

contexts (e.g. mating, foraging and avoiding predators). Behavioural ecologists, however, often specialize on behaviours in single contexts and, as a result, focus on a limited range of the organism's life history. When the interaction between two or more of these behavioural-ecological contexts is considered (e.g. foraging under high and low predation risk) different animals are typically used across treatments to satisfy assumptions of statistical independence. As a result, our understanding of the consistency of individual variation and how ecologically-important behaviours are correlated across contexts is limited (reviewed in Sih et al. 2004a, b). None the less, one recurring theme is that boldness towards predation risk may be positively correlated with behaviour in other contexts.

Wilson et al. (1993, 1994) developed the shy–bold continuum for juvenile pumpkinseed sunfish, *Lepomis gibbosus*, showing positive correlations between predator inspection, speed of acclimation to the laboratory, foraging behaviour, and parasitic infection (Wilson 1998). Boldness towards predators is positively correlated with growth and dispersal in killifish (Fraser et al. 2001), aggression and activity in a novel environment in stickleback (Huntingford 1976; Bell & Stamps 2004), social aggressiveness in wolves (Fox 1972), activity, foraging and growth in larval salamanders (Sih et al. 2003), and agonistic behaviour and wasteful killing (killing but not consuming prey) in funnel-web spiders (Riechert & Hedrick 1993; Maupin & Riechert 2001). Recently, working on the semi-aquatic fishing spider, we showed that boldness towards a predator (see below for a description of the antipredator response) is positively correlated with a female's level of aggression towards both hetero-specific prey items (crickets) and courting males (precopulatory sexually cannibalistic attacks; Johnson & Sih 2005).

In this study, we focus more closely on the antipredator response of female fishing spiders (see below for the nature of this response). We measure this behaviour in four functional contexts: (i) the control setting, in which spiders are disturbed followed by no other stimuli, (ii) the foraging context, in which spiders are disturbed and then food is immediately made available, (iii) the courtship context, in which spiders are disturbed and then a courting male is introduced, and (iv) the parental care context, in which spiders are disturbed while carrying an eggsac in their mouthparts. In addition to measuring behavioural correlations across these four functional contexts, we also address the stability of antipredator responses through ontogeny (juvenile–adult) in all but the obligate adult contexts of courtship and parental care. Finally, following the work of Bell & Stamps (2004) we test for the stability of the overall behavioural syndrome by asking whether behavioural correlations across functional contexts in one life stage are similar in other life stages.

To emphasize, the concept of a stable behavioural syndrome is different from the concept of a stable behavioural type. Even if individual behavioural types are not stable over ontogeny (e.g. some bold individuals become shy as they grow older, and vice versa), the overall behavioural syndrome can remain stable if throughout ontogeny, individuals that are more bold than others in one context also tend to be more bold than others in

another context. Given the positive correlations between juvenile foraging voracity, adult foraging voracity, sexual cannibalism and boldness reported for this species previously (Johnson & Sih 2005), we predict that we will also find a behavioural syndrome of positive correlations in antipredator responses across functional contexts and developmental stages. In contrast, the traditional adaptive paradigm predicts no such consistent individual variation across contexts, but instead predicts that individual variation in antipredator behaviour will be determined by state variables such as developmental stage, body condition, and investment in offspring.

Note that a behavioural syndrome does not conflict with the traditional adaptationist view that behaviour should be plastic and context-specific (Sih et al. 2004a, c). For example, in our study, the adaptationist view predicts that females should be bolder (emerge from hiding sooner) when a foraging or mating opportunity follows predation risk relative to their level of boldness when no foraging or mating opportunity exists. In addition, when females are brooding offspring they should be less bold as this is a period when parental investment is high. The behavioural-syndrome concept adds the prediction that within the adaptive modulation that goes on across contexts, individuals that rank relatively high for boldness in one context also rank relatively high for boldness in other contexts (see Fig. 1). Indeed, the strength of a behavioural syndromes explanation lies in the extent to which boldness in a focal context is better explained by that individual's tendency to be bold in other contexts than it is by the optimal level of boldness in the focal context.

