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Short communication

Individual trophic niche specialization in American beaver (*Castor canadensis*)

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ABSTRACT

The American beaver (*Castor canadensis*) has been described as a choosy generalist at the species/population scale, yet observational studies have shown little variation in diet among individuals. We compared isotopic values of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ taken from hair of 32 beaver, representing seven colonies in northern Alabama, USA to determine 1) if colonies of beaver show overlap in isotopic niche width as a result of the similar use of food resources and 2) if individual trophic niche specialization occurs within colonies. Total Trophic Niche Width varied across the wetland with the widest being twice the narrowest. Each of the five niche ellipses overlapped with \geq two other wetlands studied. The percentages of observed variance attributed to Within Individual Component, Between Individual Component, and Between Location Component for $\delta^{13}\text{C}$ were 37%, 33%, 30%; and those for $\delta^{15}\text{N}$ were 16%, 56%, and 28%. Dietary nitrogen differentiated the trophic niches of individual beavers. Our results revealed that colonies across the landscape showed separation in trophic niche, lending support that the choosy generalist classification is correct at the colony scale. Our results also support individual trophic niche specialization within colonies, as seen by the substantial amount variation in both $\delta^{13}\text{C}$ (33%) and $\delta^{15}\text{N}$ (56%) between individuals.

1. Introduction

The trophic niche is the spectrum of food resources used by a species, representing the role of the species and interspecific interactions in a community (Araújo et al., 2011; Bolnick et al., 2003). Trophic niche width is often measured with the diversity of proportional compositions of animal diet or with the area or size of the ellipse encompassing the 95% distributions of multivariate dietary compositions ordinated in a 2-dimensional space. Niche width is determined by a variety of biotic and abiotic factors including, but not limited to, interspecific competition, intraspecific competition, and the distribution and availability of resources (Van Valen, 1965; MacArthur and Pianka, 1966; Devictor et al., 2008). Niche width and overlap are often quantified at the species or population levels to demonstrate the role of species or interspecific interactions in a biological community. Nevertheless, individual variations in ecological niche width and individual niche specialization have been ascribed to intraspecific competition (Van Valen, 1965), and have emerged as a frontier in ecological studies (Bolnick et al., 2003; Carlson et al., 2021; Sol et al., 2021). Quantifying the trophic niche width of

individuals can be challenging, considering food resources can vary spatially among individuals (Carlson et al., 2021). In this study, we used stable isotopic analysis to quantify individual trophic niche variation of the American beaver (*C. canadensis*, hereafter beaver), a generalist herbivore representing the generalist of the specialist-generalist continuum.

There are a variety of techniques to quantify selection of specific food resources, such as direct observation of feeding activity, fecal analysis, stomach analysis, and stable isotope analysis (Roberts, 1981; Gallant et al., 2004; Phillips et al., 2005; Robertson et al., 2015). Advances in stable isotope analyses allow for comparison of resource assimilation across temporal and spatial scales (Dalerum and Angerbjörn, 2005). Stable isotope analysis has been applied to studies of beaver trophic niche, where goals were to reconstruct the general contribution of terrestrial, emergent, and aquatic vegetation in their diet (Milligan and Humphries, 2010), or determine use of woody versus herbaceous food resources (Severud et al., 2013a). Beaver have traditionally been classified as a choosy generalist herbivore, consuming a variety of woody and non-woody vegetation (Jenkins, 1975; Busher, 1996; Severud et al.,

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2013b). However, this generalization has been limited to the species level. Our goal was to examine the validity of classifying beaver as a choosy generalist across previously unexamined ecological levels of organization. If the species classification of beaver as a choosy generalist in relation to its trophic niche is correct, then we hypothesized that different colonies (i.e., family units) of beaver will show overlap in isotopic niche width as a result of the similar use of food resources (hypothesis I). Second, if individual trophic niche specialization occurs within colonies, then we hypothesized that a substantial proportion (20% or more) of the variation in total niche width will be attributed to the differences between locations (hypothesis II).

