

REVIEW AND SYNTHESIS

The ecological causes of individual specialisation

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Abstract

Many generalist populations are composed of specialised individuals, whose niches are small subsets of the population niche. This ‘individual specialisation’ is a widespread phenomenon in natural populations, but until recently few studies quantified the magnitude of individual specialisation and how this magnitude varies among populations or contexts. Such quantitative approaches are necessary for us to understand how ecological interactions influence the amount of among-individual variation, and how the amount of variation might affect ecological dynamics. Herein, we review recent studies of individual specialisation, emphasising the novel insights arising from quantitative measures of diet variation. Experimental and comparative studies have confirmed long-standing theoretical expectations that the magnitude of among-individual diet variation depends on the level of intra and interspecific competition, ecological opportunity and predation. In contrast, there is little empirical information as to how individual specialisation affects community dynamics. We discuss some emerging methodological issues as guidelines for researchers studying individual specialisation, and make specific recommendations regarding avenues for future research.

Keywords

Competition, ecological opportunity, ecology of individuals, food webs, niche variation hypothesis, optimal foraging theory, predator-prey interactions, stable isotopes.

Ecology Letters (2011) **14**: 948–958

INTRODUCTION

Ecologists have long realised that individuals within populations can differ substantially in resource use (‘niche variation’; Van Valen 1965). In many species, co-occurring individuals actively select different prey from their shared environment (e.g. West 1986; Werner & Sherry 1987; Araújo & Gonzaga 2007). Historically niche variation has been attributed to either ontogenetic niche shifts or ecological sexual dimorphism (Schoener 1986). However, resource-use variation is observed even among individuals of a given age and sex. This ‘individual specialisation’ – in which individuals use a small subset of the population’s resource base – has been shown to be a widespread phenomenon in many vertebrate and invertebrate taxa (Bolnick *et al.* 2003).

More recently, empirical studies have shown that manipulating genetic variation (a proxy for trait variation) can profoundly alter population dynamics and community structure (Hughes *et al.* 2008). Concurrently, an emerging theoretical literature is showing that among-individual variation in ecological attributes (e.g. fecundity, prey preferences, attack rates, susceptibility to predation) can substantially change population and community dynamics (Saloniemi 1993; Doebeli & Koella 1994; Okuyama 2008; Vindenes *et al.* 2008; Schreiber *et al.* In press). Bolnick *et al.* (2011) identified six distinct mechanisms through which such trait variation affects ecology. Both genetic and environmental-based variation in ecological traits can alter (1) food web network structure, (2) population stability through a portfolio effect, or (3) mean strengths of interspecific interactions if traits have a non-linear relationship with ecological attributes (Jensen’s Inequality). When trait variation is heritable, additional ecological processes may occur, including (4) the increased abundance of one phenotype owing to reproduction by a different phenotype (phenotypic subsidy), (5) adaptive eco-evolutionary feedbacks and (6) stochastic eco-evolutionary feedbacks (e.g. genetic

drift). These multifarious effects of niche variation can alter the stability, mean abundance and extinction risk of particular populations, as well as the potential for coexistence between species.

These findings are relevant because niche variation may drive among-individual differences in competition, predation or parasitism risk (Darimont *et al.* 2007; Johnson *et al.* 2009; Duffy 2010), which may in turn affect population and community dynamics. Given the potential substantial effects of individual specialisation, it is important to understand when individual specialisation is likely to be strong or weak. We propose that there is a feedback loop in which (1) ecological interactions influence the amount of among-individual variation and (2) the amount of niche variation in turn alters ecological dynamics. The second step of this loop has recently been reviewed (Hughes *et al.* 2008; Bolnick *et al.* 2011). Herein, we extend these reviews by considering the first step of the feedback loop: how do ecological interactions affect the magnitude of intraspecific niche variation? We address this question by analysing comparative and experimental studies that recently have quantified individual specialisation.

Nearly a decade ago, Bolnick *et al.* (2003) gathered published examples of individual specialisation across the animal kingdom, to make the point that among-individual resource use variation is widespread. Despite the large number of examples, very few studies at the time reported quantitative measures of individual specialisation. Most case studies simply tested (and rejected) the null hypothesis that conspecific individuals shared an identical resource distribution. Consequently, there was little information about when this niche variation was more or less pronounced. Since that earlier review, the number of examples of individual specialisation has more than doubled (see below). Importantly, many of these new studies report quantitative measures of individual specialisation (Bolnick *et al.* 2002; Araújo *et al.* 2008). Further, many studies have moved beyond merely documenting

individual specialisation, to test hypotheses as to how the strength of individual specialisation varies across ecological contexts.

The goal of this article is to summarise the insights gained by the recent shift to quantitative measures of individual specialisation. First, we present a quantitative summary of the incidence and magnitude of individual specialisation. Second, we review theoretical predictions and empirical evidence about how ecological interactions affect the magnitude of individual specialisation. Third, in view of growing interest in this topic, we discuss common methodological concerns arising in studies of individual specialisation. We end by identifying promising areas for future research.

INCIDENCE AND MAGNITUDE OF INDIVIDUAL SPECIALISATION

We identified 107 new examples of individual specialisation in 93 vertebrate, 13 invertebrate and one plant species, published since the Bolnick *et al.* (2003) review on the subject (Table S1; Online Supplementary Information), of which 97 represent new examples of individual specialisation. Combined with the instances cited by the 2003 review, the total number of species displaying some degree of individual specialisation is 189 at the time of writing. The majority of examples were for vertebrates (78% of the taxa), largely fishes, with fewer examples of birds and mammals (Fig. 1). It is unclear whether the overrepresentation of vertebrates and fishes in particular, reflects sampling bias or a real trend. Another novel observation is that cases of individual specialisation tend to be common in upper trophic levels: 23 (44% of all available cases) of the fish, 13 (38%) of the bird and 21 (70%) of the mammal species may be considered upper trophic level predators. This tentative result raises the intriguing possibility that individual specialisation varies predictably with trophic position (Matthews *et al.* 2010).

