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The Ecology of Individuals: Incidence and Implications of Individual Specialization

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abstract: Most empirical and theoretical studies of resource use and population dynamics treat conspecific individuals as ecologically equivalent. This simplification is only justified if interindividual niche variation is rare, weak, or has a trivial effect on ecological processes. This article reviews the incidence, degree, causes, and implications of individual-level niche variation to challenge these simplifications. Evidence for individual specialization is available for 93 species distributed across a broad range of taxonomic groups. Although few studies have quantified the degree to which individuals are specialized relative to their population, between-individual variation can sometimes comprise the majority of the population's niche width. The degree of individual specialization varies widely among species and among populations, reflecting a diverse array of physiological, behavioral, and ecological mechanisms that can generate intrapopulation variation. Finally, individual specialization has potentially important ecological, evolutionary, and conservation implications. Theory suggests that niche variation facilitates frequency-dependent interactions that can profoundly affect the population's stability, the amount of intraspecific competition, fitness-function shapes, and the population's capacity to diversify and speciate rapidly. Our collection of case studies suggests that individual specialization is a widespread but underappreciated phenomenon that poses many important but unanswered questions.

Keywords: individual specialization, adaptive variation, niche width, resource partitioning, frequency dependence, niche variation hypothesis, individual ecology.

Ecologists have long used niche theory to describe the ecology of a species as a whole, treating conspecific individuals as ecologically equivalent. For example, most models of intraspecific competition, predator-prey dynamics, and food web structure assume that conspecific individuals are identical (but see Lomnicki 1988; DeAngelis and Gross 1992). Similarly, the majority of articles on measuring species' niche width make no mention of the fact that individuals of the same species may use different resources (e.g., Hutchinson 1957; Colwell and Futuyma 1971; Pielou 1972; Abrams 1980; Feinsinger et al. 1981; Linton et al. 1981). This omission persisted despite a well-developed literature on niche width variation, originating with Van Valen's (1965) niche variation hypothesis. On the basis of his observations of island and mainland bird populations, Van Valen proposed that niche expansion in the absence of interspecific competition was achieved by increased between-individual variation in resource use. The role of between-individual niche variation in niche evolution was further supported by theoretical work by Roughgarden (1972, 1974). The ensuing flurry of empirical tests varied between supportive (Fretwell 1969; Rothstein 1973; Grant et al. 1976; Bernstein 1979), inconclusive (Willson 1969), and negative (Soulé and Stewart 1970; Soulé 1972; Patterson 1983; Diaz 1994). Other empirical studies downplayed the importance of interindividual diet variation. Analyzing diet data for five species of *Anolis* lizards, Roughgarden (1974) showed that between-individual variation was generally small, a conclusion that subsequently received theoretical support (Taper and Case 1985). On reviewing this debate, Grant and Price (1981, p. 797) concluded that "the status of the adaptive variation hypothesis hangs in the balance, and it is in danger of death through neglect as a result of confusion in the empirical tests and theoretical inadequacies." As predicted, discussion of individual variation trailed off in the 1980s but has revived recently with renewed interest in adaptive radiation and ecological speciation (Mousseau et al. 2000; Schluter 2000; Halama and Reznick 2001).

Given the contentious history of the niche variation

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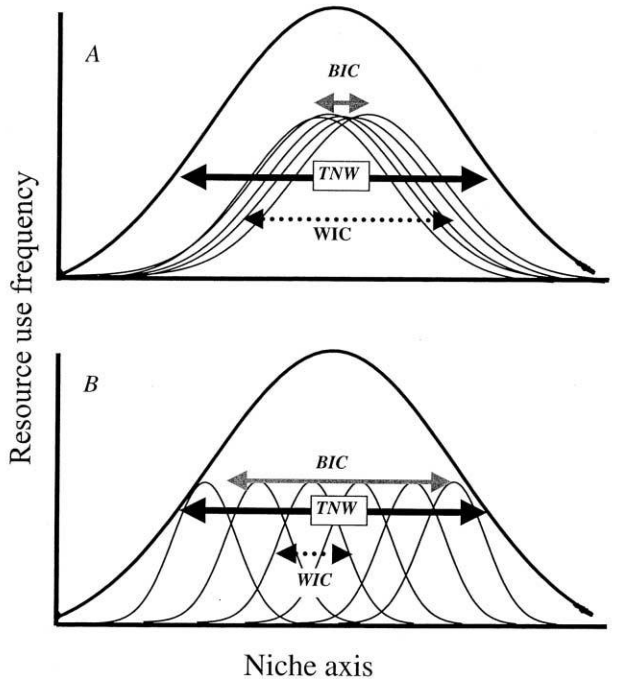

Figure 1: A schematic diagram of how individuals can subdivide the population's niche (*thick curve*). The total niche width (TNW, *black arrow*) is the variance of total resource use of all individuals (*thin curves*). TNW = WIC + BIC, where WIC (*dotted arrow*) is the average of individual niche widths, and BIC (*gray arrow*) is the variance in mean resource use among individuals. *A*, In a population of generalist individuals, WIC is a large proportion of TNW; *B*, WIC/TNW is small in a population of individual specialists. Although the idealized Gaussian curves used here are a poor description of niche shapes for many real organisms, they usefully convey the concept of between-individual variation. Real populations are likely to contain both generalized and specialized individuals, unlike the schematic diagrams shown here. Bolnick et al. (2002) describe alternative indices that do not rely on assumptions about resource distribution shapes and that can identify variation in individual niche widths.

hypothesis and its supporting theory, it is perhaps not surprising that interindividual variation has been ignored in many ecological studies. Two sources of skepticism seem particularly common. First, many ecologists believe that individual specialization is rare and/or weak (Case 1981; Patterson 1983; Taper and Case 1985; Schoener 1986). Second, even if interindividual variation is commonplace, it may have a trivial impact on ecological processes so that population averages are sufficient for understanding ecological dynamics. The primary goal of this article is to challenge both views by showing that individual specialization is widespread and that it can profoundly affect a population's ecological and evolutionary dynamics. In reviewing the incidence of interindividual niche variation, we present a summary of available case studies and discuss the range of mechanisms that can lead to individual specialization.

Defining Individual Specialization

Roughgarden (1972, 1974) provided a quantitative framework for thinking about intrapopulation niche variation. Consider an idealized niche distribution in which individuals from a population consume prey that can be described by a single continuous variable such as prey length (fig. 1). The total niche width (TNW) of the consumer population is simply the variance in the size of all captured prey and can be partitioned into two components. The within-individual component (WIC) is the average variance of resources found within individuals' diets, while the between-individual component (BIC) is the variation among individuals, such that TNW = WIC + BIC. Interindividual variation is large when BIC is a large proportion of TNW, such that WIC/TNW is small (fig. 2).

Intrapopulation niche variation can occur by subdividing the population's niche in a number of different ways. We often expect individuals of different age, sex, or ob-

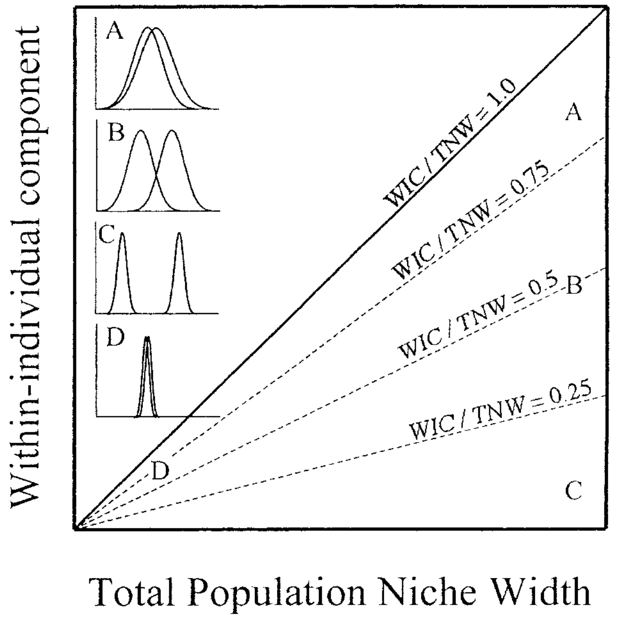

Figure 2: Individual specialization is part of a continuum from where the within-individual component equals the total niche width (on the solid diagonal WIC = TNW, BIC = 0; WIC/TNW = 1) to where WIC is a small proportion of TNW (close to the *X*-axis). *A*–*D* represent the approximate position on the diagram of hypothetical populations with (*A*) high WIC/TNW, (*B*) medium WIC/TNW, (*C*) low WIC/TNW, and (*D*) high WIC/TNW but small total niche width. Schematic diagrams represent the niche-use curves of two individuals from each of these four populations.

viously distinct morphology to have different niches, as reflected in Schoener's (1986, p. 119) statement that "for the most part, the important between-phenotype variation in populations occurs between sex and age classes." Consequently, a researcher might investigate niche variation in a population by constructing a statistical model testing the effects of sex, age, and morphology on diet, most likely dividing age and morphology into discrete age classes and arbitrary ranges of morphology (e.g., Roughgarden 1974). If a morphological trait is polymorphic (bimodal), one might reasonably choose to use categories corresponding to each morphotype, in which case the ANOVA model would look like the following:

$$\text{diet}_i = \text{sex}_i + \text{age class}_i + \text{morph}_i + \varepsilon_i, \qquad (1)$$

where the error term ε_i is the residual diet variation not attributed to these three a priori ways of classifying individuals.

We believe that a description of intrapopulation niche variation is facilitated when we can communicate the distinction between variation caused by each effect of the model. Terms are already available to describe the three main effects, and "ecological sex dimorphism" (Shine 1989, 1991), "ontogenetic niche shift" (Keast 1977; Polis 1984), and "resource polymorphism" (Wimberger 1994; Skulason and Smith 1995; Smith and Skulason 1996) have all previously been reviewed. The goal of this review is to demonstrate that there can also be important niche variation within the residual error term (among individuals), which also deserves a unique designation. We therefore define an "individual specialist" as an individual whose niche is substantially narrower than its population's niche for reasons not attributable to its sex, age, or discrete (a priori) morphological group. The phrase "individual specialization" can designate either the overall predominance of individual specialists in a population or the degree to which individuals' diets are restricted relative to their population. It is important to note that these definitions concern the relative width of individual and population niches, not their absolute values. Consequently, individual specialization is characterized not by a low WIC per se but by a low WIC relative to TNW.

