THE EVOLUTION OF ECOLOGICAL SPECIALIZATION

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INTRODUCTION

The evolution of "niche breadth," or "niche width," was a more popular topic in the evolutionary ecological literature of the 1960s and 1970s than it has been recently (109, 118, 120, 134, 155, 156). This review summarizes current hypotheses on the evolution of specialization and generalization and suggests areas in which future research might be rewarding. The topic is so broad that every area of biology bears on it. We cannot hope to offer an exhaustive review of evidence and in particular have slighted much of the ecological literature to emphasize genetic and evolutionary perspectives. We limit our discussion almost entirely to animals.

We adopt Hutchinson's (86) representation of a population's ecological niche as an n-dimensional hypervolume, the axes of which are environmental variables or resources. Along each of these, the population displays a wide or narrow tolerance or pattern of utilization, relative to other populations or species. Specialization and generalization must be defined with reference to particular axes (e.g. temperature, range of food particle sizes). Brown (9) suggests that niche breadth along different axes is positively correlated and that this explains positive correlations across species between local abundance and breadth of geographic range. Multidimensional specialization might be expected if species arise in localized regions that differ in several ecological respects from those occupied by parent species. Cody (20), however, suggested that the breadth of habitat is negatively correlated with diet breadth among certain bird species.

In practice, quantitative measurement of niche breadth can be difficult (22,

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23, 40, 109). Much of the literature uses (as will we) nonquantitative contrasts between specialized and generalized species, on the presumption, for example, that egg-eating snakes *(Dasypeltis)* are self-evidently more specialized than are colubrids with broader diets, or that the Kirtland's warbler *(Dendroica kirtlandi)* has more specialized habitat requirements than have other *Dendroica* species in that it nests only in jack pine stands with a particular physiognomy. In extreme cases, such judgments will meet little argument, but often specialization must lie in the eye of the beholder. Thus, an insect that feeds on one plant genus may be more specialized than a species that feeds on many, but if the many are chemically and morphologically similar, the species may not differ in diet breadth in a physiologically meaningful sense (23, 100). A judgment of relative degree of specialization may be most reliable if the specialist's diet or tolerance range is included within that of the generalist's. It is also important to distinguish the *fundamental* niche (with which our review is primarily concerned) from the *realized* niche that is observed in the field (86); the latter may be narrower because of the local operation of agents extrinsic to the organism, such as competition, predation, or barriers to dispersal. The fundamental niche is more nearly a manifestation of the genetic properties of the species, the evolution of which is our immediate concern.

We do not follow the common practice of equating "specialized" with a derived (apomorphic) morphology, and "generalized" with ancestral (plesiomorphic), because apomorphic characters may well enable ecological generalization. We use "generalized" and "specialized" in an ecological sense, as equivalents of "eurytopic" (or euryhaline, polyphagous, etc) and "stenotopic" (or stenohaline, oligophagous, etc) respectively. Often, of course, these ecological attributes have morphological correlates.

POSING THE QUESTIONS

Because individuals in every species succumb to unfavorable abiotic factors or to inadequacy of food, some opportunity must exist at all times for selection to broaden the species' niche, whether by polymorphism or by individual flexibility. The problem, then, is to explain specialization. (A special instance of the problem is the border of the species' geographical range.) From an evolutionary perspective, the origin of specialization within a lineage may be a different question from its maintenance, once originated. Yet a different question is why one clade should show a macroevolutionary trend toward specialization or should include more specialized species than does another clade.

It is useful to distinguish morphological or physiological properties affecting tolerance or diet breadth from specialization based on behavior (habitat selection, resource selection). For example, the limits to geographic ranges

(and some ecological ranges, such as the upper tidal limit of intertidal organisms) may be set by physiological tolerance limits; but within the geographical range, the ecological distribution may be set largely by behavior.

If an individual organism's behavior (e.g. resource selection) is responsive via learning to its history of performance, interspecific differences in behavior may to some degree be a direct, in a sense pleiotropic, consequence of the evolution of morphological or physiological (hereafter "M-P") traits. Many models (e.g. of character displacement) implicitly assume this to be the case, by mapping resource utilization (a behavior) directly onto a character such as body size. Among animals in which learning plays a substantial role, behavioral (e.g feeding) differences between very different species (e.g. gulls and sandpipers) undoubtedly have a genetic basis, but it is at least possible that the behavioral differences among similar species (e.g. of *Calidris* sandpipers) do not reflect genetic changes in behavior as such, independent of the divergence in morphology. Information on this subject is scarce. In many animals, however, resource or habitat selection is little affected by learning (for which there may be few opportunities), as in the settlement of some marine invertebrate larvae. Compare also the oviposition and feeding preferences of many phytophagous insects, some of which develop learned (conditioned) preferences, but only within a highly restricted spectrum of food plants (94, 130). Interspecific differences in resource utilization are then likely to be based on genetic differences in both behavior and M-P traits.

The behavior of an organism defines many of the selective pressures to which it is subject (112), especially on M-P adaptations for resource use. An evolutionary change in behavior frequently initiates a niche shift and directional selection on other traits, a point illustrated by organisms such as aquatic hymenopteran parasitoids (27, p. 169) and predaceous moth larvae (126, 164) that show little morphological evidence of these habits. Acceptance of introduced plants by phytophagous insects can be based on evolutionary change in behavior without apparent change in physiological adaptation (183); from phylogenetic analysis, it appears that temperature preferences have evolved more rapidly than physiological optima in Australian lygosomine skinks (83). Thus, we need to consider explicitly genetic changes in behavior, as distinct from M-P traits, in understanding the evolution of specialization. Behavior is often the mechanism by which specialization is exercised.

