Repeatability of decision-making behaviour in male threespine stickleback *Gasterosteus aculeatus*: Effects of dummy vs. live stimuli

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Abstract Individuals select from a number of behaviours when responding to various situations and the decisions they make may affect their fitness. The costs and benefits of these responses vary among individuals causing them to differ even in identical situations. One example of this type of situation is when territorial males encounter both a male and female simultaneously, generating a trade-off that likely leads to individual differences due to differing costs of various actions among males. This situation commonly occurs in threespine stickleback, *Gasterosteus aculeatus*. However, for selection to act effectively, individuals must behave in a consistent manner and measuring repeatability can aid in understanding how selection may shape such trade-offs. Males of this species exhibit consistent individual differences in their response to dummy males and females but it is unknown if patterns are similar when feedback from the stimuli is present. To assess this, male threespine stickleback were tested with dummy and live male and female conspecifics, presented separately and simultaneously. While the same trends were found regardless of stimulus type, males were more aggressive towards the live conspecifics than to the dummies. Repeatability values were similar within a treatment regardless of whether live or dummy conspecifics were used, suggesting that individuals show the same level of consistency. This study adds to our understanding of consistent individual differences by demonstrating that feedback may not affect responses to conflicting stimuli and that male threespine stickleback respond in a consistent manner to both dummy and live stimuli [Current Zoology 57 (1): 101–108, 2011].

Key words Decision-making, Stimulus efficacy, Behavioural consistency, Repeatability, Threespine stickleback

Individuals are often forced to choose from a number of behavioural responses to survive in complex and variable environments. In these situations, individuals must assess the relevant stimuli, evaluate them for useful information, and then act based on the perceived information (Blumstein and Bouskila, 1996). Given that both the social and physical environment can change rapidly, decision-making must be a dynamic process to allow individuals to respond appropriately and individuals likely differ in the consistency and/or plasticity of their responses (e.g. Coleman and Wilson, 1998; Reale et al., 2000). Behavioural plasticity, the ability to adjust one’s behaviour to environmental change, and behavioural flexibility, an individual’s tendency to respond differently when repeatedly faced with the same situation, are often used interchangeably but could reflect very different processes (Wolf et al., 2008). One factor that might affect behavioural flexibility is the presence and behaviour of social partners in the area and individuals with different behavioural profiles may be influenced differently (Fox et al., 2009). For example, male guppies shift their courtship behaviour from conspicuous displays to sneak mating attempts when predation risk is high as a result of cues from females (Evans et al., 2002) and threespine stickleback adjust their levels of exploration in relation to their partners’ levels of boldness (Harcourt et al., 2009).

Some behaviours may not be able to be performed at the same time and individuals should act as if they weigh the costs and benefits of these alternatives before responding. Social environment may influence the costs and benefits an individual faces as a result of its behavioural responses (e.g. Moore et al., 1997). For example, male white-throated sparrows may either guard their nests to prevent extra-pair copulations (EPCs) or engage in EPCs themselves and their achieved fitness is both a product of their own behavioural choices and the social landscape with which they interact (Formica and Tuttle, 2009). Therefore, the costs and benefits of performing different behaviours may vary among individuals, even...
in apparently identical situations. In addition, feedback from other individuals in the area may also influence how individuals respond. Researchers often view this feedback as a confound and use a number of different techniques, such as using models of live conspecifics or video playback to reduce feedback and provide a standardized experience to all subjects (e.g. Ryan and Lea, 1994; Rowland, 1999 for review). However, tests performed with dummies (models resembling live conspecifics) or those conducted in nonsocial situations might not reflect natural behaviour because they may fail to capture dynamic behavioural responses to social cues; therefore, the effects of conspecific cues on behavioural consistency must be explored.

