



Who dares does not always win: risk-averse rockpool prawns are better at controlling a limited food resource

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Animal 'personality', the phenomenon of consistent individual differences in behaviour within populations, has been documented widely, yet its functional significance and the reasons for its persistence remain unclear. One possibility is that among-individual behavioural variation is linked to fitness-determining traits via effects on resource acquisition. In this study, we tested this idea, using rockpool prawns, *Palaemon elegans*, to test for a correlation between 'high-risk exploration' and the ability to monopolize a limited resource. Modified open field trials (OFTs) confirmed that consistent among-individual (co)variation in high-risk exploratory behaviours does exist in this species, and multivariate analysis showed trait variation is consistent with a major axis of personality variation. Subsequent feeding trials in size-matched groups where competition was possible revealed a high repeatability of feeding duration, used here as a proxy for RHP (resource-holding potential). We found significant negative correlations between feeding duration and two 'risky' behaviours, such that individuals that took fewer risks fed more. Our results are not consistent with the widely hypothesized idea of a 'proactive syndrome' in which bolder, risk-taking personalities are positively associated with RHP. Rather they suggest the possibility of a trade-off, with some individuals successful at monopolizing limited, high-value resources, while others are more willing to engage in potentially risky exploration (which may increase the likelihood of encountering novel resource patches). We speculate that alternative strategies for acquiring limited resources might thereby contribute to the maintenance of personality variation observed in wild populations.

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The existence of consistent between-individual differences in behaviour, or 'animal personality', has been documented widely in many types of behaviours and in a variety of organisms (Bell, Hankinson, & Laskowski, 2009; Japyassú & Malange, 2014; Réale, Dingemanse, Kazem, & Wright, 2010). A key question arising from these findings is why personality persists in wild populations (Sih, Bell, & Johnstone, 2004). Superficially, complete flexibility of behaviour would appear to be the optimal strategy when the local environment is changeable. However, studies of other trait types have emphasized the need to understand costs and limits associated with plasticity (DeWitt, Sih, & Wilson, 1998; Scheiner, 1993) that are, in general, not well characterized for behaviour (Ghalambor, Angeloni, & Carroll, 2010). Such costs (including the machinery required to make accurate predictions in fluctuating

environments) are likely to limit the extent of behavioural plasticity as an adaptive strategy (Dall, Houston, & McNamara, 2004), yet the functional significance of consistent individual differences remains obscure: does personality provide adaptive advantages, act as an evolutionary constraint or is it some combination of the two (Dall et al., 2004; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Wolf & Weissing, 2010)? Theoretical treatments have proposed multiple adaptive explanations for the emergence and maintenance of personality variation (e.g. Wolf & McNamara, 2012; Wolf, Van Doorn, Leimar, & Weissing, 2007; Wolf & Weissing, 2010), and researchers are beginning to respond to the call for empirical investigations into links between behavioural types and traits that could contribute to an individual's overall fitness (Dingemanse & Réale, 2005; Smith & Blumstein, 2008).

A comprehensive explanation for the existence and maintenance of personality variation is thus likely to depend (at least in part) upon how behavioural differences contribute to life history variation (Stamps, 2007). Correlations between personality variation and life history traits have been shown in invertebrates

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(Niemełä, Lattenkamp, & Dingemanse, 2015; Sinn, Apiolaza, & Moltschaniwskyj, 2006), fish (Adriaenssens & Johnsson, 2010; Ballew, Mittelbach, & Scribner, 2017), birds (Dingemanse, Both, Drent, & Tinbergen, 2004; Patrick & Weimerskirch, 2014) and mammals (Boon, Réale, & Boutin, 2007; Seyfarth, Silk, & Cheney, 2012). While the interpretation of any such correlations is complicated by the fact that within-individual trade-offs between different life history traits largely determine fitness variation (Simpson, 1955; Stearns, 1989), a universal limiting factor to life history trait expression is resource availability (Zera & Harshman, 2001). An increased ability to acquire a limited resource would allow an individual to invest more in all traits, and thereby increase its overall fitness (Bolnick et al., 2011; Reznick, Nunney, & Tessier, 2000; Van Noordwijk & de Jong, 1986). Where intraspecific competition over a limited resource occurs, an individual's capacity to monopolize that resource also provides an indication of its competitive ability, or 'resource-holding potential' (RHP; Parker, 1974; Lindström, 1992). Observations of some measure of RHP might therefore provide insights into fitness variation (Parker, 1974; Smith, 1974), and can also be used at the individual level to determine associations with other traits of interest. While studies have typically focused on the effects of morphological differences (in particular, body size) on competitive outcomes (Briffa, Sneddon, & Wilson, 2015; Ida & Wada, 2017; Tricarico, Benvenuto, Buccianti, & Gherardi, 2008), there is increasing recognition that consistent individual behavioural differences may play a role in determining individual success (Camerlink, Arnott, Farish, & Turner, 2016; Lane & Briffa, 2017; Rudin & Briffa, 2012).