2. Study area

Our study was conducted at Redstone Arsenal, a 15,429 ha military installation managed by the Department of Defense in Madison County, Alabama, USA (34°39'00" N 86°37'52" W). Topography was relatively flat but diverse, with elevation ranging from 165 to 365 m. Land use categories included agricultural fields, bottomland hardwood forests, upland conifer forests, mixed forests and various water bodies, including many seasonal swamps that became inundated during wet seasons. Surface areas of water bodies ranged from 6 to 64 ha. Average annual temperatures ranged from 5.2°C in January to 27 °C in July, with an overall annual average of 16.7 °C. Average annual precipitation was 138 cm (Huntsville-Decatur International Airport weather station).

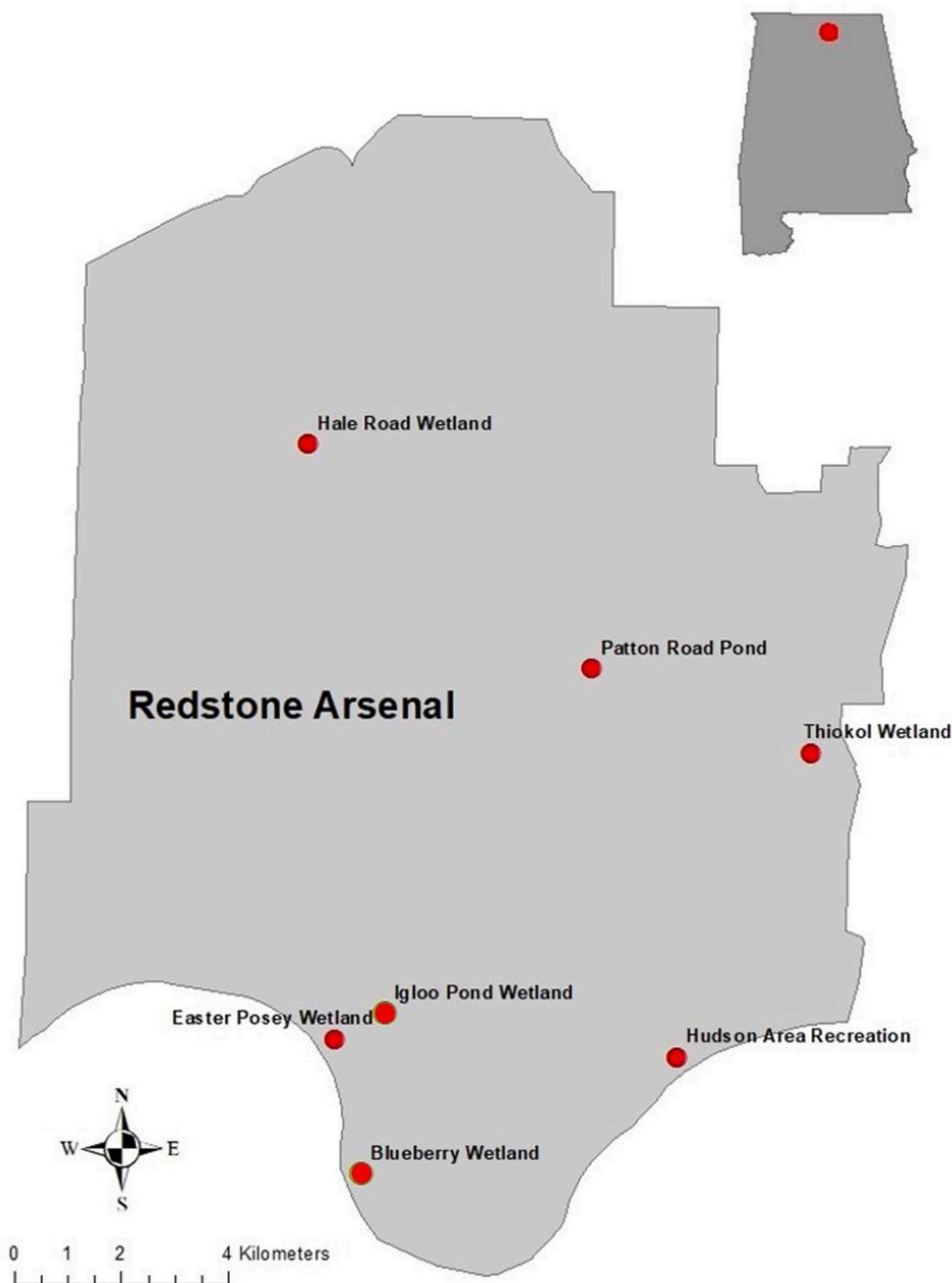


Fig. 1. Locations of hair samples collected opportunistically from seven American beaver (*Castor canadensis*) colonies across Redstone Army Arsenal (RSA), north Alabama, USA.