GENERALIZED MODELS

Levins (108, 109) introduced an optimal model in which the tolerance of individual phenotypes (e.g. to temperature) relative to the difference between two environmental states defines a concave or convex fitness set of possible

phenotypes, for narrowly or broadly tolerant phenotypes, respectively. The optimum, found by maximizing mean fitness, is a monomorphic specialized phenotype if the environment is relatively homogeneous in time and space, and either a monomorphic generalist or a polymorphism for specialists if otherwise. Intuitively appealing though this conclusion be, it has been challenged on the grounds that the quantity that should be maximized is not obvious (180) and that population genetic models may not yield the same solution.

One- and two-locus genetic models for sexual populations have been reviewed elsewhere (41, 78, 79). Most such models find conditions for the maintenance of polymorphism by variable selection ("multiple niche polymorphism"). In these models, however, the population's niche breadth may or may not depend on polymorphism. Temporal variation generally maintains polymorphism only for very restrictive conditions of the strength and temporal pattern of selection; this is also true for polygenic models. There may not even be selection for homeostatic (broadly tolerant) genotypes under some conditions of environmental autocorrelation (129). In models of spatial heterogeneity, hard selection maintains polymorphism only under rather restrictive conditions of patch frequency and selection intensity. If these conditions are not met, a specialist genotype is fixed, and the population's niche breadth will be narrower than if it were polymorphic. In additive polygenic models, likewise, environmental heterogeneity, even in the form of disruptive selection, generally fails to maintain genetic variation if phenotypes have fixed fitnesses (41, 42). Soft selection (79, 169), which generates frequency-dependent selection for genotypes that can use underutilized patch types (resources), can maintain genetic variation even if there is marginal underdominance (116, 200). Thus, with intraspecific competition, the population niche width (NW) may include both a "within-phenotype" component (WPNW), i.e. the niche width of an average phenotype, and a "between-phenotype" component (BPNW) attributable in part to genetic variation (155). In polygenic models of resource utilization, genotypes differing in some character z have Gaussian utilization functions arrayed along a resource spectrum, and they compete with neighboring genotypes in proportion to their individual niche breadths (WPNW) (155, 157, 170, 179). The genetic variance sustained decreases as WPNW increases. In a sexual (but not in an asexual) population, recombination severely constrains the genetic variance, and hence the population niche breadth attributable to variation among phenotypes (155).

These quantitative genetic models assume that resource utilization is correlated (perhaps by learning) with an M-P character (z). In one-locus models, habitat selection by each genotype of the resource conferring highest fitness broadens the conditions for polymorphism (78, 79, 121). The overall fitness of a genotype is then the sum, over habitat types, of its "performance" (viability and fecundity) in each habitat, weighted by the product of the frequency (or the carrying capacity) of that habitat and the probability of choosing it (181). Fixation of a habitat-specialized genotype can occur if it chooses a sufficiently abundant or productive habitat, even if its physiological (M-P) adaptation to this habitat is lower than to the alternative. In this case the evolution of habitat preference precedes that of M-P adaptations, and tolerance to alternative habitats will not evolve (181). Soft selection can in some cases maintain genetic variation in habitat preference alone, without concomitant variation in performance (146, 181). Presumably such a population can be invaded by a habitat generalist genotype.

If habitat preference and an M-P trait are controlled by different loci, the dynamics of their joint evolution may be complex. Tight linkage between the loci, because it promotes linkage disequilibrium, may increase the likelihood of polymorphism at the M-P locus (58). Several authors, drawing inspiration from phytophagous insects, have recognized that if host (habitat) preference and M-P adaptations are controlled by different loci, either M-P adaptation to an inferior host or avoidance of it can evolve, leading to generalization and specialization, respectively (14, 49, 68, 148). Gould (68) found that the outcome is sensitive to even slight differences in initial gene frequencies. Rausher (148) confirmed this and reported that specialization can evolve under hard, but not under soft, selection. The probability of specialization increases with a decrease in the cost of search, an increase in the cost of M-P adaptation, and an increase in the relative abundance of the superior host. The outcome is also sensitive to the intensity of selection on the M-P locus.

Finally, several authors have addressed the evolution of individual tolerance (or WPNW); physiological or ecological generalization could be attained by monomorphism for a genotype that is broadly tolerant (117), is not strongly canalized in phenotypic expression (i.e. has high environmental variance V_E; 11), or expresses adaptive plasticity, e.g. the development of different optimal phenotypes in response to environmental cues. (West-Eberhard (196) reviews developmentally irreversible "alternative adaptations" in animals, many of which are syndromes of several M-P and behavioral traits.) A developmental switch may be an ESS if the probability of making the "right" decision is greater than 1/2 (115). Treating the phenotype expressed in each of two environments as a pair of genetically correlated characters, Via & Lande (189) found that unless the genetic correlation (r_G) is exactly ±1, the joint optimum is eventually attained, although evolution of the optimum expression for a rare environment may be extremely slow. (Presumably this would provide opportunity for intervention of factors not considered, such as the evolution of avoidance.) Even if $r_G \neq \pm 1$, however, the joint optimum may not be attained if plasticity carries a cost in fitness, or if there are genetic correlations among several characters (e.g. different phenotypic optima in multiple environments; 34). Both fluctuating and dis-

ruptive selection can favor genotypes with high environmental variance (V_E) in phenotypic expression, even if it is not adaptive plasticity as such (11, 106, 158). Lynch & Gabriel (117) treat the breadth of tolerance as a quantitative trait, with fitness plotted over an environmental variable as a Gaussian function that implies a cost of generalization. Because of the cost, the optimal genotype has minimal tolerance if the environment is constant. Temporal variation favors genotypes with broad tolerance. Taper & Case (179), who treat the breadth (WPNW) of a Gaussian resource utilization function as a quantitative genetic character, found that under intraspecific competition, the population niche breadth evolves to a stable value. If either WPNW or BPNW is constrained, the other evolves to compensate. This model does not consider the effect on niche width of the resource distribution or temporal variation in resource availability.

