Biological Journal of the Linnean Society, 2007, **90**, 125–137. With 3 figures

Stable isotopic niche predicts fitness of prey in a wolf–deer system

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Received 26 August 2005; accepted for publication 1 March 2006

Interindividual variation in niche presents a potentially central object on which natural selection can act. This may have important evolutionary implications because habitat use governs a suite of selective forces encountered by foragers. In a free-living native black-tailed deer, *Odocoileus hemionus*, population from coastal British Columbia, we used stable isotope analysis to identify individual variation in foraging niche and investigated its relationship to fitness. Using an intragenerational comparison of surviving and nonsurviving *O. hemionus* over 2 years of predation by wolves, *Canis lupus,* we detected resource-specific fitness. Individuals with isotopic signatures that suggested they foraged primarily in cedar (*Thuja plicata*)-dominated and low-elevation hemlock (*Tsuga heterophylla*)-dominated forest stands were more likely to be killed by *C. lupus*. High-quality forage in *T. plicata* stands, as indexed by protein content, may be involved in maintaining this foraging phenotype. Moreover, nonsurvivors diverged more than survivors from median isotopic signatures, suggesting selection against foraging specialization. Stable isotope analysis provides a novel opportunity to integrate ecological and selective landscapes in order to identify underlying ecological mechanisms of selection and provide insight into the maintenance of variability. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **90**, 125–137.

ADDITIONAL KEYWORDS: *Canis lupus* – foraging behaviour – individual niche – natural selection – *Odocoileus hemionus* – predation – stable isotope analysis.

INTRODUCTION

Variation in niche presents a central and influential object on which natural selection can act. Habitat use, which encompasses multiple niche dimensions, determines the selective landscape and consequently influences many traits, including physiology, morphology, and behaviour. Only rarely, however, do evolutionary studies consider variability in niche at the level of the individual, or its consequences (Bolnick *et al*., 2003), perhaps because individual niche is difficult to measure. We estimated the foraging component of individual niche in a population using stable isotope analysis and examined its relationship to survival, a common fitness measure, under the risk of lethal predation. The extent to which any resource-specific fitness was linked to spatial behavioural traits, as opposed to social constraints such as natal philopatry or competition, would determine how evolution of those traits, and potentially also of the niche itself, would proceed by natural selection.

Evolution by natural selection would depend fundamentally on traits related to use of space being: (i) variable within the population, (ii) at least partially heritable, and (iii) associated with differences in relative fitness (Endler, 1986). First, as originally proposed by Van Valen (1965), individuals can diverge considerably in resource use within gender or age class. In a recent review, Bolnick *et al*. (2003) suggested that individual specialization in niche within age and gender class is widespread, but its extent varies widely among species and populations. Second, intrapopulation variability in niche is likely to have some heritable element; investigations on a variety of

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*Corresponding author. E-mail: cdarimon@uvic.ca taxa have noted genetic components to habitat preference (reviewed by Jaenike & Holt, 1991). Third, resource-specific fitness differences have traditionally been difficult to observe in the field, especially at the individual level. As a result, most studies examine changes in behavioural or foraging strategies under various levels of predation at a population level (reviewed by Lima & Dill, 1990). Embedded in these studies, however, is an understanding that some areas or niches are clearly more dangerous than are others.

Niches vary not only in predation risk but also in their profitability, and foragers can face tension when high-quality niches are also dangerous. In a large number of laboratory and field experiments, foragers have been shown to reduce energetic or protein gain in exchange for decreased risk (reviewed by Sih, 1987; Lima & Dill, 1990; Abrams, 1991). To our knowledge, however, assessments over a long period and under natural field conditions that estimates both niche quality and fitness at the individual level are very rare (but see Holbrook & Schmitt, 1992; Annett & Pierotti, 1999; Golet *et al*., 2000 for examples of association between individual niche and reproduction).

These gaps in the literature exist because, until recently, estimating individual niche has been problematic. Dietary dimensions are investigated most frequently, but traditional analyses (i.e. faecal and gut contents) are often limited by theoretical and logistical issues (reviewed by Bearhop *et al*., 2004). Individual niche can now be assessed with stable isotope analysis, which can estimate use of food resources by consumers over potentially long periods (reviewed by Peterson & Fry, 1987; Rundel, Ehleringer & Nagy, 1989; Kelly, 2000). For example, isotopic signatures in herbivores reflect those of the plants they consume (e.g. Stewart *et al*., 2003), which themselves vary among and within areas and species, mediated by abiotic and biotic factors (Adams & Grierson, 2001; Dawson *et al*., 2002; Mathewson, Hocking & Reimchen, 2003; Wilkinson, Hocking & Reimchen, 2005).

Isotopic samples are valuable because they can estimate long-term processes, which can signal persistent phenotypic variation (Bolnick *et al*., 2003). Metabolically inert tissue, such as hair, reflects diet only during growth and therefore provides an estimate of niche averaged over the growth period (Darimont & Reimchen, 2002).

Isotopic signatures not only estimate niche but also potentially track physiological processes. Individuals of different ages and genders may have different nutritional physiology, which may affect signatures (e.g. Hobson, McLellan & Woods, 2000; Roth & Hobson, 2000). Also, there is currently debate as to whether nutritional condition influences nitrogen signatures (e.g. Hobson, Alisaukas & Clark, 1993; but see Vanderklift & Ponsard, 2003). Gannes, O'Brien, & Martinez del Rio (1997) cautioned that these potentially confounding factors should be addressed to relate unambiguously isotopic signatures to foraging ecology. Relevant to our study is that age, gender and nutritional condition may be important predictors of survival in prey populations; predators often selectively kill young, old, or weakened individuals, as well as members of one gender (e.g. Temple, 1987; Shine *et al*., 2001).

Wolf (*Canis lupus*)–ungulate communities are interesting model systems for investigating predation (e.g. Peterson, Page & Dodge, 1984; Post *et al*., 1999; Vucetich & Peterson, 2004). Ungulates, and specifically deer (*Odocoileus* spp.), have wide potential niches (e.g. (Kirchhoff & Larson, 1998) and often variable isotopic signatures (e.g. Stewart *et al*., 2003). Moreover, the life histories of *Odocoileus* are shaped decidedly by their predators, which often include *C. lupus* (Leslie, Bowyer & Kie, 1999).

