



Diet selection, commonness, and rarity in a pair of smooth-toothed pocket gophers

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Understanding the determinants of species rarity is a perennial challenge for ecologists and conservation biologists. In addition to resource specialization, competitive interactions may limit the abundance and distribution of species, 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*) is restricted to areas dominated by Gardner's Saltbush (*Atriplex gardneri*); it 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. We assessed one dimension of consumer–resource interactions—diet selection—between Wyoming pocket gophers, northern pocket gophers, and Gardner's Saltbush, using a combination of path analysis, DNA metabarcoding, and cafeteria-style feeding experiments. We rejected the null hypothesis that Wyoming pocket gophers and Gardner's Saltbush co-occur solely because they require similar soil conditions. Although we 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 selection and avoidance of Gardner's Saltbush. We suggest that Wyoming pocket gophers can persist within their small geographic range by capitalizing on Gardner's Saltbush, a halophyte that probably requires some combination of physiological, morphological, and behavioral adaptations to exploit. Low abundances, restricted geographic ranges, or both are hallmarks of rarity, each of which are shaped by diet selection and other consumer–resource interactions. Quantifying consumer–resource interactions 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, fundamental specialization, interspecific competition, realized specialization, resource partitioning, rodent, *Thomomys*, Wyoming

Nearly 40 years ago, Rabinowitz (1981) detailed pathways to species rarity derived from combinations of habitat specificity, abundance, and geographic range size. Through combinations of these three variables, a species can be classified into eight categories, one of which represents common species and the other seven representing different forms of rarity. Rarity is a relative concept describing the distribution and abundance of a species (Gaston 1994; Flather and Sieg 2007), and can be defined as “the current status of an extant organism which... is restricted either in number or area to a level that is demonstrably less than the majority of other organisms of comparable

taxonomic entities” (Reveal 1981:42). Commonness falls on the opposite side of the spectrum and represents a single category in Rabinowitz's typology resulting from a large population size, over a wide geographic range encompassing many habitats (Rabinowitz 1981).

The most restrictive characteristics of Rabinowitz's 'seven 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; 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 also resulting in sparse populations and small geographic ranges (i.e., rarity; 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 from localities or entire regions (Benkman 1999; Török and Tóth 1999; Borzée et al. 2016). Alternatively, resource partitioning can relax interspecific competition and maintain subordinate species alongside ecologically similar, dominant competitors from local to continental scales (MacArthur 1958; Grant 1972; Schoener 1974; Brown et al. 2000; Stuart and Losos 2013). For example, over evolutionary time, competition between the Greater White-toothed Shrew (*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). Similarly, classic work on Melanesian ants (Wilson 1961) and Galapagos finches (Lack 1947; Grant and Grant 2006) demonstrated ecological release (sensu Herrmann et al. 2020) for species living in allopatry compared to their sympatric counterparts, patterns consistent with resource partitioning. Consequently, rare species can persist by capitalizing on foods or habitats that are unavailable or inefficiently used by otherwise-dominant competitors.

In sum, 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 (hereafter 'obligate' or 'fundamental' specialists; Shipley et al. 2009; DeVictor et al. 2010; Stephens et al. 2019); or (2) through tolerance of rare species for resources that are avoided by their more common, widespread complements (hereafter 'facultative' or 'realized' specialists; Shipley et al. 2009; DeVictor et al. 2010; Stephens et al. 2019). Each version of specialization should result in a distinct process underlying the distribution of rare species. Obligate specialization could be expected to result in competitive exclusion, through which the obligate specialist enjoys higher fitness than the generalist under a narrow range of conditions, thus outcompeting and potentially excluding ecologically similar or closely related (generalist) species. Obligate specialization typically is envisioned as an intrinsic and thus fixed (at least over ecological

time scales) property of species, while facultative specialization can be shaped by the communities within which species are embedded (DeVictor et al. 2010). Here, facultative specialists are able to persist because they can (but are not required to) use resources avoided by (or altogether unavailable to) ecologically similar or closely related (generalist) species. Although either obligate and facultative specialization can be correlated with 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 (and on which the specialist outperforms more common, widespread counterparts), while facultative specialization simply requires a tolerance for one or more resources that either are not available to or are avoided by common, widespread counterparts. Put another way, rarity often is the *result* of obligate specialization on resources that themselves are rare, while facultative specialization *might allow* rare species to persist: a resource unavailable or inefficiently used by a dominant competitor can support viable populations of subordinate species, albeit within a limited geographic range. Quantifying any flexibility (or lack thereof) surrounding diet selection (and other dimensions of consumer–resource dynamics) of rare species should therefore illuminate the mechanisms underlying 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 wide 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, United States, 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). At our study sites in south-central Wyoming, northern pocket gophers are approximately 150% heavier than Wyoming pocket gophers (81 g versus 54 g, respectively); males and females of each species do not differ in mass (Brito and Sanchez 2020). Although little is known about the ecology of the Wyoming Pocket Gopher, other *Thomomys* spp. vigorously defend small (0.01–0.02 ha) territories from conspecifics throughout the year, with the exception of the breeding season (e.g., Ingles 1952; Howard and Childs 1959; Verts and Carraway 1999). *Thomomys* spp. are strictly herbivorous, with diets of individuals containing a majority of forbs and typically some grasses (Verts and Carraway 1987, 1999; Jones and Baxter 2004). Further, shoots and leaves make up the majority of Northern Pocket Gopher diets, although consumption of at least some roots is typical (Verts and Carraway 1999). Although hybridization is relatively common in *Thomomys*