Many recent studies went beyond simply testing for the presence of individual specialisation and quantified its magnitude using recently proposed indices (Bolnick *et al.* 2002; Araújo *et al.* 2008). Whereas Bolnick *et al.* (2003) compiled just 18 quantitative measures of individual specialisation, we found an additional 241 published – a greater than 13-fold increase. These quantitative measures span nine major taxonomic groups – plants, gastropods, crustaceans, insects, fishes, amphibians, reptiles, birds and mammals. From these studies, we summarise the quantitative patterns of individual specialisation using two common metrics, IS and WIC/TNW (Bolnick *et al.* 2002).

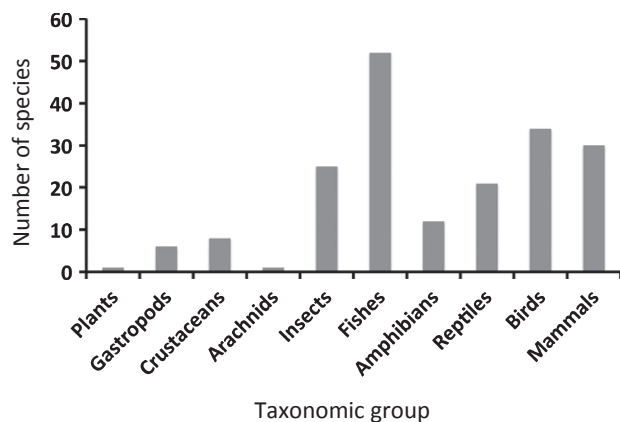


Figure 1 Number of species, classified by major taxonomic group, in which individual specialisation on diet, foraging behaviour, habitat or other niche axis has been documented. Total number of species is 189.

The IS measure of individual specialisation corresponds to the average similarity between each individual's diet and the population diet. When all individuals consume the full set of population resources, IS equals 1.0. As individuals use smaller subsets of the population diet, IS declines towards zero. The second metric, WIC/TNW, is based on a variance-partitioning framework, in which the total niche width of a population (TNW) is composed of a within- and a between-individual component (TNW = WIC + BIC; Roughgarden 1972, 1974). The ratio WIC/TNW thus measures how much smaller the average individual's niche is, compared to the population as a whole. Like IS, WIC/TNW ranges from 1.0 when all individuals are generalists and use the full population diet, towards zero when each individual uses only a single prey type whereas the population is more generalised. See the section on methodology, later in this review, for additional comments on these metrics.

Our survey reveals differences in the strength of individual specialisation among populations within species and among taxa (Fig. 2). On average, individuals' niches are 66% as broad as the population's niche (mean \pm SD; WIC/TNW = 0.66 ± 0.209 ; $n = 78$ population measures) and individuals are only, on average, 47% similar to their populations (IS = 0.47 ± 0.197 ; $n = 142$ measures). These metrics indicate, therefore, that individuals' niches are often narrower than the niches of their populations (Fig. 2a,b), consistent with the qualitative conclusions of Bolnick *et al.* (2003) that individual specialisation is substantial and common in natural populations. Of course, the predominance of strong individual specialisation in the published literature may result from publication bias. In our survey of the literature, we found only eight studies reporting cases of low or absent individual specialisation in just 12 species (Svanbäck & Persson 2004; Chérel *et al.* 2006; Poore & Hill 2006; Fontaine *et al.* 2008; Martínez del Río *et al.* 2009; Jaeger *et al.* 2010; Matich *et al.* 2011; Svanbäck *et al.* 2011). It is likely that negative results are under-published, in which case the average values reported herein may overestimate the strength of individual specialisation across all natural populations.

ECOLOGICAL CAUSES OF INDIVIDUAL SPECIALISATION

Two key questions arise from the observation of widespread individual specialisation in natural populations. First, what ecological factors determine the strength of individual specialisation? Second, does the strength of individual specialisation matter ecologically? For the remainder of this review, we focus on the first of these two questions – the latter is addressed in Hughes *et al.* (2008) and Bolnick *et al.* (2011). To understand how ecological interactions might modify the strength of individual specialisation, we first review the theory of how ecology should dictate individual niche width (WIC, as defined above), among-individual variation (BIC), and thus total niche width (TNW). To do so, we distinguish two theoretical frameworks: one based on optimal foraging theory and one on quantitative genetics. From these foundations, we review empirical results about how individual specialisation (WIC/TNW) depends on ecological interactions such as intra and interspecific competition, ecological opportunity and predation.

Theory

Foraging theory

Optimal Foraging Theory (OFT) provides a useful framework for understanding individual niche width (Stephens & Krebs 1986). Any

