

# Niche partitioning among mule deer, elk, and cattle: Do stable isotopes reflect dietary niche?<sup>1</sup>

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**Abstract:** We examined dietary niches of mule deer (*Odocoileus hemionus*), North American elk (*Cervus elaphus*), and free-ranging cattle (*Bos taurus*) that frequently co-occur in western North America. We tested the hypothesis that those three species would exhibit little overlap in diet and that mule deer, the smallest in body size of the three species, would forage more selectively than either elk or cattle. We determined diet composition from microhistological analysis and used principal components analysis to assess dietary niches. In addition to those conventional methods, we also assessed whether dietary overlap among those three ruminants would be reflected in stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) from fecal pellets. Principal component 1 represented a foraging axis based on plant classes, whereas principal component 2 represented a continuum from grazing to browsing, which revealed complete separation among those three large herbivores. Similarly,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  differed significantly among species and indicated differences in moisture regimes within habitats and types of forages used by those three ruminants. Mule deer had the greatest variability in diet and foraged on more xeric forages than did either elk or cattle. Stable isotopes elucidated differences in dietary niche among the three ruminants that were not evident from dietary analysis alone.

**Keywords:** *Bos taurus*, cattle, *Cervus elaphus*, diet,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , microhistological analysis, mule deer, niche, North American elk, *Odocoileus hemionus*, stable isotopes.

**Résumé :** Nous avons examiné les niches alimentaires du cerf mulet (*Odocoileus hemionus*), du wapiti (*Cervus elaphus*) et du boeuf (*Bos taurus*) qui se déplace librement dans ses pâturages. Ces trois espèces cohabitent souvent dans l'ouest de l'Amérique du Nord. Nous avons vérifié l'hypothèse selon laquelle il n'existe qu'un faible chevauchement dans la diète de ces trois espèces et que le cerf mulet, qui est le plus petit des trois animaux, est plus sélectif dans son alimentation que le wapiti et le boeuf. Nous avons déterminé la composition de la diète à partir d'analyses microhistologiques et utilisé l'analyse en composantes principales pour circonscrire les niches alimentaires. Pour compléter ces méthodes classiques, nous avons également vérifié à quel point le chevauchement de la diète de ces trois ruminants peut être illustré par les rapports des isotopes stables ( $\delta^{13}\text{C}$  et  $\delta^{15}\text{N}$ ) trouvés dans les fèces de ces animaux. À l'aide de la composante principale 1, qui représente un axe de la diète alimentaire basé sur les classes des plantes, et de la composante principale 2, qui représente pour sa part un continuum entre la paissance et le broutement, il est possible de séparer de façon nette les trois herbivores. De même, les isotopes  $\delta^{13}\text{C}$  et  $\delta^{15}\text{N}$  diffèrent de façon significative entre les espèces. Ils permettent également d'identifier des différences dans l'humidité des régimes à l'intérieur des habitats ainsi que les types de fourrage utilisés. C'est le cerf mulet qui possède la diète la plus variable. Il se nourrit de fourrages plus secs que le wapiti et le boeuf. Les isotopes stables ont permis de déterminer des différences entre les niches alimentaires des trois ruminants difficiles à trouver à l'aide seulement de l'analyse de la diète.

**Mots-clés :** Analyse microhistologique, bétail, *Bos taurus*, cerf mulet, *Cervus elaphus*, diète, isotopes stables, niche, *Odocoileus hemionus*, wapiti,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ .

**Nomenclature:** Grubb, 1993.

## Introduction

Resource partitioning among species traditionally has been evaluated along three niche axes: spatial separation (including use of different habitats), temporal avoidance, and dietary differences (Keddy, 1989; Ben-David, Bowyer & Faro, 1996; Kronfeld-Schor *et al.*, 2001; Stewart *et al.*, 2002). Exploring niche separation among large herbivores along all three axes is often a formidable task, because those mammals occupy relatively large home ranges and exhibit broad dietary niches. Stewart *et al.* (2002) strongly inferred competition among mule deer

(*Odocoileus hemionus*), North American elk (*Cervus elaphus*), and introduced cattle (*Bos taurus*) along two axes, spatial separation and temporal avoidance, using modern regression methods (Fox & Luo, 1996; Luo, Monamy & Fox, 1998). Stewart *et al.* (2002) reported high overlap in habitat use during summer, and postulated that this spatial distribution might result in low overlap on a dietary niche axis. High overlap on one niche axis typically is accompanied by avoidance on another axis where ecologically similar species co-exist (MacArthur & Pianka, 1966; Krebs, Ryan & Charnov, 1974; Kie & Bowyer, 1999).