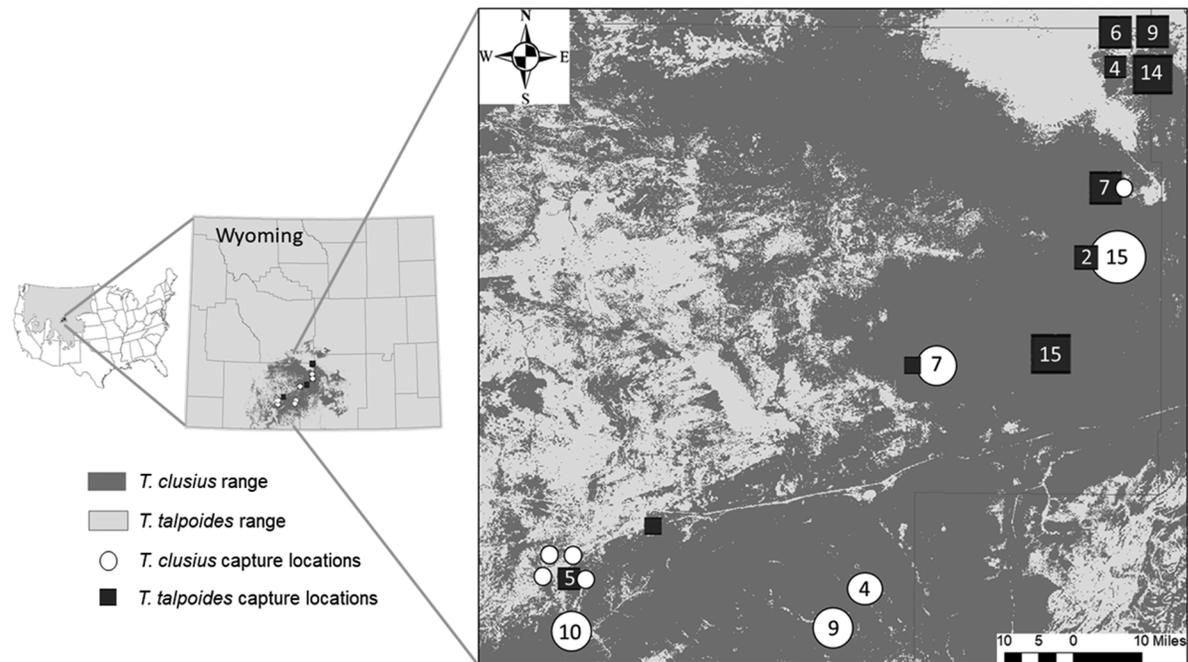


Fig. 1.—Map depicting Wyoming Pocket Gopher (*Thomomys clusius*) and Northern Pocket Gopher (*T. talpoides*) geographic ranges within the continuous United States (Keinath et al. 2014; U.S. Geological Survey—Gap Analysis Project 2017). Sites at which Wyoming pocket gophers were captured are depicted by white circles; sites at which northern pocket gophers were captured are depicted by black squares. Numbers within the circles and squares represent the number of gophers captured at a site.

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; Supplementary Data SD1).

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). Consequently, the Wyoming Pocket Gopher could be categorized as a "nondominant endemic"; that is, the most restrictive category in the typology of Rabinowitz (1981), depicted in the lower/rightmost cell in her Table 1. In contrast, the Northern Pocket Gopher is abundant throughout a wide geographic range from southern Canada through the Sierra Nevada range and New Mexico, and is roughly five times as abundant as the Wyoming Pocket Gopher in Carbon and Sweetwater Counties (Thaeler and Hinesley 1979). The Northern Pocket Gopher thus qualifies as 'common'—and could be placed in the upper leftmost cell in Table 1 of Rabinowitz (1981). With respect to the rarity of Wyoming pocket gophers, it remains unclear whether Gardner's Saltbush represents: (1) a shrub with environmental requirements (e.g., soil pH, salinity, and texture) that overlap 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.

We tested whether and how diet selection involving Gardner's Saltbush were correlated with the commonness and rarity of northern pocket gophers and Wyoming pocket gophers, respectively (Fig. 2). First, using a path analysis model, we 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, we 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; Fig. 2).

MATERIALS AND METHODS

Study area.—We conducted our work across Carbon and Sweetwater Counties in south-central Wyoming, United States. Our study area (approximately 2,000 km²) consisted mostly of public land managed by the Bureau of Land Management and land managed by private landowners. Our study area ranged from 1,950 to 2,200 m in elevation and was characterized by an average winter temperature of -4°C , an average summer temperature of 20°C , and average annual precipitation of 27