THE BEHAVIOUR AND ECOLOGY OF FISHING SPIDERS

Fishing spiders are cursorial, ambush predators of the neuston community, commonly associated with the edges of cattail ponds (Carico 1973). The natural history (Carico 1973), sensory ecology (Bleckmann & Barth 1984; Bleckmann & Lotz 1987), population ecology (Zimmerman &

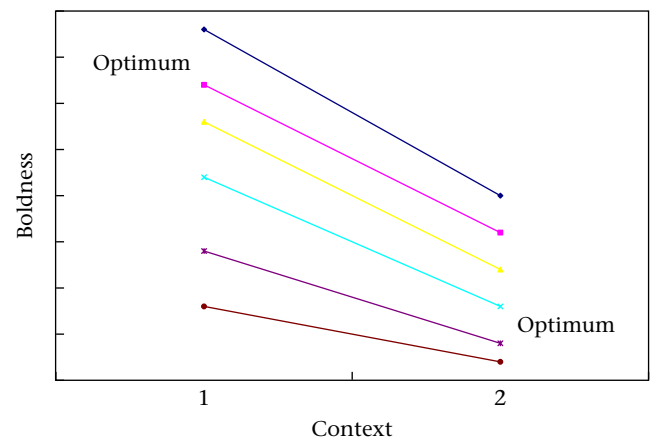


Figure 1. Hypothetical data showing rank order correlations (i.e. a boldness syndrome). Note that while all individuals show a shift in boldness in the adaptive direction, intraindividual correlations among contexts result in no single individual expressing an optimal level of boldness in both contexts.

Spence 1989, 1992) and behavioural ecology (Johnson 2001, 2005a, b; Johnson & Sih, 2005; Kreiter & Wise 2001) of fishing spiders have been well studied. While it is unclear which species most commonly prey on these spiders (e.g. birds, bats, fish), fishing spiders use an antipredator response to airborne and waterborne vibrations in which the spider dives underneath the water and clings to submerged substrate (e.g. under floating aquatic vegetation, on the underside of submerged rocks or, in the case of our experimental containers, the underside of a Styrofoam float). While submerged, the spider is enveloped in an air capsule, and thus, when healthy, can resurface completely dry.

Bishop (1924) and Carico (1973) reported submergence durations of upwards of 30 min in fishing spider. Our previous work confirms that submergence for 30 min under water is routinely seen in fishing spider, and our current record holders ($N = 3$, all healthy adult females) remained continuously submerged for an entire 90-min trial (J. C. Johnson, unpublished data). To our knowledge, no one has documented the physiological cost of submergence. As for behavioural-ecological costs, time spent submerged most likely involves lost foraging opportunities (fishing spiders primarily detect prey items through water surface vibrations), lost mating opportunities, and compromised parental care. Submergence may also allow aquatic predators (e.g. sunfish) to prey on the spider.

METHODS

The experimental approach taken here was a longitudinal study focused on quantifying female behaviour across development and in multiple behavioural-ecological contexts. The study followed 60 focal females beginning in the juvenile phase 1–2 molts (4–6 weeks) before adulthood. Following the adult molt, we tracked these same focal animals through adulthood until death (approximately 5–6 months total).

Juvenile females were collected from a pond (~60 m²) outside of Lexington, KY during the first week of April 2002. All spiders were weighed at collection and several hours before each behavioural trial. In addition, spiders were digitally imaged at collection and following each molt to estimate cephalothorax area and leg length. Body size in spiders is fixed during each stage and only increases when the spider molts. Spiders were maintained outdoors in large (60 × 41 cm and 16 cm) plastic tubs. Each experimental female ($N = 60$) was housed in a separate tub to allow us to track each individual's behaviour across the experiment. Between experimental trials, screened lids covered these tubs to allow airflow, while preventing escape of the spider and entry of prey (e.g. earwigs, wolf spiders) and predators (e.g. birds, lizards). Containers were filled with water to a depth of 2.0 cm and each contained a large Styrofoam float (10 × 6.0 cm and 0.5 cm). The sequence of behavioural trials (see below) was identical for each focal spider. Females underwent no more than one type of behavioural trial on any given day with the exception that courtship trials were

conducted in the morning and concluded a minimum of 4 h before a feeding trial.