Systems with behavioural trade-offs provide a robust measure of individual consistency in the face of changing social environments because individuals must choose from sometimes mutually exclusive responses. Territorial males are often faced with a behavioural trade-off situation when a courtship-eliciting female and an aggression-eliciting male rival are present at the same time. The threespine stickleback Gasterosteus aculeatus is a model system suitable to investigate consistent individual differences in decision-making to conflicting stimuli for a number of reasons. Extreme morphological and behavioural differences exist among populations (e.g. Bell and Foster, 1994 for review; Girvan and Braithwaite, 1998) and individuals vary in boldness and aggression, levels of which are correlated (Bell and Stamps, 2004). During the breeding season, male threespine stickleback defend territories in close proximity to one another (Ridgway and McPhail, 1987) so males likely encounter both other males and females simultaneously regularly. The presence of a rival male has been found to interfere with courtship success (Sargent and Gebler, 1980; Rowland, 1988) and males appear to use a variety of tactics to reduce these interferences. These tactics include decreasing courtship duration, nesting in a vegetated area, and concealing courtship (e.g. Sargent and Gebler, 1980; Candolin and Voigt, 1998; Dziewczynski and Rowland, 2004).

The trade-offs between foraging behaviour and predation risk (Verdolin, 2006 for review) and between mate choice and predation risk (e.g. Godin and Briggs, 1996; Lewis and Cratsley, 2008) are well documented; however, less is known about trade-offs between courtship and aggression. Males may reduce the time they spend courting a female (e.g. Santangelo et al., 2002), increase nest guarding (Scagiansi et al., 2005), or court in concealed areas (e.g. Smith et al., 2003) when a rival is present. Males may also switch mating strategies, for example from conspicuous mating displays to sneak mating attempts, based on environmental factors such as conspecific male density and increased predation risk (e.g. Matthews et al., 1997; Evans et al., 2002). Although these studies clearly demonstrate that the presence of a rival leads to behavioural changes, how males might differ from one another in their responses is rarely examined (but see Morrell, 2004 for model; Dziewczynski et al., 2009).

Repeatability, a standard quantitative genetics measure based on within- and between-individual variation, is a useful tool to the study of consistent individual differences because it measures consistency over time and can provide insight into the proximate basis of the behaviour of interest (e.g. Bell et al., 2009; Wilson and Godin, 2009). Repeatability is the proportion of the total variance measured for a trait that is explained by differences among individuals and higher repeatability scores indicate that more variation is due to between- than within-individual differences (i.e. individuals respond in a consistent manner while differing from one another) and may suggest a genetic basis for the variation (Fallen and Mackay, 1996) as well as providing the substrate on which selection may reliably act (Brodie, 1989). We examined whether male threespine stickleback respond similarly to dummy and live conspecifics when presented with a male and female simultaneously to better understand how social feedback interacts with mutually exclusive behavioural responses. We also explored whether or not males demonstrate consistent individual differences in response to live conspecifics, as has been found with dummy stimuli (Dzieweczynski et al., 2009). Feedback from conspecifics could decrease individual consistency or lead to an increase in variation between males as individuals might adjust their behaviour in response to social feedback. Threespine stickleback individuals respond differently to risky situations not only as a result of their personality but also that of other individuals (Harcourt et al., 2009) and the degree to which an individual guppy inspects a predator is affected by the antipredator behaviour of its social partners (Bleakley and Brodie, 2009). However, because decision-making to conflicting stimuli may be genetically based in this species (Bakker, 1986), we predicted that individuals will behave similarly to both dummy and live stimuli as reflected by high repeatability scores. Males were therefore presented with both dummy and live aggression-eliciting males and courtship-eliciting females.
1 Materials and Methods

1.1 Subjects

Adult threespine stickleback were collected from saltwater marshes in Biddeford, Maine just prior to their breeding season in April 2008 and 2009. Individuals were brought to the Marine Science Center at the University of New England and stored in stack trays connected to a flow-through seawater system. Males were identified based on secondary sex characteristics (e.g. red coloration on the ventral surface and blue pigmented eyes) and then placed into individual tanks (52 x 26 x 16 cm$^3$) visually isolated from one another. Tanks contained a plastic dish filled with sand, a plastic plant designed to serve as a nest site, and algae for nesting material. All subject males were tested after they had built nests, which occurred within 48 hours of being placed in a tank and indicated that they had established a territory and entered the sexual phase. All fish were fed frozen brine shrimp (Artemia spp.) once daily. Sixteen males were used in 2008 and fourteen in 2009 for a total of thirty subjects.

