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RESEARCH ARTICLE

A test of the Niche Variation Hypothesis in a ruminant herbivore

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Abstract

1. Despite the shared prediction that the width of a population's dietary niche expands as food becomes limiting, the Niche Variation Hypothesis (NVH) and Optimal Foraging Theory (OFT) offer contrasting views about how individuals alter diet selection when food is limited.
2. Classical OFT predicts that dietary preferences do not change as food becomes limiting, so individuals expand their diets as they compensate for a lack of preferred foods. In contrast, the NVH predicts that among-individual variation in cognition, physiology or morphology create functional trade-offs in foraging efficiency, thereby causing individuals to specialize on different subsets of food as food becomes limiting.
3. To evaluate (a) the predictions of the NVH and OFT and (b) evidence for physiological and cognitive-based functional trade-offs, we used DNA microsatellites and metabarcoding to quantify the diet, microbiome and genetic relatedness (a proxy for social learning) of 218 moose *Alces alces* across six populations that varied in their degree of food limitation.
4. Consistent with both the NVH and OFT, dietary niche breadth increased with food limitation. Increased diet breadth of individuals—rather than increased diet specialization—was strongly correlated with both food limitation and dietary niche breadth of populations, indicating that moose foraged in accordance with OFT. Diets were not constrained by inheritance of the microbiome or inheritance of diet selection, offering support for the little-tested hypothesis that functional trade-offs in food use (or lack thereof) determine whether populations adhere to the predictions of the NVH or OFT.
5. Our results indicate that both the absence of strong functional trade-offs and the digestive physiology of ruminants provide contexts under which populations

should forage in accordance with OFT rather than the NVH. Also, because dietary niche width increased with increased food limitation, OFT and the NVH provide theoretical support for the notion that plant–herbivore interaction networks are plastic rather than static, which has important implications for understanding interspecific niche partitioning. Lastly, because population-level dietary niche breadth and calf recruitment are correlated, and because calf recruitment can be a proxy for food limitation, our work demonstrates how diet data can be employed to understand a populations' proximity to carrying capacity.

KEYWORDS

behavioural plasticity, DNA metabarcoding, functional trade-off, genetic relatedness, microbiome, moose, Optimal Foraging Theory, social learning

1 | INTRODUCTION

Ecologists have recently come to appreciate that populations are often comprised of individuals that vary markedly in resource use, which has important implications for population and community dynamics (Araújo et al., 2011; Bastille-Rousseau & Wittemeyer, 2019; Bolnick et al., 2003, 2011). The Niche Variation Hypothesis (NVH; Van Valen, 1965) posits that the breadth of foods used by a population (hereafter 'total niche width'; sensu Roughgarden, 1972) stems from among-individual dietary diversity, wherein groups of individuals reduce intraspecific competition by specializing on subsets of food available to the population (Figure 1a; Bolnick et al., 2003; Roughgarden, 1974; Tinker et al., 2008). In contrast to the NVH, Optimal Foraging Theory (OFT) assumes that all conspecifics exploit foods in a similar manner (MacArthur & Pianka, 1966; Stephens & Krebs, 1986) and predicts that the total niche width of a population reflects within-individual dietary diversity (Figure 1b; Krebs et al., 1977; Pyke, 1984). Despite contrasting assumptions about how individuals use food resources, both the NVH and OFT predict that total niche width expands as food becomes limiting (Figure 1a,b; Krebs et al., 1977; Roughgarden, 1974; Svanbäck & Bolnick, 2007), with the alternative pathways proposed by the NVH and OFT being repeatedly demonstrated in both natural and laboratory settings (Figure 1c; Araújo et al., 2011). Although expansion of total niche width ultimately is caused by intraspecific competition, the more proximate mechanisms that determine whether individuals contract or expand their diets in accordance with the NVH or OFT are poorly understood.

Functional trade-offs that constrain individuals from broadening their diet have been hypothesized to promote the among-individual dietary diversity that underlies individual diet specialization, and

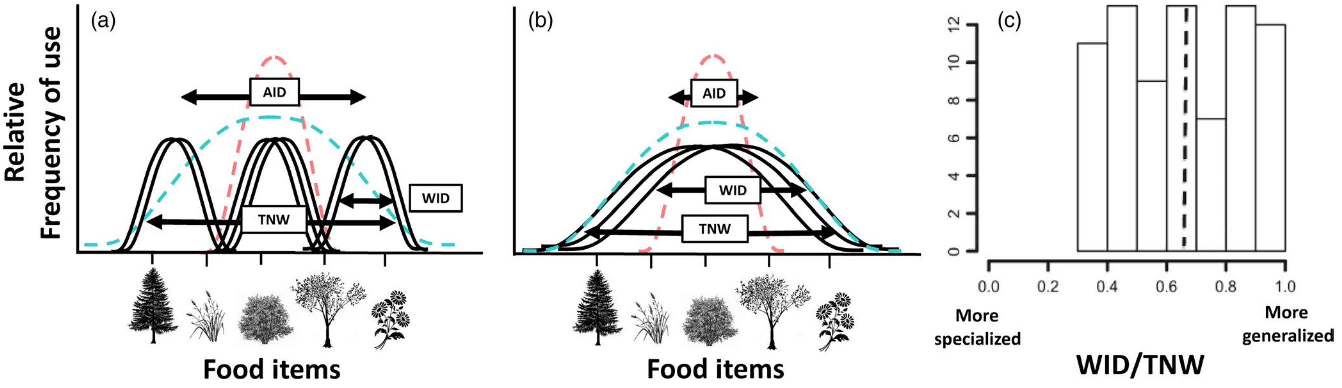

FIGURE 1 Heuristic illustration of individual dietary niches (solid curves) under food limitation according to (a) the Niche Variation Hypothesis (NVH), and (b) Optimal Foraging Theory (OFT). Salmon-coloured curves illustrate the total niche width (TNW) of a population when food is abundant, whereas teal-coloured curves represent the TNW of a population under food limitation. The width of the solid curves represents within-individual dietary diversity (WID) when food is limiting, whereas the distance between the peaks of the solid curves reflects the amount of among-individual diversity (AID) when food is limiting. The NVH predicts that groups of individuals specialize on subsets of food (i.e. WID is small relative to TNW; panel a). In contrast, OFT predicts that TNW is primarily a reflection of individual diet breadth (i.e. WID is large relative to TNW; panel b). (c) Evidence for the NVH (left side of histogram corresponding to low WID/TNW ratio indicating dietary specialization; panel a) and OFT (right side of histogram corresponding to high WID/TNW ratio indicating increased generalization; panel b). The dashed, vertical line reflects the average level of dietary specialization observed across all studies reviewed by Araújo et al. (2011). Figure adapted from Bolnick et al. (2003) and Araújo et al. (2011)

thus determine whether expansion of total niche width conforms to the predictions of the NVH or OFT (Araújo et al., 2011; Bolnick et al., 2003). Functional trade-offs require that individual variation in cognition, physiology or morphology gives rise to variation in foraging efficiency, such that individuals are efficient at extracting energy from some foods but not others (Araújo et al., 2009; Araújo & Gonzaga, 2007; Bolnick et al., 2003; Costa-Pereira & Pruitt, 2019; Svanback & Bolnick, 2005). Individual variation in cognition, physiology or morphology may be accentuated by disruptive selection to generate the dietary specializations illustrated in Figure 1a (Bolnick, 2004). Additionally, innovation of new foraging behaviours is commonplace in nature, suggesting that diet specializations also may arise rapidly and in the absence of disruptive selection (for review, see Reader et al., 2016 and references within). Regardless of the mechanism by which variation in food use might occur, such variation promotes the increased among-individual dietary diversity predicted by the NVH (Figure 1a).

Alternatively, individuals within a population may differ minimally with respect to their cognition, physiology or morphology, causing diet selection among individuals to be similar. Under these circumstances, all individuals increasingly rely on secondary or tertiary foods as competition for food increases, thereby increasing the within-individual dietary diversity consistent with OFT (Figure 1b; Araújo et al., 2011; Bolnick et al., 2003; Svanback & Bolnick, 2005). Thus, weak or non-existent functional trade-offs should result in (a) diet selection that does not vary among individuals within a population; and (b) a broadening of the total dietary niche width (TNW) stemming from increased within-individual dietary diversity (Figure 1b,c; Araújo et al., 2011; Bolnick et al., 2003).

Ruminants are a diverse (~200 species) group of herbivorous mammals that rely on their gut microbiome for handling and breaking down cellulosic compounds (i.e. cellulose, hemicellulose, lignin) and chemical defences (e.g. tannins), suggesting that among-individual variation in diet may be linked to among-individual variation in gut microbiome (Barboza et al., 2010). Such specialization of the gut microbiome can be viewed as a direct analogue to the specialized feeding morphology and physiology of three-spined sticklebacks *Gasterosteus aculeatus* (Matthews et al., 2010), Eurasian perch *Perca fluviatilis* (Olsson et al., 2007) and yellow-rumped warblers *Dendroica coronate* (Afik & Karasov, 1995), each of which has enabled individuals of these species to specialize on subsets of food. Additionally, many foraging behaviours are inherited via social learning and improve foraging efficiency (Aplin et al., 2015; Jesmer et al., 2018; Leadbeater & Chittka, 2007; Slagsvold & Wiebe, 2011; Sweanor & Sandegren, 1989; Weigl & Hanson, 1980), suggesting that the among-individual variation predicted by the NVH may be promoted and maintained by social learning (Estes et al., 2003; Kopps et al., 2014; Tinker et al., 2008; van de Waal et al., 2013). Like social learning of diet selection, the gut microbiome may be transmitted from mother to offspring during parturition, and post-parturition through contact with maternal faeces, milk and skin (Barboza et al., 2010; Ducluzeau, 1983). Indeed, the gut microbiome has been implicated in facilitating dietary specialization in domestic goats *Capra aegagrus hircus* (Jones & Lowry, 1984) and helps maintain the dietary specializations consistent with the NVH in woodrats *Neotoma lepida* (Kohl et al., 2014). Social transmission of diet selection, the rumen microbiome or both may therefore constrain individuals from broadening their diet when food is limiting and result in substantial among-individual dietary diversity (Figure 1a,c).