Individual specialization is one of many factors contributing to intrapopulation niche variation. Although the case studies collected here are restricted to examples of individual specialization, much of our discussion of the causes and consequences of individual specialization is also pertinent to other forms of niche variation. However, there are some good biological reasons to distinguish between sex- or age-based variation and individual-level niche variation. Ecological differences between males and females can arise as side effects of sexual selection, breeding behavior (Magurran and Garcia 2000), or nutritional or energetic requirements associated with reproduction (Belovsky 1978), mechanisms that are potentially (but not necessarily) different from those generating individual specialization. Similarly, age-based niche shifts may arise as a necessary consequence of body-size changes and development so that niche partitioning is an incidental byproduct of ontogeny.

In contrast, our distinction between polymorphism and individual variation is primarily semantic. We follow Smith and Skulason (1996, pp. 111–112) in defining a polymorphism as "discrete intraspecific morphs," implying that the morphological distribution has more than one mode and that members of the population can generally (though not necessarily always) be unambiguously assigned to a particular group. By taking this definition, we are ensuring that the word "polymorphism" is not simply synonymous with the term "variation."

In reality, individual variation and polymorphism are ends of a continuum of increasingly discrete variation. This review focuses on the less discrete end of this continuum, in which individuals cannot clearly be assigned to distinct morphotypes because either morphological variation is continuous or resource use variation is not clearly tied to morphology. We do so because individual-level variation has been neglected rather than because it is fundamentally different from polymorphism. Where examples cited in this review overlap with Smith and Skulason's (1996), either it reflects our feeling that the case in question is not composed of discrete morphs (e.g., Werner and Sherry 1986) or we are referring to populations in which the variation is less discrete than those used for their review. Examples of the latter include three-spine sticklebacks *Gasterosteus aculeatus* and arctic char *Salvelinus alpinus.* In each species, benthic/limnetic variation is continuous in some populations (Amundsen 1995; Robinson 2000; D. I. Bolnick, unpublished manuscript) and discrete in others (Schluter and McPhail 1992; Skulason et al. 1993; Snorrason et al. 1994).

Incidence of Individual Specialization

We surveyed the literature for examples of individual specialization on resources, such as prey taxa, host plants, or oviposition sites, collecting a list of examples from 93 animal species (table 1). We excluded cases where ecologically differentiated individuals could not be considered sympatric or where diet groups showed significant reproductive isolation, because such variation cannot be said to occur within a population. We also omitted cases of within-colony niche variation in eusocial insects (Heinrich 1976; Rissing 1981; Johnson 1986; Wells and Wells 1986;

Table 1: Examples of individual specialization for populations with substantial interindividual variation in diet, microhabitat preference, foraging behavior, oviposition preference, or other niche axis

Study species	Morphological distribution	Genetic basis	Timescale consistency	Evidence for consistency	Trade-offs	Spatial context	Summary	Reference
Gastropods:								
Marisa cornuarietis (giant ramshorn snail)			>4 d	RO		Lab	Individuals' foraging strategies vary from time minimizing to energy maximizing	Grantham et al. 1995
Nucella emarginata			3 mo	RO	Handling time	O	Individuals' diets varied substantially; individuals ignored less preferred prey while foraging	West 1986
Nucella lapillus (dogwhelk)		E	>27 d	RO		MS	Snails at adjacent exposed/protected coastal sites varied in preference for mussels, even after transplants	Burrows and Hughes 1991
Nucella melones			3.5–13 mo	RO	Handling time	O	Individuals' diets varied substantially; individuals ignored less preferred prey while foraging	West 1988
Placida dendritica	IM		2–3 wk	RO	Handling time	O	Individuals starved to death on nonpreferred species of algae	Trowbridge 1991
Crustaceans:								
Asellus aquaticus		G	Seasonal	G		MS	Habitats within pond associated with different amylase allozymes, active microhabitat choice	Christensen 1977
Daphnia pulex		G	P	G		MS	Vertical separation of genotypes in water column during daily migration	Weider 1984
Daphnia pulicaria		G, E	P	G		MS	Vertical separation of genotypes in water column during daily migration	Leibold et al. 1994
Gammarus palustris		G	P	G		MS	Across-habitat heterozygote deficiency, indicating genotype-based habitat choice	Borowsky et al. 1985
Proasellus coxalis			12 d	RO	Reproductive	Lab	Wild-caught isopods had variable but restricted diets in laboratory trials	Basset and Rossi 1987
Insects:								
Battus philenor (pipevine swallowtail)			10 min	RO		O	Individual females prefer to alight on either narrow-leaved or broad-leaved host plants	Rausher and Papaj 1983
Bombus fervidus (bumblebee)		E	1 mo	RO	Limited learning	O	Queens "majored" on specific flower species while establishing a colony	Heinrich 1976
Bombus vagans (bumblebee)		E	1 mo	RO	Limited learning	O	Queens "majored" on specific flower species while establishing a colony	Heinrich 1976
Colias eurytheme (orange sulphur butterfly)		G?	P	RO		O	Individual preference for one of two oviposition plants; independent of experience	Tabashnik et al. 1981
Colias philodice (clouded sulphur butterfly)		E	Final instar	RO	Physiological	Lab	Host plant used at end of penultimate instar becomes obligate host for final instar	Karowe 1989
Drosophila tripunctata		G	P	G		O	Genetic variation for preference for tomatoes vs. mushrooms	Jaenike and Grimaldi 1983; Jaenike 1985
Euphydryas editha (Edith's checkerspot butterfly)		G	P	G	Larval performance	O	Heritable variation for host preference, correlated with larval performance; some females specialize on individual plants within a host species	Ng 1988; Singer et al. 1989

Heliaula rufa (rufous grasshopper)			1 yr	I		O	Gut contents correlated with isotope ratios; isotope ratios exceptionally variable (range = 9.8, SD = 4.27)	Fry et al. 1978
Liriomyza brassicae (serpentine leafminer)		G	P	G	Growth rate	O	Host-specific performance differences among individuals	Tavormina 1982
Liriomyza sativae (vegetable leafminer)	IM	G?	P	G	Growth rate	Lab	Heritable variation in oviposition preference for one of two plants; correlated with larval performance	Via 1986
Melanoplus arizonae (Arizona spur-throat grasshopper)			1 yr	I		O	Gut contents correlated with isotope ratios; isotope ratios exceptionally variable (range = 3.7, SD = 1.33)	Fry et al. 1978
Melanoplus gladstoni (Gladstone grasshopper)			1 yr	I		O	Gut contents correlated with isotope ratios; isotope ratios exceptionally variable (range = 5.6, SD = 2.12)	Fry et al. 1978
Melanoplus lakinus (Lakin grasshopper)			1 yr	I		O	Gut contents correlated with isotope ratios; isotope ratios exceptionally variable (range = 6.8, SD = 2.8)	Fry et al. 1978
Megachilidae (leaf cutter bee)						O	Pollen on individual bees caught in mixed flower fields showed individual specialization	A. Muller 1996
Pieris rapae (cabbage butterfly)			<1 d	RO	Handling time	Lab	Butterflies continue to choose the flower species first encountered on a specific day due to search image	Lewis 1986
Plutella xylostella (diamondback moth)						Lab	Between-individual variation in oviposition and larval performance is higher for low-density populations	Bigger and Fox 1997
Polygonia c-album (comma butterfly)		G	P	RO, G	Larval growth	Lab	Females vary in rank-order preference for host plants, correlated with larval performance	Janz et al. 1994; Janz 1998
Taeniopoda eques (horse lubber grasshopper)			11 d	RO		Lab	Individuals had distinct feeding preferences when experimentally exposed to 10 novel food plants	Howard 1993
Fishes:								
Amia calva (bowfin)			>1 yr	I		O/MS	Unexpectedly large isotopic differences between individuals indicated variable diets within population	Fry et al. 1999
Bidyanus bidyanus (silver perch)		E				?	Gut contents reveal individual dietary differences throughout a season; patchy prey not ruled out	Warburton et al. 1998
Dorosoma cepedianum (gizzard shad)			>1 yr	I		O/MS	Unexpectedly large isotopic differences between individuals indicated variable diets within population	Fry et al. 1999
Dorosoma petenense (threadfin shad)			1 yr	I		O/MS	Unexpectedly large isotopic differences between individuals indicated variable diets within population	Fry et al. 1999

Table 1 (*Continued*)