Boldness Control

Boldness control trials (that ran for 30 min each) were conducted twice weekly throughout the experiment (i.e. on juveniles and adults). We used a females' average score for each developmental period (juvenile versus adult) in data analyses. The goal in all trials was to begin by provoking submergence behaviour. After opening each container, females were 'disturbed' by being firmly poked from behind with a pencil. Following submergence, the substrate each female had submerged under was struck with the pencil. If females submerged before we could prod them, the substrate they had submerged under was struck with the pencil. The few females that refused to submerge after being prodded for 30 s were scored as unwilling to submerge and received a submergence duration score of 0 s. Although, females were not disturbed again after the initial disturbance, females often resurfaced and submerged again over the course of a trial; thus we also calculated the proportion of a trial spent submerged. Females were scored as resurfacing when at least 4 legs had returned to the water surface. Assays described below used this same basic method; however, others involved conflicting demands (foraging, mating opportunities, parental care, see below) that should affect boldness. In all cases, we calculated two measures of boldness: (1) latency to resurface and (2) proportion of trial spent above the water's surface.

Foraging and Boldness

Females underwent 30-min foraging trials twice weekly and these were the only foraging opportunities afforded females through the duration of the experiment. Feeding regimes of this regularity have been used in the past and have resulted in successful growth to adulthood and offspring production within the range of that seen in the field (Johnson, 2001; unpublished data). Foraging trials were conducted on females as juveniles and adults, but not when adult females were defending their eggsacs. Females rarely attack prey while carrying an eggsac in their mouthparts (Carico, 1973; Johnson, personal observation). Foraging trials began with a 'disturbance' as described for the boldness control trials described above. Thirty seconds following submergence, one 4-week-old cricket (*Acheta domesticus*) was introduced to the water surface at a point 30 cm from the submerged female. Previous work showed that while underwater, females can detect and respond to surface prey and to males (see *Courtship and Boldness*). Thus, we obtained 2 submergence scores in the foraging context per female each week and used a female's average score for each developmental period in data analyses.

Courtship and Boldness

Adult females underwent 30-min courtship trials conducted 4 times per week beginning on each female's

3rd day following adult emergence and continuing through the second week of adulthood. Thus, we obtained 4 courtship submergence scores for each female each of 2 weeks and used a females' average score in data analyses. Mating generally requires that a pair be together for over an hour. As a result, mating never occurred during courtship trials and all courtship submergence scores reported were from virgin females. In accord with the protocol for boldness control and foraging trials, courtship trials began with a 'disturbance'. Thirty seconds following submergence, a mature male was introduced to the water surface at a point 30 cm from the submerged female. Courtship in this species involves rhythmic leg waving and tapping of the water surface with the front legs. Courtship is triggered by the presence of female, silk-based pheromone, and males are known to court (1) in a female's container despite her absence (Arnqvist, 1992) and (2) when females are submerged (J. C. Johnson, unpublished data). All males initiated courtship within 10 min of their introduction.

Parental Care and Boldness

Parental care trials were identical to the boldness control trials described above except that they were conducted when females were defending their eggsacs. Eggsacs are produced approximately 10–14 days following mating and are carried in the female's mouthparts. Eggsac defence by the female is vigorous to the point that eggsacs cannot be removed from the female's mouthparts without ripping the outer lining of the eggsac.

