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Shy–Bold Continuum in Pumpkinseed Sunfish (*Lepomis gibbosus*): An Ecological Study of a Psychological Trait

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The shy–bold continuum is recognized as a fundamental axis of behavioral variation in humans, but 3 major issues have not been addressed. First, the taxonomic distribution of shyness and boldness is unknown. Second, the ecological consequences of shyness and boldness have not been studied in natural populations. Third, no one has tried to predict and test patterns of shyness and boldness that might result from natural selection. We show that a shy–bold continuum, which influences diet, predator risk, and parasite fauna, exists in juvenile pumpkinseed sunfish (*Lepomis gibbosus*). Individual differences are relatively stable in nature but seem to disappear when the fish are held in social and ecological isolation in the laboratory. Thus, phenotypic stability may not reflect innate tendencies to be shy or bold but rather environmental conditions that maintain differences between phenotypically plastic individuals.

In humans and at least some other species, individual organisms vary along a behavioral continuum from extreme shyness to extreme boldness (for humans, Kagan, 1991; Kagan, Reznick, & Snidman, 1988; Matheny, 1989; Plomin & Dunn, 1986; Thomas & Chess, 1977; for primates, Stevenson-Hinde, Stillwell-Barnes, & Zung, 1980; Suomi, 1983, 1987, 1991; for canids, Bekoff, 1977; Fox, 1972; Goddard & Beilharz, 1985; MacDonald, 1983; for rats, Blanchard, Flannelly, & Blanchard, 1986; Blizard, 1981; Cooper, Schmidt, & Barrett, 1983; for goats, Lyons, Price, & Moberg, 1988). Shy individuals react to unfamiliar situations by retreating or becoming quiet and vigilant. Bold individuals act normally or become actively exploratory in the same situations.

Although psychologists regard the shy–bold continuum as a fundamental axis of behavioral variation, they have not addressed three major issues. First, the ecological consequences of shyness and boldness have never been studied in a natural population of any species. Second, an evolutionary perspective is lacking. The biological basis of shyness and boldness is treated as a central issue, but existing studies focus on heritability, phenotypic stability, and physiological mechanisms. No one has tried to predict and test adaptive patterns of shyness and boldness that might result from natural selection. Third, because research has been confined to humans and a few other mammalian species, the taxonomic distribution of shyness and boldness is largely unknown.

These unresolved issues in the psychological literature are precisely those that behavioral ecologists may be expected to address. Curiously, however, behavioral ecologists have not yet focused on shyness and boldness as an important subject that requires an ecological or evolutionary explanation (Clark & Ehlinger, 1987). In addition, it is important to distinguish behavioral variation within populations from behavioral variation between populations. For example, in some fish species populations that experience different degrees of predation have been shown to differ in their behavioral response to predators in ways that could be interpreted as *shy* and *bold* (for the guppy *Poecilia reticulata,* Fraser & Gilliam, 1987; Magurran & Seghers, 1990; for the stickleback *Gasterosteus aculeatus* L., Giles & Huntingford, 1984; Tulley & Huntingford, 1987a, 1987b; for the minnow *Phoxinus phoxinus,* Magurran, 1986b, 1990). These and other studies explain differences between populations, but they tend to ignore the profound individual differences that can exist within populations (but see Altmann, 1980; Armitage, 1986; Huntingford, 1976; Huntingford & Giles, 1987; Magurran, 1986a, 1986b; Murphy & Pitcher, 1991). Thus, the same gaps that exist in the psychological literature on shyness and boldness also exist in the behavioral ecology literature.

In this article we examine shyness and boldness in populations of juvenile pumpkinseed sunfish. We focus on the following questions: (a) Does a shy–bold continuum exist in juvenile pumpkinseed sunfish? (b) How does shyness and boldness correlate with age, sex, and size? (c) What are the ecological consequences of shyness and boldness? (Possibilities include differences in spatial movement, feeding behavior, growth rate, mortality, and parasite load.) (d) Are individual differences phenotypically stable?

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Method

Subjects

Field work was conducted during 1990 and 1991 at Cornell University's experimental pond facility. The ponds are square shaped, 30 m on each side with a bottom that slopes gradually to 2 m. The littoral zone was dominated by a rather homogenous layer of water milfoil (*Myriophyllum spicatum*). The ponds contained adult and juvenile pumpkinseed sunfish (*Lepomis gibbosus*) and fathead minnows (*Pimephales promelas*). Predators included great blue heron (*Ardea herodias*) and belted kingfisher (*Megaceryle alcyon*). Fish predators, such as largemouth bass (*Micropterus salmoides*) and pike (*Esox lucius*), were absent from the ponds but are common in the nearby natural lakes from which the adult pumpkinseeds in the experimental ponds were obtained. Thus, the juveniles used in this study are derived from populations that evolved in the presence of fish predators.

Novel Object Tests

Psychologists frequently classify humans as shy or bold by monitoring their reaction to a novel object (e.g., Kagan et al., 1988). We used the same criterion to classify juvenile pumpkinseeds by conducting novel object tests in the experimental ponds. The novel objects were cylindrical wire minnow traps (6-mm mesh size, 44 cm long and 23 cm in diameter, with openings 3.5 cm in diameter), placed 1 m from the shore at a depth of approximately 0.5 m for a period of 10 min. Several traps were placed simultaneously at intervals of 6 to 12 m, depending on the experiment (see later description). The maximum distance between a fish along the shore and a trap was 6 m, which is easily within the perceptual range of juvenile pumpkinseed sunfish. The traps contained no bait but nevertheless were approached and entered by many pumpkinseeds, which in anthropomorphic terms can only be described as *curious.*

Immediately after the traps were retrieved, a 30-m seine (3-mm mesh size) was used to capture the fish that did not enter the traps. First, the seine was stretched parallel to the shore and approximately 2 m from the water's edge until it blocked off the section of shoreline that contained the traps. Then the seine was pulled toward the shore, to capture only the fish that had been in close proximity to the traps.

