

## MEASURING INDIVIDUAL-LEVEL RESOURCE SPECIALIZATION

DANIEL I. BOLNICK,<sup>1,3</sup> LOUIE H. YANG,<sup>1</sup> JAMES A. FORDYCE,<sup>1</sup> JEREMY M. DAVIS,<sup>1</sup> AND RICHARD SVANBÄCK<sup>2,4</sup>

<sup>1</sup>*Section of Evolution and Ecology, Center for Population Biology, Storer Hall, University of California, Davis, California 95616 USA*

<sup>2</sup>*Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden*

**Abstract.** Many apparently generalized species are in fact composed of individual specialists that use a small subset of the population's resource distribution. Niche variation is usually established by testing the null hypothesis that individuals draw from a common resource distribution. This approach encourages a publication bias in which negative results are rarely reported, and obscures variation in the degree of individual specialization, limiting our ability to carry out comparative studies of the causes or consequences of niche variation. To facilitate studies of the degree of individual specialization, this paper outlines four quantitative indices of intrapopulation variation in resource use. Traditionally, such variation has been measured by partitioning the population's total niche width into within- and between-individual, sex, or phenotype components. We suggest two alternative measures that quantify the mean resource overlap between an individual and its population, and we discuss the advantages and disadvantages of all four measures. The utility of all indices depends on the quality of the empirical data. If resources are measured in a coarse-grained manner, individuals may falsely appear generalized. Alternatively, specialization may be overestimated by cross-sectional sampling schemes where diet variation can reflect a patchy environment. Isotope ratios, parasites, or diet–morphology correlations can complement cross-sectional data to establish temporal consistency of individual specialization.

**Key words:** adaptive variation; diet analysis; gut contents; individual specialization; niche variation; proportional similarity; resource partitioning.

### INTRODUCTION

Traditionally, ecologists have viewed the niche as a property of the species or population as a whole. However, many apparently generalized species are in fact composed of individual specialists that use small subsets of the population's niche. For example, a population of the intertidal snail *Nucella melones* was recorded consuming 21 prey taxa, yet individuals consumed no more than 1–5 taxa, often ignoring prey species that other conspecifics preferred (West 1988). Although individual specialization occurs in a broad range of taxa (Bolnick et al., *in press*), few studies calculate the degree to which individuals vary. Such quantitative measures are necessary for any comparative or experimental study attempting to explain the

origins or effects of variation in the degree of individual specialization. The goal of this paper is to outline the major problems in quantifying individual specialization. We describe and evaluate four indices of intrapopulation niche variation, and review methods of establishing its temporal consistency. The methods discussed in this paper can be applied to any axis of niche variation, including oviposition sites, habitat, temperature, etc., though we primarily discuss the methods in terms of analysis of diet data, as individual specialization is most commonly demonstrated in diet analyses. A program, IndSpec1, to calculate all of the indices discussed in this paper is available in the Supplement.

### INDICES OF INDIVIDUAL SPECIALIZATION

All four indices discussed here share a feature that sets them apart from related measures of species-level niche width. Most measures of species niche breadth compare the frequency distributions of the species' resource use with that of all available resources (Hurlbert 1978, Feinsinger et al. 1981). To do this, a researcher must determine the frequency distribution of resources

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<sup>3</sup> E-mail: dibolnick@ucdavis.edu

<sup>4</sup> Present address: Department of Limnology, Evolutionary Biology Centre, Uppsala University, Norbyv. 20, SE-752 36 Uppsala, Sweden.

in the environment, a process that is difficult and may be riddled with assumptions. In contrast, indices of individual specialization use the population's total diet to define resource availability so that individuals are compared to their population rather than to the environment.