Study species	Morphological distribution	Genetic basis	Timescale consistency	Evidence for consistency	Trade-offs	Spatial context	Summary	Reference
Embiotoca lateralis (striped surfperch)	IM		na	RO	High competition vs. low resource quality	MS	Diet correlated with algal substrate on defended territories; different diets had different fitness	Holbrook and Schmitt 1992
Esox lucius (northern pike)			1 yr	I		?	Specialization on invertebrate or fish prey was a long-term trait in some individuals	Beaudoin et al. 1999
Gambusia affinis (mosquitofish)		E	<1 wk	RO	Limited learning	MS/Lab	Field and lab specialization due to trade-offs in learned handling time, affecting optimal foraging	Bence 1986
Gasterosteus aculeatus (three-spined stickleback)	U/M	G, E	P	M	Feeding efficiency	B/L, O	Benthic and limnetic fish have different mean phenotypes and diet in single-species lakes	Milinski 1987; Robinson 2000; Reimchen and Nosil 2001*a*; D. I. Bolnick, unpublished manuscript
Haplochromis nyererei	U		na	M		?	Intrapopulation diet variation associated with ecomorphological variation	Fermon and Cibert 1998
Heterandria formosa (least killifish)			>1 yr	I			Unexpectedly large isotopic differences between individuals indicated variable diets within population	Fry et al. 1999
Lepidiolamprologus profundicola	IM	E	3 mo	RO	Feeding efficiency	O	Individual-specific foraging behavior, correlated with microhabitat but not prey type	Kohda 1994
Lepisosteus platyrhincus (Florida gar)			>1 yr	I		O/MS	Unexpectedly large isotopic differences between individuals indicated variable diets within population	Fry et al. 1999
Lepomis gibosus (pumpkinseed sunfish)	U	G, E	P	M	Growth rate trade-offs	B/L	Benthic and limnetic fish have different mean phenotypes, diet, and foraging efficiencies	Robinson et al. 1993, 1996; Robinson and Wilson 1996
Lepomis macrochirus (bluegill sunfish)	U	E	>3 mo	P, M, I	Feeding efficiency	B/L	Phenotype-specific feeding efficiency, habitat use, isotope content, and parasitism rates	Werner et al. 1981; Ehlinger and Wilson 1988; Ehlinger 1990; Wilson et al. 1996; Fry et al. 1999
Lepomis microlophus (redear sunfish)			1 yr	I		O/MS	Unexpectedly large isotopic differences between individuals indicated variable diets within population	Fry et al. 1999
Micropterus salmoides (largemouth bass)			>1 yr	RG, I		O	17% average pairwise dietary overlap due to learned prey preferences	Schindler et al. 1997; Fry et al. 1999
Notemigonus crysoleucas (golden shiner)			>1 yr	I		O/MS	Unexpectedly large isotopic differences between individuals indicated variable diets within population	Fry et al. 1999
Oncorhynchus nerka (sockeye salmon)			na	P		B/L	Morphological variation associated with diet and parasite load differences	Konovalov 1995
Oreochromis aureus (blue tilapia)	U		1 yr	I		?	Isotope data indicate individual specialization	Gu et al. 1997
Perca flavescens (yellow perch)	U					O/Lab	Individual differences in prey preferences	Chabot and Maly 1986; Ansari and Qadri 1989

Perca fluviatilis (Eurasian perch)	U	E	?	RO	Feeding efficiency	B/L	Benthic and limnetic populations differ in morphology and foraging efficiency	Hjelm et al. 2001; Svanbäck and Eklöv 2002; R. Svanbäck and P. Eklöv, unpublished manuscript
Plecodus straeleni			1 h	RO		O	Within-age and within-sex variation in hunting technique and prey species	Nshombo 1994
Pomoxis nigromaculatus (black crappie)			1 yr	I		O/MS	Unexpectedly large isotopic differences between individuals indicated variable diets within population	Fry et al. 1999
Salmo clarki (cutthroat trout)			6 mo	RG		?	Repeated gut-content analysis on recaptured fish revealed persistent individual specialization	Bryan and Larkin 1972
Salmo gairdneri (rainbow trout)			6 mo	RG		?	Repeated gut-content analysis on recaptured fish revealed persistent individual specialization	Bryan and Larkin 1972
Salmo trutta (brown trout)	U		1 yr	RG		O/MS	Repeated gut-content analysis shows degree of individual specialization varies by habitat and season	Bridcut and Giller 1995
Salvelinus alpinus (arctic char)	U/M	G[a]	>3 mo	P	Feeding efficiency	MS	Char have discrete polymorphisms but also individual specialization in nonpolymorphic lakes	Frandsen et al. 1989; Sandlund et al. 1992; Amundsen 1995; Amundsen et al. 1995; Curtis et al. 1995
Salvelinus fontinalis (brook char)	U		1 season	RO		B/L	Telemetry and repeated gut contents on individuals, 50% always benthic, 18% always limnetic; stream-dwelling fry specialize on fast- or slow-running water	Bryan and Larkin 1972; McLaughlin et al. 1992; McLaughlin and Grant 1994; Bourke et al. 1997
Salvelinus namaycush (lake trout)	U		>1 yr	I		?	78% of variation in trophic position accounted for by between-lake variation, 22% intrapopulation	Vander Zanden et al. 2000
Reptiles and amphibians:								
Ambystoma gracile (northwestern salamander)						MS/lab	Wild individuals specialized on benthic or mid-water prey; in lab, preferences reflect larval experience	Henderson 1973
Ambystoma tigrinum (tiger salamander)	U[b]	E			Disease risk vs. energy intake	O	Within cannibal morphs, smaller snout-vent length eat 50% larvae, larger eat 100% larvae	Collins et al. 1993; Maret and Collins 1997
Anolis marmoratus ferreus (Marie-Galante anole)	U						BPC = 30% of TNW in some populations	Roughgarden 1974
Anolis sagrei (brown anole)	U				Handling time	T	BPC is higher in populations with larger total niche width	Lister 1976*a*, 1976*b*
Python brongersmai (blood python)	…[c]	G	P	G		O	Color correlated with morphology and with diet, mechanism unclear, discreteness of colors unclear	Shine et al. 1998
Birds:								
Arenaria interpres (ruddy turnstone)	U	E	2–3 yr	RO		MS[d]	Individuals specialize on one of six alternative foraging methods	Whitfield 1990
Branta bernicla (brant geese)			2 yr	RO		O	Dominant pairs monopolize preferred food plants	Prop and Deerenberg 1991
Cepphus columba (pigeon guillemot)			Brooding	RO		O	Specialists (>50% of one fish species) have higher productivity and fledgling success than generalists	Golet et al. 2000

Table 1 (*Continued*)

Study species	Morphological distribution	Genetic basis	Timescale consistency	Evidence for consistency	Trade-offs	Spatial context	Summary	Reference
Columba livia (feral pigeon)			Season?	RO		MS/lab	Individual differences in seed choice in field and lab; specialization stronger when competition is higher	Giraldeau and Lefebvre 1985; Inman et al. 1987
Corvus caurinus (common crow)			Months	RO		O	Individual birds (captive and free ranging) have color preferences for real and artificial fruits	Willson and Comet 1993
Cuculus canorus (common cuckoo)	…[e]	G	P	M	Nestling survival	O	Interfemale variation in choice of host species to parasitize; egg color varies accordingly	Marchetti et al. 1998
Geospiza fortis (medium ground finch)	U	G	4 mo, P	RO, M	Handling time	O	Bill size correlated with seed choice	Grant et al. 1976; Price 1987
Haematopus ostralegus (oystercatcher)	U	E	3 yr	RO	Foraging efficiency	O	Dominance, morphology, and learned prey-handling behaviors determine an individual's prey type	Norton-Griffiths 1967; Goss-Custard and Durell 1983; Sutherland 1987; Sutherland et al. 1996
Larus argentatus (herring gull)			2 mo, 2 yr	RO	Reproductive	MS/O	Nest site associated with distinct diets (mussels, birds, refuse), also preferences vary within site	McCleery and Sibly 1986; Pierotti and Annett 1987, 1991
Larus occidentalis (western gull)			Years	RO		MS	Specialists on fish have higher lifetime reproductive success than generalists or specialists on refuse	Annett and Pierotti 1999
Lonchura punctulata (spice finch)			>1 wk	RO		Lab	Individual differences in seed choice in laboratory	Beauchamp et al. 1997
Numenius arquarta (curlew)			Years	RO		O	Persistent variation in prey-handling behaviors adapted to alternative prey types	Ens and Zwarts 1980
Parus ater (coal tit)	U		2 mo	RO		O	Within age groups, morphological variation affects foraging site selection and hence diet composition	Gustafsson 1988
Parus major (great tit)		E	50 trials	RO	Handling time	L	Individual preferences correlated with differences in efficiency in alternate artificial environments	Partridge 1976
Phalacrocorax albiventer (king cormorant)	IM		3 mo	RO		O	Individual females specialize on shallow or deep foraging dives	Kato et al. 2000
Phalacrocorax atriceps (blue-eyed shag)			1 mo	RO		O	Regurgitated pellet contents correlate with consistent diving duration measured by radiotelemetry	Wanless et al. 1992
Phoenicurus ochruros (black redstart)	IM		2 yr	RO			Fecal contents collected at individual's roosting sites revealed variation in selectivity among available prey	Hódar 1998
Pinaroloxias inornata (cocos finch)	IM	E?	10 mo	RO		O	Species as a whole is highly generalized; individuals use limited range of resources	Werner and Sherry 1986
Turdus migratorius (American robin)	U					O	Body size associated with preference for three alternate fruits, independent of sex and age	Jung 1992
Tyrannidae (Neotropical flycatchers)						?	Species with broader diets had more interindividual gut content variation; patchy resources not ruled out	Sherry 1984

Mammals:								
Alopex lagopus (arctic fox)			1 yr	I		T	Isotope data show individual dietary differences due to habitat heterogeneity and territoriality	Angerbjorn et al. 1994
Balaenoptera acutorostrata (minke whale)		E?	>2 yr	RO		O	Individuals use one of two possible hunting techniques	Hoelzel et al. 1989
Martes americana (American pine marten)			Season	I		T	Territory location associated with diet differences	Ben-David et al. 1997
Molossus ater (black mastiff bat)	U					O	Most captured bats preferred hydrophilid beetles; a few had unique diets; consistency unknown	Fenton et al. 1998
Mustela lutreola (European mink)	IM		1 yr	RO		MS	Scat from radiotagged individuals showed persistent diet variation reflecting localized prey abundance	Sidorovich et al. 2001
Mustela vison (American mink)	IM		1 yr	RO		MS	Scat from radiotagged individuals showed persistent diet variation reflecting localized prey abundance	Sidorovich et al. 2001
Otaria byronia (southern sea lion)			na	RO		O	Very few males fed on fur seals, but those that did attacked seals repeatedly	Harcourt 1993
Peromyscus boylii (brush mouse)	U		na	M		MS	Correlation between gut contents, tail length, and degree of arboreality	Smartt and Lemen 1980
Peromyscus truei (pinyon mouse)	U		na	M		MS	Correlation between gut contents, tail length, and degree of arboreality	Smartt and Lemen 1980
Scotophilus leucogaster (Mexican fishing bat)						O	Individuals preferred different insect orders, based on fecal analyses	Barclay 1985
Ursus arctos (grizzly bear)	U		Years	RO	Territoriality	T	Individuals with streamside territories ate fish but suffered higher intraspecific predation	Mattson and Reinhart 1995

Note: Morphological distribution: U, diet depends on unimodal morphological trait; IM, morphology was measured but diet is independent of morphology; U/M, unimodal in some populations, multimodal in others. Genetic basis: G, known genetic component; E, known environmental basis; ?, some evidence for heritability. Consistency timescale: Where the study documented the duration over which consistency was observed, we use that duration. Where stable isotope data were used, we use 1 yr (the average time span over which muscle isotope ratios indicate past diet). Where the trait has a genetic basis, there is reason to believe that it is a permanent trait (P), but further evidence is preferred; na, known to be consistent, timescale not available. Evidence for consistency: I, isotope; M, morphological correlation; P, parasitological; RO, longitudinal study with repeated observations; RG, repeated gut contents; G, genetic basis. Spatial context: O, overlapping, differentiated individuals forage in the same locations, encounter the same prey; MS, microspatial differences, individuals specialize on particular microhabitats but are capable of switching habitats; B/L, benthic/limnetic difference within a single lake; ?, insufficient data to assess whether individuals are overlapping or microspatially distributed; lab, laboratory tests of individual preferences, field spatial context not reported; T, territorial organisms, diet differences associated with microhabitat differences in territory location.