1.2 Decision-making to conflicting stimuli: dummy presentations

Testing started 24 hours after a male had built his nest. Males were presented with one of three treatments in random order: dummy female alone, dummy male alone, or a dummy male and dummy female presented simultaneously. Dummies were made using the methods described in Rowland (1999) and the same two dummies were used throughout testing. Dummies were suspended from the middle of a thin metal rod that was positioned in the front quadrant of the tank with the dummies positioned to face the subject male’s nest. The male dummy was positioned in the aggressive “head-down” position while the dummy female was positioned in the receptive “head-up” position. To prevent side-bias in the paired treatment, the side on which each dummy was presented was randomized. Trials lasted for 5-min and started after the first dummy-directed behaviour. Males received 3 trials for each of the 3 treatments with no more than 2 trials a day that were at least 4 hours apart. Treatment order was randomized and males never received the same treatment type twice in a row. All trials were recorded on videotape for later analysis.

1.3 Decision-making to conflicting stimuli: live fish presentations

After males completed all 9 trials with the dummy stimuli, they were tested with live stimuli. As with the dummy stimuli, males received three 5-min trials for each of the three treatments: single live female, single live male, and live male and female presented simultaneously. Live conspecifics were presented in clear plastic containers placed in the front quadrant of the subject’s tank. When the male and female were presented together, these bottles were placed equidistant from one another in the front quarter of the tank. To rule out the behaviour of the live conspecific as a factor influencing the subject’s behaviour, the time the live stimulus fish spent orienting to the subject was then used as a covariate in later analyses. Different live stimulus fish were used in every trial.

1.4 Behaviours Measured

We measured all stimulus-directed behaviours including zigzags (the most common courtship behaviour) and bites (the most common aggressive behaviour) to both the male and female as well as dorsal pricking and leading to the female. Dorsal pricking occurs when a male extends his dorsal spines and rubs them along the belly or side of a female (Wilz, 1970). A male leads by turning sharply away from the female and moving in a direct path towards his nest (Wilz, 1970). Time spent fanning at the nest, gluing events, and whether or not the male crept through his nest during a trial were also noted (see Wootton, 1976 for descriptions). We used an event recording program (Event-PC) to analyze the data tapes.

1.5 Statistical Analyses

ANOVA's were conducted to assess if trial number influenced behaviour in any of the treatments when either dummy or live stimuli were used. In other words, these were used to determine whether males changed their responses over subsequent stimulus presentations or remained consistent. When trial order was not found to affect any of the behaviours during dummy presentations ($F_{2,15} \leq 2.33, P \geq 0.08$) or live presentations ($F_{2,15} \leq 2.91, P \geq 0.07$), the mean scores for each individual for each behaviour within a treatment were calculated and used for subsequent analyses. To determine if stimulus fish behaviour influenced that of the focal male, Pearson’s correlations between the behaviours of the focal male and the time a stimulus fish spent orienting towards him were tested. When stimulus fish behaviour was found to not affect male response (female-directed behaviours: $r \leq 0.09, P \geq 0.20$; male-directed behaviours: $r \leq 0.10, P \geq 0.19$), two-way repeated measures analyses of variance (RMANOVA) with post-hoc t-tests were then run to determine if treatment type (single female, single male, paired fe-
male-male) or stimulus type (dummy or live) influenced behaviour. Bonferroni adjustments at \( \alpha = 0.05 \) were applied to all comparisons to reduce compounding Type 1 error.

Repeatability scores for zigzags and bites were calculated to determine the consistency of individual responses and if individuals differed from one another in their responses within a given treatment. Repeatability (R) can be estimated by taking repeated measures and then calculating the ratio of the among-individual variance (\( \sigma^2_w \)) to the total variance (i.e. the sum of both the among-individual and within-individual variances; \( \sigma^2_w + \sigma^2_a \)) with \( R = \sigma^2_w / (\sigma^2_w + \sigma^2_a) \) (Falconer and Mackay 1996). These variance components were calculated by dividing the appropriate mean squares obtained from ANOVAs with individual as the main effect (Lessels and Boag 1987) and standard errors were calculated per Becker (1984).

