



The effects of the social environment and physical disturbance on personality traits

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The environment can have a considerable impact on behaviour. The social environment is predicted to be a particularly important driver of behavioural variation and evolution through the indirect genetic effects that arise whenever individuals interact with conspecifics. We used male Australian field crickets, *Tel-eogryllus oceanicus*, to examine the effects of changes in the social environment (recorded acoustic sexual signals of other males) on the expression and consistency of boldness, activity and exploration, and their between-individual covariation. Switching from a silent environment to being exposed to male acoustic sexual signals resulted in crickets becoming less bold, active and explorative. Switching from an acoustic to a silent environment resulted in increased boldness and activity. We also looked at the effects of changes in the nonsocial environment via a physical disturbance that mimicked the presence of a potential predator (mechanical shaking). The effects of physical disturbance (and changes thereof) on behaviour were far less pronounced than the effects of changes in the social environment. Neither the repeatability of nor correlations between behaviours were affected by changes in physical disturbance. Only the average level of exploration was affected significantly when crickets were moved from an undisturbed to a disturbed environment, with crickets becoming less explorative. Although changes in the social and the nonsocial environment affected the repeatability of and correlations between some of the behaviours measured, changes in the social environment had the greater effect. We discuss the ecological and evolutionary implications of our findings and how they relate to our current understanding of social and nonsocial environmental effects on behaviour.

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The effect of environmental factors on animal phenotypes is well established. In particular, the behaviour of an animal can be profoundly influenced by its social environment. In honeybees, *Apis mellifera*, for example, brood pheromone has been found to affect the age at which workers start foraging (Le Conte, Mohammadi, & Robinson, 2001) and in bank voles, *Myodes glareolus*, male expenditure on the ejaculate can be affected solely by the presence of rival male pheromones in the environment (delBarco-Trillo & Ferkin, 2004). Similarly, we have known for some time that different levels of predation risk affect both nonbehavioural (Creel, Christianson, Liley, & Winnie, 2007; Hawlena & Schmitz, 2010) and behavioural traits (Briffa, Rundle, & Fryer, 2008; Lima & Dill, 1990; Werner, Gilliam, Hall, & Mittelbach, 1983) that serve in predator avoidance in both vertebrate and invertebrate taxa.

Investigating between-individual (animal personality) and within-individual behavioural variation (phenotypic plasticity) together (Dingemanse, Kazem, Réale, & Wright, 2010) has attracted increased interest in recent years. Different explanations for such behavioural variation have been proposed. Besides adaptations to endogenous attributes such as cognitive ability (Sih & Del Giudice, 2012) and metabolism (Wolf & McNamara, 2012), between-individual behavioural variation may be shaped by exogenous factors such as predation threats (e.g. Bell & Sih, 2007; Sih, Kats, & Maurer, 2003) or social environments (Montiglio, Ferrari, & Réale, 2013; Wolf & McNamara, 2013). When individuals interact with conspecifics in a way that influences their own behaviour (interacting phenotypes; Moore, Brodie III, & Wolf, 2009), indirect genetic effects (IGEs) are predicted to arise, where the genes of interacting individuals affect the expression of traits in one another (Moore et al., 2009; Wolf, Brodie, Cheverud, Moore, & Wade, 1998). A diverse range of selective pressures can therefore result from social interactions which might prove to be especially important drivers of behavioural variation (Bailey, Marie-Orleach, & Moore, 2017). Similarly, we can expect behavioural plasticity in the light of

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predation risks. However, plasticity in response to such risks may be more costly (and therefore lower) because incorrect decisions often lead to death (which is not the case for plasticity in response to social cues). Thus, behaviour may be optimized to maximize survival in different environments. In a recent review, [Bailey et al. \(2017\)](#) suggested that behaviour is particularly prone to variation in the social environment. Such variation should therefore have a greater impact on behavioural plasticity than other aspects of the environment such as the presence of predators. Some recent theoretical papers suggest that there are coevolutionary processes that lead to the existence of both socially responsive and consistent individuals as a result of negative frequency dependence ([Johnstone & Manica, 2011](#); [McNamara, Stephens, Dall, & Houston, 2009](#); [Wolf, Van Doorn, & Weissing, 2011](#)). Although predators and prey coevolve, the presence of different predators and a diversity of prey may dilute these effects in comparison to social interactions within species. Thus, we may expect social interactions to have more pronounced effects on behavioural plasticity. Much remains to be learned about the ways in which environmental cues shape between- and within-individual behavioural variation. Here we investigated the effects of different environmental cues (social versus nonsocial) on behavioural plasticity within the same experimental framework.

