PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1998 **353**, 199-205
doi: 10.1098/rstb.1998.0202

The Royal Society

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Phenotypic differences can exist between species, between local populations of the same species and between individuals within single local populations. At all scales, phenotypic differences can be either adaptive or non-adaptive. Using natural selection to explain differences between closely related species was controversial during the 1940s but had become common by the 1960s. Similarly, the adaptive nature of differences between local populations was initially controversial but had become widely accepted by the 1980s. The interpretation of differences at the finest scale—between individuals within single populations—is still unresolved. This paper reviews studies of adaptive individual differences in resource use and response to risk. A general conceptual framework for thinking about adaptive individual differences within populations can unite subjects as seemingly different as speciation and personality psychology.

Keywords: adaptation; natural selection; individual differences; trophic polymorphisms; personality differences; frequency-dependence

1. INTRODUCTION

In 1947 David Lack published a book on Darwin's finches that helped to define the modern study of ecology and evolution. By the time the second edition was published in 1961, so much had changed that Lack felt obliged to add the following preface (p. xii):

> A condition of the 1961 reprint is that the text should not be changed. The reader may therefore be reminded that this text was completed in 1944 and that, in the interval, views on species-formation have advanced. In particular, it was generally believed when I wrote the book that, in animals, nearly all of the differences between subspecies of the same species, and between closely related species in the same genus, were without adaptive significance... Sixteen years later, it is generally believed that all, or almost all, subspecific and specific differences are adaptive, a change of view which the present book may have helped to bring about.

Lack's preface reveals that using natural selection to explain differences between closely related species was controversial during the 1940s but had become accepted by the 1960s. This transition was the beginning of a larger historical trend involving the use of natural selection to explain differences between organisms at increasingly finer scales. Lack presumably would have been surprised to learn that guppies from upper and lower sections of the same stream differ in ways that can be explained by natural selection, yet by the 1980s the concept of local adaptation in guppies and many other species had become widely accepted (reviewed by Endler 1986).

The next step in this progression is to explain differences between individuals within a single population as the product of natural selection. Of course, some adaptive individual differences have been known for a long time, such as polymorphisms in mimicry (reviewed by Gilbert 1983). Another outstanding example that has been studied more recently is male mating polymorphism, in which a population consists not only of recognizably different males and females, but also different kinds of males that succeed in mating with females in different ways (e.g. Shuster & Wade 1991). Nevertheless, despite these examples, differences between individuals within a single population are often regarded as the raw material on which natural selection acts, rather than as the end product of natural selection. For example, virtually all studies of optimal foraging theory assume that there is a single best way to forage, which is tested against the average foraging behaviour of the study population (reviewed by Stephens & Krebs 1986). Individual differences in foraging behaviour are assumed to be non-adaptive variation that surrounds an adaptive mean. Imagine the confusion that would result if this reasoning was applied to male mating behaviour. In short, evolutionary biologists have yet to adopt a general set of expectations about adaptive individual differences within single populations that can be applied to all traits.

This paper reviews individual differences in foraging behaviour and response to risk in bluegill and pumpkinseed sunfish populations (Centrarchidae: *Lepomis macrochirus* and *L. gibbosus*), in an effort to understand the general nature of individual differences within single populations.

2. VARIATION IN FORAGING BEHAVIOUR

A natural environment such as a lake affords many ways to survive and reproduce, which account for many of the differences between species. Coexisting species are often said to occupy different niches whereas single species occupy a single niche. Often, however, even a single population of a single species occupies a diverse natural environment that affords more than one way to survive and reproduce. If single populations inhabit multiple-niche environments, then the same ecological and evolutionary forces that create differences between species can create differences within species. An example is provided by bluegill sunfish, which occupy both the littoral zone and open-water zone of North American freshwater lakes. Species that are restricted to these two habitats differ in ways that are obviously functional. Open-water species tend to be fusiform and have small pectoral fins to minimize drag, whereas littoral zone species tend to be deep-bodied with large pectoral fins to manoeuvre through their spatially complex habitat. Bluegill have been thought to be ecological generalists with an intermediate body form that allows them to occupy both habitats. However, Ehlinger & Wilson (1988) showed that bluegill collected from the open water of one lake were more fusiform and had shorter pectoral fins than individuals collected from the littoral zone of the same lake. Thus, morphological variation existed within a species that could be interpreted in the same way as morphological variation between species. This does not mean that the population consists of two discrete morphological types. On the contrary, discriminate function analysis showed that the morphological distribution of the population is unimodal, with roughly the upper and lower halves of the distribution occupying the different habitats (figure 1).