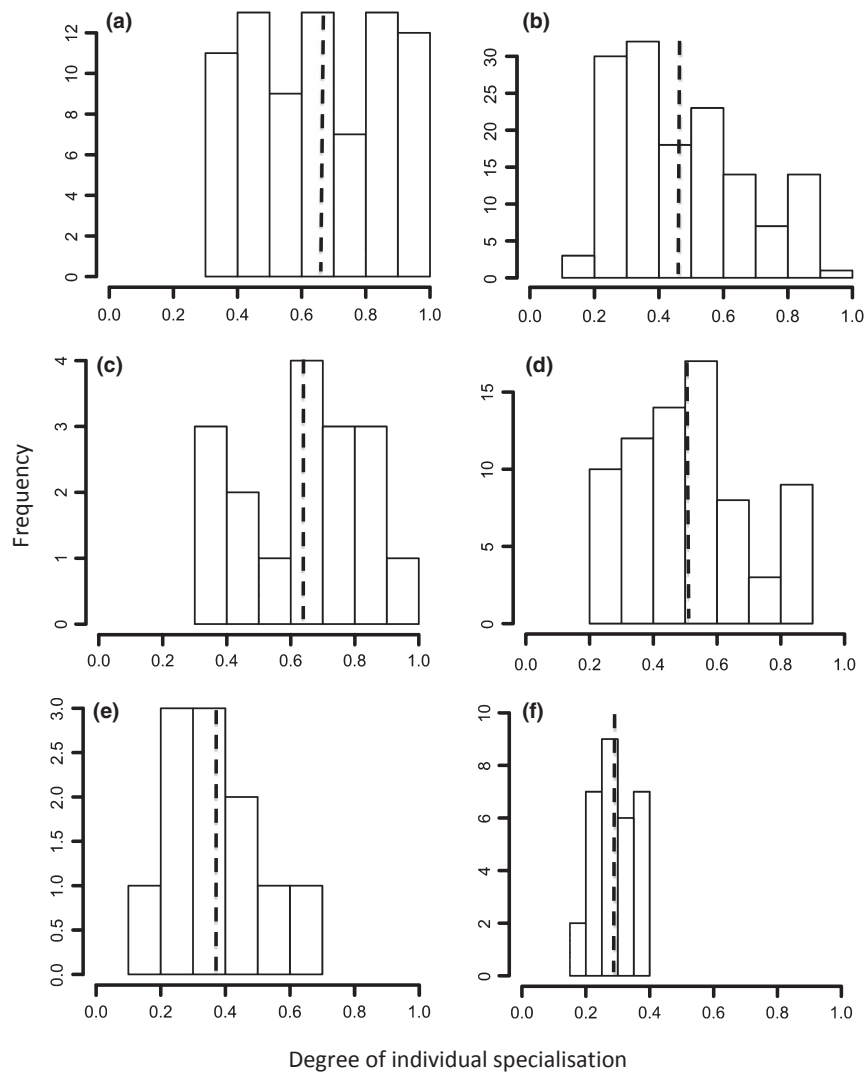


Figure 2 Empirical values of the (a) WIC/TNW and the (b-f) IS indices of individual specialisation calculated for plants, gastropods, crustaceans, insects, fishes, amphibians, reptiles, birds and mammals. (a,b) Combined measures for all taxa; (c) Crustaceans; (d) Fishes; (e) Amphibians; and (f) Reptiles. Values closer to zero indicate stronger individual specialisation. Dashed bars indicate average values.

individual occupies an environment with a particular diversity of potential resources, setting an upper bound on the individuals' niche width. OFT seeks to explain why individuals may consume only a subset of the available resource diversity. Typically, OFT models assume that individuals rank alternative resources according to their energetic value per unit handling time, which depends on resource traits and individuals' phenotypic capacity to capture, handle and to digest those resources. OFT suggests that individuals will always feed on the most valuable resources, ignoring lower-value resources when search and handling time could be better spent searching for more valuable ones. When preferred resources are scarce, individuals will expand their niche to accept previously unutilised resources. Thus, individual niche width (WIC) depends on the diversity of available resources ('ecological opportunity'), the individual's phenotypic traits and resource abundance.

The next question is why co-occurring individuals might consume different resources, leading to between-individual diet variation (BIC, the between-individual component of total niche width). Foraging theory suggests three general scenarios. First, individuals may have different optimal diets due to different rank preferences. For instance, phenotypic variation (genetic or environmental) can

produce among-individual differences in ability to detect, capture, handle, or digest alternative prey, leading to divergent rank preferences. Second, individuals may have different optimal diets because they use different optimisation criteria (Schoener 1971). For instance, within populations some individuals choose resources to minimise predation risk, while other individuals are less risk-averse and act to maximise energy intake. Similarly, individuals might differ in diets because they have different physiological requirements, for example when lactating females consume otherwise sub-optimal resources to obtain specific nutrients (Belovsky & Jordan 1978). Third, individuals may differ in their ability to attain their optimal diet. For instance, if socially dominant individuals secure the best areas or resources, subordinates may be unable to access preferred resources (Sol *et al.* 2005). Thus, between-individual diet variation relies on some amount of phenotypic variation affecting consumer's resource preferences, foraging behaviour, physiological requirements and/or social status.

Next, to understand the degree of individual specialisation (WIC/TNW), we consider how ecological interactions might differentially affect WIC or BIC. Intraspecific competition will tend to reduce availability of preferred resources, driving individuals to