Roughgarden (1972) suggested that the total niche width of a population (TNW) can be broken down into two components: the variation in resource use within individuals (within-individual component, WIC), and the variance between individuals (between-individual component, BIC) so that  $TNW = WIC + BIC$ . Originally developed for within- and between-phenotype (or between-sex; Ebenman and Nilsson 1982) variation, it can be applied at the individual level. Assuming that variation in niche parameters can be expressed along a single continuous dimension  $x$  (e.g., prey size), let  $\mathbf{X}$  be a matrix of diet data where each element  $x_{ij}$  is the size (or other measure) of the  $j$ th prey item in individual  $i$ 's diet. Then,

$$TNW = \text{Var}(x_{ij}) \tag{1}$$

$$WIC = E[\text{Var}(x_j | i)] \tag{2}$$

$$BIC = \text{Var}[E(x_j | i)]. \tag{3}$$

The relative degree of individual specialization can be measured as the proportion of TNW explained by within-individual variation,  $WIC/TNW$ . As this value approaches 1, all individuals utilize the full range of the population's niche, whereas smaller values indicate decreasing inter-individual overlap and hence higher individual specialization.

Roughgarden's  $WIC/TNW$  is limited to continuous diet data. To carry this approach over to discrete data such as the frequency of alternate prey taxa in the diet, Roughgarden (1979:510) proposed a measure that uses the Shannon-Weaver index as a proxy for variance. The following formulae are equivalent to Roughgarden's formulation, although we use different notation for consistency within this paper. Let  $\mathbf{N}$  be a matrix of diet data, where elements  $n_{ij}$  represent the number (or mass) of diet items in individual  $i$ 's diet that fall in category  $j$ . This raw data matrix is then transformed into a proportion matrix  $\mathbf{P}$ , with elements  $p_{ij}$  describing the proportion of the  $j$ th resource category in individual (or phenotype)  $i$ 's diet. Then,

$$WIC_s = \sum_i p_{i\cdot} \left( - \sum_j p_{ij} \ln p_{ij} \right) \tag{4}$$

$$BIC_s = \sum_i p_{i\cdot} \ln(p_{i\cdot}) - \left\{ \sum_j q_j \left[ - \sum_i \gamma_{ij} \ln(\gamma_{ij}) \right] \right\} \tag{5}$$

$$TNW_s = - \sum_j q_j \ln q_j \tag{6}$$

where the subscript "s" distinguishes this from the continuous index. The variable  $p_{i\cdot}$  is the proportion of all resources used by the population that are used by individual  $i$ ,  $q_j$  is the proportion of the  $j$ th resource category in the population's niche, and  $\gamma_{ij}$  is the proportion of the population's total use of resource  $j$  that was used by individual  $i$ , so that

$$p_{ij} = \frac{n_{ij}}{\sum_j n_{ij}} \quad p_{i\cdot} = \frac{\sum_j n_{ij}}{\sum_i \sum_j n_{ij}}$$

$$q_j = \frac{\sum_i n_{ij}}{\sum_i \sum_j n_{ij}} \quad \gamma_{ij} = \frac{n_{ij}}{\sum_i n_{ij}}$$

As before,  $TNW_s = BIC_s + WIC_s$ , and one can easily calculate  $WIC_s/TNW_s$  (see Ebenman and Nilsson 1982 for a worked example).

Two distribution-overlap measures provide discrete-data alternatives to  $WIC_s/TNW_s$ , measuring the mean pairwise overlap between each individual and the population. Both Schoener (1968) and Feinsinger et al. (1981) advocated a proportional similarity index (PS) for measuring interspecific diet overlap. Adapted to individual-level analyses, the diet overlap between an individual  $i$  and the population is

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j| = \sum_j \min(p_{ij}, q_j) \tag{7}$$

where  $p_{ij}$  and  $q_j$  are the same as above. For individuals that specialize on a single diet item  $j$ ,  $PS_i$  takes on the value  $q_j$ . For individuals that consume resources in direct proportion to the population as a whole,  $PS_i$  will equal 1. The population-wide prevalence of individual specialization (IS) is then measured by the average of individuals'  $PS_i$  values.

