

Correlation between boldness and body mass in natural populations of the poeciliid *Brachyrhaphis episcopi*

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(Received 29 January 2007, Accepted 22 June 2007)

The boldness of individual *Brachyrhaphis episcopi*, collected from regions of high and low predation, was investigated using two independent assays: (1) the time to emerge from cover and (2) the propensity to leave shoal mates and investigate a novel object. A strong correlation between the two assays was revealed such that fish that emerged from shelter sooner were also more likely to approach a novel object. This is indicative of a boldness personality axis acting across both behavioural contexts. Fish from high-predation areas were bolder than those from low-predation areas and males were bolder than females. A significant correlation between body mass, standard length (L_S) and boldness score was also found. In general, bold fish had a greater body mass at a given L_S than shy fish. These results suggest that personality traits are strongly influenced by population-specific ecological variables and may have fitness consequences in wild populations.

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Key words: boldness; fitness; personality; poeciliids; predation pressure.

INTRODUCTION

In recent years, there has been growing interest in personality traits exhibited in animals, and a number of these studies have focused on personality traits in fishes (Huntingford, 1976; Bell, 2005; Brown *et al.*, 2005a). Personality traits are expected to be relatively stable over time and across a variety of different contexts but are susceptible to change through life experiences. Recent evidence emerging from studies conducted on animals ranging from invertebrates to primates suggest that personality traits widely exist across the Animal Kingdom, and it has been proposed that they will have profound ecological and evolutionary consequences (Wilson *et al.*, 1994; Gosling, 2001; Reale & Festa-Bianchet, 2003; Dingemanse *et al.*, 2004; Sih *et al.*, 2004). Until recently, many behavioural ecologists assumed that variation in individual behavioural traits was indicative of random scatter around a locally adaptive average behavioural

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phenotype (Dall *et al.*, 2004). An alternative view is supported, which suggests that some of this variation represents different, adaptive behavioural strategies influenced by underlying personality traits (Wilson, 1998).

One of the commonly considered dimensions of personality is the shy–bold continuum. The terms shy and bold refer to the propensity to take risks, especially in novel situations. Shy individuals react to novelty by retreating, reducing activity levels and becoming more vigilant (similar to symptoms of mild stress), whereas bold individuals are more likely to approach novel objects, increase activity levels and exploratory behaviour. The shy–bold behavioural continuum tends to cut across demographic variance in behaviour although each demographic category (*e.g.* males or females and young or old) may display different levels of shyness and boldness (Wilson *et al.*, 1994). An individual's position on the boldness–shyness continuum is determined both by its experiences during ontogeny as well as an underlying heritable component (van Oers *et al.*, 2004; Sinn *et al.*, 2006; Brown *et al.*, 2007) and is likely to be under strong selective pressure, the magnitude of which is likely to vary between habitats (Huntingford, 1976; Brown *et al.*, 2005a).

Comprehensive studies examining whether personality traits affect the fitness of individuals in wild populations have been conducted in very few organisms (Wilson *et al.*, 1993; Armitage & Van Vuren, 2003; Dingemanse *et al.*, 2004). These, and additional laboratory-based studies, indicate that individual variation in boldness can have potential fitness consequences by influencing mate choice, parental care, reproductive success, dispersal, anti-predator behaviour, invasion or colonization ability and speciation potential (Godin & Davis, 1995; Godin & Dugatkin, 1996; Budaev *et al.*, 1999; Reale *et al.*, 2000; Fraser *et al.*, 2004; Martin & Fitzgerald, 2005). Bold pumpkinseed *Lepomis gibbosus* (L.), for example, are more likely to forage in open waters, away from cover and hence their diet and parasite load differs from shy fish (Wilson *et al.*, 1993). Studies examining the fitness consequences of expressing different personality traits in a range of habitats, however, have rarely been conducted and some personality types would probably be better suited to a given environment than others.