Models that predict that the breadth of tolerance should evolve to match environmental variability envision the organism as responding passively to what the environment presents. Insofar as unsuitable conditions can be avoided, however, there may be no simple correspondence between the evolved breadth of tolerance and the degree of environmental heterogeneity that an investigator measures. In temporally stable but spatially heterogeneous environments, selection favors alleles that increase the fidelity of habitat selection (82) or that reduce the propensity for dispersal (5). This is one mechanism that could yield a correlation, over species, between dispersal rate and niche breadth (73, 90). Moreover, with precise habitat fidelity, selection may shape many characters toward the optimum for a specific environment. This might result in narrow tolerances in each of several respects, i.e. a positive correlation in breadth along several niche axes.

In general models, then, the evolution of specialization tends to be favored (a) by environmental constancy coupled with trade-offs in fitness under different environmental states, (b) by hard selection rather than the intraspecific competition implied by soft selection, and (c) by abundance of one or another environmental state or resource (e.g. if there is little cost of search). Coupling of M-P characters with appropriate habitat selection is assumed in some models; when these vary independently, specialization may evolve as an alternative to generalization (148), or as the consequence of the instability of multiple-niche polymorphism (58, 121). The assumption of a cost of adaptation—the trade-off principle that "a jack of all trades is master of none" (118)—is fundamental in all of these models of specialization.

SOME EMPIRICAL CONSIDERATIONS

Empirical evidence on the prevalence of multiple-niche polymorphism and of genetic variation in resource use has been reviewed elsewhere (78, 79; for

insects see 54, 66a). Although both quantitative genetic variation and discrete polymorphisms have been documented, the "niche-variation hypothesis" (186), according to which greater population niche breadth should be correlated with greater phenotypic variation in trophic structures, seems to find little support (54, 132, 154), except perhaps in resource-associated sexual dimorphism (71, 114, 154, 159, 166, 171). In vertebrates, BPNW may account for only a small fraction of population niche breadth (179, 195). Certainly a broad niche at the population level does not always depend on genetic variation (97). For much of the rest of this paper, we do not consider polymorphism further except insofar as studies of genetic variation shed light on the origin of species-typical specializations.

One such context is the question of the nature and magnitude of a correlation between M-P traits affecting habitat or resource use, and habitat or resource selection ("preference") (54, 185). Across species, such a correlation is frequently evident, but the evidence from genetic correlations within populations is less clear. Phenotypic correlations have been described between beak size and preferred seed size in birds (69, 140, 172), between body size and preferred seed size in seed-harvesting ants (28), and, in some but by no means all instances, between tongue length and the corolla depth of flowers preferred by bumblebees (75a, 76, 88, 127). Such correlations are thought to arise as an individual learns what it can handle best. Interspecific differences in habitat and resource selection may be so striking, though, that genetic divergence of behavior as such surely occurs—at least if we consider such contrasts as the frugivorous oilbird (Steatornis) and the insectivorous nightjars among the Caprimulgiformes. Greenberg (72) made the intriguing suggestion that innate differences in aversion to unfamiliar stimuli may account for differences in niche breadth (foraging patterns) among parulid warblers.

Color polymorphisms in cryptic insects are sometimes associated with preference for a matching substrate, and sometimes not (54, 63, 64). Feeding and habitat preference are apparently pleiotropically, and adaptively, associated with enzyme polymorphisms in some crustaceans (7, 19) and in Drosophila (15, 59). A genetic correlation between adult oviposition preference and offspring growth rate on different plant hosts has been reported for two species of phytophagous insects (168, 188), but it was not found in another case (96). Whether the rather weak correlations reported are caused by pleiotropy or linkage disequilibrium is not known. In contrast, there is abundant, although often indirect, evidence that in phytophagous insects, host preference is poorly correlated with growth and survival (54, 122, 185). The rank order of preference for different plant species is sometimes very different from that of suitability for growth (24, 122, 197), and the correlation between the deterrent and postingestive effects of plant secondary compounds

is quite poor (6). Genetic variation in preference may exist without correlated variation in performance and vice versa (51, 66, 178, 193). Closely related species with different preferences, including specialists that feed on a subset of a congeneric generalist's hosts, may not differ in performance when reared on a common host (57, 98). Thus, host preference and M-P adaptation appear to be largely under independent genetic control. In *Drosophila tripunctata*, oviposition preference for either of two foods is controlled by at least two major loci with epistasis, which as Jaenike (96) notes, would make it difficult to establish linkage disequilibrium between preference and the loci governing physiological adaptation.

ECOLOGICAL BASES OF THE EVOLUTION OF SPECIALIZATION

Environmental Constancy

It is not surprising that narrow physiological tolerances are sometimes found in organisms that inhabit relatively constant environments. For example, the range of salinities over which osmoregulation is effective in full-salinity marine species and freshwater species is frequently narrower than in closely related species that typically experience varying salinity, the K_m of enzymes such as the sodium pump enzyme $Na^+K^+ATPase$ falling within the usual range of Na^+ concentration in the environment (81). Short-term thermal tolerances of pupfish *(Cyprinodon)* from constant-temperature springs are narrower than for populations from inconstant environments (80), and tropical salamanders have a lower capacity for thermal acclimation than do temperate zone species (39). The supposition that diet breadth should be narrower in relatively constant environments than in variable ones (133, 134) is seemingly supported by a few observations such as the greater host-specificity of tropical than of temperate zone bruchid beetles (99). However, this hypothesis has received little empirical study, perhaps because of the difficulty of assessing variation in resources. Vertebrates may be difficult subjects for testing this idea because of their behavioral flexibility; invertebrates have received little attention in this context. Differences in host range between Drosophilidae that breed in mushrooms versus decaying vegetation, and among mycophagous drosophilids, have been attributed to differences in the predictability and/or temporal duration of these resources (93, 105).