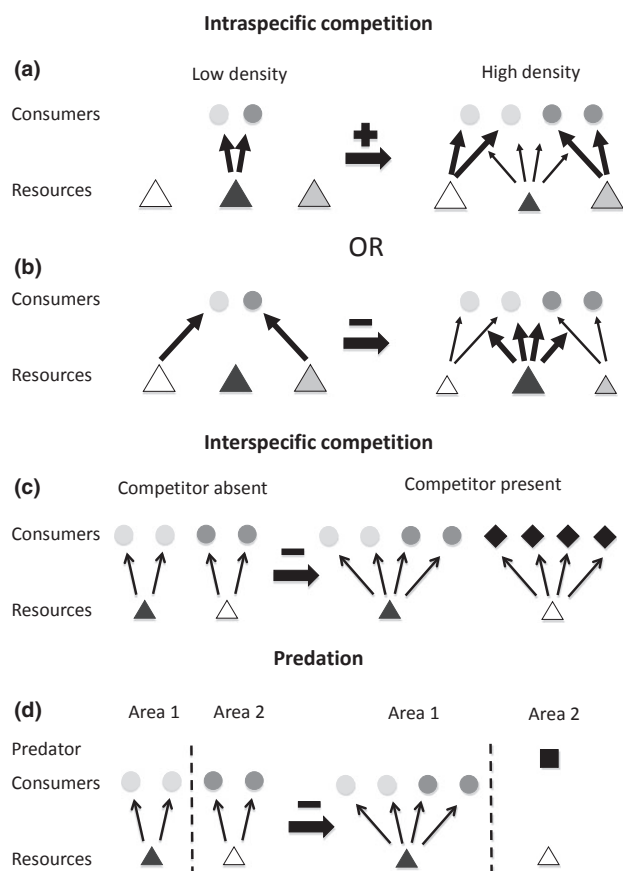


Figure 3 Illustration of how ecological mechanisms may affect the degree of individual specialisation. Arrows linking resources to individual consumers indicate resource consumption (relative thickness indicates proportional contribution). Horizontal arrows indicate the sign (positive or negative) of the effect on the degree of individual specialisation. (a) Consumers with different phenotypes (different shades of grey) share the same preferred resource (dark gray triangle), but have different alternative resources (white and light gray triangles). At low density consumers with both phenotypes consume the preferred resource; at higher densities, as the preferred resource becomes scarce (smaller sized triangle) due to higher intraspecific competition, consumers add alternative resources to their diets, increasing the degree of individual specialisation. (b) Alternatively, consumers with different phenotypes may have distinct preferred resources, so that at low density there are distinct diets. At higher densities all individuals converge to the same alternative resource (dark gray triangle), reducing diet variation. (c) In the absence of a competitor species (black diamonds), consumers with different phenotypes exploit different resources and individual specialisation is high. In the presence of a competitor, the population niche is constrained to one resource (dark gray triangle) limiting the degree of individual specialisation. The converse of interspecific competition is ecological opportunity, which may increase due to competitive release and should have a positive effect on individual specialisation (see text). (d) If resources occur in different microhabitats (e.g. littoral vs. pelagic zones of a lake), presence of a predator in one of the microhabitats may constrain consumers to the safe area, reducing the scope for individual specialisation.

expand their niche to less valuable resources (increased WIC). The corresponding change in BIC is less predictable (Svanbäck & Bolnick 2005). If individuals all prefer the same top-ranked resource but resort to different secondary resources, then as individuals expand their niches they will tend to diverge (Fig. 3a). As a result, intraspecific competition may increase individual specialisation as BIC increases faster than WIC (leading to smaller WIC/TNW). Alternatively, individuals may initially prefer different resources but converge onto

shared secondary resources as competition intensifies (Fig. 3b), thereby reducing BIC and individual specialisation. As such, foraging theory predicts that intraspecific competition can either increase or decrease individual specialisation, depending on the pattern of rank-preference variation. By extension, interspecific competition also is expected to alter individual specialisation. The direction of this effect is variable, depending on the type of rank-preference variation in the focal species as well as the nature of diet overlap with the competing species (e.g. competing for preferred or lower-valued prey). These changes in individual specialisation can occur within a generation, as they depend on individuals changing foraging behaviour in response to shifting ecological conditions.

Quantitative genetic theory

From an evolutionary standpoint, niche variation is unsurprising: without heritable variation in resource use, a population's dietary niche would be unable to evolve. Thus, individual specialisation plays a key role in several models of niche evolution (Roughgarden 1972; Slatkin 1980; Taper & Case 1985; Ackermann & Doebeli 2004). This body of theory on individual specialisation uses tools from quantitative genetics, focusing on heritable evolutionary change. Individual niche width (WIC) is presumed to be a fixed (Roughgarden 1972) or strictly heritable trait (Taper & Case 1985; Ackermann & Doebeli 2004), as opposed to the behaviourally flexible trait assumed by OFT. Between-individual diet variation (BIC) is assumed to arise from heritable phenotypic variance, which can be eroded or amplified by stabilising or disruptive selection. The problem is thus reduced to the question of when ecological processes promote or lessen genetic variation in resource use.

Generally speaking, intraspecific competition is expected to generate selection for increased total niche width, because adding new resources reduces the overall severity of resource limitation. Interspecific competition has the opposite effect, limiting a population from certain resources and thereby decreasing population niche width (e.g. ecological character displacement; Slatkin 1980). All these changes are predicted to occur by altered individual niche width (WIC), because selection is expected to remove between-individual variation and thus eliminate individual specialisation ($WIC/TNW \sim 1$; Taper & Case 1985; Ackermann & Doebeli 2004). The exception is when functional trade-offs prevent the evolution of an effective generalist strategy (Taper & Case 1985; Wilson & Turelli 1986). Placing an upper bound on individual niche width means that changes to total niche width can only occur via changes in between-individual variation (individual specialisation). Therefore, release from interspecific competition should occur largely via increased inter-individual variation and individual specialisation (Fig. 3c; Niche Variation Hypothesis or NVH, Van Valen 1965).

Empirical evidence

Intraspecific competition

As noted above, both foraging and quantitative genetic models suggest that intraspecific competition favours the evolution of increased individual niche width. But the actual outcome depends on the form of rank-preference variation (OFT) or the strength of trade-offs limiting individual niche width (quantitative genetic models). Recent empirical studies consistently find that intraspecific competition increases individual specialisation (Table S1). Several correlational studies have demonstrated a positive relationship between population density (a proxy for intraspecific competition)

and the degree of individual specialisation (Svanbäck & Persson 2004; Svanbäck *et al.* 2008; Svanbäck & Persson 2009; Frederich *et al.* 2010). Other studies showed that lower resource abundance coincided with behavioural diversification in microhabitat use (Kobler *et al.* 2009) or the inclusion of novel resources via increased interindividual variation (Tinker *et al.* 2008; Yeakel *et al.* 2009; Svanbäck *et al.* 2011).

Two experimental studies also found a positive relationship between intraspecific competition and individual specialisation (Svanbäck & Bolnick 2007; Huss *et al.* 2008). Svanbäck & Bolnick (2007) manipulated population density of stickleback (*Gasterosteus aculeatus*) in small (9 m²) field enclosures, and found that competition drove increased individual specialisation over a 2 week period. Competition drove increased population niche width via greater between-individual variation. Huss *et al.* (2008) manipulated population density of YOY Eurasian perch (*Perca fluviatilis*) and found that under high competition larger YOY switched from zooplankton to macroinvertebrates, increasing interindividual diet variation. As such, multiple experimental and observational studies indicate that intraspecific competition increases individual specialisation, a body of evidence that stems directly from the recent shift towards quantitative hypothesis-testing of individual specialisation.

Interspecific competition

The Niche Variation Hypothesis states that ecological release from competing species leads to population niche expansion largely via increased between-individual variation (Van Valen 1965). The NVH has received limited support from studies looking at the variation in size or trophic morphology (used as a proxy for diet variation; e.g. Diaz 1994; Meiri *et al.* 2005). Recent quantitative studies of individual specialisation have been more supportive of the NVH, typically finding a positive correlation between the population niche width and degree of inter-individual diet variation (Bolnick *et al.* 2007; Costa *et al.* 2008; Araújo *et al.* 2009; Darimont *et al.* 2009). The discrepancy between morphological and dietary results seems obvious in retrospect: ultimately the NVH is about changing patterns of resource use, whereas morphological variance is a rather indirect proxy. Diet variance, therefore, provides a more direct test of the NVH than morphological variance.