Here, we set out to test the existence of a link between personality and the ability to monopolize a limited food resource using the rockpool prawn, *Palaemon elegans*. One of the most frequently studied personality traits is 'boldness', usually defined as an axis of variation in tendency to engage in risky behaviours (e.g. exploration of novel environments; Wilson, Clark, Coleman, & Dearstyne, 1994). A previous study on this species used a variety of assays that each recorded a single behaviour nominally considered a distinct personality trait, finding some evidence of consistent individual differences and correlations across time and situations (Chapman, Hegg, & Ljunberg, 2013). However, the explanatory importance of single behaviours can vary between contexts and species (Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013). Consequently, empirical investigations of personality are increasingly seeking to infer personality variation by placing individuals on axes of variation defined from repeated observations of multiple behaviours (e.g. Carter & Feeney, 2012; Houslay, Vierbuchen, Grimmer, Young, & Wilson, 2018; White, Kells, & Wilson, 2016). We followed that trend in this study: we observed individuals repeatedly in modified open field trials (OFT; Walsh & Cummins, 1976), measuring movement behaviours in a novel and 'risky' environment. At the end of the OFT period we created small groups of these individuals for repeated group resource acquisition trials. In crustaceans, a limited food resource is expected to induce intraspecific competition for its acquisition (e.g. Barki, Karplus, & Goren, 1992; Sneddon, Huntingford, & Taylor, 1997; Stewart, McKenzie, Simon, & Baker, 2010). Since the ability to monopolize a limited resource is already known to be influenced by size in *P. elegans* (Evans & Shehadi-Moacdieh, 1988), we size-matched individuals in these groups to better identify any additional influence of among-individual behavioural variation as measured by the OFTs.

We predicted that (1) there would be consistent individual differences between multiple exploratory and/or risk-related behaviours assayed in the modified OFTs, (2) these behaviours would be correlated in such a way as to be consistent with a continuum of parameters traditionally described as being 'shy–bold' (Wilson et al., 1994) and (3) there would be a clear association between

these correlated risk-related behaviours and an individual's repeatable RHP (measured as the among-individual variation in feeding duration in group resource acquisition trials). We did not, however, have a clear prediction for the direction of such an association. Boldness is commonly positively correlated with resource acquisition (Biro & Stamps, 2008) and/or competitive ability (e.g. Sih, Cote, Evans, Fogarty, & Pruitt, 2012), a relationship that suggests the presence of a 'proactive syndrome' (reviewed in Briffa et al., 2015). However, there is increasing recognition that the sign of such correlations may be dependent on the details of the study system in question (Briffa et al., 2015). In *P. elegans*, alternative strategies for resource acquisition may be present and maintained through balancing selection (Wolf & McNamara, 2012). For instance, individuals that take more risks through exploration might find new resources quickly but be unable to defend them, while more socially dominant individuals may be better able to monopolize existing resources. In such a scenario, individuals with higher RHP could be seen to exhibit nominally 'shy' behaviours such as increased refuge use, when in fact this 'shyness' is borne out of an ability to control limited shelter space and thus a reduced necessity to take risks. This would be in line with the results of Evans and Shehadi-Moacdieh (1988), who found that shelter residents are more likely to repel intruders, suggesting that refuge space itself is a limited resource in this species. It would also support their prediction that it appears to be 'more adaptive' for weaker *P. elegans* to avoid direct confrontation, as competitive scenarios produce fewer agonistic interactions when individuals are competitively asymmetrical. In their case weaker individuals were smaller, but in our size-matched trials other competitive asymmetries could arise. In this case, we predicted a negative correlation between nominally 'bold' tendencies (to engage in risky exploration when shelter was available) and RHP.

METHODS

Capture and Tagging

We collected data in four blocks between 16 April and 12 June 2016. Each block comprised a 2-week period during which wild-caught animals were housed in the laboratory and subjected to behavioural trials and morphological measurements. At the start of each data collection block we captured 40 prawns ($N = 160$ in total) from rock pools on Gyllyngvase Beach, Falmouth, on the south coast of Cornwall, U.K. (latitude 50.144116, longitude -5.068408) and transported them to the laboratory in a sealed container filled with sea water and enriched with rock shelters. In the laboratory prawns were kept in an aerated home tank (120×60 cm and 30 cm deep), filled to a depth of 25 cm, which was maintained at a constant temperature of 11.5 °C and a salinity of 33–35 parts per thousand. The home tank was kept on a regular 12:12 h day:night cycle (lights on at 0700 hours) and was enriched with rocks and sections of 3 cm diameter plastic piping for prawns to use as refuges.

After a 24 h acclimatization period we weighed and tagged the prawns. We used coloured implant elastomer for tagging (Northwest Marine Technology, <http://www.nmt.us/products/vie/vie.shtml>), allowing us to differentiate between individuals during data collection blocks and when taking pre and post mortem measurements. Tagging involved the injection of a small amount of elastomer under the left and right sides of the third tail carapace segment. By using six colours and injecting two tags for each individual (one on either side of the tail) it was possible to uniquely tag 36 prawns. The other four individuals were retained for use in case of mortality. Pretrial weight was also recorded during tagging, for use when size-matching individuals.

We then allowed a further 24 h for recovery before starting behavioural trials. Trials consisted of a 'boldness' test phase followed by assays of resource acquisition (described below). Prawns

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