



Overlap and partitioning of the ecological and isotopic niches

Elizabeth A. Flaherty and Merav Ben-David

E. A. Flaherty (lizf@uwyo.edu) and M. Ben-David, Dept of Zoology and Physiology, Univ. of Wyoming, 1000 E. University Ave., Dept 3166, Laramie, WY 82071, USA.

Recently, it was proposed that stable isotope patterns can be used to quantify the width of the ecological niche of animals. However, the potential effects of habitat use on isotopic patterns of consumers have not been fully explored and consequently isotopic patterns may yield deceptive estimates of niche width. Here, we simulated four different scenarios of a consumer foraging across an isotopically heterogeneous landscape to test the combined effects of habitat and diet selection on the widths of the isotopic niche. We then modeled the actions of a naive researcher who randomly sampled consumers from the simulated populations, and used these results to assess the overlap and partitioning of the isotopic and the ecological niches when habitat-derived differences among isotope signatures are not considered. Our results suggest that populations of dietary specialists exhibited broader isotopic niches than populations composed of dietary generalists, and habitat generalists exhibited narrower isotopic niche widths compared with populations of individuals that foraged in specific habitats. The conversion of isotopic niches to ecological niches without knowledge of foraging behavior and habitat-derived isotopic differences transformed an informative IS-space into 'a blurry p-space'. Therefore, knowledge of habitat-derived differences in stable isotope values and understanding of habitat use and individual foraging behavior are critical for the correct quantification of the ecological niche.

The idea that stable isotopes of carbon and nitrogen can reflect dietary niches and food niche partitioning (Genner et al. 1999, Feranec and MacFadden 2000, Power et al. 2002), as well as trophic niches (Post 2002, Schneider et al. 2004, Layman et al. 2007) of animals was eloquently summarized by Newsome et al. (2007). Newsome et al. (2007) emphasized that stable isotope analysis can yield quantitative information on resource use and width (or breadth) of the ecological niche of organisms. Newsome et al. (2007) also cautioned that the isotopic niche may yield deceptive estimates of niche width or breadth, because consumers feeding on resources (i.e. end-members) with greater differences in isotopic values will seem to have a broader isotopic niche than consumers feeding on resources with fewer differences in isotopic values. Therefore, Newsome et al. (2007) recommended the use of linear mixing-models (Phillips 2001, Phillips and Koch 2002, Phillips and Gregg 2003), which correct for the distribution of isotopic values of end-members.

Although they presented the isotopic niche as an emergent property of both habitat use and foraging, Newsome et al. (2007) concentrated their discussion on the potential effects of diet. Several investigators have highlighted the importance of understanding the effects of habitat use on isotopic patterns in animals. For example, Lee et al. (2005) used stable isotope analyses to show that although subadult bowhead whales *Balaena mysticetus* feed more in the eastern Beaufort Sea than adults, they do not acquire sufficient food there and thus rely on stored resources. In a study of niche partitioning among mule deer *Odocoileus hemionus*, North American elk

Cervus elaphus, and free-ranging cattle *Bos taurus* in Oregon, Stewart et al. (2003) reported that mule deer were displaced by elk and cattle and consequently foraged in more xeric habitats. Darimont et al. (2007) observed that in coastal British Columbia, individual black-tailed deer *O. h. columbianus* with isotopic signatures indicative of foraging in stands of cedar *Thuja plicata* and low-elevation hemlock *Tsuga heterophylla*, were more likely to be killed by wolves *Canis lupus* than conspecifics foraging in other habitats. Thus, habitat use may add complexity and additional sources of variation to values of stable carbon and nitrogen isotopes that confound the interpretation of the isotopic niche. Indeed, Bearhop et al. (2004) suggested that "foraging location" could affect the isotopic variance of a consumer population when individuals forage across an isotopically heterogeneous landscape. Under such conditions, wide-ranging individuals would exhibit more variation in their isotopic signatures than sedentary ones (Bearhop et al. 2004).

While studying the dietary ecology of several species in the fragmented, temperate rainforest of Prince of Wales Island, southeast Alaska, we observed differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among individual soil macro-invertebrates of the same taxa captured in different habitats (Flaherty et al. in press). These habitat-related differences likely stem from differences in evapo-transpiration and water-use efficiency of plants (Ehleringer et al. 1993, Lajtha and Marshall 1994, Dawson et al. 2002) in old-growth forest, young-growth stands, and clearcuts. Those habitat-related isotopic patterns raised questions concerning the emergent isotopic niche

breadth of consumers with different degrees of habitat and dietary specializations. Moreover, we were curious to know how ignoring habitat variation in isotopic values and habitat use would influence the overlap between the isotopic and ecological niches.

Here we report on results from simulation models exploring the effects of habitat use and foraging of individuals that are generalists or specialists (Bolnick et al. 2003) on the isotopic niche of a consumer. Matthews and Mazumder (2004) and Bearhop et al. (2004) demonstrated that populations of generalists will have narrower isotopic niche breadth compared to populations of dietary specialists. In contrast, Bearhop et al. (2004) predicted that habitat generalists would exhibit more variation in their isotopic signatures than habitat specialists. Thus, in our simulations we included four scenarios: 1) $D_S H_g$ - dietary specialists and habitat generalists; 2) $D_g H_g$ dietary and habitat generalists; 3) $D_S H_S$ - dietary and habitat specialists; and 4) $D_g H_S$ - dietary generalists and habitat specialists. We then modeled the actions of a naive researcher, ignorant of the spatial foraging behaviors of consumers, to assess the influence of habitat use on isotopic niche breadth. We also evaluated the degree of overlap and partitioning that occur between the isotopic and the ecological niches when habitat-derived differences among isotope signatures are not considered.