Foraging Theory

The greatest recent elaboration of models for diet specialization has been in foraging theory (144, 175). Analogous models have been developed for oviposition decisions by phytophagous and parasitic insects (17, 89, 92). These models are meant to predict the momentary "decisions" of behaviorally flexible individual organisms, usually assuming complete knowledge of the available resources. They can be taken to predict the evolution of an optimal diet (e.g. specialization on the most rewarding kind of resource) only by supposing that the optimal decision becomes genetically fixed. This would require that M-P features, which are constraints on the optimal behavior, do not evolve at the same time. When an organism with individually flexible behavior, such as a redshank, is found to forage optimally, there is some question whether this means that redshanks have evolved optimal behavior, or whether, by feedback from morphology through experience to subsequent behavior, they instead possess a quasi-optimal decision-making machinery that evolved much earlier, say in the origin of the Scolopacidae or of the Aves.

Although some models find the optimal diet as a function of the variance in the resources (149), the classical prediction of foraging theory is that if types of food are ranked by their profitability per item E_i/h_i (energy reward/handling time), an animal should specialize on the highest ranking type if the encounter rate λ_i is high enough, and should always take it when encountered. Less profitable types are taken in decreasing rank order if superior types are scarce, but it is never profitable to specialize on a lower-ranking type of resource, no matter how abundant it is. Students of behavioral ecology differ in their assessment of the conformity of observation to the theory (102, 104, 175). Moreover, the optimal diet can be broader if different resources are complementary (e.g. containing different toxins or nutrients), if recognition time is substantial, if each type of resource provides a variable reward, or if there is intra-specific competition (which favors an "ideal free distribution" of consumers over resources). Specialization on a less profitable type of item can be optimal if the several kinds of items are sufficiently clumped, because the optimal clump type is then the item of choice.

Aside from the usual reservations applying to optimal models, and the difficulty of knowing a priori which foraging model is appropriate to a given species, the utility of foraging theory as a theory of the evolution of specialization may be limited by its assumption of fixed λ_i, E_i, and h_i. These, however, are evolutionary variables corresponding to genetic variation in such features as perceptual abilities (λ_i), digestive efficiency (E_i), and M-P traits affecting handling time (h_i). Sufficient abundance of a less profitable food type may select for improvement in any of these traits, so that its profitability and effective encounter rate might be increased. Optimal foraging theory thus does not address the evolution of those properties of any particular species that specify why specialization should be optimal. Models that include genotype-specific resource preference and fitness may differ from those of optimal foraging theory, e.g. in predicting specialization for a sufficiently abundant but less profitable resource (e.g. 181).

Interspecific Interactions

Specialization can be attributed to interspecific competition in three ways. First, in purely ecological dynamics, specialists may exclude generalists if they use resources more efficiently (119). Possibly the clearest evidence that specialized species may be more efficient and exclude generalists has been provided by chemostat populations of bacteria (but see below) (36, 65).

Second, a facultative behavioral change in resource use may occur in response to interspecific competition (143, 160, 161); if an exploitative competitor lowers the abundance of certain resources, the optimal response is either to restrict search to a less exploited habitat or patch type (if resource distribution is coarse-grained) or to expand diet breadth (if resource distribution is fine-grained and the competitor depletes the superior resource). Thus, the immediate behavioral response to competition may be either increased or decreased specialization.

The third effect of interspecific competition, evolution of the pattern of resource use, is the subject of models of character displacement (3, 170, 179). ESS models (107) and one-locus models (e.g. 44) for two species and two resources predict displacement (and consequently specialization) if for each species there is a negative correlation (trade-off) in the efficiency with which the two resources are used.

In polygenic models (12, 170, 179), the magnitude of character displacement can be very slight, or convergence may occur, if the distribution of resources is narrow relative to the species' niche breadths (but see 124). The evolution of niche breadth under interspecific competition has been treated explicitly by Taper & Case (179). If WPNW is fixed, the genetic variance in the character is reduced as the breadth of the Gaussian competition function or the between-species variance in character means increases. Taper & Case found that if not only the character z but also the breadth of individual resource utilization (WPNW) is genetically variable, interspecific competition reduces both BPNW and WPNW (Case, in litt.).

Evidence on the impact of interspecific competition on niche breadth (as distinct from central tendency) comes chiefly from the greater amplitude of resource and habitat utilization (ecological release) on species-poor islands compared to species-rich islands and continents, especially in lizards (114, 160) and birds (1, 69). Although WPNW seems generally to be much greater than BPNW (179), individual organisms sometimes have different specialized behaviors, which at least in the Cocos Island finch are acquired by learning (195). There appears to be little evidence that differences in ecological amplitude among island populations are genetic, rather than nongenetic behavioral responses to resources freed by the paucity of competitors. We have referred earlier to the virtual lack of evidence for the niche-variation hypothesis except, perhaps, in relation to sexual dimorphism.