It is possible that the bluegill occupying the extremes of the morphological distribution act as ecological specialists, spending most of their time in their respective habitats, whereas the majority of the population occupying the middle portion of the distribution act as ecological generalists, as previously envisioned for the entire population. Wilson *et al.* (1996) examined this possibility by using parasites as an indicator of long-term habitat use. Trematode parasites use snails as an intermediate host and therefore are largely restricted to the littoral zone habitat. If morphologically intermediate bluegill use both habitats, they should also be intermediate in their trematode parasite loads. Figure 2 shows that this is not the case. Two trematode parasite species were over five times more abundant in fish collected from the littoral zone than fish collected from the open water. Within a habitat, however, there was no correlation between morphology and parasite load. Morphologically intermediate fish collected in the open water had the same average load as morphologically extreme fish from the open water and a much smaller load than morphologically intermediate fish from the littoral zone. Even the few trematodes that were found in open-water fish could have been acquired during the juvenile stage of the life cycle (when all bluegill are confined to the littoral zone) or during the mating season (which also takes place in the littoral zone). The parasite data suggest that there are no bluegill in this lake that act as ecological generalists. Even morphologically intermediate fish commit themselves to one habitat or the other and spend most of their time within that habitat.

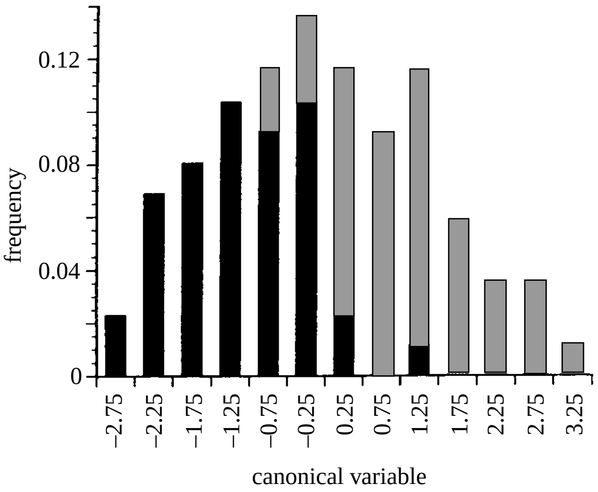

Figure 1. Discriminate function analysis of bluegill sunfish morphology in Holcomb Lake, Michigan, USA. Black represents fish captured in the open water and grey represents fish captured in the littoral zone. The two groups are morphologically different from each other but the overall morphological distribution of the population is unimodal. See Ehlinger & Wilson (1988) and Wilson *et al.* (1996) for more information.