2 Results

2.1 Female-directed behaviours

Treatment type (single female or paired female-male) influenced zigzags to the female \( (F_{1, 29} = 19.56, P < 0.0001) \) but not bites, leads or dorsal pricks to the female \( (F_{1, 29} \leq 2.80, P \geq 0.06) \). Males performed more zigzags to the female when she was presented alone than when she was presented with the male for both the dummy and live stimuli \( (t \geq 4.42, n = 30, P \leq 0.0001; \) Figure 1a). Stimulus type (dummy vs. live conspecific) affected dorsal pricks, bites, and leads to the female \( (F_{1, 29} \geq 4.33, P \leq 0.04) \). Males performed more dorsal pricks and leads to the dummy than the live female \( (t \geq 2.08, n = 30, P \leq 0.04) \) but bit the live female more than the dummy female \( (t = 5.68, n = 30, P < 0.0001; \) Fig. 1b). No interaction effects were found between treatment and stimulus type for any female-directed behaviours \( (F_{1, 29} \leq 3.18, P \geq 0.08) \).

2.2 Male-directed behaviours

An interaction was found between treatment and stimulus type for zigzags only \( (F_{1, 29} = 35.59, P < 0.0001) \), with subject males zigzagging to the male more in the dummy single male condition than in all other conditions \( (t \geq 8.17, n = 30, P \leq 0.0001; \) Fig. 2A). Both treatment \( (F_{1, 29} = 24.90, P < 0.0001) \) and stimulus type \( (F_{1, 29} = 5.57, P = 0.02) \) affected the number of bites males delivered to the stimulus male. Males bit the male more in the single male than paired male-female treatment \( (t = 4.10, n = 30, P < 0.0001) \) and when a live stimulus was used \( (t = -6.61, n = 30, P < 0.0001; \) Fig. 2B).

Head down displays to the male were not affected by treatment or stimulus type \( (F_{1, 29} \leq 1.05, P \geq 0.31) \).

2.3 Nest-directed behaviours

Both treatment \( (F_{2, 29} = 21.82, P = 0.0001) \) and stimulus type \( (F_{1, 29} \geq 8.13, P \leq 0.005) \) influenced the time males spent fanning at their nests. Males fanned more when a single female was present \( (t \geq 4.67, n = 30, P < 0.0001) \) and when dummies were used \( (t \geq 2.79, n = 30, P \leq 0.006) \). Males also glued and crept through their nests more in the single dummy female treatment \( (t \geq 2.52, n = 30, P \leq 0.01) \) than when a male was present or

Fig. 1 The two main behaviours directed towards the female, zigzags (A) and bites (B), in the paired and single treatments when dummy and live stimuli were used

Error bars represent ± 1 SEM. Differing letters represent significant post-hoc comparisons.
Fig. 2 The mean number of the two main behaviours directed toward the male, zigzags (A) and bites (B), in the paired and single treatments. Error bars represent ± 1 SEM.

2.4 Repeatability

Repeatability values (Table 1) of 0.500 or greater reflect high repeatability and, therefore, more variation due to between- than within-individual differences (i.e. at least 50% or more of the variance is due to differences among individuals, which can only happen if individuals are consistent). Both zigzags to the female and bites to the male showed high repeatability in all conditions, suggesting that males were consistent for these behaviours while differing from one another within a context (Table 1). Repeatability for zigzags to the female was slightly lower when a male stimulus was present compared to the single female treatment. Bites to the female were only highly repeatable in the male-female treatment although male responses varied between the single and paired female treatments (Table 1). Repeatability scores were calculated for all other behaviours (e.g. leads, dorsal pricks, and all nest-directed behaviours); however they were more modest (< 0.180) and were similar across contexts for each behaviour (varying no more than 0.030 from one another).