If interspecific competition weakens individual specialisation, we would predict individual specialisation to be weaker in species-rich communities, where interspecific competition should be stronger (assuming richness correlates with interspecific competition and other factors being equal). Two recent studies confirmed this prediction (Knudsen *et al.* 2007; Costa *et al.* 2008). Arctic charr, *Salvelinus alpinus*, in a lake with few other fishes showed more interindividual resource use variation than another nearby population with more competing fish species (Knudsen *et al.* 2007). Second, in 17 Brazilian lizard species across 18 localities, Costa *et al.* (2008) did not find any effect of species richness *per se* on individual specialisation, but found a negative relationship between individual specialisation and an index of phylogenetic diversity. That is, individual specialisation was higher when interacting species were less closely related. Assuming that more closely related species are also ecologically more similar (and therefore stronger competitors), these results also argue for a negative effect of interspecific competition on the degree of individual specialisation.

The only experimental study of how interspecific competition affects individual specialisation yielded conflicting results. Threespine stickleback, *Gasterosteus aculeatus*, released from competition with juvenile cut-throat trout, *Oncorhynchus clarki*, showed increased popu-

lation niche width and more individual specialisation, consistent with the Niche Variation Hypothesis (Bolnick *et al.* 2010). However, release from competition with prickly sculpins, *Cottus asper*, had the opposite effect: individual niches expanded while population niche width remained constant, thus reducing individual specialisation. At present it is unclear why these competitors have such different effects on stickleback diet variation.

In sum, comparative and experimental evidence support the notion that interspecific competition reduces (or competitive release increases) individual specialisation, but this is not a universal outcome. One important future direction would be to consider effects of different kinds of competition; existing models are exclusively focused on exploitative competition, whereas interference competition (for instance) may have very different effects (Huss *et al.* 2008; Svanbäck *et al.* 2011).

Ecological opportunity

Interspecific competition and ecological opportunity are related, but distinct, concepts. Typically, interspecific competition is presumed to reduce ecological opportunity, but opportunity also depends on factors such as patch size, microhabitat diversity, resource diversity and environmental stability (Nosil & Reimchen 2005; Parent & Crespi 2009). Thus, opportunity can vary independently of the number or abundance of competing species, and have correspondingly independent effects on population and individual niche width. For example, habitat fragmentation in estuarine tidal wetlands leads to lower resource diversity and simplified food webs, which in turn decreases individual specialisation in a predatory fish, the grey snapper *Lutjanus griseus* (Layman *et al.* 2007b). Similarly, individual specialisation in the grey wolf, *Canis lupus*, is positively related to resource diversity (Darimont *et al.* 2009; Semmens *et al.* 2009). Populations with access to both marine and terrestrial resource pools exhibited stronger individual specialisation than populations restricted to one of these resource pools. In addition, seasonal dynamics of resources and consumer niche variability offers additional support to the idea that the degree of individual specialisation should increase with higher diversity of resources. For example, in the fruit bat, *Rousettus aegyptiacus*, the degree of individual specialisation was higher in spring, when the number of plant species bearing fruits was also higher (Herrera *et al.* 2008). Available correlational studies (Table S1), therefore, seem to support the longstanding suggestion that higher levels of ecological opportunity should favour individual specialisation (Roughgarden 1974). Although this result might seem intuitive, these quantitative studies are the first to provide solid empirical evidence of this prediction.

Predation

Individual specialisation can be affected by predation in either of two ways: (1) density-mediated effects (changes in prey abundance) or (2) changes in prey behaviour in response to predation risk. Either mechanism could plausibly lead to increased or decreased individual specialisation. By regulating the populations of their prey, predators may promote low intraspecific competition among prey, which may result in either low or high individual specialisation. If a predator is restricted largely to one microhabitat, prey may all take refuge in a protected microhabitat and thus converge in resource use (Fig. 3d; Werner *et al.* 1983). Alternatively, if individuals vary in risk aversion, predation risk might exaggerate individual diet differences as risk-averse individuals shift to less profitable refuges while others forage in more risky areas (Coleman & Wilson 1998).

One experiment found that the presence of a predator (larval dragonfly) reduced size variation in cohorts of bullfrog tadpoles, *Rana catesbeiana*, by suppressing natural variation in the expression of behavioural traits (e.g. activity levels; Peacor & Pfister 2006). Though this study did not measure diet variation, if diet is correlated with size then predation would tend to reduce individual specialisation. A similar outcome was found by Eklöv & Svanbäck (2006), who exposed young-of-the-year (YOY) Eurasian perch, *Perca fluviatilis*, to a predatory adult perch constrained to one of two habitats (pelagic or littoral). Without predators, YOY perch utilised both habitats and showed strong individual specialisation. With predators, YOY perch remained in the safer habitat, suppressing diet variation (Eklöv & Svanbäck 2006). Thus, the limited available evidence suggests that predation reduces individual specialisation, but there is no theoretical reason why this should be a general result. There has been no consideration of how other natural enemies (e.g. parasitoids, parasites or pathogens) affect the magnitude of individual specialisation.

METHODOLOGICAL CONSIDERATIONS

The conclusions discussed above were only possible because researchers have begun quantifying individual specialisation in both comparative and experimental studies. Although the trend towards more quantitative studies of individual specialisation is encouraging, these quantitative approaches have potential pitfalls. We summarise several methodological issues that are critical to consider when exploring the incidence and degree of individual specialisation.

Relevant data

The central challenge in studying individual specialisation is the need to acquire replicated observations of each individual's resource use decisions to calculate an index of diet variation among individuals (Bolnick *et al.* 2002; Araújo *et al.* 2008). Most ecological studies treat the individual as the level of replication (e.g. the error term in a statistical linear model). In contrast, to quantify individual specialisation, individual is a random-effect term whose variance we wish to estimate; residual error is provided by multiple observations per individual. Thus, one's ability to estimate individual specialisation depends on the number of independent feeding decisions recorded per individual, as well as the number of individuals. Ecologists typically employ two types of data to measure individual specialisation.

