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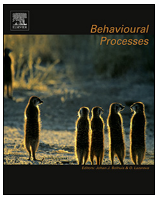

To hide or to feed: an evaluation of personality traits in the sand bubbler crab, *Dotilla wichmanni*, when responding to environmental interference

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ABSTRACT

Behaviour plays a crucial role in a species' ability to cope with environmental challenges. However, this ability may be affected by repeatable individual differences in behaviour, a pattern described as animal personality. The consideration of animal personality is therefore essential when understanding how a species copes with its environmental stressors. For sand bubbler crabs, feeding is often disrupted by environmental interference, in the forms of predatory events and human recreational activities. How these crabs deal with such disruption is, however, not well documented. Here, we characterised the foraging and risk-taking behaviours of *Dotilla wichmanni* when responding to induced disruption. Whether these are personality traits and if they form part of a behavioural syndrome were also examined. We quantify both behaviours by taking four measures (two per behaviour). All behavioural measures were consistently different among individuals, suggesting that *D. wichmanni* exhibits personality. Results further suggest that they could cope with some environmental interference, although this is limited. Crabs did not vary the time spent hiding in burrows with each repeated disruption nor did behavioural plasticity differ between individuals. Notwithstanding these, the absence of support for a foraging–risk propensity behavioural syndrome points to possible complexity in the crabs' coping ability.

1. Introduction

Behaviour, being the most pliant of phenotypes, plays an important role in animals' ability to deal with quick temporal changes in the environment (DeWitt et al., 1998). How a species copes with environmental stressors, therefore, hinges on its behavioural traits. However, not all individuals behave alike. Individuals of many species exhibit repeatable differences in behaviours (e.g., Carere et al., 2005; Lopez et al., 2005; Mowles et al., 2012); these patterns are often described as behavioural types or personality traits (Wolf and Weissing, 2012). Personality traits can covary and form a suite, which is often referred to as a behavioural syndrome (Sih et al., 2004; Groothius and Carere 2005).

Understandably, the cause and maintenance of animal personality and behavioural syndrome can appear counterintuitive (Wolf et al., 2013). Presented with the same problem, individuals should have the same optimal response. Furthermore, the correlation in personality traits could result in behavioural inflexibility, which is maladaptive (Wolf et al., 2013). However, between-individual differences in states, variations in spatiotemporal environment, frequency-dependent selection and non-equilibrium dynamics, among others, can favour multiple behavioural optima to the same problem (Wolf et al., 2008, 2013). These, in turn, may be maintained through trade-offs and state-dependent feedbacks (Sih et al., 2015; Wolf et al., 2007). Similarly, common underlying behavioural architecture and correlational selection are some reasons why a suite of personality traits might correlate (Wolf et al., 2013; Sinervo and Calsbeek, 2006). Together, they may explain why animal personality and coping style are so widespread across animals (e.g., Dochtermann and Jenkins, 2007; Briffa et al., 2008; Conrad et al., 2011; Dingemanse et al., 2012).

Animal personality, though reduces behavioural flexibility, does not equate to the absence of behavioural plasticity or the inability to adjust to changes in the environment (e.g., Sih et al., 2004; Briffa et al., 2008); this is a misconception (Frost et al., 2007; Dingemanse et al., 2010). Individuals can adjust to the environment while maintaining consistent behavioural differences (i.e., personality) (e.g., Frost et al., 2007; Briffa et al., 2008; Dingemanse et al., 2012; Kim, 2016). However, the amount of variation in plasticity could either be fixed (e.g., Kim, 2016), or varied among individuals (e.g., Frost et al., 2007; Briffa et al., 2008; Dingemanse et al., 2012; Stamps et al., 2012;). In the latter, plasticity

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might be linked to personality traits (e.g., Frost et al., 2007; Dingemanse and Wolf, 2013; Brown and Robinson, 2016). In fact, both traits are thought to have co-evolved (Wolf et al., 2008). Yet, increasingly, individual variation in plasticity is not shown to associate so much with a specific personality type (e.g., Frost et al., 2007; Briffa et al., 2008), as with a specific coping style (Wolf et al., 2008; Dingemanse et al., 2010; Mathot et al., 2012; Dingemanse and Wolf, 2013). Regardless, the association between personality and plasticity suggests that the behavioural repertoire of individuals can be more limited than what is available to the population.

