000	0.000	1.000
10	73964	(14)	1	1.000	0.000	1.000	0.000	0.000	1.000
11	73968	(15)	1	0.000	1.000	0.000	1.000	1.000	0.000
12	73961	(3)	1	0.000	1.000	0.000	1.000	1.000	0.000
13	73962	(25)	1	0.000	1.000	0.000	1.000	1.000	0.000
14	73963	(0)	1	1.000	0.000	1.000	0.000	0.000	1.000
15	73965	(5)	1	1.000	0.000	1.000	0.000	0.000	1.000
16	73966	(0)	1	1.000	0.000	1.000	0.000	0.000	1.000
17	73971	(4)	1	1.000	0.000	1.000	0.000	0.000	1.000

18	73973	(4)	1	1.000	0.000	1.000	0.000	0.000	1.000
19	73974	(8)	1	1.000	0.000	1.000	0.000	0.000	1.000
20	73976	(13)	1	0.000	1.000	0.000	1.000	1.000	0.000
21	73978	(5)	1	1.000	0.000	1.000	0.000	0.000	1.000
22	73971	(0)	1	1.000	0.000	1.000	0.000	0.000	1.000
23	73974	(12)	1	0.000	1.000	0.000	1.000	1.000	0.000
24	73975	(2)	1	1.000	0.000	1.000	0.000	0.000	1.000
25	73981	(11)	1	0.000	1.000	0.000	1.000	1.000	0.000
26	73982	(12)	1	1.000	0.000	1.000	0.000	0.000	1.000
27	73983	(2)	1	0.000	1.000	0.000	1.000	1.000	0.000
28	73984	(5)	1	1.000	0.000	1.000	0.000	0.000	1.000
29	73985	(1)	1	1.000	0.000	1.000	0.000	0.000	1.000
30	73988	(12)	1	1.000	0.000	1.000	0.000	0.000	1.000
31	73989	(4)	1	1.000	0.000	1.000	0.000	0.000	1.000
32	73983	(8)	1	0.000	1.000	0.000	1.000	1.000	0.000
33	73984	(16)	1	0.000	1.000	0.000	1.000	1.000	0.000
34	73986	(17)	1	0.000	1.000	0.000	1.000	1.000	0.000
35	73990	(1)	1	0.000	1.000	0.000	1.000	1.000	0.000
36	73992	(17)	1	0.000	1.000	0.000	1.000	1.000	0.000
37	73993	(0)	1	1.000	0.000	1.000	0.000	0.000	1.000
38	73995	(14)	1	0.000	1.000	0.000	1.000	1.000	0.000
39	73996	(20)	1	0.000	1.000	0.000	1.000	1.000	0.000
40	73997	(1)	1	1.000	0.000	1.000	0.000	0.000	1.000

41	73998	(8)	1	0.000	1.000	0.000	1.000	1.000	0.000
42	73991	(14)	1	0.000	1.000	0.000	1.000	1.000	0.000
43	73992	(4)	1	1.000	0.000	1.000	0.000	0.000	1.000
44	73994	(18)	1	0.000	1.000	0.000	1.000	1.000	0.000
45	73910	(3)	1	0.000	1.000	0.000	1.000	1.000	0.000
46	73911	(0)	1	1.000	0.000	1.000	0.000	0.000	1.000
47	73913	(15)	1	0.000	1.000	0.000	1.000	1.000	0.000
48	73915	(2)	1	1.000	0.000	1.000	0.000	0.000	1.000
49	73917	(4)	1	1.000	0.000	1.000	0.000	0.000	1.000
50	73912	(0)	1	1.000	0.000	1.000	0.000	0.000	1.000
51	73913	(0)	1	1.000	0.000	1.000	0.000	0.000	1.000
52	73915	(18)	1	0.000	1.000	0.000	1.000	1.000	0.000
53	73916	(3)	1	1.000	0.000	1.000	0.000	0.000	1.000
54	73920	(17)	1	1.000	0.000	1.000	0.000	0.000	1.000
55	73924	(27)	1	0.000	1.000	0.000	1.000	1.000	0.000
56	73926	(4)	1	1.000	0.000	1.000	0.000	0.000	1.000
57	73927	(27)	1	0.000	1.000	0.000	1.000	1.000	0.000
58	111	(4)	1	1.000	0.000	1.000	0.000	0.000	1.000
59	112	(5)	1	1.000	0.000	1.000	0.000	0.000	1.000
60	113	(18)	1	0.000	1.000	0.000	1.000	1.000	0.000