Thus, measures of female condition during parental care trials describe the female's mass while carrying the eggsac. We obtained 2 parental care submergence scores for each female in each of the first 2 weeks of eggsac defence and used a female's average score in data analyses. These trials were discontinued after 2 weeks so as to not compromise the hatching success of eggsacs.

Statistical Analyses

Given the within-subjects design used here, we ran a one-way repeated measures ANOVA to test for developmental factors (juvenile, adult) and behavioural contexts (control, foraging, courtship and parental care). Because the data did not conform to the assumption of sphericity, we report multivariate statistics that do not make such assumptions. Paired contrasts are reported to identify contexts that differed significantly.

Using the formula from Lessells & Boag (1987), we used intraclass correlation coefficients to estimate the repeatability of each female's boldness response within each context studied. Finally, univariate correlations were used to examine the hypothesis that an individual's behaviour in one context is consistent with its behaviour in other contexts, thus explaining the nature of the variation seen in mean submergence behaviour within a context. Because females commonly resurfaced and resubmerged multiple times during a trial, we determined that boldness in this species is best estimated as the total

proportion of a trial spent above the water surface. Thus, we report only data analyses using these proportions, however, analyses using the latency to first resurfacing yielded identical results. Proportional data were arcsine transformed to satisfy assumptions of normality. To test for correlations across developmental and behavioural contexts we include a stringent, sequential Bonferroni adjustment to account for the multiple tests performed. In addition, we inspect correlations between female condition before a trial (mass/cephalothorax area) and her boldness to test the traditional adaptive idea that behaviour should reflect state variables such as condition. Throughout our analyses, different treatments display varying sample sizes because some animals could not be sampled in each context. Most notably, analyses on the parental care context are limited to the subset of spiders ($N = 12$) that successfully produced eggsacs.

RESULTS

Mean Behaviours across Contexts

Our analysis revealed significant differences in boldness across the six contexts measured ($F_{5,55} = 52.155$, $P < 0.0001$; Fig. 2). Within control trials and foraging trials there were no developmental differences in mean boldness between juveniles and adults. However, spiders (both as juveniles and adults) were significantly bolder in foraging trials than control trials (juvenile: $t = 0.307$, $P < 0.0001$; adult: $t = 0.387$, $P < 0.0001$). In addition, restricting the analysis to adult behavioural contexts, adult spiders were significantly bolder in foraging trials than courtship trials ($t = 0.259$, $P < 0.0001$), and parental care trials ($t = 0.225$, $P < 0.0001$), and significantly bolder in the parental care context relative to the control boldness setting ($t = 0.161$, $P < 0.0001$), and the courtship context ($t = 0.146$, $SE = 0.05$, $P = 0.004$). Finally, spiders were significantly bolder in the courtship context relative to the control context ($t = 0.128$, $P < 0.0001$).

Individual Variation within and across Contexts

The above analysis does not consider the possibility that individual variation may be correlated across these contexts. First, within each of the contexts studied except for parental care, females displayed significantly high repeatability of behaviour across trials (juvenile control: $r = 0.612$, $F_{1,52} = 1.53$, $P = 0.023$; adult control: $r = 0.512$, $F_{1,58} = 2.36$, $P < 0.0001$; juvenile foraging: $r = 0.562$, $F_{1,52} = 2.61$, $P < 0.0001$; adult foraging: $r = 0.633$, $F_{1,58} = 2.40$, $P < 0.0001$; courtship: $r = 0.815$, $F_{1,58} = 5.30$, $P < 0.0001$; parental care: $r = 0.624$, $F_{1,11} = 1.73$, $P = 0.124$). To address the extent to which boldness is stable across an individual's development and/or correlated across behavioural contexts we reported a series of univariate correlations (see Table 1). Throughout we used a sequential Bonferroni adjustment for the 21 tests performed to determine the statistical significance of correlations.