As the behaviours of individuals can have constraints and these may be related to their coping styles, the mere consideration of a species' behavioural traits is insufficient in understanding how it copes with stressors in its environment. Further examinations of whether these behaviours are consistently different between individuals (i.e., are relevant behaviours personality traits?) and if they are in any way correlated (i.e., are behavioural traits part of a behavioural syndrome?) are, therefore, necessary. Accordingly, we seek to understand, in this study, the ability of Dotillid crabs to cope with environmental disruption while taking into consideration the influence of animal personality.

Dotillid crabs or sand bubblers, of the genus *Dotilla*, predominantly inhabit tropical sandy intertidal shores (Hartnoll, 1973; Fishelson, 1983; Bradshaw and Scoffin, 1999). During high tide, these crabs remain burrowed and emerge only when the tide recedes (Ansell et al., 1988). Whether the sand bubblers exhibit burrow fidelity and what activity they undertake during high tide remain unclear. However, at low tide, foraging constitutes the most conspicuous activity (Ansell 1988; pers. obs.). Sand bubblers feed by ingesting and processing sediment as they move to and fro around their burrow entrances. Due to their usual abundance and ability to process extensive amounts of sediment, though they are usually not more than three centimetres in carapace width, these crabs likely function as important bioturbators (Lee, 2015). An estimation placed the daily amount of sediment processed by *Dotilla myctiroides* at 1.47 kg m^{-2} (Bradshaw and Scoffin, 1999), while *D. fenestrata* could process up to six kilogram of sediment per square metre (Fishelson, 1983).

Yet, feeding and other surface activities are disrupted whenever the crabs sense threats. Sand bubblers will scurry back to their burrows and only re-emerge after having perceived that the threat has passed (Ansell 1988). Threats usually come in the form of predators, but also as interference caused by recreational activities. Animals often regard humans as potential predators (Frid and Dill, 2002; Beale and Monaghan, 2004). Thus, sand bubblers might respond to human recreational activities as potential threats although they are seldom harmed. Interference—arising from predatory events or human activities—can translate to the loss of foraging opportunities for low-tide activities in sand bubblers, which if substantial could affect their survival. Yet, how these crabs cope with such environmental stressor (i.e., disruption to their feeding activities) has remained unexamined.

To understand how *Dotilla wichmanni* deals with interference to their feeding activities, we examined its responses to induced disruption. Of its behavioural repertoire, foraging habit and the propensity to take risk probably function importantly in influencing its ability to cope with environmental disruptions. We, therefore, investigated how these behaviours vary in response to repeated disruption while controlling for size, sex and distance of individual to disruption and to its burrow. Since animal personality could affect individuals' ability to cope with environmental interference, we also checked for the presence of personality (i.e., repeatable individual differences) and individual variation in plasticity (i.e., if response between individuals varies with accumulating disruption) in these behaviours. In addition, we explored the presence of a foraging–risk-taking behavioural syndrome and the validity of the behavioural measures used in this study.

Here, we hypothesise that *D. wichmanni* will respond adaptatively to repeated disruptions in its feeding and risk-taking behaviours. Many animals can habituate when repeatedly exposed to novel events (Chapman et al., 2012; Mccleery, 2009; Metcalf et al., 2000). In other words, we predict that crabs will feed faster and further from their burrows, take more time to respond to and less time to recover from each repeated disturbance. Nevertheless, the ubiquity of personality and, in the broader sense, behavioural syndrome in animals (e.g., Carere et al., 2005; Lopez et al., 2005; Mowles et al., 2012), proposes that these behaviours are personality traits that will form part of a behavioural syndrome. Therefore, the adaptive responses of *D. wichmanni* to repeated disruption are predicted to differ (i.e., presence of personality) between individuals and correlate (i.e., part of a behavioural syndrome) with each other.