It may well be that individual differences in personality traits represent adaptive patterns of behaviour that have arisen through natural selection in response to varying environmental conditions. The manner in which individuals assess risk appears to vary between populations with individuals from various environmental backgrounds willing to accept varying amounts of risk for a given payoff (Brown *et al.*, 2005a). Such variation in boldness is likely to manifest itself in environments that differ markedly in the average or ambient level of risk. One important variable that many animals experience, which can lead to behavioural and physiological differences between individuals within the same species, is differential exposure to predation (Lima & Dill, 1990; Endler, 1995). Three-spined sticklebacks *Gasterosteus aculeatus* L. from high- and low-predation areas, for example, differ in their average level of aggression (Huntingford, 1976). A recent study by Brown *et al.* (2005a) found that *Brachyrhaphis episcopi* (Steindachner) from high-predation locations are generally bolder than those from low-predation sites, suggesting that habitat-specific selection pressures are likely to result in population variation in personality traits. These

differences were maintained in fish reared in the laboratory and further exposure to simulated predatory attacks increased boldness scores (Brown *et al.*, 2007). Similar observations have been made in wild populations of big horn sheep *Ovis canadensis* Shaw (Reale & Festa-Bianchet, 2003). Likewise, lizards reared in captivity and exposed to differential rates of simulated predator attack also develop different personalities (Lopez *et al.*, 2005). Such observations strongly suggest that boldness traits in animals are not only heritable but also heavily influenced by experiences during ontogeny. Behavioural variations along the boldness–shyness spectrum may be produced under artificial selection in captivity resulting in traits that may or may not be favourable depending on the management objectives. Research into this area, therefore, has serious implications for aquaculture and hatchery production of fishes (Huntingford & Adams, 2005).

The boldness of the tropical poeciliid *B. episcopi* from eight predator sympatric or allopatric populations was examined in two independent assays to examine the role of the environment in shaping boldness traits. It was hypothesized that boldness scores would generalize across a range of contexts (domain general perspective of personality traits; Sih *et al.*, 2004). In addition, the relationship between boldness and body mass was examined, using the latter as a proxy for fitness. In fishes, body condition (mass per unit length) is highly correlated with a wide range of fitness measurements (Le Cren, 1951; Reznick & Braun, 1987; Neff & Cargnelli, 2004). Based on previous studies in this system, it was hypothesized that heavier mass per unit length would be associated with bold individuals in the high-predation areas, whereas the reverse may be true in the low-predation areas. Thus, there were three primary objectives: (1) to examine how variation in boldness scores observed in wild fish is partitioned between, predation regime, sex and body-length, (2) determine the generality of the boldness measurement by comparing it with an alternative boldness assay and (3) examine the relationship between boldness and body mass.

MATERIALS AND METHODS

The study species, *B. episcopi*, is a small, live-bearing poeciliid occupying the headwaters of streams in the Republic of Panama. Its widespread distribution offers an excellent opportunity to examine the influence of various habitats on the evolution and development of behavioural traits. The boldness of *B. episcopi* from eight sites (two sites in each of four tributaries) was examined. These paired sites were separated by waterfalls such that *B. episcopi* in downstream sites below the waterfall barriers were predator sympatric, while fish from upstream sites were predator naïve. Waterfall barriers prevent the upstream migration of all piscivorous fish species and observations suggest that avian predation is equally spread above and below the waterfalls (Brown & Braithwaite, 2004; Brown *et al.*, 2005b). The fish came from three independent rivers running into the Panama Canal: Rio Limbo (RL), Rio Macho (RM) and Quebrada Juan Grande (QJG). In RL, two separate tributaries (RL1 and RL2) were sampled both of which contained high- and low-predation populations (see Table 1). Despite being part of the same river drainage, the RL1 and RL2 sites were considered geographically isolated as the distribution of the study species did not extend downstream to the junction where both branches met.