3. Methods

3.1. Hair sample collection and processing

Beaver were trapped between March 2016 and August 2016 by DOD personnel or their designated representative in accordance with Alabama state permit #8551 as part of a program to reduce wildlife damage. We opportunistically collected hair samples from deceased beaver that were trapped from seven different beaver colonies across Redstone Arsenal (Fig. 1). Hair was sampled prior to beaver beginning their prolonged annual molt (Ling, 1970), likely representing food assimilated over several months. Hair types collected were guard hair, undercoat hair, and foot hair. We obtained a total of 56 hair samples from 32 individuals. We stored samples at -20°C , no later than 4 h after collection. We washed hair thoroughly in 98% pure ethanol to remove surface contaminants and oils. We considered samples clean after inspection under a dissecting microscope revealed no apparent debris particles. We then filtered samples through inert gas filters to remove excess ethanol and clipped hair samples 8–10 mm from the follicle (Milligan and Humphries, 2010).

3.2. Stable isotopic analysis

We ground samples, packaged them in 2.0 mg tin capsules, and shipped them to University of Windsor (Windsor Ontario, Canada) for analysis. Analysis was performed in a Delta V Advantage Mass Spectrometer (Thermo Scientific, Waltham, Massachusetts, USA), coupled to a Costech 4010 Elemental Combustion system (Costech Analytical Inc., Valencia, California, USA) and a ConFlo IV gas interface (Thermo Scientific, Waltham, Massachusetts, USA). Precision was assessed by the standard deviation of replicate analyses of four standards (NIST1577c, internal lab standard (tilapia muscle), USGS 40 and Urea ($n = 7$ for all), and was measured $\leq 0.2\text{‰}$ for $\delta^{15}\text{N}$ and $\leq 0.09\text{‰}$ for $\delta^{13}\text{C}$ for all the standards. The accuracy, based on the certified values of USGS 40 ($n = 7$) analyzed throughout the analysis, showed a difference of 0.14‰ for $\delta^{15}\text{N}$ and -0.02‰ for $\delta^{13}\text{C}$ from the certified value. Instrumentation accuracy was checked throughout the analysis based on NIST standards 8573, 8547 and 8574 for δN^{15} and 8542, 8573, 8574 for $\delta^{13}\text{C}$ ($n = 10$ for all). The mean differences from the certified values were -0.16 , -0.03 , -0.04‰ for δN^{15} and -0.03 , -0.05 and -0.09‰ for $\delta^{13}\text{C}$, respectively.

3.3. Statistical analyses

To account for potential bias isotopic values collected from guard hair, undercoat hair, and foot hair (DeNiro and Epstein, 1978; Deniro and Epstein, 1981), we conducted an ANOVA in R to assess if hair types differed in $\delta^{13}\text{C}$ or δN^{15} (R Core Team, 2016). We used the *shapiro.test* function in R to test for multivariate normality in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Jarek, 2012). We used the package *SIBER* in R, which applies Bayesian-centered analysis to infer the niche separation and niche width of user defined groups (Jackson et al., 2011). We defined groups by wetland trapping locations and used one hair sample per individual to avoid over representing niche overlap (Jackson et al., 2011).

We applied a linear mixed-effect model to all hair samples ($n = 56$) with animal individual identification (ID) and wetland ID as random effects for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Individual IDs were nested within wetlands. We built four models of different combinations of random effects, with $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values as the dependent variable using the package *glmmTMB* in R (Table 1) (Brooks et al., 2017). Model selection was performed using Akaike's Information Criterion corrected for small sample size (AICc), with the most parsimonious model having the lowest AICc and highest Akaike weight (Bozdogan, 1987).