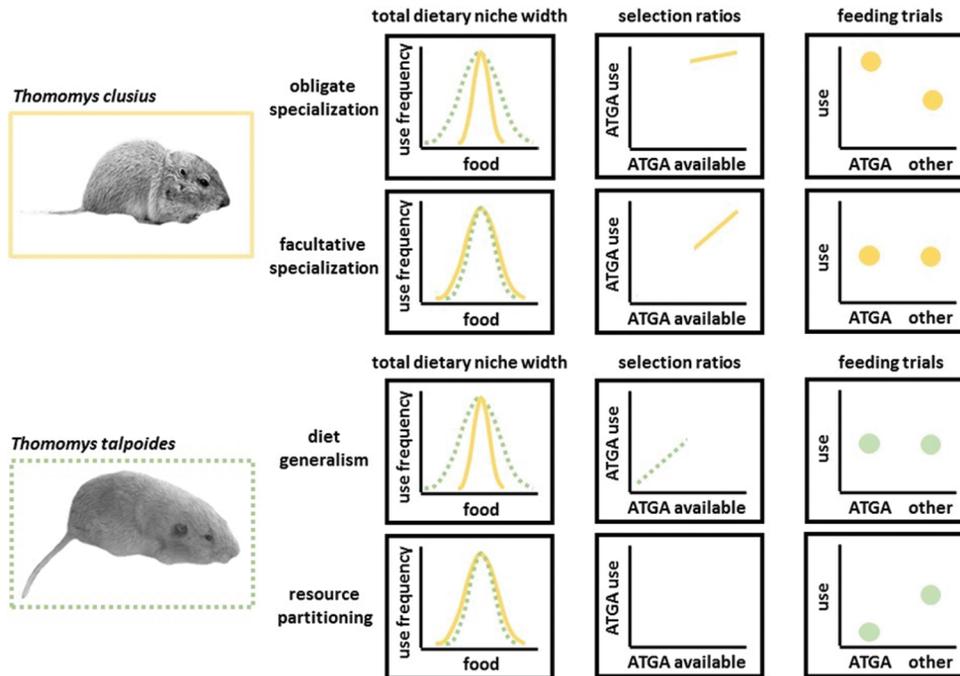


Fig. 2.—Hypotheses and associated predictions regarding consumer–resource interactions among Gardner’s Saltbush (*Atriplex gardneri* [“ATGA”]), Wyoming pocket gophers (*Thomomys clusius*, solid line), and northern pocket gophers (*T. talpoides*, dashed line). The ‘obligate specialization’ and ‘facultative 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. Graphical predictions associated with each hypothesis are arranged in rows; metrics (or methods) to assess predictions are arranged in columns. The ‘obligate specialization’ and ‘diet generalism’ hypotheses both predict that populations of Wyoming pocket gophers should exhibit narrower dietary niche width relative to populations of northern pocket gophers (left column). Under the ‘obligate specialization’ hypothesis, Wyoming pocket gophers should use Gardner’s Saltbush more than expected based on its availability; under the ‘facultative specialization’ hypothesis, Wyoming pocket gophers should use Gardner’s Saltbush (and other food plants) in proportion to its availability. Both hypotheses predict that availability of Gardner’s Saltbush is high (middle column, top panels). Under the ‘diet generalism’ hypothesis, northern pocket gophers should use Gardner’s Saltbush in proportion to its availability (which is low); under the ‘resource partitioning’ hypothesis, northern pocket gophers should neither use nor have available Gardner’s Saltbush (middle column, bottom panels). When food availability is held constant, Wyoming pocket gophers should prefer Gardner’s Saltbush under the ‘obligate specialization’ hypothesis, but should display no such preference under the ‘facultative specialization’ hypothesis (right column, top panels). When food availability is held constant, northern pocket gophers should display no preferences under the ‘diet generalism’ hypothesis, but avoid Gardner’s Saltbush under the ‘resource partitioning’ hypothesis (right column, bottom panels).

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, we surveyed for the presence of pocket gophers at eighteen 640-km² (i.e., 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 2020). Upon identifying active mounds at 16 sites, we livetrapped pocket gophers from June to October 2017–2019. All sites were sampled at

least once in each of the 3 years; two 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. We checked traps hourly from 0800 to 1800, and left traps open overnight for three consecutive days, after which the number of unique individuals captured did not increase (Supplementary Data SD2).

At each site, we randomly collected three soil samples within 20 m² of a focal (livetrapped) gopher mound. We collected samples using a 17.78-cm tubular soil sampler with a 1.27-cm diameter. Soil samples were analyzed at the Environmental Analytical Laboratory (Brigham Young University, Provo, Utah) for pH, salinity (EC dS/m), and soil texture (proportion of sand, silt, and clay-sized particles). We calculated the average of each soil characteristic from each site (mean # of soil

samples $\pm SE$) for use in path analysis modeling (see below). We 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, we collected fecal pellets directly from pocket gophers during processing. Fecal samples were processed at Jonah Ventures (Boulder, Colorado). Plant DNA from fecal samples was extracted using the DNeasy 96 PowerSoil Pro Kit. A forward (CGAAATCGGTAGACGCTACG) and reverse (CCATTGAGTCTCTGCACCTATC) primer was used during PCR amplification (Taberlet et al. 2007). A portion of the chloroplast *trnL* intron was PCR-amplified from each genomic DNA sample using the c and h *trnL* primers. Both forward and reverse primers also contained a 5′ adaptor sequence to allow for subsequent indexing and Illumina sequencing. Each 25 μ L PCR reaction was mixed according to the Promega PCR Master Mix specifications (Promega catalog #M5133, Madison, Wisconsin). A second round of PCR was performed to give each sample a unique 12-nucleotide index sequence. Final indexed amplicons from each sample were cleaned and normalized using SequelPrep Normalization Plates (Life Technologies, Carlsbad, California). Using the Life Technologies SequelPrep Normalization kit, 25 μ L of PCR amplicon was purified and normalized according to the manufacturer’s protocol. Samples were then pooled together by adding 5 μ L of each normalized sample to the pool.

Sample library pools were sent for sequencing on an Illumina NovaSeq 6000 (San Diego, California) at the Texas A&M Agrilife Genomics and Bioinformatics Sequencing Core facility using the SP Reagent Kit v1.5 (500 cycles). Necessary quality control measures were performed at the sequencing center prior to sequencing. Raw sequence data were demultiplexed using phenix (v2.1.0; Galanti et al. 2021) enforcing strict matching of sample barcode indices (i.e., no errors). Cutadapt (v3.4; Martin 2011) was then used to remove gene primers from the forward and reverse reads, discarding any read pairs where one or both primers were not found at the expected location (5′) with an error rate < 0.15. Read pairs were then merged using vsearch (v2.15.2; Torbjørn et al. 2016), discarding resulting sequences with a length of <100 bp or with a maximum expected error rate > 0.5 bp (Edgar and Flyvbjerg 2015). For each sample, reads were then clustered using the unnoise3 denoising algorithm (Edgar 2016) as implemented in vsearch, using an alpha value of five and discarding unique raw sequences observed less than eight times. Counts of the resulting exact sequence variants (ESVs) were then compiled and putative chimeras were removed using the uchime3 algorithm, as implemented in vsearch.

For each final ESV, a consensus taxonomy was assigned using a custom best-hits algorithm and a reference database consisting of publicly available sequences (GenBank; Benson et al. 2005) as well as Jonah Ventures voucher sequences records. Reference database searching used an exhaustive semi-global pairwise alignment with vsearch and match quality was quantified using a custom, query-centric approach, where

the percent match ignores terminal gaps in the target sequence, but not the query sequence. The consensus taxonomy was then generated using either all 100% matching reference sequences or all reference sequences within 1% of the top match, accepting the reference taxonomy for any taxonomic level with >90% agreement across the top hits.