A second overlap measure is an adaptation of Petraitis' (1979) likelihood approach to measuring species' niche width. If we assume that the population resource use distribution (the vector of  $q_j$ 's) is a given, we can determine the probability that any individual  $i$ 's diet (the vector of  $n_{ij}$ 's or  $p_{ij}$ 's) was drawn randomly from the population distribution. This multinomial probability is proportional to the likelihood function, which can be compared to the maximum likelihood in which the individual and population have the same resource use distribution. The resulting likelihood ratio is

$$\lambda_i = \prod_j \left( \frac{q_j}{p_{ij}} \right)^{n_{ij}} \tag{8}$$

and has the same quantitative behavior as  $PS_i$ , ranging from generalization ( $\lambda = 1$ ) towards  $q_j$  as an individual specializes on resource  $j$ . However, the precise value of  $\lambda_i$  is sensitive to the sample size of diet items used

TABLE 1. Summary of the alternative indices for quantifying individual specialization.

Index	Description	Type of data	Advantages	Disadvantages
WIC/TNW	Proportion within-individual component of total niche width (WIC/TNW).	continuous	Estimates individual specialization and population niche width.	Continuous data only. Assumes resource-use distribution is normal.
WIC <sub>s</sub> /TNW <sub>s</sub>	Shannon index approximation to WIC/TNW.	discrete	Estimates individual specialization and population niche width.	Can be biased when some individuals are monophagous. Assumes even resource distribution in environment. Statistical properties unknown.
IS	Mean proportional similarity (PS <sub>i</sub> ) between individuals and population.	discrete	Estimates individual specialization for each individual.	Published statistical properties unreliable.
$\bar{W}$	Mean likelihood ( $W_i$ ) of individual's diet being drawn from population diet.	discrete	Estimates individual specialization for each individual. Known statistical properties.	Assumes the observed population diet distribution is the "true" population diet.

by individual  $i$  ( $n_i$ ), and number of resource categories ( $r$ ). Consequently, Petraitis proposed a standardization procedure,

$$W_i = (\lambda_i)^{1/n_i} \quad (9)$$

that corrects for this. It is possible to generate a  $P$  value to test whether the individual's diet represents a significant deviation from the population's diet, as the  $-2 \ln(\lambda_i)$  has an approximately chi-square distribution with  $(r - 1)$  degrees of freedom. As with PS<sub>i</sub>, one can use the mean  $W_i$  of the sample as an estimate of the overall predominance of individual specialization in the population ( $\bar{W}$ ).

Overlap measures have also been used to quantify average pairwise diet overlap between individuals (Brodin 1994, Schindler et al. 1997). Rather than comparing each individual's diet with the population diet distribution ( $p_{ij}$  vs.  $q_j$ ), this approach calculates the proportional similarity between pairs of individuals ( $p_{ij1}$  vs.  $p_{ij2}$ ). Although this approach is qualitatively similar to the four indices discussed here, in that it ranges from 0 (strong specialization) up to 1 (generalization), it is not tightly correlated with the other measures when applied to the same data (D. I. Bolnick et al., unpublished simulations). Furthermore, the small within-individual sample sizes limit the application of parametric and nonparametric statistical tests (discussed below), and the average degree of pairwise overlap has the undesirable statistical property that many pairwise comparisons are not independent. Consequently, we do not consider pairwise diet overlap in any detail.

#### CHOOSING AMONG INDICES

All four indices vary from values close to 1, indicating individual generalists, to near 0, indicating

strong individual specialization. The different indices, when applied to the same data, consistently yield very similar, though not identical values. In unpublished simulations, we calculated all four indices on a wide range of simulated data sets (>500 000 diet matrices with varying degrees of specialization and resource-use evenness) and found that regressions relating the various indices had very high goodness-of-fit ( $r^2 > 0.9$ ). PS<sub>i</sub> and  $W_i$  also yield very similar results for a given individual. Using gut content data from 65 threespine sticklebacks, *Gasterosteus aculeatus* (D. I. Bolnick, unpublished data), PS<sub>i</sub> and  $W_i$  for a given individual were highly correlated ( $r^2 = 0.933$ , Bartlett chi-square = 129.4, df = 1,  $P < 0.001$ ; regression intercept =  $-0.039 \pm 0.22$ , regression slope =  $1.027 \pm 0.05$ ; mean  $\pm 1$  SE).