Methods

Modeling approach

We simulated the foraging behavior of a common raptor on Prince of Wales Island (Van Horne 1983); the American kestrel *Falco sparverius*. This avian predator largely eats invertebrates (Callopy and Koplin 1983), and forages on the ground across a habitat mosaic of variable-aged clearcut, young-growth, and old-growth habitats (Elliot and Cowan 1983). We identified the modeled kestrels as either generalists, individuals using a wide range of dietary resources, or specialists, those individuals concentrating on few food types (Bolnick et al. 2003). Our simulations included: 1) $D_S H_g$ - all kestrels were habitat generalists (i.e. each individual foraged in all three habitat types) but different individuals specialized on only one of five taxa of soil macro-invertebrates. Such dietary specialization in individuals of the same population was observed in American martens *Martes americana* in southeast Alaska (Ben-David et al. 1997a), river otters in southcentral Alaska (Blundell et al. 2002), and sea otters *Enhydra lutris* in California (Tinker et al. 2008; also see Bolnick et al. 2003); 2) $D_g H_g$ - all kestrels were habitat and dietary generalists (i.e. consumed all possible macro-invertebrates in all three habitats in different proportions); 3) $D_S H_S$ - all kestrels consumed only one and the same diet item but different individuals specialized on foraging in one of the specific habitats (i.e. habitat specialists). Such habitat segregation among individuals of the same population was previously observed in northern goshawks *Accipiter gentilis* in southeast Alaska (Ben-David 1999); and 4) $D_g H_S$ - all kestrels were dietary generalists (i.e. consumed all possible prey macro-invertebrates) and habitat specialists (i.e. each foraged in only one habitat).

Study site and sampling methods for soil macro-invertebrates

Study areas were located throughout the northern portion of Prince of Wales Island, southeast Alaska (55°53'28"N, 133°9'57"W). This island, part of the Tongass National Forest, has experienced 40-50 years of industrial timber harvest beginning in the 1950s, creating a mosaic of clearcut (cc), young-growth (yg) and old-growth (og) habitats of varying ages (USDA Forest Service 1997). Old-growth habitats contain large, old sitka spruce *Picea sitchensis*, western hemlock *Tsuga heterophylla* and yellow cedar *Chamaecyparis nootleanensis* trees, downed and decaying logs and snags, and an understory dominated by *Vaccinium* spp. Young-growth habitats are mostly 'doghair' (i.e. densely stocked, small diameter trees) stands of spruce and hemlock in which little sunlight and often little rain reaches the forest floor. Clearcuts have no canopy and generally have an herbaceous layer that includes skunk cabbage *Lysichitum americanum* and *Vaccinium* spp.

During spring 2004 and 2005 and fall 2005, we sampled soil macro-invertebrates in the three habitat types. We sampled 15 stands of each habitat with three line-transect surveys in each stand. The transect locations in each stand were chosen randomly and were 20 m long with five pitfall traps spaced every 5 m. The pitfall traps were a 473-ml plastic cup buried in the earth with the lip flush with the ground-level. The cup height and surface prevented escape by trapped invertebrates eliminating the need for a preservative. A plastic plate was placed over the cup to prevent it from filling with rainwater. The traps were left for approximately three days after which the contents were emptied into a plastic bag and frozen until analysis and identification in the laboratory at the Univ. of Wyoming. A total of 225 traps were collected from each of the three habitat types for a total of 675 traps.

Stable isotope analysis

In the lab, all macro-invertebrates were identified to at least order using a dissecting scope and guide books (Kaston et al. 1978, White 1983, Borror and White 1998). We dried samples, individual invertebrates, at 60°C for 48 h and ground them to a fine powder using a mixer mill. A subsample (0.57-0.63 mg) was weighed into a miniature tin weigh boat (4 X 6 mm) for combustion and sent to the Stable Isotope Facility at the Univ. of Wyoming for analysis with an elemental analyzer attached to a mass spectrometer. Each sample was analyzed in duplicate and accepted only if difference between samples did not exceed 0.15‰ and machine linearity did not deviate from 0.99 (Ben David et al. 1997a, 1997b). We used multivariate analysis of variance (MANOVA; Zar 1999) to test for differences in stable isotope values of the soil macro-invertebrates among the three habitat types.