Predation and parasitism can have effects analogous to those of competition, although they have received little theoretical treatment. In numerous cases, a species suffers greater parasitism or predation in one habitat, or in association with one resource, than another, and may even be excluded from some habitats (101, 139). Students of phytophagous insects, especially, have proposed that selection for the use of "enemy-free space" may commonly be responsible for host specificity (4, 61, 101, 139). The evidence to date is circumstantial, e.g. the broader host ranges of species of lycaenid butterfly that have ant-protected larvae than of species that lack such protection (135), and the narrower host ranges of aposematic chrysomelid beetles that sequester defensive compounds from their host plants, compared to cryptic species (131). Selection for α-amanitin tolerance in mycophagous Drosophila species may have been imposed by parasitic nematodes that cannot survive in amanitin-containing mushrooms (95).

Specificity of association of an insect with its host plant (or of a predator with its prey) may be attributable to factors extrinsic or intrinsic to the relationship. Extrinsic factors may include community-level pressures such as interspecific competition or predation ("ecological monophagy:" 60). Intrinsic factors, inherent in the properties of the insect and its host, have sometimes been attributed to coevolution ("coevolved monophagy:" 60). This could happen in two ways. In a coevolutionary "arms race," an insect might track the evolution of a host and become increasingly restricted to it as the host diverges from other plants; or some plants, by evolving new defenses, may escape the insect's diet (38). Both scenarios imply a cost of generalization. Although morphologically and chemically divergent plants indeed support different, specialized, insects, this may simply represent adaptation to a preexisting array of diverse hosts, as to any other array of resources (48, 123); it is exceedingly difficult to show that one-on-one reciprocal coevolution has occurred (48, 56, 184).

Mating Rendezvous

Several authors (21, 151) have suggested, and provided indirect evidence, that host- or habitat-specificity may arise through frequency-dependent selection for finding mates at low population densities. Using a simple model, Colwell (21) suggests that a frequency-dependent runaway process analogous to sexual selection may cause rapid local shifts in host association, leading to speciation, and that this explains host specificity in hummingbird-transmitted flower mites. The host as mating rendezvous is an appealing hypothesis for parasites and phytophagous insects with ephemeral populations, especially because the apparent abundance of unutilized resources (52, 138, 145, 151, 177) leads some authors to doubt the force of interspecific competition.

TRADE-OFFS AND CONSTRAINTS

Trade-offs between adaptations in two environments, i.e. the cost of broad tolerance, are central to both mathematical models and verbal arguments for the evolution of specialization. A negative correlation in fitness over environments is inherent in models of the maintenance of genetic polymorphism for habitat or resource use, and in some models of the evolution of reaction norms (e.g. 117).

In general, trade-offs cannot be assumed a priori since the tolerance function of individual phenotypes, which determines the cost or fitness function, is precisely what needs explanation. Empirical analysis of biochemical, physiological, or morphological function is necessary to determine if a postulated trade-off actually exists. Examples of both negative and positive correlations over environments have been found. Many examples of negative correlations, however, involve interspecific comparisons in which each of two species performs better on its own typical resource than that of the other species. These examples are perhaps less relevant than interspecific comparisons. The hypothesis that specialization originates because of trade-offs requires that the fitness of genotypes within populations be negatively correlated among environments. Because a specialized association with a particular resource or habitat imposes selection for special adaptation in numerous characters, many of the features of specialized species are not causes but consequences of a history of specialization. Thus, negative correlations between species may exist because they have evolved a posteriori as a *consequence* of specialization; they may exist only for large interspecific differences (and not for smaller between-genotype differences within a population); or they may exist simply because neither species has been selected for adaptation to the other's environment (e.g. that tropical and Antarctic fish die at each others' temperature is no evidence for a cost of broad thermal tolerance).

Even negative correlations within species do not necessarily imply absolute constraints. In Via & Lande's (189) polygenic model, a population can eventually evolve the optimal adaptation to each environment in the face of a negative genetic correlation between environments, as long as there exists some uncorrelated genetic variation and there is no negative interaction between the fitness functions for the two environments, i.e. no cost of plasticity. This model can represent the evolution of the norm of reaction of an individual with a "labile" character, i.e. one which, as in physiological acclimation, can be altered repeatedly within an individual's lifetime in response to different environments. It may also be applied to nonlabile characters (those which, like beak size in birds, become fixed during ontogeny) if we consider the norm of reaction not of the character itself, but of the performance of the character in different environments. For example, optimal performance of a particular beak size on two types of foods might be achieved by different handling behaviors or by using tools (as in the Galápagos woodpecker finch). Similarly, trade-offs in the temperature dependence of an enzyme may be circumvented by regulation of enzyme concentration. A trade-off at a reductionist level of analysis may not operate at the organismal level, at which compensatory changes come into play. However, as more compensatory changes become necessary, more characters are involved, and new constraints may arise. For n characters, the maximum average genetic correlation that allows characters to evolve freely to their optima is $-1/(n-1)$ (34). The optimal norm of reaction will also be prevented from evolving if the characters' fitness functions interact, as in the interference between enzymes in the *lac* system mentioned below. Such interactions may impose a cost to plasticity.

Nonlabile Traits

For certain inflexible traits, i.e. those that at some point in ontogeny become incapable of compensatory adjustments to changes in environment, trade-offs at the phenotypic level may be inherent and predictable from knowledge of function. An individual organism can have only a single phenology, for example. Clonal genotypes of the fall cankerworm *(Alsophila pometaria)* that hatch at the time of budbreak have the advantage of rapid growth before the foliage of their hosts becomes nutritionally unsuitable; later-hatching genotypes avert the risk of starvation when budbreak is delayed (125). Biomechanical analyses (191) can often specify trade-offs in structural design for different environments. For example, the design for burrowing versus fleetness is incompatible in myriapods; in sessile marine organisms such as corals, rigid and compliant phenotypes are incompatible adaptations for life in still as opposed to turbulent waters.