(1) Longitudinal data, in which multiple individuals' foraging decisions are observed repeatedly over time, is ideal for studies of individual specialisation. Importantly, replicate observations of each individual's feeding bouts should be spaced far enough apart in time to ensure they are independent events. The duration over which independent longitudinal observations are made (e.g. days, months or years) should be tailored to the biological question at hand and the study species. Observations made over a few days can provide a valid measure of among-individual variation, with the caveat that one does not know the duration over which individual specialisation persists ('consistency'). Long sample periods provide better measures of consistency, but may gloss over episodes of strong individual specialisation. Approximately one-third of the studies in Table S1 employed longitudinal sampling.

(2) Cross-sectional samples of individuals' feeding events are frequently used when longitudinal data are unobtainable. Stomach contents are the most commonly used source of cross-sectional diet data, but a variety of other approaches are employed (analysis of animal scat, direct feeding observations, etc.). Obviously, one can only use stomach data to draw an inference about a very limited window of time (unless one uses gastric lavage to non-lethally acquire stomach contents repeatedly from the same individual). Using a cross-sectional sample rests on several important assumptions. This approach can be used to quantify individual specialisation if, and only if:

- (i) *there are multiple prey items per stomach.* This is important because the number of prey items per individual determines statistical power, rather than the number of individuals. For example, piscivorous fishes often have a single item in their stomachs (Layman *et al.* 2005), rendering them unsuitable for cross-sectional stomach content analyses of individual specialisation. Low sample sizes per individual will tend to artificially inflate estimates of individual specialisation. However, this inflation can be tested using any of a number of statistical tests, ranging from contingency tables (e.g. chi-squared test) or Monte Carlo resampling procedures (Bolnick *et al.* 2002; Araújo *et al.* 2008). These methods allow one to test whether the observed diet variation exceeds a null expectation, with the null hypothesis being that individuals sample randomly from a single population diet distribution. Often times the null expectation will vary between populations, for instance if there are different numbers of prey items per stomach. In this case, the average null index (from Monte Carlo samples) should be used as a covariate in subsequent analyses comparing different populations.
- (ii) *multiple prey items represent independent prey-capture decisions.* This is necessary to ensure that the multiple prey items per individual consumer are statistically informative. Non-independence among prey items (e.g. if prey are spatially clumped) may lead to over-estimation of diet variation. This criterion is typically the hardest to evaluate, and must be carefully evaluated in any particular study organism. Note that the Monte Carlo resampling methods, which are used to test for departures from a null hypothesis, rely on this assumption.
- (iii) *the sampled diet is representative of the overall diet of the individual.* If individuals feed on multiple prey items, the single diet sample must be a reasonable approximation of the individual's longer-term diet. If there are substantially fewer items in the sampled diet, then the degree of individual specialisation will tend to be overestimated. Since many organisms (e.g. piscivorous fishes) have relatively few diet items at a given time, this assumption is often violated in studies of diet variation. Null model approaches can help avoid this pitfall (see below). However, null models cannot fix bias introduced by sampling individuals who have undergone a temporary diet shift.
- (iv) *individuals being compared must be drawn from a small spatial range, and a single point in time.* Any spatial or temporal heterogeneity among specimens may introduce variance in resource availability that artificially inflates measures of individual specialisation. In principle it should be possible to calculate a measure of individual specialisation after statistically

removing temporal or spatial trends in population diet, but these methods have not yet been applied in practice.

Testing a null hypothesis

For both longitudinal and cross-sectional data, the null hypothesis is that all individuals sample prey with similar probabilities from a shared set of taxa (e.g. $WIC/TNW = 1$). This null hypothesis can be tested using Monte Carlo resampling methods. To begin with, a researcher uses any of a number of indices to quantify individual specialisation (Bolnick *et al.* 2002; Araújo *et al.* 2008). The indices are all correlated, but have slightly different interpretations – see Bolnick *et al.* (2002) for details. For each of perhaps several thousands of iterations, every individual in the sample is reassigned its original number of prey, drawn randomly from the population diet distribution (multinomial sampling), and then the index of diet variation is recalculated. Biologically real diet variation is inferred when the observed value falls outside the range of the null values. Therefore, null models provide a useful test for the presence of individual specialisation, and can identify cases where small numbers of prey per individual artificially generate the appearance of individual specialisation. The null values generated by Monte Carlo resampling can also be used as a covariate in statistical comparisons of the degree of individual specialisation across different populations (see below).

However, available null models also have serious limitations, particularly that they do not test for independence of feeding events (criterion ii above) or spatial or temporal sources of variance (criterion iv). Moreover, current null models can only be used with prey count data, not total prey mass or volume, because counts are assumed to represent independent feeding events (Bolnick *et al.* 2002; Araújo *et al.* 2008). However, when prey taxa differ greatly in size, resampling procedures can generate biologically implausible results. For example, in the Eurasian perch, *Perca fluviatilis*, individuals in the same cohort may feed on zooplankton or fishes (Urbatzka *et al.* 2008). One cannot resample based on grams, because a predator does not choose to capture a large fish prey on a per-gram basis. On the other hand, one cannot simply resample randomly when the consumer would be satiated either by eating a single fish, or hundreds of *Daphnia*. A useful future development would be to develop null models that sample individual prey while taking into account prey size and predator satiation. Until such tools exist, resampling routines are most appropriate for predators with similar-sized prey items per stomach.

A final limitation of null models is that, at present, they do not automatically adjust the estimated degree of individual specialisation to variation in baseline expectations. For example, the index E measures the average pairwise dissimilarity among individuals, and varies from 0 (no individual specialisation) to 1 (each individual uses a unique set of prey). However, stochastic sampling will always generate a null value larger than zero – much larger when there are few samples per individual. Imagine sampling two populations, one with actual individual specialisation and many observations per individual ($E = 0.7$, null $E = 0.2$), another with weak actual individual specialisation but few observations per individual ($E = 0.7$, null $E = 0.6$). Proceeding to use the raw E values would falsely imply equal individual specialisation. Thus, in comparative studies of individual specialisation, it is vital to use the mean null value as a covariate to account for variation in individual specialisation measures that arise simply from sampling effects (Bolnick *et al.* 2007).