Using a taxonomic reference library, we identified ESVs to the lowest taxonomic resolution possible. We adjusted taxonomic identities when the plant species (diagnosed by the reference library) was absent from our study area, but a closely related species (i.e., in the same genus) occurred in our study area (Soininen et al. 2013). We 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; Kartzin et al. 2015) for each fecal sample, excluding plant taxa with RRA < 1% (Kartzin et al. 2015; Iwanowicz et al. 2016).

To assess food availability, we recorded the percent cover of shrubs, forbs, and grasses using line-intercept transect methods (Canfield 1941). We centered four 10-m transects at cardinal and intercardinal directions on each mound at which a gopher was captured. Each set of four transects was paired with a set of four predetermined transects, centered on a point generated randomly within sites (ArcMap v. 10.1). Each plant was identified to the lowest taxonomic resolution possible. To quantify site-specific food availability, we combined all line-intercept data (both from capture points and associated random points).

Feeding trials.—We 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 Gardner’s Saltbush relative to three other species of plants. Selection indices inform whether and how individuals choose among resources that differ in their availabilities within individual home ranges or entire study sites (Litvaitis 2000). In contrast, feeding trials generate data on preferences (in which availability of foods is held constant) and, when conducted among different populations or species, are most useful in informing how such populations (Goheen et al. 2003) or species (Ivan and Swihart 2000; Otieno et al. 2019) differ in the perceived value of foods. Further, resource use by individuals may depend on resource availability, such that use of a particular resource may intensify when that resource is rare (i.e., functional responses; Chan et al. 2017; Holbrook et al. 2019). Feeding trials therefore provide opportunity to understand food use in the absence of confounding variation in food availability, to understand preferences for foods that are not regularly encountered, or both.

Feeding trials were conducted simultaneously with trapping efforts from June to October in 2019. Individual gophers ($n = 6$ per species) were held separately for 24 h in plastic enclosures (61 \times 46 \times 48 cm) containing ca. 20 cm of locally collected soil. To mimic natural tunnels, we 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. We 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 ± 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 our study sites. We 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), we were 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 (Fig. 2). Additionally, preliminary results from DNA metabarcoding of diets indicated that, on average, ca. 60% of Wyoming Pocket Gopher 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, we conducted two 12-h feeding trials. After the first trial, we 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-h 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.—We 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 our live-trapping efforts. In employing this analysis, our goal was not to characterize the soil properties preferred by Wyoming pocket gophers, but rather to test the null hypothesis that associations between Wyoming pocket gophers and Gardner's Saltbush were not merely due to overlapping soil requirements. Consequently, we did not attempt to quantify an exhaustive suite of soil properties determinative of the distributions of other fossorial rodents (e.g., Luna and Antinuchi 2006; Lövy et al. 2015; Galiano and Kubiak 2021), but instead focused on predictors known to constrain the distribution of Gardner's Saltbush and other members of the genus *Atriplex* (Stubbendieck et al. 1981; Ansley and Abernethy 1984). Additionally, we included distance to natural gas infrastructure because of its hypothesized effects on soil compaction, which could influence gopher presence.

We developed an a priori path analysis model (Fig. 3A) based on research by Keinath et al. (2014) using the *piecewiseSEM* package (Lefcheck 2016) in Program R. In the event that our a priori path model—in which gopher and saltbush distributions would be purely associational—had been supported, we would have focused our efforts on quantifying a broader range of soil properties, particularly soil resistance (which might be expected to differentially affect energetic

costs of burrowing in the smaller Wyoming Pocket Gopher relative to the larger Northern Pocket Gopher; Brito and Sanchez 2020; see also Perissinotti et al. 2009). We inspected variance inflation factors of covariates to check for collinearity. Given the high collinearity between the soil texture variables (i.e., proportion clay, sand, and silt), we only retained clay content in our final model. We modeled Gardner's Saltbush and Wyoming pocket gophers as binary responses (i.e., presence/absence) using logistic regression, and we 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). We 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, we calculated Jacobs' *D* index: $D_i = (r_i - p_i)/r_i + p_i - 2r_i p_i$, 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 zero indicate use in proportion to availability. We 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. We excluded four individuals (two Wyoming pocket gophers, two northern pocket gophers) with sequence reads of plant species that did not occur (i.e., were not available) at our study site (Soininen et al. 2015). To compare the degree of diet selection between species for different food plants, we computed Jacobs' *D* using the *dietr* package (Borstein 2019). Because of the unequal number of fecal samples between species, we randomly sampled Jacobs' *D* values associated with each food from 14 Wyoming pocket gophers, without replacement, 1,000 times. For each food plant, we compared the mean observed Jacobs' *D* index of northern pocket gophers to this distribution of resampled Jacobs' *D* values. To compare diet breadth of Wyoming pocket gophers and northern pocket gophers, we calculated total niche width (TNW) using the *RInSp* package in Program R (Zaccarelli et al. 2013). TNW is the summation of the within-individual component and the between-individual component of niche width and is synonymous with diet breadth in this study (Roughgarden 1972; Bolnick et al. 2002).

Following cafeteria-style feeding trials, we used linear mixed models to explore if trial and individual affected feeding preferences. Food plant species, gopher species, and initial plant biomass were treated as fixed effects, with a food plant \times gopher species interaction. Trial and individual were treated as random effects in the linear mixed models. All linear mixed models resulted in singular fit with variance estimates for random effects of zero or nearly zero. As such, we concluded the random effects of trial and individual did not significantly influence feeding preferences, so we removed all random effects from our models. Trial and individual were then treated as fixed effects (along with food plant species, gopher species,