Kestrel foraging models

We created the kestrel foraging models using MATLAB (Mathworks). Inputs for all four models were mean $\delta^{13}C$ and $\delta^{15}N$ values and associated variance for five macro-invertebrate taxa in each of the three habitat types (Table 1). We used only the largest invertebrates sampled in pitfall traps (those with body lengths > 10 mm) as they are more likely to be

of energetic value to a foraging raptor. This included two genera of carabid beetles (*Scaphinotus* and *Pterostichus* spp.), a large millipede (*Halpaphe baydeniana*), spiders (Order Araneae, Families Araneidae and Lycosidae), and earthworms (Order Haploraxida), which comprised >58% of the total invertebrate biomass sampled in all habitats combined. In the models, isotopic signature for each bird was derived from normal distributions of macro-invertebrate values. Foraging strategies were randomly assigned to each individual using the following decision rules:

1. D_5H_g - In this scenario, we modeled 250 kestrels foraging on only one of the five taxa of soil macro-invertebrates (50 birds foraging on each invertebrate) and across all three habitat types. In the model, we simulated random habitat contribution (h) by choosing a number between 0 and 1 using a 'broken stick' model (i.e. the range is randomly divided into three values totaling 1) for each of the birds. For each prey group, we randomly assigned an isotopic signature from the normal distribution for both $\delta^{13}C$ and $\delta^{15}N$ for each habitat type. The sum of the products of the isotope values times the randomly chosen habitat-contribution values resulted in the final isotopic signature for each bird ($\delta^{13}C_k$ and $\delta^{15}N_k$).

$$\delta^{13}C_k = (h_{cc} \times \delta^{13}C_{cc}) + (h_{yg} \times \delta^{13}C_{yg}) + (h_{og} \times \delta^{13}C_{og})$$

$$\delta^{15}N_k = (h_{cc} \times \delta^{15}N_{cc}) + (h_{yg} \times \delta^{15}N_{yg}) + (h_{og} \times \delta^{15}N_{og})$$

$$h_{cc} + h_{yg} + h_{og} = 1$$

where h_{cc} is proportion of foraging in clearcuts, h_{yg} is the proportion of foraging in young growth, and h_{og} is the proportion of foraging in old growth.

2. D_5H_g - In this model we simulated random habitat contribution with the broken stick model using the same approach as in model 1 for 150 kestrels. Similarly, the final $\delta^{13}C$ and $\delta^{15}N$ values for each bird were calculated using the same equations listed in model 1, but including a random assignment of diet contribution of the five invertebrates and randomly assigning the proportion of each resource consumed from each habitat.
3. D_5H_s - In this model, kestrels only consumed one genus of soil macro-invertebrates, the carabid beetle *Pterostichus* spp. We modeled 50 individuals that specialized on foraging in each of the three habitats for a total of 150 birds. In this model, we assigned each bird a $\delta^{13}C$ and $\delta^{15}N$ value from the normal distribution of *Pterostichus* in each of these three habitats.
4. D_5H_s - This model simulated three populations of 50 kestrels each foraging upon all five invertebrate taxa in only one of the three habitats.

For each of the models, we made many of the same assumptions as Matthews and Mazumder (2004): each macro-invertebrate group had the same percentage of carbon and

Table 1. Values of stable C and N isotopes (mean and standard deviation) for the five soil macro-invertebrates collected in clearcuts, young-growth and old-growth stands in southeast Alaska 2004–2005. Global means were calculated for pooled samples ignoring the effect of habitat.

Invertebrate	Global means			Old-growth			Young-growth			Clearcut		
	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$
Polydesmida: <i>Halpaphe haydeniana</i>	36	-24.55 (0.84)	1.18 (1.65)	17	-24.75 (0.45)	2.95 (1.66)	3	-26.04 (0.73)	1.28 (0.67)	16	-24.07 (0.79)	0.71 (0.75)
Araneae	72	-25.27 (0.84)	5.57 (1.20)	28	-25.45 (0.91)	5.67 (1.27)	23	-25.26 (0.82)	6.07 (0.99)	21	-24.94 (0.70)	4.74 (0.78)
Haplotaxida	64	-23.74 (0.99)	2.74 (2.09)	30	-23.69 (0.80)	3.08 (2.32)	20	-24.34 (1.10)	2.73 (1.77)	14	-22.98 (0.60)	2.04 (1.94)
Coleoptera: <i>Pterostichus</i> spp.	85	-26.08 (1.32)	4.12 (1.25)	28	-26.49 (1.37)	4.76 (1.32)	29	-26.48 (0.99)	4.32 (1.00)	28	-25.25 (1.22)	3.27 (0.95)
Coleoptera: <i>Scaphinotus</i> spp.	76	-26.72 (0.77)	3.15 (1.48)	30	-26.73 (0.81)	3.75 (1.80)	29	-26.94 (0.63)	2.74 (1.08)	17	-26.33 (0.81)	2.79 (1.12)

nitrogen per unit biomass, each assimilated macro-invertebrate group provided a homogenous $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signature, assimilation of prey $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was instantaneous (i.e. tissue turnover rate is ignored), and we did not account for the effects of elemental routing into specific tissues (Karasov and Martinez del Rio 2007).

Evaluation of the overlap and partitioning of the isotopic and ecological niches

To assess the influence of habitat on isotopic niche breadth we calculated the mean and variance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each simulated kestrel population. We used the among-individual variance as a surrogate of niche width or breadth because our modeling approach did not produce within-individual variation (Araujo et al, 2007, Newsome et al. 2007), and compared these values among models with Levene's test of homogeneity of variance (SPSS 15.0 for Windows). To evaluate the degree of overlap and partitioning between the isotopic and the ecological niches when habitat differences among isotope signatures are not accounted for, we modeled the actions of a naive researcher on Prince of Waies Island who randomly sampled 15 kestrels from each of the simulated populations. This naive researcher, who is unaware of the foraging habits of kestrels, determined their ecological niche following the procedures described by Newsome et al. (2007). Using the global means of the isotopic values for the five soil macro-invertebrates (Table 1) and diet-consumer discrimination factors of 1‰ for $\delta^{13}\text{C}$ and 3‰ for $\delta^{15}\text{N}$ (DeNiro and Epstein 1981, Peterson and Fry 1987, Kelly 2000, McCutchan et al 2003), the naive researcher employed a multiple source, dual-isotope linear mixing-model (Phillips and Gregg 2003; SISUS: stable isotope sourcing using sampling; Erhardt 2007) to convert the isotopic data from d-space to p-space (i.e. convert isotopic contribution of the diet sources to the consumer into dietary proportions; Newsome et al. 2007).