Categorising prey

Individual specialisation can be calculated using a number of prey attributes. The first quantitative metric of individual specialisation (WIC/TNW) was developed for prey body size data (or any other continuous measure; Roughgarden 1974). Roughgarden (1979) subsequently adapted this metric to categorical prey data such as prey taxonomic composition, using the Shannon diversity index in place of variances. Most other metrics of individual specialisation are intended for taxonomic composition data (Bolnick *et al.* 2002; Araújo *et al.* 2008). Inevitably, the quantitative value of the metric will depend on the resolution at which one defines prey categories. Consider the above-mentioned index E applied to a population that uses two prey categories in equal proportion. If individuals in this population are complete specialists on either of the two categories, any given individual has an average pairwise dissimilarity of 0.5 (complete similarity with half its conspecifics, complete dissimilarity with the other half). Thus, the maximum value E can take is 0.5. However, if we subdivide the prey into 10 taxonomic categories (used equally by the population overall), then the maximum value E can take is 0.9. Consequently, metrics of individual specialisation can depend on how resource taxa are lumped into functional categories. This problem is shared by all indices that use prey category frequency data. A solution is to not only rescale one's index by the null value (as discussed above), but also by the theoretical maximum. For instance, if E really varies between a null of 0.3 and a maximum of 0.9, then one can calculate an adjusted value ($E_{adj} = \frac{E_{observed} - E_{null}}{E_{max} - E_{null}}$), which will range from 0 to 1 and be comparable across samples with different nulls and maxima.

Few studies clearly report their taxonomic resolution, making it difficult to directly compare values across studies. At the very least, it would be beneficial if authors reported the mean and variance of the number of prey items and prey categories per individual. In practice, however, different lumping strategies often yield only slightly different outcomes (Bolnick, pers. obs.) that do not confound comparative or experimental results.

Sample size

There has been no systematic analysis of sample size requirements for estimates of individual specialisation. Sample size in such studies has two facets: the number of individuals sampled and the number of resource use events observed per individual. Current resampling procedures only account for sampling of prey items within individuals. An important next step would be to incorporate the sampling of individuals of a population into randomisation procedures to generate confidence intervals around estimates of individual specialisation. This would aid researchers to determine the number of individuals of a population that need to be sampled to allow reliable inferences about the population's degree of individual specialisation. This will be an especially important issue when the number of individuals sampled is small and/or when individuals vary substantially in their degree of specialisation, as the inclusion of a single additional individual might substantially change the estimate.

Stable isotopes

In view of the caveats associated with stomach content analysis, additional sources of evidence for individual consistency in resource

use are always desirable when studying individual specialisation. For example, stable isotope ratios reflect individuals' diet over a longer time-frame (typically weeks to months; Dalerum & Angerbjörn 2005). Isotopes may thus provide a powerful tool to infer temporal consistency and supplement measures from stomach contents. Not surprisingly, this technique is becoming increasingly more popular in studies of individual specialisation (Table S1). Several new analytical approaches based on stable isotopes have been proposed in the last few years, offering new possibilities that might greatly improve ecologists' ability to investigate individual specialisation.

The basic idea of these isotopic approaches is that individuals' tissues will have isotope signatures that reflect their diet (Layman *et al.* 2007a; Newsome *et al.* 2007). If individual predators have different diets (and prey differ isotopically), then the predators will also differ in their isotope signatures. Therefore, the variance in isotope values among individuals in a population can be used to infer the degree of diet variation. This inference requires information about the isotopic variance among available resources. Recently developed methods include (1) null models providing the possibility of testing for the presence of individual specialisation after adjusting for prey isotopic signatures (Matthews & Mazumder 2004), (2) indices of individual specialisation (Araújo *et al.* 2007) and (3) Bayesian hierarchical models that allow the partitioning of isotope variation between different levels (e.g. sex, social group, individual; Semmens *et al.* 2009).

Isotopes also can be used to infer changes in diet variation through time. Different tissue types (e.g. liver, muscle) have different turnover rates, and therefore integrate resource use over different time scales (Bearhop *et al.* 2004). As a consequence, individuals that consistently specialise on the same resource(s) over time should have similar isotope values in different tissues (after correcting for among tissue differences in fractionation rates), whereas individuals that switch resources over time (e.g. seasonally) should show a mismatch between faster and slower tissues (Martínez del Río *et al.* 2009; Matich *et al.* 2011). Alternatively, metabolically inert tissues, such as hair and feathers, represent a consumer's diet at the time of deposition, so that if the rate of tissue deposition is known, these tissues can represent a timeline of the consumer's isotopic history (Newsome *et al.* 2009).

So far, isotopic approaches have largely been used to test for the presence/absence of individual specialisation, rather than to quantify it for comparative purposes (but see Araújo *et al.* 2007; Matich *et al.* 2011). Importantly, however, isotopic variance can be well correlated with stomach content-based measures of individual specialisation (Araújo *et al.* 2007) and can thus provide validation that cross-sectional measures of individual specialisation can be reasonably robust.

Studies using isotopes must sample prey and consumers at relevant temporal and spatial scales, and preferably should account for isotopic variance within prey taxa, variation in fractionation among consumers, and rates of isotopic turnover. Recent Bayesian approaches that allow the incorporation of some of these sources of error as priors offer a promising analytical tool (Semmens *et al.* 2009). Despite these caveats, stable isotope data will continue to be critical in the study of individual specialisation, especially when used in conjunction with direct dietary information (Layman & Post 2008).