At each site fish were sampled opportunistically and were tested individually in two different boldness–shyness assays. The apparatus for both experiments was set-up on level ground beside each river. Eight individuals from a given pool were collected using

TABLE I. The number of fish collected at each location and their mean standard length (L_S). Individuals of <15 mm were excluded from the data set

River	Predation regime	Number of males	Number of females	Total n	L_S (mm) males	L_S (mm) females
Rio Macho (RM)	High	16	14	30	23.7	26.1
	Low	7	21	28	24.0	36.5
Rio Limbo	High	15	18	33	22.7	27.7
Trib.1 (RL1)	Low	8	24	32	24.5	30.8
Rio Limbo	High	7	21	28	19.4	24.4
Trib.2 (RL2)	Low	10	21	31	22.2	31.9
Quebrada Juan	High	11	15	26	21.7	27.2
Grande (QJG)	Low	9	23	32	24.7	25.6
Total		83	157	240		

small dip-nets and placed in a 20 l bucket. Two individuals were then chosen at random and tested concurrently in the two experiments (*i.e.* one in each experiment). The fish were then transferred to the alternative experiment. After each fish had been tested in both experiments, their standard length (L_S), mass (M) and sex were recorded. Individuals <15 mm could not be sexed (the male gonopodium had not yet formed), so they were considered to be juveniles and removed from the data set. After all eight fish had been tested, the water in both sets of apparatus was refreshed and a further eight fish collected from the stream. This was repeated until *c.* 30 adult fish had been tested at each site (Table I). Note that due to heavily biased sex ratios, it was difficult to sample large numbers of males in some locations. All fish that had been exposed to the tests were retained in a separate bucket to ensure none of the fish in a given pool were re-sampled. All fish were released back into their home pool at the end of the experiments.

EXPERIMENT 1. TIME TO EMERGE FROM SHELTER

The apparatus consisted of a circular, pale blue, paddling pool (1 m diameter) filled to a depth of 100 mm. A box (190 mm high \times 80 mm wide \times 100 mm long, as described in Brown *et al.*, 2005a) was positioned at the edge of the pool. Opening of the vertically sliding trapdoor allowed access to the paddling pool *via* a doorway (30 mm wide \times 50 mm high) at the front of the box. A white plastic sheet in the form of a 'D' was placed underneath the box to provide a strong background contrast to the colour of the fish. Fish were placed in the start box and a lid was positioned on top. An individual was kept in darkness for 2 min before the trapdoor was opened. An observer sat motionless, 1 m from the edge of the pool, directly in front of the box and recorded the time taken for the fish to emerge from the box using a stopwatch. The criterion for this was the individual's head crossing the line of the door. Any fish failing to emerge from the start box after 15 min was given a ceiling value of 900 s.

Brachyrhaphis episcopi is sexually dimorphic with females generally being larger than males. In addition, fish from low-predation regimes tend to be larger than those from high-predation regimes (Table I). Previous studies revealed that L_S has a large impact on boldness traits (Brown & Braithwaite, 2004; Brown *et al.*, 2005a), therefore, the relationship between size and boldness was closely scrutinized. The time to emerge data were analysed using a mixed-effects linear model with L_S , predation regime and sex as fixed effects and river as a random effect. Variables that did not explain significant amounts of variability were excluded from the model.

EXPERIMENT 2. TIME SPENT INVESTIGATING A NOVEL OBJECT

A small, transparent, plastic aquarium (240 × 390 mm) was divided along its length into thirds by drawing black lines on its underside. Water depth was maintained at 150 mm. A pair of stimulus fish ('the shoal') consisting of a male and a female captured from the same pool as the test fish was placed in a transparent, plastic cylinder (100 mm diameter) at one end of the aquarium. A novel object was positioned at the other end (bright pink and yellow rubber ball of 40 mm diameter). A single test fish was placed in a clear cylinder (80 mm diameter) located in the centre of the aquarium equidistant from the shoal and the novel object. After 2 min, the cylinder constraining the test fish was gently lifted clear by pulling on a monofilament line leaving the fish free to move around the aquarium for 5 min. After 5 min, the subject was restrained in the clear cylinder, while the shoal and novel object were switched between the ends of the tank and the test was repeated for an additional 5 min. An observer, sitting motionless 1 m away, recorded the amount of time the test fish spent in the third of the aquarium closest to the novel object (and hence furthest from the shoal) for the 10 min experimental period.

Owing to the high incidence of fish not leaving the safety of the shoal to investigate the novel object (c. 38% of individuals), the inspection data were converted into a binomial statistic (1 = inspected the novel object, 0 = did not inspect the novel object) and the proportion of individuals within each population for each sex that left the shoal and inspected the novel object was analysed. The model used for the analysis of these proportion data was similar to that used in experiment 1, with the exception of the incorporation a binomial error structure.