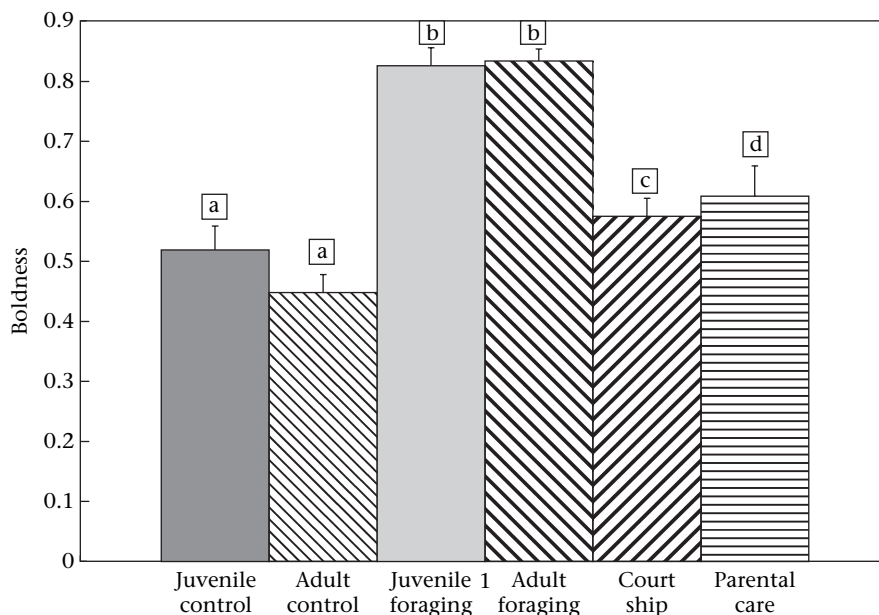


Figure 2. Repeated measures ANOVA shows that average boldness in this experiment was significantly different across behavioural contexts (see text for details), but no differences were observed for boldness across developmental stages (juvenile–adult).

Developmental Stability

Looking first at the developmental stability of behaviours within the control context, we found a trend for a positive correlation between a spider's boldness as a juvenile and as an adult (see Table 1 for all test statistics). This result, however, was not robust enough to meet the more stringent criteria of the Bonferroni correction. In contrast, we found significant developmental stability of submergence behaviours when the disturbance was followed immediately with a foraging opportunity.

Correlations across Functional Contexts

We found no evidence for a juvenile syndrome of boldness across the control and foraging contexts. In contrast, three of the four adult behavioural contexts measured were strongly intercorrelated (control, foraging

and courtship). Boldness in the parental care context, however, was not correlated with any other context measured. Thus, univariate correlations suggest a behavioural syndrome of boldness is absent in juveniles but present among foraging, courtship and control contexts in adults, indicating that the adult behavioural syndrome shown here is not stable across development.

Boldness and Female Condition

Surprisingly, a female's condition (mass/carapace area) at the time of a behavioural trial was not a significant predictor of her boldness in that trial (see bottom row of Table 1). Note, however, that in all contexts before eggsac production, the trend is for boldness to be positively correlated with condition. In contrast, in the parental care context boldness is negatively correlated with condition.

Table 1. Correlations among boldness behaviours in several behavioural contexts and developmental phases

$r=$, $N=$ $P=$	Juvenile control	Juvenile foraging	Adult control	Adult foraging	Courtship	Parental care
Juvenile foraging	0.128, 41, 0.427					
Adult control	0.370, 37, 0.024*	0.148, 46, 0.330				
Adult foraging	0.09, 43, 0.550	0.512, 51, <0.0001**	0.497, 53, <0.0001**			
Courtship	0.393, 43, 0.009*	0.503, 51, <0.0001**	0.560, 53, <0.0001**	0.624, 59, <0.0001**		
Parental care	0.02, 22, 0.910	0.202, 22, 0.367	0.340, 19, 0.150	0.102, 24, 0.560	0.105, 24, 0.510	
Female condition	0.268, 43, 0.043*	0.188, 49, .098	0.016, 52, 0.456	0.206, 57, 0.063	0.287, 57, .015*	-0.442, 24, .016*

The bottom row shows correlations between boldness and female condition (mass/carapace area).

