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Does repeatable behaviour in the laboratory represent behaviour under natural conditions? A formal comparison in sea anemones

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Animal personality studies rely on collecting repeated behavioural data either in the field or under laboratory conditions. Conditions in the field should be far less stable than controlled laboratory conditions, and hence represent a potential source of variation in behaviour. Here we report on the first experiment to our knowledge that formally compares the repeatability of identical behaviours in the laboratory and the field, and across the transition from laboratory to field. Using a design that controls for observation number we compared two groups of sea anemones, observed across two experimental phases, either (1) in the field followed by the laboratory or (2) in the laboratory only. We analysed differences in behaviour across a range of levels including repeatability and its between- and within-individual variance components. Although mean startle response durations varied between the laboratory and field, there was no significant difference in repeatability across situations. Within-individual variance differed between the two periods of the experiment for animals observed only in the laboratory but this effect was not present for those that transitioned from field to laboratory. Furthermore, the rank order of individual responses was stable for animals observed only in the laboratory but changed for those that transitioned from field to laboratory. These results show that although repeatability estimates in the laboratory can yield results like those obtained in the field, the underlying components of consistent variation in behaviour might be influenced by an interaction between prior experiences and the current situation in which the animals are observed.
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Consistent between-individual differences in behaviour have now been described in a wide array of animal taxa (Carere & Maestripieri, 2013) and although most studies have been performed on vertebrates there are several examples across invertebrate phyla including arthropods and cnidarians (Kralj-Fiŝer & Schuett, 2014). Usually referred to as animal personality (Dall, Houston, & McNamara, 2004; Sih, Bell, & Johnson, 2004) consistent between-individual variation can be quantified as repeatability, *R* (Bell, Hankison, & Laskowski, 2009). This metric describes the proportion of total variation attributed to between-individual variation, once other obvious covariates (e.g. body size) have been accounted for. Thus $R = V_{BI}/(V_{BI} + V_{WI})$, where V_{BI} denotes between-individual variance and V_{WI} denotes within-individual variance, typically the residual variance in statistical models that also include terms for V_{BI} (Cleasby, Nakagawa, & Schielzeth, 2015; Royauté, Buddle, & Vincent, 2015; Stamps, Briffa, & Biro, 2012; Westneat, Wright, & Dingemanse, 2014). Residual within-individual variance (also called intra-individual variation, IIV; Stamps et al., 2012) has itself been the focus of recent interest. Along with understanding what factors might influence overall measures of repeatability, the effects of external conditions on IIV are also of interest across a range of fields including psychology (Asendorpf, 1992), cognitive neuroscience (MacDonald, Nyberg, & Bäckman, 2006) and latterly behavioural ecology (e.g. Westneat et al., 2014). This measure quantifies the predictability or consistency of behaviour. In addition to biotic covariates that could influence V_{BI} and V_{WI} abiotic aspects of the environment could also influence repeatability and its variance components (Briffa, Bridger, & Biro, 2013; Royauté et al., 2015). For example, in poikilotherms metabolic rate and hence behaviour should fluctuate with temperature. For aquatic animals, we also expect temporal fluctuations in a suite of physicochemical parameters that might influence behaviour including pH, dissolved oxygen and conductivity or salinity. Furthermore, spatial variation in these parameters can lead to between-individual variation in microhabitat, especially in sessile or sedentary animals. There has therefore been some

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concern that there may be a disjoint between repeatability estimates made under relatively stable (temporally and spatially) laboratory conditions and those made under variable field conditions (e.g. Fisher, James, Rodríguez-Muñoz, & Tregenza, 2015). Temporal variation in the field might increase V_{WI}, reducing repeatability (compared to laboratory conditions) whereas stable between-individual variation in microhabitat may increase V_{BI}, increasing repeatability (compared to laboratory conditions). Such concerns are especially pertinent when laboratory repeatability estimates are obtained for wild-caught animals, which have been bought into a novel environment, and when studies aim to make inferences about the fitness consequences of animal personality variation (Fisher, James, et al., 2015). Specific experimental paradigms where these concerns are important include 'two-step' studies where animals are observed in the laboratory and assigned to a given behavioural type (e.g. 'shy' or 'bold', or given a value along a shy—bold continuum) before being released and observed in the field (Niemelä & Dingemanse, 2014), or when captive-bred populations are used in personality research (Archard & Braithwaite, 2010).