To test predictions of the NVH and OFT, we quantified whether and how food limitation resulted in diet shifts by a broadly distributed ruminant, the moose *Alces alces*. Specifically, we evaluated whether the total niche width of populations expanded under resource limitation according to (a) the NVH, wherein the expansion of total niche width is accompanied by substantial among-individual dietary diversity and individual specialization (Figure 1a), or (b) OFT, which posits that total niche width expands because of increased within-individual dietary diversity (Figure 1b). Furthermore, we tested two potential pathways by which individual specialization might arise: social transmission of the microbiome and social transmission of diet selection (Figure S3). In light of the importance of social transmission in shaping diet selection in ruminants and other taxa, and given that moose form mother–offspring dyads for the first year of their lives, we expected any support for individual specialization (and thus the NVH) to be further attended by inheritance of the microbiome, inheritance of diet selection, or both.

2 | MATERIALS AND METHODS

2.1 | Study area

We studied six populations of moose in Wyoming, northern Colorado, and northern Utah, USA (Figure S1), where habitats were characterized by riparian shrublands dominated by Booth's willow *Salix boothii*, Geyer's willow *Salix geyeriana*, and planeleaf willow *Salix planifolia*. Within riparian shublands, several other willow species, deciduous shrubs (e.g. family Rosaceae and *Betula glandulosa*), cottonwoods (*Populus* spp.) and a number of grasses (family Poaceae), sedges (*Carex* spp.) and forbs (e.g. families Asteraceae, Onagraceae) were also common. In addition to riparian shrublands, moose also used upland habitats that interspersed riparian habitats (hereafter ‘uplands’; Baigas et al., 2010; Becker, 2008; Oates, 2016) characterized by mixed conifers (*Abies lasiocarpa*, *Picea engelmannii*, *Pinus contorta*, *Pseudotsuga menziesii*), aspen (*Populus tremuloides*), sagebrush (*Artemisia* spp., also family Asteraceae) and other upland shrubs in the subfamily Dryadoideae [i.e. mountain mahogany (*Cercocarpus* spp.) and bitterbrush *Purshia tridentate*]. All six populations were exposed to high seasonality, with winters characterized by deep snow (mean February snow depth 78 ± 15 cm) and cold temperatures (mean February low temperature −15 ± 1°C), while summers were characterized by low precipitation (mean July rainfall 4 ± 1 cm) and mild temperatures (mean July high temperature 23 ± 2°C; Western Regional Climate Center).

2.2 | Study design and sampling

In the absence of strong top-down forcing (i.e. predation, disease), rates of calf recruitment are a sensitive measure of food limitation for ruminant herbivores (Eberhardt, 2002; Gaillard et al., 1998; Jesmer et al., in press). We obtained estimates of population-level calf recruitment for each of the six study populations from the Wyoming Game and Fish Department, Colorado Division of Parks and Wildlife, and Utah Division of Wildlife Resources. To estimate calf recruitment, biologists counted and classified the age (adult, yearling or juvenile) and sex (male or female for yearlings and adults) of individual moose from helicopters and fixed wing aircraft during winter (i.e. December to February). Calf recruitment was measured as the number of calves observed per 100 cows. From 1947 to 1987, moose were translocated from historical (native) populations in western Wyoming and northern Utah (i.e. Jackson, Sublette and Uinta) to mountain ranges in eastern Wyoming and northern Colorado (i.e. Bighorn, Snowy Range, North Park; Brimeyer & Thomas, 2004; Jesmer et al., 2018). Combined with variation in climate and plant productivity, these translocations created a threefold difference in food limitation (as indexed by calf recruitment) among the six populations (Jesmer et al., in press). Only one (i.e. Jackson) of six study populations possessed appreciable numbers of large carnivores. Although grizzly bears *Ursus arctos horribilis* and wolves *Canis lupus* in Jackson consume calves and influence recruitment (Oates, 2016), Jackson moose are also highly food limited (Berger et al., 1999; Jesmer et al., in press). Thus, calf recruitment provides an accurate proxy for food limitation across our study region.

To quantify diet and microbiome composition of individuals in each population, we collected faecal samples via stratified random sampling along transects within two strata: riparian shrublands and uplands. Faecal samples were collected over 10-day sampling periods during the winters of 2012 and 2013 and the summer of 2013. We constrained sampling to areas where moose were likely to occur (hereafter ‘core habitat’), which we modelled using random forests (Breiman, 2001; Evans et al., 2011; Liaw & Wiener, 2002; see site selection in Appendix S1 for detailed modeling procedure) and locations derived from 174 GPS-collared individuals (n = 1,523,829 locations) distributed across the Jackson, Sublette and Snowy Range study regions from 2006 to 2014 (Baigas et al., 2010; Oates, 2016). We then used the National Land Cover Database (Homer et al., 2015) to further constrain sampling within core habitat to riparian shrubland and upland habitat strata. Within each stratum, we identified 20 locations for each population using a spatially balanced stratified random design (Kincaid et al., 2012; Stevens & Olsen, 2004). At each location, we randomly selected a direction that would allow us to remain within the habitat strata for the entire 2-km sampling transect. We used detection dogs to find faecal samples along transects during summer when faecal samples scattered across vast areas, were hidden by thick vegetation, and were required to be recently defecated (<48 hr old) for DNA analysis (Dahlgren et al., 2012). During winter, however, visual detection of faecal samples was feasible because faeces were concentrated on winter ranges, readily detected in snow and were frozen shortly after defaecation by the cold winter conditions in our study area. All samples were collected according to a sterile protocol and frozen at −20°C within 8 hr.

2.3 | Genetic analyses

To identify individual moose and their sex, we developed multi-locus genotypes from faecal samples using nine microsatellite loci and a sex marker (Table S1). Genotyping errors are common, however, when working with low-quality DNA such as that extracted from faecal samples (for review, see Lampa et al., 2013; Miller et al., 2002; Taberlet et al., 1996). Genotyping errors have the potential to cause downstream errors in inference regarding inheritance of foraging behaviour and microbiome (Waits et al., 2001). We therefore took several precautionary steps to limit any potential confounds associated with genotyping error (see mitigating the effects of potential genotyping errors in Appendix S1). Following recommendations for faecal DNA extraction and amplification (Lampa et al., 2013), we extracted DNA using a sterile protocol (Qiagen Inc.; Adams et al., 2011; Woodruff et al., 2014) and amplified nine microsatellites and a sex marker via a standard multiplexing protocol (Qiagen Inc.; Table S2). We employed a multiple tubes approach, wherein a minimum of three PCR reactions were conducted for each faecal sample (Taberlet et al., 1996). All PCR products were then prepared for fragment analysis in a dedicated room that was physically separated from the laboratory where DNA extraction was performed (Goldberg et al., 2016). Each fragment analysis was genotyped by two independent observers using GeneMarker® (SoftGenetics, LLC). We used the probability that two genotypes were indeed unique individuals and not simply siblings with similar genotypes [i.e. probability siblings (Psibs) <0.05] as a conservative measure of individual identification (Waits et al., 2001).

To quantify diet and microbiome composition of individual moose identified via multilocus genotyping, we used DNA metabarcoding. DNA was extracted from faecal samples using the MoBio PowerSoil htp-96 well Isolation Kit (Qiagen Inc.) according to the manufacturer's protocol. Diet composition was determined by sequencing the P6 loop of the chloroplast trnL(UAA) intron using c and h trnL primers (Taberlet et al., 2007; Table S1), whereas microbiome composition was quantified by sequencing the 16sRNA region of bacteria and archea using 515F and 806R primers (Bergmann et al., 2015; Taberlet et al., 2007; Table S1). See Appendix S1 for detailed information regarding DNA extraction, PCR conditions, and metabarcoding informatics.

If multiple faecal samples belonged to the same individual, we randomly selected a single faecal sample to represent the diet and microbiome of that individual over the preceding ~48–72 hr. To ensure that our single sample estimates of diet selection were appropriate for evaluating individual specialization, we followed the recommendations of Araújo et al. (2011): (1) that stomach samples have multiple foods, (2) these multiple foods represent independent foraging decisions, (3) the sampled diet is representative of the overall diet of the individual, (4) individuals being compared must be drawn from a small spatial range and a single point in time. The digestive physiology and movement behaviour of moose inherently align with recommendations 1 and 2 because digesta is mixed in the gut for ~48–72 hr, thereby causing faecal samples of moose to represent tens of foraging bouts (Clauss et al., 2007; Hofmann, 1989; Meyer et al., 2010). Moose traverse their home ranges ~1 time per day (Noonan et al., 2020), meaning faecal samples for this species likely represent the overall seasonal diet of the individual (recommendation 3). And lastly, we ensured individual samples were collected across small spatiotemporal windows (recommendation 4) by collecting samples within the seasonal ranges of each population over short periods of time (i.e. 10 days) to avoid changes in diet related to changing plant phenology.

2.4 | Statistical analyses

Distinct metabolic demands of male and female moose (and other ruminants) combine with seasonality to shape diet selection (Barboza & Bowyer, 2000). Therefore, we used multivariate analysis of variance to test for differences in diet among years, seasons and sexes. Additionally, DNA metabarcoding techniques recover both highly digested foods and rare operational taxonomic units (OTUs; i.e. taxonomic order, family, or genus; Taberlet et al., 2007), meaning diet compositions may contain large numbers of OTUs that contribute little (<0.01%) to overall composition. We therefore calculated cumulative read curves and omitted all plant OTUs that did not contribute to the top 95% of cumulative reads (Bergmann et al., 2015).

To estimate total niche width, and among and within-individual dietary diversity (hereafter, 'niche components'; sensu Roughgarden, 1972), we used package RInSp in Program R (R Core Team, 2018; Zaccarelli et al., 2013). We converted the number of plant OTU reads into proportions for each individual so that individuals (i.e. faecal samples) with greater total OTU reads would not have undue influence on estimates of total niche width, among-individual dietary diversity, or within-individual dietary diversity (Zaccarelli et al., 2013). We then used the Shannon–Weaver approximation of within-individual and among-individual variance in resource use, which sum to equal the total niche width of a population (Bolnick et al., 2002; Roughgarden, 1979). Lastly, we estimated individual specialization as the ratio between the amount of within-individual dietary diversity and total niche width (i.e. WID/TNW). The WID/TNW ratio provides a measure of the relative degree of specialization and results in values between zero and one. When WID/TNW values approach zero, within-individual dietary diversity is small and among-individual dietary diversity is high, indicating a high degree of specialization (Figure 1a). In contrast, when WID/TNW values approach one, populations are comprised of generalized individuals that use a more complete range of foods available to the population (Figure 1b; Bolnick et al., 2002; Roughgarden, 1979).

