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FORUM

Determining trophic niche width: a novel approach using stable isotope analysis

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Summary

1. Although conceptually robust, it has proven difficult to find practical measures of niche width that are simple to obtain, yet provide an adequate descriptor of the ecological position of the population examined.
2. Trophic niche has proven more tractable than other niche dimensions. However, indices used as a proxy for trophic niche width often suffer from the following difficulties. Such indices rarely lie along a single scale making comparisons between populations or species difficult; have difficulty in combining dietary prey diversity and evenness in an ecologically meaningful way; and fail to integrate diet over ecological time-scales thus usually only comprise single snapshots of niche width.
3. We propose an alternative novel method for the comparison of trophic niche width: the use of variance of tissue stable isotope ratios, especially those of nitrogen and carbon.
4. This approach is a potentially powerful method of measuring trophic niche width, particularly if combined with conventional approaches, because: it provides a single measure on a continuous axis that is common to all species; it integrates information on only assimilated prey over time; the integration period changes with choice of tissue sampled; and data production is theoretically fast and testing among populations simple.
5. Empirical studies are now required to test the benefits of using isotopic variance as a measure of niche width, and in doing so help refine this approach.

Key-words: carbon isotope, diet, generalist, nitrogen isotope, specialist.

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Introduction

Hutchinson's (1957) conceptualization of niche as an *n*-dimensional hypervolume was a crucial foundation upon which ecologists have tried to understand the development of community structure. Occupied niche space implies resource use, and understanding factors that lead to change in niche parameters is central to understanding the evolutionary process. For example ecological character displacement is regarded as a key driving force by evolutionary ecologists (Losos 2000) and cladogenesis can be viewed as an emergent property of competition for resources (Bridle & Jiggins 2000).

Niche parameters can respond very rapidly to changes in intraspecific and interspecific competition as well as prey abundance. For example, competition for niche space is relaxed on islands as a consequence of species impoverishment, thus insular forms typically show an expanded niche width relative to their mainland counterparts (MacArthur, Diamond & Karr 1972). Differences in niche width are conventionally demonstrated using proxies such as bill size (Grant 1965; Gosler & Carruthers 1994), body size (Grant 1968; Clegg & Owens 2002), feeding ecology or prey preferences

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(Carrascal, Moreno & Valido 1994; McDonald 2002) and habitat choice (Diamond 1970; MacArthur *et al*. 1972; Blondel, Chessel & Frochot 1988).

Niche width is usually expressed by calculating the heterogeneity within a set of ecological measurements, often borrowing indices derived as measures of evenness and richness (Shannon & Weaver 1949; Simpson 1949; Margalef 1958). Trophic niche width, often assessed using dietary diversity, is the most tractable and frequently studied component of niche space. However, there are practical problems associated with quantifying trophic niche width using conventional dietary analysis.

1. It is difficult to measure accurately the relative abundance of differing dietary prey items, and over- or underestimates are possible. For example, pellet-contents analyses overestimate the proportion of birds in the diet of great skuas *Catharacta skua* (Brunnich) (Votier *et al*. 2001).

2. Temporal integration of dietary information is often difficult to quantify, such that many dietary studies are 'snapshots' of dietary prey at a point in time.

3. Conventional dietary analysis techniques, in most instances, are unable to take account of variation in prey assimilation rates.

In addition to these observational biases, conventional dietary analysis is often intrusive and can be cumbersome and labour-intensive. For example, a crucial question to ask of a population that appears to show a large dietary niche width is whether it is composed of generalist individuals all taking a wide range of food types (Type A generalization), or individuals each specializing on a different but narrow range of food types (Type B generalization) (Van Valen 1965; Grant *et al*. 1976). Distinguishing the form of population generalization is important for constructing evolutionary hypotheses (e.g. Clegg & Owens 2002), but discriminating between the alternatives using conventional approaches requires laborious sampling of individuals over extended time periods followed by integration of the information, which is often difficult to achieve.

Criteria defining a useful and robust measure of dietary niche width should (i) allow direct comparison amongst individuals, populations and species through the arrangement of samples along a single diversity scale; (ii) combine information on richness and evenness of dietary composition; and (3) allow temporal integration of dietary information over different timescales, preferably from a single sampling event.