Although the indices are quantitatively very similar, each has particular advantages and disadvantages (Table 1). WIC/TNW offers the attractive advantage of quantifying both relative specialization and population niche width. This approach facilitates testing several hypotheses such as Van Valen's (1965) hypothesis that niche expansion during competitive release occurs by increased inter-individual variation, implying that higher TNW is associated with greater individual specialization (low WIC/TNW). This pattern has been observed in the lizard *Anolis sagrei* (using data from Listers 1976: Fig. 5a,  $F_{1,3} = 11.069$ ,  $P = 0.045$ ).

Both of Roughgarden's indices make assumptions about the resource distribution. The continuous version assumes niches are normal distributions, while the Shannon-Weaver index assumes that resources are evenly distributed, maximized both by many diet categories and equal utilization of each (Feinsinger et al.

1981). If prey items vary in their availability, then equal utilization indicates a degree of preference for rare prey items, in which case Shannon-Weaver-based measures are inaccurate indicators of generalization or specialization.

The Shannon-Weaver-based index can also be biased to overestimate individual specialization (low  $WIC_s/TNW_s$ ) due to its use of the natural log of a proportion. This problem is particularly likely when a population primarily uses a single resource, with lesser dependence on a wide variety of other resources at low frequency. For example, the snail *Nucella emarginata* has a strong preference for the barnacle *Balanus*, but is known to consume six other taxa at low frequencies (West 1986: site B, Table 3). Any individual that consumed only *Balanus* would closely resemble the population's diet, but have a niche breadth of  $\ln(1) = 0$ , depressing the mean WIC. Diet data for *Nucella emarginata* (West 1986: site B, Table 3) yields  $WIC_s/TNW_s = 0.58$ , but 12 out of 31 individuals ate only *Balanus*. To demonstrate the sensitivity of this index to monophagy, we randomly assigned each monophagous individual only one extra non-*Balanus* prey item, and  $WIC_s/TNW_s$  increased to 0.81. Proportional similarity and Petraitis'  $W$  circumvent this bias (IS changed from 0.824 to 0.85). Two additional advantages of the two overlap measures are that they make no assumptions about the shapes of the resource distributions, and they yield estimates of specialization for each individual. The latter property makes it possible to study the variation in  $PS_i$  or  $W_i$  among individuals in a population so one could study the ecological or fitness consequences of individual specialization.

Both  $PS_i$  and  $\lambda_i$  have published statistical properties, which  $WIC_s/TNW_s$  does not. The currently available formula for  $\text{Var}(PS)$  (Feinsinger et al. 1981, Smith 1984) appears to be incorrect, and can yield misleadingly low variances even when sample sizes for an individual are extremely small (D. I. Bolnick, *personal observation*). This is because the sample size of the individual's diet distribution can be completely omitted from the calculation of this formula when  $p_{ij}$  is greater than  $q_j$  or equal to zero for all resource categories  $j$ . In contrast, Petraitis'  $W_i$  allows a parametric statistical test of the null hypothesis that an individual draws randomly from a common diet, using the log-likelihood ratio.

Nonparametric Monte Carlo techniques are possible for any of the indices discussed here. The program IndSpec1 (see Supplement) generates replicate null diet matrices by assigning each individual  $n_r$  diet items drawn randomly from the population's resource distribution. Recalculating the index for each replicate data set provides a null distribution against which to test the observed index value. The log-likelihood method

appears to provide a more conservative test of individual specialization. Using diet data from three-spine sticklebacks (D. I. Bolnick, *unpublished data*), we compared the  $P$  values from the likelihood ratio to the values approximated by resampling (the proportion of resampled indices less than the observed index value). For any given individual, the  $P$  values were either both significant at  $P < 0.05$  ( $N = 36$ ), both nonsignificant ( $N = 19$ ), or only significant for the Monte Carlo method ( $N = 11$ ), indicating that the likelihood approach is less likely to reject the null hypothesis. Individuals that did not significantly differ from the population diet included both individuals with large and small  $W_i$  values, the latter failing to reject the null hypothesis due to insufficient sample size.

#### SAMPLING CONSIDERATIONS

In measuring niche variation, it is important that the niche axis or categories have been chosen appropriately. Coarse-grained niche studies that pool functionally distinct resources may underestimate individual specialization. For example, an analysis of diet variation in the Eurasian Oystercatcher, *Haematopus ostralegus*, might reveal that most individuals feed on the same species of bivalve. A diet description using prey species would miss significant intraspecific variation in shell morphology of their mussel prey that affects prey-handling technique (Sutherland and Ens 1987). When resources that a forager distinguishes among are lumped together by an ecologist, individuals may appear more generalized than they really are.