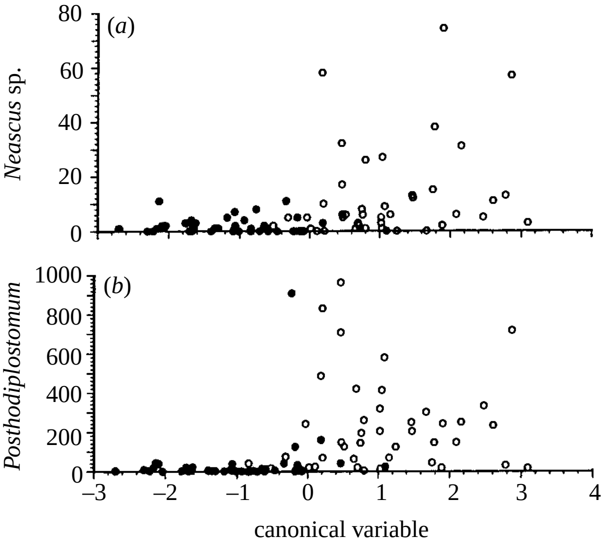

Figure 2. Parasite infestation as a function of morphology and habitat use for the same sample of fish shown in figure 1. (*a*) *Neascus* and (*b*) *Posthodiplostomum* are trematode parasites that use snails as intermediate hosts and therefore are confined largely to the littoral zone. Fish captured from the littoral zone were infected by approximately five times as many parasites as fish captured from the open water. Within a habitat, there was no relationship between morphology and parasite load, suggesting that all fish, including morphological intermediates, spend most of their time in a single habitat. See Wilson *et al.* (1996) for more information.

In this lake and virtually all other lakes of the mid-western US, bluegill sunfish coexist with pumpkinseed sunfish. Bluegill are usually 6–10 times more abundant and occupy both habitats, whereas pumpkinseed are confined to the littoral zone and specialize in crushing hard-bodied prey, such as snails. The geographical distributions of the two species only partially overlap, however, and pumpkinseed sunfish are the only sunfish species in thousands of lakes in the north-eastern US. With Beren Robinson and our colleagues, I conducted a series of studies to determine if the absence of a closely related species influences intraspecific variation in the pumpkinseed sunfish. Our results can be summarized as follows.

North-eastern lakes are similar to mid-western lakes as far as the bluegill–pumpkinseed interaction is concerned. One criticism that is often levelled against studies of character displacement and release is that the allopatric region may differ in other ways than the absence of the closely related species. However, bluegill sunfish have been introduced to some lakes in the north-eastern US, providing a natural experiment to test this possibility. We examined two large lakes in the Adirondack mountain region with introduced bluegill, and in both cases the pumpkinseeds were confined to the littoral zone, as in all mid-western lakes (Robinson *et al.* 1998).

In the absence of bluegill, pumpkinseeds usually occupy both habitats. Pumpkinseeds inhabited the open water of 12 out of 12 large lakes (>91 ha) and 10 out of 14 small lakes (<33 ha) that were censused (Robinson *et al.* 1998).

Morphological differences between open-water and littoral-zone pumkinseeds ranged from statistically nonsignificant to bimodally distributed. The differences were statistically significant in 10 out of the 12 large lakes and 5 out of the 10 small lakes. Figure 3 shows examples for three large lakes, which range from very modest differences to almost no overlap in morphological space (Robinson *et al.* 1998).

Both genetic differences and phenotypic plasticity contribute to the morphological differences between habitats. Figure 3*b* is from Paradox Lake, New York. Adults were collected from the open water and littoral zone of this lake and allowed to breed separately in artificial ponds. Their progeny were then raised in enclosures in both the littoral zone and open water of another artificial pond (Robinson & Wilson 1996). The progeny of open-water and littoral-zone adults differed morphologically, even when they were raised in the same habitat. However, progeny of both types raised in the open water also differed morphologically from progeny raised in the littoral zone. Genetic differences accounted for roughly 30% of the morphological variation.

In the absence of bluegill, pumpkinseeds appear to inhabit a two-peak adaptive landscape (disruptive selection). Robinson *et al.* (1996) measured two components of fitness (relative growth rate and the concentration of lipids in the muscle) as a function of morphology. Natural selection appears to be directional in the open-water habitat, favouring the extreme open-water morphology. Similarly, the extreme littoral-zone morphology appears to be favoured in the littoral-zone environment. Individuals occupying the extremes of the morphological distribution are almost never found in the 'wrong' habitat and therefore enjoy the advantages of their specializations without the costs. Morphologically intermediate individuals are always at a disadvantage, compared to one extreme or the other, and therefore appear to occupy an adaptive valley, even though the majority of the population is morphologically intermediate.