Currently we have no robust measure of niche width that satisfies all of these basic requirements for practical application. Of the criteria least frequently met by current techniques, is the ability to compare between populations and species on a single scale. Here we propose a new method that meets all of the basic requirements listed, is theoretically strong, and is simple to apply; namely the use of variance in stable isotope ratios of consumer tissues (see also Matthews & Mazumder 2004).

Conventional applications of stable isotope analysis to ecology

Over the past 15 years, stable isotope ratios of nitrogen and carbon have been used increasingly by animal ecologists to elucidate patterns in food webs. Their utility lies in the fact that stable isotope ratios in the proteins of consumers reflect those of the proteins in their diet in a predictable manner (Hobson & Clark 1992a; Hobson 1999a). Conventionally expressed as $\delta^{15}N$ (‰), the ratio of ^{15}N to ^{14}N generally exhibits a stepwise enrichment (increase in the value of $\delta^{15}N$) at each trophic level and consequently the $\delta^{15}N$ values in the tissues of consumers tend to be between 2·5‰ and 5‰ greater than those of their diets (e.g. DeNiro & Epstein 1981; Hobson & Clark 1992b; Bearhop *et al*. 2002). The ratio of ^{13}C to ^{12}C ($\delta^{13}C$) also increases with trophic level, but to a much lesser degree than $\delta^{15}N$, in the order of 1‰ (e.g. DeNiro & Epstein 1978).

Carbon and nitrogen stable isotope ratios at the base of food webs may also vary spatially, and this is reflected in spatial variability in isotopic composition among food webs. Such spatial variability can be on a grand scale – for example the difference in $\delta^{15}N$ and $\delta^{13}C$ of basal marine food webs resources from that of a terrestrial food web is reflected throughout all of the species within each web (Hobson 1999a) – or on a smaller scale – geographical differences in baseline $\delta^{15}N$ signatures may occur within the same category of ecosystem (Hobson 1999b; Vander Zanden & Rasmussen 2001). Such differences are often to the observer's advantage. For example, spatial variability in $\delta^{13}C$ can reveal the relative importance of other carbon pools to a consumer, discriminating between inshore and offshore feeding at a variety of spatial scales, from the open sea (Hobson, Piatt & Pitocechelli 1994) to relatively small freshwater lakes (France 1995), or by helping distinguish animals feeding in moist primary forests from those feeding in drier second growth scrub (Marra, Hobson & Holmes 1998).

The carbon and nitrogen isotopic composition of consumer tissues are thus a function of: $\delta^{15}N$ and $\delta^{13}C$ of each prey species; the relative proportions of each prey species assimilated; the isotopic fractionation associated with converting prey tissue into consumer tissue; and in certain instances, foraging location. Moreover, the stable isotope signatures of tissues generally reflect the diet over the period during which the tissue was synthesized (Hobson & Clark 1992a; Bearhop *et al*. 2002), such that tissues with different turnover rates will integrate dietary information over different temporal periods. For example, blood is a short-term integrator whereas bone integrates the dietary nitrogen over a much longer time-scale (Hobson & Clark 1992a; Haramis *et al*. 2001; Bearhop *et al*. 2002; Pearson *et al*. 2003). Finally, tissues that are metabolically inert after formation, such as hair, feathers, baleen or claws, will preserve this record indefinitely (Schell, Saupe & Haubenstock 1989; Hobson 1999a; Bearhop *et al*. 2003).

Combined, such qualities render stable isotope analysis a powerful tool to study diet. However, to date relatively few studies have given thought to the variation associated with the mean isotopic signature (e.g. Genner *et al*. 1999; Bearhop *et al*. 1999), which when combined with conventional assessment of diet, we propose has the potential to be a powerful integrative measure of foraging niche width.