We used Australian field crickets, *Teleogryllus oceanicus*, to test the hypothesis that the environment, and changes therein, can affect behavioural expression (phenotypic plasticity), the repeatability of behaviours (a phenomenon often referred to as 'animal personality': [Bell, Hankison, & Laskowski, 2009](#); [Gosling, 2001](#)) and correlations between multiple behavioural traits ('behavioural syndromes': [Bell, 2007](#); [Sih, Bell, Johnson, & Ziemba, 2004](#)). We manipulated two aspects of the environment, the social environment via acoustic cues from conspecifics, and the physical environment via mechanical disturbance, and examined the effects of the presence and absence of these cues on male behaviour. In crickets, acoustic sexual signals have been found to affect aggression, dominance, female mate choice and alternative mating tactics ([Bailey & Zuk, 2008](#); [Bailey, Gray, & Zuk, 2010](#); [DiRienzo, Pruitt, & Hedrick, 2012](#)). Males from various cricket species have been found to be attracted to conspecific song, forming clusters in which individuals remain relatively stationary while broadcasting acoustic sexual signals ([Campbell & Shipp, 1979](#); [Simmons, 1988](#); [Tinghitella, Wang, & Zuk, 2009](#)). Based on these findings, we predicted that males would be more likely to engage in searching behaviour (emerge quickly from a shelter and be more explorative and active in search of conspecifics) in the absence than the presence of conspecific calls. Different levels of predation or parasitism risk can affect how cautiously individuals behave ([Hedrick & Kortet, 2006](#); [Lewkiewicz & Zuk, 2004](#)). Therefore, we might expect the presence of a physical disturbance to render crickets less active and less bold than crickets that are not exposed to disturbances. However, we expected the effect of disturbances in the environment to be small compared to changes in the social environment owing to the special role that the social environment is imputed to have in the evolution of animal behaviour ([Bailey et al., 2017](#)).

In a previous study ([Rudin, Tomkins, & Simmons, 2017](#)), we found that changes in dominance status eroded the repeatability of some behaviours, but that boldness (latency to emerge from a shelter) remained relatively stable. Additionally, changes in social status had a disruptive effect on the correlation between boldness and activity, but not on the correlation between boldness and exploration. Because of the links between social status and acoustic sexual signals (e.g. [Brown, Smith, Moskalik, & Gabriel, 2006](#); [Callander, Kahn, Hunt, Backwell, & Jennionsa, 2013](#); [Simmons, 1986](#)), we predicted that changes in such signals will similarly affect the repeatability of and correlations between behaviours.

Previous studies have investigated environmental effects on the repeatability and expression of behaviours by exposing animals to different environments, measuring them repeatedly in the same environment. There is a distinct lack of studies that have investigated the effects of relatively short-term environmental changes on the repeatability and expression of and correlations between behaviours. Our experimental design allowed us to investigate the effects of such changes. Additionally, comparing individuals that experienced a switch in environments to those that did not allowed us to infer the presence or absence of between-individual variation in behavioural plasticity, or individual-by-environment interactions (IxEs; [Alonzo, 2015](#); [Dingemans & Wolf, 2013](#); [Mathot, Wright, Kempnaers, & Dingemans, 2012](#); [Stamps, 2016](#)). Although researchers have recently begun to focus on IxEs, much remains to be learned about them, especially in the light of changes in the social environment ([Bailey et al., 2017](#)).

METHODS

Study Population

The animals used in this experiment came from a large outbred laboratory stock population (>1000 individuals) which is restocked annually with freshly collected individuals from Carnarvon (Western Australia). Animals were reared with ad libitum access to food and water and held at 26 °C on a 12:12 h light:dark cycle. At the final larval instar, males ($N = 208$) were taken from the stock population and housed in individual clear plastic containers (7×7 cm and 5 cm high). Individuals were checked daily and placed into experimental treatments the day following their final moult to adulthood.

Experiment 1: Sociosexual Environment

In our first experiment, crickets were exposed to the presence and absence of acoustic sexual signals from conspecific males. Four groups of 26 crickets each (total $N = 104$) were assigned to four separate environmental chambers, two silent and two acoustic. We clipped the tegmen of all crickets to ensure they could not produce song. Within the acoustic chambers, 5 min recordings of about 30 sexually mature males housed with an equal number of females were played back continuously. These recordings included a mixture of calling, courtship and aggressive song. The playback devices were MP3 players (iPod nano 7th Gen and iPod classic 6th Gen) and speakers (Logitech Z200 Multimedia Speakers and Philips Speaker Dock SBD8000/79). The light:dark cycles of all chambers were set to 12:12 h light:dark and all were held at 26 °C. After 1 week of exposure to either the silent or acoustic environments, behavioural trials were conducted as described below. After behavioural trials, half of the crickets were returned to the same treatment they had been exposed to previously, while the other half switched treatment, either from the silent to the acoustic or from the acoustic to the silent treatment. Crickets were again exposed to these treatments for a week after which behavioural trials were repeated. This resulted in four groups of individuals at the end of the two trials: AA (acoustic environment for first week, acoustic environment second week), AS (acoustic environment for first week, silent environment second week), SS (silent environment for first week, silent environment second week) and SA (silent environment for first week, acoustic environment second week) ([Fig. 1](#)). Each of these groups consisted of 26 individuals.

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