CORRELATION BETWEEN BOLDNESS ASSAYS

A simple linear regression between \log_{10} (time to emerge) and \log (time spent inspecting the novel object) was conducted. In addition, the binomial inspection data were utilized to split the data set into those individuals that did investigate the novel object and compared their time to emerge from shelter with those that did not investigate the novel object.

BOLDNESS AND BODY MASS

Condition factor is traditionally based on the relationship between \log_{10} (length) and \log_{10} (body mass) (Le Cren, 1951). Regression analysis determined the relationship between M and L_S in the current data set was best represented by a cubic function of L_S , therefore, L_S was entered as a third order polynomial in the analysis. The relationship between boldness and M was investigated using a mixed-effects linear model with M as the dependent variable, and time to emerge from shelter, location, sex and L_S (as a cubic polynomial) as fixed independent variables and river as a random variable. The time to emerge was used as a proxy for boldness since it was considered the most reliable of the two boldness assays and both assays were highly correlated. The model was minimized by the removal of higher order interactions that did not explain significant amounts of variation.

RESULTS

EXPERIMENT 1. TIME TO EMERGE FROM SHELTER

The mixed-effects analysis revealed a highly significant relationship between L_S and time to emerge from shelter. Small fish emerged sooner than large fish (linear model, $F_{1,230}$, $P < 0.01$). Additionally, fish from locations with a

high-predation regime emerged from shelter sooner than those from locations with a low-predation regime (linear model, $F_{1,230}$, $P < 0.05$; Fig. 1). Males tended to emerge from shelter sooner than females, although not significant (linear model, $F_{1,230}$, $P > 0.05$). A significant interaction between sex and predation regime suggested that this difference between high- and low-predation areas was primarily driven by male behaviour (linear model, $F_{1,230}$, $P < 0.05$).

EXPERIMENT 2. TENDENCY TO APPROACH NOVEL OBJECT

The minimized, binomial, general linear model was reduced to the main factors (L_S , predator regime and sex) as there were no significant interactions between any of these terms. Small fish were more likely to approach the novel object than larger fish (linear model, $F_{1,231}$, $P < 0.001$). The model revealed no significant difference in the probability of males and females approaching the novel object (linear model, $F_{1,231}$, $P > 0.05$), although males tended to approach the novel object more often than females. Nor was there a significant difference between fish from high- and low-predation regimes (linear model, $F_{1,231}$, $P > 0.05$).

CORRELATION BETWEEN TWO BOLDNESS ASSAYS

Linear regression revealed a significant relationship between the two assays of boldness (linear model, $F_{1,236}$, $P < 0.001$). This close relationship was emphasized when the mean time to emerge from shelter for males and females from each location was examined by regression against the mean time spent inspecting a novel object ($r^2 = 0.46$; Fig. 2). Taking a binomial approach, individuals that left the safety of the shoal and investigated the novel object

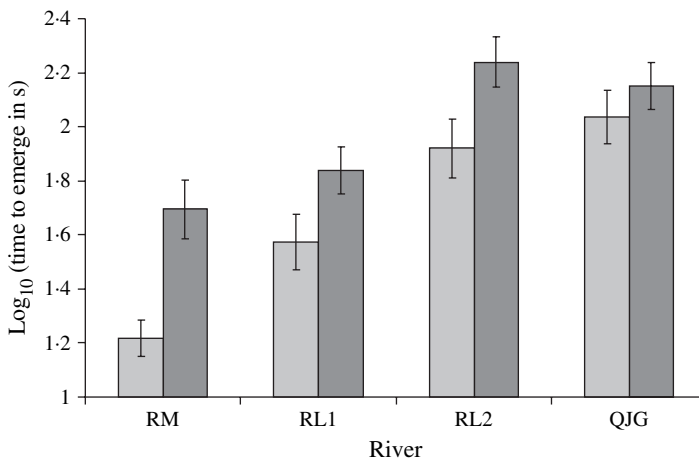


FIG. 1. The mean \pm s.e. \log_{10} time taken for fish from each population (see Table I) to emerge from shelter. Fish from low-predation areas (■) emerged from shelter before those from high-predation areas (□).