Stable isotope variance as a measure of niche width

For this approach to provide a useful measure of niche width we make the following theoretical assumptions.
1. Prey species must differ isotopically. This can be assessed by isotopic characterization of potential prey items. If variation does not exist then this assumption would be invalid, and further consideration of niche width (through isotopic variance of the consumer) would be futile.
2. The isotope signatures at the food-web base, and the diets of prey species remain relatively invariant over time. Several studies have shown that baseline isotope signatures can change over time as a consequence of primary production shifts or nutrient inputs, and dietary preferences of prey may also change (Yoshioka, Wada & Hayashi 1994). In practice, if the isotopic signature of the (combined) prey exhibits temporal variation, as long as this variance is less than the variance resulting from a consumer dietary shift (revealed by sampling of prey items), stable isotope signature variance should remain a robust measure of trophic niche width.
3. The tissue analysed reflects the period over which the niche width is expressed. In a population of generalists (particularly Type A generalists) variability in diet amongst individuals will tend to exist at only shorter temporal scales, and this variation is likely to become lost through averaging of the stable isotope signature over longer periods. In this case, tissues with integration times slightly shorter than the period of niche width assessment will likely provide the best indicators of niche width. However, where a whole population shifts diet synchronously for comparison with a population where individuals shift asynchronously, serial sampling of tissues integrating relatively short-term information would be required. In keeping with more traditional approaches to trophic niche-width estimation, the detail of the question being asked will determine the most appropriate choice of tissue.

Where these assumptions are met, we propose the following will influence the isotopic variance exhibited by a consumer population, or an individual serially sampled over time:
1. the range of prey species consumed;
2. the evenness (in its ecological sense) of prey components in the diet over time;
3. the range of trophic levels from which prey is drawn;
4. foraging location;
5. variability in individual physiology; and
6. variability in diet-tissue fractionation.

Numbers 1–4 have been used previously as indicators of foraging niche width; numbers 5 and 6 should, in most cases, result in small variations in stable isotope variance and thus add only a small amount of noise to variance estimates. Here we consider the effect each control will exert in more detail and derive specific predictions relating to the use of stable isotope analyses as a measure of foraging niche width. At this stage in isotope ecology studies, due to larger trophic differences and proportionally smaller measurement precision, variance in $\delta^{15}N$ is the most powerful parameter to consider, thus much of the following discussion will focus on this, although with respect to geographical foraging area $\delta^{13}C$ may offer considerable utility.

(1) The range of prey species consumed

Prediction 1: in general, populations that consume a wide range of prey species will exhibit wider variation in their tissue isotopic signatures than those consuming a narrow range of prey items. For example, a population of shags *Phalacrocorax aristotelis* (L.) that fed exclusively on a single prey type at a single foraging site had a smaller variance in $\delta^{15}N$ (feather) (0·33‰) than feathers of cormorants *Phalacrocorax carbo* (L.) which had been feeding on multiple prey types at multiple sites (4·04‰) (Bearhop *et al*. 1999).

(2) The evenness of prey components in the diet over time

Prediction 2: populations where individuals consume widely differing proportions of each of their prey items over time will tend to show less variation in tissue stable isotope ratios than will those consuming a constant proportion of each prey type. This is demonstrated in Fig. 1. Further, asynchronous population diet switching would lead to large isotopic variability, synchronous population variation would lead to small isotopic variability. Detecting whether variation was asynchronous

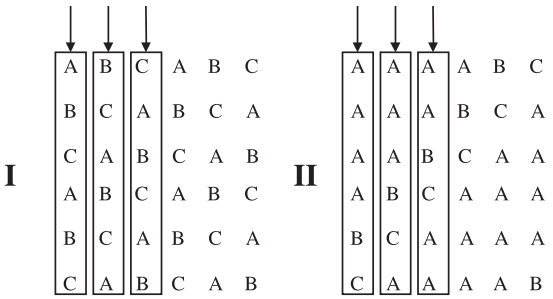
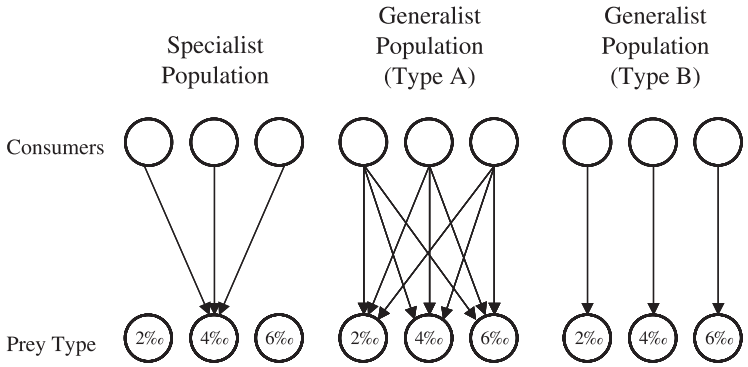