Monitoring predation can permit simultaneous comparisons between living and dead individuals in a population, and this can provide direct evidence for selection and its targets (Endler, 1986; Shine *et al*., 2001). We conducted such an intragenerational comparison of surviving and nonsurviving black-tailed deer, *O. hemionus,* subject to predation by *C. lupus*, in order to: (1) test whether stable isotope analysis reliably tracks the niche of *O. hemionus* prey, (2) test whether different niches carry different probabilities of mortality by predation, and if so, (3) examine how the niches of survivors and nonsurvivors differ. We also examined the potential association between forage quality and risk of predation. An inductive process defined our approach; we predicted that predation would be nonrandom with respect to isotopic niche but we did not predict how survivors might differ from nonsurvivors ecologically.

METHODS

STUDY AREA

On the central coast of British Columbia, Canada (Fig. 1), coniferous forests dominate this archipelago. This nearly road-less and mostly unsettled region is characterized by a wet and temperate climate (Pojar & Mackinnon, 1994). There is a wide potential niche available to *O. hemionus*, with dozens of suitable herbs, shrubs and trees (Kirchhoff & Larson, 1998). This vegetative diversity is structured by nutrient and moisture regimes that dictate which tree species dominate (Krajina, 1965).

Canis lupus can occur on all landmasses in the archipelago (Paquet *et al*., 2006), and their potential prey base is diverse, including *O. hemionus*, moose (*Alces alces*), mountain goats (*Oreamnos americanus*), ursids, mustelids, rodents, birds, and marine resources (Darimont, Reimchen & Paquet, 2003; Darimont *et al.*, 2004; Price *et al.*, 2005). During the periods of this study (winter and spring), however, *O. hemionus* comprise more than 80% of the items in *C. lupus* faeces (Darimont *et al.*, 2004; C.T. Darimont, unpubl. data).

Our samples originated from three sampling areas: Haida Gwaii, 'central coast multiwatershed', and 'central coast – Yeo Island'. We sampled Haida Gwaii *O. hemionus* with known gender, nutritional condition and size (as a proxy for age) to examine the potential influence of these factors on isotopic signature. To address the relationship between individual niche and survival, we then sampled surviving and nonsurviving *O. hemionus* from the adjacent central coast (Fig. 1). Multiwatershed samples originated from sites across roughly 1500 km^2, consisting of four mainland and four island watersheds, which are within the territories of eight different *C. lupus* social groups. To gain increased resolution on the potential ecological differences between surviving and *C. lupus*-killed *O. hemionus*, we sampled intensively Yeo Island (100 km^2), which included a watershed sampled in the multiwatershed surveys. The south and west portions of Yeo Island had undergone logging within the last 8 years. One social group of *C. lupus* has used this island continuously for at least 5 years and numbered five to ten animals (counted in late autumn).

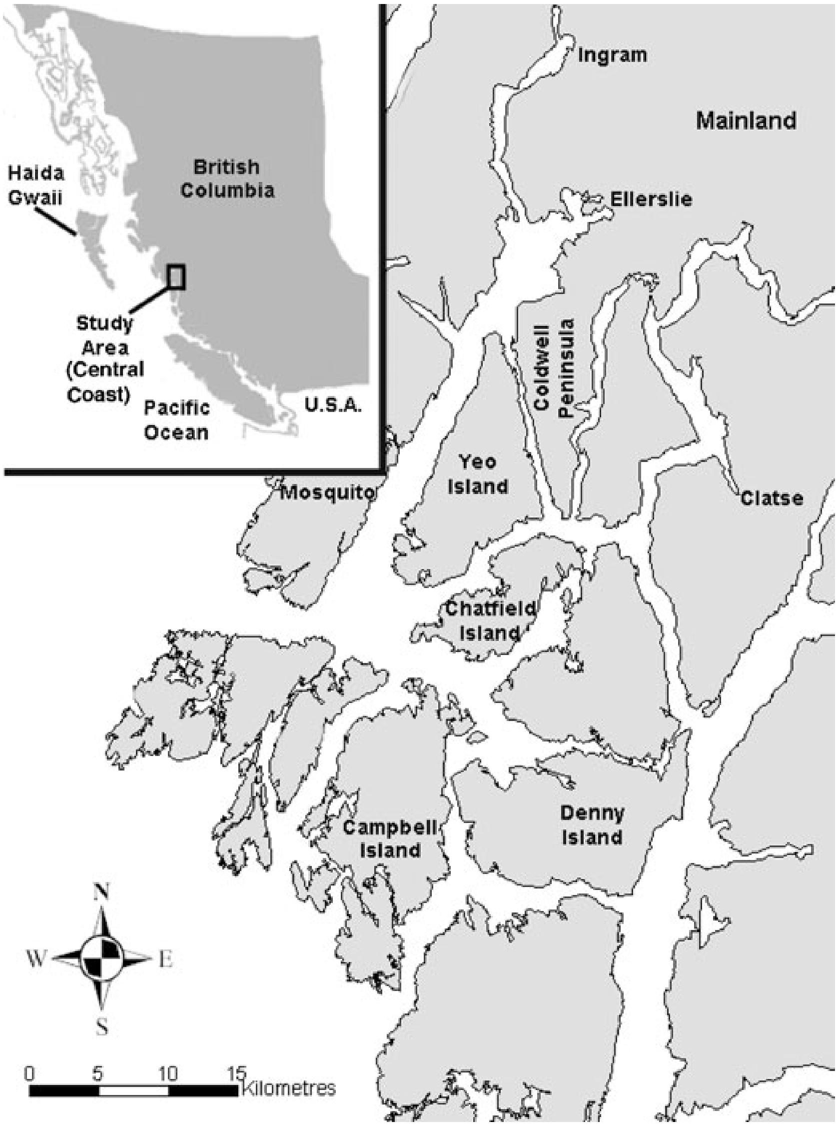

Figure 1. Study area where isotopic samples from surviving and nonsurviving deer (*Odocoileus hemionus*) under risk of predation by wolves (*Canis lupus*) were collected; central coast of British Columbia during spring 2002 and 2003. Nine sampling locations are named. See inset for Haida Gwaii, from where additional samples originated.