Multiple-niche polymorphisms appear to be extremely widespread. The patterns that we have documented for bluegill and pumpkinseed sunfish may appear exceptional to those who have been taught that single species occupy single niches and that natural selection usually favours the middle of a phenotypic distribution and trims the edges. Nevertheless, dozens of examples are emerging for other species, suggesting that multiple-niche polymorphisms may be more the rule than the exception (reviewed by Robinson & Wilson 1994; Smith & Skulason 1996). A recent example involves the little greenbul (*Andropadus virens*), a passerine bird that inhabits both forested and adjacent open habitats in the tropics (Smith *et al.* 1997). Individuals collected from the two habitats differ both morphologically and genetically, just as we have described for pumpkinseed sunfish.

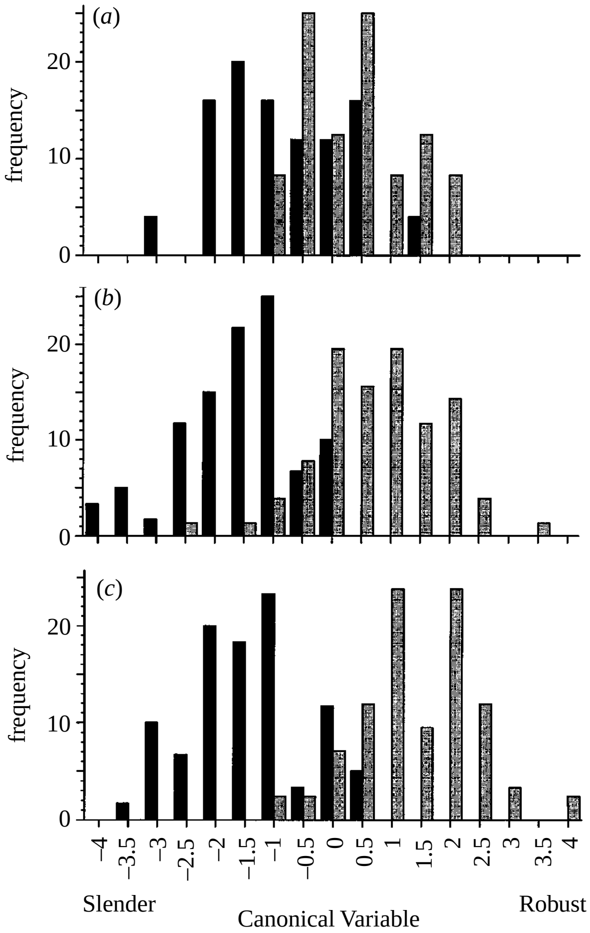

Figure 3. Discriminate function analysis of pumpkinseed sunfish morphology in three large lakes that lack bluegill sunfish. Pumpkinseeds occupy both the littoral zone and open water of all three lakes, but the morphological differences between habitats range from slight to almost no overlap. See Robinson *et al.* (1998) for more information.

Multiple-niche polymorphisms are not always obvious and sometimes must be looked for to be found. Sunfish were studied for many years without the adaptive nature of individual differences being detected. In other cases the differences are so large that members of the same species are mistaken for different species. This leads to the question of whether adaptive individual differences within a single population can ultimately result in the formation of new species.

3. VARIATION IN RESPONSE TO RISK

Imagine stocking a lake with fish that are identical in their behavioural disposition. The first fish to be added will wisely select the safest habitats and the safest ways of obtaining resources within a habitat. Subsequent fish will be faced with a more difficult choice between safe opportunities that are already being exploited and more risky opportunities that are so far unexploited. As the density of fish in the lake increases, a range of opportunities will ultimately be exploited, from safe to risky, despite the fact that the fish are identical in their behavioural dispositions. This conclusion follows from the concept of the ideal free distribution, which has many applications in evolutionary biology (Bulmer 1994).

Against this background, consider a mutant fish that is especially well-adapted for life in risky situations. This individual may still choose safer options when available, but will be among the first to shift to riskier options as density increases. Similarly, a mutant fish that is especially well-adapted for life in crowded-but-safe situations will be among the last to adopt risky behaviour. In this fashion, the original population of fish that were identical in their behavioural disposition might evolve into a more complex mix that includes risk-prone and risk-averse 'specialists'.