[a] Genetic in polymorphic populations; basis in unimodal populations unknown.

[b] Unimodal variation within the cannibal morph.

[c] Color is reported to be polymorphic; morphology is unimodal.

[d] Individuals within a single flock of birds will specialize on different microhabitats.

[e] Egg color polymorphism.

Waller 1989) because of ambiguity over what constitutes an individual.

The case studies collected in table 1 indicate that individual specialization occurs in a broad array of vertebrate and invertebrate taxa. Many of these examples explicitly excluded the effects of sex (e.g., Rausher and Papaj 1983; Janz and Nylin 1997; Marchetti et al. 1998) and/or age (e.g., Jung 1992; Nshombo 1994). Other cases highlight the utility of distinguishing between individual variation and discrete polymorphism. For example, although populations of the tiger salamander *Abystoma tigrinum* often contain two discrete morphs (normal and cannibal), diet variation can also occur within a given morph. Within the cannibals, individuals with longer snout-vent lengths consume a greater proportion of conspecific larvae (Collins et al. 1993; Maret and Collins 1997). Alternatively, diet variation can be associated with unimodal, continuous morphological variation, as in the 23 cases collected here (e.g., Lister 1976*a*; Smartt and Lemen 1980; Price 1987; Fenton et al. 1998; Svanbäck and Eklöv 2002), while in nine other cases, morphology-diet correlations could not be detected at all (e.g., Werner and Sherry 1986; Trowbridge 1991; Holbrook and Schmitt 1992; Kohda 1994). These collected examples support our claim that significant interindividual variation can occur even within sex, age, or a priori morphological groups.

Although table 1 clearly demonstrates that individual specialization exists, this collection of case studies does not lend itself to any generalizations about its frequency or degree. The paucity of negative results, where populations are composed of generalized individuals, makes it impossible to treat this collection as a random sample from which to draw broad conclusions. This bias reflects a file-drawer effect in which the lack of significant diet variation is not considered worthy of publication. A notable exception is the diet study of the tilapia *Sarotherodon mossambicua*, in which Bowen (1979) expressed surprise at the uniformity of the gut contents of 1,262 individuals examined.

While it is important to test the null hypothesis that individuals sample randomly from a common niche, treating individual specialization as either present (null rejected) or absent (null not rejected) ignores substantial variation in the degree of individual specialization. Indices of the degree of individual specialization (Bolnick et al. 2002) such as WIC/TNW can uncover differences among species, among conspecific populations, and even among individuals within populations. For example, the degree of individual specialization varied between two neighboring populations of the intertidal snail *Nucella emarginata* (fig. 3). Even within each snail population, individuals varied in the degree to which their diet resembled the population diet, so that each population was composed of both relatively generalized and relatively specialized individuals.

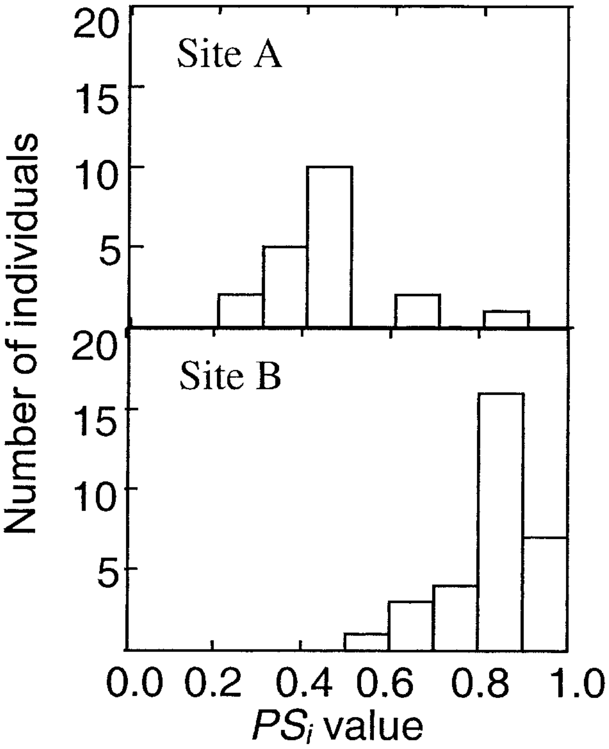

Figure 3: Individual specialization varies both among different populations and among individuals within a population of the snail *Nucella emarginata* (data from table 3 in West 1986). Each individual's degree of specialization is quantified by measuring the proportional similarity (PS_i) between the resource distribution of the individual and the distribution of the population as a whole (Bolnick et al. 2002). PS_i varies from 1 (complete overlap between the individual and the population) toward 0 (increasing individual specialization). The average PS_i is lower (more specialization) in population A than in population B, while individuals within each population also vary in their degree of specialization.

Despite the large number of cases of significant individual specialization, indices of the degree of specialization are available for only 18 species (table 2). The proportion within-individual variation (WIC/TNW) varies widely among species and populations. Roughgarden (1974) surveyed WIC/TNW values for five *Anolis* lizard species and concluded that BIC was generally low. For example, between-individual variation accounted for only 1.4% of the niche width of the *Anolis shrevei* population on Valle Nuevo (WIC/TNW = 0.986). In contrast, between-individual variation in the Cocos Island finches *Pinoroloxias inornata* is 49.4% of TNW (Werner and Sherry 1986) and 62.2% of TNW in a population of the snail *Nucella melones* (West 1988). It is unsafe to draw solid conclusions from so few examples, but it does appear that BIC is generally smaller than WIC, although the two niche width components are often nearly equal (fig. 4). One barrier to further generalization is the difficulty in interpreting variation in the ratio WIC/TNW. As with any statistic based on a ratio, it is difficult to tell when variation in the value of the ratio is driven by changes in the numerator or the denominator. A second problem is the fact that different authors may use measures of individual specialization that cannot be directly compared. For example, Schlindler et al. (1997) calculated the average pairwise diet overlap between same-age individuals of the largemouth bass *Micropterus salmoides.* Although the average overlap was strikingly low (17.3%), there is no way to compare this result to measures of WIC/TNW, making it less useful for comparative studies. Alternative indices for measuring individual specialization are discussed in more detail in Bolnick et al. (2002).

Temporal Consistency

Measures of resource-use variation such as WIC/TNW need to be interpreted with great care because they do not directly convey the timescale over which the niche variation was observed. Low WIC/TNW can result both from short-term processes, such as the stochastic effects of foraging in a patchy environment, and from long-term effects, such as persistent phenotypic or behavioral variation. When prey are clumped (e.g., swarms of copepods; Byron et al. 1983), individuals' gut contents can vary greatly, reflecting extremely localized prey abundance rather than forager preference. In contrast, many studies have followed individuals through time to demonstrate that individual specialization is consistent over months (18 cases) or years (30 cases; table 1).

Determining the timescale over which niche variation persists is important because the temporal consistency of individual specialization will have implications for both evolution and ecology. Resource competition and selection will operate very differently when interindividual variation is stochastic, temporary, or a permanent feature of the individuals in the population. In the cabbage butterfly *Pieris rapae* (Lewis 1986), individuals specialize on a single flower species over the course of any given day because of a search image established during the first flower encounter of the day. The search image is reestablished daily, so that individuals are always specialized, but the preferred flower species changes regularly. Frequency-dependent competition, or selection, is unlikely to operate on such short-term specialists because they can quickly alter their preferences when their currently preferred resource becomes rare or risky. Populations composed of long-term individual specialists are unable to respond as quickly and so are more subject to frequency-dependent effects.

A wide range of methods are available for testing the temporal consistency of individual specialization. Longitudinal sampling, in which the researcher collects repeated observations on individuals over time, is the most direct method. Longitudinal studies have used direct observation of prey capture (West 1986), foraging behavior (Werner and Sherry 1986), radiotelemetry of microhabitat choice (Bourke et al. 1997), and repeated gut-content sampling of individuals (Bryan and Larkin 1972). Niche data can also be collected by cross-sectional sampling, such as the analysis of gut contents from a collection of specimens. While this approach may reveal diet differences among individuals, it cannot exclude the effects of foraging in a patchy environment (Warburton et al. 1998) or identify the duration of the specialization.

Three approaches have been used to supplement cross-sectional data in order to infer the temporal consistency of individual specialization (Bolnick et al. 2002). Stable isotope ratios have been used to estimate the contribution of different prey to a predator's diet (Vander Zanden et al. 2000). Because stable isotope ratios turn over slowly, they represent a long-term average of prey use (Hesslein et al. 1993). High intraspecific variance in isotope ratios indicates large and consistent diet variation (Fry et al. 1978). In some studies, isotope variation was parallel to cross-sectional gut-content variation (Gu et al. 1997; Beaudoin et al. 1999), while in other studies, diet variation was inferred directly from variation in isotope ratios (Angerbjorn et al. 1994; Fry et al. 1999). Similarly, individuals that specialize on particular prey species will have a higher exposure to parasites whose life cycles use that species as an intermediate host. As many macroparasites remain in the host's body for a long period of time, the prevalence of a particular parasite indicates temporally consistent specialization (Curtis et al. 1995; Konovalov 1995; Wilson et al. 1996). Finally, consistency can be inferred if niche variation is due to variation in functional morphology or physiology. Correlations between morphology and resource use provide particularly strong evidence for consistency when the correlation is in a direction predicted a priori by biomechanical, functional, or physiological reasons (Wainwright 1996; Ferry-Graham et al. 2002).