*Indicates statistical significance; ** indicates statistical significance in a given sequential Bonferroni adjustment.

DISCUSSION

Adaptive Shifts in Boldness

Some of our results test standard optimality-based predictions of the effects of developmental stage and behavioural context on average boldness. With regard to alternative contexts, as expected, females were more bold (spent more time on the water, and less time submerged) when food was available than otherwise. In addition, females were significantly bolder in the presence of courting males (that either represent mates or food) than they were in the control context. Finally, females were significantly bolder in the parental care context than they were in the courtship or control context. This goes against our *a priori* hypothesis that females carrying offspring should be extremely wary, but likely reflects either the physical difficulty/energetic costs to females of staying underwater with an eggsac (see below), or perhaps egg development costs incurred when eggsacs are held underwater for long periods.

Over ontogeny, because adults are larger and probably less vulnerable to predation than juveniles, we expected adults to be bolder than juveniles. In addition, Kreiter and Wise (2001) suggested that food limitation is particularly strong in adult fishing spider (as opposed to juveniles); accordingly, adults tend to be more active (and should presumably be more bold) than juveniles. Contrary to these predictions, we found that mean boldness did not change significantly over ontogeny. Perhaps the costs of staying submerged were higher for juveniles than adults. More study on the size, age and/or stage-dependent costs and benefits of boldness will be valuable.

A Multicontext Syndrome of Boldness

Beyond contrasts of average behaviour, our main interest is in the existence of a behavioural syndrome of boldness in fishing spider, across development and among behavioural contexts. First, females displayed highly repeatable responses across time within each context except for the parental care context. Across contexts, correlations were apparent between some contexts but not between others. Specifically, we found boldness in the foraging context to be a stable trait across development, a trend which also existed within the control context but did not meet statistical significance. Looking across behavioural contexts, we found an adult boldness syndrome that included control, foraging and courtship contexts, but did not include the parental care context. Given the lack of repeatability in parental care boldness it is not surprising that it is not included in an adult boldness syndrome. Finally, we found no evidence for a syndrome of boldness in juveniles, indicating a lack of developmental stability for the syndrome. Below we discuss the implications of these findings.

Developmental Stability of Boldness

We observed a general tendency for an individual's expression of boldness to carry over from the juvenile

period to adulthood. To the extent that an individual's behaviour is correlated across developmental switch points that individual will be constrained in its ability to adaptively modulate behaviour according to current environmental conditions across ontogeny. Nevertheless, developmental correlations like the ones shown herein for boldness in fishing spiders have been noted for aggression in stickleback (Bakker 1986; but see Bell & Stamps 2004), and exploratory behaviour in great tits (Dingemanse et al. 2002). More often than not, however, behaviour is not measured in the same individuals across development, making it impossible to quantify developmental constraints via behavioural correlations.

Boldness Correlations across Functional Context

Within the adult stage, we found a boldness syndrome among control, foraging and courtship contexts similar to that reported for a number of other species (see Introduction; reviewed in Sih et al. 2004a, b). The coupling of boldness among multiple contexts in such a diverse array of animals suggests that we need to reconsider whether the motivational states of fear and aggression are generally distinct and independent of each other (Riechert & Maynard-Smith 1989). Multi-context behavioural syndromes have profound ecological and evolutionary implications. In the same way that developmental correlations indicate limited behavioural plasticity across development, behavioural correlations across contexts suggest that animals are often predisposed to show individual variation that is consistent across disparate contexts. Studies that address the mechanistic underpinnings (Ketterson & Nolan 1999), ecological consequences (Rehage & Sih 2004) and evolutionary implications (Dingemanse et al. 2004) of behavioural syndromes should prove valuable in our attempt to fully understand the dynamic process of behavioural adaptation.