We conducted a sensitivity analysis to ensure that among-population differences in sample size did not influence inference regarding the relationship between food limitation and niche components (see assessing relationship between sample size and niche components in Appendix S1). We tested predictions of the NVH and OFT by regressing total niche width, among-individual dietary diversity, within-individual dietary diversity and individual specialization on food limitation (as indexed by calf recruitment). We tested for different intercepts and slopes between seasons when assessing the relationship between total niche width, among-individual dietary diversity and within-individual dietary diversity by including season as a fixed effect and assessing statistical support for an interaction between season and the aforementioned niche components.

We evaluated support for cognitive and physiological trade-offs by quantifying the relationship between individual diets, rumen microbiome, and genetic relatedness while accounting for spatial autocorrelation in diet composition by fitting spatially explicit structural equation models (SEMs; Lamb et al., 2014; Figure S3). We quantified pairwise relatedness following the methodology of Lynch and Ritland (1999) implemented in GeneAlEx 6.5 (Peakall & Smouse, 2012), and we used Jaccard dissimilarity to estimate pairwise differences in diet and microbiome composition. Spatially explicit SEMs apply non-spatial SEMs to subsets of data within distance bins, thereby incorporating spatial autocorrelation into the SEM and testing the null hypothesis that diets are more similar among close relatives simply because relatedness and foods are spatially autocorrelated. We developed a simple SEM to test the relationship between relatedness, diet selection and microbiome composition (Figure S3) and fit the SEM within lag distances corresponding to twice the diameter of a moose home range (7 km; i.e. the distance at which two individuals were unlikely to have overlapping home ranges; Baigas, 2008; Becker, 2008; Oates, 2016). If diet or microbiome were inherited via mother–offspring transmission, we expected pairwise dissimilarity to decline with increased relatedness (i.e. a negative path coefficient). If diet was constrained by microbiome composition, we expected diet dissimilarity to increase with microbiome dissimilarity (i.e. a positive path coefficient). In other words, individuals with more similar diets would have more similar microbiomes.

To visualize how diet selection changed as a function of food limitation, and to facilitate comparison between moose diet composition and classical tests of the NVH based on prey size (Bolnick et al., 2007; Roughgarden, 1974), we converted our categorical diet data into a continuous variable by ranking diet items by their importance in the study-level diet. We ranked the most important food as zero and all subsequent ranks as increasingly negative and positive integers. By ranking the diet data in this way, we were able to plot categorical diet data as a smoothed histogram (i.e. a density plot depicting relative frequency of use) and visualize our categorical data in the same manner that several authors have graphically dichotomized predictions of the NVH and OFT (e.g. Araújo et al., 2010, Bolnick et al., 2003, Bolnick et al., 2007, Newsome et al., 2009; see also Figure 1).

3 | RESULTS

3.1 | Sampling and genetic analyses

We obtained genotypes for 709 of 1,176 (60%) faecal samples across populations, seasons and years representing 218 individuals (Table 1). Consistently, the diet composition of moose shifted from season to season (PERMANOVA, p-values ranged from <0.01 to 0.05) and occasionally among years ($p < 0.01$–0.35) but was similar between males and females ($p = 0.07$–0.79; Table S4). We therefore subset the data from each population by season and year, but pooled data between sexes. The mean number of individuals identified per population-year-season was 11.75 ± 1.53 *SE*. Population-level niche components stabilized when population-level datasets included six or more diet samples (Figure S5). Thus, we excluded 2 of the 24 season by year datasets because they had fewer than six samples (see Table 1).

Microsatellite polymorphism was variable across loci (range = 3–6; Table S3). Genotyping error was low and consisted primarily of allelic dropout and false alleles (Table S3). Metabarcoding of the trnL amplicon identified 143 OTUs of plants (107 orders, 4 families, 32 genera). Analysis of cumulative read curves resulted in winter diets characterized by 37 OTUs and summer diets characterized by 24 OTUs (Figure S4). Metabarcoding of 16sRNA primers identified 4,411 OTUs of bacteria and archea (33 phyla and 66 classes). Analysis of cumulative read curves resulted in the microbiome being characterized by 500 OTUs in both winter and summer faecal samples.

3.2 | Food limitation and components of the dietary niche

During summer, increased food limitation resulted in a near doubling of total niche width between the most and least food limited populations (Figure 2a; $\beta = -0.03$, $p < 0.01$, $R^2 = 0.92$). For populations with greater food limitation (i.e. calf:cow decreased), individual specialization did not increase (Figure 2b; $\beta = -0.003$, $p = 0.15$), yet within-individual dietary diversity increased and explained nearly all variation in total niche width among populations (Figure 2d; $\beta = -0.024$, $p < 0.01$, $R^2 = 0.98$). Among-individual dietary diversity was not associated with food limitation (Figure 2c; $\beta = -0.004$, $p = 0.37$).

During winter, food limitation did not explain observed variation in total niche width (Figure 2e; $\beta = 0.00$, $p = 0.98$), individual specialization (Figure 2f; $\beta = 0.00$, $p = 0.79$), among-individual dietary diversity (Figure 2g; $\beta = 0.00$, $p = 0.88$), or within-individual dietary diversity (Figure 2h; $\beta = 0.00$, $p = 0.99$). Interestingly, average total niche width, among-individual dietary diversity and within-individual dietary diversity during winter was similar to that of the most food limited populations during summer (Figure 2). Neither the strength nor directionality of relationships between food limitation and total niche width, among-individual dietary diversity, within-individual dietary diversity and individual specialization were altered by sub-setting each population's dataset to six samples (Figure S6).

The intercept, but not the slope, of the relationship between total niche width and individual specialization differed between seasons (Figure 3a; $p < 0.01$ and $p = 0.48$ respectively). Neither intercept nor slope differed between seasons when assessing the relationship between total niche width, among-individual dietary diversity and within-individual dietary diversity (Figure 3b,c; $p = 0.17$–0.90). Contrary to the NVH, as the total niche width of a population increased, individuals became increasingly generalized in both summer and winter (Figure 3a; $\beta = 3.74$, $p = 0.03$, $R^2 = 0.43$). Although among-individual dietary diversity increased with increased total niche width (Figure 3b; $\beta = 2.33$, $p < 0.01$, $R^2 = 0.48$), within-individual dietary diversity again explained nearly all variation in total niche width among populations [Figure 3c; $\beta = 1.17$, $p < 0.01$, $R^2 = 0.93$; note that total R^2 for the two aforementioned models is >1.0 because among-individual dietary diversity and within-individual dietary diversity are correlated ($r = 0.44$)]. Together, our results indicate that the increased total niche width observed under increased food limitation

TABLE 1 Number of individual moose identified per herd, sex, season and year via faecal DNA

	Summer			Winter					
	2012			2012			2013		
Herd	**F**	**M**	**Total**	**F**	**M**	**Total**	**F**	**M**	**Total**
Bighorn	14	11	25	13	1	14	7	4	11
Jackson	2	4	6	11	7	18	4	5	9
North Park	9	6	15	8	5	13	3	5	8
Snowy range	9	10	19	5	2	7	3	2	5[a]
Sublette	10	4	14	4	2	6	3	3	6
Uinta[b]	14	15	29	6	6	12	1	0	1[a]

[a] Note that less than six individual diet samples were obtained for the Uinta and Snowy Range populations during winter of 2013. Those samples were therefore omitted from the dataset prior to statistical analysis.

[b] Also note that no recruitment data were available for Uinta in 2013, so those data were omitted from summer analysis.

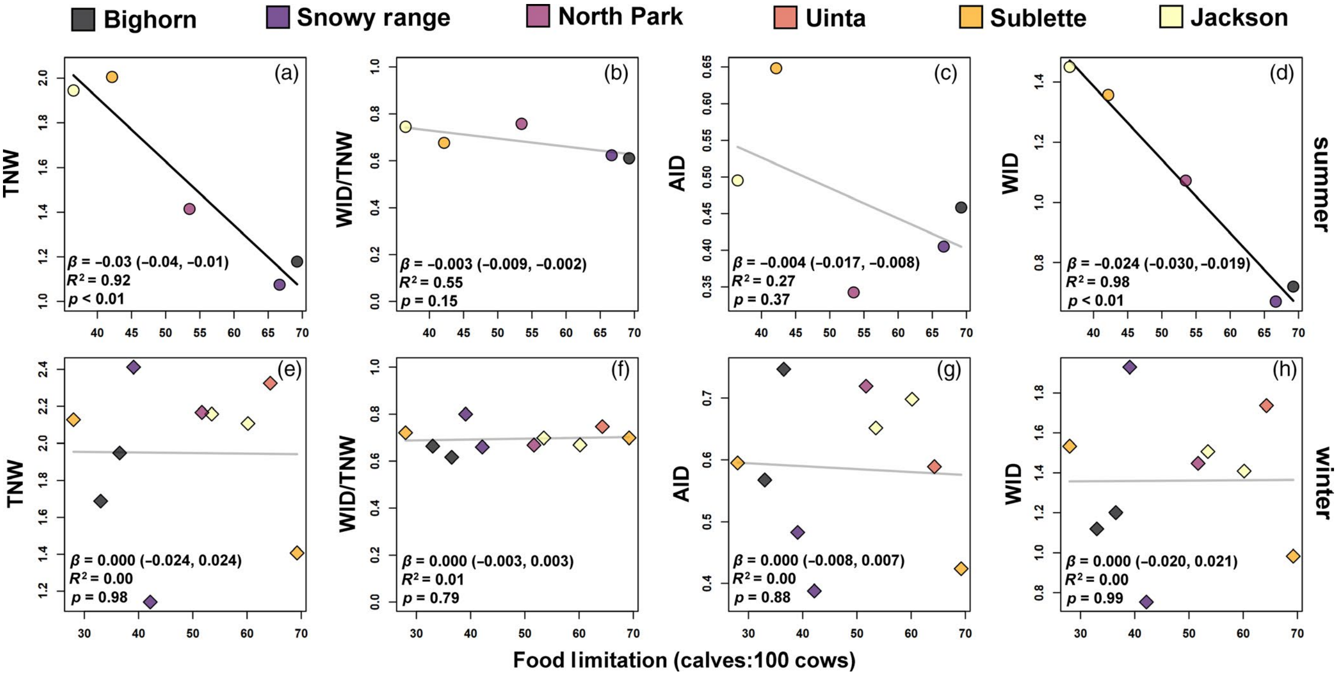

FIGURE 2 Relationship between resource limitation (number of calves per 100 cows; lower values represent stronger resource limitation) and (a, e) total niche width (TNW), (b, f) individual specialization (WID/TNW), (c, g) among-individual diversity (AID) and (d, g) within-individual diversity (WID). Summer data for each population are represented by circles, whereas winter data are represented by diamonds. Uinta was excluded from summer analysis because recruitment surveys were not completed. Black lines represent statistically significant relationships, whereas grey lines represent non-significant relationships. During winter of 2012 and 2013, average total niche was broad (e), which is consistent with strong resource limitation, but resource limitation did not explain patterns of individual specialization (f), among-individual diversity (g) or within-individual diversity (h). Winter 2013 data for both Uinta and Snowy Range were excluded from analysis because of <6 estimates of individual diets. During summer, and in accordance with both the NVH and Optimal Foraging Theory (OFT), total niche width increased as resource limitation increased (a). In contrast with the NVH, however, increased resource limitation did not result in increased individual specialization or among-individual diversity (b, c). Instead, and in accordance with OFT, increased total niche width under resource limitation stemmed primarily from increased within-individual diversity (d)