Nevertheless, the assumption that slight differences in morphology imply efficiency differences on different resources can be hard to verify. No one would doubt that the beaks of woodpeckers, warblers, and finches equip them poorly for each others' food, but it is less evident that optimal size or hardness of seed is correlated with beak size among finches. The expected contrast has been reported in at least one case (172), but in other intra- and interspecific comparisons, it is ambiguous whether or not large-beaked finches handle small seeds less effectively than do small-beaked finches (although they are clearly more effective on large seeds than are small-beaked birds) (69, 70, 142, 198). The curve relating efficiency to seed size for a large beak may embrace that for a small beak. Nevertheless, the optimal diet for a large-beaked finch may consist of large seeds because of their greater energy reward (142). Reviewing numerous comparisons, Wilson (199) found little evidence

that the size distribution of prey is symmetric about a mode that varies with predator body size; the diet of the larger form commonly includes that of the smaller. Compared to short-tongued bees, long-tongued bees can feed in deeper flowers, but they have only a slight disadvantage, if any, on shallower flowers. Under some but not all conditions, optimal foraging should yield a correlation between tongue length and the type of flowers visited (75, 76).

Labile Traits

The reality of trade-offs in performance may be more difficult to demonstrate in characters capable of adjustment to changes in environment. At the biochemical level, optimal temperature, pH, or pressure commonly dictates trade-offs in the function of enzyme and other protein variants among and sometimes within species (81, 136). However, because regulation of enzyme levels and multiplicity of isozymes frequently provide greater physiological flexibility than could be predicted from the biochemical properties of an enzyme, it is not clear how frequently protein function restricts ecological amplitude.

Detoxifying enzymes have been considered an important source of tradeoffs favoring host specialization in phytophagous insects because of the cost thought to be involved in detoxifying or otherwise handling the diverse toxic compounds of different plants (31, 100). However, insects sometimes grow well on chemically very different nonhosts, if they can be induced to feed, e.g. by sensory deprivation (30, 192). Measures of digestive efficiency sometimes do not differ between host specialists and related generalists (57, 165) and do not necessarily reveal trade-offs when conspecific populations associated with different hosts are compared (51, 147). Reports of genetic correlations in performance on different host plants have been more frequently positive or insignificant than negative (55, 77, 98, 147, 187, 194; J. Jaenike, in preparation).The cytochrome P450 system of detoxifying enzymes is thought to consist of nemerous isozymes with overlapping substrate specificity (182). There is some indirect evidence (163) that maintenance of high levels of these inducible enzymes is energetically costly, but little evidence that enzyme activity is higher in polyphagous than in stenophagous insects (67, 152). The inability of many insects to survive on plants other than their natural hosts may often be more a consequence than a cause of specialization (47).

The little evidence we have encountered on trade-offs in physiological functions (i.e. a cost of plasticity) appears ambiguous. Acclimation to low salinity can lower tolerance to high salinity and vice versa, and freshwater invertebrates derived from marine ancestors have generally lost tolerance to higher salinity (103). We have not encountered evidence on the cost of acclimation or adaptation to salinity in euryhaline compared to stenohaline organisms. "Broad-niched" species of Drosophila may have a greater capa-

city for temperature acclimation than do "narrow-niched" species (110), but there is no information on the cost of acclimation, if any. Individual variation in sprint speed in a lizard showed no trade-offs at different temperatures (85), but an interspecific comparison in lizards revealed a negative correlation between burst speed and endurance, for which physiological and anatomical correlates were found (84). In a species of garter snake, however, the genetic correlation between speed and endurance is positive (58a).

Trade-Offs in Perception and Information Processing

Avoidance of some palatable food species because of their resemblance to unpalatable species can restrict diet breadth, as illustrated by mimicry. Levins & MacArthur (111) postulated that host specificity in phytophagous insects may be advantageous if some suitable plants cannot be distinguished from toxic species; instances of oviposition on toxic introduced plants may provide examples (18). Feeding in specialized phytophagous insects in some instances depends on chemoreceptors tuned specifically to a stimulatory compound in the host, but more often on central nervous integration of numerous receptors with overlapping sensitivity to a broad range of both stimulatory and deterrent compounds (32, 33, 122, 162); sensory constraints might therefore be weak. Some evidence suggests that higher taxa made up primarily of host generalists have more chemoreceptors than do taxa comprised mostly of specialists, but the number of chemoreceptors is so great in most species that limitations on sensory discrimination may be an unlikely explanation for specificity of diet (16).

Search image-like behavior, however, which in some instances increases the rate of resource harvest (29, 128, 130, 173), implies that constraints may exist on information processing that may favor restriction of diet (25). If such constraints hold for genetically based differences in "search image," they might contribute to the evolution of diet specialization (47, 148).

The Energy Conservation Hypothesis

Trade-offs are frequently assumed to lie in an energetic cost of maintenance of enzymatic or morphological features that serve different functions. The most precise and carefully controlled experiments addressing this hypothesis have been tests of auxotrophic mutants of bacteria, either in pure culture or in competition with wild-type strains, when provided with an excess of the requisite for which the enzyme function has been deleted (35, 36, 37). Although mutants lacking unnecessary enzymes (e.g. deletion mutants) sometimes have greater growth rates and a selective advantage over wild type, numerous lines of evidence indicate that the selective advantage does not lie in energy conservation, but in "resource interference;" for example, unnecessary lactose permease in a constitutive lac operon mutant appears to

interfere with uptake of other sugars. Such results suggest that at the biochemical, and even more probably at the organismal, level, trade-offs may be caused primarily by mechanical interference between traits. Thus, the functional properties peculiar to individual characters and complexes of characters may determine if there are functional trade-offs among character variants. If a universally generalizable basis for trade-offs, such as energy conservation, does not exist, trade-offs cannot be assumed in the absence of functional analysis.