If a shy–bold continuum exists in juvenile pumpkinseeds, the average trapped fish ought to be bolder than the average seined fish, as revealed by subsequent tests. However, the two groups might have differed for other reasons. For example, it is possible that one capture method (presumably seining) was more traumatic than the other and created behavioral differences between groups that did not exist prior to capture. This possibility is addressed in Experiment 1. The two trapping methods may also have sampled different microhabitats, despite the fact that the shoreline habitat looked homogenous to the human observer and despite our effort to restrict sampling to the same section of shore. This possibility is addressed in Experiments 3 and 4.

It is important to emphasize that the novel object test does not completely segregate fish into groups on the basis of their behaviors. For example, fish that approached and explored the traps but did not actually enter are included in the seined sample. Also, the existence of two discrete categories is an artifact of the sampling procedure and says nothing about the distribution of phenotypes along the shy–bold continuum, which is presumably continuous. Nevertheless, if individual differences exist along the shy–bold continuum, they should manifest themselves as statistical differences between the two groups.

Differences Between Trapped and Seined Fish

Four novel object tests were performed, each followed by subsequent tests of differences between groups.

Experiment 1. The main purpose of this experiment was to examine behavioral differences under controlled laboratory conditions. On June 8, 1990, one side of Pond 228 was selected for sampling. Sixty-four pumpkinseeds were captured in three traps spaced at 12-m intervals, and 172 fish were captured by the seine. A randomly selected subset of the trapped fish were then placed in the seine, the seine was folded over to prevent the trapped fish from escaping or new fish from being caught, and the seine was dragged through the water for a period of 30 s (roughly the amount of time required to drag the seine onto the shore during the actual seining operation). These fish were therefore captured in traps but given the additional experience of being seined.

Twenty fish from traps (T), 20 fish from the seine (S), and 20 fish from traps that were given a seined experience (TS) were maintained in 10-gal (37.85-L) aquaria on a metal rack against the wall of a large fish room. Each aquarium was partitioned into five sections with opaque dividers, and each section contained a single fish. The three groups alternated among adjacent sections (e.g., T1, S1, TS1, . . . T20, S20, TS20; the systematic design of Hurlbert, 1984). The remaining fish were first anesthetized and then killed with Tricaine Methanesulfunate (ethyl 3-aminobenzoate methanesulforic acid salt; Aldrich Chemical, No. E1,052–1, Milwaukee, WI) and preserved in 10% buffered formalin. Scales from the preserved fish were taken from a standardized area of the body (between the posterior end of the dorsal fin and the anal fin) and used to estimate growth rate by measuring the width of the outer growth margin in relation to scale size (Doyle, Talbot, & Nicholas, 1987).

Acclimation to the laboratory was monitored by videotaping the fish during feeding. The camera was trained on a single aquarium, a measured amount of floating food pellets was placed in each partition, and the experimenter then left the room for 5 min before returning to repeat the operation on the next aquarium. From the videotapes each fish was scored for the number of seconds that elapsed before feeding during the 5-min interval, hereinafter termed *feeding latency.* If a shy–bold continuum exists for pumpkinseeds, we expected trapped fish to acclimate sooner, on average, than seined fish.

After fish had acclimated to the laboratory, a series of five behavioral tests were run on each individual. The first test was *response to handling.* On Day 25 after capture, fish were fed and videotaped as usual. Each fish was then captured with a small net (for the first time since the beginning of the experiment), handled for approximately 30 s, and returned to its section of the aquarium. The next morning fish were fed and videotaped as usual. Feeding latency before and after the handling event provided an index of stress associated with handling. We expected trapped fish to commence feeding sooner than seined fish. The second test was *Novel Environment Test A.* On Days 47–49, each fish was removed from its partition and placed by itself in a 10-gal (37.85-L) aquarium with a gravel bottom and various objects, such as stones and artificial plants. The typical response was for the fish to remain motionless for a period of time and then to explore the novel environment. The movement of each fish was measured at 1, 5, 10, 15, 20, 25, and 30 min by noting its position against a grid placed on the back of the aquarium for twelve 5-s intervals. We expected trapped fish to begin exploring the novel environment sooner than seined fish. *Novel Environment Test B* was the third test. On Days 86–88, we withheld food for 24 hr from all 20 seined fish and 20 of the trapped fish but fed the remaining 20 trapped fish according to the regular schedule. We then repeated the novel environment test. We expected hungry trapped fish to explore the environment sooner than satiated trapped fish and the difference between hungry trapped and hungry seined fish to be greater than the difference between two groups of satiated fish in Test A. In the fourth test we measured *stress and respiration rate.* Several studies of humans and mammals have established a relation between behavioral measures of shyness–boldness and physiological measures, such as heart-rate response during mildly stressful experiences (Fox, 1972; Gunnar, 1987; Kagan, Reznick, & Gibbons, 1989; Kagan, Reznick, & Snidman, 1987). In fish the opercula open and close rhythmically to pump water past the gills at a rate that correlates with heart rate (Shelton, 1970). On Days 61–64, we placed fish in a small Plexiglas container (a mildly stressful experience), videotaped them at close range for 30 min, and measured opercular pumping rate at 3-min intervals. The typical response was for pumping rate to start high and decline to a plateau during the course of the test. We expected trapped fish to reach their plateau more quickly than seined fish. The last test measured *social interactions.* On Day 96, aquaria were divided by opaque partitions into three sections. One trapped fish and one seined fish ($N = 19$ pairs), matched for both standard length and weight, were introduced into each section. Aggressive (chases and nips) and submissive (avoidance) interactions were recorded immediately after the introduction and again after 5 days, by which time one member of each pair was clearly dominant. We tentatively expected seined fish to dominate trapped fish (see Discussion for our rationale) but also envisioned scenarios that might lead to the opposite situation (see Fox, 1972; Huntingford, 1976).