2. Material and methods

2.1. Collection and set-up

During four spring diurnal low tides in March 2017, we observed and recorded the behaviours of 38 individuals of *Dotilla wichmanni* (23 males and 15 females) found at Changi Beach in Singapore (N 1.374°, E 104.007°), using a camcorder (SONY HDR-XR260VE) mounted onto a PVC frame. The camcorder was positioned as perpendicular as possible to the surface of the shore, so that observations from the top view could be made and distance measurements during video and image processing facilitated. A Singapore third series 50 cents coin, with a diameter of 23 mm, was placed within the image frame as a length reference scale. Each crab was tracked continuously throughout the behavioural observations using video recording and was captured after all observations were completed to determine its carapace width (measured to the nearest 0.01 mm) and sex. All individuals were adults, but none of the females was berried. Subsequently, they were returned to their natural environment.

2.2. Behavioural observations

When setting up the camcorder for behavioural observations, we ensured that interference was kept to a minimum. In addition, the crabs were given 10 min to acclimate to our setup. In no instance did we observe any crab cease surface activities due to our setup. Moreover, all crabs took no longer than two minutes to resume surface activity after our setup.

The foraging habit and risk propensity of *D. wichmanni* were each determined using two behavioural measures/tests. Because disruption may have carryover effects (*sensu* Díaz-Uriarte, 2002), we recorded foraging measures before the risk-taking measures in each set of observation. An observational set, therefore, consists of a behavioural assay (five minutes; for details see below) followed immediately by a risk-taking behavioural assay, initiated by an induced disruption. It was considered to have ended five minutes after the induction of the disruption. In total, five sets of foraging–risk-taking observations were conducted with 10 min interval between the sets (see Figure S1). The order in which each set of observation was made or the observation number (one to five) was noted.

2.3. Foraging assay

We employed the rate of the area covered during feeding (hereafter referred to as RAC) and the maximum foraged distance from the burrow (hereafter referred to as MFD) to quantify the individual feeding habit of *D. wichmanni*. A five-minute video recording of activity, prior to the induction of disruption, was first converted into image sequence using Adobe Photoshop (version 13.0.6).

To calculate the RAC of each individual, we first measured the surface area of sediment fed on by each individual, using image-processing software ImageJ (version 1.51n, Wayne Rasband, National Institute of Health, USA), during the five-minute period. The time spent feeding within that period by each individual was also obtained

Table 1
GLMM analyses of factors influencing foraging and risk-taking behaviours of *Dotilla wichmanni*, with individual identity fitted as random intercept, and estimates of between- and within-individual variances, and adjusted repeatability.

Fixed effects	Foraging				Risk-taking			
	Rate of area covered (RAC) (mm^2/sec, log-transformed)		Maximum foraged distance (MFD) (mm)		Response Time to Disruption (RT) (sec; log-transformed)		Latency to re-emergence (LR) (sec; log-transformed)	
	β (95% CI)	ΔDIC	β (95% CI)	ΔDIC	β (95% CI)	ΔDIC	β (95% CI)	ΔDIC
Sex	−0.273 (−0.462, 0.177)	−0.08	−26.290 (−59.906, −1.211)	0.02	−0.078 (−0.396, 0.187)	−0.44	0.183 (−0.098, 0.504)	−0.09
Carapace width (mm)	0.255 (0.124, 0.378)	0.73	20.768 (8.850, 30.703)	0.60	0.041 (−0.060, 0.169)	0.58	0.206 (0.108, 0.364)	2.18
Order of observation	−0.030 (−0.063, 0.002)	3.68	3.611 (0.576, 9.012)	5.33	−0.068 (−0.110, −0.004)	18.32	−0.018 (−0.063, 0.027)	−2.01
Individual's mean distance to disruption	–	–	–	–	< 0.001 (> −0.001, 0.001)	−0.56	> −0.001 (> −0.001, < 0.001)	−0.50
Distance to disruption (centred within-individual)	–	–	–	–	0.001 (−0.001, 0.002)	−1.04	−0.001 (−0.002, < 0.001)	2.22
Distance to burrow (centred within-individual)	–	–	–	–	0.005 (0.003, 0.007)	51.50	−0.002 (−0.003, > −0.001)	5.83
Variances	σ^2 (95% CI)	ΔDIC	σ^2 (95% CI)	ΔDIC	σ^2 (95% CI)	ΔDIC	σ^2 (95% CI)	ΔDIC
Between-individual	0.151 (0.084, 0.253)	131.12	1411.660 (755.040, 2339.14)	85.59	0.084 (0.033, 0.204)	30.44	0.11 (0.05, 0.20)	58.91
Within-individual	0.092 (0.075, 0.120)		1412.451 (1237.500, 1969.135)		0.295 (0.221, 0.348)		0.18 (0.16, 0.24)	
Adjusted Repeatability	$r_{adj.}$ (95% CI) 0.658 (0.481, 0.755)		$r_{adj.}$ (95% CI) 0.458 (0.328, 0.626)		$r_{adj.}$ (95% CI) 0.203 (0.106, 0.444)		$r_{adj.}$ (95% CI) 0.396 (0.242, 0.560)	