ISOTOPIC DATA FROM *O. HEMIONUS* OF HAIDA GWAII – AGE, GENDER, AND NUTRITIONAL CONDITION

To examine the potential influence of age, gender, and nutritional condition on stable isotopic signatures, we sampled hair from 35 (17 male and 18 female) *O. hemionus* killed in late September and October 1997 in a government-sponsored eradication program on Reef Island (2 km^2) in the Haida Gwaii archipelago (S. Sharpe & H. Schwantje, unpubl. data), where *O. hemionus* are an introduced species (Cowan & Guiguet, 1975; Fig. 1). A veterinarian scored each individual's gender, as well as nutritional condition on a scale of 1–5 with 0.5 increments, based on the amount of fat visible on the back and ribs, and surrounding the organs (Kistner, Trainer & Hartmann, 1980). Teeth were unavailable for age estimation, so we used shoulder height as an age proxy, and consider this a good surrogate because gender and nutritional condition were known (and controlled for in analyses). *O. hemionus* take several years to attain maximum size, and the variation in size in adults sampled across British Columbia is 67.5–90 cm (Cowan & Guiguet, 1975). Shoulder height in our samples ranged from 53 to 82 cm, which is greater in relative range (range divided by lower value), so our samples likely included yearlings to adults of various ages. In sika deer (*Cervus nippon yesoensis*), Suzuki *et al*. (2001) found that values for shoulder height were predicted well from age data.

ISOTOPIC DATA FROM *O. HEMIONUS* OF CENTRAL COAST – MULTIWATERSHED AND YEO ISLAND

We sampled 'survivors', or individuals that survived to the spring moult, by collecting their winter hair, which had been shed in day beds. In late May and early June, we sampled random 1-km upslope transects, starting at either sea level or a low-elevation road, and often terminating in the subalpine region (up to 800 m). We conducted two transects in each of eight watersheds in 2002, and six on Yeo Island in 2003, supplemented by opportunistic shorter transects in areas not well represented by previous sampling on Yeo Island. We also collected seven samples from *O. hemionus* beds on the closest landmass, Coldwell Peninsula, where we occasionally observed Yeo Island *C. lupus* (Fig. 1). We used these samples to examine the possibility that most or all of the nonsurviving *O. hemionus* ('nonsurvivors', see below) originated from this location and not from Yeo Island.

During the same periods and in the same areas, we also collected faeces from *C. lupus*, which often contained the remains of *O. hemionus*, including their winter hair. We refer to these samples as 'nonsurvivors', as these *O. hemionus* died prior to or during the spring moult. We sampled these faeces from transects established earlier in our research program, which covered a broad range of available habitat for *O. hemionus* and *C. lupus*, following wildlife trails in riparian areas adjacent to the shoreline or waterways and on forest ridgelines. Transects also followed power-line right-of-ways and road networks. Faeces decompose rapidly in this wet environment (Wallmo *et al*., 1962; C.T. Darimont, unpubl. data), so we assumed that *O. hemionus* in faeces were killed in the winter and spring prior to or during the spring moult. We soaked faeces in hot water, and then rinsed the remains in a 1-mm mesh sieve until only hair, bones, and other macroscopic components remained. Identification of *O. hemionus* hair followed Ciucci *et al*. (1996).

All hair samples from *O. hemionus* in this study (central coast and Haida Gwaii, British Columbia; Calgary Zoo, Alberta [see below]) reflect the same dietary (and isotopic) time windows and age classes. Isotopic signatures in winter hair collected from day beds (survivors), *C. lupus* faeces (nonsurvivors), and carcasses from management control (Haida Gwaii) tracked the foraging behaviour of *O. hemionus* between July and October. Winter pelage grows from mid July to the end of October and is carried through the winter before shedding in the spring, when the summer pelage begins to grow (until July when winter pelage again re-grows; Cowan & Raddi, 1971). We observed shedding in our study area between April and June. *O. hemionus* are born in the spring and summer and thus all individuals were at least a few months old at the time of sampling. Once fawns moult into their first winter coat, their pelage cannot be separated from that of older individuals (Scott & Shackleton, 1980; Milne, Harestad & Atkinson, 1989).

LINKING *O. HEMIONUS* HABITAT TO SURVIVORSHIP – YEO ISLAND

To allow insight into how isotopic signatures in *O. hemionus* hair can give information about their niche (i.e. food resources consumed), we collected habitat data and fresh *O. hemionus* pellets ($N = 84$), which contain leftover plant material. Isotopic data from pellets describe short-term diet (i.e. over the last several days). Signatures of herbivore faeces are similar to bulk diet, and variability among individuals given the same feed is small (Jones *et al*., 1979; Sponheimer *et al*., 2003a, b). We conducted pellet transects on Yeo Island in September 2003, when *O. hemionus* are roughly midway through winter pelage growth (Cowan & Raddi, 1971). Five uphill transects (~1.5–2.5 km) began from either sea level or a low-elevation road and terminated at subalpine summits. Although following a compass bearing, we zigzagged to search a belt at least 50 m wide. At collection sites, we classified forest cover into five categories based on the dominant tree species (> 50% occurrence): cedar (*Thuja plicata*), pine (*Pinus contorta*), disturbed areas (clearcuts and areas within 500 m of clearcuts); low-elevation hemlock (*Tsuga heterophylla*; below 425 m) and high-elevation *T. heterophylla* (above 425 m). Unlike other stand types, *T. heterophylla* spans a large range in elevation, and has corresponding variance with elevation in carbon signatures (Pearson's correlation; $r^2 = 0.860$; $P < 0.001$). Accordingly, we divided *T. heterophylla* forests into two categories, below and above 425 m, an elevation at which we observed a sharp discontinuity in signatures.

To provide visual interpretation of how forest stand types with differing isotopic signatures could influence the signatures in *O. hemionus*, we placed *O. hemionus* pellet and *O. hemionus* hair values on a comparable isotopic level (see Fig. 3). Accordingly, isotopic signatures in pellets were corrected for net fractionation from forage-faeces (–0.9 and 2.2‰) and from forage-hair (3.2 and 3.8‰) for carbon and nitrogen, respectively (based on grand means of multiherbivore experiments; Sponheimer *et al*., 2003a, b, c; M. Sponheimer, *pers. comm*., 2004).

Using the same *O. hemionus* pellets, we were able to evaluate resource quality for *O. hemionus* in different stand types. We examined carbon to nitrogen ratios and percent nitrogen (hereafter C : N and %N) in pellets. These metrics have been used to assess the protein quality of ungulate food in both forage and ungulate faeces (e.g. van der Wal *et al*., 2000; Sponheimer *et al*., 2003c).