This thought experiment suggests that multiple resources are not the only foundation for the evolution of adaptive individual differences. Response to risk provides another foundation, leading to behavioural dispositions that in human terms would be described as 'shy' and 'bold' (Clark & Ehlinger 1987; Wilson *et al.* 1994). Wilson *et al.* (1993) examined this possibility for juvenile pumpkinseed sunfish by placing unbaited wire minnow traps at 5 m intervals along the shore of a pond. Each trap was soon surrounded by a cloud of juvenile pumpkinseeds who eagerly explored its contours. As the traps contained no food, in everyday terms these fish appeared to be motivated entirely by curiosity. The traps were retrieved after 10 min and the same section of shore was swept with a seine to capture the fish in the immediate vicinity that did not enter the traps. If juvenile pumpkinseeds differ along a shy–bold continuum, then the traps should contain the boldest fish and the seine should contain a mix of shy fish who avoided the traps and bold fish who approached but did not happen to enter. Average differences between the two groups could therefore be used to test for the existence and consequences of individual differences in shyness and boldness. We performed this basic experiment several times, with the following results.

Trapped fish began to feed in laboratory aquaria five days sooner, on average, than seined fish. Most wild fish require a period of time to acclimatize to laboratory conditions before they will feed. However, the same behavioural disposition that caused some fish to explore the traps also caused them to acclimatize much sooner than the seined fish. It is possible that seined fish are slower to acclimatize because the experience of being seined is more traumatic than the experience of being trapped. To test this possibility we placed some trapped fish in a seine and dragged them through the water before conveying them to the laboratory. The experience of being seined had no effect on habituation to laboratory conditions.

Trapped fish had ingested over three times more copepods, on average, than seined fish immediately prior to capture. In a separate experiment trapped and seined fish were sacrificed immediately after capture to examine their stomach contents. The only difference was in the number of copepods ingested. Copepods are probably a risky prey because they inhabit the open-water column and are difficult to capture, requiring concentration that detracts from the ability to detect predators (Krause & Godin 1996).

Seined fish seek the proximity of other fish in their natural environment. The most informative experiment involved marking the trapped and seined fish, returning them to the pond, and observing their behaviour over a period of weeks. Fish from the two groups became thoroughly intermixed, with no tendency to interact preferentially or segregate into different microhabitats. However, seined fish were far more likely than trapped fish to swim within three body lengths of another fish.

In a separate study, T. Dearstyne and D. S. Wilson (unpublished data) examined shyness and boldness in individually marked adult pumpkinseed sunfish. When two marked fish were observed at the same time, one almost invariably swam closer to the diver than the other, providing a convenient measure of relative shyness and boldness. Not only was this difference consistent for a given pair, but it was also transitive across pairs. In other words, if A swam closer than B and B swam closer than C, then A would swim closer than C when they were observed together. The shy member of one pair that was observed intensively was so inhibited that it never fed in the presence of a diver, even though its bold partner often fed. When the bolder fish was captured and removed from the lake for three days, its shy partner spent the entire period under a submerged tree stump, at least in the presence of divers. When the bolder fish was returned, it swam directly to the stump and both members of the pair were observed on their home range during the following observation period. We were unable to observe the response of the bold fish to the removal of its shy partner because the latter would not allow itself to be captured. This fish would probably be judged as 'pathologically shy' by human standards, but if the diver had been a predator, it would have been the surviving member of the pair.

These studies suggest that profound differences in behavioural dispositions, which are described by the word 'personality' in our own species, probably exist in many other species and may often be adaptive. However, studying personality differences from an evolutionary perspective leads to some interesting departures from traditional psychological approaches to the subject. Psychologists frequently study personality by measuring large numbers of traits (usually with the use of questionnaires) and analysing the results with a factor analysis. A number of factors are identified that are interpreted as major dimensions of personality. For example, the 'big five' dimensions of human personality identified by many studies include extroversion (shyness–boldness), agreeableness, conscientiousness, emotional stability, and intellect (reviewed, from an evolutionary perspective, by Buss 1991; MacDonald 1995). This framework assumes that an individual's personality is relatively domain-general. For example, an individual who scores high on the extroversion dimension is presumably bold in most respects, such as social interactions, response to predators, exploration of the physical environment and so on.