Fundamental versus Realized Specialists

The word "specialization" has many connotations and so can engender confusion among researchers who use different definitions. For some evolutionary ecologists, specialization implies an evolved morphological or physiological adaptation to use a specific resource. For others, specialization may simply imply the act of consuming a relatively limited fraction of the range of available resources. These two views are often but not necessarily

Table 2: Available measures of the degree of individual specialization, measured as the proportion within-individual niche variation (WIC/TNW)

Species	WIC/TNW	Sample size	Niche axis (TNW)	No. of diet categories	Reference
Acmaea scutum (northern face)	.884[a]	16	Prey species	3	Kitting 1980
A. scutum (southern face)	.826[a]	17	Prey species	3	Kitting 1980
Anolis cybotes	.882	73	Prey size (36 mm^2)	Continuous	Roughgarden 1974
Anolis marmoratus ferreus	.675	44	Prey size (243 mm^2)	Continuous	Roughgarden 1974
Anolis sagrei (Jamaica)	.97	389	Prey size (42 mm^2)	Continuous	Lister 1976*b*
A. sagrei (Abaco)	.95	390	Prey size (56 mm^2)	Continuous	Lister 1976*b*
A. sagrei (Cayman Brac)	.91	271	Prey size (73 mm^2)	Continuous	Lister 1976*b*
A. sagrei (Exuma)	.89	418	Prey size (85 mm^2)	Continuous	Lister 1976*b*
A. sagrei (Swan Island)	.78	287	Prey size (92 mm^2)	Continuous	Lister 1976*b*
Anolis shrevei	.986	41	Prey size (38 mm^2)	Continuous	Roughgarden 1974
Antennaria parlinii	.98	22	Light	5	Michaels and Bazzaz 1989
A. parlinii	.97	22	Light	5	Michaels and Bazzaz 1989
A. parlinii	.91	22	Light	5	Michaels and Bazzaz 1989
A. parlinii	.94	28	Nutrients	5	Michaels and Bazzaz 1989
A. parlinii	.98	28	Nutrients	5	Michaels and Bazzaz 1989
A. parlinii	.97	28	Nutrients	5	Michaels and Bazzaz 1989
A. parlinii	.82	28	Nutrients	5	Michaels and Bazzaz 1989
A. parlinii	.96	28	Nutrients	5	Michaels and Bazzaz 1989
A. parlinii	.84	28	Nutrients	5	Michaels and Bazzaz 1989
Apis mellifera (trial 1)	.471[a]	11	Artificial flower color	3	Wells and Wells 1986
A. mellifera (trial 2)	.541[a]	10	Artificial flower color	3	Wells and Wells 1986
Arenaria interpres (CG flock 1982)	.818[a]	28	Foraging behavior	3	Whitfield 1990
A. interpres (CG flock 1983)	.632[a]	24	Foraging behavior	3	Whitfield 1990
A. interpres (PS-FS 1982)	.680[a]	33	Foraging behavior	3	Whitfield 1990
A. interpres (PS-FS 1983)	.619[a]	32	Foraging behavior	3	Whitfield 1990
A. interpres (Car rock 1982)	.823[a]	21	Foraging behavior	3	Whitfield 1990
A. interpres (Car rock 1983)	.765[a]	21	Foraging behavior	3	Whitfield 1990
Fringilla coelebs (island)[b]	.85	83	Substratum	4	Ebenman and Nilsson 1982
F. coelebs (island)[b]	.86	83	Foraging height	Continuous	Ebenman and Nilsson 1982
F. coelebs (island)[b]	.92	83	Distance from trunk	4	Ebenman and Nilsson 1982
F. coelebs (island)[b]	.89	83	Tree part	5	Ebenman and Nilsson 1982
F. coelebs (island)[b]	.96	83	Technique	3	Ebenman and Nilsson 1982
F. coelebs (mainland)[b]	.99	51	Substratum	4	Ebenman and Nilsson 1982
F. coelebs (mainland)[b]	.90	51	Foraging height	Continuous	Ebenman and Nilsson 1982

Table 2 (*Continued*)

Species	WIC/TNW	Sample size	Niche axis (TNW)	No. of diet categories	Reference
F. coelebs (mainland)[b]	.95	51	Distance from trunk	4	Ebenman and Nilsson 1982
F. coelebs (mainland)[b]	.83	51	Tree part	5	Ebenman and Nilsson 1982
F. coelebs (mainland)[b]	1.0	51	Foraging technique	3	Ebenman and Nilsson 1982
Gasterosteus aculeatus	.301	68	Prey taxon	14	D. I. Bolnick, unpublished data
Geospiza fortis	.89	91	Seed type	3	Price 1987
Mustela lutreola	.790[a]	9	Prey taxon	10	Sidorovich et al. 2001
Mustela vison	.720[a]	10	Prey taxon	11	Sidorovich et al. 2001
Nucella emarginata (site A)	.388[a]	20	Prey taxon	7	West 1986
N. emarginata (site B)	.680[a]	31	Prey taxon	3	West 1986
Nucella melones (site A 1980)	.459[a]	42	Prey taxon	8	West 1988
N. melones (site B 1982)	.489[a]	21	Prey taxon	13	West 1988
N. melones (site B 1983)	.375[a]	32	Prey taxon	16	West 1988
Phalacrocorax atriceps	.514[a]	30	Dive duration	10	Wanless et al. 1992
Phoenicurus ochruros	.790[a]	14	Prey taxon	13	Hódar 1998
Pinoroxalis inornata	.506	89	Foraging behavior	9	Werner and Sherry 1986

Note: Values close to 1 indicate generalized individuals, with increasing individual specialization as values approach 0. For continuous niche axes such as prey size, the index is calculated with formulas from Roughgarden (1974). Most diet data are discrete rather than continuous, in which case a Shannon-Weaver diversity index approximation to niche width is used (Roughgarden 1979, p. 510). We report the degree of individual specialization, the sample size of individuals used to collect resource use data, the niche axis, and the number of diet categories where niche data are discrete. Note that many of the species included in this table have high WIC/TNW scores and are not included in table 1 as examples of individual specialists.

[a] Where complete diet data matrices were published but WIC/TNW was not reported, we calculated the index from the published data.

[b] WIC/TNW calculated between sexes rather than between individuals.

related because an individual's phenotype may not always map perfectly onto its actual resource use.

If a population is composed of multiple (heritable) phenotypes, each of which prefers and performs better on a particular subset of the resources, few would object to considering such individuals specialists. In contrast, more debate might ensue over whether or not a population is composed of specialists if individuals have similar phenotypes, preferences, and performances but consume different resources as a result of social status or territory location. From an evolutionary standpoint, few would regard subordinate individuals as specialists on poor-quality resources, yet such individuals may be restricted to a subset of the population's resources. Conversely, individuals with heritable variation for resource preference may nevertheless use the same resource when options are limited or a shared high-value resource is available (Robinson and Wilson 1998), in which case they would be specialized in their fundamental but not their realized niches.

The potential disconnect between the evolutionary and ecological views of specialization has been clearly articulated at least since Hutchinson (1957) made a distinction between the fundamental and the realized niche. Fundamental individual specialization reflects preference or performance variation due to intrinsic traits such as morphology or behavior and generally must be measured experimentally. Conversely, realized specialization is measured as variation in actual resource use and may result from intrinsic and/or extrinsic (resource patchiness, social interactions) mechanisms. The extent to which extrinsic factors influence an individual's diet will determine the degree to which the realized and fundamental niches differ. Because the vast majority of cases of individual specialization rely mostly or entirely on data reflecting realized niche variation such as habitat use or diet, table 1 primarily documents realized individual specialization. However, any consideration of the causes of individual specialization must take into account both the determinants of individuals' fundamental niche and the extrinsic factors that determine its realization.

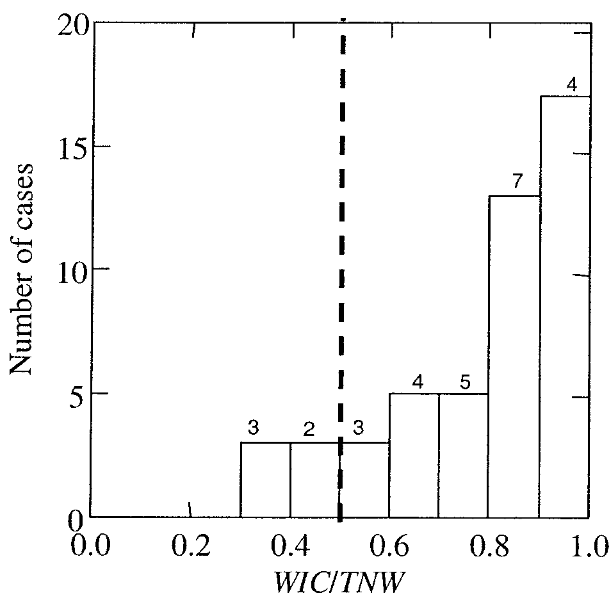

Figure 4: Histogram of available WIC/TNW values (from table 2) including multiple observations within a species (18 species total, 49 observations). The number on top of each histogram bar indicates the number of species that had one or more populations fall within the corresponding range of WIC/TNW. The dotted vertical line marks the point at which WIC = BIC. Note that variation in this ratio does not identify whether specialization varies because of changes in WIC or BIC, nor is there any obvious null distribution for this index. It is possible that the relative paucity of cases where WIC < BIC (*left of the dotted line*) would change had we included cases of ecological sex dimorphism, ontogenetic niche shifts, or discrete polymorphisms.