STABLE ISOTOPE PREPARATION AND LABORATORY ANALYSIS

We sonicated hair samples (between ten and 30 hairs in each) in distilled water, then soaked them in 2 : 1 chloroform : methanol solution for approximately 24 h to remove oils and debris. After drying at 60 °C for at least 48 h for hair and 2 weeks for pellets, we powdered samples in a Wig-L-Bug grinder (Cresent Dental Co, Chicago, IL, USA). Approximately 1 mg was subsampled for continuous-flow isotope ratio mass spectrometry analysis at the stable isotope facility, University of Saskatchewan, using a Europa Scientific ANCA NT gas/solid/liquid preparation module coupled to a Europa Scientific Tracer/20 mass spectrometer. Isotopic signatures are expressed in delta notation (δ) as ratios relative to PeeDee limestone (carbon) and atmospheric N_2 (nitrogen) standards as follows: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - (1) \times 1000$, where X is ^{13}C or ^{15}N, and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. This data set also provided C : N and %N results. Thirteen replicates on separate mass spectrometer runs showed precision averaging of 0.05 (±0.04 SD)‰ for carbon and 0.06 (±0.05 SD)‰ for nitrogen.

STATISTICAL ANALYSES

For data on *O. hemionus* from Haida Gwaii, we used a multivariate general linear model to examine potential contributions of age (shoulder height), gender, nutritional condition, and all two-way interaction terms in explaining *O. hemionus* $\delta^{13}C$ and $\delta^{15}N$.

We used a conservative subsampling protocol in comparisons of survivors and nonsurvivors. Isotopic signatures could be similar between or among individuals because of comparable diets. However, although our field sampling was broad geographically and *O. hemionus* densities were high in these productive forests, it was also possible that we collected the same individual more than once in bed sites or faeces. Therefore, if two or more samples from the same area had highly similar isotopic signatures (±mean measurement error and SD), we randomly removed all but one. It may be that in so doing we unnecessarily excluded individuals, although this approach resulted in the removal of only one of 54 samples in the multi-watershed data and 16 of 109 samples from Yeo Island, but inclusion of all samples yielded comparable results in all analyses.

We were concerned that the mechanical and chemical treatment of hair during digestion by *C. lupus* could affect the isotopic signatures in *O. hemionus* hair. Accordingly, we conducted one wild and three zoo feeding trials in which *O. hemionus* carcasses were consumed by *C. lupus*. For each trial, we calculated the mean isotopic signatures, among three to five samples each, of hair from the carcasses and within the resulting *C. lupus* faeces. Digestion caused a marginal but consistent increase in isotopic signatures across trials. Mean shifts in $\delta^{15}N$ and $\delta^{13}C$ were +0.84 (±0.66 SD; range, 0.30–1.66) and +0.49 (±0.15 SD; range, 0.28–0.61), respectively. The grand means were thus subtracted from faecal hair samples (nonsurvivors) to correct for digestion effects.

We investigated potential differences among surviving and *C. lupus*-killed *O. hemionus* using three techniques. First, we used chi-square analysis to determine if there was an association between survivorship and areas of isotopic niche space inhabited by *O. hemionus*. We separated isotopic niche space, which was distributed continuously along two axes, into four quadrats or categories. Quadrat/category assignments were based on *Z*-scores of each individual *O. hemionus* for both isotopes (difference between sample and mean, standardized by the SE; SPSS Inc., Chicago, IL, USA), with category divisions at median values (which are less sensitive to outliers than are mean values).

Second, we used an information-theoretic approach to predict survivorship among *O. hemionus* based on more complex components of their isotopic niche. From a priori hypotheses, we developed a set of candidate logistic regression models, restricted to combinations of one to three isotopic parameters and two-way interaction terms. For 2002 multiwatershed models, we used *Z*-scores calculated for each valley separately (to remove interwatershed effects; see Results), whereas 2003 Yeo Island models included only untransformed data. For both analyses, in addition to δ^{13}C and δ^{15}N signatures, we included a 'Euclidean distance' metric as a third parameter, which calculates for two or more traits (i.e. δ^{13}C and δ^{15}N signatures) the deviation of a sample from central tendency (the population median in this case, which is less sensitive to outliers than is the mean). Measured in *Z*-scores, this metric ensures both traits contribute equally to this distance and it has been used to test for stabilizing selection across multiple traits simultaneously (Manley, 1985). We examined 2002 multiwatershed and 2003 Yeo Island data separately because they were collected on different spatial scales.

A Hosmer–Lemeshow goodness-of-fit statistic based on global models (i.e. all possible parameters) showed that the data did not depart from a logistic-regression model for the multiwatershed ($P = 0.659$) and Yeo Island ($P = 0.185$) data. Moreover, both models performed well ($P = 0.001$ and $P = 0.002$, respectively). We found no evidence of multicollinearity among predictor variables (variance inflation factors range, 1.05–1.24 and 1.07–1.33 for the two areas, respectively).

For each model, we calculated Akaike information criteria (AIC) following the general formula: $\text{AICc} = -2(\log \text{likelihood}) + 2\text{K} + 2\text{K}(\text{K} + 1)/(\text{n} - \text{K} - 1)$, where K is the number of parameters and n is the sample size. We then evaluated ΔAICc to select best approximating model(s) and make appropriate inferences, using $\Delta\text{AICc} < 2$ to describe the top model set (offering substantial level of empirical support). Finally, we summed Akaike weights (ω_i) across the top model set for each variable to rank them according to importance (Burnham & Anderson, 1998).

Third, to cross-validate earlier results, we conducted discriminant function analyses to determine which variables best discriminated between surviving and nonsurviving *O. hemionus*. All tests were performed using SPSS 11.0.

RESULTS

ISOTOPIC DATA FROM *O. HEMIONUS* OF HAIDA GWAII – AGE, GENDER, AND NUTRITIONAL CONDITION

Age, gender, and nutritional condition did not affect isotopic signatures of free ranging *O. hemionus* from Haida Gwaii. Separate models for each isotope explained a very low proportion of overall variance (δ^{15}N model, adjusted $R^2 < 0.001$; δ^{13}C model, adjusted $R^2 = 0.011$). No effect was significant in multivariate tests (all $P > 0.21$).

ISOTOPIC DATA FROM *O. HEMIONUS* OF CENTRAL COAST – MULTIWATERSHED AND YEO ISLAND

Nitrogen and carbon signatures of *O. hemionus* of central coast BC were spatially variable, indicating diversity in foraging niche. In 2002, when we sampled *O. hemionus* hair ($n = 53$) from eight watersheds, δ^{15}N ranged from –0.44–6.46 with a mean of 3.66 (±2.00 SD), whereas δ^{13}C values varied from –29.43 to –25.61, averaging –27.87 (±0.77 SD). Nitrogen signatures in *O. hemionus* varied by watershed in which they where sampled ($F_{7,45} = 7.81$; $n = 53$; $P < 0.001$).