3.4. Analysis of individual trophic niche specialization

Total Niche Width (TNW) is a measure of the number of resources

Table 1

Candidate linear mixed models to explain the variation of $\delta^{13}\text{C}$ (Model A) and $\delta^{15}\text{N}$ (Model B) in the diet of American beaver (*Castor canadensis*) using Akaike Information Criteria corrected for small sample size (AICc). Most parsimonious models for $\delta^{13}\text{C}$ (Model A) and $\delta^{15}\text{N}$ (Model B) have the lowest AICc and are identified with an asterisk (*).

	K	AICc	Akaike weight
Model A ($\delta^{13}\text{C}$)			
C ~ 1 + (1 location) + (1 location:beaver)	4	150.67*	0.67
C ~ 1 + (1 beaver)	3	152.75	0.24
C ~ 1 + (1 location)	3	154.628	0.09
Model B ($\delta^{15}\text{N}$)			
N ~ 1 + (1 location) + (1 location:beaver)	4	132.18*	0.68
N ~ 1 + (1 beaver) + location	3	133.72	0.32

consumed by a population or species, which satisfy a specific biological need (Bolnick et al., 2002). The Within Individual Component (WIC) of TNW represents the total number of different resources utilized by a typical individual, while TNW can apply to other organizational scales (Bolnick et al., 2002). Contrastingly, the Between Individual Component (BIC) represents the difference in resource utilization between individuals within a population (Bolnick et al., 2003). Between Location Component (BLC) explains the variation of the niche between geographic locations and is required if geographically separate individuals are being compared. Examinations of individual niche specialization require comparing the proportion of variation of TNW explained by WIC and BIC, respectively (Bolnick et al., 2003).

The variances of WIC, BIC, and BLC were calculated as the variances for residual, individual ID, and wetland ID from the mixed models. Total Niche Width (TNW) is the sum of the WIC, and BIC, and BLC variances. We used formulas similar to Bolnick et al. (2002) to calculate the proportions of the WIC, BIC, and BLC variances within TNW. The amount of variation considered substantial to confirm the pattern of individual trophic niche specialization is $>10\text{--}20\%$. These proportions are not strict and are further strengthened when phenotypic or behavioral differences between individuals are observed (Bolnick et al., 2003; Araujo et al., 2011).

4. Results

Data were normally distributed ($W = 0.95$, $p = 0.24$) and isotopic value of $\delta^{13}\text{C}$ ($F_{2, 53} = 2.66$, $p = 0.08$) nor $\delta^{15}\text{N}$ ($F_{2, 53} = 2.8$, $p = 0.07$) differed among guard, foot, and undercoat hair samples. The *SIBER* output showed niche separation between wetlands (Fig. 2). Both BB and IPW had too few samples to run as an individual wetland in *SIBER* and were thus combined with the nearest wetland (EPW) approximately 2.5 and 1.4 km away, respectively. These data were analyzed with and without the inclusion of BB and IPW, and the results were consistent. The 95% ellipse areas for wetlands were: EPW = 0.87, HRW = 0.70, HUD = 1.70, PRP = 1.39, and TW = 0.84 and represented the TNW for each wetland. Each ellipse overlapped with \geq two other wetlands (Fig. 2). The greatest amount of niche overlap was between EPW and PRP at 34% percent of the ellipse.

The mixed model with the lowest AICc included wetland ID as a random effect, and individual ID nested within wetlands ID as a random effect for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 1). Residuals of the mixed models were normally distributed for both $\delta^{13}\text{C}$ (Shapiro test: $p = 0.09$) and $\delta^{15}\text{N}$ (Shapiro test: $p = 0.17$). The quantile-quantile (QQ) plots also suggested normality for the residuals of the two best models. WIC, BIC, and BLC estimated variance of $\delta^{13}\text{C}$ were 0.39, 0.35, and 0.31; WIC, BIC, and BLC estimated variance of $\delta^{15}\text{N}$ were 0.16, 0.56, and 0.28. The proportion of estimated variance attributed to WIC, BIC, and BLC for $\delta^{13}\text{C}$ were 0.37, 0.33, 0.30; and those for $\delta^{15}\text{N}$ were 0.16, 0.56, and 0.28 (Fig. 3 A and B).