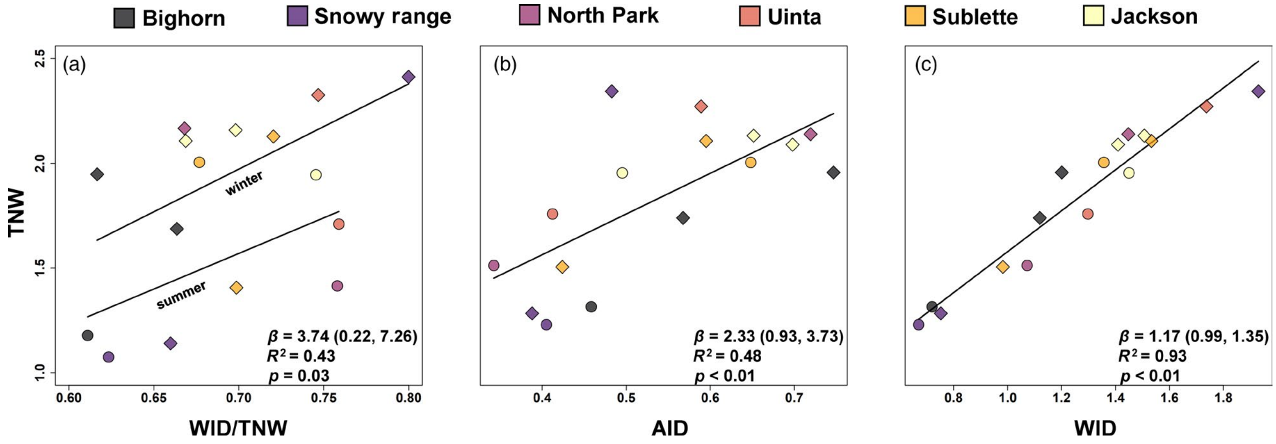

FIGURE 3 Relationship between total niche width (TNW) and (a) individual specialization (WID/TNW), (b) among-individual diversity (AID), and (c) within-individual diversity (WID). Summer data for each population are represented by circles, whereas winter data are represented by diamonds. In panel a, separate lines were fit for winter and summer because intercepts were statistically significant (see Section 3). The NVH predicts that TNW increases because individual specialization increases (i.e. WID/TNW decreases), whereas Optimal Foraging Theory (OFT) predicts that TNW increases because individuals broaden their diets (i.e. WID/TNW increases). In both summer and winter, TNW increased because of increased WID/TNW (panel a) primarily because of increased WID (panel c)

stemmed from individuals broadening their diets (i.e. increased within-individual dietary diversity; Figures 2 and 3), thereby supporting the predictions of OFT (Figure 1b).

During summer, populations with abundant food (as indexed by calf production) foraged largely on willows (*Salix* spp.; Figure 4) and exhibited narrower total niche widths and less within-individual

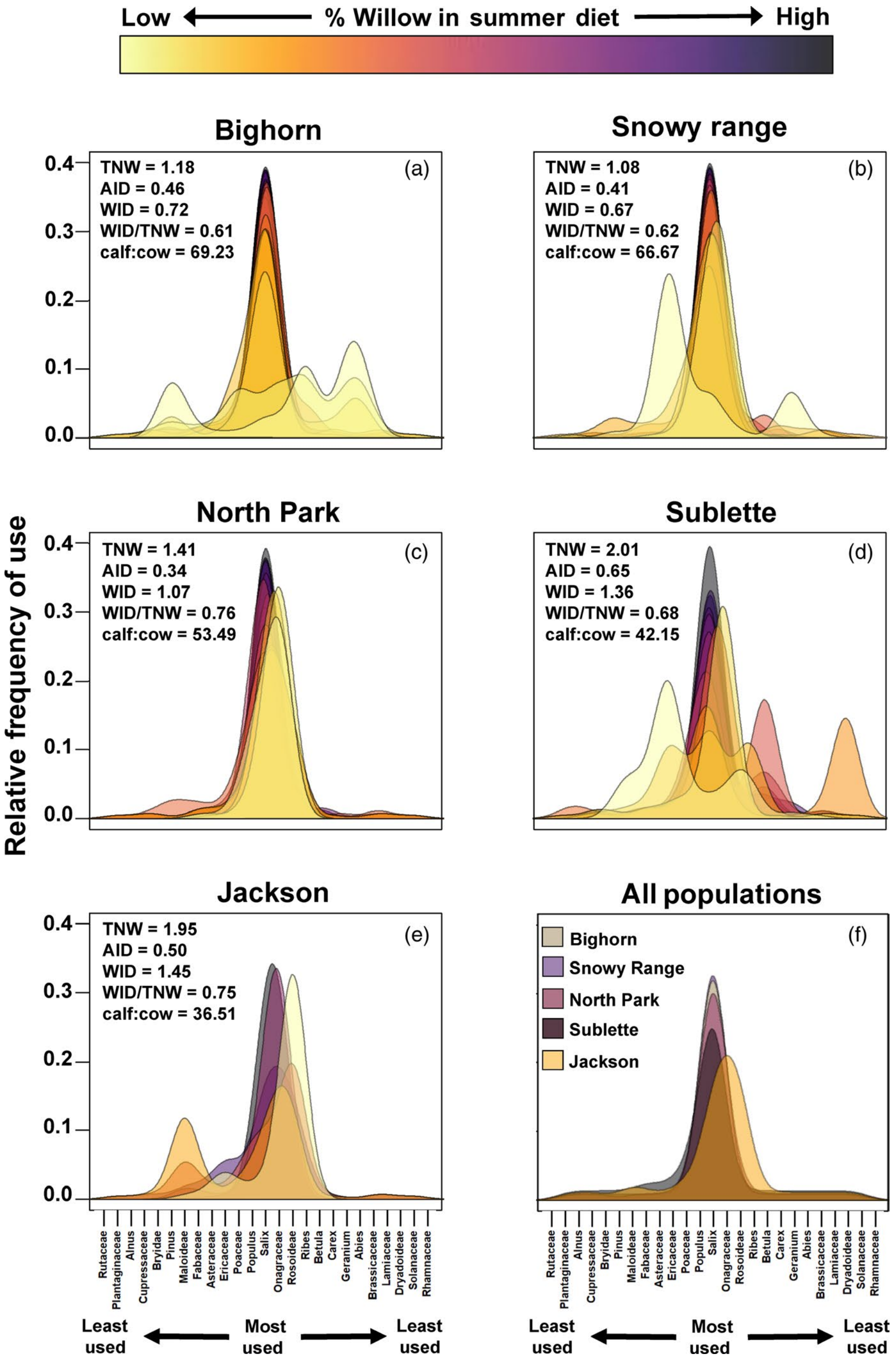

FIGURE 4 Density plots of the 25 most frequently used foods used during summer. Foods were ranked from most used (centre of *x* axis) to least used (left and right-hand sides of *x* axis). Density (*y* axis) reflects relative frequency of foods in diets. Panels are presented in increasing order of resource limitation (decreasing calf:cow). Individuals were plotted in order from those with the highest proportion of their diet consisting of willow to lowest. Individual density plots were set to 50% transparency, so more saturated colours indicate greater overlap among individuals and less saturated colours indicate rare foraging strategies within a population. (a–e) Diet composition of individuals within each of the five populations for which resource limitation data (calf:cow) were available in 2013. (f) Population-level diet composition. Expansion of total niche width (TNW) is driven by within-individual dietary diversity (WID) rather than from increased among-individual dietary diversity (AID; also see Figures 1 and 2). Note that individuals from resource-limited populations increasingly incorporate 'novel' foods into their diets

dietary diversity than individuals during winter. As food limitation intensified, individuals reduced willow consumption and broadened their diet to include greater amounts aspen and cottonwood (*Populus* spp.), willow herbs (Onagraceae; *Epilobium* spp.), grasses (family Poaceae) and species from the subfamily Rosoideae [e.g. cinquefoil (*Potentilla* spp.)]. Individuals within populations facing the most severe food limitation (i.e. the Sublette and Jackson populations) further broadened their diet by also increasing use of species from the family Maloideae [e.g. serviceberry (*Amelanchier* spp.)] and the diverse Ericaceae family (Figure 4).

During winter, willow continued to dominate diets, yet within-individual dietary diversity increased compared to summer (Figure 2d,h) and among-individual dietary diversity remained negligible (Figures 2g and 5). During this time of food limitation, individuals consumed less willow than during summer and relied more heavily on fir (*Abies* spp.), species from the subfamily Dryadoideae [e.g. mountain mahogany (*Cercocarpus* spp.), bitterbrush (*Purshia tridentate*)], pine (*Pinus* spp.), grasses, sedges (*Carex* spp.) and species within the family Rhamnaceae [e.g. ceanothus (*Ceanothus* spp.); Figure 5].