3 Discussion

Individual differences in behaviour have been widely studied in recent years and have recently been viewed as adaptive in themselves rather than simply being ‘noise’ around an adaptive mean (Wilson, 1998; Dall et al., 2004). It has already been established that male threespine stickleback vary from one another in their behaviour when a male and a female are presented simultaneously (Dziewczynski et al., 2009); it was not known, however, whether individuals would still respond when live stimuli were used. Males rarely crept through or glued their nests when live stimuli were used (only two males ever performed these behaviours with live stimuli present) so these behaviours were not analyzed.

| Table 1 | Repeatability scores (R ± SE) for the two main behaviours: zigzags to female, bites to female, zigzags to male and bites to male |
|-------------|-----------------|-----------------|-----------------|-----------------|
|            | Single Dummy    | Paired Dummy    | Single Live     | Paired Live     |
| Zigzag female | 0.831 ± 0.05;  | 0.596 ± 0.09;  | 0.836 ± 0.05;  | 0.606 ± 0.09;  |
|              | $F_{29, 89} = 15.80, P < 0.0001$ | $F_{29, 89} = 15.26, P < 0.0001$ | $F_{29, 89} = 16.07, P < 0.0001$ | $F_{29, 89} = 13.18, P < 0.0001$ |
| Bite female  | 0.207 ± 0.12;  | 0.712 ± 0.08;  | 0.246 ± 0.12;  | 0.708 ± 0.08;  |
|              | $F_{29, 89} = 6.18, P = 0.01$ | $F_{29, 89} = 13.99, P < 0.0001$ | $F_{29, 89} = 3.40, P = 0.003$ | $F_{29, 89} = 8.29, P < 0.0001$ |
| Zigzag male  | 0.179 ± 0.12;  | 0.192 ± 0.12;  | 0.041 ± 0.11;  | 0.104 ± 0.11;  |
|              | $F_{29, 89} = 1.49, P = 0.10$ | $F_{29, 89} = 1.71, P = 0.07$ | $F_{29, 89} = 0.89, P = 0.63$ | $F_{29, 89} = 1.35, P = 0.16$ |
| Bite male    | 0.706 ± 0.08;  | 0.758 ± 0.07;  | 0.767 ± 0.07;  | 0.801 ± 0.06;  |
|              | $F_{29, 89} = 8.21, P < 0.0001$ | $F_{29, 89} = 10.37, P < 0.0001$ | $F_{29, 89} = 18.22, P < 0.0001$ | $F_{29, 89} = 19.55, P < 0.0001$ |

P values are Bonferroni corrected and high repeatability values (i.e. ≥ 0.500) are given in bold. The F statistic and associated P values reported are the results from the repeated measures ANOVA used to calculate each repeatability value.
consistently when the stimuli could interact with the focal animal (but see Bell et al., 2009). As predicted, male threespine stickleback in this study exhibited consistent differences in their responses when a male-female pair was presented simultaneously and this consistent individual variation was found regardless of whether dummy or live stimuli are used. While males reacted the same way within a given treatment regardless of stimulus type, their responses decreased when the male and female were presented simultaneously. There was one exception to this; males were more aggressive to both the female and male when live stimuli were used. The decrease in courtship may result from males dividing their time between the two stimuli and is consistent with the reduction in aggression between the single male and paired treatments as well. However, these explanations are not mutually exclusive and courtship reduction when a rival male is present is common across territorial fish species (e.g. Rowland, 1988; Kangas and Lindström, 2001; Wong, 2004). It could be advantageous for a male to reduce his courtship attempts when other males are present. The male may switch from courting to attempting to remove the rival from the area because rivals are detrimental to courtship success in this species. Males in our study divide their time between courtship and aggression in our study, perhaps as a way to deter rivals.

Increased aggression to the live female compared to the dummy female may be explained by live females not always adopting the head-up posture of the dummy female, as male threespine stickleback switch from courtship to aggression when a dummy female is presented in a horizontal posture; yet this does not occur when the dummy female is presented in a head-up courtship posture (Rowland, 2000). Males may also view live stimuli as more threatening than dummy stimuli, which is consistent with both the increase in aggression to the female and male and the decrease in time spent at the nest when live conspecifics were used. Finally, live conspecifics could simply elicit a greater response than dummy conspecifics. If this was the case, however, we would expect to see an increase in all conspecific-directed behaviours and not just bites. Together, our data demonstrate that males remain consistent in their responses to conspecifics even when feedback from these conspecifics is present. This indicates that social feedback does not override differences between individuals or lead to greater within individual variability. The ability to interact with the stimulus does appear to influence the nature of interactions to some degree, however, since males exhibit greater responses to live conspecifics compared to dummy stimuli.