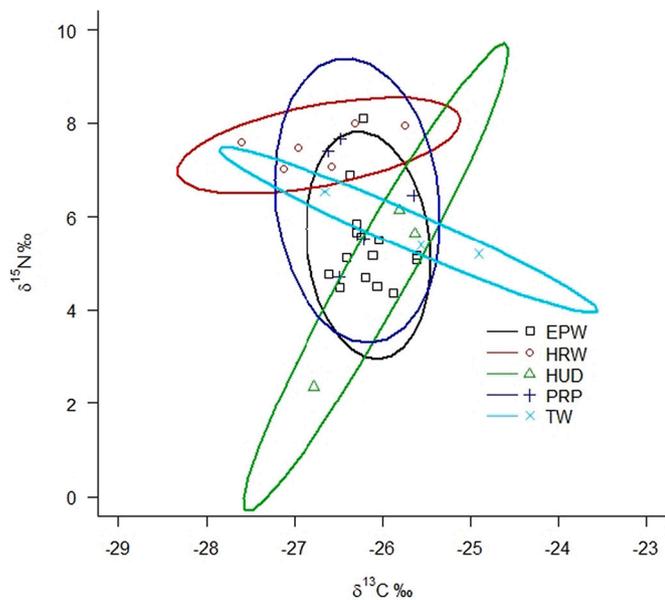


Fig. 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ bi-plot of the trophic niche of American beaver (*Castor canadensis*) as measured by stable isotope analysis in Redstone Arsenal, Alabama, USA. Colored lines are 95% ellipses for each wetland: Easter Posey Wetland (EPW), Hale Road Wetland (HRW), Hudson Area Recreation (HUD), Patton Road Pond (PRP), and Thiokol Wetland (TW).

5. Discussion

Our results revealed colonies across the landscape showed separation in trophic niche, lending mild support for the choosy generalist classification at the colony scale (hypothesis I). Low overlaps among the 95% ellipse of trophic niches of five wetlands offers evidence that beaver may utilize different food resources over small geographic distances. Our results also support hypothesis II; that is, individual trophic niche specialization does occur, as seen by the substantial amount estimated variation in both $\delta^{13}\text{C}$ (0.33) and $\delta^{15}\text{N}$ (0.56) of BIC among individuals within colonies of beaver. Ultimately, our findings support the definition of beaver as a choosy generalist at the species/population scale (Jenkins, 1975; Gerwing et al., 2013).

On Redstone Arsenal, beaver have seasonally reduced their home range sizes following patterns of increased Normalized Difference Vegetation Index, which represented the amount of vegetation growth vigor in an area (McClintic et al., 2014a). Such patterns offer indirect

evidence that beaver may shift its trophic niche in relation to the availability, or accessibility, of herbaceous or woody vegetation. $\delta^{15}\text{N}$ has been shown to be more variable in woody species while $\delta^{13}\text{C}$ is variable in herbaceous aquatic and emergent vegetation (Milligan et al., 2010). The high BIC of $\delta^{15}\text{N}$ showed that individuals utilized isotopically different woody food resources. Currently, our data set is unable to attribute the amount of forage to woody, emergent, or aquatic vegetation, although our direct observations indicated that beaver do not feed exclusively on woody vegetation during winter months on Redstone Arsenal (unpublished data).

Foraging decisions by beaver are shaped by energy constraints and predation risk (Salandre et al., 2017) and may be associated with their central place foraging strategy (Jenkins, 1980; Busher, 1996; Gerwing et al., 2013; McClintic et al., 2014b). On Redstone Arsenal, beaver moved faster with increasing distance from lodges in wetlands and hourly distances moved from lodges were distributed bimodally during the breeding season (McClintic et al., 2014b). It is possible the implications of optimal foraging theory, to optimize nutrition while avoiding risk, influences trophic niche specialization.