In contrast, thinking about personality from the adaptive standpoint leads to the expectation of domain-specificity. The selection pressures that favour individual

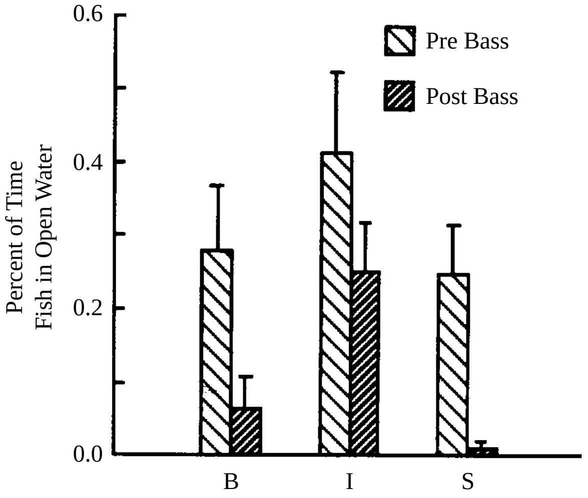

Figure 4. Behavioural differences between juvenile pumpkinseed sunfish classified as shy (S), intermediate (I) and bold (B) according to their response to an observer approaching them with a red-tipped stick (a threatening situation). Intermediates were more likely to spend time in the open water, especially in the presence of bass. See Coleman & Wilson (1998) for more information.

differences in one context (e.g. response to predators) can be very different from the selection pressures operating in other contexts (e.g. intraspecific social interactions). It is even plausible to expect negative correlations across domains. An individual who is shy with respect to predators may find itself in a crowded habitat, favouring boldness with respect to social interactions. In general, the question of whether natural selection promotes individual differences within a population must be asked separately for each adaptive problem encountered by members of the population.

Coleman & Wilson (1998) looked for context-sensitivity in shyness and boldness with the following study. Juvenile pumpkinseed from a pond without major predators were marked so that individuals could be identified at a distance of several metres. Repeated measures of shyness and boldness were obtained in two contexts: (i) by extended a red-tipped stick toward an individual and recording when it retreated from this threatening situation; and (ii) by introducing a ball of aquatic vegetation wrapped in netting and rich in invertebrate prey into the pond and observing which fish approached and fed most quickly. These measures of shyness and boldness were related to each other and to focal observations of behaviour taken from a glass-bottomed observation vessel. Finally, largemouth bass (*Micropterus salmoides*) were added half-way through the experiment to measure behaviour in the presence and absence of a major predator.

Individual differences were stable for each context but did not correlate across contexts. In other words, a fish that quickly fled from the stick during one trial was likely to behave the same way in subsequent trials, but this same individual could be consistently among the first to approach and feed from the ball of vegetation. This result confirmed our suspicion that individual differences are often stable within contexts but not necessarily across contexts. A single measure of shyness and boldness does

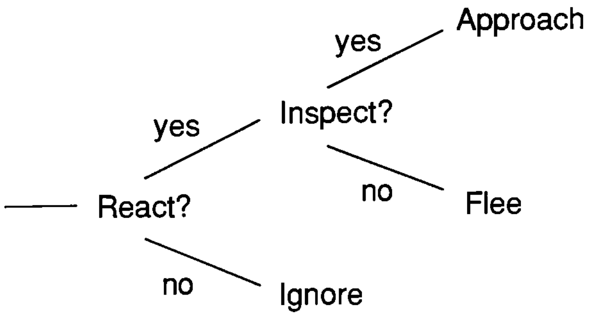

Figure 5. Individual differences as a decision tree rather than a one-dimensional continuum of behaviours. The first decision concerns reactivity to a threatening situation (ignore versus react) and the second decision refers to the particular reaction (flee versus inspect). Individuals that tend to ignore threatening situations may appear as intermediates when individual differences are represented as a one-dimensional continuum of behaviour.

not suffice to characterize individual differences in the population.