Results

All invertebrate taxa differed in isotopic values among habitats (MANOVA, $p < 0.05$; Table 1). These habitat-derived differences ranged from 0.61‰ in $\delta^{13}\text{C}$ for *Scaphinotus* to 1.970/00 for *Harpaphe*, and 1.01‰ in $\delta^{15}\text{N}$ for *Pterostichus* to 2.24‰ for *Harpaphe*. In general, individuals trapped in clearcuts had enriched $\delta^{13}\text{C}$ and depleted $\delta^{15}\text{N}$ values compared with the same taxa from young-growth and old-growth habitats, except for *Scaphinotus* spp. Similarly, individuals captured in old-growth stands had enriched $\delta^{15}\text{N}$ values compared with young-growth and clearcut habitats, although no distinct patterns were observed for $\delta^{13}\text{C}$ (Table 1).

Results from our simulations revealed that the isotopic niches (in 8-space) of the populations of kestrels that were dietary generalists (D_gH_g and D_gH_g) were significantly narrower in bivariate space than those that were composed of dietary specialists (D_sH_g and D_sH_s), regardless of whether they were habitat specialists or generalists (Fig. 1, Table 2,3). The width of the isotopic niche in $\delta^{13}\text{C}$ was 4.8 and 5.7 times greater for populations of dietary specialists than generalists,

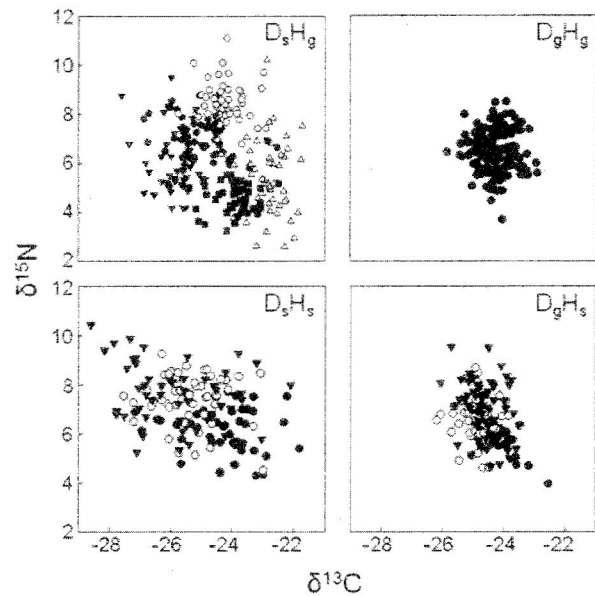


Figure 1. Output from four models simulating habitat use and foraging behaviors of American kestrels in southeast Alaska. Model 1 simulated diet specialists and habitat generalists – kestrels that foraged in all three habitat types but different individuals specialized in foraging on only one of the five taxa of soil macro-invertebrates: *Pterostichus* (full circles), *Araneae* (open circles), *Scaphinotus* (full triangles), *Harpaphe* (open triangles), and *Haplotaenidia* (open squares); (D_sH_g). Model 2 simulated habitat and dietary generalists (D_gH_g). Model 3 simulated diet specialists and habitat specialists (D_sH_s) – all kestrels consumed only *Pterostichus* spp. but different individuals specialized on foraging in specific habitats, clearcuts (full circles), young-growth (open circles), or old growth (full triangles). In model 4, all kestrels were dietary generalists and habitat specialists: clearcuts (full circles), young-growth (open circles), or old growth (full triangles); (D_gH_s).

and 1.4-4.0 times broader in $\delta^{15}\text{N}$ when comparing the variance (Table 2). Similarly, the isotopic niches of populations of kestrels that were habitat generalists were narrower ($\delta^{13}\text{C}$: 1.1 and 1.3 times; $\delta^{15}\text{N}$: 1.5 - model 4 vs model 2; Table 2) than those composed of individuals foraging in specific habitats, except for $\delta^{15}\text{N}$ when kestrels were dietary specialists (D_sH model 1; $\delta^{15}\text{N}$: 0.5 - model 3 vs model 1; Table 3). Nonetheless, kestrels that consumed only *Pterostichus* in all habitats (i.e. habitat generalists; model 1, Table 2), had a narrower isotopic niche ($\delta^{13}\text{C}$: 2.7 times; $\delta^{15}\text{N}$: 2.4;

Table 2. Mean and variance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for simulated American kestrels *Falco sparverius* populations. Model 1 represents diet specialists and habitat generalists (D_sH_g); model 2 diet and habitat generalists (D_gH_g); model 3 diet and habitat specialists (D_sH_s); and model 4 diet generalists and habitat specialists (D_gH_s).