All reported values are estimated posterior means with 95% credible intervals in parentheses. ΔDIC is the change in deviance information criterion between a model without a specific factor and a full model. Positive values that are less than 0.001 are written as < 0.001. Negative values that are more than −0.001 are stated as > −0.001.

through the review of video recordings. The RAC for each individual was determined as $\frac{Surface\ area\ fed\ on\ (mm^2)}{Time\ spent\ feeding\ (s)}$. Similarly, using ImageJ, we measured MFD as the maximum distance at which each individual foraged from the burrow during the five-minute period prior to the onset of disruption (see Figure S1). As crabs tend to foraged to-and-fro their burrows in a radial fashion, food depletion in a patch will not necessarily increase MFD. Therefore, MFD could measure the foraging behaviours of individuals.

2.4. Risk-taking assay

To quantify the risk propensity of individual crabs, we measured the response time to induced disruption (hereafter referred to as RT) and the latency to re-emergence (hereafter referred to as LR) after being interfered. Disruption was induced each time by an experimenter (Chen, P.Z.), wearing the same attire, approaching the crabs at a walking pace from a fixed point (approximately 10 m away) to a pre-established reference line near the crabs and immediately walking away. In every trial, crabs retreated into their burrows before the experimenter reaches the reference line. The distances of the individual, from the reference line and its burrow, prior to induced disruption, were then measured using ImageJ; after video recordings of the observation were converted into image sequences using Adobe Photoshop. To differentiate the within- from the between-individual effects (see van de Pol and Wright, 2009), we employed within-individual centring on the distance measurements. This was achieved by subtracting an individual's mean value from all its values (i.e., $x_{(B/D)ij} - \bar{x}_{(B/D)j}$, where x_{Bij} is the distance of individual j to its burrow at observation i, while x_{Dij} is the distance of individual j to the induced disruption at observation i). In every instance, the crabs retreated into their burrows when disturbed and took no more than three minutes to re-emerge.

We defined an individual's RT as the time taken for the experimenter to reach the reference line after initiation of burrow retreat—always by halting its surface activity and dashing back to its burrow. A high RT value would indicate quick initiation of burrow retreat (lower risk propensity), while a low RT value suggests a slow initiation of burrow retreat (higher risk propensity). Conversely, the LR of an individual was defined as the time taken to re-emerge from the burrow completely after the disruption. Individuals with high LR values would suggest a lower propensity for risk while individuals with low LR values have higher risk propensity. Both durations were obtained through the review of video recordings (see Figure S1).

2.5. Statistical analyses

Although 38 individuals (23 males and 15 females) were observed, not all individuals had all five sets of foraging–risk-taking measures. Some individuals (6 out of 38 individuals) either failed to forage or moved out of view during one or two sets of observation. As such, some behavioural measures could not be obtained for these individuals in those replicates. These replicates were thus excluded from the analyses. We employed univariate and bivariate Generalised Linear Mixed Models (GLMMs), with Gaussian distribution error, to evaluate the feeding habit and risk propensity of *D. wichmanni* in response to induced disruption. All analyses were conducted within a Bayesian framework, using the R package *MCMCglmm* (Hadfield, 2010) in RStudio (RStudio Team, 2017) with R version 3.4.1 (R Core Team, 2017). All our models ran with uninformative priors, for 4,000,000 iterations (nitt)—of which the first 50,000 (burn-in) were discarded—and had a specified thinning interval of 10,000 (thin). The trace and density plots of the models for each parameter were also evaluated to ensure no autocorrelation. We reported the modes of the posterior distribution as the point estimates, while the 95% highest posterior densities were reported as 95% credible intervals.