This adult boldness syndrome did not extend, however, to boldness in the parental care context. As noted above, females carrying eggsacs displayed remarkably high levels of boldness given that eggsacs represent a large material investment. Thus, two questions remain to be answered concerning boldness in the parental care context: why are females, on average, so bold when carrying their eggsac, and why doesn't an adult syndrome of boldness extend into the parental care context? Both questions may be answered if the indicator of boldness used here (tendency to resurface after a disturbance) reflects something other than boldness when females are carrying eggsacs. Spiders tending their eggsac may resurface quickly and remain on the surface not due to boldness, but instead because the nature of the antipredator response in this species entails energetic costs and/or physical constraints that are inflated when females are carrying an eggsac in their mouthparts. This idea is supported by the finding that, while boldness in this study was generally positively correlated with female condition, boldness in the parental care context was instead negatively correlated with condition (see bottom row of Table 1). In other words,

in the parental care context, only females in the best condition are capable of remaining submerged for significant periods. Thus, physical constraints on eggsac carrying females appear to limit a spider's ability to use submergence behaviour as an antipredator defence, thus dissolving behavioural correlations with the parental care context and making spiders appear strikingly bold given their state of reproductive investment. This disassociation illustrates that behavioural syndromes do not require across the board correlations. Instead, we view behavioural syndromes as predispositions to behave in a consistent manner. To the extent that such predispositions incur costs, and to the extent that genetic variation is available for selection to modify costly behaviour, it is not surprising at all that some contexts (here the parental care context) are not included in a behavioural syndrome.

The Developmental Stability of a Boldness Syndrome

We found no boldness syndrome for juvenile spiders. Thus, a boldness syndrome is not stable across development as it is absent in juveniles but present following the adult molt. What factors could cause females to display a boldness syndrome in adulthood but not before that? The discontinuous nature of growth and development in spiders through molts provides a very distinct switch point between developmental stages including the juvenile–adult transition. This may allow for a significant reorganization of behaviour (and mechanisms underlying behaviour) between phases, which would explain the appearance of a syndrome only after the adult molt.

Bell & Stamps (2004) present similar findings for stickleback, *Gasterosteus aculeatus*. In stickleback a behavioural syndrome of boldness and aggression is weak in the sub-adult phase but robust in adults. They too favour the idea that the reorganization of behaviour at adulthood may account for this lack of stability across development, citing the importance of rapid hormonal changes before adulthood. However, as they note, syndromes could also fluctuate through development if different selective environments faced at different stages make it such that a suite of correlated traits is favourable in one stage but not another. This 'developmental-environment' hypothesis is perhaps further supported by their finding that, while a boldness syndrome was a defining feature of one population associated with a high degree of predation risk, the boldness syndrome was absent in some life stages of a population from a distinct drainage that experiences a significantly lower degree of predation risk. Future work, preferably in a variety of taxa, should test the prediction that high levels of predation risk, experienced throughout all stages of the life history, may be associated with tightly integrated phenotypes characterized by behavioural syndromes.

In conclusion, the most notable and general result here is that even when populations of animals show adaptive shifts in their mean behaviour, as was apparent here in boldness responses, an examination of individual variation in behaviour can tell a more complete story. As we

argued elsewhere (Sih et al. 2004c) behavioural syndromes need not be mutually exclusive with adaptive flexibility, but instead may complement and complicate adaptive shifts in mean behavioural response.

Allowing for this level of complexity may be required if we wish to fully understand the relationship between behaviour at the individual level, population dynamics, and critical issues in ecology such as invasive species and population extinctions. A boldness syndrome such as the one outlined here may commonly include other ecologically important behaviours such as dispersal ability (Gilliam & Fraser 2001; Dingemanse et al. 2003; Rehage & Sih 2004), which need to be considered to understand the success of some species and the failure of others. For these reasons, we hope that future studies of behavioural adaptation will use designs that allow for an investigation of both shifts in mean behaviour and the extent to which individual variation changes across developmental stages and relevant behavioural contexts.

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