Among ruminants, physiological and nutritional requirements differ in relation to body size (Jarman,

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1974; Demment & Van Soest, 1985; Hoffman, 1985; Robbins, 1993; Barboza & Bowyer, 2000; 2001). Interactions among different nutritional requirements, availability of forages, and occurrence of competitors help determine diet selection of individuals in community assemblages of ruminants (Anthony & Smith, 1977; Singer, 1979; Smith, 1987; Mower & Smith, 1989; Jenkins & Wright, 1988). Diets also may be constrained by mouth architecture (Illius & Gordon, 1987), which likewise increases with body mass (Spaeth *et al.*, 2001).

Conventional methods for determination of diet usually yield valuable information on dietary overlap. Nonetheless, recent studies demonstrated the utility of ratios of stable isotopes in exploring differences in diet composition for numerous species, including ruminants (Cormie & Schwarcz, 1994; 1996; Ben-David, Shochat & Adams, 2001). For example, isotope ratios for moose (*Alces alces*) and caribou (*Rangifer tarandus*) from Denali National Park and Preserve reflected diets of each species and indicated seasonal changes in foraging strategies and animal condition (Ben-David, Shochat & Adams, 2001); therefore, we restricted our analysis to summer, when the greatest quantity of forage was available.

In this study, we explored niche separation among mule deer, elk, and cattle and hypothesized that these three herbivores would exhibit low overlap in use of forages in summer (when the greatest spatial overlap among species occurs; Stewart *et al.*, 2002). Further, we hypothesized that the smaller-bodied species, mule deer, would be more selective in its diet as indicated by less variability among individual diets and by use of higher-quality forages. Finally, we hypothesized that dietary differences among these three species would be reflected in their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures.

## Methods

We conducted research on the Starkey Experimental Forest and Range (hereafter, Starkey) of the United States Forest Service. Starkey (45° 12' N, 118° 3' W) is situated in the Blue Mountains of northeastern Oregon, U.S.A., with elevations ranging from 1,120 to 1,500 m. Starkey encompasses 10,125 ha and is surrounded by a 2.4-m-high fence that prevents immigration or emigration of large herbivores (Rowland *et al.*, 1997). Population sizes were approximately 500 adult female cattle (with young) in the main study area (7,762 ha) and 75 mule deer and 130 elk in the northeast study area (1,453 ha), as determined from stocking rate and helicopter censuses (Rowland *et al.*, 1997; Stewart *et al.*, 2002).

Both study areas consisted of four major habitats: *i*) mesic forest with the overstory dominated by grand fir (*Abies grandis*) and understory consisting of forbs and shrubs; *ii*) ponderosa pine (*Pinus ponderosa*) forest, xeric community with the understory dominated by elk sedge (*Carex geyeri*); *iii*) xeric grasslands dominated by a few grasses and forbs; and *iv*) logged forest, harvested during 1991-1992 (Rowland *et al.*, 1998; Stewart *et al.*, 2002).

We collected fresh (<2 days old) fecal pellets opportunistically from mule deer ( $n=28$ ), elk ( $n=27$ ), and range cattle ( $n=20$ ) while sampling vegetation during

summer (July-August) 1997. Cattle feces were collected from the main study area and feces from mule deer and elk were collected from the northeast study area. Habitats and forages available were similar for main and northeast areas, and mule deer and elk were present in both areas. Feces were collected across large portions of the study areas to ensure that samples were representative of available habitats and to minimize the possibility that the same individual was sampled repeatedly. Each fecal sample was analyzed for diet composition and for values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