3.3 | Functional trade-offs

Both spatially explicit and non-spatially explicit SEMs indicated that among-individual variation in microbiome composition and

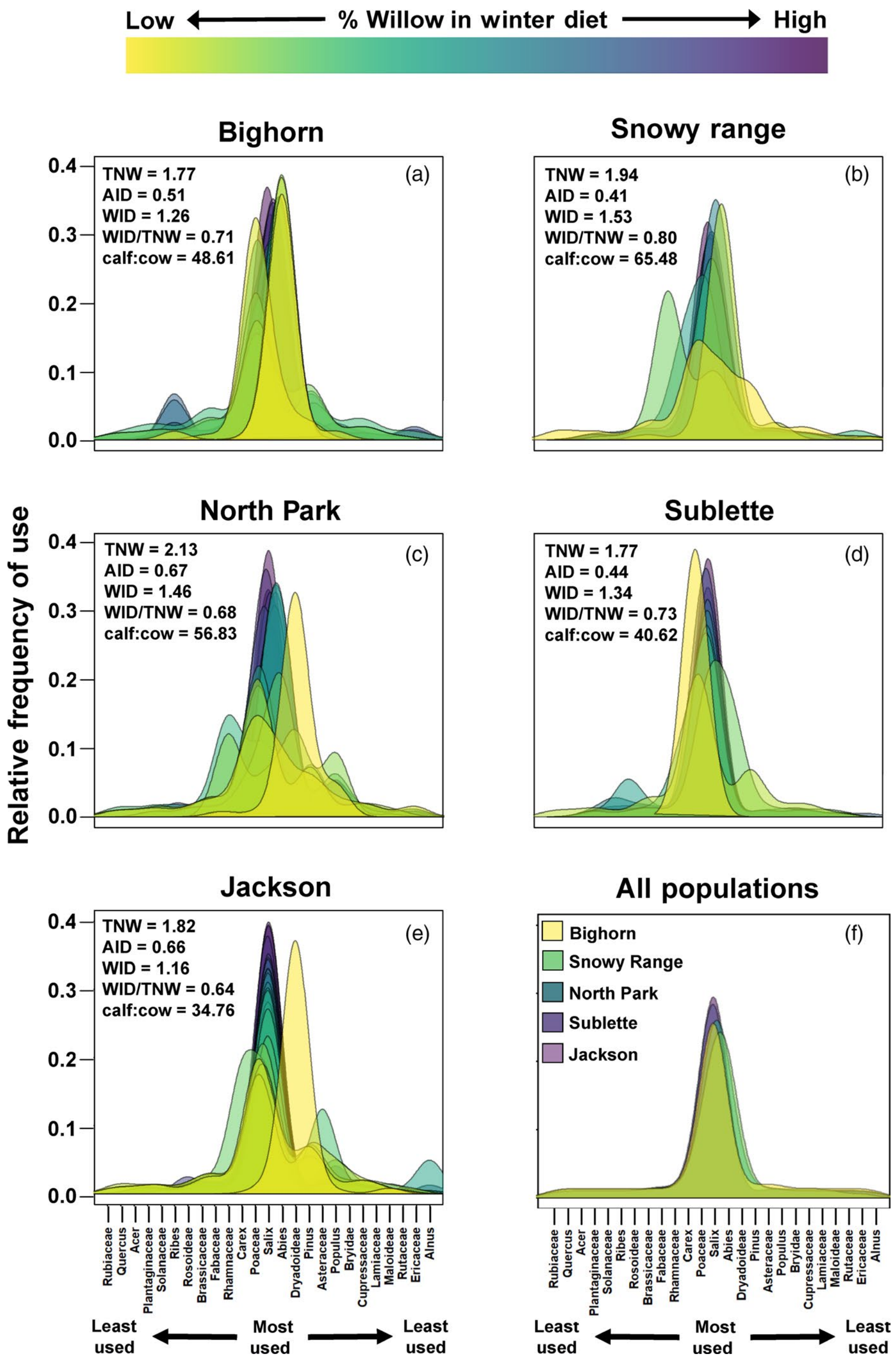

FIGURE 5 Density plots of the 25 most frequently used foods used during winter. (a–e) Foods were ranked from most used (centre of *x* axis) to least used (left- and right-hand sides of *x* axis). Density (*y* axis) reflects relative frequency of foods in diets. Individuals were plotted in order from those with the highest proportion of their diet consisting of willow to lowest. Individual density plots were set to 50% transparency, so more saturated colours indicate greater overlap among individuals and less saturated colours indicate rare foraging strategies within a population. (a–e) Diet composition of individuals within five populations across 2 years (2012–2013) for which resource limitation data (calf:cow) were available. (f) Population-level diet composition. Niche components and calf:cow ratios are reported as the 2-year mean. Note that average total niche width (TNW) and average within-individual dietary diversity (WID) across populations in winter is approximately 25% greater than in summer (see Figures 2 and 4)

relatedness explained <1% of among-individual variation in diet composition ($R^2 < 0.01$). The spatially explicit SEM indicated weak relationships between diet similarity, microbiome similarity and genetic relatedness (all $b < 0.04$). In accordance with the results of the spatially explicit SEM, the non-spatial SEM also indicated weak relationships between diet similarity, microbiome similarity and genetic relatedness (all $b < 0.012$).

During both winter and summer, diet and microbiome were significantly correlated at some lag distances, but effect sizes were small ($b < 0.04$) and the directionality of the relationship was not consistently positive or negative (Figure 6a,b). In winter, the effect of relatedness on diet dissimilarity was consistently small ($b < 0.02$) across all distance lags and directionality of the relationship was not consistent (Figure 6d). More closely related individuals in close proximity to each other tended to have more similar microbiomes in summer (i.e. a negative path coefficient), but the effect of relatedness on microbiome similarity was small ($b < 0.005$; Figure 6e). The effect of genetic relatedness on microbiome similarity was similarly small in winter ($b < 0.01$) and related individuals tended to have more distinct microbiomes across most lag distances (Figure 6f). Together, these results suggest that a lack of strong functional trade-offs (i.e. social transmission of foraging behaviour or microbiome) promotes within-individual dietary diversity and thus foraging in accordance with OFT (Figures 1–3).

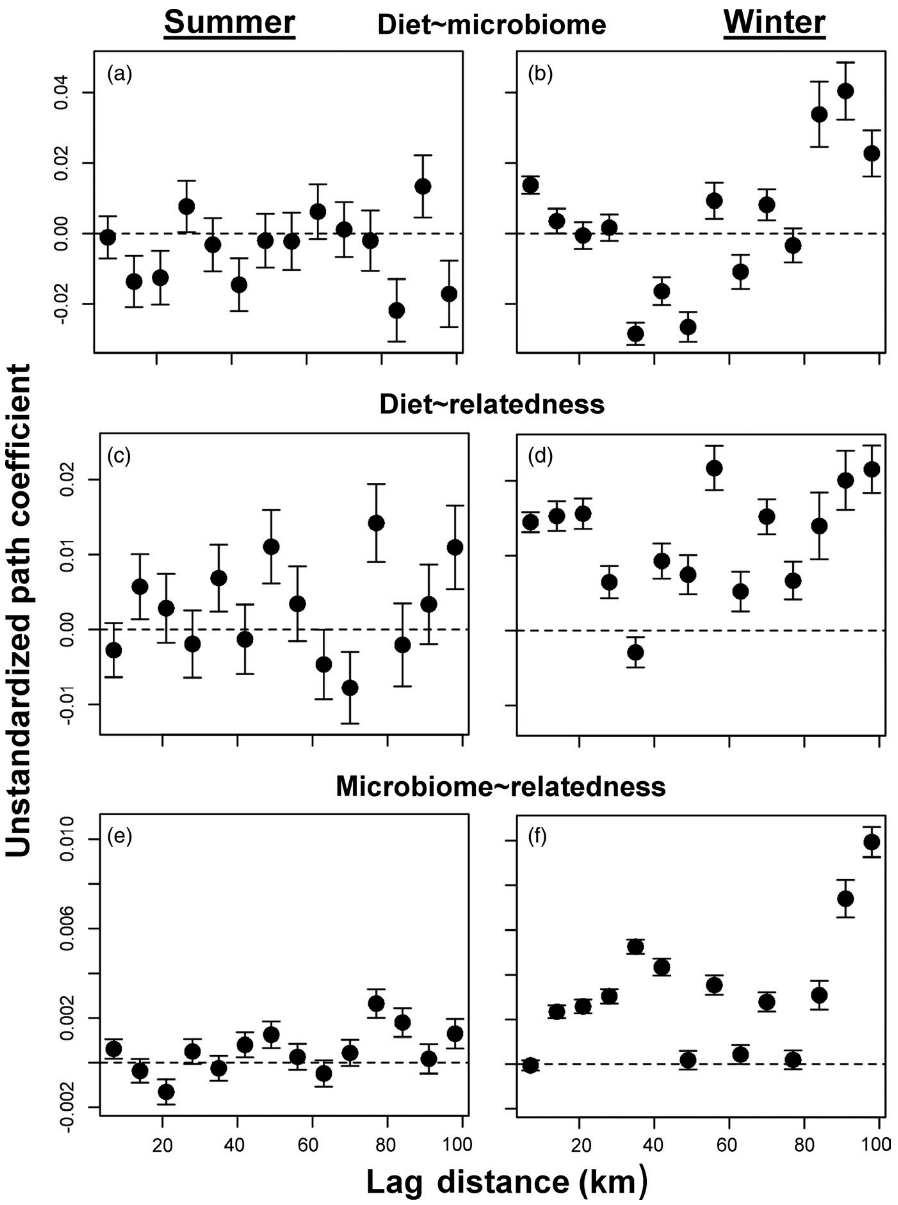

FIGURE 6 Path coefficients for the relationship between (a, b) diet dissimilarity and rumen microbiome dissimilarity, (c, d) diet dissimilarity and relatedness, and (e, f) microbiome dissimilarity and relatedness. Dissimilarity and relatedness measures are pairwise associations between individuals during summer (left panels) and winter (right panels). Error bars represent 95% confidence intervals for unstandardized path coefficients. Note small effect sizes (all path coefficients <0.04). Total variation in among-individual diet dissimilarity explained by microbiome and relatedness combined is <1% ($R^2 < 0.01$)

4 | DISCUSSION

Despite the shared prediction that total niche width should expand as food becomes limiting, the NVH (Van Valen, 1965) and OFT (Krebs et al., 1977; MacArthur & Pianka, 1966; Stephens & Krebs, 1986) offer contrasting views about how animals should alter diet selection when intraspecific competition for food intensifies (Figure 1). In accordance with both the NVH and OFT, the total niche width of moose in the Intermountain West, USA, increased as food became more limited (Figures 2 and 4). Increased total niche width arose primarily from increased within-individual dietary diversity rather than increased among-individual dietary diversity and individual specialization (Figures 2 and 3), thereby supporting the predictions of OFT (Figure 1b). Accordingly, we demonstrated that the total niche width expanded as a consequence of individuals adding 'novel' foods to their diet rather than forming groups of specialized individuals that foraged on narrow subsets of foods available to the population (Figure 4).