Conversely, high between-individual variation may not be biologically significant if it is based on "snapshot" sampling regimes. If individuals forage in an environment with patchy resources, even a generalist predator might appear specialized if it encountered a swarm of one prey species immediately prior to capture for gut content analysis (Warburton et al. 1998). This risk can be minimized by several sampling schemes that allow one to establish the temporal consistency of diet variation. The most direct method for determining niche consistency is to follow individuals through time. Longitudinal sampling schemes are widely used, and include repeated observations of prey-capture events (West 1986), foraging behaviors (Werner and Sherry 1986), scat contents (Sidorovich et al. 2001), microhabitat use (Bourke et al. 1997), and even repeated samples of gut contents from the same individual (Bryan and Larkin 1972).

Significant phenotype-diet correlation provides strong inferential support for consistent diet differentiation, as it suggests that diet variation is due to functional morphology rather than random effects such as patchy prey distributions. This is particularly true when the correlation is in a direction predicted a priori by

biomechanical, functional, or physiological reasons (Wainwright 1996), or when identical correlations occur convergently in many taxa. For example, phenotypic variation in bluegill sunfish (*Lepomis macrochirus*) produces trade-offs in search and prey-handling efficiency (Ehlinger 1990), consistent with functional measures of swimming performance, and parallel phenotype-diet correlations in other species (Robinson et al. 1996, Svanbäck and Eklöv 2002).

Stable isotope ratios can be used to estimate the contribution of different prey types to a predator's diet, as prey have characteristic isotope signatures. Isotope ratios in a predator's tissues turn over slowly, so isotope levels at any point in time represent a long-term average of prey use, depending on the organism's growth rate and the type of tissue used (Fry and Arnold 1982). Several studies have shown that stable isotope data are consistent with cross-sectional diet studies, indicating that the observed gut content variation reflects long-term foraging strategies (Gu et al. 1997, Beaudoin et al. 1999).

Many parasites have life histories that use particular prey species as intermediate hosts. As many macro-parasites remain in the host's body for a long time, the prevalence of a particular parasite indicates that the intermediate host has been a preferred prey for a significant period of time (Konovalov 1995, Wilson et al. 1996). For example, in a population of Arctic charr (*Salvelinus alpinus*), Curtis et al. (1995) found that similar-sized charr tended to have either benthic or limnetic prey in their guts, and that an individual's parasite fauna was strongly associated with a particular diet.

#### CONCLUSIONS

Interindividual niche variation is known to occur in a wide variety of species and environments (Durell 2000; Bolnick et al., *in press*). To date, most studies only claim to show individual specialization by statistically rejecting the null hypothesis that individuals draw from a common pool of resources. However, two problems arise out of this hypothesis-testing approach. First, studies that fail to reject the null hypothesis (individual generalists) end up in file drawers rather than manuscripts, leading to a biased record of the relative frequency of individual specialization. Second, treating individual variation as either present or absent obscures important variation in the degree of individual specialization.

Applying quantitative methods to measuring, as well as testing, individual specialization, should help circumvent these problems. By measuring the degree of individual specialization, the methods outlined in this paper give more value to negative results, allow us to distinguish more and less specialized individuals within a population, and facilitate comparisons of the prev-

alence of interindividual variation among populations or species. For example, Ebenmann and Nilsson (1982) applied  $WIC_s/TNW_s$  to within- and between-sex variation in island and mainland populations of Chaffinches (*Fringilla coelebs*). Their comparative approach was able to confirm that habitat use partitioning by sexes is more pronounced in environments with low interspecific competition. Such quantitative approaches are necessary to further dissect the ecological causes of individual specialization, its fitness consequences for individuals, and its overall prevalence.

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#### SUPPLEMENT

IndSpec1, a program to calculate measures of individual specialization, is available in ESA's Electronic Data Archive: Ecological Archives E083-056-S1.