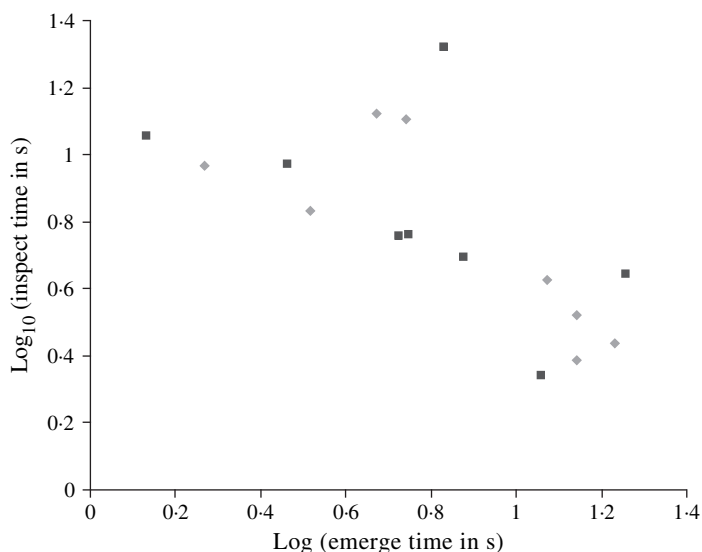


FIG. 2. The relationship between the two measurements of boldness, \log_{10} time to emerge from cover and the log time spent inspecting a novel object [data averaged for females (◆) and males (■) at each location for clarity].

emerged from shelter sooner than those that did not approach the novel object (t -test, d.f. = 236, $P < 0.001$; Fig. 3).

BODY MASS

The results of the minimal model exploring the association between M and boldness (\log_{10} time to emerge) revealed that M was strongly influenced by L_S

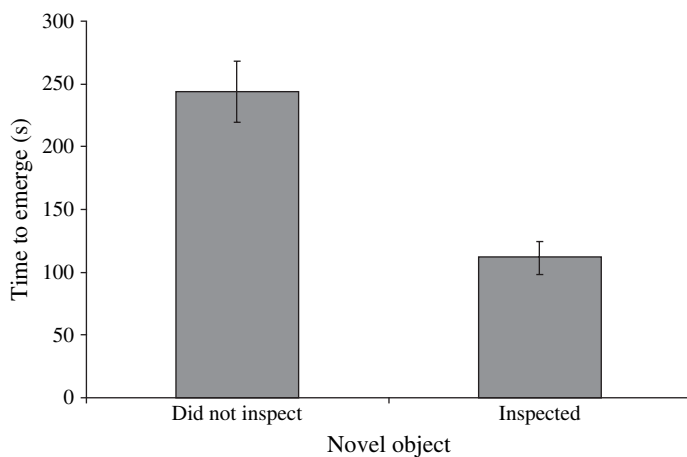


FIG. 3. Mean \pm S.E. time to emerge from shelter for individuals that approached or did not approach the novel object.

(linear model, $F_{1,226}$, $P < 0.001$) and sex (linear model, $F_{1,226}$, $P < 0.01$) as expected. The influence of the time to emerge from shelter on M , however, was of primary interest. A significant interaction between boldness (\log_{10} time to emerge) and L_S was revealed (linear model, $F_{1,226}$, $P < 0.001$). At any given L_S , bold fish were heavier than shy fish and this difference in M increased with increasing L_S (Fig. 4).

DISCUSSION

Few studies have ever attempted to investigate the fitness consequences of expressing personality traits, least of all in natural populations occupying a range of habitats. The analysis in this paper revealed a strong relationship between boldness scores and body mass. Body mass is closely associated with fitness in fishes and is known to affect a number of fitness characteristics ranging from the probability of overwinter survival through to reproductive success (Le Cren, 1951; Reznick & Braun, 1987; Schultz & Conover, 1999; Neff & Cargnelli,