At the level of variation within populations, which is where the origin of specialization must be sought, it appears that trade-offs are easier to assume than to demonstrate. We do not find that the evidence is so abundant as to justify this assumption, and we feel that the study of specialization warrants more extensive physiological and functional morphological study of intraspecific variants, as well as more attention to hypotheses for the origin of specialization that do not depend on this assumption. An experiment that fails to provide evidence for trade-offs may be challenged: the trade-off may exist in some other, untested, respect, just as one can postulate elusive niche differences to account for the coexistence of competitors. Sensitive tests for trade-offs will require careful design and full awareness of the biological properties of the characters and organisms examined.

MACROEVOLUTIONARY ASPECTS

Because species in a clade may share a specialized habit through common ancestry, they do not provide independent evidence on the advantage of specialization. The proportion of specialized species may be affected by three macroevolutionary biases: differential rates of evolution from generalization to specialization and vice versa, and differential rates of speciation and extinction of generalized and specialized forms.

Far more phylogenetic analysis is required than has been done, to document patterns of evolution of generalized and specialized habits (cf 123, 153 for examples). It is commonly presumed that specialists evolve from generalists, and this is surely true in many instances, as in the derivation of egg-eating and snail-eating snakes from more generalized colubrids, of leaf-eating monkeys (e.g. *Colobus*) from generalized cercopithecids, and of *Acacia*-associated *Pseudomyrmex* species from less host-specific pseudomyrmecine ants. In at least some cases, isolated generalists in an otherwise specialized clade have doubtless arisen from specialized ancestors; the polyphagous habit of the swallowtail butterfly *Papilio glaucus*, for example, is probably a derived condition within a tribe consisting mostly of specialized feeders on Lauraceae and Rutaceae (123). Many, perhaps most, specialists arise from other specialists with either the same or different habits. In some groups a particular

specialization is phylogenetically conservative; for example, among Lepidoptera the troidine swallowtails all feed on Aristolochiaceae, and among Hymenoptera the Eucharitidae are parasitoids of ants, the Evaniidae of roach oothecae, and the Sclerogibbidae of auchenorrhynchous Homoptera. Such instances may imply that stabilizing selection maintains a *particular* specialization. In other groups, however, each species, although specialized, uses a very different resource; for example, sibling species of *Calligrapha* (Coleoptera: Chrysomelidae) feed on plants in the Salicaceae, Ulmaceae, Malvaceae, Cornaceae, and others (10); and sibling species of *Yponomeuta* (Lepidoptera: Yponomeutidae) feed on Celastraceae, Rosaceae, Salicaceae, and Crassulaceae (79a). In such instances the lineage appears not to be "committed" by its physiology and morphology to a particular resource, but there appears to be selection for "specialization *per se*," owing perhaps to ecological factors (e.g. competition, sexual rendezvous) or to disruptive selection. In butterflies, congeneric species appear to vary more radically in host affiliation in groups that use the host as a focus for mating than in those that do not (60).

In many instances the successive evolution of numerous adaptations to a special resource or habitat constitutes an increasing commitment that makes reversion to a generalized habit, or a shift to a very different specialization, increasingly unlikely. Characters are frequently reduced or lost in specialized groups (e.g. wings, eyes, and foraging behavior in inquilinous arthropod associates of social insects, teeth in several groups of "anteaters," many characters in parasites). Whether vestigialization is mostly a consequence of selection, or of mutation pressure alone, is one of the major unsolved and largely neglected questions in evolution (8, 26, 141). Compared to specialists in which characters have been highly modified, reduced, or lost, generalists often must have a richer repertoire of features from which to evolve new variations; thus specialization is often thought to lead to an evolutionary *cul de sac* (87, 150, 167). Implicit in this idea, however, is the assumption of a constant and monotonic relationship between characters and functions and between function and evolutionary potential: each modification or loss of a character represents loss of another function and therefore of "evolutionary potential." But because a monotonic relationship may not hold, it is not always apparent how much modification is necessary for the loss of other functions, or if this loss would indeed restrict "evolutionary potential." Turtles have exchanged teeth for slicing blades that enable them to feed in a way no other living reptiles can, and so to have diverse feeding habits.

That specialization is often irreversible may well be true, but this is difficult to test because, like evolutionary constraints generally (62, 174), *culs de sac* are identified by nonevents. A taxon of specialists (e.g. the burrowing "blind

snakes," Typhlopidae) is evidence for irreversible commitment to specialization only if it has not given rise to species with different or more generalized habits. Snakes are ecologically an extraordinarily diverse group, even though they display extreme skeletal modifications and reductions and are derived from a burrowing ancestor (137). A test of the hypothesis that specialization leads irreversibly to a *cul de sac* should include comparisons among sister taxa derived from specialized versus generalized ancestors. At least in principle, generalists could be as committed to their way of life, as subject to stabilizing selection, and as phylogenetically constrained as specialists. The hypothesis that specialization is a special cause of phylogenetic constraint would not be strongly supported if the generalized habit were just as phylogenetically conservative.