Repeatability levels were comparable when either dummy or live conspecifics were used (Table 1). Males were consistent in all measured behaviours except for zigzags to the live male and behaved similarly across trials of a given treatment type. While an increase in bites and a decrease in courtship were observed when live stimuli rather than dummy stimuli were used, repeatability values did not differ for either of these behaviours. Although males were more aggressive to the live stimuli, individual responses did not change as a result of stimulus type. Repeatability quantifies variation between individuals or populations while consistency quantifies variation within individuals. Because repeatability is a ratio, it is expressed relative to the variation between individuals and can be considered to place an upper bound on heritability (Boake, 1989 but see Dohm, 2002), although it should not be viewed as a substitute for actual heritability studies. Thus, it is useful to conduct these studies before assumptions about the genetic basis of these traits can be made as behaviours with low repeatability are unlikely to have high heritability. Additional studies on the repeatability and heritability of behavioural tradeoffs are needed to examine whether the observed consistent individual differences have a genetic basis.

In numerous species, individuals differ consistently from one another in their behavioural responses. Central to this theory of animal personality is the notion that individual behaviour should be repeatable, or consistent over time (Dall et al., 2004). This does not mean, however, that trait expression must be absolutely constant across contexts but rather that the relative level of expression by an individual in relation to others in the population will be correlated across contexts (Johnson and Sih, 2007; Sih and Bell, 2008). Social environment may interact with personality to generate behaviour within and across contexts (e.g. Sih and Watters, 2005; Nelson et al., 2008; Schuett and Dall, 2009). For example, male sagebrush lizards vary consistently from one another in their courtship behaviour yet alter their courtship intensity based on female receptivity (Ruiz et al., 2008). Also, any evidence of behavioural syndromes disappears when the behaviour of male chickens is analyzed in the absence of a dominance hierarchy (Nelson et al., 2008).

Alternatively, behaviour across contexts may involve behavioural plasticity, defined as a degree of flexibility within an individual’s repertoire that allows him or her to adjust their behaviour based on the present context.
(Dall et al., 2004). Even if individuals are consistent within a given context factors in the physical or social environment may reduce consistency. For example, increased competition leads garter snake males to switch mating tactics from obvious courtship behaviours to sneak attempts (Shine et al., 2003) while an increase in male density causes male two-spotted gobies to court more (de Jong et al., 2009). Two conclusions emerge from our data, however. First, we observed biologically relevant responses in every situation with both the dummy and live stimuli, and thus conclude that dummies therefore can be used effectively to understand individual consistency and trade-offs in this system. Second, males changed their responses when a male and female were presented together compared to when they were presented singly while behaving consistently within a given treatment, demonstrating consistent behavioural flexibility. Although selection may not act on traits with low repeatability because individuals are not acting consistently (Brodie and Russell, 1999), selection may act on plasticity if it is expressed in a consistent manner (reviewed in Pigliucci, 2001). Therefore, even behavioural flexibility may be predictable which would allow selection to act while still allowing males to adjust their behaviour appropriately to changes in the social environment.

This study was designed to explore whether or not male threespine stickleback exhibited consistent individual differences when faced with feedback from live stimuli. Individuals were consistent in their responses within a treatment while varying from one another, indicating that male behaviour can be reliably predicted across time and/or contexts. However, males were more aggressive when live rather than dummy stimuli were used, regardless of whether these stimuli were presented alone or together. Although males were more aggressive, the responses of each individual remained similar regardless of stimulus type. Repeatability values were also similar regardless of whether live or dummy stimuli were present. This study suggests that variation between threespine stickleback is due, at least partially, to inherent, permanent differences within individuals because males did not change their behaviour as a result of feedback from live stimulus fish. Therefore, consistent individual variation in decision-making to conflicting stimuli exists in this species and the mechanisms and consequences of this variation can be further explored.

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