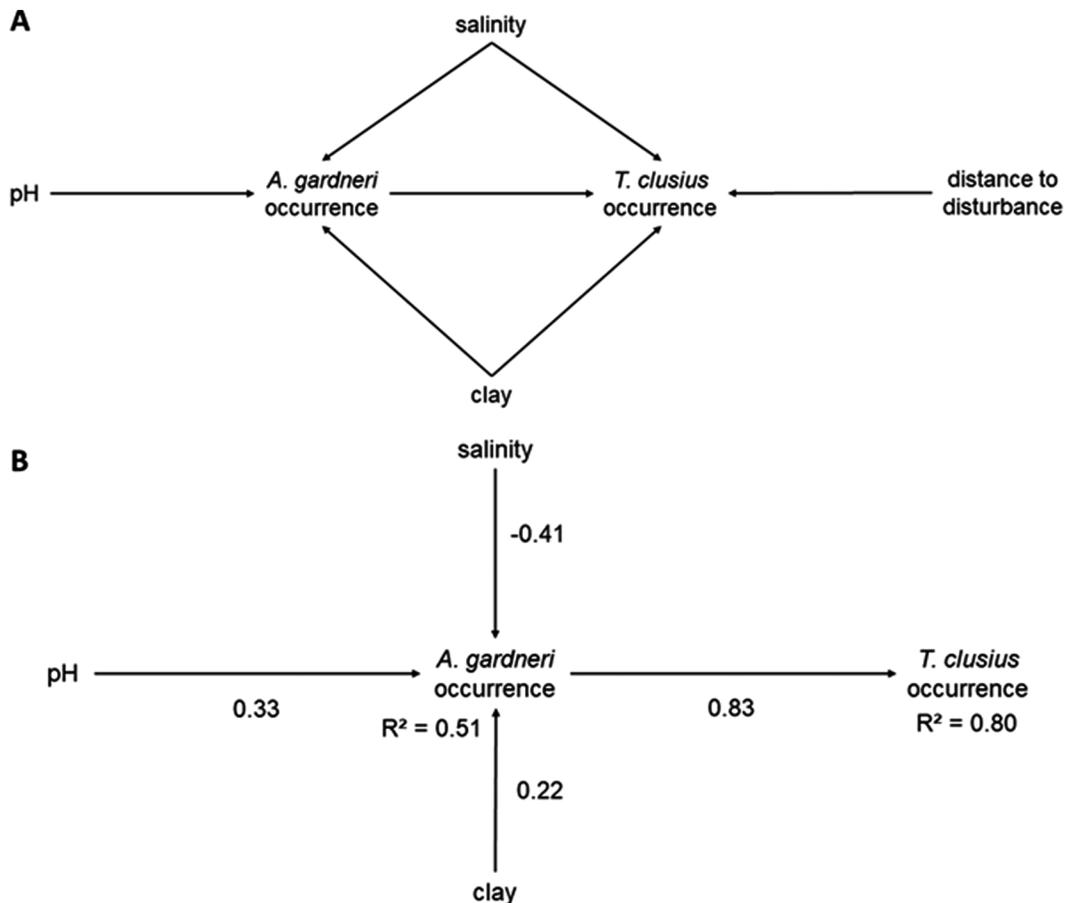


Fig. 3.—(A) Conceptual a priori path analysis model illustrating the hypothesized influences of pH, salinity, clay content, distance to human disturbance, and Gardner’s Saltbush (*Atriplex gardneri*) occurrence on Wyoming Pocket Gopher (*Thomomys clusius*) occurrence. (B) Path analysis model quantifying 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.

and initial plant biomass, with a food plant \times gopher species interaction) in subsequent linear models. Since the interaction between food plant species and gopher species was the only significant effect, we used Jacob’s D index to calculate selection of food plants (Jacobs 1974). All statistical analyses were conducted in Program R (R Core Team, 2020).

RESULTS

We captured 64 northern pocket gophers (at 10 out of 16 sites) and 50 Wyoming pocket gophers (at 10 out of 16 sites) from June 2017 to October 2019. Both species were captured at 4 out of 16 sites. We 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 our data adequately, suggesting no important paths were excluded (Fisher’s $C = 4.09$, d.f. = 6, $P = 0.67$; Fig. 3B). 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 (Family Poaceae) and plant species in the Family Asteraceae (Table 1, Fig. 4A). Big Sagebrush (*A. tridentata*) was the most common species 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 plant species in the Family Asteraceae (Fig. 4A); however, unlike areas where northern pocket gophers were captured, Wyoming Pocket Gopher capture

Table 1.—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* = 14) 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.

Family	Species	<i>Thomomys talpoides</i>			<i>Thomomys clusius</i>		
		Availability	Use	Jacobs' <i>D</i> ± <i>SD</i>	Availability	Use	Jacobs' <i>D</i> ± <i>SD</i>
Amaranthaceae	<i>Atriplex gardneri</i>	2.46	4.58	-0.01 ± 0.95	26.16	57.63	0.47 ± 0.51
	<i>Grayia spinosa</i>	—	—	—	0.58	0.00	-1.00 ± 0.00
	<i>Neokochia americana</i>	0.05	0.00	-1.00 ± 0.00	1.32	1.40	-0.47 ± 0.75
	<i>Krascheninnikovia lanata</i>	0.84	3.47	-0.73 ± 0.69	2.39	5.44	-0.65 ± 0.67
	<i>Salsola tragus</i>	—	—	—	0.11	1.63	-0.51 ± 0.99
Asteraceae	Asteraceae	43.55	30.64	-0.34 ± 0.65	42.89	11.13	-0.79 ± 0.30
Brassicaceae	<i>Descurainia</i> spp.	0.07	0.00	-1.00 ± 0.00	0.78	0.96	-0.68 ± 0.75
Caryophyllaceae	<i>Arenaria</i> spp.	1.29	3.14	-0.40 ± 0.84	0.55	0.00	-1.00 ± 0.00
Fabaceae	<i>Lupinus</i> spp.	0.60	0.44	-0.40 ± 0.85	—	—	—
	Other Fabaceae	0.96	8.33	-0.17 ± 0.96	—	—	—
Malvaceae	<i>Sphaeralcea coccinea</i>	—	—	—	0.01	2.95	-0.75 ± 0.71
Orobanchaceae	<i>Cordylanthus ramosus</i>	0.66	0.31	-0.67 ± 0.66	0.96	0.00	-1.00 ± 0.00
Poaceae	<i>Achnatherum hymenoides</i>	2.01	0.09	-0.94 ± 0.24	3.47	0.56	-0.92 ± 0.31
	<i>Hesperostipa comata</i>	1.57	17.70	-0.07 ± 0.98	0.17	0.00	-1.00 ± 0.00
	Triticeae	15.23	16.83	-0.37 ± 0.79	7.72	11.43	-0.06 ± 0.65
	Other Poaceae	27.59	10.62	-0.64 ± 0.50	11.48	1.76	-0.76 ± 0.44
Polemoniaceae	<i>Linanthus pungens</i>	0.18	0.14	-0.80 ± 0.61	0.29	0.00	-1.00 ± 0.00
	<i>Phlox hoodii</i>	2.47	1.28	-0.70 ± 0.59	0.87	0.37	-0.89 ± 0.38
Polygonaceae	<i>Eriogonum</i> spp.	0.18	0.00	-1.00 ± 0.00	0.27	4.74	-0.62 ± 0.78
Santalaceae	<i>Comandra umbellata</i>	0.28	2.45	0.49 ± 0.44	—	—	—