	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
	Mean	Variance	Mean	Variance
Model 1 (<i>Pterostichus</i> only)	-24.36	1.43	6.36	2.89
Model 2	-24.28	0.30	6.49	0.73
Model 3	-25.18	1.88	7.11	1.56
Model 4	-24.61	0.33	6.61	1.11

Table 3. Differences in variance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between models for simulated American kestrel populations. Model 1 represents diet specialists and habitat generalists (D_sH_g); model 2 diet and habitat generalists (D_gH_g); model 3 diet and habitat specialists (D_sH_s); and model 4 diet generalists and habitat specialists (D_gH_s).

Compared models	Levene's statistic	DF	p-value
Model 1 vs model 2 ($\delta^{13}\text{C}$)	82.305	(1,398)	< 0.001
Model 3 vs model 4 ($\delta^{13}\text{C}$)	92.873	(1,298)	< 0.001
Model 1 vs model 2 ($\delta^{15}\text{N}$)	90.832	(1,398)	< 0.001
Model 3 vs model 4 ($\delta^{15}\text{N}$)	4.575	(1,298)	0.033
Model 1 vs model 3 ($\delta^{13}\text{C}$)	3.927	(1,398)	0.048
Model 2 vs model 4 ($\delta^{13}\text{C}$)	0.094	(1,298)	0.759
Model 1 vs model 3 ($\delta^{15}\text{N}$)	25.038	(1,398)	< 0.001
Model 2 vs model 4 ($\delta^{15}\text{N}$)	5.784	(1,298)	0.017
Model 1 (<i>Pterostichus</i> only) vs model 3 ($\delta^{13}\text{C}$)	14.132	(1,198)	< 0.001
Model 1 (<i>Pterostichus</i> only) vs model 3 ($\delta^{15}\text{N}$)	13.356	(1,198)	< 0.001

Table 2) compared with their conspecifics that consumed the same prey but specialized in foraging in different habitats (i.e. habitat specialists).

In models 1, 3 and 4, isotopic values of several of the 15 birds that were randomly sampled by the naïve researcher fell outside the mixing space (Fig. 2) when the global means of prey signatures were used. This deviation was especially pronounced for model 1. For all populations, however, the average values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the 15 kestrels occurred within the mixing space (Fig. 2).

Despite distinct differences in δ -space (Fig. 1, 3) among models, the conversion to p-space using the dual-isotope linear mixing model yielded a relatively uniform pattern.

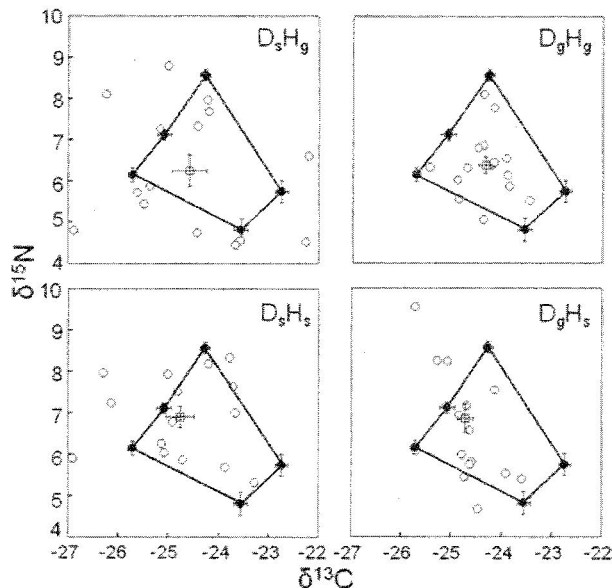


Figure 2. Mixing space represented by the polygon connecting the global means ($\pm$ SD) of $\delta^{13}\text{C}$ and depleted $\delta^{15}\text{N}$ for the five taxa of soil macro-invertebrates (full circles) and data for 15 American kestrels (open circles) randomly chosen from the simulated population of each of the four models (D_sH_g , D_gH_g , D_sH_s , D_gH_s). The mean kestrel isotope signature (open box; $\pm$ SD) is also depicted.

With the exclusion of model 1, in which three birds were used in the conversion because most birds fell out of the mixing space, these models suggested that kestrels ate few *Pterostichus*, even for model 3 (D_sH_s ; Fig. 3), where all kestrels were exclusively feeding on this resource in different habitats. The variance in p-space was nearly 2.9 times higher for model 4 (D_gH_s) compared with model 2 (D_gH_g ; 0.020 and 0.007, respectively), and 2.4 times higher for model 3 (D_sH_s) compared with model 2 (D_gH_g ; 0.017 and 0.007, respectively), which was comparable to variance differences in d-space.

Discussion

We suggest that populations of dietary specialists exhibit broader isotopic niches than populations composed of dietary generalists (Matthews and Mazumder 2004), likely because generalist consumers sample and therefore integrate (or average) their diets. Under such conditions, the isotopic differences among individuals will be smaller than among populations of specialists (Bearhop et al. 2004, Feranec and McFadden 2006). A similar pattern emerged from differential use of habitat. Contrary to the prediction that wide-ranging individuals vary more in their isotopic signatures than sedentary ones (Bearhop et al. 2004), habitat generalists in our simulations exhibited narrower isotopic niches compared with a population of individuals that forage in specific habitats. Our findings on the effects of habitat use on isotopic niche breadth add another layer of complexity to a growing list of challenges in relating isotopic niche breadth to ecological niche breadth, including problems associated with missing prey items, the spread of prey isotopic signatures (Araujo et al. 2007), effects of diet quality, elemental routing, and tissue turnover rate (Bearhop et al. 2004, Matthews and Mazumder 2004, Newsome et al. 2007).