In addition, this study included a result that we had not expected. We had assumed that shyness and boldness within a single context could be represented as a one-dimensional continuum of behaviour. For example, we classified those fish who fled immediately from the stick as shy, those who allowed the stick to approach within a few centimetres as bold (some even approached the stick and nipped at it) and those who allowed the stick to approach within an intermediate distance as intermediate in their behavioural disposition. When we related response to the stick to behaviour during focal observations, however, we discovered that the fish classified as intermediate behaved most boldly in their natural environment in several respects. Figure 4 shows one example in which intermediates spent more time in the open water, especially in the presence of bass, than the fish classified as shy and bold based on response to the stick.

These results begin to make sense if we think of shyness and boldness as a decision tree rather than a one-dimensional continuum of behaviour, as shown in figure 5. The first branch of the tree involves reactivity to predators and other threatening situations. The second branch involves the behavioural response of the reactive fish. The individuals that we classified as 'shy' and 'bold' may have been similar in terms of reactivity but different in their particular response to the threatening situation (fleeing vsersus inspecting). The individuals that we classified as intermediate may have differed from both the shy and the bold (as we classified them) by simply ignoring predators and other threatening situations, at least until the risk became too great. This working hypothesis needs to be confirmed by future studies, but it illustrates the dangers of assuming, without evidence, that behaviours can be arranged along a one-dimensional continuum, even within a single context.

Huntingford & de Leaniz (1997) have recently provided another example of domain-specific individual differences in juvenile Atlantic salmon (*Salmo salar*). Individuals were first measured with respect to dominance in small tanks with a single localized resource and then released into an artificial stream. The so-called dominant fish were less likely than so-called subordinants to establish feeding stations and were more likely to emigrate from the stream. Huntingford & de Leaniz (1997) suggest that the behaviours promoting success in high density situations and localized food resources are different from the behaviours promoting success at low densities and more complex physical environments.

4. DISCUSSION

Adaptive individual differences in resource utilization and response to risk are interesting in their own right, but they also serve as examples of a more general process. In both cases, the fitness of an individual depends not only on how it behaves, but also on how many other individuals in the population are doing the same thing. In the absence of density-dependence there is no reason to expect different activities to have the same consequences for survival and reproduction. One activity should be better than the others and all members of the population should evolve to do that one thing. Negative density-dependence causes any activity to become inferior if enough individuals perform it, favouring the performance of a diversity of activities in single populations. This principle can apply to resource utilization, response to risk, mating and many other behaviours, providing a general framework for the study of adaptive individual differences within single populations.

Negative density-dependence is a highly intuitive concept and an integral part of some theoretical frameworks, such as the ideal free distribution and evolutionary game theory, but it is lacking from other frameworks. Optimal foraging theory focuses on the behaviour of an individual forager whose prey are characterized by parameters that are held constant (e.g. energy value, handling time, encounter rate, distance between patches). The lack of density-dependent processes in the theory leads to the expectation that there should be a single best way to forage. When we consider the feedback loops that cause populations of foragers to change the parameters of their prey environment, it becomes obvious that multiple foraging strategies can be favoured in a single population, just as multiple mating strategies can be favoured. The study of adaptive individual differences for one subject (foraging) has lagged behind another subject (mating) when both should be studied under a common framework that recognizes the importance of density-dependent processes.

Early theories of speciation also tended to be naive about density-dependent processes. Typically, two incipient species were imagined to come into contact after a period of isolation (e.g. Dobzhansky 1970). Mating within incipient species yields offspring of high fitness, while mating between incipient species yields hybrid offspring of low fitness. If mating is random and one incipient species is more common than the other, the less common will produce mostly (unfit) hybrid offspring and ultimately will go extinct. This is a density-dependent process, but one that eliminates rather than favours diversity. Given these assumptions, many speciation theorists concluded that incipient species cannot coexist long enough to evolve reproductive isolation mechanisms. The entire process of speciation must take place in allopatry (e.g. Paterson 1978, 1980).

