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Predicting multifarious behavioural divergence in the wild

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Many animals show complex behaviours that can have important ecological and evolutionary consequences. Environmental variation can lead to divergent selection that consistently favours particular behaviours in different environments; but how predictably multiple aspects of animal behaviour diverge in response to different environmental conditions remains unclear. We tested whether populations evolving under different levels of predation risk show predictable and repeatable population-level behavioural differences in all five primary components of animal personality: aggression, sociability, boldness, activity and exploration. We formulated and tested a priori predictions of divergence for each behaviour using the adaptive radiation of Bahamas mosquitofish, *Gambusia hubbsi* (family Poeciliidae), inhabiting vertical water-filled caves (blue holes) where they have evolved for thousands of years in either the presence or absence of predatory fish. Mosquitofish behaviours differed consistently, and largely predictably, between predation regimes: low-predation mosquitofish showed reduced sociability and greater exploration of a novel environment compared to high-predation counterparts. However, some differences were sex dependent: only females showed greater boldness and only males displayed reduced aggressiveness in low-predation populations. Activity levels did not differ between predation regimes. All populations showed a behavioural syndrome characteristic of either proactive or reactive stress-coping styles with regard to exploration. Exploration behavioural syndromes were more similar among populations that evolved in similar predation regimes, regardless of genetic relatedness. Using laboratory-born, high-predation mosquitofish, we confirmed that exploratory behaviours have a genetic basis and show significant within-individual repeatability. Our results suggest that environmental variation, such as chronic predation risk, can lead to repeatable, and often predictable, changes in multifarious animal behaviours, and that various aspects of behaviour can diversify more or less independently of one another. Considering the ecological importance of these behaviours, the ability to forecast behavioural shifts in a rapidly changing world could serve as a valuable conservation tool.

Many animals regularly display distinct behaviours that have important fitness consequences and influence ecological patterns (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Westneat & Fox, 2010; Wolf & Weissing, 2012). Selection from environmental factors, especially stressors such as predation risk, could consistently and simultaneously act on multiple behaviours, favouring different suites of behavioural types under different conditions (Bell, 2005; Dingemanse et al., 2007). Predation risk is known to affect complex social behaviours in diverse prey taxa (Langerhans, 2006; Lima & Dill, 1990; Réale & Festa-Bianchet, 2003) and may concurrently drive repeatable and predictable evolution in multifarious animal behaviours. However, we currently have a poor understanding of how predictably multiple aspects of animal behaviour evolve in the wild.

Réale, Reader, Sol, McDougall, and Dingemanse (2007) described five broad behavioural categories of animal 'temperament' or 'personality': (1) aggression, (2) sociability, (3) boldness, (4) activity and (5) exploration (for definitions, see Table 1). Although these behaviours are frequently investigated within the context of animal personality per se (i.e. within-individual repeatability), they appear to capture the major axes of variation in complex animal behaviour more broadly. Recent years have witnessed growing interest in understanding why individual animals, populations or species may differ in these behavioural categories. Yet to our knowledge, no prior study has investigated

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Table 1
Description of the five categories of animal behaviour examined in this study (from Réale et al., 2007), and our a priori predictions of divergence (see text for details and references)

Behavioural category	Definition and prediction rationale
Aggression	An individual's agonistic reaction toward conspecifics
Prediction: lower in LP	Reduced selection for grouping behaviours that can lead to aggression in LP Greater survivorship of aggressive individuals in HP
Sociability	An individual's tendency to avoid or associate with conspecifics
Prediction: lower in LP	Increased intraspecific competition in LP Survival advantages of social grouping in HP
Boldness	An individual's reaction to a risky, but not novel, situation
Prediction: greater in LP	Absence of lethal agents in LP Selection for wariness in HP, especially with abundant resources
Activity	An individual's general level of activity in a non-novel situation
Prediction: no difference	Similar overall needs for foraging, mating, social interactions
Exploration	An individual's reaction to a novel situation
Prediction: greater in LP	Foraging advantages of exploration in LP Mortality risks of exploratory behaviours in HP

LP: low predation; HP: high predation.

population-level responses of all five behavioural categories to environmental variation within a single study system. Such a study could provide critical insights into the sources of among-population variation in diverse aspects of animal behaviour, the extent to which different behaviours show adaptive responses versus physiological or genetic constraints and our ability to predict complex behavioural changes a priori.