After the behavioral tests the fish were anesthetized and killed with Tricaine Methanesulfunate, measured (standard length in millimeters), sexed by dissection, and aged by counting the annuli of scales collected from between the posterior end of the dorsal fin and the anal fin. Although determination of age from scale annuli can be difficult for older fish, it is straightforward for juvenile sunfish (Osenberg, Werner, Mittelbach, & Hall, 1988; Tesch, 1968). Finally, each fish was examined for parasites. Livers, hearts, and gonads were pressed between two microscope slides and examined at low power under a compound microscope to count cysts of two internal parasites, white grub (*Posthodiplostomum minimum centrarchi*) and bass tapeworm (*Proteocephalus ambloplitis*). The entire body was examined for blackspot (*Neascus* spp.), which encysts subcutaneously, and yellow grub (*Clinostomum* spp.), which encysts in muscle tissue.

Experiment 2. The main purpose of this experiment was to examine the diets of trapped and seined fish. On July 4, 1990, a second side of Pond 228 was sampled under the same procedure that was described for Experiment 1. Twenty-five trapped fish and 25 seined fish were immediately killed in Tricaine Methanesulfunate for gut content analysis. Stomachs were removed and preserved in 70% ethanol. Stomach contents were placed in a 6-cm plastic petri dish with 1-cm grid marks scratched on the bottom. All recognizable prey items were counted under a dissecting microscope and grouped into major taxa (see Table 1). Blackspot cysts were also counted to confirm the results of Experiment 1. Other parasites were not counted because they are difficult to detect in preserved specimens.

Experiment 3. The main purpose of this experiment was to observe trapped and seined fish in their natural habitat. On July 29, 1991, 25 traps were placed around all four sides of Pond 233 at intervals of approximately 6 m. Numbered flags were placed at 3-m intervals around the pond to identify spatial location. After the traps were retrieved, the east and west sides of the pond were simultaneously seined. These sides provided a sufficient number of fish for the experiment, and the other two sides were not seined. A total of 196 trapped fish and 215 seined fish between 40 and 50 mm in standard length were measured and marked with a 2-mm circular numbered tag threaded onto colored rubber thread that was passed through the dorsal musculature just anterior to the dorsal fin and tied into a loop. This is a common marking technique for larger fish that we have miniaturized for use with small fish. Fish could be identified through binoculars as trapped or seined by the color of the thread and could be individually identified in hand by the number on the tag. An additional sample of 64 trapped and 64 seined fish were measured and weighed to calculate a condition index (Schreck & Moyle, 1990).

The fish were released on all four sides of the pond, without respect to their capture location, within 5 hr of their removal. The fish were then visually censused on Days 2, 4, 9, 15, 18, 30, and 32 after capture. The observer walked slowly around the pond, approximately 3 m from the water's edge, scanning the shallow water with binoculars for marked fish. Sightings were reported to a second person who recorded the color of the thread and the flag nearest the observer. Care was taken to record the fish as they were sighted; for example, if the observer was walking from left to right and came upon 3 marked fish, they were recorded in left-to-right order. If 2 or more marked fish were within three body lengths of each other, they were noted as an *aggregation.* Some censuses were hampered by wind conditions, and the windward (east) side of the pond could not be observed on Days 2 and 9. On Day 36, all four sides of the pond were seined, and 69 marked fish were captured and identified by their numbered tags and remeasured to estimate growth rate.

Experiment 4. On Sept 4, 1991, Experiment 3 was repeated in Pond 233 with the following modifications. Three sides of the pond were both trapped and seined. An effort was made to record the location of capture for seined fish, as well as trapped fish, by placing a line of buckets along the shore and putting fish from the seines into the nearest bucket. Thirty-two trapped fish and 32 seined fish were marked with three colored beads rather than numbered tags, which allowed individual fish to be identified from a distance. Fish from all three sides were released at a single location on the fourth side. Fish were censused on Days 2, 8, 9, 11, 13, 15, 22, 25, 27, 29, 31, and 34. Censuses were made both from the shore with binoculars and from the water with a mask and snorkel. For observations from the water, an observer swam a transect along the shore, recorded the identify of each fish on a waterproof writing tablet, and then lifted his or her head above the water to record the nearest flag on the shore.

Statistical procedures. Comparisons of the trapped and seined groups are complicated by two factors. First, standard statistics are designed for comparing samples from two large, independent populations, whereas our seined samples are biased by the prior removal of the trapped fish from a relatively small population. We therefore compared results from standard statistical tests with a randomization test in which differences between groups of size n_1 and n_2 were compared to a distribution that was generated by randomly allocating individuals into groups of size n_1 and n_2 1000 times (Sokal & Rohlf, 1981, pp. 791–795). The results were virtually identical to the results of standard tests so only the latter are reported here. Second, it is difficult to determine appropriate significance levels when multiple statistical comparisons are made; for example, with 20 comparisons, at least one seemingly significant result at the $\alpha = .05$ level is expected by chance alone. We therefore used the Bonferroni inequality test (Neter, Wasserman, & Kutner, 1985; O'Brien, 1984), which sets the significance level to $\alpha \div m$, where m is the number of comparisons. Thus, if $\alpha = .05$ and $m = 20$, a probability of $p < .0025$ is required to declare a result significant. If anything, the Bonferroni inequality test is too conservative because it assumes that the multiple variables that are compared are uncorrelated with each other (Manly, McAlevey, & Stevens, 1986). SYSTAT (Wilkinson, 1989) was used for all analyses except the randomization test, which we programmed ourselves.