Causes of Individual Specialization

In all of the examples in table 1, individuals use a subset of their population's niche. However, the mechanisms that cause individual specialization vary widely among these examples. To understand the causes of individual specialization, we first consider some determinants of an individual's resource use and then discuss how these determinants vary among individuals. In particular, we describe the role of trade-offs in constraining individual resource use so that different phenotypes do not use the same broad set of resources.

Determinants of an Individual's Resource Use

To develop a mechanistic view of individual specialization, it is first necessary to understand why a particular individual uses a given set of resources, a problem often addressed by optimal foraging theory (Schoener 1971; Werner 1974) and related models. Although optimal foraging theory is not uniformly successful in generating quantitative or qualitative predictions of foraging behavior (Sih and Christensen 2001), it can usefully serve as a rough guide to the strategic decision making an individual might use to choose its resources. An individual is expected to choose among the available range of resources to approximately maximize some benefit such as net energy income or reproductive success. This net benefit depends on a variety of factors: the rate at which alternative resources are encountered, resource values (e.g., energy content of different prey), prey escape rates, handling times, and risks such as predation. While each of these factors is in part a function of the resource (its population density, evasiveness, caloric content, and defenses), they are also influenced by the predator's experience (Werner et al. 1981), search or handling behavior (Goss-Custard and Durell 1983), morphology (Price 1987), and physiology (Afik and Karasov 1995). Consequently, an individual's rank preferences for alternative resources reflect a complex interaction between resource traits, resource abundance, and the individual's phenotype. These preferences then interact with prey availability, escape rates, environmental heterogeneity, and social interactions to mold the individual's actual resource use.

Mechanisms of Interindividual Variation

Why would a group of individuals, each acting strategically to choose resources, arrive at different outcomes despite sharing a common environment? The most proximate answer is that individuals will use different resources if they have different preferences or resource-use efficiencies, reflecting variable morphological, behavioral, or physiological capacity to handle alternative resources. Yet, this poses a second problem: why does phenotypic variation result in preference or efficiency variation? Without some trade-offs constraining efficiency on alternative resources, phenotypic variation would not produce functional variation, and all individuals would be equally capable of using all resources. This was reflected in a theoretical study by Taper and Case (1985), who concluded that TNW expansion would generally involve increased within-individual niche width (WIC). Only when WIC is constrained does between-individual variation (BIC) become large during niche expansion. Trade-offs remain one of the most plausible mechanisms for limiting an individual's niche breadth (but see Fry 1996; Whitlock 1996). By trade-offs, we mean that an individual adopting one strategy (e.g., specialize on prey A) loses the ability to efficiently perform an alternative strategy (capture prey B). In such a situation, a generalist (consuming A and B) may be unable to perform either strategy as well as the respective specialist and hence may be selected against. Such trade-offs are known to occur in many aspects of foraging, including prey recognition, capture, and digestion.

Resource recognition and search efficiency can be subject to strong trade-offs (Bernays 1998; Bernays and Funk 1999) when individuals have a limited neural capacity to retain search images or capture behaviors (Pieyrewicz and Kamil 1979). In many species, individuals that specialize on a single food type form more effective search images and have greater foraging success. In bluegill sunfish *Lepomis macrochirus*, foraging efficiency improved fourfold over six to eight feeding trials on the same prey (Werner et al. 1981), while foraging efficiency of perch *Perca fluviatilis* was reduced in the presence of multiple prey types (Persson 1985). Individual cabbage butterflies *Pieris rapae* learned to extract nectar efficiently from one flower species but were less efficient after being exposed to a second flower species (Lewis 1986). An individual's repertoire of prey capture or handling behaviors can also be restricted by learning constraints. When specific techniques are best suited for particular prey, an individual that can master a limited range of behaviors will be restricted to a limited range of prey (Sutherland and Ens 1987; Hoelzel et al. 1989; Kohda 1994; Kato et al. 2000).

Trade-offs can also be based on functional morphological traits that affect resource handling ability (Robinson 2000). Many aspects of locomotion and prey capture are governed by lever systems that have fundamental trade-offs between force and velocity (Frazzetta 1962; Bock 1964; Badoux 1975; Westneat 1990; M. Muller 1996). Biomechanical features of prey capture subject to trade-offs include jaw-closing strength/speed (Wainwright and Richard 1995) and foraging speed versus maneuverability (Ehlinger 1990; Svanbäck and Eklöv 2002). Physiological trade-offs can occur after prey are ingested, when alternative prey require different digestive conditions, enzymes, or detoxification mechanisms (Burrows and Hughes 1991). For example, yellow-rumped warblers *Dendroica coronata* modulate their digestive enzyme production to suit their current diet. However, at any given time, an individual is restricted to a particular digestive strategy so that it can digest certain prey more efficiently than others (Afik and Karasov 1995).

Negative synergistic interactions between prey can also restrict generalization. When defensive chemicals of different plant species interact so that the combined toxins are more detrimental than either toxin singly, generalists will be at a disadvantage (Feeny 1975; Root 1975; Kitting 1980). Negative synergy might also result from parasite exposure. Generalist predators are likely to encounter a wider variety of parasite species because they consume a larger number of potential intermediate hosts. If there are trade-offs in mounting immune response to alternative parasites, then exposure to multiple parasite species at low frequencies may be worse than higher exposure to a limited number of parasite species.

Any of the above trade-offs can limit the range of resources used by a particular individual. When such limits exist, two individuals with different phenotypes or experience may place different values on the same prey item because their foraging, capture, or digestive efficiencies for that prey differ. Consequently, interindividual variation in resource use can reflect intrapopulation variation in a wide range of individual traits that determine resource-specific efficiency and preferences. Individual variation can even reflect differences in optimization strategies themselves. Grantham et al. (1995) suggest that individuals of the giant ramshorn snail *Marisa cornuarietis* vary in the extent to which they minimize foraging time, or maximize energy intake. Diet variation in the western gull *Larus occidentalis* may reflect individual variation in risk aversion (Annett and Pierotti 1999).

This range of proximate causes of individual specialization is nicely illustrated by the detailed ecological studies that have been carried out on the bluegill sunfish *L. macrochirus*. This species is a classic example of a strategic forager because optimal foraging theory has yielded accurate quantitative predictions of resource use (Werner 1974). Individuals vary in their prey-specific efficiency because of search image formation (Werner et al. 1981) and variation in body and fin shape affecting prey capture rates (Ehlinger and Wilson 1988; Ehlinger 1990). Furthermore, individuals appear to vary in their "personality type," some being more risk averse than others, possibly reflecting different optimization rules (Wilson et al. 1994; Wilson 1998). All of these factors interact to produce variation in rank preference, microhabitat choice, and hence individual specialization. When a population of bluegills was experimentally introduced to a pond, individuals quickly sorted into benthic or limnetic specialists (Werner et al. 1981). The remaining generalists constituted 10%–30% of the population and appeared to have a lower intake rate of food.

Not all diet variation need reflect variation in rank preference. Even individuals with identical rank preferences can nevertheless have highly differentiated diets, reflecting variation in social status, mating strategy, or microhabitat. Consider a case in which the optimal diet favors specialization on a single valuable prey type (Schoener 1971; Werner 1974). In such a situation, competitively dominant individuals may defend and monopolize the optimal resource. Subordinate individuals will then be forced to rely on lower-quality alternate resources (Krebs 1971; Morse 1974). For example, competitively dominant surfperch *Embiotoca lateralis* specialize on caprellid amphipods and defend their more profitable resource against smaller, competitively inferior conspecifics who by default become gammarid specialists or generalists (Holbrook and Schmitt 1992). Such interference competition is facilitated when the optimal resource is patchy and can be defended by territorial individuals. Territoriality in a patchy environment causes individual specialization in several mammal species. In both bears (Mattson and Reinhart 1995) and pine martens (Ben-David et al. 1997), individuals whose territories abut streams consume significantly more fish in their diet than neighbors whose territories do not include streamside habitat.

Dominance relationships, territory locations, and mating strategies can of course interact with an individual's fundamental niche. In the oystercatcher *Haematopus ostralegus*, individual birds specialize both on prey species and on particular prey-capture techniques such as probing mud for worms or hammering bivalves (Goss-Custard and Durell 1983). Even individuals that use the same bivalve species tend to specialize on different hammering or stabbing techniques that reflect intraspecific variation in prey shell morphology (Sutherland and Ens 1987). Individuals are limited to learning a small repertoire of handling behaviors, while additional trade-offs are introduced by functional variation in bill morphology (Sutherland et al. 1996). However, the various feeding strategies do not provide equal fitness payoffs, and subdominant and juvenile birds are often restricted to suboptimal diets other than those they would choose in the absence of interference competition (Goss-Custard et al. 1984).

In conclusion, realized niche variation can result from a vast array of mechanisms. Functional variation in intrinsic traits such as morphology or experience can lead strategic foragers to arrive at alternative optimal resource-use patterns when trade-offs constrain individual's ability to generalize. The resulting fundamental specialization may or may not produce realized specialization. Depending on resource availability, individuals with similar fundamental niches may nevertheless be realized individual specialists because of a range of social and environmental factors, or individuals with different fundamental niches may nevertheless use the same resources.

Evolution of Individual Specialization

To begin our discussion of the evolutionary causes of individual specialization, we assume that populations of individual specialists are derived from more generalized ancestors through one of two pathways. In the first, a population of individual generalists expands its total niche width (TNW) by increased interindividual variation, while individual niche widths (WIC) remain constant (path *A* in fig. 5). This corresponds to the niche variation hypothesis (Van Valen 1965). In the second pathway, a population with a broad niche is composed of generalist individuals that evolve to subdivide the resources more finely so that TNW is constant and WIC decreases (path *B* in fig. 5). These two alternative pathways highlight the fact that variation in the ratio WIC/TNW can evolve by changing the numerator and/or the denominator.