2.5.1. Use of ΔDIC as statistical support

Throughout, support for an effect was determined using Deviance Information Criterion (DIC), which is a generalisation of Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC). It is used in model selection whenever parameters were estimated from Markov Chain Monte Carlos simulation (Spiegelhater et al. 2002). Like AIC or BIC, models with change in DIC (ΔDIC) value of more than two are considered to differ in support. The model with the lower DIC is preferred. Here we considered a ΔDIC value of more than two as having "support for the presence" and less than negative two as having "support for the absence" of the effect in question.

2.5.2. Factors affecting foraging and risk-taking measures

We used univariate GLMM analyses to investigate factors influencing variation in all four behavioural tests (two foraging and two risk-taking behavioural measures). The individual identity was fitted, in each analysis, as a random effect (random intercept). The measures of foraging behaviour—RAC (log-transformed) and MFD—were each evaluated with three fixed effects: carapace width, sex and observation number (see Table 1). The observation number was centred and entered as a continuous variable. Conversely, for each analysis of risk-taking behaviours—RT (log-transformed) and LR (log-transformed), three other factors were added to the previous fixed effects (see Table 1). They were the individuals' mean distance to disruption ($\bar{x}_{Dj}$), the distance to disruption (centred within-individual; $x_{Dij} - \bar{x}_{Dj}$), and distance to burrow (centred within-individual; $x_{Bij} - \bar{x}_{Bj}$). Support for each fixed effect of each behavioural measure was determined by taking the ΔDIC between a model that excluded the effect in question and a full model.

2.5.3. Presence of personality in foraging and risk-taking measures

To estimate repeatability, we calculate the adjusted repeatability of each measure as: the between-individual variance over sum of between- and within-individual variance ($r_{adj.} = \frac{V_{ind_0}}{V_{ind_0+V_{e0}}}$, where V_{ind_0} is the between-individual variance and V_{e_0} is the within-individual variance; Dingemanse and Dochtermann, 2013). The 95% credible intervals (CI) of the respective adjusted repeatability were also estimated. As with the main effects, statistical support for the presence of personality for each behavioural measure was determined by taking the ΔDIC between a model that excluded the random effect and a full model. A ΔDIC of more than two suggests that the model with individual identity as a random effect is more parsimonious. Therefore, coupled with CI of adjusted repeatability, ΔDIC of more than two lends evidence for the presence of personality (see Dingemanse et al., 2012).

2.5.4. Presence of individual variation in plasticity with accumulating disruption

In addition, we examined whether behavioural test responses vary between individuals with accumulating interference by fitting observation number (centred) as a random slope to previous univariate GLMM analyses (see Table 2). Random slope models estimate the variance between-individual differences in the intercept ($\sigma^2_{\mathrm{elevation}}$), the slope ($\sigma^2_{\mathrm{slope}}$) and the residuals ($\sigma^2_{\varepsilon}$), and the covariance between intercept and slope ($\sigma_{\mathrm{\ elevation,\ slope}}$). Evidence for individual variation in plasticity was determined by taking the ΔDIC between a model that only contained random intercept and a constrained or an unconstrained model fitted with random intercept and slope (see Dingemanse et al., 2012). A constrained model is one where the covariance between intercept and slope is set to zero, while in an unconstrained model, the covariance between intercept and slope can vary. When the support for individual variation in plasticity was present (ΔDIC > 2), we calculated the conditional repeatability as $r_{cond.} = \frac{\sigma^2{}_{elevation}}{\sigma^2{}_{elevation} + \sigma^2{}_{\varepsilon}}$. This is the repeatability at the average accumulated level of disruption (i.e., the repeatability when the covariate is zero; Nakagawa and Schielzeth, 2010).

Table 2

Between-individual variance in the relationship between behavioural measurements and order of observation (accumulated interference).