The conclusion that ignoring habitat use may lead to problems in estimating the ecological niche was obvious from the attempts of our naïve researcher to convert the isotopic niche from d-space to p-space for the 15 kestrels sampled at random from each of the four simulated populations. In all of those attempts, isotopic values for several birds fell outside of the mixing space derived from the global means of prey values (Fig. 2; Phillips 2001, Phillips and Gregg 2003). This was especially pronounced for model 1 (D_sH_g ; Fig. 2). In all our models, no prey items have been missed per se, diet quality (or the C:N ratio of the prey; Phillips and Koch 2002) was similar for all prey (averaging 45; 11 for all items), we did not use different consumer-diet discrimination factors in generating the kestrel isotopic values, nor did we add variation related to tissue turnover rate. Here, especially for model 3 (D_sH_s), ignorance of habitat-specific isotopic variation for the same taxa, and lack of knowledge of the foraging behavior of the simulated kestrels resulted in misalignment of consumers and their prey. The relatively high cost of isotope analyses and the increasing demand for synthesizing information from multiple studies leads to use of published data (Blundell et al. 2002, Mowat and Heard 2006, Herreman et al. 2009). Use of such data without complete knowledge of the processes and mechanisms that generated the observed

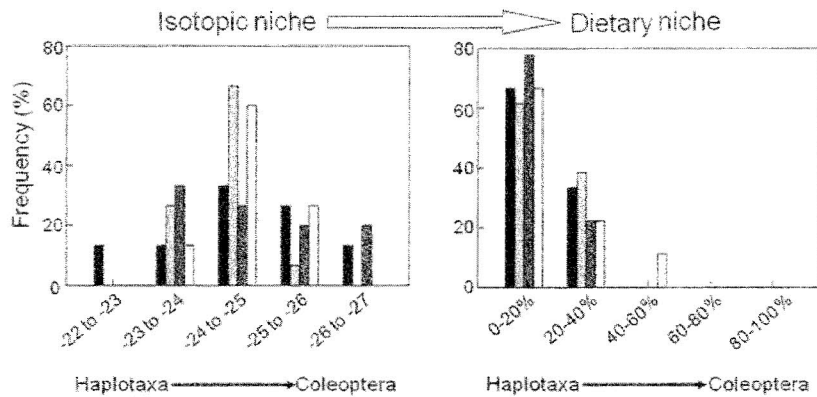


Figure 3. Frequency of observation of the diet of 15 kestrels randomly chosen from the simulated population of each of the four models (D_3H_8 – black, D_5H_8 – medium gray, D_6H_8 – dark gray, D_7H_8 – light gray). The x-axis represents a continuum of isotope values for the invertebrates ranging from the order with the highest fraction of $\delta^{13}C$ to the order that was the most depleted in $\delta^{13}C$. The dietary niche in p-space does not reflect the width or pattern of the isotopic niche for any of the four models.

isotopic panerns may result in misinterpretation and misrepresentation of the ecological niche.

Although disconcerting, the observation that the proportion of birds that fell outside of the mixing space differed among models, could lead to the identification of potential effects of habitat use on the isotopic niche. By employing similar simulations to ours or those described by Matthews and Mazumder (2004), one could generate expectations for individual specializations based on foraging behaviors and habitat use and compare those to observed panerns. Such comparisons will likely elucidate which of the problems listed above most contribute to the misalignment of consumers and their prey.

The most unsettling result of our naive researcher's efforts to convert kestrel data from d-space to p-space was the observation that while the mixing models maintained a similar level of variation, the distinct isotopic panerns were eliminated. Indeed, as Newsome et al. (2007) stated the mixing models transformed an informative d-space into 'a blurry p-space'. It is especially rroublng that for model 3 where Kestrels fed exclusively on *Pterostichus* but in different habitats, results of the mixing model suggest most individuals consumed little of this resource. This lack of correspondence between isotopic and dietary niches is clearly a function of the poor definition of all potential end-members (i.e. prey or isotopic sources; Phillips 2001); but in this case, a result of introducing too many sources (global means of all prey taxa) rather than too few. To properly represent the dietary niche of the simulated kestrels, we should have provided the frequency distributions of all solutions for all prey taxa (Phillips and Gregg 2003), which would have resulted in five niche axes. We have elected to show only the axis representing *Pterostichus*, because we wanted to mimic, as much as possible, the presentation of similar data by Newsome et al. (2007) for comparison. We do not advocate the single-axis presentation and suggest following the guidelines provided by Phillips and Gregg (2003), especially when the number of diet items exceeds $n + 1$ isotopes.