Results

Results are organized conceptually, rather than chronologically, to clarify the objectives of the research. For example, growth rates are estimated by different methods in Experiments 1 and 3. These are presented together in a section entitled *Growth Rates,* rather than separately in sections for Experiment 1 and Experiment 3.

Age, Sex, and Size

Experiment 1 provided the most complete information on age, sex, and size composition. Excluding seined fish that were too large to enter the opening of the minnow traps, the size distributions of trapped and seined fish were virtually identical ($M \pm SD$ = 37.43 ± 2.25 mm vs. 37.39 ± 2.04 mm respectively). Scale annuli revealed that all fish belonged to the same cohort that was born the previous year. The sex ratio of both groups was close to 1:1; 50% of 40 trapped fish and 45% of 20 seined fish were male. Thus, behavioral differences between trapped and seined fish cannot be explained by size, age, or sex.

Effect of Seining Experience

No significant differences existed between the trapped only and trapped and seined groups in Experiment 1 (Mann-Whitney U tests for one acclimation and five postacclimation tests, $n_T = 20$ and $n_{TS} = 20$, $183 < U < 233$, $.247 < p < .780$). Differences between trapped and seined fish can therefore be attributed to differences before capture and not to the effects of the trapping method per se.

Spatial Distributions in the Field

Experiments 3 and 4 demonstrated, unexpectedly, that the juvenile pumpkinseeds were strongly site specific and returned to their home range when displaced. Seined fish were virtually always sighted on the two sides of the pond that were originally seined, despite the fact that they were released on all four sides of the pond (94% of 171 sightings). (Comparable observations could not be made for trapped fish because they were captured from all four sides of the pond.) At the end of Experiment 3, 76% of 21 trapped fish and 85% of 34 seined fish were recaptured on the same side of the pond from which they were originally captured. Experiment 4, which allowed us to identify individual fish from a distance, revealed that 82% of 50 trapped fish and 85% of 26 seined fish were sighted within 9 m of their capture site (this analysis was restricted to observations from the water to maximize probability of correct identification). In both experiments trapped and seined fish did not differ significantly in their site specificity, $\chi^2(1, N = 55) = 0.723$, *ns,* for Experiment 3, and $\chi^2(1, N = 76) = 0.083$, *ns,* for Experiment 4, respectively.

The spatial distribution of trapped and seined fish along the shoreline was analyzed by treating each census in Experiment 3 as a linear string of data (e.g., T-T-S-S-S-T-S-T . . .) representing the order of trapped and seined fish sighted as the observer worked his or her way down the shore. If trapped and seined fish are spatially segregated, either because of social interactions or preferences for microhabitats not obvious to the human observer, trapped and seined fish ought to be nonrandomly distributed along the string. Accordingly, a Wald-Wolfowitz runs test was performed for each census. Analysis was restricted to the east and west sides of the pond (because seined fish were virtually absent from the other two sides), and each side was analyzed separately. Only censuses that included more than 15 fish were included, and this led to a total of eight tests. One test was significant at the $p = .001$ level (and exceeded the Bonferroni inequality test's significance level of $p < .0063$), but the others were far from significant ($.098 < p < .985$), which suggests that on most days the trapped and seined fish were randomly distributed along the shoreline with respect to each other. Segregation into social groups was also examined by restricting analysis to the aggregations. The average trapped and seined fish experienced the same relative frequency of trapped and seined neighbors in its aggregation, which shows that the two types were randomly distributed among aggregations, $t(66) = 0.471$, $p = .651$.

Finally, marked fish were never observed in the interior of the pond, although unmarked juvenile pumpkinseeds were common. These results demonstrate that trapped and seined fish were drawn from the same population of fish that restricted their movements to a particular section of shore. If differences exist between trapped and seined fish, it is not because they were drawn from different sections of the pond or from different microhabitats but because of differences in their behavioral response to a novel object (the trap).

Behavioral Differences in the Pond

Although trapped and seined fish in aggregations were randomly distributed with respect to each other, they may still have had different tendencies to join aggregations. This possibility was examined in Experiment 3 by calculating the proportion of sightings of trapped and seined fish that were in aggregations. The east and west sides of the pond were analyzed separately to maximize the homogeneity of the samples. For the west side, 54% of 76 sightings of seined fish were in aggregations, compared with 24% of 108 sightings of trapped fish, $\chi^2(1, N = 184) = 10.900$, $p < .009$. For the east side, 21% of 95 sightings of seined fish were in aggregations, compared with only 2% of 56 sightings of trapped fish, $\chi^2(1, N = 151) = 9.400$, $p < .005$. Thus, fish that were apt to enter traps also appear likely to forage at greater distances from other fish.

In Experiment 4, the ratio of trapped to seined fish sighted from the shore with binoculars was 43:31, which is not significantly different from 1:1, $\chi^2(1, N = 74) = 1.940$, *ns.* The ratio of trapped to seined fish sighted from the water was 52:25, which is biased toward trapped fish, $\chi^2(1, N = 77) = 9.40$, $p < .005$. Thus, fish that were apt to enter traps were also attracted to, or less inclined to flee from, a human observer in the water.