Even within Yeo Island, there was substantial variation in foraging niche. Values in *O. hemionus* hair ($n = 93$), ranged from –0.04–4.69 with a mean of 2.45 (±1.17 SD) for δ^{15}N, whereas δ^{13}C varied from –29.17 to –25.71, averaging –27.28 (±0.79 SD).

ISOTOPIC COMPARISON OF SURVIVING AND *C. LUPUS*-KILLED *O. HEMIONUS*

Surviving and *C. lupus*-killed *O. hemionus* occupied different areas of isotopic niche space. In multiwatershed comparisons, *C. lupus*-killed *O. hemionus* ($N = 23$) occurred disproportionately more than did survivors ($N = 30$) in quadrats characterized by lower δ^{15}N (Fig. 2A; $\chi^2 = 18.097$; d.f. = 3; $N = 53$; $P < 0.001$). On Yeo Island, *C. lupus*-killed *O. hemionus* ($N = 39$) showed a similar pattern, but they also occurred disproportionately more than did survivors ($N = 54$) in the quadrat defined by relatively enriched δ^{15}N and depleted δ^{13}C (Fig. 2B; $\chi^2 = 18.097$; d.f. = 3; $N = 93$; $P < 0.001$). Results were similar, using data uncorrected for digestion effects ($\chi^2 = 7.79$; d.f. = 3; $N = 53$; $P = 0.050$ and $\chi^2 = 7.94$; d.f. = 3; $N = 93$; $P = 0.047$ for multiwatershed and Yeo Island, respectively).

To further evaluate which aspects of individual isotopic niche space best differentiated *C. lupus*-killed from surviving *O. hemionus*, we used AIC based on output from logistic regression analyses. In multiwatershed data, all three models in the top model set contained δ^{15}N (Table 1). Summing Akaike weights across top models ranked δ^{15}N ($\Sigma\omega_i = 0.65$) higher than δ^{13}C and their interaction term ($\Sigma\omega_i = 0.47$ and 0.15) by factors of 1.4 and 4.4, respectively. The direction of parameter coefficients indicated that lower δ^{13}C and especially δ^{15}N signatures increased the probability of mortality. Our Euclidean distance metric did not occur in any of the top models. Discriminant function

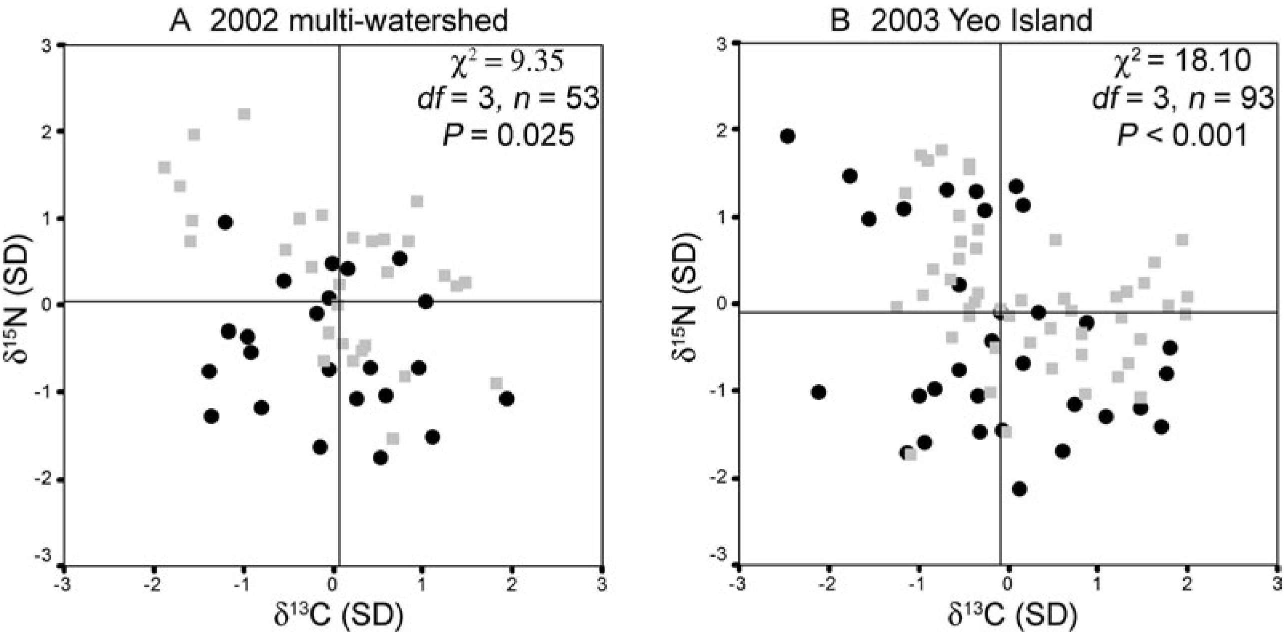

Figure 2. δ^{15}N and δ^{13}C of surviving (■) and nonsurviving (●) deer (*Odocoileus hemionus*) under risk of predation by wolves (*Canis lupus*), in coastal British Columbia in 2002 and 2003. Data are *Z*-scores, calculated (A) separately in each of eight watersheds sampled in 2002, and (B) for all of Yeo Island (100 km^2), which was sampled intensively in 2003. Reference lines are drawn at medians.

Table 1. Top logistic regression model sets to predict the probability of mortality of deer (*Odocoileus hemionus*) from predation by wolves (*Canis lupus*) based on isotopic signatures of survivors and nonsurvivors, with model structure, number of parameters (# K), deviance, and corresponding (ΔAIC_c) and Akaike weight (ω_i)

Dataset	Model	# K	Deviance	AIC$_c$	ΔAIC$_c$	ω_i
Multiwatershed	zδ15N, zδ13C	3	55.64	62.13	0.00	0.32
	zδ15N	2	58.97	63.21	1.08	0.19
	zδ15N, zδ13C, zδ15N × zδ13C	4	54.83	63.67	1.54	0.15
Yeo Island	zδ15N, zδ13C, Euc	4	110.46	118.91	0.00	0.39
	zδ15N, zδ13C, zδ15N × zδ13C	4	111.17	119.62	0.71	0.27

Samples in multiwatershed dataset collected from eight watersheds on the central coast of British Columbia during winter and spring 2002 (*N* = 53 *O. hemionus*: 30 survivors, 23 nonsurvivors). Samples in Yeo Island dataset collected on Yeo Island on the central coast of British Columbia during winter and spring 2003 (*N* = 93 *O. hemionus*: 54 survivors, 39 nonsurvivors). zδ15N and zδ13C are nitrogen and carbon isotopic signatures, respectively, both in *Z*-scores calculated separately in each valley. 'Euc' is Euclidean distance to population median, a measure of distance from central tendency in population isotopic niche.

analysis provided output consistent with modelling results; pooled within-group correlations between discriminating variables and standardized canonical discriminant functions were highest for δ^{15}N at 0.866, low for δ^{13}C at 0.079, and negligible for Euclidean distance at 0.002.