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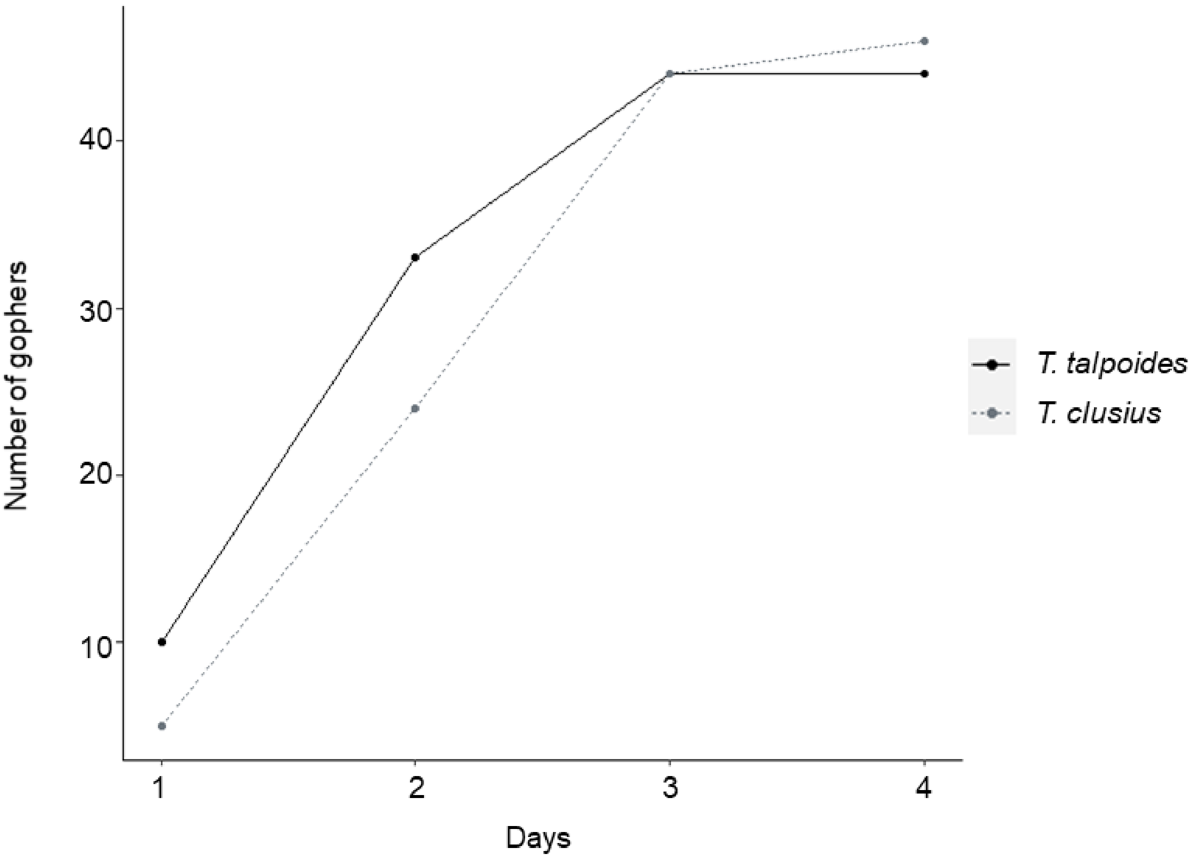
Supplementary Data SD2. — Assessment of unique gophers trapped during a trapping bout.



Supplementary Figure 1. The number of unique northern pocket gophers (*Thomomys talpoides*) and Wyoming pocket gophers (*T. clusius*) captured during a trapping bout. The number of unique individuals captured did not increase after three consecutive days of trapping.

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