Table 1
Prey Items in the Stomachs of Fish Captured by Traps (n = 25) and Seine (n = 25)

	Trapped	Seined	
Prey	*M* ± *SD*	*M* ± *SD*	*p*
Copepods	50.75 ± 41.75	17.31 ± 18.73	.000
Cladocerans	3.32 ± 4.12	4.65 ± 8.54	.825
Ostracods	4.21 ± 5.38	4.50 ± 5.14	.827
Chironomids	6.57 ± 8.38	8.42 ± 10.24	.578
Mites	1.61 ± 2.90	1.00 ± 2.43	.226
Snails	0.61 ± 1.32	1.27 ± 1.99	.112
Terrestrial insects	0.50 ± 0.92	1.81 ± 4.28	.138

Note. Significance values are from Mann-Whitney *U* tests.

Stomach Contents

Table 1 shows the major categories of prey items found in the pumpkinseed stomachs. Trapped fish had ingested over three times more copepods than seined fish before capture (Mann-Whitney *U* test, $n_T = 28$ and $n_S = 26$, $U = 588$, $p < .0001$, which exceeds the Bonferroni inequality test's significance value of $p < .0071$). All other prey categories were consumed equally by both groups ($290 < U < 423$, $.266 < p < .939$).

Growth Rate

No differences in growth rate, measured as the width of the outer growth margin of scales, were observed in Experiment 1 (analysis of covariance with scale radius as covariate), $F(1, 44) = 1.327$, $p = .256$. In Experiment 3, no differences in weight were observed when length was held constant (the condition index; analysis of covariance with length as a covariate), $F(1, 117) = 0.063$, $p = .803$. Direct estimates of growth rates in Experiment 3 revealed no differences between trapped and seined fish, $t(54) = 0.647$, $p = .521$. In fact, neither group increased in standard length during the course of the experiment, which suggests that the pumpkinseed population in Pond 233 was food limited. Other studies of juvenile pumpkinseeds have demonstrated measurable growth within 1 month (e.g., Mittelbach, 1988)

Mortality

Although mortality can theoretically be estimated from the census and recapture data of Experiment 3, a variety of practical problems intervene. The proportion of the original marked population of 411 fish that was actually counted during a given census varied from .04 to .55. Fish were easily concealed by vegetation, and riffles from wind made observations much harder on some days than others. The number of censused fish did not decline systematically during the course of the experiment, nor did the number of trapped fish decline in relation to the number of seined fish. On the other hand, only 21 trapped fish and 44 seined fish were recaptured on Day 36. The total of 55 fish represents 16% of the original marked population and is significantly biased toward seined fish, $\chi^2(1, N = 65) = 6.170$, $p < .05$. This may reflect differential mortality toward the end of the experiment but may also reflect other factors, especially because the trapped and seined fish were not distributed equally around the four sides of the pond. Mortality therefore cannot be reliably estimated from Experiment 3.

Parasites

From Experiment 1, three genera of parasites, blackspot, white grub, and yellow grub, were sufficiently common to allow comparison between groups (see Table 2). All are digenetic trematodes that use snails as their first host, enter the fish by direct contact through the skin, and complete their life cycle in fish-eating birds (Hoffman, 1967). Blackspot were over twice as abundant in trapped fish (t test with log-transformed data to equalize variance), $t(58) = 4.330$, $p < .001$; white grub were over twice as abundant in seined fish, $t(58) = 3.407$, $p < .001$; and yellow grub were equally abundant in both groups, $t(58) = 0.574$, $p = .568$ (Bonferroni criterion of $p < .016$).

Acclimation to the Laboratory

Because no significant differences existed between the trapped only and trapped and seined groups, they were lumped into a single group of 40 trapped fish for comparison with the seined only group. Figure 1 shows the proportion of fish that fed during the 5-min period (*y* axis) as a function time after capture (*x* axis) in Experiment 1. Trapped fish acclimated more readily to the laboratory. The proportion of trapped fish that fed exceeded the proportion of seined fish for Days 6–15 after capture (seven chi-square tests; $2.970 < \chi^2 < 5.680$, $.005 < p < .042$). The same results can be expressed another way by regarding each fish as acclimated when it fed during the 5-min interval for 2 days in succession. By this measure the average trapped fish acclimated to the laboratory 5 days sooner than the average seined fish ($M \pm SD = 11.75 \pm 5.41$ for trapped fish vs. 16.30 ± 6.48 for seined fish; Mann-Whitney *U* test, $n_T = 40$ and $n_S = 20$, $U = 226$, $p = .006$).

Postacclimation Behavior

No differences were detected between the trapped and seined groups for any of the postacclimation tests. Trapped fish did not recover sooner from the experience of being handled (Mann-Whitney *U* test, $n_T = 40$ and $n_S = 20$, $U =$

Table 2
Parasite Faunas of Fish Captured in Traps in Seines

	Trapped	Seined	
Parasite	*M* ± *SD*	*M* ± *SD*	*p*
Blackspot	12.82 ± 6.40	5.66 ± 3.50	.001
White grub	7.84 ± 7.93	16.33 ± 11.20	.01
Yellow grub	6.76 ± 5.66	6.33 ± 6.27	.568

Note. Significance values are from *t* tests with log-transformed data to equalize variance.

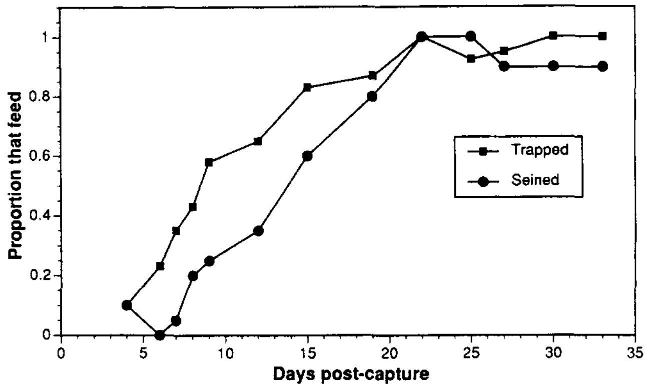

Figure 1. The proportion of fish captured by traps or by a a seine that fed during 5-min feeding trials.