Van Valen (1965) observed that, for many bird species, island populations had broader niches than their mainland progenitors. This niche expansion could be achieved in two (not mutually exclusive) ways. Every individual in the population could eat a broader array of foods (path *C* in fig. 5), or there could be greater interindividual variation (path *A*). In light of increased phenotypic variance on islands, Van Valen suggested that TNW expansion was achieved by greater between-individual variation. For example, populations of *Anolis sagrei* with higher niche width have higher between-individual variation. Linear regression of WIC/TNW versus TNW shows a significant negative slope ($F = 11.069$, $\mathrm{df} = 1, 3$, $P = .045$; data from fig. 5*a* in Lister 1976*b*). Beaudoin et al. (1999) found that northern pike *Esox lucius* had higher levels of interindividual diet variation when they were the only fish species present in a lake. Sexually dimorphic ecological traits also show character release in environments with fewer competitors (Lister 1974; Hamilton and Johnston 1978; Ebenman and Nilsson 1982), although it is unclear what role niche partitioning plays in the evolution of sex dimorphisms (Shine 1989). Eusocial insects appear to show competitive release in the degree of among-worker foraging

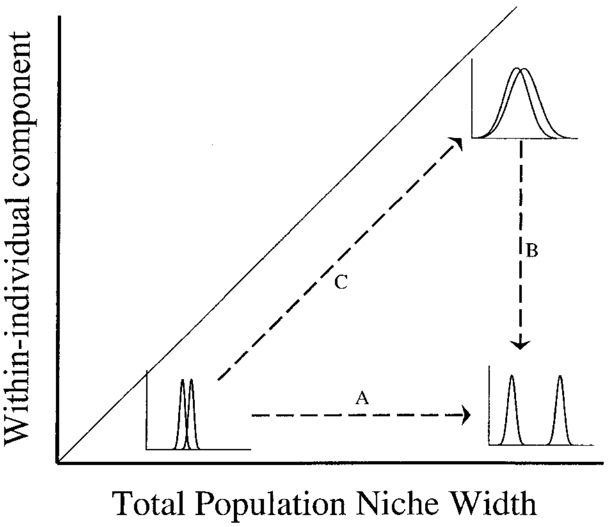

Figure 5: Possible pathways by which individual specialization could evolve. In path *A*, the population niche width expands, while individual niches remain constant or increase slightly because WIC is constrained (e.g., by trade-offs). In path *B*, individual niche widths are reduced, while the population niche width remains constant. Path *C* represents total niche width expansion achieved by increased within-individual niche breadth rather than greater between-individual variation, hence not resulting in individual specialization.

variation (Bernstein 1979). To understand why a population would evolve individual specialization in this way, we first address why TNW should increase and then why WIC might not increase in proportion to TNW.

Population niche breadth is thought to represent a balance between the diversifying effect of intraspecific competition and the constraints imposed by interspecific competition (Roughgarden 1972; Grant and Price 1981; Taper and Case 1985). Intraspecific competition is diversifying in the sense that any individual able to use a new, exclusive resource efficiently will experience reduced intraspecific competition and have higher fitness (Roughgarden 1972). As competitive pressures increase, selection to switch to new resources becomes stronger so that previously suboptimal resources may confer a benefit (Wilson and Turelli 1986; Bolnick 2001). However, if heterospecifics already use the novel resource, interspecific competition may nullify the selective benefit of niche expansion. Consequently, niche expansion and, hence, individual specialization are expected to be more pronounced in environments with fewer competing species. Nonadaptive population niche expansion is also possible, resulting from selectively neutral diet changes or introgression. Introgression of ecologically differentiated genotypes from other finch species elevated the genetic diversity and morphological variance of the recipient *Geospiza fortis* population (Grant and Grant 2000). Support for the inter/intraspecific competitive balance stems largely from theory and from observational studies of character release and character displacement (Grant 1972; Robinson and Wilson 1994; Robinson and Schluter 2000).

Whether or not individual specialization evolves will reflect the degree to which changes in TNW are due to individual niche expansion or interindividual differences. Theory suggests that most TNW expansion should be due to elevated WIC (path *C*) unless WIC is constrained, in which case BIC will increase to compensate (Taper and Case 1985). As discussed earlier, WIC may be constrained by trade-offs, interference competition, or negative synergy between prey that are maintained during competitive release. Before niche expansion, resource-use trade-offs may be relatively unimportant for a population but are uncovered as TNW expands and a greater variety of functionally distinct resources are available. Individuals continue to be constrained to narrow niches even as the population as a whole diversifies. If trade-offs themselves are able to evolve, they may decay over time if selection favors generalized individuals not subject to trade-offs. Several cases of individual specialization are actually populations with both individual specialists and generalists (Werner et al. 1981; Basset and Rossi 1987; Holbrook and Schmitt 1992; Golet et al. 2000). These cases are particularly interesting for their potential to reveal trade-offs between specialist and generalist strategies that could maintain a mixed population.

In path *B*, the population niche width is constant while individuals partition resources more finely. We propose two hypotheses as to why individuals might reduce their niche widths. First, intense intraspecific competition may select for individuals that use particular resources more efficiently at a cost to their generality. Optimal foraging theory can lead to this result when trade-offs are asymmetrical as individuals switch from a shared high-value resource to partitioning lower-value resources (for which trade-offs are higher) as competition increases (Robinson and Wilson 1998). Supporting this theory, Inman et al. (1987) found that pigeons *Columba livia* foraged more selectively when feeding with conspecifics than when alone. In a population of the Eurasian perch *Perca fluviatilis*, WIC/TNW fluctuated with population density because individual specialization was more pronounced when population density was high (R. Svanbäck and P. Eklöv, unpublished data). Second, if deleterious mutations have resource-specific effects, mutation accumulation in a population will produce individuals with restricted resource-use ability (analogous to processes modeled by Kawecki 1994; Kawecki et al. 1997).

Consequences of Individual Specialization

In the introduction to this article, we noted that most niche studies overlook intraspecific niche variation. We have shown that it is not always accurate to assume that individuals are ecologically identical, although it remains unclear how widespread individual specialization is and how it evolves. Even if individual specialization proves to be widespread, is it necessary to incorporate individual-level data in ecological studies? Describing a species as the sum or the average of its parts can vastly simplify both empirical data collection and theoretical models. What is gained by adding an extra level of complexity to our description of a population or a community? We briefly discuss the ecological, evolutionary, and conservation implications of individual specialization.

Ecological Implications

Acknowledging individual-level variation can benefit ecological studies in three ways. First, it represents a more complete description of a biological system. Second, information on individual resource use is necessary if we are to make the transition from phenomenological models of population dynamics to mechanistic models in which the dynamics of a population are predicted from the properties of its components. Third, population models that incorporate individual variation can result in profoundly different dynamical behavior because of the added capacity for frequency-dependent effects.

In describing a population's ecology, researchers often focus on the intensity of intraspecific competition, the types of social interactions, and the risk of predation or parasitism from a range of natural enemies. However, all of these effects can depend on an individual's resource use. Diet-specific risk factors are common because foraging individuals can be particularly vulnerable to predators and parasites (Aeschlimann et al. 2000). For example, open-water three-spined sticklebacks *Gasterosteus aculeatus* may be more vulnerable to piscivorous predators, while benthic sticklebacks may experience greater risks from invertebrate predators (Reimchen 1980). Stickleback exposure to parasites also varies with prey type (Reimchen and Nosil 2001*b*) as it does in other fish species (Curtis et al. 1995; Konovalov 1995; Wilson et al. 1996; Shine et al. 1998). Microhabitat partitioning can lead to greater proximity between individuals of like diets so that social and competitive interactions between individuals are strongest among individuals using the same subset of resources (Goss-Custard et al. 1984). Individual specialization can also produce a delayed response to fluctuations in prey availability. Experimental populations of bluegill sunfish *Lepomis macrochirus* switched from vegetation to open-water habitats long after the latter habitat began to be more profitable because learning constraints limited the capacity for benthic specialists to recognize the potential value of the alternative resource (Werner et al. 1981).

Ideally, models of population dynamics should incorporate such variation. For example, consider an application of a host-parasite dynamic model (Anderson and May 1979) to a population of individual specialists whose parasite exposure depends on their diet. It would be inaccurate to equate the overall population density with the density of potential hosts because a large proportion of the population may never consume the intermediate host. It is possible that this additional level of complexity may help to stabilize the chaotic dynamics of many host-parasite models. Similarly, high between-individual niche variation substantially reduces the number of conspecifics that a given individual will compete with (Van Valen 1965; Roughgarden 1972; Feinsinger and Swarm 1982; Polis 1984; Smith 1990; Holbrook and Schmitt 1992; Collins et al. 1993; Kohda 1994; Amundsen 1995; McLaughlin et al. 1999). A population with large between-individual variation will be divided into subgroups that may compete within themselves but with low between-group competition. Consequently, censuses of total population size will not serve as a good proxy for the level of intraspecific competition. Instead, exploitative competition will be both density and frequency dependent, reflecting both the number of individuals within dietary subgroups and pairwise diet overlaps between groups (Abrams 1980).

Ideally, empirical recognition of individual specialization will lead to more precise modeling approaches that use the behavior of individuals to build descriptions of population dynamics. Whether such individual-based models will improve our predictive power enough to justify the additional work required remains to be seen. However, theoretical work on frequency-dependent intraspecific competition suggests that profoundly different population dynamics can emerge when individual variation is acknowledged. Highly variable populations may be more stable in the face of competition or predation (Lomnicki 1978, 1980, 1984), exert different forms of selection on prey species (Sherratt and MacDougall 1995), and diversify more readily (Abrams et al. 1993; Doebeli and Dieckmann 2000). It is likely that many of these ecological consequences will be affected by the timescale over which individual specialization occurs. Frequency-dependent effects operate differently when individuals can choose a different strategy each day, as with the cabbage butterflies, than when individuals retain particular specializations throughout their lives. To our knowledge, no theoretical treatments have taken into account the effects of varying temporal consistency.