A proper understanding of density-dependent processes forces a radical revision of this scenario. Negative density-dependence can allow incipient species to coexist indefinitely, despite random mating and the production of hybrid offspring. Not only can incipient species that diverged in allopatry coexist when they come together, but the initial process of divergence can occur in sympatry. Wilson & Turelli (1986; see, also, Wilson 1989) provide a theoretical example of a polymorphism that remains stable even though the majority of individuals in the population are relatively unfit heterozygotes. Pumpkinseed sunfish appear to provide an empirical example: the morphologically extreme individuals are most fit (as measured by growth rate and lipids), even though the majority of the individuals in the population are morphologically intermediate. Instead of an adaptive mean surrounded by maladaptive variation that is typically imagined for stabilizing selection, the tails of the distribution are adaptive and the mean is maladaptive.

Disruptive selection that is stable in the face of random mating provides a new background for the study of speciation. Early theorists assumed that the long-term coexistence of incipient species would result in the evolution of reproductive isolation, completing the process of speciation. After all, if mating with one's own type produces better offspring than mating with other types, then genes for assortative mating should easily evolve. In retrospect, this expectation seems naive. Reproductive isolation requires not only assortative mating, but complete assortative mating. Choosing mates of variable quality is similar to choosing food items of variable quality (Wilson & Hedrick 1982; Parker, this volume). Even though the best are preferred, the inferior are often accepted when the best are not available. Individuals should evolve to be choosy maters in polymorphic populations, but choosy mating does not necessarily result in the complete assortative mating required for speciation to occur. Ironically, early theorists believed that the first phase of sympatric speciation (the evolution and coexistence of incipient species) was difficult and the second phase (the evolution of reproductive isolation) was straightforward. It now appears that the first phase is relatively straightforward, but the second phase is problematic.

Examples of trophic polymorphisms, similar to those we have documented for bluegill and pumpkinseed sunfish, are accumulating for species of many taxa and may ultimately prove to be more the rule than the exception. However, few if any studies have examined the effects of trophic polymorphisms on the evolution of mating decisions and the degree to which adaptive mate choice results in assortative mating. One possibility is that trophic polymorphisms are extremely common, but require certain mating systems to result in the creation of new species. For example, individuals should be choosiest about the quality of their mate when reproduction involves a large investment of time, energy and risk. Adaptive mate choice might result in extreme assortative mating (speciation) more often in species that practice biparental care than species in which one or both sexes invest little in their offspring. Perhaps this kind of reasoning can explain why trophic polymorphisms remain intraspecific in some taxa and result in multispecies adaptive radiations in others (e.g. cichlid fish; Greenwood 1984).

There is a tendency to be interested in trophic polymorphisms primarily in connection with speciation, but they are equally interesting and important when they remain intraspecific. The bluegill trophic polymorphism that we documented within a single lake may never result in two species, but it has resulted in two ecologically isolated subpopulations that differ by a factor of five in their trematode parasite loads. Any detailed study of the bluegill, their parasites or the lake ecosystem in which they are embedded must take these kinds of individual differences into account.

A general conceptual framework for studying adaptive individual differences within single populations allows seemingly different subjects to be related to each other. It would be hard to imagine two subjects more superficially different than speciation and personality psychology, yet the same basic principles apply to both. Psychologists tend to think of personality in terms of a few domain-general factors that can be regarded as one-dimensional continua of behaviour. An evolutionary perspective leads to a different set of expectations in which individual differences favoured in one context (e.g. reaction to predators) may or may not be adaptive in other contexts and may or may not exist as a one-dimensional continuum of behaviour. The study of personality in non-human species has lagged so far behind other subjects that it still exists mostly in the future. Not only does the general study of adaptive individual differences encourage us to study personality along with foraging and mating behaviour in non-human species, but it encourages us to think differently about our own personalities as well.

This paper reviews research done in collaboration with a number of colleagues, including Anne Clark, Kristine Coleman, Ted Dearstyne and Beren Robinson, all of whom I thank. I also thank the Ecology, Evolution and Behavior group at Binghamton University for stimulating discussions. Finally, I thank Anne Magurran and Sir Robert May for organizing the symposium. The research on trophic polymorphisms was funded by NSF grant # DEB-9212954.

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