We analyzed feces for diet composition using micro-histological analyses, conducted at Washington State University (B. Davitt, Pullman, Washington, U.S.A.). Microhistological analysis is used to estimate diet composition through microscopic identification of epidermal fragments of plant species present in feces of herbivores (Sparks & Malecheck, 1968). We used multivariate analyses of variance (MANOVA) with planned contrasts to test for differences in composition of forage classes among species (Neter *et al.*, 1996). We used arcsine, square-root transformations to ensure additivity of treatment effects (Gilbert, 1973; Kie & Bowyer, 1999). We conducted principal components analysis (PCA) based on the variance-covariance matrix to reduce dimensionality of those data (SAS Institute, 1988; McGarigal, Cushman & Stafford, 2000). We plotted means with 95% confidence intervals as bivariate ellipses for the first two principal components to examine differences among herbivores.

Fecal samples were analyzed for ratios of stable isotopes of carbon and nitrogen following the methods of Ben David *et al.* (1998) and Ben David, Hanley, and Schell (1998). We used multi-response permutation procedures (MRPP; BLOSSOM: Slauson, Cade & Richards, 1991) to investigate differences among species in stable isotopes of carbon and nitrogen for fecal samples.

## Results

Mule deer, elk, and cattle exhibited diverse diets as estimated from microhistological analyses of feces: mule deer (74 plant species); elk (80 plant species); and cattle (51 plant species). Mule deer consumed mostly sedges, but also ate about equal portions of grasses, forbs, conifers, and shrubs. Elk concentrated on forbs, with some grasses and shrubs in their diets, whereas cattle fed principally upon grasses and some sedges (Table I). Diets of mule deer are highly variable: forbs ranged from 0% to 70% and sedges from 0% to 88% of individual diets (Table I). Diets of elk were generally less variable, although grasses ranged from 4% to 54%; cattle diets had the lowest variability among forage classes (Table I).

Significant differences occurred among species in use of forage classes (Wilk's Lambda  $F_{10, 136}$ ;  $p < 0.0001$ ). Pairwise comparisons between species demonstrated that range cattle and mule deer differed in use of forage categories ( $p < 0.05$ ) except forbs ( $p = 0.075$ ); range cattle and elk differed in use of forage classes ( $p < 0.05$ ) except for small amounts of conifers ( $p = 0.92$ ). Mule deer and elk differed in use of forage classes ( $p < 0.01$ ) except for other foods ( $p = 0.97$ ; Table I).

We reduced dimensionality of those data to two principal components that explained 70% of the variation in

TABLE I. Descriptive statistics for diet composition (%) of feces of cattle ( $n=20$ ), mule deer ( $n=28$ ), and elk ( $n=27$ ) during summer 1997 on the Starkey Experimental Forest and Range, northeastern Oregon, U.S.A.

Species and forage class	$\bar{x}$	SD	Minimum	Maximum
<b>MULE DEER</b>				
Conifers	8.4	13.13	0	56.2
Forbs	14.4	21.33	0	70.4
Grasses	16.6	8.55	3.5	33.3
Sedges	47.4	29.90	0	88.0
Shrubs	8.5	9.51	0	40.9
Other foods	4.8	6.72	0	34.2
<b>ELK</b>				
Conifers	0.8	1.28	0	4.2
Forbs	44.7	11.07	24.9	46.7
Grasses	31.2	10.80	4.4	53.8
Sedges	11.7	6.16	1.5	26.4
Shrubs	6.9	4.67	0	18.2
Other foods	4.8	3.29	0	12.7
<b>CATTLE</b>				
Conifers	0.6	0.68	0	2.1
Forbs	6.6	3.26	0.7	11.3
Grasses	53.4	12.84	23.8	53.0
Sedges	36.6	12.06	19.8	50.9
Shrubs	1.5	1.94	0	6.9
Other foods	1.4	1.50	0	5.8

diets among those three large herbivores. Means with 95% confidence intervals indicated separation of groups of principal components scores based upon forage classes dominant in fecal pellets (Figure 1). We considered principal component 1 (39%), a forage-class axis ranging from conifers (negative loadings) to shrubs (positive loadings); diets dominated by graminoids loaded slightly negative (0-1.5), and those containing mostly forbs loaded more positively (1-2; Figure 1). Principal component 2 (31%) ostensibly represented a continuum from grazing (negative loadings) to browsing (positive loadings; Figure 1). Diets that reflected a grazing strategy (dominated by grasses and sedges) loaded negatively for principal component 2, whereas those diets dominated by shrubs and conifers, which represented a browsing strategy, loaded strongly positive on that same axis (PC2). Moreover, 95% confidence ellipses, based upon scores for principal components 1 and 2, clearly separated mule deer, elk, and cattle based upon those putative forage-class (PC1) and feeding-strategy (PC2) axes (Figure 1).