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 14 plant taxa (Supplementary Data SD3) and the diets of Wyoming pocket gophers contained 12 plant taxa (Supplementary Data SD4); seven plant taxa were present in the diets of both pocket gopher species (Table 1, Fig. 4B and C). All Wyoming pocket gophers consumed Gardner's Saltbush (mean RRA = 57.63% ± *SD* 29.04). Two northern pocket gophers consumed Gardner's Saltbush (mean RRA = 4.58% ± *SD* 11.63). Jacob's *D* indices are presented in Table 1 (Fig. 4C). Diet breadth (TNW) was higher for northern pocket gophers (1.77) than Wyoming pocket gophers (1.62, Fig. 5).

In cafeteria-style feeding trials, northern pocket gophers showed no preference for Fringed Sagebrush ($D = 0.02 \pm SD 0.24$) or Indian Ricegrass ($D = 0.05 \pm SD 0.13$), preferred Spiny Phlox ($D = 0.19 \pm SD 0.22$), and avoided Gardner's Saltbush ($D = -0.46 \pm SD 0.34$; Fig. 6). In contrast, Wyoming pocket gophers neither preferred nor avoided any food plants during feeding trials (Fig. 6).

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, we rejected the null hypothesis that associations between Wyoming pocket gophers and Gardner's Saltbush arose from overlapping environmental

(soil) requirements. However, it is possible that soil hardness, compaction, or bulk density—properties that we did not quantify—might have further influenced the distribution of Wyoming pocket gophers. Such physical properties of soils are correlated with the distributions of members of the genus *Ctenomys* (tuco-tucos), subterranean rodents with ecologies comparable to those of pocket gophers (e.g., de Freitas et al. 2012; Galiano et al. 2014a). Further, *Ctenomys* spp. with weak bite forces tend to be restricted to low-density soils, perhaps because of high-density soils are more difficult to excavate (Borges et al. 2017). Finally, pocket gophers, tuco-tucos, and other subterranean rodents can influence soil properties themselves (Reichman and Seabloom 2002; Davidson et al. 2012; Galiano et al. 2014b; Chu et al. 2020). Whether and the extent to which soil density shapes (or responds to) the distributions of Wyoming and northern pocket gophers—either exclusively or in tandem with the influence of Gardner's Saltbush—remains an open question for future research.

Our results suggest that the strong affiliation for Gardner's Saltbush by Wyoming pocket gophers likely reflects differential food selection by Wyoming pocket gophers and northern pocket gophers. All Wyoming pocket gophers sampled during our study consumed Gardner's Saltbush, supporting the 'obligate specialization' hypothesis (Fig. 2) and highlighting a mechanism by which Wyoming pocket gophers might competitively exclude northern pocket gophers from saltbush-dominated areas. However, Wyoming pocket gophers exhibited no preference for Gardner's Saltbush during feeding trials, supporting the 'facultative specialization' hypothesis (Fig. 2). In contrast, Gardner's Saltbush was avoided in feeding trials by northern pocket gophers and was unavailable to them in the field (with the exception of two individuals), lending support for the 'resource partitioning' hypothesis (Fig. 2).