In 2003 (Yeo Island), the three top models all contained δ^{15}N and δ^{13}C parameters, whereas their interaction term and Euclidean distance occurred twice (Table 1). Parameters δ^{15}N and δ^{13}C ranked equivalently ($\Sigma\omega_i = 0.92$), about 1.4 and 1.7 times higher than Euclidean distance and their interaction term ($\Sigma\omega_i = 0.64$ and 0.53, respectively). The direction of parameter coefficients was similar to that in multiwatershed models, though lower δ^{13}C signatures were more important than was lower δ^{15}N in predicting mortality. Greater Euclidean distance increased the likelihood of predation by *C. lupus*. Nonsurvivors had greater Euclidean distances than had survivors, and this difference approached significance (*t*-test; $t = -1.801$; $N = 93$, d.f. = 91, $P = 0.075$). Discriminant function analysis again provided output consistent with modelling results; pooled within-group correlations between discriminating variables and standardized canonical discriminant functions were highest for δ^{13}C at 0.463, followed by Euclidean distance and δ^{15}N at –0.429 and 0.375, respectively. Logistic regression and discriminant function analyses using data uncorrected for digestion effects yielded comparable results for both multiwatershed and Yeo Island samples. Moreover, it is unlikely that these results were influenced by the possibility that *C. lupus* deposited the remains of *O. hemionus* killed on the closest landmass. Coldwell Peninsula *O. hemionus* ($N = 9$) averaged 1.88 (±0.54) in δ^{15}N and –27.10 (±0.72) in δ^{13}C, which did not correspond to areas of isotopic niche space dominated by *C. lupus*-killed *O. hemionus* collected on Yeo Island (see below, and Fig. 3).

LINKING *O. HEMIONUS* HABITAT TO SURVIVORSHIP – YEO ISLAND

Isotopic signatures of *O. hemionus* pellets, which reflect foraging habitat, describe the isotopic variability in *O. hemionus* food available in different stand types and thus can aid in the interpretation of the observed isotopic niches of consuming *O. hemionus*. Pellet signatures differed among stand types in which they were collected in δ^{13}C (ANOVA; $N = 84$; $F_{4,79} = 19.198$; $P < 0.001$) and δ^{15}N (ANOVA; $N = 84$; $F_{4,79} = 14.706$; $P < 0.001$; Table 2; Fig. 3). Isotopic boundaries were demarcated by low-elevation *T. heterophylla* stands (relatively depleted in both isotopes), *T. plicata* stands (low δ^{13}C, high δ^{15}N) and disturbed stands (low/moderate δ^{15}N, highly enriched δ^{13}C; Fig. 3).

Isotopic data from *O. hemionus* and their pellets plotted simultaneously (and adjusted for fractionation; see Methods) showed three main patterns describing foraging differences between survivors and nonsurvivors (Fig. 3). Specifically, nonsurvivors outnumbered survivors in two isotopic niches and the opposite was observed in a third niche. First, many nonsurvivors foraged primarily or exclusively in low-elevation *T. heterophylla* stands. Second, there was a cluster of nonsurvivors with depleted δ^{13}C and enriched δ^{15}N, isotopically distant from the nearest survivors. This region of isotopic niche space would be derived from foraging primarily or exclusively in *T. plicata* or *P. contorta* stands. Finally, survivors outnumbered nonsurvivors in an isotopic niche defined by intermediate δ^{13}C and δ^{15}N, which would characterize generalized foraging strategies, or use of a mosaic of stand types (Fig. 3).

Protein content in pellets also differed among stand types. *T. plicata* stands had the highest protein, disturbed stands the lowest, and the remaining types fell among these and did not differ (C : N ANOVA; $N = 84$ $F_{4,79} = 3.48$; $P = 0.011$; %N ANOVA; $N = 84$ $F_{4,79} = 3.92$; $P = 0.009$; Table 2).

DISCUSSION

Evolutionary and ecological studies tend to examine population-level responses to predation and there has not been much interest in individual variation or its consequences, especially in the context of fitness (but see Clutton-Brock, 1988; Stuart-Smith & Boutin, 1995). In a *O. hemionus* population, we have shown that isotopic signatures track resource use reliably, and demonstrate considerable intrapopulation variability in niche. Importantly, we then showed a direct fitness cost (mortality via predation) among individuals that occupied different long-term isotopic (and ecological) niche space than did foragers that survived the same period. If the observed variability in niche

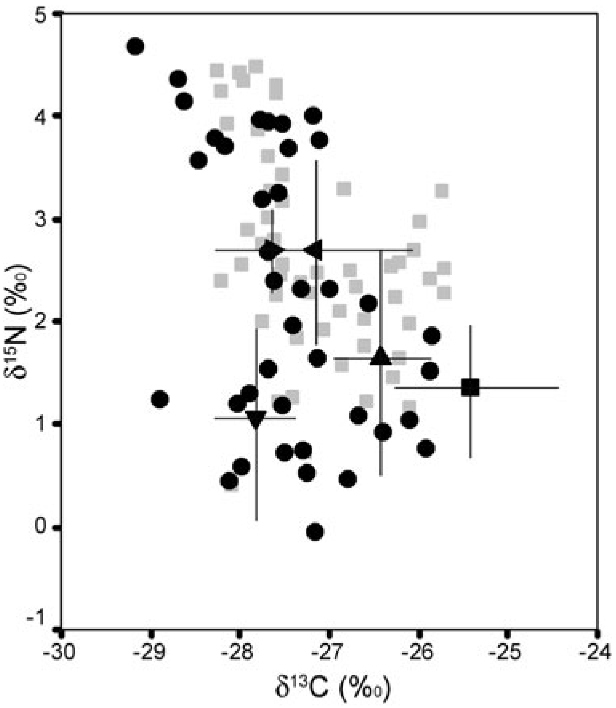

Figure 3. Mean δ^{15}N and δ^{13}C (±1 SD) in deer (*Odocoileus hemionus*) pellets from five different stand types, as well as isotopic signatures from the hair of surviving (▨) and nonsurviving (●) *O. hemionus* in Yeo Island, British Columbia, in 2003. To provide for increased visual interpretation, we placed pellet and *O. hemionus* hair values at a comparable isotopic level (the level of *O. hemionus* hair) using fractionation factors estimated from multiherbivore experiments (Sponheimer *et al*., 2003a, b, c; M. Sponheimer *pers. comm.*, 2004). Stand types were: low-elevation hemlock, *Tsuga heterophylla* (▼); high-elevation *T. heterophylla* (▲); disturbed (■); cedar, *Thuja plicata* (◀); pine, *Pinus contorta* (▶).