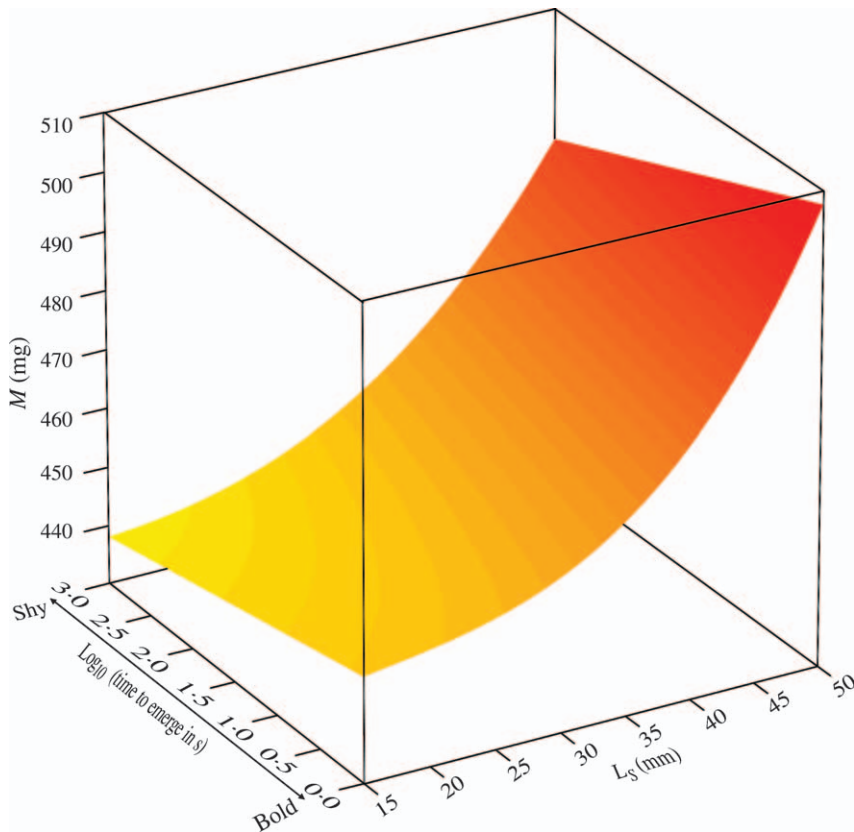


FIG. 4. Relationship between boldness [\log_{10} (time to emerge from shelter)], standard length (L_S) and body mass (M) showing the characteristics of a classic growth curve. Note that bold fish are always heavier than shy fish at any given L_S . In addition, the rate of mass gain per unit length is significantly higher in bold fish than shy fish.

2004). Regardless of the expected strong cubic relationship between L_S and M , the relationship between L_S and M was strongly affected by boldness scores. Bold fish were not only heavier at any given L_S than shy fish, but this mass differential increased as L_S increased. It is often difficult to assign cause and effect in correlative studies. It is possible, for instance, that an individual's M per unit L_S could result in a shift in motivational state (*e.g.* hunger), thus causing a change in behaviour (and hence boldness scores). This could not have been the case here as it would be generally expected lighter fish to be more inclined to take great risks by emerging from shelter sooner to resume foraging. In the present study, the reverse was true (Fig. 4) suggesting that this relationship could not be explained by hunger levels or some similar motivating factor. Furthermore, differences in boldness traits remain even when measured in the laboratory following feeding to satiation (Brown *et al.*, 2007) and similar increased growth rates have been reported in bold three-spined sticklebacks in laboratory studies (Ward *et al.*, 2004). Taking these facts into account, it would seem that the variability in boldness observed in these experiments is responsible for the body mass of the fish, not *vice versa*.