Stable isotope ratios indicated high variability in diet for all three herbivores, with mule deer exhibiting the greatest variability (Table I, Figure 2). MRPP indicated significant ( $p < 0.01$ ) differences among mule deer, elk, and cattle for isotope ratios of both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . Moreover, pairwise comparisons of ratios of stable isotopes revealed significant differences between mule deer and cattle ( $p < 0.001$ ), mule deer and elk ( $p < 0.001$ ), and elk and cattle ( $p = 0.004$ ).

### Discussion

We hypothesized that mule deer, elk, and cattle would exhibit little overlap in dietary niche. Indeed, both dietary and stable isotope analyses indicated complete sep-

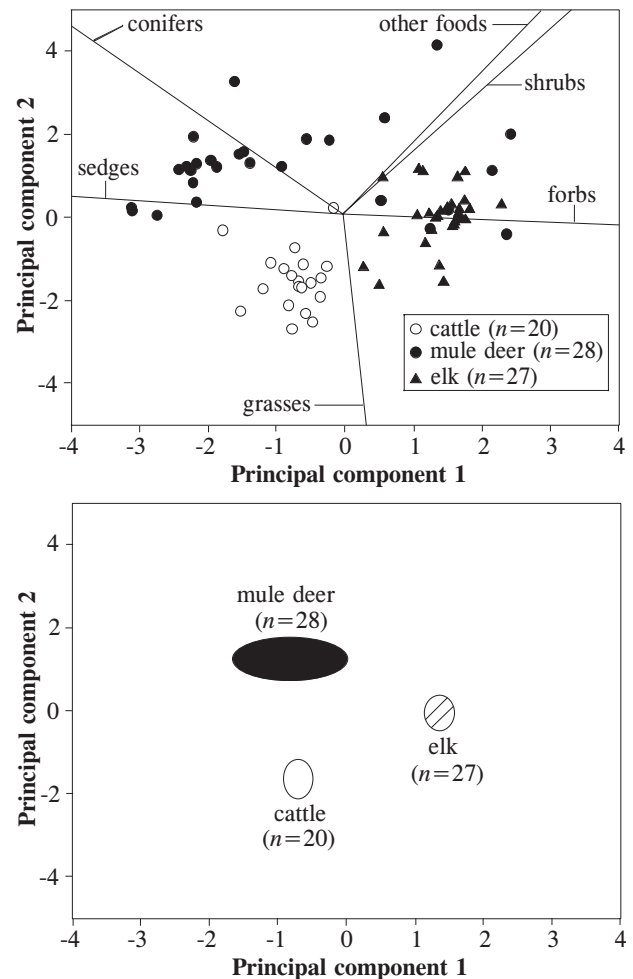


FIGURE 1. Results of principal components analysis (PCA) on forage classes determined from microhistological analysis of feces of cattle, mule deer, and elk with plots of principal components 1 and 2 (70% of variation explained). The top graph is a biplot scatter of principal component scores with loadings for forage classes indicated by lines. Principal component 1 is a forage type axis, whereas principal component 2 represents a browsing versus grazing continuum. The bottom graph contains 95% confidence intervals for principal component scores for cattle, mule deer, and elk during summer on the Starkey Experimental Forest and Range, northeastern Oregon, U.S.A., 1997.

aration of diets among those three species (Figures 1 and 2). Stewart *et al.* (2002) reported significant overlap in habitat use among these three large herbivores during summer; thus, mule deer, elk, and cattle used similar habitats while diverging strongly in diets. Principal component 2 clearly separated these three ruminants by foraging strategy. Despite diets containing large amounts of sedges, mule deer followed a browsing strategy, elk were intermediate or mixed-feeders, and cattle were grazers during summer.