Evolutionary Implications

Intrapopulation niche variation presents an important target for natural selection. Resource-specific ecological interactions mean that individuals within the same population can be subject to different selective pressures. In the striped surfperch, the competitively dominant caprellid specialists had a large fitness advantage over generalists and gammarid specialists (Holbrook and Schmitt 1992). In other cases, disruptive selection maintains specialists on multiple resources. Pigeon guillemots *Cepphus columba* with specialized diets (regardless of which prey) had higher fledging rates than generalists (Golet et al. 2000). Likewise, reproductive efficiency was lower for generalized isopods (Basset and Rossi 1987). In western gulls *Larus occidentalis*, individuals adopting a high-risk diet of fish had significantly higher long-term reproductive success than individuals specializing on a lower-risk diet of human refuse (Annett and Pierotti 1999). Whether such effects lead to trait evolution will depend on the heritability and temporal consistency of the interindividual variation.

Resource-specific fitness and individual specialization facilitate frequency-dependent interactions that can produce complex fitness functions such as stable fitness minima (disruptive selection) and unstable fitness maxima (Abrams et al. 1993). For example, under frequency-dependent competition, phenotypically intermediate individuals (or generalists) can experience exaggerated per capita competition and hence have lower fitness (Doebeli 1996*a*). Theory suggests that this frequency-dependent disruptive selection plays a critical role in niche expansion (Van Valen 1965), the evolution of polymorphisms (Wilson and Turelli 1986; West-Eberhard 1989; Smith and Skulason 1996), the evolution of reproductive isolation (Gibbons 1979; Seger 1985; Kondrashov and Mina 1986; Dieckmann and Doebeli 1999), and adaptive radiation (Schliewen et al. 1994; Schluter 2000).

Individual specialization may also facilitate rapid adaptive speciation. The evolution of reproductive isolation (speciation) has long been thought to be restricted by sympatry and extensive gene flow (Mayr 1963). While sympatric speciation still appears to be relatively rare (Barraclough and Vogler 2000; Coyne and Price 2000), many of the candidate cases of sympatric speciation (Via 2001) involve a period of individual specialization. Theoretical models of competitive speciation rely on relatively large between-individual niche variation (BIC) to generate strong enough disruptive selection to drive reinforcement and the evolution of assortative mating (Rosenzweig 1978; Kondrashov and Shpak 1998; Dieckmann and Doebeli 1999). Far simpler scenarios have been envisioned for phytophagous insects, many of which are composed of host races that specialize on particular host plants (Via 1999). When such host races mate on the same plant on which they feed, reproductive isolation among races flows directly from host choice. Consequently, populations of individual specialists may in time evolve into isolated host races (Wood et al. 1999). However, intrapopulation variation need not always lead to reproductive isolation, and the conditions under which speciation will or will not occur are still poorly understood.

Conservation Implications

Recognizing individual specialization can benefit conservation biology in several ways. Most immediately, management plans that aim to protect a species' resource base by targeting some "average" resource for the population may harm individual specialists. This may pose the greatest danger when intrapopulation variation is due to age or sex, so that a demographically important subset of the population is put at risk (Durell 2000). However, individual specialization may also yield some positive benefits. Theoretical models suggest that populations of individual specialists may be more stable (Lomnicki 1988) and more open to future evolutionary diversification (Rosenzweig 1978; Wilson and Turelli 1986; Doebeli 1996*b*; Dieckmann and Doebeli 1999). Niche variation within a population may help to buffer against loss of particular habitats or resources and provide genetic variation needed to adapt to changing environments (Durell 2000).

Indices of the degree of individual specialization may also provide a measure of ecologically significant intrapopulation diversity (Bolnick et al. 2002). Recently, conservation biology has begun to emphasize preserving intraspecific variation, with the aim of preserving a species' genetic diversity and hence its ability to adapt to environmental change (Moritz 1994; Coates 2000; Smith et al. 2001). Populations are often ranked for conservation priority based on morphological or genetic variation of uncertain functional or selective value (Vogler and Desalle 1994; Petit et al. 1998; Kark et al. 1999). In contrast, measures of intrapopulation niche variation estimate ecologically functional diversity that is more likely to facilitate population stability and evolutionary potential.

Despite the potential benefits of incorporating individual specialization into conservation biology, little empirical evidence is available to confirm that populations of individual specialists are more stable than generalists or more likely to adapt to environmental change. Furthermore, choosing to protect a highly variable population may come at a cost. If individual specialization is negatively correlated with the number of co-occurring species (as predicted by the niche variation hypothesis), then protecting a high-variance population of one species may require preserving a low-diversity habitat, while reserves designed to include high-interspecific biodiversity may minimize intraspecific diversity.

Conclusions

In an article that measured the proportion within phenotype component (WIC/TNW) in five species of *Anolis*, Roughgarden (1974, p. 433) concluded that BIC "is not a large proportion, perhaps never a majority, of the total niche width, at least among adult male anolis lizards." This conclusion received theoretical support from a model of character displacement that allowed WIC and BIC to evolve freely, indicating that "the within-individual component of the niche width will be much larger than the between-individual component" (Taper and Case 1985, p. 355). In contrast to these statements, the large collection of case studies presented in this review indicates that individual specialization occurs in many populations distributed across a broad array of taxa. When combined with other forms of intrapopulation variation such as ecological sex dimorphisms (Shine 1989), ontogenetic niche shifts (Polis 1984), and discrete polymorphisms (Smith and Skulason 1996), it is clear that niche variation is widespread. Nevertheless, it does appear to be true that within-individual variation is generally larger than the between-individual variation (table 2, WIC/TNW > 0.5), although there are exceptions such as the stickleback *Gasterosteus aculeatus* (D. I. Bolnick, unpublished manuscript) and the snails *Nucella emarginata* (West 1986) and *Nucella melones* (West 1988). In a number of other species, BIC was only marginally less than WIC. These data, together with the case studies collected in this review, strongly suggest that individual specialization is neither rare nor always weak.

Despite this conclusion, it is extremely tempting to accept the generality of simple ecological models that treat individuals as interchangeable because individual specialization can be difficult to measure and model. We argue that such simplification has several failings. First, it is simply inaccurate to describe a population as a homogenous unit when individuals consume different resources, use different habitats, and are exposed to different predators and parasites. Second, models that do incorporate individual variation can result in complex frequency-dependent dynamics not seen in simpler theory (Emlen 1985; Christiansen 1988; Lomnicki 1988). These models include interesting evolutionary dynamics such as stable fitness minima (Abrams et al. 1993; Doebeli and Dieckmann 2000), niche expansion (Roughgarden 1972, 1974; Wilson and Turelli 1986), and speciation (Rosenzweig 1978; Udovic 1980; Dieckmann and Doebeli 1999). Finally, recognizing individual variation (a prerequisite for natural selection) at an ecological level is a necessary component for building a truly integrative approach to evolutionary ecology.

Many traditional evolutionary models emphasize stabilizing selection and optimization, in which a single phenotype has the highest fitness. Under such models, variation is maintained by mutation, drift, immigration, or fluctuating selection. While stabilizing selection and optimization are important phenomena, it is likely that much variation persists through complex frequency-dependent processes in which variation is a product of, as well as a prerequisite for, natural selection (Van Valen 1965; Roughgarden 1972, 1974; Grant and Price 1981; Wilson 1998; Mousseau et al. 2000; Halama and Reznick 2001). We hope that this review will remind ecologists that adaptive variation is a significant phenomenon that should be accounted for in more ecological studies and that poses many unanswered questions.

Future Directions

Many of the most pressing questions about individual specialization revolve around its basic natural history. What proportion of species or populations within a species exhibit significant interindividual niche variation? What is the distribution of the degree of individual specialization (e.g., WIC/TNW), how does this degree vary between conspecific populations, and is it stable across space or time? Are populations of individual specialists generally composed entirely of individuals with small niches, or do individual niche widths vary so that a population may contain both specialists and generalists? Over what timescale is an individual's specialization consistent? Such questions can only be answered by the accumulation of far more studies that quantify interindividual niche variation using standardized indices that can be compared across studies (see Bolnick et al. 2002), documenting both the timescales involved and associated environmental conditions. Given the long history of diet analyses in ecology, there are a vast number of relevant data sets already in existence, waiting to be analyzed for niche variation. Populations with no significant intrapopulation niche variation should also be documented because they serve an important role as a contrast against which individual specialists can be compared.

Where possible, investigators should not stop at documenting the degree of individual specialization but should attempt to identify the mechanisms that generate interindividual variation. Such an endeavor is likely to require a combination of detailed field observation to record the effects of social interactions or territoriality and experimental studies to test for cognitive, biomechanical, or physiological trade-offs that limit individual niche width. Examples of individual specialization may prove to be particularly fertile ground for the study of trade-offs because one can eliminate the confounding effect of independent evolutionary histories that has plagued between-species studies of trade-offs (Futuyma and Moreno 1988). Where the degree of specialization varies among conspecific populations, comparative methods may help document the ecological conditions that favor the evolution of individual specialists. Nonadaptive causes of individual specialization may also prove interesting, particularly the role of introgression in increasing WIC or BIC.

As discussed earlier in this article, individual specialization (and intrapopulation niche variation in general) has potentially profound implications for our understanding of ecological and evolutionary processes and hence for conservation programs. Individual specialization should be incorporated into models of food webs, competition, and predator-prey and host-parasite interactions (e.g., Lomnicki 1988; DeAngelis and Gross 1992). The resulting increase in complexity and capacity for frequency-dependent effects may greatly change the stability of many population dynamic models. Food web models in particular threaten to become far more complex because species may no longer be treated as discrete units occupying a particular node of a food web. Such models should also investigate the effects of complications such as populations composed of both specialists and generalists and varying temporal consistency of specialization. Of course, the theoretical advances should be matched by empirical tests such as experimental studies of adaptation or population stability in populations with varying degree of individual specialization. The effect of individual specialization on the stability of population dynamics and on the rate of adaptation should be of particular concern for conservation biologists. The possibility that reserves designed to maximize species diversity may tend to minimize intraspecific ecological diversity is also of some concern.

Variation within populations is necessary for natural selection and hence adaptation. By extension, ecological variation among individuals is necessary for the evolution of ecological traits and interactions. The realization that ecological traits vary among individuals is not new but has often been underappreciated. Further empirical and theoretical analysis of individual specialization and other forms of intrapopulation niche variation will vastly improve our understanding of the complexity and evolution of ecological interactions.

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