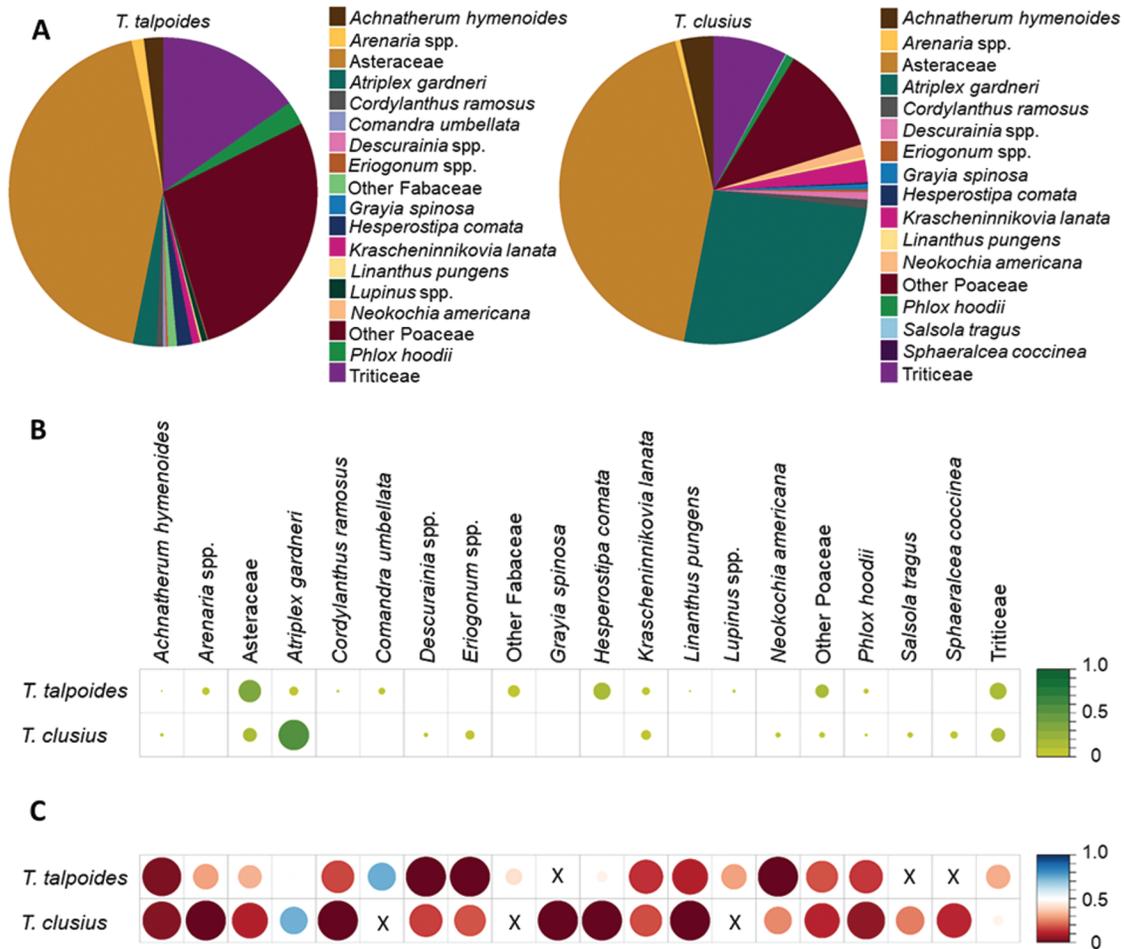


Fig. 4.—Mean food availability, utilization, and selection for Northern Pocket Gopher (*Thomomys talpoides*) and Wyoming Pocket Gopher (*T. clusius*) across 16 sites in south-central Wyoming. (A) Relative availability of plant taxa for each pocket gopher species that were consumed by at least one species 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). Xs indicate a food plant that was not available to a particular pocket gopher species.

Irrespective of whether they are obligate or facultative specialists, our results indicate that Wyoming pocket gophers persist within a restricted geographic range by capitalizing on a resource that is neither consumed by nor available to northern pocket gophers.

We hypothesize that Wyoming pocket gophers may exhibit adaptations similar to other rodents that consume halophytes (e.g., Schmidt-Nielsen 1964; Abdallah and Tawfik 1969; Kenagy 1972, 1973; Degen 1988; Mares et al. 1997), thus permitting them to consume high quantities of Gardner's Saltbush. Given that its larger, common congener is uncommon where Gardner's Saltbush occurs in the field, and avoids Gardner's Saltbush in feeding trials, we suspect that such high quantities of consumption by Wyoming pocket gophers on Gardner's Saltbush represent a strategy by which to minimize competition and partition resources with northern pocket gophers. A correlation 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 (Thaaler and Hinesley 1979; Keinath et al. 2014; Brito and Sanchez 2020), suggesting that they are confined to areas unusable by the competitively superior Northern Pocket Gopher.

To test this hypothesis, experimental removals (or exclusions) of each species of gopher might be conducted in conjunction with removal of Gardner's Saltbush. Exclusion and removal experiments provide some of the best evidence for the effect of competition in restricting the local abundance and distribution of species (e.g., Hairston 1980; Neet and Hausser 1990; Hamel et al. 2013; Pasch et al. 2013; Eurich et al. 2018). If Wyoming pocket gophers are able to competitively exclude northern pocket gophers by virtue of obligate specialization on Gardner's Saltbush, the removal of Wyoming pocket gophers, Gardner's Saltbush, or both should result in the expanded

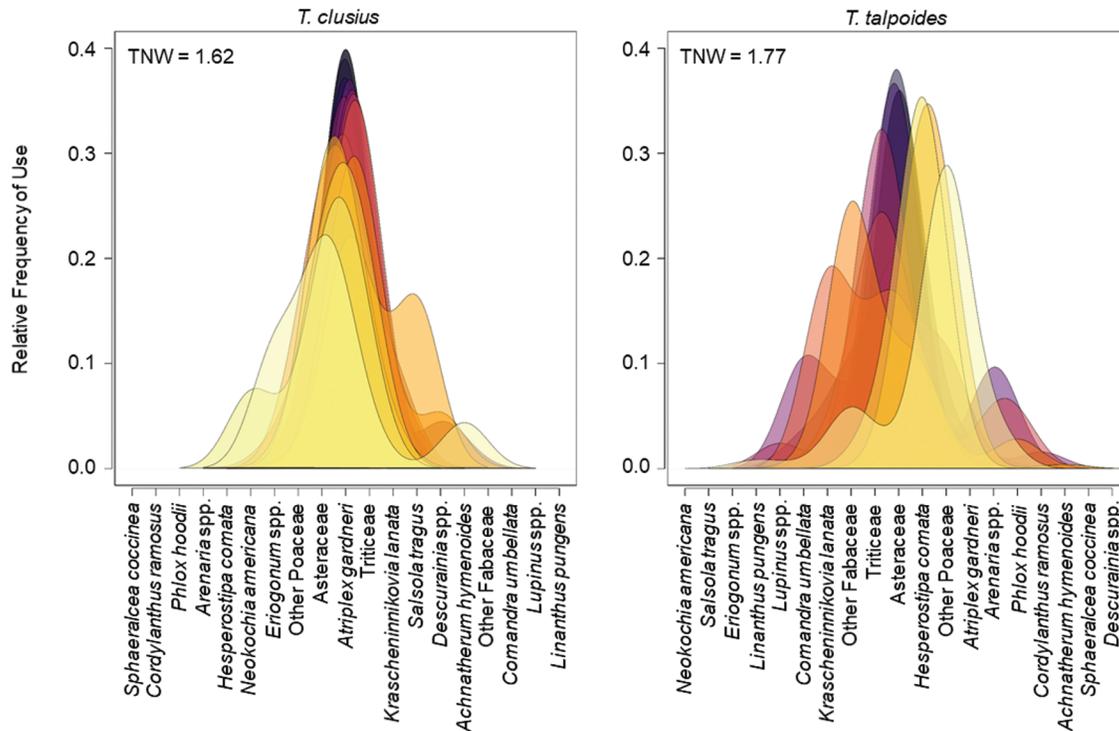


Fig. 5.—Density plot depicting the most frequently used food plants for Wyoming Pocket Gopher (*Thomomys clusius*, $n = 21$) and Northern Pocket Gopher (*T. talpoides*, $n = 14$). Food plants were ranked from the most frequently used items (center of x-axis) to the least used items (left and right sides 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 24 Wyoming Pocket Gopher (*Thomomys clusius*) and 16 Northern Pocket Gopher (*T. talpoides*) diets. 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.