Table 2. $\delta^{13}C$, $\delta^{15}N$, C : N and percentage nitrogen (%N) data for deer (*Odocoileus hemionus*) pellets ($N = 84$) collected in different stand types dominated by cedar (*Thuja plicata*), hemlock (*Tsuga heterophylla*), or pine (*Pinus contorta*) trees, or those that were disturbed by logging

		$\delta^{13}C$			$\delta^{15}N$			C : N			%N		
Stand type	*N*	Mean	SD	Group	Mean	SD	Group	Mean	SD	Group	Mean	SD	Group
T. plicata	30	–31.25	1.12	a	1.10	0.90	a	15.54	2.26	a	3.29	0.55	a
Low *T. heterophylla*	12	–31.92	0.44	a	–0.54	0.93	b	16.04	1.69	a,b	3.00	0.31	a,b
High *T. heterophylla*	5	–30.54	0.56	a,b	0.04	1.14	a,b,c	16.17	0.95	a,b	3.04	0.34	a,b
P. contorta	3	–31.75	0.12	a	1.09	0.42	a,c	14.96	0.12	a,b	3.48	0.03	a,b
Disturbed	34	–29.52	0.93	b	–0.24	0.66	b,c	17.22	1.85	b	2.93	0.33	b

Low *T. heterophylla* stands were below 425 m elevation. Samples were collected in autumn 2003 from Yeo Island, British Columbia. Group membership was based on posthoc tests on ANOVA output (Tukey's HSD for %N, Bonferroni for others).

was related not only to social constraints but also to underlying spatial behavioural traits, one would predict the evolution of the traits and the niche itself.

Age, gender, and nutritional condition were poor predictors of isotopic signatures in Haida Gwaii *O. hemionus* and therefore probably likewise in nearby central coastal British Columbia. In contrast, *O. hemionus* pellets (which contain leftover plant material) from different stand types in coastal British Columbia had divergent isotopic signatures, suggesting that variable signatures in *O. hemionus* hair reflected differences in habitat use. We infer, therefore that the isotopic variability we observed represents different foraging strategies among individuals, and that stable isotopic signatures in our system are predictors of mortality independent from physiological processes associated with age, gender, and nutritional condition (which are commonly investigated variables in predator–prey examinations in mammals (e.g. O'Karma, 1984; Longland & Jenkins, 1987; Huggard, 1993) and other taxa (e.g. Temple, 1987)). Although ultimately age (and condition) may be the best predictors of predation in natural systems, and especially in ungulates (Gaillard, Festa-Bianchet, Yoccz, 1998), we have demonstrated here that predation can also be ecologically selective independent of age, gender, and condition, and specifically at the level of the individual niche.

O. hemionus showed considerable intrapopulation variability in isotopic niche across the landscape. For multiwatershed data, isotopic niches of *O. hemionus* differed not only within but also among sites. Nitrogen signatures were particularly useful in distinguishing between survivors and nonsurvivors, perhaps because there was more variability in nitrogen signatures compared with those of carbon. Lacking habitat and vegetative data from these watersheds, however, we cannot assign this variability to specific differences in resource use. For *O. hemionus* sampled on Yeo Island, however, the distribution of *O. hemionus* signatures corresponded to isotopic variability among different forest stand types. Carbon signatures were more important in the Yeo Island data to predict survival, likely because the disturbed stands introduced greater variability into available habitat (and $\delta^{13}C$ distribution), compared with the multiwatershed data that lacked disturbed areas.

Overlaying isotopic data from *O. hemionus* pellets from each stand type onto *O. hemionus* hair signatures, one can observe how foraging strategies differed among individuals (Fig. 3). For example, many *O. hemionus* had intermediate isotopic signatures with respect to available stand types, representative of a general foraging strategy or broad niche (i.e. foraging in multiple stand types). In contrast, some foragers appeared to specialize in *T. plicata* or *P. contorta* stands, between which we could not discriminate, because $\delta^{15}N$ and $\delta^{13}C$ were very similar. We suspect most of these individuals foraged in *T. plicata* stands because they are common on Yeo Island, whereas *P. contorta*-dominated stands are rare. Other specialists converged on isotopic signatures representative of low-elevation *T. heterophylla* stands. In contrast, no individuals specialized on disturbed stands (Fig. 3).

Although qualitative inference is valuable, we were unable to estimate quantitatively how different stand types contributed to the niches of individual *O. hemionus*. Isotopic signatures in faeces reflect an integrated and time-averaged diet over several days (Jones *et al.*, 1979; Sponheimer *et al.*, 2003b), and the *O. hemionus* that deposited the pellets we collected could have traveled among stand types during this time. The isotopic signatures of our a priori food source categories would therefore converge towards each other isotopically, and so are not discrete food items suitable for isotopic mixing models (Phillips & Gregg, 2001). The limitations of this pellet-sampling protocol could explain why some *O. hemionus* occurred outside the distribution of mean and standard deviations of vegetation in different stand types as estimated by pellet signatures (e.g. upper left individuals in Fig. 3).

Intrapopulation variability in foraging strategies could be a function not only of spatial variability but also of temporal variability in feeding. Specifically, it is possible that embedded within a homogenized sample of whole hair strands is temporal isotopic variability during hair growth. For example, individuals could converge on similar (and central tendency-biased) isotopic signatures with foraging strategies varying from one characterized by the use of two or more stand types each day to another characterized by a seasonal migration between habitats. Intratissue isotopic signatures could discriminate between or among scenarios by providing finer temporal information about resource use over time (e.g. Darimont & Reimchen, 2002).