457, $p = .365$), did not explore novel environments more readily (Test A and Test B; Mann-Whitney *U* tests for six time intervals per test, $n_T = 40$ and $n_S = 20$, $337 < U < 496$, $.105 < p < .956$), did not respond to stress with a lower opercular pumping rate (Mann-Whitney *U* tests for eight time intervals, $349 < U < 413$, $.309 < p < .838$), and were equally likely to be dominant or subordinant in social interactions, $\chi^2(1, N = 38) = 1.778, p = .182$. These results do not even approach significance for single comparisons, much less the Bonferroni inequality tests for multiple comparisons.

The first novel environment test (Test A) provides an example of our negative results (Figure 2). When trapped and seined fish were analyzed as a single group, the results showed that the fish gradually increased their movements during the first 10 min of the 25-min period, $t(57) = 3.751$, $p < .001$, for 0 min vs. 5 min, and $t(57) = 2.77$, $p < .01$, for 5 min vs. 10 min. However, trapped fish did not respond more quickly than seined fish, despite the fact that they acclimated more quickly to laboratory conditions.

It is important to remember that the categories *trapped* and *seined* cannot be equated directly with *bold* and *shy*. The seined sample in particular ought to contain a mixture of shy and bold fish, including fish that approached the traps but did not enter them during the original novel object test. The acclimation date of individual fish may therefore provide a better index of shyness and boldness than the status of trapped or seined. Accordingly, for each postacclimation test we used acclimation date as the independent variable in a linear regression. The squared correlation values ranged from 0 to .130 and in all cases were nonsignificant in comparison with the Bonferroni inequality test. Thus, individual differences that are highly significant in the field and during the acclimation process seem to disappear after a period of social and ecological isolation in the laboratory.

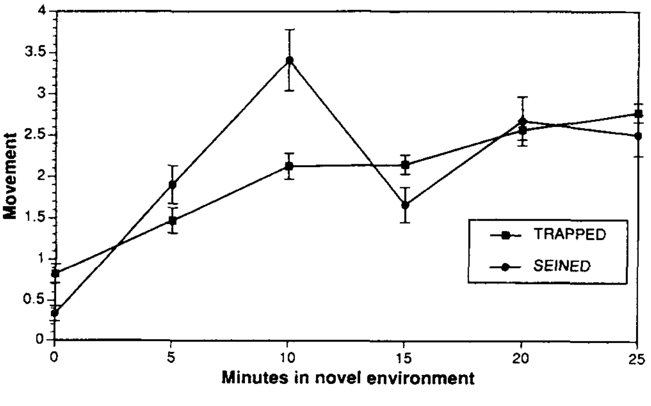

Figure 2. Movement (in grid units) in a novel environment as a function of time spent in the novel environment. (Vertical bars represent the standard errors.)

Discussion

Although everyone that works with animals knows that they have different personalities, the nature of individual differences in a population has seldom been the focus of study, at least compared with differences between species and between populations of the same species (Clark & Ehlinger, 1987; Magurran, 1986a; Slater, 1981). Two factors contribute to this neglect. First, phenotypic variation is ubiquitous in populations, as it must be if natural selection is to operate. Individual differences per se therefore do not seem to require a special explanation. Second, optimization models usually predict a single optimal behavior for a particular set of assumptions about the organism and the environment. Empirical tests of optimization models almost always compare the averaged behavior of a population to the model's predictions and offer no explanation for variation around the average (e.g., Table 9.1 in Stephens & Krebs, 1986). The implicit assumption is that all individuals of the same size, age, sex, and state (in dynamic models) behave in the same way and that deviations from the optimum can be attributed to various forms of error or perhaps to nonadaptive genetic variation that is continually produced by recombination and reduced by stabilizing selection (Mangel, 1991).

More recently, the nature of individual differences in populations has emerged as an object of study in its own right (e.g., Altmann, 1980; Armitage, 1986; Bruton, 1989; Colgan, Gotceitas, & Frame, 1991; Francis, 1990; Gotceitas & Colgan, 1988; Maynard Smith, 1982; Rosenzweig, 1991; Wilson, 1989). The most striking examples involve behavioral, morphological, and life history differences among males that constitute alternative strategies for mating with females (reviewed for fish by Turner, 1986). In these and other studies, individual differences are interpreted not as the raw material on which natural selection acts but as the end product of natural selection. This represents a fundamental shift in thinking because the averaged behavior of the population becomes meaningless and individual differences become the essence.

This shift in thinking has, however, proceeded unevenly. The focus on alternative strategies that has become common in studies of male mating behavior, for example, remains rare in studies of foraging behavior and predator avoidance (but see Brodie, 1989; Burghardt, 1974; Colgan et al., 1991; Gotceitas & Colgan, 1988; Herzog & Burghardt, 1988; Huntingford & Giles, 1987; Robinson, Wilson, Margosian, & Lotito, in press; Smith, 1990; Wilson, 1989). In addition, the interpretation of discrete forms (such as male mating types) has seldom been extended to continuous phenotypic distributions (such as shyness and boldness). We think that adaptive individual differences—continuous or discrete—must be expected in many contexts and often cut across the categories of age, size, and sex traditionally recognized as important by behavioral ecologists. One likely candidate is shyness and boldness, which has already been recognized as an important behavioral continuum by psychologists.

Our study begins to address three major questions about the shy–bold continuum in natural populations.

Does a Shy–Bold Continuum Exist in Juvenile Pumpkinseed Sunfish?