Fig. 1. The matrices represent two populations, one with high evenness in the diet (I) the other with low evenness in the diet (II). Each row represents the diet of a different individual over time and each letter a different type of prey item. The arrows indicate a sampling event and the boxes show the population sampled at each sampling point. Because the prey preferences of the consumer populations do not fluctuate synchronously, sampling a population with high dietary evenness will tend to yield higher variances than one with low evenness.



If we assume that diet/tissue fractionation is constant (4‰), prey isotope ratios remain constant over time and that Type A individuals consume all prey types in equal amounts then:

(A) Sampling a tissue that integrated dietary information over long temporal scales would likely give consumer population values (mean ± s^2) of

Specialist	Generalist (Type A)	Generalist (Type B)
8‰ ± 0	**8‰ ± 0**	**8‰ ± 4**

(B) Sampling a tissue that integrated dietary information over short temporal scales (with a large sample size) would likely give consumer population values (mean ± s^2) of

Specialist	Generalist (Type A)	Generalist (Type B)
8‰ ± 0	**8‰ ± 4**	**8‰ ± 4**

(C) Assuming that the tissue being sampled integrates dietary information over a shorter period than the diet varies over, serial sampling the same tissue (integrating very short-term dietary information, such as blood plasma samples, or short sections from feathers, hair or possibly whiskers) from the same individual over time would likely give individual values (mean ± s^2) of

Specialist	Generalist (Type A)	Generalist (Type B)
8‰ ± 0	**8‰ ± 4**	**6, 8 or 10‰ ± 0**

Fig. 2. Sampling regimes that could enable the use of stable isotope variance in animal tissues to discriminate between Type A and Type B generalism. For clarity, the examples represent idealized predator–prey systems, where dietary specializations represent extremes of the specialist/generalist and type I/type II continua and the problems of estimating population-level variances are ignored.

/synchronous between two populations would be possible through a sampling regime similar to Fig. 2 (part (c)).

(3) THE RANGE OF TROPHIC LEVELS FROM WHICH PREY IS DRAWN

Prediction 3: populations where individuals consume prey over a broad spectrum of trophic levels will tend to show more isotopic variance than those which feed on the same number of prey species, but all drawn from the same trophic level.

(4) GEOGRAPHIC FORAGING AREA

Prediction 4: since spatial variation at the food-web base is reflected throughout the food web, populations where individuals forage in a range of geographical areas are likely to show more variation in the stable isotope signatures of their tissues than those from sedentary populations.

(5) VARIABILITY IN INDIVIDUAL PHYSIOLOGY

Prediction 5: physiological differences among individuals within the population (or within the same individual over time) will cause some variance in tissue-isotope signatures. A first consideration should be variability in nutritional condition. For example, the tissues of individuals in poor nutritional condition had elevated $\delta^{15}N$ compared to those of individuals in better condition (Hobson, Alisauskas & Clark 1993). Variability in metabolic rates may also lead to inter-individual variation in tissue isotope signatures (observed during studies of captive individuals; Hobson & Clark 1992a; Bearhop *et al.* 2002). However the magnitude of this effect on population or serially sampled individual variance is likely to be small and would manifest in noise, rather than forcing error between populations or individuals. Nevertheless, despite recent advances, our understanding of how variability in physiology influences tissue stable isotope signatures is still limited, and more work is required in this area.

(6) VARIABILITY IN DIET-TISSUE FRACTIONATION

Prediction 6: diet-tissue isotopic fractionation may vary with the type of food being consumed or through differential mobilization of stored resources (Adams &

Sterner 2000). Captive birds subject to artificial diet switches exhibited variation in diet-tissue isotopic fractionation (Bearhop *et al*. 2002), perhaps as a function of diet quality. However, since enrichment factors for different diets to the same tissue type differ by up to 2‰ for $\delta^{15}N$ and by just over 1‰ for $\delta^{13}C$ (Hobson & Clark 1992b; Haramis *et al*. 2001; Bearhop *et al*. 2002), such variability may only account for a large proportion of the variance when the dietary isotopic variance is small.