The realized niches of individual *O. hemionus* that we measured would reflect not only traits that underlie foraging behaviour but also their interaction with social constraints. In a review, Jaenike & Holt (1991) noted that genetic variation for habitat preference is common. As one example, Lemon (1993) demonstrated that foraging patch choice had a heritable component in zebra finches, *Taeniopygia guttata*. Although never investigated to our knowledge, on first principles we would expect heritable influences to underlie foraging strategies in *O. hemionus*. On a landscape scale, however, the realized niche would be modified by social constraints; principal among these in northern forest ungulates is natal dispersal, which is influenced by, among other factors, gender, density, and territorial aggression (Hjeljord, 2001). Cultural transmission of foraging strategies from mothers to young may also occur; Estes *et al*. (2003) postulated that individual dietary patterns in sea otters, *Enhydra lutris*, were transmitted along matrilines via learning. On the other hand, we postulate that sufficient microspatial heterogeneity, a function of the mosaic of forest stands that characterize coastal British Columbia, may exist to permit *O. hemionus* to demonstrate trait-determined preferences on smaller scales, within the constraints of sociality. Such expressed variability in heritable traits would lead to their evolution if accompanied by differential fitness.

The variability in niche that we detected among foraging *O. hemionus* was associated with relative fitness differences during the following winter. Logistic regression model selection and multimodel inference allowed us to estimate not only how nonsurvivors differed in niche but also which components of isotopic niche were most important in predicting mortality across the study area (Tables 1, 2; Figs 2A, B). In the multiwatershed data, isotopic differences between survivors and nonsurvivors varied among sites, which we would expect if the 'arena of predation' was variable across the study area and/or niches of the *C. lupus* themselves differed among groups. A larger data set from Yeo Island revealed a readily interpretable pattern of mortality with respect to niche. Clusters of nonsurvivors inhabited niches that included disproportionately more *T. plicata* (or *P. contorta*) and especially low-elevation *T. heterophylla* stands (Fig. 3). McLoughlin, Dunford & Boutin (2005) documented a similar association between individual niche (as estimated by radio collar relocations) and fitness (as estimated by differential mortality) in a *C. lupus*–caribou (*Rangifer taradus*) system. Upland areas (primarily mixed deciduous and coniferous forest) presented *R. taradus* with higher than expected levels of predation risk (McLoughlin *et al*., 2005).

Why are dangerous areas used by foragers? Optimal foraging theory predicts that to maximize fitness, individuals will trade off benefits associated with resources against the costs of acquiring those resources, which often take the form of increased predation risk (Sih, 1987; Abrams, 1991). For *T. plicata*- and *T. heterophylla*-dominated foraging phenotypes to be maintained, there must be fitness benefits derived from these stand types. We are unclear of benefits derived in *T. heterophylla* stands but for *T. plicata* stands, we suggest a plausible trade-off regarding nutritional benefits: C : N ratio and %N data imply that *T. plicata* stands provide high protein, which is the most important nutritional currency for survival and reproduction in ungulates, including *Odocoileus* (Robbins, 1983). Such trade-offs would function to maintain variability in foraging niche, and if any aspect of this foraging variability had a heritable component, this would promote genetic diversity.

Variability in niche may also be maintained via selection favouring generalists. In our larger dataset (Yeo Island), survivors were more likely to occur closer to central tendency in isotopic niche space, which represents the most general of foraging strategies (i.e. mixtures of all stand types). *O. hemionus* that diverged most from central tendency, indicating specialization, were more likely to be killed by *C. lupus*. If any aspect of this is heritable, this produces a selective landscape promoting individual niche breadth. This differs from other studies examining associations between individual niche and fitness (though all measured reproductive output, not survival), which have found selection for increased specialization (Holbrook & Schmitt, 1992; Annett & Pierotti, 1999; Golet *et al*., 2000).

Resource-specific fitness may have broader evolutionary implications. If selection for generalization is occurring, it could influence not only habitat preference but also other traits, because habitat use determines the suite of selective forces that an individual forager encounters (Jaenike & Holt, 1991). Also, because mating occurs after dispersal (and habitat selection), variable spatial behaviour could encourage assortative mating. This would increase genetic variance for habitat preference and its heritability (Nagylaki, 1982). Jaenike & Holt (1991) proposed that variance in habitat preference would be maintained subsequently by preference-performance correlations or density-dependent regulation within different habitats (i.e. frequency-dependent selection).

The potential for individual niche variability (and specialization) within populations (Van Valen, 1965; Bolnick *et al*., 2003), its ability to be detected using stable isotopic analysis (Bolnick *et al*., 2002; Matthews & Mazumder, 2004), and a coupling with fitness measures present rich opportunities to unify ecological and evolutionary concepts. This can play an important role in the continued evaluation of the relative roles of random and deterministic processes in evolution. Indeed some of the most noteworthy demonstrations of natural selection are supported by detailed information about the ecological theatre in which selection occurred (e.g. Grant & Grant, 2002). Moreover, our general approach of linking individual isotopic niche to survivorship offers prospects of adding evolutionary context to existing and well-established predator–prey research programmes, such as *C. lupus–A. alces* systems on Isle Royale (Peterson *et al*., 1984) and large-mammal predator–prey systems in Africa (Sinclair & Arcese, 1995). Finally, we suggest that isotopic analysis can also be informative by allowing individual phenotypes (i.e. morphology) to be coupled with information on resource use and fitness on the timescales on which selection occurs, thus integrating the morphological, ecological, and selective landscapes. Notably, this may aid in identifying the underlying ecological mechanisms of selection and lend insight into the maintenance of niche variability, including multiniche polymorphisms, within populations.

ACKNOWLEDGEMENTS

We thank the Heiltsuk Nation for their permission and participation, and the Raincoast Conservation Society for financial and logistical support. We also thank C. Aries, P. Clement, J. Gordon-Walker, G. Pfleuger, S. Neo-Liang, and C. Starr for fieldwork, H. Schwantje and S. Sharpe for Haida Gwaii *O. hemionus* samples and age, sex, and nutritional status data, and the Calgary Zoo for feeding trials. The McCaw Foundation, National Geographic Society, Wilburforce, Vancouver Foundation, World Wildlife Fund Canada, and private donors kindly provided funding. While preparing the manuscript, C.T.D. was supported by a Natural Sciences and Engineering Research Council (NSERC) Industrial Post-graduate Scholarship and T.E.R. by an NSERC operating grant (N2354).

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