As in the evolution of the nonplanktotrophic from the planktotrophic habit in some molluscs (73, 90), irreversibility of specialization implies a macroevolutionary explanation for the incidence of specialized species. Differential speciation and extinction rates (species selection) may also have an effect. A common idea is that specialized species, because of their narrow tolerances, have more fragmented distributions and are therefore more prone to allopatric speciation than are generalists. Fryer (45, 46) has invoked this explanation for the great diversity of *Haplochromis* and other African lake cichlids, which are generally more habitat- and food-specific, and have more patchy distributions, than is *Tilapia*, which has few species. The similar feeding habits of many of the species argue against interspecific competition as an explanation of the individual species' specialized habits. Vrba (190) has likewise argued that the greater habitat specialization of the Alcelaphini (Bovidae) has caused a greater speciation rate than in their less diverse sister group, the Aepycerotini. A markedly lower speciation rate of eurytopic species relative to stenotopic species of marine invertebrates has been attributed to their higher dispersal propensity, a result of their tendency to have planktotrophic larvae and thus a prolonged planktic stage (74, 90, 91). Price (138) argued from the positive correlation between the total number of species and the number of specialized species across parasitic and phytophagous taxa of insects that host specialization promotes speciation. However, because most of the taxa compared are distantly related, the meaning of the correlation is unclear.

Related to, but distinct from, the hypothesis that specialization promotes speciation is the hypothesis that speciation in itself generates specialization. In the controversial hypothesis of sympatric speciation by host shifts in phytophagous insects (13, 43, 53), host-specialized species arise by disruptive selection on host preference, which will constitute an isolating mechanism if the organism mates on the preferred host. Futuyma (50) has suggested that speciation in allopatric populations may confer evolutionary permanence on characters (such as specializations) that would otherwise be lost

to recombination upon secondary contact with other populations. (The same argument could apply to the retention of a derived generalized habit.)

The phylogenetic information necessary to test the relationship between specialization and rate of diversification is scarce. For example, in preparing this article, we sought, using Linsley's monograph (113), to contrast the number of species per genus in genera of North American Cerambycidae (Coleoptera) comprised mostly of host plant specialists versus generalists. We examined this family because abundant host records exist and because unlike many other taxa of phytophagous insects, it includes numerous groups of both generalists and specialists. Contrary to our expectation, genera of generalists and specialists seem not to differ in species richness, but the genera cannot be equated with clades: the profusion of very small genera suggests that many of the larger genera may be paraphyletic. The appropriate comparison would be between sister clades of specialists and generalists.

Simpson (167) suggested that generalized taxa persist longer than do specialized taxa, which if true would tend to reduce the incidence of specialization. However, although some ecological attributes seem to affect duration (73, 90), the claim that specialization is one such attribute has not been properly documented. Bryozoan taxa with a higher index of morphological complexity have been more susceptible to mass extinctions, although not to "normal" extinctions (2), but the relation between morphological complexity and ecological specialization is uncertain.

Knowledge of phylogenetic history is crucial for determining the reality of the macroevolutionary patterns we have discussed. Only by knowing the history and direction of evolution can we hope to detect phenomena like specialization-driven irreversibility, and to test statistically their frequency against null expectation.

CONCLUSIONS

1. The sources of natural selection that may favor the evolution of ecological specialization in diet, habitat use, or physiological tolerance are many. No one factor can be assumed, a priori, to explain any individual instance.

2. The evolution of specialized behavior (e.g. diet selection) must be distinguished from the evolution of morphological and physiological traits. The extent to which both behavior and morphology have diverged genetically among related species that are capable of learning appears not to have been extensively studied. In some instances, specialized behavior may be, in a sense, a pleiotropic consequence of morphology. Intraspecific correlations between behavior and morphological or physiological traits, and their basis in learning or genetic covariation, are a neglected aspect of the evolution of specialization.

3. Optimal foraging theory predicts specialization in diet, but it may not be a theory of the evolution of specialization in the particular species studied. Moreover, the coevolution of optimal foraging with the morphological and physiological traits that dictate an individual's optimal choice has not been modelled. Optimal foraging theory treats these traits as constants, not as evolutionary variables.

4. At least superficially, a common immediate effect of interspecific competition, facultative expansion of diet, appears to conflict with its evolutionary effect, which at least under some conditions is to narrow diet breadth. There is little firm evidence on the evolutionary effect of interspecific competition on diet breadth. Likewise, although predation, parasitism, and mate finding are likely sources of selection for specialization, the evidence on their role is circumstantial at best.

5. Trade-offs in the function of character variants in different environments, if invoked to explain specialization, must be tested by intraspecific rather than interspecific comparisons, because many of the properties of specialized species are the consequences rather than the causes of specialization. Physiological and functional morphological studies are needed to determine if costs can be discerned among slightly different phenotypes. A trade-off discerned by a reductionist analysis of a single character may not operate at the level of the organism, in which compensatory features come into play. At the same time, the more characters come into play, the more likely genetic correlations are to constrain evolution. It is possible that constraints on perception and information processing contribute to specialization.

6. The number of specialized species is affected by the rates of speciation and extinction of specialists compared to generalists, and by the relative rates of evolution between generalized and specialized habits. There is little explicit information, of the kind that phylogenetic analysis could provide, on these patterns. Phylogenetic information may cast light on some evolutionary mechanisms, e.g. on the postulate that specialization promotes speciation by reducing gene flow.

7. Both the frequency and the causes of irreversibility in the evolution of specialization have been little analyzed. The common supposition that specialization is irreversible (hence invariably a derived condition) and that it restricts "evolutionary potential" is difficult to test, both because "evolutionary potential" is best recognized with hindsight and because a simple correspondence between characters and functions should not be assumed without justification. Commitment to, and phylogenetic conservatism of, a generalized habit is also possible, at least in principle. There is a need for statistical testing of phenomena like irreversibility of specialization.

8. It appears possible to distinguish between clades in which a particular specialization is phylogenetically conservative and clades in which species have different specializations. In the former case, trade-offs in morphological and physiological traits may enforce commitment to a historically acquired particular specialization ("phylogenetic constraint"). In the latter, selection for "specialization *per se*" may be imposed by ecological factors such as competition or mating success.

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