The simulations we present here are, if anything, very conservative. First, we only used five food sources and only three different habitats. In reality, most animals, even

specialized foragers, usually consume more than five food sources (Bolnick et al. 2003, Tinker et al. 2008). Second, the isotopic variation among habitats in our study is well within the observed variation in other systems (Stewart et al. 2003, Lee et al. 2005, Darimon et al. 2007). In fact, if one considers the differences between marine and freshwater habitats (Ben-David et al. 1997b), or forests and grasslands (Feranec and McFadden 2006), our simulations represent a gross underestimate of the potential effects of habitat specializations of individuals in a single population. Furthermore, in modeling consumers feeding on only one prey (model 3), we selected an item that had moderate habitat-derived variation (*Pterostichus*) rather than the most extreme one (*Harpaphe*). Therefore, the scenarios represented by our models are neither extreme nor unique. Yet, our models illustrate that in addition to knowledge of all potential food sources and the spread of prey isotopic signatures (Bearhep et al. 2004, Matthews and Mazumder 2004, Araujo et al. 2007, Newsome et al. 2007), knowledge of habitat-derived differences in stable isotope values, and an understanding of habitat use and foraging behavior of individuals, are critical for the correct quantification of the ecological niche. We also suspect that future simulation models similar to ours that will address the effects of diet quality, elemental routing, tissue turnover rates and variation in the length of the assimilation period (Karasov and Martinez del Rio 2007), will demonstrate that the relation between the isotopic and ecological niches is convoluted, and thus attempts to quantify the ecological niche with isotopic data may be complicated. Indeed, Semmens et al. (2009) proposed hierarchical Bayesian mixing models that incorporate both dietary differences across multiple population levels and variance in diet sources. In their analyses Semmens et al. (2009) found that variation in diet choice among individuals and subpopulations can significantly influence the niche width of a population. Their model, like ours, demonstrates that prey isotopic variability, in addition to, or in the absence of diet or ecological variability, can result in a broader than anticipated ecological niche (Semmens et al. 2009).

Because it is rarely possible to obtain data to account for all factors that enable the conversion of isotopic data to

reliable estimates of ecological niches, we think that efforts should be directed elsewhere. Indeed, we believe the principal value of stable isotope analysis in vertebrate ecology is the ability to investigate the responses of individuals to the conditions they encounter in their environment (such as habitat and food availability, competition, predation and predation risk; Ben-David et al. 1997a, 2004, Stewart et al. 2003, Lee et al. 2005), and ultimately to explore how the variable responses of individuals influence fitness components (such as reproductive success and survival; Bolnick et al. 2003, Darimont et al. 2006), which in turn, affect the dynamics of populations, community structure (Post et al. 2008) and ecosystem processes (Ben-David et al. 1998, 2005).

Acknowledgements - We thank D. Doak for his suggestions and assistance with constructing the models. 'We are grateful to I. Abernathy, C. Boser, D. Caton, R. Choi, D. Haynes, K. Keffer, S. Scott, C. Shanley, K. Van Dyke and G. Yenni and to all of our EARTHWATCH volunteers for assistance in the field and E. Averil for her help in the lab. M. Araujo, R. O. Hall, A. Krist, C. Martinez del Rio and W. P. Smith provided valuable comments on earlier versions of this manuscript. This research was funded in part by the USDA Forest Service Pacific Northwest Research Station, Univ. of Wyoming, and an EARTHWATCH grant to W. P. Smith and S. Pyare. MBD was supported by a grant from the National Science Foundation (DEB-0454474).