Despite a thorough literature review, finding empirical studies to support these predictions has proved extremely difficult since data have not been collected with these hypotheses in mind (to our knowledge). For example there are few studies of wild populations where serial sampling of the same tissue type (or individual) has been undertaken contemporaneous with monitoring isotopic composition of the diet, or insufficient individuals from comparable populations have been measured to allow the appropriate statistical analyses. However, with relatively simple sampling protocols, and the appropriate experimental design, there is the potential to address a number of questions with respect to niche width. For example, the question posed in the introduction regarding the manner in which niche width is expressed (i.e. Type A or Type B generalists) could be investigated in the manner described in Fig. 2.

DISCRIMINATING BETWEEN POPULATION AND INDIVIDUAL GENERALISM

Using conventional methods to address this problem has required labour intensive field observations and often populations of identifiable individuals. However, either by serial sampling or utilizing the differential rate of tissue turnover, stable isotope analysis offers a powerful approach to estimate the relative prevalence of population, and individual, generalism. Because different animal tissues integrate dietary signatures over different temporal scales (Hobson & Clark 1992a; Bearhop *et al*. 2002), in a population of generalists we predict the variance among tissues that integrate diet over short temporal scales (shorter than period of trophic variation) to be larger than the variance for tissues that integrate diet over longer temporal scales (that cover the period of trophic variation). Thus for example, tissues that integrate over days and weeks, such as blood plasma, blood cells or individual feathers (Hobson & Clark 1992b; Hilderbrand *et al*. 1996; Bearhop *et al*. 2002), are much more likely to discriminate dietary generalism than tissues which integrate variation over much longer time-scales, such as bone, groups of feathers, fish otoliths or scales (Hobson & Clark 1992a; Begg & Weidman 2001). It follows that if we have a population of specialists we would predict little or no change in variance between long- and short-term integrators (Fig. 2, parts (a) and (b)).

If individuals within the population were identifiable, serial sampling from the same individuals would also distinguish Type A and Type B generalists. Serial sampling could comprise multiple blood samples, sampling sections of feathers grown at different times in the moult cycle or sampling multiple subsections of long hairs such as vibrissae. We would expect the variation measured sequentially within individuals from population of Type A generalists to be approximately equal to the variation found in sample representative of the population, whilst for Type B generalism, we would expect variance derived from sequentially measured individuals to be low compared with the variance derived from a single sample of the population at any one time (Fig. 2, part (c)). This latter approach, although potentially increasing animal stress in the case of blood due to multiple re-captures, would in general be more desirable than the multiple tissue approach, which may require the sacrifice of animals.

Closing remarks

We conclude that using variance in stable isotope analysis, particularly of $\delta^{15}N$, may offer a significant addition to the range of techniques for estimating trophic niche width in animals and comparisons can be undertaken using a simple variance ratio test (*F*-test). The technique, potentially at its most powerful when combined with conventional approaches, would be best applied in closed systems, or where nutrient inputs or changes in production could be easily quantified, such as freshwater lakes or islands. Under certain circumstances marine systems, which tend to be more isotopically homogeneous (over moderate spatial and temporal scales), may be suitable. Potential confounding effects of physiology should also be considered. While our understanding of physiological effects upon tissue stable isotope signatures has increased considerably in recent years due to an increase in the number of controlled dietary studies (Hobson & Clark 1992a, 1992b; Hilderbrand *et al*. 1996; Haramis *et al*. 2001; Bearhop *et al*. 2002; Pearson *et al*. 2003), more work of this nature is required. We suggest that the technique could provide valuable insights into the processes underlying insular evolution and the impacts of alien introductions upon the communities they invade. The challenge now lies with the ecological community to evaluate fully the usefulness of this approach through the design and execution of empirical studies that use isotopic variance as a measure of niche width.

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