CONCLUSIONS AND FUTURE DIRECTIONS

As of the 2003 review by Bolnick *et al.*, most studies of individual specialisation simply tested the null hypothesis that individuals feed

opportunistically from a common pool of resources. This hypothesis-testing approach was sufficient to establish that individual specialisation exists. Many of the more recent studies have taken a more quantitative approach, providing empirical evidence for several predictions from theory. A number of observational and experimental studies support the qualitative prediction that intraspecific competition and ecological opportunity should promote individual specialisation (Table S1). On the other hand, interspecific competition can increase or decrease individual specialisation depending on the context. The reason for this heterogeneity is unclear. The effect of predation on individual specialisation has received insufficient attention. Future investigations should reveal the generality of these findings and the relative importance of different ecological mechanisms (e.g. intra vs. interspecific competition; Svanbäck *et al.* 2008) in maintaining individual specialisation in natural populations.

The results so far are in line with the limited available theory on the mechanisms of individual specialisation. Unfortunately, available theory makes largely qualitative predictions on the degree of individual specialisation, depending on assumptions (Roughgarden 1972, 1974; Taper & Case 1985). For example, intraspecific competition may increase or decrease individual specialisation depending on phenotypic variance in rank preferences (Svanbäck & Bolnick 2005). Rigorous tests of theory will therefore require empirically parameterised models (e.g. phenotypic variance in rank preferences) to yield specific predictions for a given study system (Svanbäck & Bolnick 2005; Tinker *et al.* 2009). This foraging theory approach could allow more complex scenarios as well, such as the presence of a top predator, or a patchy distribution of resources in space. Alternatively, game theoretical approaches, which have been used to investigate a wide range of ecological and evolutionary questions (McGill & Brown 2007), can also provide promising avenues for future research. For example, ideal free distribution theory (IFD, Fretwell & Lucas 1969) predicts that as population density increases, individuals within a population will distribute themselves among patches so that fitness is equalised in all patches. If we draw an analogy between patches and resources (or for that matter assume that resources are heterogeneously distributed in space), it is easy to predict that individuals will switch to novel resources as a consequence of increased density. More complex scenarios in which individuals have different competitive abilities, so that superior competitors secure the best patches/resources (Houston & McNamara 1988) could also be incorporated in such models. Finally, another important future direction would be to integrate these mechanistic behavioural models with population dynamic and/or quantitative genetic models. Individual based models (IBMs, Grimm & Railsback 2005) could provide a useful analytical tool in such endeavour.

At a proximate level, it is relatively well established that individual specialisation is usually associated with functional trade-offs, where the use of different resources by a single individual is constrained by functional morphology, cognitive ability or digestive ability (Persson 1985; Afik & Karasov 1995; Robinson 2000; Svanbäck & Eklöv 2003, 2004; Olsson *et al.* 2007). These trade-offs might cause individuals with different phenotypes to rank resources differently in terms of energy gain per unit time, providing a proximate explanation for among-individual niche variation (Bolnick *et al.* 2003). Recent studies on animal culture and social learning suggest that culturally transmitted foraging behaviours, including tool use, may also be an

important mechanism underlying individual specialisation (Estes *et al.* 2003; Sargeant *et al.* 2005; Hunt & Gray 2007; Mann *et al.* 2008; Sargeant & Mann 2009; Torres & Read 2009). More information is needed, however, about the neurological, biomechanical or physiological basis of constraints on individual niche width.

We still know very little about the genetic basis of individual specialisation, which will ultimately determine its potential for evolutionary change (Agashe & Bolnick 2010) and is, therefore, of utmost importance. Studies on the topic have usually measured genetic variation in quantitative traits assumed to correlate with diets (e.g. trophic morphology). For the most part, they have found evidence of a genetic basis (Grant & Price 1981; Hermida *et al.* 2002), but also a potentially large component of phenotypic plasticity (Svanbäck & Eklöv 2006; Urbatzka *et al.* 2008). The investigation of feeding behaviour has highlighted the genetic component of several aspects of foraging, such as prey recognition or preference (Gibbons *et al.* 2005; Latshaw & Smith 2005). Empirical evidence, therefore, suggests a potentially important genetic component of diet variation, but studies directly measuring the heritability of individual specialisation are lacking.

Another important future direction is to expand beyond single-species studies of individual specialisation (e.g. Svanbäck *et al.* 2008). It is quite plausible that diet variation might vary systematically across trophic positions. Trophic position can influence the relative role of top-down or bottom-up density regulation and, as discussed above, both predation and competition can alter the strength of individual specialisation. Our review found a large number of top predators among the empirical cases of individual specialisation. Confirming such patterns will be critical in developing biologically justifiable models of the community effects of individual specialisation. For instance, mobile top predators have the opportunity to link spatially separate food chains (McCann *et al.* 2005), which may have important stabilising effects on community dynamics (Rooney *et al.* 2006). However, this effect may be nullified if individual specialisation is particularly strong in top predators, because although top predators may be population generalists, individual predators may be specialised and thus rarely disperse among patches with separate food chains (Quevedo *et al.* 2009; Matich *et al.* 2011). In this context, individual specialisation may tend to undermine the typically stabilising effects of these keystone predators, clearly affecting the role that predators play in structuring communities. Thus, individual specialisation may both alter and be altered by, community ecology interactions. A long-term research goal would be to study both directions of this feedback loop.

ACKNOWLEDGEMENTS

This work was conducted as a part of the *Ecology of Niche Variation* Working Group at the National Institute for Mathematical and Biological Synthesis, sponsored by the National Science Foundation, the U. S. Department of Homeland Security and the U. S. Department of Agriculture through NSF Award #EF-0832858, with additional support from The University of Tennessee, Knoxville. Research was also supported by NSF grants OCE #0746164 and DEB # 0842196. MSA thanks CAPES for financial support. DIB was supported by the Howard Hughes Medical Institute and the David and Lucille Packard Foundation. We thank John Fryxell, Mike Heithaus, Mark Novak, Richard Svanbäck and two anonymous reviewers for comments on earlier versions of the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Empirical cases of species/populations with individual specialisation (IS) in diet, foraging behaviour, habitat preferences, or other niche axis documented since 2003.

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Editor, John Fryxell

Manuscript received 2 May 2011

First decision made 4 June 2011

Manuscript accepted 18 June 2011