We predicted that small-bodied mule deer would exhibit a narrower dietary niche, with forage of higher quality, than either larger-bodied elk or cattle (Mackie, 1970; Schoener, 1971; Demment & Van Soest, 1985; Robbins, 1993; Kie & Bowyer, 1999). In contrast to that prediction, mule deer exhibited greater variability in dietary niche when compared with elk and cattle (Figures 1 and 2). Sedges dominated mule deer diets, but varied

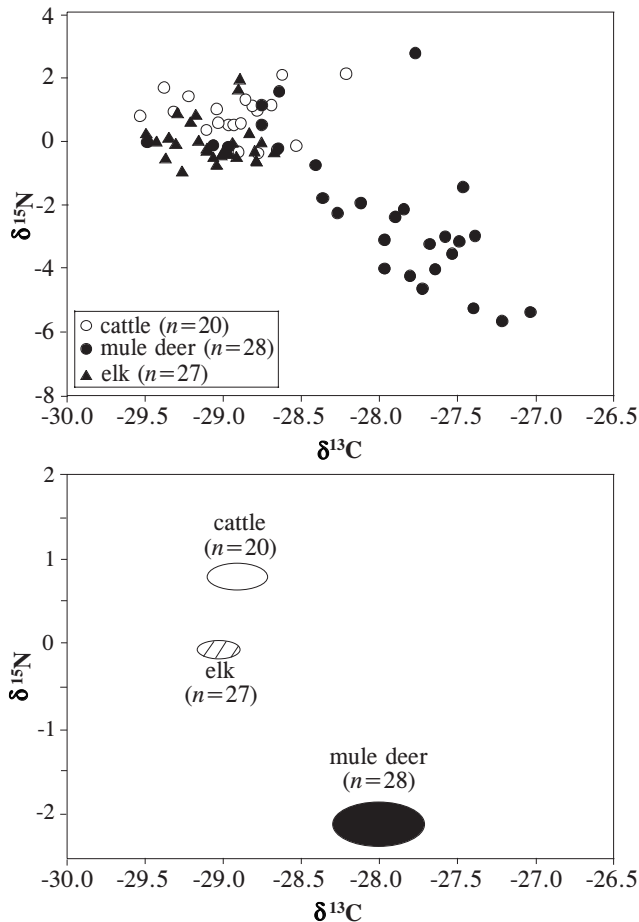


FIGURE 2. Results of stable isotope analyses from feces of cattle, mule deer, and elk. The top graph is a scatter plot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios. The ellipses in the bottom graph are 95% confidence intervals for stable isotope ratios of cattle, mule deer, and elk during summer on the Starkey Experimental Forest and Range, northeastern Oregon, U.S.A., 1997. Values of  $\delta^{13}\text{C}$  are derived from comparison of the ratio of the heavy ( $^{13}\text{C}$ ) and light ( $^{12}\text{C}$ ) isotopes in the sample with the ratio of those two isotopes in a standard (PDB limestone) using the equation  $\delta^{13}\text{C} = \left\{ \left[ \frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}}}{(^{13}\text{C}/^{12}\text{C})_{\text{standard}}} - 1 \right] \times 10^3 \right\}$ . Because PDB limestone is highly enriched in  $^{13}\text{C}$  relative to most biological samples, values of  $\delta^{13}\text{C}$  are usually negative. Values of  $\delta^{15}\text{N}$  are calculated in a similar manner. The value of the standard, atmospheric nitrogen, is set by convention to 0 (Nadelhoffer & Fry, 1994).

greatly from 0% to 88% of individual diets (Table I). Nonetheless, mule deer consumed numerous forbs, shrubs, and conifers, indicating that deer were opportunistic feeders compared with elk and cattle, which foraged primarily on forbs and grasses, respectively. This result was somewhat unexpected and may indicate that mule deer foraged on plants of lower quality than either elk or cattle. Perhaps, by increasing variability in their diet by feeding opportunistically, mule deer increased overall diet quality. More research into this question, however, is required.