Optimal foraging for ruminants may be distilled into a single rule: maximize energy and nutrient intake while minimizing ingestion of plant chemical defences (Afik & Karasov, 1995; Belovsky, 1978; Freeland & Janzen, 1974). The co-evolution of plants and herbivores has resulted in nearly all plants possessing chemical defences (Bryant et al., 1983; Bryant & Kuropat, 1980; Karban & Agrawal, 2002). Although ruminants counteract these defences with proline-rich saliva and symbiotic gut microbes capable of breaking down plant toxins (Bryant et al., 1991; Hofmann, 1989), chemical defences nevertheless limit energy and nutrient assimilation (Barboza et al., 2010; McArt et al., 2009). As such, ruminants forage on a diverse array of plants to prevent over-ingestion of any single defence compound (Barboza et al., 2009; Parikh et al., 2017) and we observed such dietary diversity in our study (Figures 4 and 5). Reconstructing moose diets with DNA metabarcoding resulted in 24 families and genera of plants contributing to the top 95% of the diet in summer, and more than 37 families and genera in winter (Figure S4). Ruminant diet selection should be flexible to match phenological changes in the composition, quality and quantity of plants (Provenza et al., 2003). We observed such flexibility in our study, with total niche widths and within-indvidual dietary diversity increasing approximately 25% from summer to winter (Figures 2, 4 and 5). Moreover, average total niche width, among-individual dietary diversity and within-individual dietary diversity during winter was similar to that of the most food limited population during summer (Figure 2), indicating that a flexible diet capable of exploiting seasonal shifts in food availability likely is adaptive. Consequently, moose did not specialize on subsets of food and therefore did not adhere to predictions of the NVH. We hypothesize that specializing on subsets of plants is physiologically costly for ruminants (Parikh et al., 2017); doing so would require reformulation of the microbiome and detoxification mechanisms to ingest relatively small subsets of chemical defences in large quantities (for review, see Barboza et al., 2010; Forbey & Foley, 2009; Forbey et al., 2009). The digestive constraints of an herbivorous lifestyle may therefore represent one context under which foraging in accordance with OFT should be expected (Figure 1c).

Like the socially learned foraging behaviours underlying individual specialization in California sea otters (*Enhydra lutris nereis*; Estes et al., 2003; Tinker et al., 2008), juvenile moose spend the first year of their life in mother–offspring dyads (Bubenik, 2007) and may learn to select forage from their mothers (Edwards, 1976). While social learning early in life is important for the survival of juveniles (Thornton & Clutton-Brock, 2011), such learned behaviour may erode overtime in long-lived vertebrates as they experience variable environmental conditions (Teitelbaum et al., 2018). Furthermore, rigid adherence to socially learned diet selection may prove maladaptive in changing environments (Keith & Bull, 2017; Laland & Williams, 1998), such that behavioural plasticity or trial-and-error learning are better foraging strategies for long-lived species experiencing variation in environmental conditions throughout their lifetime (Galef & Whiskin, 2001; Provenza & Balph, 1987; Stephens et al., 2007). Accordingly, diet similarity in moose was weakly correlated with relatedness (Figure 6c), indicating that even if social transmission of diet selection occurred early in life, such learned behaviour dwindled as individuals foraged outside their natal ranges and as environmental conditions shifted over time. Because diet selection was either not inherited or adherence to inherited diet selection waned over time, individual specialization in moose did not occur (Figures 2 and 3). Instead, we hypothesize that flexible diets are promoted by the presence of plant chemical defences and a diverse rumen microbiome; and such flexibility facilitates increased within-individual dietary diversity under food limitation (Figures 2–4).

Although transmission of the microbiome has been demonstrated to constrain diet selection and promote individual specialization (e.g. Kohl et al., 2014), the plethora of digestive enzymes produced by the rumen microbiome may facilitate a flexible diet and minimize physiological constraints that lead to individual specialization. We found weak association between diet and microbiome composition in moose (Figure 6a; see also Bergmann et al., 2015), a finding supported by previous research indicating that the core microbiome of ruminants across the globe is comprised of orders Bacteroidales (phylum Bacteroidetes), Clostridiales (phylum Firmicutes) and Methanobacteriales (phylum Euryarchaeota) despite different diets within and among species (Henderson et al., 2015; Sundset et al., 2007). The lack of strong association between microbiome and diet was nevertheless surprising because, as with domestic goats, desert woodrats and two-toed sloths *Choloepus hoffmanni*, 'secondary' (non-core) microbial groups play an important role in promoting ingestion of novel foods and foods with abundant chemical defences (Dill-McFarland et al., 2016; Jones & Lowry, 1984; Kohl et al., 2014). As individual moose diversified their diets when food became limiting (Figures 2, 4 and 5), more diverse microbiomes were expected. In contrast to this expectation, our work demonstrates that changes in moose diet do not require large concomitant changes in the microbiome (Figure 6a,b), suggesting that the cellulolytic and detoxifying capacities of a diverse microbiome facilitate the dietary flexibility required to expand and contract diets with changing levels of food abundance.

An emergent notion in ecology and evolutionary biology is that individual specialization, and thus the NVH, stems from inter-individual differences in cognition, physiology or morphology that cause diet selection to vary among individuals (see examples within Araújo et al., 2011; Bolnick, 2004). Yet the reciprocal notion—that a lack of functional trade-offs should yield support for predictions of OFT—has received considerably less attention. We found support for the predictions of OFT in moose (Figures 1–3), suggesting that functional trade-offs are weak or absent. In accordance with this notion, moose foraging was not constrained by either of the two key functional trade-offs for ruminants: (a) social learning of diet selection (Figure 6c,d), or (b) social transmission of the gut microbiome (Figure 6e,f). The natural history and ecophysiology of ruminants has resulted in foraging strategies that promote continuous sampling of foods so that individuals can adjust to ever-changing plant quantity and quality (Provenza, 1995; Stephens et al., 2007). Therefore, specializing on a subset of plants may be challenging for ruminants (Figures 4 and 5), which may limit rigid constraints on diet selection. Instead, the broadening of individual diets (i.e. within-individual dietary diversity) as a mechanism to reduce intraspecific competition likely represents a more adaptive strategy than individual specialization in ruminants (Figures 2–4; Provenza & Balph, 1987; Provenza et al., 2003; but see Pansu et al., 2019). Our work therefore supports the hypothesis that the occurrence of cognitive, physiological or morphological constraints on diet selection should at least partly determine whether the predictions of the NVH or OFT are upheld.

Regardless of the mechanisms underlying expansion of total niche width, total niche width increased with increased food limitation (Figure 2a), a result with at least two basic and applied implications. First, expansion of total niche width is hypothesized to reduce intraspecific competition when food is limiting (Bolnick, 2004; Roughgarden, 1972; Svanbäck & Bolnick, 2007). Niche expansion should, however, increase the potential for interspecific competition because of diet overlap with heterospecifics (MacArthur & Levins, 1967; Pringle et al., 2019). For example, Kartzinel et al. (2015) and Pansu et al. (2019) used bipartite networks to quantify plant–herbivore interactions across a community of ruminants in East Africa.

Our results suggest that such plant–herbivore networks are dynamic, shifting over time as density dependence and variable abiotic conditions cause food limitation to ebb and flow. Thus, the notion that a species' or population's total niche width is plastic, rather than static, should be considered in future research. Second, and since the time of Aldo Leopold (1933), wildlife ecologists have sought tools for detecting food limitation to inform harvest and conservation programmes (e.g. see Ali et al., 2017; Boertje et al., 2009; Jesmer et al., in press). Because total niche width and within-individual dietary diversity were strongly correlated with calf recruitment, diet data can be used to quantify food limitation and thus proximity to nutritional carrying capacity. In summary, our work contributes to a growing literature indicating that food limitation alters intra- and interspecific interactions, which in turn has important implications for understanding the ecology of individuals, populations and communities.

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AUTHORS' CONTRIBUTIONS

B.R.J., M.J.K. and J.R.G. conceptualized and funded the study; B.R.J. carried out the field and laboratory work; M.A.M. provided guidance on, and laboratory space for, all genetic analysis; M.A.M. also provided guidance for the random forest spatial distribution modelling; B.R.J., M.J.K. and J.R.G. drafted the manuscript and all authors revised the manuscript.

DATA AVAILABILITY STATEMENT

Data used in this study are available on the Dryad Digital Repository: https://doi.org/10.5061/dryad.bcc2fqz9q (Jesmer, 2020).

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REFERENCES

Adams, J. R., Goldberg, C. S., Bosworth, W. R., Rachlow, J. L., & Waits, L. P. (2011). Rapid species identification of pygmy rabbits (*Brachylagus idahoensis*) from faecal pellet DNA. *Molecular Ecology Resources*, *11*, 808–812. https://doi.org/10.1111/j.1755-0998.2011.03020.x

Afik, D., & Karasov, W. H. (1995). The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology*, *76*, 2247–2257. https://doi.org/10.2307/1941699

Ali, A. H., Ford, A. T., Evans, J. S., Mallon, D. P., Hayes, M. M., King, J., Amin, R., & Goheen, J. R. (2017). Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope. *Journal of Applied Ecology*, *54*, 1720–1729. https://doi.org/10.1111/1365-2664.12856

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, *518*, 538–541. https://doi.org/10.1038/nature13998

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, *14*, 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Araújo, M. S., Bolnick, D. I., Martinelli, L. A., Giaretta, A. A., & Dos Reis, S. F. (2009). Individual-level diet variation in four species of Brazilian frogs. *Journal of Animal Ecology*, *78*, 848–856. https://doi.org/10.1111/j.1365-2656.2009.01546.x

Araújo, M. S., & Gonzaga, M. O. (2007). Individual specialization in the hunting wasp *Trypoxylon* (*Trypargilum*) *albonigrum* (Hymenoptera, Crabronidae). *Behavioral Ecology and Sociobiology*, *61*, 1855–1863. https://doi.org/10.1007/s00265-007-0425-z

Araújo, M. S., Martins, E. G., Cruz, L. D., Fernandes, F. R., Linhares, A. X., Dos Reis, S. F., & Guimarães, P. R. (2010). Nested diets: A novel pattern of individual-level resource use. *Oikos*, *119*, 81–88. https://doi.org/10.1111/j.1600-0706.2009.17624.x

Baigas, P. E. (2008). *Winter habitat selection, winter diet, and seasonal distribution mapping of Shiras moose (Alces alces shirasi) in southeastern Wyoming*. University of Wyoming.

Baigas, P. E., Olson, R. A., Nielson, R. M., Miller, S. N., & Lindzey, F. G. (2010). Modeling seasonal distribution and spatial range capacity of moose in southeastern Wyoming. *Alces*, *46*, 89–112.