References

- Araujo, M. S. et al. 2007. Using $\delta^{13}\text{C}$ stable isotopes to quantify individual-level diet variation. - *Oecologia* 152: 643-654.
- Bearhop, S. et al. 2004. Determining trophic niche width: a novel approach using stable isotope niches. - *J. Anim. Ecol.* 73: 1007-1012.
- Ben-David, M. 1999. Diet analysis of northern goshawks using stable isotope ratios. Progress report. - In: Titus, K. et al. (eds), Goshawk ecology and habitat relationships on the Tongass National Forest. Federal Aid in Wildlife Restoration 1999, field progress report. Alaska Dept Fish Game Study SE-4-2.
- Ben-David, M. et al. 1997a. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. - *Oecologia* 111: 280-291.
- Ben-David, M. et al. 1997b. Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. - *Can. J. Zool.* 75: 803-811.
- Ben-David, M. et al. 1998. Social behavior and ecosystem processes: river otter latrines and nutrient dynamics of terrestrial vegetation. - *Ecology* 79: 2567-2571.
- Ben-David, M. et al. 2004. Consumption of salmon by Alaskan brown bears: a tradeoff between nutritional requirements and the risk of infanticide? - *Oecologia* 138: 465-474.
- Ben-David, M. et al. 2005. Communication in river otters: creation of variable resource sheds for terrestrial communities. - *Ecology* 86: 1331-1345.
- Blundell, G. M. et al. 2002. Sociality in river otters: cooperative foraging or reproductive strategies? - *Behav. Ecol.* 13: 134-141.
- Bolnick, D. et al. 2003. The ecology of individuals: incidence and implications of individual specialization. - *Am. Nat.* 161: 1-28.
- Borror, D. J. and White, R. E. 1998. A field guide to the insects: America north of Mexico. - Houghton Mifflin.
- Callopy, M. W. and Koplin, J. R. 1983. Diet, capture success, and mode of hunting by female American kestrels in winter. *Condor* 85: 369-371.
- Darimont, C. T. et al. 2007. Stable isotopic niche predicts fitness of prey in a wolf-deer system. - *Biol. J. Linn. Soc.* 90: 125-137.
- Dawson, T. E. et al. 2002. Stable isotopes in plant ecology - *Annu. Rev. Ecol. Syst.* 33: 507-559.
- DeNiro, M. J. and Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. - *Geochim. Cosmochim. Acta* 45: 341-351.
- Ehleringer, J. R. et al. 1993. Stable isotopes and plant carbon-water relations. - Academic Press.
- Elliot, C. L. and Cowan, C. A. 1983. The food habits of an American kestrel (*Falco sparverius*...) in interior Alaska. - *Murrelet* 64: 63-64.
- Erhardt, E. B. 2007. 'SISUS: stable isotope sourcing using sampling Retrieved [15 November 2007] - <<http://statacumen.com/sisus/>>.
- Feranec, R. S. and MacFadden, B. J. 2000. Evolution of the grazing niche in Pleistocene mammals from Florida: evidence from stable isotopes. - *Palaeogeogr. Palaeoclimatol.* 162: 155-169.
- Feranec, R. S. and MacFadden, B. J. 2006. Isotopic discrimination of resource partitioning among ungulates in C_3 -dominated communities from the Miocene of Florida and California. - *Paleobiology* 32: 191-205.
- Flaherty, E. A. et al. Diet and food availability: implications for foraging and dispersal of Prince of Wales northern flying squirrels across managed landscapes. - *J. Mamm. in press*.
- Genner, M. J. et al. 1999. Niche segregation among Lake Malawi cichlid fishes? Evidence from stable isotope signatures. - *Ecol. Lett.* 2: 185-190.
- Herreman, J. K. et al. 2009. Evidence of bottom-up control of diet driven by top-down processes in a declining harbor seal (*Phoca vitulina richardsi*; population. - *Mar. Ecol. Prog. Ser.* 374: 287-300.
- Karasov, W. H. and Murrin, C. 2007. Physiological ecology. - Princeton Univ. Press.
- Kaston, B. et al. 1978. How to know the spiders. - McGraw-Hill.
- Kelly, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian ecology. - *Can. J. Zool.* 78: 1-27.
- Lajtha, K. and Marshall, J. D. 1994. Sources of variation in the stable isotopic composition of plants. - In: Lajtha, K. and Michener, R. H. (eds), Stable isotopes in ecology and environmental science. Blackwell, pp. 1-21.
- Layman, C. A. et al. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? - *Ecology* 88: 42-48.
- Lee, S. H. et al. 2005. Regional and seasonal feeding by bowhead whales *Balaena mysticetus* as indicated by stable isotope ratios. - *Mar. Ecol. Prog. Ser.* 285: 271-287.
- Matthews, B. and Mazunder, A. 2004. A critical evaluation of intrapopulation variation of $\delta^{13}\text{C}$ and isotopic evidence of individual specialization. - *Oecologia* 140: 361-371.
- McCutchan, J. H. Jr. et al. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. - *Oikos* 102: 378-390.
- Mowat, G. and Heard, D. C. 2006. Major components of grizzly bear diet across North America. - *Can. J. Zool.* 84: 473-489.
- Newsome, S. D. et al. 2007. A niche for isotopic ecology. - *Front. Ecol. Environ.* 5: 429-436.
- Peterson, B. J. and Fry, B. 1987. Stable isotopes in ecosystem studies. - *Annu. Rev. Ecol. Syst.* 18: 293-320.
- Phillips, D. L. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. - *Oecologia* 127: 166-170.

- Phillips, D. L. and Koch, P. L. 2002. Incorporating concentration dependence in stable isotope mixing models. - *Oecologia* 130: 114-125.
- Phillips, D. L. and Gregg, J. W. 2003. Source partitioning using stable isotopes: coping with too many sources. - *Oecologia* 136: 261-269.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. - *Ecology* 83: 703-718.
- Post, D. M. et al. 2008. Intraspecific variation in a predator affects community structure and cascading trophic interactions. - *Ecology* 89: 2019-2032.
- Power, M. et al. 2002. Growth and dietary niche in *Salvelinus alpinus* and *Salvelinus fontinalis* as revealed by stable isotope analysis. - *Environ. Biol. Fish.* 64: 75-85.
- Schneider, K. et al. 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios ($\delta^{15}\text{N}/\delta^{14}\text{N}$). - *Soil Biol. Biochem.* 36: 1769-1774.
- Semmens, B. X. et al. 2009. Quantifying inter- and intra-population niche variability using hierarchical Bayesian stable isotope mixing models. - *PLoS One* 4: 1-9.
- Stewart, K. M. et al. 2003. Niche partitioning among mule deer, elk and cattle: do stable isotopes reflect dietary niche? - *Ecoscience* 10: 297-302.
- Tinker, M. T. et al. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. - *Proc. Natl. Acad. Sci. USA* 105: 560-565.
- USDA Forest Service 1997. Land and resource management plan - Tongass National Forest. - US For. Service R10-MB-338dd, **Alaska Region, Juneau.**
- Van Horne, B. 1983. Summertime activity pattern of the longrail vole in Alaska. - *Ecography* 6: 199-203.
- White, R. E. 1983. A field guide to the beetles of North America. - Houghton Mifflin.
- Zar, J. H. 1999. Biostatistical analysis (4th ed.), - Prentice-Hall.