Individual x Order of observation	Foraging				Risk-taking			
	Rate of area covered (RAC) (mm^2/sec, log-transformed)		Maximum foraged distance (MFD) (mm)		Response Time to Disruption (RT) (sec; log-transformed)		Latency to re-emergence (LR) (sec; log-transformed)	
	Estimate (95% CI)	ΔDIC	Estimate (95% CI)	ΔDIC	Estimate (95% CI)	ΔDIC	Estimate (95% CI)	ΔDIC
$\sigma^2_{\text{elevation}}$	0.153 (0.081, 0.310)		342.853 (0.627, 1580.785)		0.140 (0.061, 0.374)		0.247 (0.105, 0.530)	
σ^2_{slope}	0.041 (0.023, 0.061)	−23.37	4.971 (0.197, 88.657)	3.69	0.053 (0.029, 0.092)	−36.62	0.048 (0.025, 0.077)	−14.55
$\sigma_{\text{elevation, slope}}$	−0.002 (−0.047, 0.021)	−25.04	94.529 (−37.717, 202.170)	1.83	−0.029 (−0.103, 0.005)	−37.96	−0.032 (−0.111, 0.009)	−14.09
Conditional Repeatability	$r_{cond.}$ (95% CI) –		$r_{cond.}$ (95% CI) 0.477 (0.237, 0.657)		$r_{cond.}$ (95% CI) –		$r_{cond.}$ (95% CI) –	

All estimates are from GLMM analyses with individual identity fitted as random intercept and order of observation as random slope. 95% credible intervals of estimates are given in parentheses. ΔDIC is the change in deviance information criterion between a model that only contained random intercept and a constrained or an unconstrained model fitted with random intercept and slope.

2.5.5. *Behavioural syndrome and validity of measures*

Subsequently, we used multivariate GLMMs to explore both the presence of foraging-risk-taking behavioural syndrome and the validity (*sensu* Burns, 2008) of the behavioural measures. We fitted *trait-1* as the fixed effect (so that the mean of each measure was estimated) and the individual identity as the random effect. We then examined the correlations of all the measures at the phenotypic, between- and within-individual levels (see Table 3). The correlations at each level were calculated as the covariance between two measures divided by the square root of the product of their variances. The phenotypic covariances and variances are the sum of their respective between- and within-individual components. To ascertain support for the presence of correlation, we took the ΔDIC between a model that has its between- or within-individual covariances constrained and an unconstrained model.

A correlation between behavioural measures at the phenotypic level could result from a correlation at the between- and/or within-individual level (Dingemanse and Dochtermann, 2013). However, only correlations at the between-individual level can constitute as convergent validity and behavioural syndrome (Carter et al., 2013; Dingemanse and Dochtermann, 2013). A between-individual level correlation between measures of the same behaviour—either foraging or risk-taking behaviours— would suggest convergent validity (i.e., both measures are likely measuring the same behaviour; Carter et al., 2013), while a between-individual level correlation of different behaviours would suggest the presence of a behavioural syndrome (Carter et al., 2013).

2.6. *Ethical note*

While prior licensing and approval are not needed in our case, experimental procedures were, nevertheless, in accordance with the guidelines laid out by the university's Institutional Animal Care and Use Committee. We also minimise, as far as possible, the number of animals used. As such, our work complies with the guidelines laid out in Animal Behaviour (1991, 41, 183–186).

3. Results

3.1. *Factors affecting foraging and risk-taking measures*

Among the factors considered to predict foraging measures (RAC, MFD), the order of observation was the only effect that had support (Table 1; Fig. 1). With increasing order of observation, dotillids' RAC decreased ($\beta = -0.030$, 95% CI [-0.063, 0.002]; $\Delta DIC = 3.68$), while their MFD increased ($\beta = 3.611$, 95% CI [0.576, 9.012]; $\Delta DIC = 5.33$).

For risk-taking measures (RT, LR), however, the factors that had support varied (Table 1) (Table 1; Fig. 2). Despite the small effect sizes, we found strong support for the distance of individual from burrow and the order of observation in explaining variance in RT. Crabs that were further away from their burrows were quicker in initiating burrow

Table 3

Correlation matrices at the phenotypic, between-individual and within-individual level.