distribution of northern pocket gophers. Alternatively, if areas dominated by Gardner's Saltbush simply represent refugia for Wyoming pocket gophers (because they are unusable by northern pocket gophers), the removal of northern pocket gophers should result in the expanded distribution of Wyoming pocket gophers. While results of our study suggest that competitive exclusion by northern pocket gophers may delineate the geographic range of Wyoming pocket gophers, exclusions and removals would provide a stronger, more definitive test of this hypothesis. Such field manipulations would be difficult. 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 demanding to determine if all northern pocket gophers were removed from areas 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. While challenging, such a series of experiments could disentangle the causal mechanisms underlying the distributions of these species, and thus remains a potential direction for future research.

The tendency for rare species to exploit a resource that is unused or avoided by common species is a recurrent pattern across taxa. For example, narrow endemism by some

jewelflowers (*Streptanthus* spp.) and by whistling-thorn trees (*Acacia drepanolobium*) is promoted by harsh physical conditions in the serpentine soils of California and the 'black cotton' soils of East Africa, respectively; these species are competitively subordinate to congeners inhabiting neighboring soil types (Cacho and Strauss 2014; Pringle et al. 2016). Reciprocally, when dominant competitors are naturally absent or experimentally removed, other (subordinate) species often increase in population size (i.e., density compensation), expand their diets and microhabitat use (i.e., niche expansion), or both (e.g., Lister 1976; Boag and Grant 1984; Brown and Munger 1985; Golcher-Benavides and Wagner 2019), suggesting that facultative specialization is widespread geographically and taxonomically. In sum, dietary specialization need not preclude dietary flexibility, but instead is a pathway through which rare species can persist in proximity to dominant competitors.

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

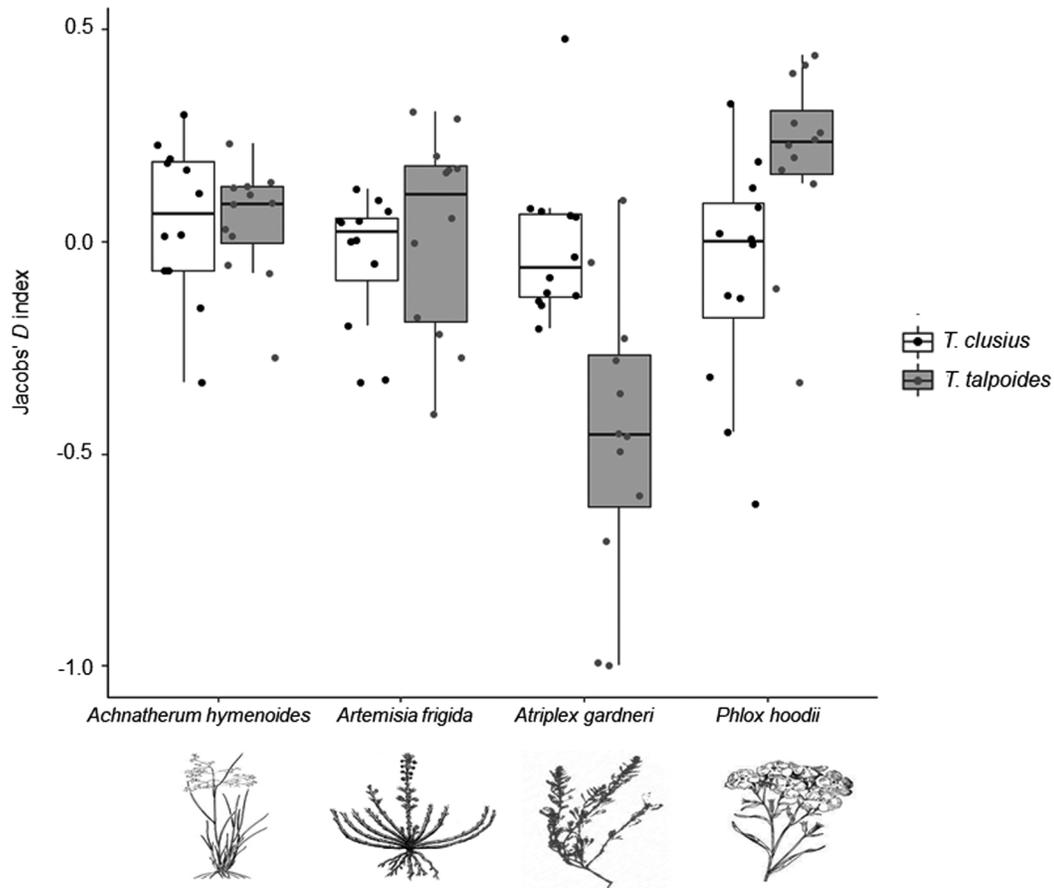


Fig. 6.—Food preferences of Wyoming Pocket Gopher (*Thomomys clusius*) and Northern Pocket Gopher (*T. talpoides*) in multiple-choice cafeteria-style feeding trials. Jacob's *D* ranges from -1 to 1 , where negative values indicate avoidance, positive values indicate preference, and values indistinguishable from 0 indicate use in proportion to availability.

allows Wyoming pocket gophers to persist by capitalizing on a resource that is unavailable to and avoided by northern pocket gophers, a more common, more generalized, and more widespread congener. We 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 the mechanistic basis for commonness and rarity.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Assessment of pocket gopher hybridization frequency.

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

Supplementary Data SD3.—Bipartite food network depicting Northern Pocket Gopher (*Thomomys talpoides*) diet composition.

Supplementary Data SD4.—Bipartite food network depicting Wyoming Pocket Gopher (*Thomomys clusius*) diet composition.

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