Barboza, P. S., Bennett, A., Lignot, J. H., Mackie, R. I., McWhorter, T. J., Secor, S. M., Skovgaard, N., Sundset, M. A., & Wang, T. (2010). Digestive challenges for vertebrate animals: Microbial diversity, cardiorespiratory coupling, and dietary specialization. *Physiological and Biochemical Zoology*, *83*, 764–774. https://doi.org/10.1086/650472

Barboza, P. S., & Bowyer, R. T. (2000). Sexual segregation in dimorphic deer: A new gastrocentric hypothesis. *Journal of Mammalogy*, *81*, 473–489. https://doi.org/10.1644/1545-1542(2000)081<0473:SSIDDA>2.0.CO;2

Barboza, P. S., Parker, K. L., & Hume, I. D. (2009). *Integrative wildlife nutrition*. Springer-Verlag.

Bastille-Rousseau, G., & Wittemyer, G. (2019). Leveraging multidimensional heterogeneity in resource selection to define movement tactics of animals. *Ecology Letters*, *22*, 1417–1427. https://doi.org/10.1111/ele.13327

Becker, S. A. (2008). *Habitat selection, condition, and survival of Shiras moose in northwest Wyoming*. University of Wyoming.

Belovsky, G. E. (1978). Diet optimization in a generalist herbivore: The moose. *Theoretical Population Biology*, *14*, 105–134. https://doi.org/10.1016/0040-5809(78)90007-2

Berger, J., Testa, J. W., Roffe, T., & Monfort, S. L. (1999). Conservation endocrinology: A noninvasive tool to understand relationships between carnivore colonization and ecological carrying capacity. *Conservation Biology*, *13*, 980–989. https://doi.org/10.1046/j.1523-1739.1999.98521.x

Bergmann, G. T., Craine, J. M., Robeson II, M. S., & Fierer, N. (2015). Seasonal shifts in diet and gut microbiota of the American bison (*Bison bison*). *PLoS ONE*, *10*, e0142409. https://doi.org/10.1371/journal.pone.0142409

Boertje, R. D., Kellie, K. A., Seaton, C. T., Keech, M. A., Young, D. D., Dale, B. W., Adams, L. G., & Aderman, A. R. (2007). Ranking Alaska moose nutrition: Signals to begin liberal antlerless harvests. *Journal of Wildlife Management*, *71*, 1494–1506. https://doi.org/10.2193/2006-159

Bolnick, D. I. (2004). Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution*, *58*, 608–618. https://doi.org/10.1111/j.0014-3820.2004.tb01683.x

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, *26*, 183–192. https://doi.org/10.1016/j.tree.2011.01.009

Bolnick, D. I., Svanbäck, R., Araújo, M. S., & Persson, L. (2007). Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 10075–10079. https://doi.org/10.1073/pnas.0703743104

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Darrin Hulsey, C., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, *161*, 1–28. https://doi.org/10.1086/343878

Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M., & Svanbäck, R. (2002). Measuring individual-level resource specialization. *Ecology*, *83*, 2936–2941. https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2

Breiman, L. (2001). Random forests. *Machine Learning*, *45*, 5–32.

Brimeyer, D. G., & Thomas, T. P. (2004). History of moose management in Wyoming and recent trends in Jackson Hole. *Alces*, *40*, 133–143.

Bryant, J. P., Chapin III, F. S., & Klein, D. R. (1983). Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*, *40*, 357–368. https://doi.org/10.2307/3544308

Bryant, J. P., & Kuropat, P. J. (1980). Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. *Annual Review of Ecology and Systematics*, *11*, 261–285. https://doi.org/10.1146/annurev.es.11.110180.001401

Bryant, J. P., Provenza, F. D., Pastor, J., Reichardt, P. B., Clausen, T. P., & du Toit, J. T. (1991). Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics*, *22*, 431–446. https://doi.org/10.1146/annurev.es.22.110191.002243

Bubenik, A. B. (2007). Behavior. In A. W. Franzmann & C. C. Schwartz (Eds.), *Ecology and management of the North American moose* (pp. 173–222). University of Colorado Press.

Clauss, M., Schwarm, A., Ortmann, S., Streich, W. J., & Hummel, J. (2007). A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *148*, 249–265. https://doi.org/10.1016/j.cbpa.2007.05.024

Costa-Pereira, R., & Pruitt, J. (2019). Behaviour, morphology and microhabitat use: What drives individual niche variation? *Biology Letters*, *15*, 20190266.

Dahlgren, D. K., Elmore, R. D., Smith, D. A., Hurt, A., Arnett, E., & Connelly, J. (2012). Use of dogs in wildlife research and management. In N. J. Silvy (Ed.), *Wildlife techniques manual* (pp. 140–153).

Dill-McFarland, K. A., Weimer, P. J., Pauli, J. N., Peery, M. Z., & Suen, G. (2016). Diet specialization selects for an unusual and simplified gut microbiota in two- and three-toed sloths. *Environmental Microbiology*, *18*, 1391–1402. https://doi.org/10.1111/1462-2920.13022

Ducluzeau, R. (1983). Implatation and development of the gut flora in the newborn animal. *Annales de Recherches Veterinaires*, *14*, 354–359.

Eberhardt, L. L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology*, *83*, 2841–2854. https://doi.org/10.1890/0012-9658(2002)083[2841:APFPAO]2.0.CO;2

Edwards, J. (1976). Learning to eat by following the mother in moose calves. *The American Midland Naturalist*, *96*, 229–232. https://doi.org/10.2307/2424583

Estes, J. A., Riedman, M. L., Staedler, M. M., Tinker, M. T., & Lyon, B. E. (2003). Individual variation in prey selection by sea otters: Patterns, causes and implications. *Journal of Animal Ecology*, *72*, 144–155. https://doi.org/10.1046/j.1365-2656.2003.00690.x

Evans, J. S., Murphy, M. A., Holden, Z. A., & Cushman, S. A. (2011). Modeling species distribution and change using random forest. In C. Drew, Y. Wiersma, & F. Huettmann (Eds.), *Predictive species and habitat modeling in landscape ecology* (pp. 139–159). Springer. https://doi.org/10.1007/978-1-4419-7390-0_8

Forbey, J. S., & Foley, W. J. (2009). PharmEcology: A pharmacological approach to understanding plant–herbivore interactions: An introduction to the symposium. *Integrative and Comparative Biology*, *49*, 267–273. https://doi.org/10.1093/icb/icp020

Forbey, J. S., Harvey, A. L., Huffman, M. A., Provenza, F. D., Sullivan, R., & Tasdemir, D. (2009). Exploitation of secondary metabolites by animals: A response to homeostatic challenges. *Integrative and Comparative Biology*, *49*, 314–328. https://doi.org/10.1093/icb/icp046

Freeland, W. J., & Janzen, D. H. (1974). Strategies in herbivory by mammals: The role of plant secondary compounds. *The American Naturalist*, *108*, 269–289. https://doi.org/10.1086/282907

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, *13*, 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Galef, B. G., & Whiskin, E. E. (2001). Interaction of social and individual learning in food preferences of Norway rats. *Animal Behaviour*, *62*, 41–46. https://doi.org/10.1006/anbe.2000.1721

Goldberg, C. S., Turner, C. R., Deiner, K., Klymus, K. E., Thomsen, P. F., Murphy, M. A., Spear, S. F., McKee, A., Oyler-McCance, S. J., Cornman, R. S., Laramie, M. B., Mahon, A. R., Lance, R. F., Pilliod, D. S., Strickler, K. M., Waits, L. P., Fremier, A. K., Takahara, T., Herder, J. E., & Taberlet, P. (2016). Critical considerations for the application of environmental DNA methods to detect aquatic species. *Methods in Ecology and Evolution*, *7*, 1299–1307.

Henderson, G., Cox, F., Ganesh, S., Jonker, A., Young, W., Collaborators, G. R. C., & Janssen, P. H. (2015). Rumen microbial community composition varies with diet and host, but a core microbiome is found across a wide geographical range. *Scientific Reports*, *5*. https://doi.org/10.1038/srep14567

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia*, *78*, 443–457. https://doi.org/10.1007/BF00378733

Homer, C., Dewitz, J., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N., Wickham, J., & Megown, K. (2015). Completion of the 2011 National Land Cover Database for the conterminous United States – Representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing*, *81*, 345–354.

Jesmer, B. (2020). Data from: A test of the niche variation hypothesis in a ruminant herbivore, v3, Yale. *Dataset*, https://doi.org/10.5061/dryad.bcc2fqz9q

Jesmer, B. R., Kauffman, M., Kilpatrick, S., Monteith, K. L., Thomas, T., Yost, J., & Goheen, J. R. (in press). Life-history theory provides a framework for detecting resource limitation: A test of the Nutritional Buffer Hypothesis. *Ecological Applications*.

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., Hurley, M. A., McWhirter, D. E., Miyasaki, H. M., Monteith, K. L., & Kauffman, M. J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science*, *361*, 1023–1025. https://doi.org/10.1126/science.aat0985

Jones, R. J., & Lowry, J. B. (1984). Australian goats detoxify the goitrogen 3-hydroxy-4(1H) pyridone (DHP) after rumen infusion from an Indonesian goat. *Experientia*, *40*, 1435–1436. https://doi.org/10.1007/BF01951931

Karban, R., & Agrawal, A. A. (2002). Herbivore offense. *Annual Review of Ecology and Systematics*, *33*, 641–664. https://doi.org/10.1146/annurev.ecolsys.33.010802.150443

Kartzinel, T. R., Chen, P. A., Coverdale, T. C., Erickson, D. L., Kress, W. J., Kuzmina, M. L., Rubenstein, D. I., Wang, W., & Pringle, R. M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(26), 8019–8024.

Keith, S. A., & Bull, J. W. (2017). Animal culture impacts species' capacity to realise climate-driven range shifts. *Ecography*, *40*(2), 296–304.