Foraging decisions by beaver also are affected by plant chemistry within and between sites (Jenkins, 1975). Therefore, post-ingestive feedback from secondary plant metabolites may also influence central place foraging. Beaver have been shown to have strict preference for woody vegetation in cafeteria feeding style experiments as well as preference for few plant species in natural settings (Henry and Bookhout, 1970; Fryxell, 1992; Gallant et al., 2004), leading to potential misclassification of preference. For example, Svendsen (1980) and Busher (1996) observed beaver consuming large proportions of red maple (*Acer rubrum*), while Muller-Schwarze et al. (1994) found that red maple was a least preferred species. Beaver also have been shown to manipulate the palatability of tree species by soaking bark in water (Muller-Schwarze et al., 2001). Generalizing preference to plant genera (e.g., willow [*Salix* sp.], alder [*Alnus* sp.], or maple) also can lead to spurious management decisions. Gerwing et al. (2013) found that beaver selected three species of willow (*Salix scouleriana*, *Salix drummondiana*, and *S. sitchensis*) while avoiding *S. bebbiana*, suggesting that beaver were able to differentiate among closely related species.

Limited resources result in increased intraspecific competition between individuals within a single colony. Intraspecific trophic competition has been shown to be a common mechanism prompting individual niche specialization in other taxa (Roughgarden, 1974; Bolnick et al., 2003; Araújo et al., 2011), including other semi-aquatic mammals such as California sea otter (*Enhydra lutris nereis*) (Tinker et al., 2008). Reduced resource availability due to territoriality and resource fragmentation also increases intraspecific competition, subsequently

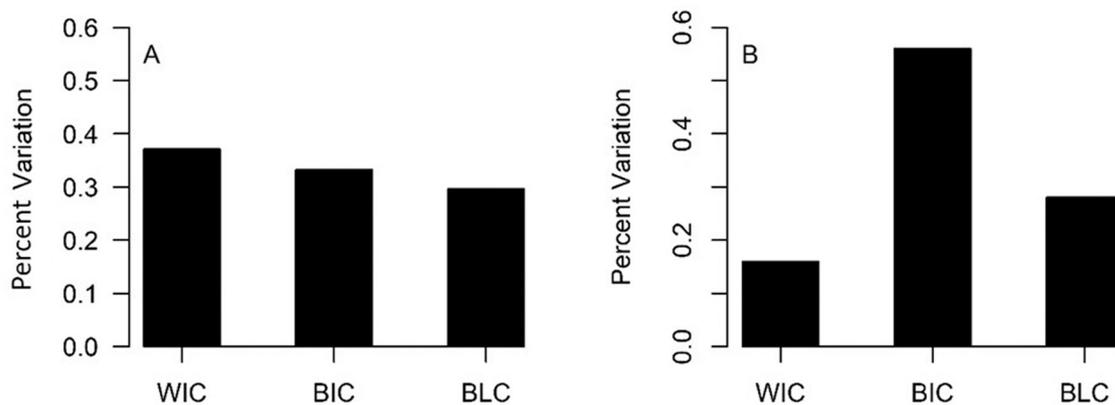


Fig. 3. Comparisons of the proportion of variation of the Total Niche Width (TNW) explained by the Within Individual Component (WIC), Between Individual Component (BIC), and Between Location Component (BLC) for (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ calculated using the most parsimonious linear mixed model. Variation greater than 20% in the BIC supports the occurrence of individual trophic niche specialization with colonies of American beaver (*Castor canadensis*) during winter and early spring on Redstone Arsenal, Alabama, USA.

promoting individual niche specialization. Territoriality has been positively correlated with individual trophic niche specialization within another social mammal, the European badger (*Meles meles*) (Robertson et al., 2015).

With our isotopic data, we are unable to strictly say which mechanisms are driving individual trophic niche specialization, nor can we differentiate between species that beaver foraged upon. Nevertheless, we found variation within, between, and among colonies in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Overall, these data suggest individuals within a colony exploit different food resources, possibly during times of limited resource availability or accessibility (i.e., late winter and early spring) or based on choices related to palatability or nutritional quality. Our results for beaver are similar to other taxa that exhibit individual niche specialization (Werner et al., 1981; Robertson et al., 2014). These findings are novel for beaver because observational studies showed little to no difference in food selection based on age or sex (Svendsen, 1980; Roberts, 1981).

Declaration of Competing Interest

None.

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