



Predator-induced changes in the boldness of naïve field crickets, *Gryllus integer*, depends on behavioural type

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In recent years, using a personality approach for studies of animal behaviour has increased our ability to predict an individual's or population's behavioural responses to external stimuli. At a population level, different behavioural types (e.g. bold and shy) often exist, and the behaviour of different types may not be free to vary across different situations. In the present study, we examined whether a predator introduction induced shifts in boldness and if predator-induced changes in behaviour depended on the individual's original behavioural type in the field cricket *Gryllus integer*. We also studied whether exposure to a natural predator affected the formation of a behavioural syndrome between aggression and boldness or the consistency of boldness. We define a behavioural syndrome as an association between functionally different behaviours or consistency in a behaviour over time or contexts. We found that exposure to a predator affected behavioural antipredator responses, measured as the time to recover from freezing (immobility). Moreover, we found that the different behavioural types expressed different behavioural responses to predator introduction (i.e. shy individuals became bolder and bold individuals more shy). However, an aggressiveness–boldness behavioural syndrome was not detected in either the treatment or control groups, and early antipredator responses were rank order repeatable only in the control group. We suggest that individuals' behavioural antipredator responses under increased predation risk depend on the individual's original behavioural type and that increased risk may break apart the consistency of behaviour.

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Behavioural ecologists have studied the plasticity of behaviour for several decades, but studying behavioural plasticity with respect to behavioural syndromes is a more recent phenomenon. A behavioural syndrome approach assumes that at the population level, different behavioural types are found (e.g. 'bold' and 'shy' individuals), and that behavioural plasticity is limited so that the individual's behavioural type is relatively consistent across time or between different ecological contexts (Sih et al. 2004; Stamps & Groothuis 2010). According to recent theoretical studies regarding behavioural syndromes (i.e. an association between functionally different behaviours or consistency in a behaviour over time or contexts) and their relationship to behavioural plasticity, the level of plasticity of behaviour may vary among different behavioural types (Wolf et al. 2008; Dingemans et al. 2010; Stamps & Groothuis 2010). This is expected, since plasticity can have significant energetic and mortality costs compared to nonplasticity and

individuals differ in their abilities to pay these costs (Dewitt et al. 1998; Ernande & Dieckmann 2004; Wolf et al. 2008; Auld et al. 2010). Additionally, individuals may vary in their abilities to perform costly behaviours such as predator escape, resulting in different behavioural responses to environmental stimuli (Cressler et al. 2010).

In technical terms, individual behavioural reaction norms (i.e. behaviour * environmental interactions) may differ so that an individual can only produce a limited set of behavioural responses to certain environmental stimuli (Dingemans et al. 2010). This is possibly because reactive (shyer) and proactive (bolder) individuals may differ in the precision and efficiency of their information acquisition or usage potential (Koolhaas et al. 1999; McElreath & Strimling 2006; Wolf et al. 2008), making different behavioural responses between behavioural types beneficial. According to the proactive–reactive axis for behavioural types, reactive individuals, which are shyer and less aggressive, should search their environment more thoroughly and therefore should be more sensitive and reactive to environmental cues and express more behavioural plasticity (Koolhaas et al. 1999) than proactive behavioural types.

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Despite the apparently conflicting interaction between the behavioural plasticity and behavioural syndrome approaches (the latter of which implies limited behavioural plasticity), the two ideas are not mutually exclusive. The behavioural syndrome approach is not violated by plastic expression of behaviours if relative differences between individuals remain stable (Wolf et al. 2008). Plastic individuals have the potential advantage of being able to adapt their behaviour to multiple environments (Sih 1992; Dewitt et al. 1998; Sih et al. 2004). However, extremely variable environments may make plasticity overly costly, because individuals cannot keep up with changes in the environment or required plasticity is simply too expensive and thus maintaining a single behavioural strategy may be more adaptive. In a stable environment less plastic individuals may have an advantage over plastic ones because of the energetic costs of plasticity.

Predation is a major ecological force affecting the behaviour and survival of individuals (Lima & Bednekoff 1999; Preisser et al. 2005; Cressler et al. 2010; Kortet et al. 2010; Luttbeg & Sih 2010). Individuals can respond in life historical, morphological and behavioural ways to predators (Boeing et al. 2006; Cressler et al. 2010). The magnitude of and associations between predation pressure, an individual's state and different feedback mechanisms may facilitate the formation of stable behavioural differences between individuals (i.e. behavioural types; Luttbeg & Sih 2010). Predation pressure may even determine whether or not behavioural syndromes develop in a population or species (Bell 2005; Dingemanse et al. 2007; but see Pruitt et al. 2010). For example, Bell & Sih (2007) found that exposure of three-spined sticklebacks, *Gasterosteus aculeatus*, to a piscivore predator created a positive aggressiveness–boldness syndrome that did not exist prior to exposure. The syndrome was caused by both predation-induced selection and behavioural plasticity (Bell & Sih 2007). Therefore, environmental factors, such as predation pressure, can change the behaviours and alter the associations between behaviours leading to the formation of a behavioural syndrome as a response to the current environment (see also Dingemanse et al. 2007).