The two assays of boldness measured in two independent contexts were highly correlated. Individuals that emerged from the shelter sooner were more likely to leave their shoal mates to investigate a novel object (Fig. 3). The high concordance of boldness in different contexts across all of the populations examined could indicate that underlying mechanistic constraints are limiting the expression of behavioural optima (domain general view; Sih *et al.*, 2004) or, alternatively, similar selective regimes operate across both contexts under examination (domain specific view). Some treat the domain general view of personality with scepticism suggesting that any individual that breaks free of such constraints, and thus shows greater behavioural flexibility, would have greater fitness across all contexts (Neff & Sherman, 2004). The domain specific view, on the other hand, highlights the importance of context specific selection. A growing number of studies support the domain specific view (Coleman & Wilson, 1998; Reale *et al.*, 2000; D'Eath & Burn, 2002), posing that correlations between behavioural traits, when they do arise, may be a by-product of independent selection acting on single traits in a number of different contexts rather than acting on a common underlying mechanism. The behaviour of *B. episcopi* in both of the assays used herein does not appear to be maladaptive and could, theoretically, support either perspective. Leaving the safety of a shoal and approaching novel objects, or early emergence from cover following a disturbance, may seem like a dangerous occupation in high-predation areas, but it is likely to be adaptive if competition for food and mates is fierce. These fish must emerge from shelter and 'get on with their lives' even though the risk of doing so is potentially high. The fact that fish from high-predation areas were slightly more inclined to leave the safety of the shoal and inspect the novel object is even more surprising given that fish in high-predation areas tend to school very strongly. Fish in these areas must first overcome the need to school and then overcome their shyness before approaching the novel object. Incidentally, this may explain why the second measurement of boldness did not show the same degree of variability as the first. It appears that in regions of high predation pressure bold behaviour is likely to lead to

increased foraging and reproductive success, whereas the selective pressure favouring boldness is lacking in regions of low-predation pressure. Fish in high-predation areas simply cannot afford to spend their entire lives hiding from predators and must be prepared to accept a higher risk for any given pay-off (Brown *et al.*, 2005a).

The results of both of the boldness assays presented here were highly correlated with L_S . Independent of predation regime, small fish tend to emerge from shelter sooner than large fish and they also show a greater tendency to approach a novel object. This result is consistent with previous studies conducted both in the laboratory and *in situ* (Brown & Braithwaite, 2004; Brown *et al.*, 2005a). It suggests that fish can alter their behaviour as they grow, perhaps through experience or a state-dependent mechanism, or alternatively, that there is heavy selection against bold individuals across all environments. This latter explanation seems unlikely given the lack of aquatic predators in low-predation areas (Brown & Braithwaite, 2004). A number of studies have shown that personality traits can vary with demography, especially with age (Gosling & John, 1999; Lee & Hotopf, 2005) and the results of the present study support these observations. Thus, it appears that the shift in personality traits with age is geared towards maximizing fitness potential as selection regimes, life-history priorities and individual experiences change during ontogeny.

Much of the differences in boldness between the sexes were encompassed by variation in body size, bearing in mind that females are far larger than males in this species. Nevertheless, there was some indication that males were more likely to leave the safety of a shoal to investigate novel objects and emerge from shelter sooner than females even after body size was controlled for. Moreover, the differences in boldness between the high- and low-predation populations was primarily driven by male behaviour as indicated by the significant interaction term in the first boldness assay. Differences in the boldness scores between the sexes might be explained by variation in life-history priorities (Magurran & Garcia, 2000). In a range of animals, males tend to be risk takers and risk taking usually emerges in the sex that suffers from the intense reproductive competition (Wilson & Daly, 1985). Like guppies *Poecilia reticulata* Peters, male *B. episcopi* persistently pursue females for the purposes of mating, even in the presence of predators (Reznick & Endler, 1981; Evans *et al.*, 2003). The heavy competition between males for access to females is intensified in downstream areas where sex ratios are less skewed in favour of females (see Table I; Brown *et al.*, 2005a). This variation in intra-sexual competition may also favour bolder males. Moreover, female guppies prefer bold males in a predator inspection context (Godin & Dugatkin, 1996).

In conclusion, it is evident that an individual's position on the boldness–shyness personality continuum is likely to have fitness consequences in wild populations given the close relationship between boldness and body mass. Boldness personality traits are heritable and partly predicted by demographic variables such as age and sex. These results show that boldness traits shift during ontogeny, possibly due to life experiences, and that these traits vary considerably in response to varying selective pressures emanating from an individual's environment.

We thank the Smithsonian Tropical Research Institute for their continued support. The fish were collected under licence from the Panamanian authorities (ANAM permit# 31503 and # SEX/A-88-03). This work was funded by NERC (grant # NER/A/S/01/00608). We also thank the referees whose comments contributed to this manuscript.

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