Although some animal personality studies have compared laboratory and field data, few have been designed to formally test the idea that estimates of repeatability could vary between the two situations (Fisher, James, et al., 2015; Fisher, David, Tregenza, & Rodríguez-Muñoz, 2015; McCowan, Mainwaring, Prior, & Griffith, 2015; Yuen, Pillay, Heinrichs, Schoepf, & Schradin, 2016). In a recent example by Fisher, James, et al., 2015 wild field crickets, *Gryllus campestris*, were observed both in situ and in the laboratory through repeated cycles of recapture and release. They found that while three traits were significantly repeatable in the laboratory, only activity and exploration were repeatable in the field setting. Furthermore, while exploration and activity in the laboratory correlated with the same traits in the field, there was no correlation between boldness in laboratory and field conditions. Similarly, McCowan et al. (2015) found that although laboratory and field measures of exploration were both repeatable in zebra finches, *Taeniopygia guttata*, there was no correlation between the two situations. Results such as these imply that there is a mismatch between personality traits under laboratory and natural conditions, and therefore interpreting the evolutionary and ecological significance of laboratory-based personality studies may be less than straightforward. Similarly, laboratory measures related well to field measures in blue tits, *Cyanistes caeruleus* (Herborn et al., 2010), red squirrels, *Tamiasciurus hudsonicus* (Boon, Réale, & Boutin, 2008) and African striped mice, *Rhabdomys pumilio* (Yuen et al., 2016) but for Siberian chipmunks, *Tamias sibiricus*, there was no correlation between behaviours observed across the different situations (Boyer, Réale, Marmet, Pisanu, & Chapuis, 2010). While these studies have compared repeatabilities or mean level effects across laboratory and field settings, an aspect that has yet to be investigated is how the specific variance components, V_{BI} and V_{WI}, might be affected by the experimental setting. Studies focusing on these components could identify the causes of differences in behaviour between the laboratory and field.

Beadlet sea anemones, *Actinia equina*, are sedentary cnidarians, common on the intertidal zone in northwestern Europe. Mature polyps attach their basal disc to rocky substrata, a condition that can be reproduced in the laboratory (Rudin & Briffa, 2011, 2012). At the opposite end of the column (the main mass of the body) is the oral disc through which they ingest food and eject waste. The oral disc is surrounded by six rows of feeding tentacles, used to trap prey and detritus from the water column and then to guide it to the oral disc. Polyps also possess a single row of specialized acrorhagial tentacles, which are only easily visible during agonistic encounters (Fish & Fish, 2011). When disturbed, *A. equina* will retract its feeding tentacles to cover the oral disc. Following retraction of the tentacles, the anemone will slowly reopen so that the tentacles and oral disc are again visible. In previous studies of behavioural variation in sea anemones the duration of tentacle retraction, also termed the 'startle response duration', has been used as an index of boldness and this is significantly repeatable in *A. equina* (Briffa & Greenaway, 2011; Rudin & Briffa, 2012) and in the Caribbean giant sea anemone, *Condylactis gigantea* (Hensley, Cook, Lang, Petelle, & Blumstein, 2012). In *A. equnia*, significant repeatability has been found in studies based in the field (Briffa & Greenaway, 2011) and in the laboratory (Rudin & Briffa, 2012) but these studies differed in key experimental details (e.g. number of within-individual replicates, presence of aggression) hindering the direct comparison of laboratory and field data. Since the retraction response can be elicited in both situations, using identical methods to disturb the anemones, *A. equina* is an ideal study subject for experiments specifically designed to compare laboratory- and field-based repeatabilities (e.g. see Carter, Marshall, Heinsohn, & Cowlishaw, 2012; Dochtermann & Nelson, 2014). Here we investigated personality differences between typical laboratory conditions and field conditions, using an experimental design that controls for the duration of the experiment and the number of observations conducted in each situation: One group of anemones was repeatedly observed in the field for the first period of the experiment and then in the laboratory for the second period. A second group was observed concurrently with the first group and on an equal number of occasions but only in the laboratory, across both periods of the experiment.

First, we asked whether sample level mean behaviour (i.e. the average of all individuals in the experiment) differed between laboratory- and field-based observations. Second, we asked whether repeatability differed between the two situations and whether its variance components (V_{BI} and V_{WI}) differed between situations. Third, we investigated the specific effects of transitioning individuals from the field to the laboratory. For those anemones observed in the field, we also analysed key physicochemical sea water parameters that might influence their behaviour. If laboratory-based estimates of repeatability are comparable to those made in the field, we would expect no significant differences in repeatability (or its variance components) across the two situations. If the transition from field to laboratory is important, we would expect to see differences between the two periods of the experiment in the group that transitioned from field to laboratory, but not in the group that spent the whole experiment in the laboratory.

METHODS

Study Animals

Anemones were collected from tidepools at the base of rocky outcrops at the intertidal zone at Portwrinkle harbour beach, Cornwall, U.K. (50.361°N, 4.315°W), during July 2014. We identified 78 individuals of the red colour morph of *A. equina*, separated from one another by a distance of at least 1 m, for use in the experiment. Previous molecular studies have shown that individuals separated by this distance are unlikely to be clone mates (e.g. Foster & Briffa, 2014; Turner, Lynch, Paterson, León-Cortés, & Thorpe, 2003). We immediately removed 39 individuals from the rocks, by inserting the edge of a thin silicone spatula under the pedal disk allowing them to be prized from the substrate. These were placed in individual containers and transported back to the laboratory. The remaining 39 individuals were left in situ during the first period of the experiment. For these individuals, we applied unique

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