Using field crickets, *Gryllus integer* that had no prior experience with predators, we studied whether exposure to a natural predator affects subsequent boldness and whether there were differences in predator-induced shifts in behaviour between different behavioural types. Previously, we had found that there are stable behavioural types in a *G. integer* population originating from Davis, California (Hedrick & Kortet 2012; Niemelä et al. 2012, unpublished data), where our study was conducted. Moreover, we examined whether our treatments affected the formation of behavioural syndromes, that is, consistency of boldness or association between aggression and boldness, which has previously been found in several taxa (Bell 2005; Moretz et al. 2007; Kortet & Hedrick 2007). First, we predicted that individuals in the predator treatment should change their behaviour more than those in the control group and that different behavioural types might have different behavioural responses to a predator threat so that shy individuals would change their behaviour more (Coleman & Wilson 1998; Koolhaas et al. 1999). The directions of these shifts in behaviours are probably context-dependent. Second, we predicted that the positive association between aggressiveness and boldness would only develop in the predator treatment (Bell 2005; Bell & Sih 2007; Dingemanse et al. 2007).

METHODS

The crickets we used were first-generation offspring of parents collected from a wild population (Davis, California, U.S.A.). Crickets were maintained in a laboratory at the University of California, Davis, U.S.A., under a constant 12:12 h light:dark cycle at $25 \pm 1^\circ\text{C}$ with ad libitum food and water. All the experimental crickets were reared in

sibling boxes (300 × 150 mm and 100 mm high) and moved to individual containers (100 mm diameter × 80 mm height) when they reached the fifth to sixth larval instar. At 6–10 days past sexual maturation, the males were placed individually in plastic containers (i.e. one male in one container; 540 × 270 mm and 135 mm high) to mimic their natural territories. These containers included a cardboard shelter. Water and food were supplied ad libitum. Crickets were given 24 h to acclimate in a container after which most males started calling, indicating that they viewed the containers as territories. We conducted experiments on one 20-male group/week for 9 weeks (altogether 180 males). Males were selected randomly for these groups.

After 24 h of acclimation, the first boldness trials (B1; see below) were conducted. Based on B1 results, the males were ranked from the most bold to the least bold in groups of 20 individuals. Each male was then paired with the closest ranked male that was within a 10% range of his body mass (i.e. shy paired with shy and bold paired with bold). After pairs were designated, individual males were anaesthetized using CO₂ for marking with nontoxic white paint on the left or right side of their pronotum for identification during the later aggression trials (after B2). We randomly divided the 154 males into a predator treatment (77) and a control group (77). Our sample size did not reach 180 individuals (see above) owing to natural mortality and since we were unable to pair all of the males for the aggression trials based on body mass.

Forty-eight hours following the B1 trials, we divided the crickets according to their treatments (predator treatment and control). We used the western toad, *Bufo boreas*, as a predator, which is an opportunistic natural predator on field crickets in Davis, California where the crickets were obtained. We had three toads, which were randomly assigned to predation treatments. The toads were collected from Davis, California as per a Scientific Collecting Permit issued by the California Department of Fish and Game. Previous to the experiment the toads were fed live crickets. Toads were maintained in the laboratory in individual plastic containers (540 × 270 mm and 135 mm high) with ad libitum access to water and field crickets. After the experiments in this study, toads remained in the laboratory in their plastic containers for additional experiments. In the predator treatment we placed a toad inside the 'territory' containers. The toad was allowed to move freely inside a cricket's territorial container. Some of the crickets were eaten by the toad ($N = 2$). In the control group we just opened and closed the lids of the containers to control for the disturbance caused by placing the toad inside the predator treatment containers. The duration of the treatments was 30 min after which we performed the second boldness trials (B2). All B2 trials were conducted within 5–10 min following the treatment. Both B1 and B2 trials lasted for 20 min. After B2 trials we conducted aggression trials (see below; 60–120 min after B2 trials).

All behavioural trials were performed in a sound-proof, temperature-controlled dark room ($27 \pm 1^\circ\text{C}$) in which the experimental setting was composed of a computer, a desk and experimental arenas. Since *Gryllus* spp. probably cannot see long (red) wavelengths properly (Briscoe & Chittka 2001), dim red light mimics dark conditions. We therefore used a dim red light (25 W red incandescent bulb) to minimize potential disturbance by the observer. All the experiments were carried out at approximately the same time, between 0900 and 1300 hours.

The research conformed to the legal requirements of the U.S. (California Department of Fish and Game Scientific Collecting Permit 006354, and University of California Davis IACUC protocol 15745).

Boldness Trials

We used the same methods of behavioural testing to assess the 'boldness' of individual crickets as described previously in Hedrick

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