Fish that were quick to explore a novel object (a trap) in their natural habitat also differed behaviorally in three other ways. First, they were less likely to swim in close proximity to other fish; second, they were more likely to approach (or less likely to flee from) a human observer in the water; and third, they acclimated more quickly to a novel environment (the laboratory). All of these differences indicate a degree of fearlessness, as compared with the seined group. For example, small fish are well known to respond to perceived danger by staying close to conspecifics (reviewed by Lima & Dill, 1990; Pitcher, 1986).

These differences are especially impressive because the novel object test did not completely segregate fish into groups on the basis of their behaviors; for example, fish that approached and explored the traps but did not actually enter them were included in the seined sample. The differences between bold and shy fish are therefore presumably more extreme than the average difference between fish that are trapped and seined.

Behavioral differences between trapped and seined fish are unlikely to be caused by the sampling process itself or an artifact of sampling different microhabitats within the pond. Both groups were derived from a sedentary shoreline population occupying a rather homogenous physical environment. Even if habitat segregation had been observed, it would not necessarily imply the absence of a shy–bold continuum. Habitat segregation caused by behavioral differences is at least as plausible as behavioral differences caused by habitat segregation. Clearly, the primary difference between trapped and seined fish in our study is a difference in behavioral disposition that causes some to approach a novel object and others to avoid it.

What Are the Ecological Correlates of Shyness and Boldness?

Fish that were trapped and seined in the same location and that were identical with respect to age, size, and sex nevertheless differed by a factor of three in the number of copepods eaten before capture and by a factor of two in the number of specific parasites acquired over a longer time interval. These differences suggest that a fish's position on the shy–bold continuum has important ecological consequences. The precise interpretation of the consequences, however, is not obvious. At this point it is useful to review a number of ecological scenarios that may contribute to a shy–bold continuum in nature.

Trade-off between foraging success and risk of predation. In many species the best places to find food and the most efficient behaviors for capturing food are also most dangerous for the forager (Gilliam & Fraser 1987; Godin & Smith, 1988; Metcalfe, Huntingford, & Thorpe, 1987; Milinski, 1986; Mittelbach, 1981; Werner & Hall, 1988). Theoretical models on this subject often predict a single optimal solution to the trade-off, which all individuals of a given size are expected to follow (e.g., Werner & Gilliam, 1984). However, it is easy to envision situations that would promote a spectrum of risk-prone (i.e., bold) and risk-averse (i.e., shy) individuals. For example, consider a range of foraging tactics that can be characterized by energy return and risk of predation. Consumers initially choose the safest, most productive tactic, but their own foraging depletes the resources. As consumer density increases, fitness associated with the safe-but-overused tactics eventually equilibrates with fitness associated with risky-but-unused tactics. This scenario includes the frequency- and density-dependent processes that can balance the fitness of phenotypically different individuals (Fretwell & Lucas, 1970; Rosenzweig, 1991; Slatkin, 1978; Wilson, 1989; Wilson & Turelli, 1986).

Although our results do not provide solid evidence for this scenario, they are broadly consistent with it. Resource depletion is well documented for sunfish in small ponds (Werner & Mittelbach, 1981). The low growth rate in Experiment 3 and the high frequency of ingested copepods in Experiment 2 suggests that more vulnerable prey, such as *Daphnia*, have been overexploited. Copepods are encountered primarily in the water column, and their capture probably increases exposure to piscivorous birds and fish. Finally, the fact that trapped fish are observed less often in clusters suggests that they are accepting a higher risk, presumably for higher foraging returns. On the other hand, differences in growth rate that are expected from this scenario were not observed.

Social interactions. Many studies have shown that fish take greater risks to obtain food when they are hungry than when they are well fed (reviewed by Lima & Dill, 1990). Social interactions can create a dominance hierarchy in which some individuals have more access to resources than others. If subordinant individuals are hungrier, they may be more likely to investigate novel objects and forage in novel environments. Our results conflict with this scenario in several ways. Trapped fish are not in poorer condition and, if anything, have a higher overall feeding rate than seined fish. Body size is an important determinant of dominance, yet trapped and seined fish are similar in size. Trapping method had no effect on dominance in the postacclimation experiment. Finally, despite the fact that pumpkinseed sunfish readily form dominance hierarchies in aquaria (Beacham, 1988; Dugatkin & Ohlsen, 1990), members of natural populations engage much less frequently in aggressive interactions (Coleman & Wilson, 1993), and the importance of dominance is unclear.

Although this scenario equates boldness with social subordinance, an equally plausible scenario equates boldness with social dominance. For example, Huntingford (1976) showed that the most aggressive sticklebacks in social interactions also were most fearless toward predators (see also Fox, 1972, for wolves). Clearly, more empirical work is required to understand the interplay, if any, between social interactions and the shy–bold continuum in juvenile pumpkinseeds.

Manipulation by parasites. Several studies have shown that sticklebacks parasitized by the cestode *Schistocephalus solidus* recover from frightening stimuli more quickly than nonparasitized sticklebacks (Giles, 1983, 1987; Godin & Sproul, 1988; Milinski, 1984, 1985). The infected fish may simply have been hungrier, because their body cavities were often filled with the parasite. Alternatively, the parasites may have evolved to manipulate the behavior of their fish host to facilitate transmission to their next host (fish-eating birds). In either case, parasites can plausibly increase their host's boldness, as operationally defined.

Our results do not fit easily into this scenario. All three common species of parasites in our study have the same basic life cycle, which includes fish-eating birds as the final host. All would presumably benefit in the same way by emboldening their host, yet only blackspot were more abundant in trapped fish, and white grub were significantly less abundant. Blackspot cercariae encyst close to the skin and appear less likely to alter host behavior, directly or indirectly, than white grub that encyst primarily in the liver or yellow grub that can encyst close to the brain. If parasites directly manipulate the behavior of their host, we ought to have continued to observe differences in the postacclimation tests. With respect to the fish's hunger, infestations of all three species combined were negligible compared with those of *Schistocephalus solidus,* whose combined mass sometimes even exceeded the body weight of their stickleback hosts.