We hypothesized that these three large herbivores would differ in stable-isotope signatures and that divergence in those ratios would reflect differences in diets among mule deer, elk, and cattle. Indeed, those three species of ungulates differed significantly on both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  axes, further indicating complete separation on

the dietary niche axis (Figures 1 and 2). Although differences in isotopic ratios among ungulates were not large, feces of mule deer were significantly depleted in  $\delta^{15}\text{N}$  and enriched in  $\delta^{13}\text{C}$  compared with either elk or cattle (Figure 2). Depletion of  $\delta^{15}\text{N}$  in feces of mule deer, in concert with enrichment of  $\delta^{13}\text{C}$ , likely resulted from consumption of forages occurring in more xeric habitats dominated by sedges. Enrichment in  $\delta^{13}\text{C}$  has been reported as a result of higher soil temperature or water stress in plants (Lipp *et al.*, 1991; Michelsen *et al.*, 1996; Panek & Waring, 1997; Barber, Juday & Finney, 2000), an outcome consistent with xeric forages used by mule deer. Consumption of C4 plants may affect values of  $\delta^{13}\text{C}$  in feces, but C4 plants were not present on either study area or in herbivore diets we sampled. Other studies have noted that mule deer occupied more xeric habitats, characterized by ponderosa pine overstory with an elk sedge dominated understory, than those habitats used by elk or cattle (Johnson & Clausnitzer, 1992; Johnson *et al.*, 2000; Coe *et al.*, 2001; Stewart *et al.*, 2002).

Elk and cattle separated on the  $\delta^{15}\text{N}$  axis (Figure 2). Such differences in values of  $\delta^{15}\text{N}$  probably reflected reliance of elk on forbs (including legumes) and cattle on grasses. Elk likely fed more on leguminous forbs that rely on atmospheric  $\text{N}_2$ -fixation, resulting in  $\delta^{15}\text{N}$  values near 0 in feces of elk, which is consistent with signatures of plant species that fix atmospheric nitrogen (Nadelhoffer & Fry, 1994; Ben-David *et al.*, 1998).

Comparisons of 95% confidence intervals of PC1 from dietary analysis with ratios of stable isotopes highlight the differing results obtained by those two methods. PC1 indicated strong overlap of forage classes between mule deer and cattle, but differences between cattle and elk (Figure 1). Stable isotopes indicated the opposite (Figure 2). Although elk and cattle separated on the  $\delta^{15}\text{N}$  axis, significant overlap occurred in the  $\delta^{13}\text{C}$  axis, precluding the interpretation that cattle also utilized more xeric types of forages, similar to mule deer diets. Stewart *et al.* (2002) frequently observed cattle at low elevations on shallow slopes with mesic vegetation. Thus, isotopic data may reflect differences in use of forages between cattle and mule deer more clearly than dietary data, because of differences in xeric conditions of those habitats and types of forages contained therein. Stable isotopes may provide an added dimension to understanding dietary partitioning among large herbivores that inhabit landscapes consisting of diverse habitats. Nonetheless, stable isotopes may not reflect differences in habitat use between cattle and elk as efficiently as for mule deer, because of similar moisture regimes and more mesic conditions of the forages consumed.

Niche separation traditionally is evaluated along spatial, temporal, and dietary axes, and conclusions about niche dynamics from a single axis alone may lead to misinterpretation of results (Keddy, 1989; Ben-David, Bowyer & Faro, 1996; Kronfeld-Schor *et al.*, 2001). Although mule deer, elk, and cattle were reported to overlap in use of habitats, our examination of diets indicated strong partitioning of dietary niche and some separation of habitats related to moisture regimes, with mule deer using more xeric habitats than either elk or cattle. Contrary to our prediction,

mule deer exhibited the greatest variability in dietary niche and used lower-quality forages occurring in xeric habitats. Although mule deer consumed large amounts of sedges, they continued to follow a browsing strategy. Stable isotope analysis was useful in determining moisture regimes of forages eaten by ungulate species and indicated some partitioning of habitats in addition to forages, which was not evident from simply examining diets. Thus, we hypothesize that the arrangement of forages in a heterogeneous landscape (*sensu* Kie *et al.*, 2002) may be as important as body size in determining dietary niche; more research on this complex topic is needed.

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