Kincaid, T., Olsen, A., Stevens, D., Platt, C., White, D., & Remington, R. (2012). spsurvey: Spatial survey design and analysis. R package version 2.6. https://r.meteo.uni.wroc.pl/web/packages/spsurvey/spsurvey.pdf

Kohl, K. D., Weiss, R. B., Cox, J., Dale, C., & Dearing, M. D. (2014). Gut microbes of mammalian herbivores facilitate intake of plant toxins. *Ecology Letters*, *17*, 1238–1246. https://doi.org/10.1111/ele.12329

Kopps, A. M., Ackermann, C. Y., Sherwin, W. B., Allen, S. J., Bejder, L., & Krutzen, M. (2014). Cultural transmission of tool use combined with habitat specializations leads to fine-scale genetic structure in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1782), 20133245. https://doi.org/10.1098/rspb.2013.3245

Krebs, J. R., Erichsen, J. T., Webber, M. I., & Charnov, E. L. (1977). Optimal prey selection in the great tit (*Parus major*). *Animal Behaviour*, *25*, 30–38. https://doi.org/10.1016/0003-3472(77)90064-1

Laland, K. N., & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, *9*, 493–499. https://doi.org/10.1093/beheco/9.5.493

Lamb, E. G., Mengersen, K. L., Stewart, K. J., Attanayake, U., & Siciliano, S. D. (2014). Spatially explicit structural equation modeling. *Ecology*, *95*, 2434–2442. https://doi.org/10.1890/13-1997.1

Lampa, S., Henle, K., Klenke, R., Hoehn, M., & Gruber, B. (2013). How to overcome genotyping errors in non-invasive genetic mark-recapture population size estimation – A review of available methods illustrated by a case study. *The Journal of Wildlife Management*, *77*, 1490–1511. https://doi.org/10.1002/jwmg.604

Leadbeater, E., & Chittka, L. (2007). Social learning in insects – From miniature brains to consensus building. *Current Biology*, *17*, R703–R713. https://doi.org/10.1016/j.cub.2007.06.012

Leopold, A. (1933). *Game management*. C. Scribner's Sons.

Liaw, A., & Wiener, M. (2002). *Classification and regression by random forest*. R News.

Lynch, M., & Ritland, K. (1999). Estimation of pairwise relatedness with molecular markers. *Genetics*, *152*, 1753–1766.

MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, *101*, 377–385. https://doi.org/10.1086/282505

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*, 603–609. https://doi.org/10.1086/282454

Matthews, B., Marchinko, K. B., Bolnick, D. I., & Mazumder, A. (2010). Specialization of trophic position and habitat use by sticklebacks in an adaptive radiation. *Ecology*, *91*(4), 1025–1034. https://doi.org/10.1890/09-0235.1

McArt, S. H., Spalinger, D. E., Collins, W. B., Schoen, E. R., Stevenson, T., & Bucho, M. (2009). Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. *Ecology*, *90*, 1400–1411. https://doi.org/10.1890/08-1435.1

Meyer, K., Hummel, J., & Clauss, M. (2010). The relationship between forage cell wall content and voluntary food intake in mammalian herbivores. *Mammal Review*, *40*, 221–245. https://doi.org/10.1111/j.1365-2907.2010.00161.x

Miller, C. R., Joyce, P., & Waits, L. P. (2002). Assessing allelic dropout and genotype reliability using maximum likelihood. *Genetics*, *160*, 357–366.

Newsome, S. D., Tinker, M. T., Monson, D. H., Oftedal, O. T., Ralls, K., Staedler, M. M., Fogel, M. L., & Estes, J. A. (2009). Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology*, *90*, 961–974.

Noonan, M. J., Fleming, C. H., Tucker, M. A., Kays, R., Harrison, A.-L., Crofoot, M. C., Abrahms, B., Alberts, S. C., Ali, A. H., Altmann, J., Antunes, P. C., Attias, N., Belant, J. L., Beyer Jr., D. E., Bidner, L. R., Blaum, N., Boone, R. B., Caillaud, D., de Paula, R. C., … Calabrese, J. M. (2020). Effects of body size on estimation of mammalian area requirements. *Conservation Biology*, *34*(4), 1017–1028. https://doi.org/10.1111/cobi.13495

Oates, B. A. (2016). *Effects of predators and resource limitation on demography and behavior of moose in the Greater Yellowstone Ecosystem*. University of Wyoming.

Olsson, J., Quevedo, M., Colson, C., & Svanbäck, R. (2007). Gut length plasticity in perch: Into the bowels of resource polymorphisms. *Biological Journal of the Linnean Society*, *90*, 517–523. https://doi.org/10.1111/j.1095-8312.2007.00742.x

Pansu, J., Guyton, J. A., Potter, A. B., Atkins, J. L., Daskin, J. H., Wursten, B., Kartzinel, T. R., & Pringle, R. M. (2019). Trophic ecology of large herbivores in a reassembling African ecosystem. *Journal of Ecology*, *107*(3), 1355–1376.

Parikh, G. L., Forbey, J. S., Robb, B., Peterson, R. O., Vucetich, L. M., & Vucetich, J. A. (2017). The influence of plant defensive chemicals, diet composition, and winter severity on the nutritional condition of a free-ranging, generalist herbivore. *Oikos*, *126*, 196–203. https://doi.org/10.1111/oik.03359

Peakall, R., & Smouse, P. E. (2012). GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research – An update. *Bioinformatics*, *28*, 2537–2539.

Pringle, R. M., Kartzinel, T. R., Palmer, T. M., Thurman, T. J., Fox-Dobbs, K., Xu, C. C. Y., Hutchinson, M. C., Coverdale, T. C., Daskin, J. H., Evangelista, D. A., Gotanda, K. M., Man in 't Veld, N. A., Wegener, J. E., Kolbe, J. J., Schoener, T. W., Spiller, D. A., Losos, J. B., & Barrett, R. D. H. (2019). Predator-induced collapse of niche structure and species coexistence. *Nature*, *570*, 58–64. https://doi.org/10.1038/s41586-019-1264-6

Provenza, F. D. (1995). Tracking variable environments: There is more than one kind of memory. *Journal of Chemical Ecology*, *21*, 911–923. https://doi.org/10.1007/BF02033798

Provenza, F. D., & Balph, D. F. (1987). Diet learning by domestic ruminants: Theory, evidence and practical implications. *Applied Animal Behaviour Science*, *18*, 211–232. https://doi.org/10.1016/0168-1591(87)90218-8

Provenza, F. D., Villalba, J. J., Dziba, L. E., Atwood, S. B., & Banner, R. E. (2003). Linking herbivore experience, varied diets, and plant biochemical diversity. *Small Ruminant Research*, *49*, 257–274. https://doi.org/10.1016/S0921-4488(03)00143-3

Pyke, G. H. (1984). Optimal foraging theory: A critical review. *Annual Review of Ecology and Systematics*, *15*, 523–575. https://doi.org/10.1146/annurev.es.15.110184.002515

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reader, S. M., Morand-Ferron, J., & Flynn, E. (2016). Animal and human innovation: Novel problems and novel solutions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*. https://doi.org/10.1098/rstb.2015.0182

Roughgarden, J. (1972). Evolution of niche width. *The American Naturalist*, *106*, 683–718. https://doi.org/10.1086/282807

Roughgarden, J. (1974). Niche width: Biogeographic patterns among anolis lizard populations. *The American Naturalist*, *108*, 429–442. https://doi.org/10.1086/282924

Roughgarden, J. (1979). *Theory of population genetics and evolutionary ecology: An introduction*. Macmillan.

Slagsvold, T., & Wiebe, K. L. (2011). Social learning in birds and its role in shaping a foraging niche. *Philosophical Transactions of the Royal*

Society B: Biological Sciences, *366*, 969–977. https://doi.org/10.1098/rstb.2010.0343

Stephens, D. W., Brown, J. S., & Ydenberg, R. C. (2007). *Foraging: Behavior and ecology*. University of Chicago Press.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton University Press.

Stevens, D. L., & Olsen, A. R. (2004). Spatially balanced sampling of natural resources. *Journal of the American Statistical Association*, *99*, 262–278. https://doi.org/10.1198/016214504000000250

Sundset, M. A., Praesteng, K. E., Cann, I. K. O., Mathiesen, S. D., & Mackie, R. I. (2007). Novel rumen bacterial diversity in two geographically separated sub-species of reindeer. *Microbial Ecology*, *54*, 424–438. https://doi.org/10.1007/s00248-007-9254-x

Svanbäck, R., & Bolnick, D. I. (2005). Intraspecific competition affects the strength of individual specialization: An optimal diet theory method. *Evolutionary Ecology Research*, *7*, 993–1012.

Svanbäck, R., & Bolnick, D. I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 839–844. https://doi.org/10.1098/rspb.2006.0198

Sweanor, P. Y., & Sandegren, F. (1989). Winter-range philopatry of seasonally migratory moose. *Journal of Applied Ecology*, *26*, 25–33. https://doi.org/10.2307/2403648

Taberlet, P., Coissac, E., Pompanon, F., Gielly, L., Miquel, C., Valentini, A., Vermat, T., Corthier, G., Brochmann, C., & Willerslev, E. (2007). Power and limitations of the chloroplast trnL (UAA) intron for plant DNA barcoding. *Nucleic Acids Research*, *35*, e14. https://doi.org/10.1093/nar/gkl938

Taberlet, P., Griffin, S., Goossens, B., Questiau, S., Manceau, V., Escaravage, N., Waits, L. P., & Bouvet, J. (1996). Reliable genotyping of samples with very low DNA quantities using PCR. *Nucleic Acids Research*, *24*, 3189–3194. https://doi.org/10.1093/nar/24.16.3189

Teitelbaum, C. S., Converse, S. J., & Mueller, T. (2018). The importance of early life experience and animal cultures in reintroductions. *Conservation Letters*, *12*(1), e12599. https://doi.org/10.1111/conl.12599

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 978–987. https://doi.org/10.1098/rstb.2010.0312

Tinker, M. T., Bentall, G., & Estes, J. A. (2008). Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 560–565. https://doi.org/10.1073/pnas.0709263105

Van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, *99*, 377–390. https://doi.org/10.1086/282379

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, *340*, 483–485.

Waits, L. P., Luikart, G., & Taberlet, P. (2001). Estimating the probability of identity among genotypes in natural populations: Cautions and guidelines. *Molecular Ecology*, *10*, 249–256. https://doi.org/10.1046/j.1365-294X.2001.01185.x

Weigl, P. D., & Hanson, E. V. (1980). Observational learning and the feeding behavior of the red squirrel (*Tamiasciurus hudsonicus*): The ontogeny of optimization. *Ecology*, *61*, 213–218. https://doi.org/10.2307/1935176

Woodruff, S. P., Adams, J. R., Johnson, T. R., & Waits, L. P. (2014). Rapid species identification of Sonoran pronghorn from fecal pellet DNA. *Wildlife Society Bulletin*, *38*, 842–848. https://doi.org/10.1002/wsb.477

Zaccarelli, N., Bolnick, D. I., Mancinelli, G., & Giuggioli, L. (2013). RInSp: An R package for the analysis of individual specialization in resource use. *Methods in Ecology and Evolution*, *4*, 1018–1023.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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