We suggest that the causal relation between parasites and host behavior may be reversed: Rather than parasites altering the behavior of their hosts, pumpkinseeds that vary along the shy–bold continuum may interact with their environment in different ways that influence their acquisition of parasites. For example, exploratory fish may encounter more cercariae than do sedentary ones (Poulin, Rau, & Curtis, 1991). The stickleback studies did not consider this possibility but merely assumed that behavioral differences between parasitized and unparasitized fish were caused by the parasites. Of course, without additional information, neither scenario can explain the strong associations observed between shyness–boldness and parasite fauna.

These multiple scenarios show that individual differences along the shy–bold continuum can plausibly be influenced by a large number of factors. The main purpose of this article is to document the basic phenomenon and a broad spectrum of ecological correlates. Obviously, our study does not rigorously exclude or support any of the scenarios that we outline and merely serves as an initial survey of possibilities.

Are Phenotypic Differences Stable, and If So, Are They Caused by Innate Differences?

Psychologists are very interested in the possibility that shyness and boldness have a biological basis (i.e., a heritable component). Phenotypic stability is often used as evidence for innateness. For example, Kagan et al. (1988) argued for a biological basis because children who occupy the extremes of the shy–bold continuum at 2 years of age differ significantly from each other at 7 years of age. Phenotypic stability of traits related to shyness and boldness has also been demonstrated for nonhuman species (e.g., Colgan et al., 1991; Gotceitas & Colgan, 1988; Huntingford, 1976; Lyons et al., 1988; MacDonald, 1983).

Behavioral differences between trapped and seined pumpkinseeds persisted for the duration of the field experiments (approximately 30 days). In addition, behavioral differences presumably extended far enough into the past for the trapped and seined fish to accumulate different parasite faunas. Shyness and boldness therefore appear to be phenotypically stable in nature. Contrary to our own expectations, however, behavioral differences seem to disappear after a period of social and ecological isolation in the laboratory.

These results can be interpreted in two ways. First, despite the negative results of our postacclimation experiments, it is still possible that shyness and boldness reflect innate temperaments of organisms that can be revealed by additional behavioral tests. Suomi (1983, 1987) has made the point that shyness and boldness are best revealed by intermediate levels of stress. Our own acclimation data provide a good example; trapped and seined fish did not differ at the beginning, when all fish were highly stressed, or at the end, when all were familiar with their new setting, but only during an intermediate period. Perhaps our postacclimation tests failed to elicit the degree of stress required to reveal innate differences.

Alternatively, it is possible that phenotypic stability in natural populations is caused less by innate individual differences than by ecological and social forces that create and maintain differences among phenotypically plastic individuals (e.g., MacDonald, 1983). For example, in the frequency-dependent scenario that we outline earlier, some phenotypically plastic individuals may become shy, and others may become bold. These individuals have little opportunity to change their phenotypes as long as ecological conditions remained stable. However, when individuals are removed from their natural environment and placed in the laboratory, individual differences may well disappear along with the ecological factors that caused them. More generally, the assumption that phenotypic stability implies innate differences between individuals is questionable. Environmental factors can reinforce differences between flexible individuals as easily as erasing them.

The question of genetic polymorphism versus phenotypic plasticity is a general issue that extends beyond the specific subject of shyness and boldness. Evolutionary models make it clear that both can be favored as mechanisms for the production of phenotypic diversity, either alone or in combination, depending on details of the external environment (e.g., Lively 1986; Stearns, 1989; Wilson & Yoshimura, 1993).

Thus, even if innate differences in shyness–boldness are not found in juvenile pumpkinseeds, they may still exist in other species, including humans.

Our study suggests that the shy–bold continuum is an important axis of behavioral variation that deserves more attention from behavioral ecologists. In addition, behavioral ecologists can provide a naturalistic context for a trait that has long fascinated human psychologists.

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Call for Nominations

The Publications and Communications Board has opened nominations for the editorships of *Behavioral Neuroscience*, the *Journal of Experimental Psychology: General*, and the *Journal of Experimental Psychology: Learning, Memory, and Cognition* for the years 1996–2001. Larry R. Squire, PhD, Earl Hunt, PhD, and Keith Rayner, PhD, respectively, are the incumbent editors. Candidates must be members of APA and should be available to start receiving manuscripts in early 1995 to prepare for issues published in 1996. Please note that the P&C Board encourages participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. To nominate candidates, prepare a statement of one page or less in support of each candidate.

- For *Behavioral Neuroscience*, submit nominations to J. Bruce Overmier, PhD, Elliott Hall—Psychology, University of Minnesota, 75 East River Road, Minneapolis, MN 55455 or to overmier@vx.cis.umn.edu.

- For the *Journal of Experimental Psychology: General*, submit nominations to Howard E. Egeth, PhD, Chair, *JEP: General* Search, Department of Psychology, Johns Hopkins University, Charles & 34th Streets, Baltimore, MD 21218, to egeth@jhuvm.bitnet, or to fax number 410-516-4478.

- For the *Journal of Experimental Psychology: Learning, Memory, and Cognition*, submit nominations to Donna M. Gelfand, PhD, Dean, Social and Behavioral Science, 205 Osh, University of Utah, Salt Lake City, UT 84112-1102 or to fax number 801-585-5081.

Names of members of the search committees will be printed in late fall and early winter issues of the journals and in the *APA Monitor*. First review of nominations will begin December 15, 1993.