As a first step in the evaluation of the predictability of multifarious behavioural changes in response to ecological variation between populations, we should (1) generate clear, a priori predictions of changes in all five behavioural categories based on theory, prior empirical study and natural history of the relevant system, (2) investigate intraspecific divergence to avoid confounding variables inherent in among-species comparisons, (3) examine multiple, independent populations to avoid confounding effects of shared ancestry and gene flow and (4) use a relatively simple natural system where populations vary in a small number of readily identifiable ecological factors to avoid confounding effects of other environmental variables (e.g. see Langerhans, 2010; Martin, McGee, & Langerhans, 2015). We accomplished this by developing and testing predictions of divergence in all five behavioural aspects of personality within a model system for adaptive diversification: Bahamas mosquitofish, *Gambusia hubbsi*, inhabiting vertical water-filled caves (blue holes) across Andros Island. *Gambusia* fishes are well studied in personality research, showing many individually consistent complex behaviours readily amenable to field and laboratory study (e.g. Biro & Adriaenssens, 2013; Blake & Gabor, 2014; Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010, 2011; Ward, 2012; Wilson, Godin, & Ward, 2010). However, we know little about how populations might jointly diverge in mean values of multiple behavioural components of personality when evolving in environments with different selective pressures.

Bahamas mosquitofish are small, livebearing fish that have repeatedly evolved different adaptive traits in either the presence (high predation) or absence (low predation) of predatory fish during the past ~15 000 years (e.g. Heinen-Kay & Langerhans, 2013; Langerhans, 2010; Langerhans, Gifford, & Joseph, 2007; Martin, Riesch, Heinen-Kay, & Langerhans, 2014; Riesch, Martin, & Langerhans, 2013). Variation in the presence of piscivorous fish represents the primary source of environmental variation in these populations, resulting in two major categories of populations of Bahamas mosquitofish: (1) low-predation populations experience low mortality rates, and consequently face high levels of resource competition due to elevated conspecific densities, and (2) high-predation populations experience high levels of mortality from predatory fish (primarily bigmouth sleeper, *Gobiomorus dormitor*) and have relatively low conspecific densities (Heinen et al., 2013). No other environmental factor measured to date systematically covaries with the presence of predatory fish (e.g. productivity, salinity, turbidity, water transparency, depth, dissolved oxygen, temperature, pH; Heinen et al., 2013; Langerhans & Gifford, 2009; Langerhans et al., 2007). This allows us to focus more or less exclusively on the effects of predation regime in driving phenotypic divergence in this system.

For all five focal behaviours, we explicitly sought a simple, directional a priori prediction of population-level differences between predation regimes based on hypotheses of natural selection, assuming that each behavioural category could independently respond to selection (Table 1). For low-predation populations, we predicted lower aggressiveness to contend with living in high densities (monopolization or defence of resources are not particularly relevant in this system), combined with greater survivorship often experienced by aggressive individuals under threat of predation (Bell, 2005; Bell & Sih, 2007; Lung & Childress, 2007; Quinn & Kokorev, 2002). We predicted lower sociability in low-predation populations owing to increased intraspecific competition for resources in high-density conditions (Heinen et al., 2013), as well as the survival advantages of social grouping (e.g. schooling or shoaling) in the presence of predators (Krause & Ruxton, 2002; Pitcher & Parrish, 1993). We predicted that low-predation populations would show greater boldness in the presence of a potentially threatening stimulus due to the absence of selection from lethal agents, along with selection favouring wariness under chronic predation risk, particularly when resources are abundant (Bell, 2005; Herczeg, Gonda, & Merila, 2009; Riechert & Hall, 2000). For activity, we predicted no change across predation regimes, as selection should favour similar levels of overall activity for foraging, mating and other social interactions since Bahamas mosquitofish are highly social fish and activity is not known to affect predation risk from bigmouth sleepers. We predicted increased exploratory behaviours in low-predation populations due to foraging advantages of exploration under high resource competition, as well as selection against exploratory behaviours in environments with abundant ambush predators (Bell, 2005; Riechert & Hall, 2000). Alternative predictions could be made for some of the traits using different assumptions or different hypotheses of natural selection. For instance, aggression could be higher in low-predation populations if correlation with boldness or sociability prevents an independent response (Archard & Braithwaite, 2011a; Herczeg et al., 2009; Magurran & Seghers, 1991), and selection could favour increased boldness in high-predation populations as has been previously observed in some systems (Brown, Jones, & Braithwaite, 2005; Godin & Davis, 1995; Harris, Ramnarine, Smith, & Pettersson, 2010; Smith & Blumstein, 2010). However, we wished to assess our ability to predict changes in behaviour using simple predictions (i.e. assuming trait independence, ample genetic variance, closed system) most suitable for this particular study system. In this way, we can begin to gauge how accurately researchers can predict how multiple behaviours change in response to ecological variation.