Phenotypic		Foraging				Risk-taking	
		Rate of area covered (RAC)		Maximum foraged distance (MFD)		Response time to disruption (RT)	
Foraging	Rate of area covered (RAC)	–	–	–	–	–	–
	Maximum foraged distance (MFD)	0.344 (0.213, 0.544)	–	–	–	–	–
Risk-taking	Response time to disruption (RT)	0.063 (−0.275, 0.250)	–	0.060 (−0.378, 0.230)	–	–	–
	Latency to re-emergence (LR)	0.029 (−0.365, 0.237)	–	−0.142 (−0.637, 0.129)	–	0.146 (−0.186, 0.308)	–
Between-Individual			ΔDIC		ΔDIC		ΔDIC
Foraging	Rate of area covered (RAC)	–	–	–	–	–	–
	Maximum foraged distance (MFD)	0.558 (0.506, 0.721)	5.16	–	–	–	–
Risk-taking	Response time to disruption (RT)	0.058 (−0.558, 0.346)	−0.55	0.021 (−1.165, 0.235)	−0.81	–	–
	Latency to re-emergence (LR)	0.018 (−0.509, 0.283)	−0.39	−0.095 (−0.899, 0.221)	−0.61	0.443 (0.064, 0.578)	5.36
Within-Individual							
Foraging	Rate of area covered (RAC)	–	–	–	–	–	–
	Maximum foraged distance (MFD)	0.032 (−0.125, 0.187)	−1.52	–	–	–	–
Risk-taking	Response time to disruption (RT)	0.080 (−0.125, 0.174)	−1.11	0.087 (−0.039, 0.239)	1.39	–	–
	Latency to re-emergence (LR)	0.048 (−0.197, 0.144)	−1.71	−0.192 (−0.435, −0.011)	4.40	−0.064 (−0.324, 0.048)	1.39

All estimates are from multivariate GLMM analyses with trait-1 fitted as fixed effect and individual identity as random intercept. 95% credible intervals of estimates are given in parentheses. ΔDIC between a model that has its between- or within-individual covariances constrained and an unconstrained model.

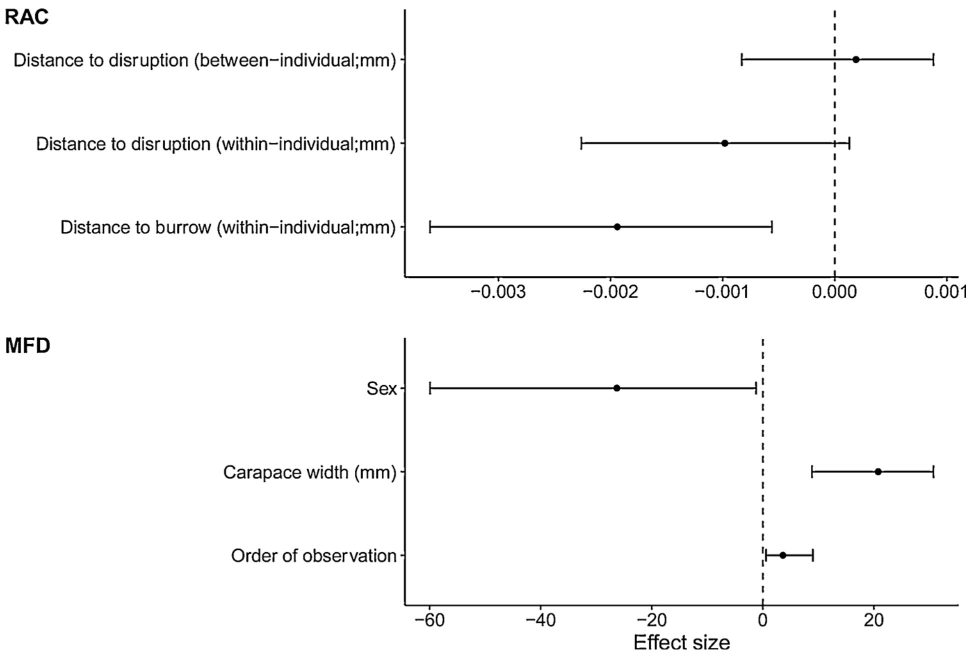

Fig. 1. Plot showing the estimated effect size and corresponding 95% credible interval of the influence sex, carapace width and order of observation have on behavioural measures RAC and MFD (foraging behaviours).

retreat ($\beta = 0.005$, 95% CI [0.003, 0.007]; ΔDIC = 51.50), while the responses were slower with increasing order of observation ($\beta = -0.068$, 95% CI [-0.110, -0.004]; ΔDIC = 18.32). Conversely, carapace size, distance to disruption (centred within individual) and distance to burrow (centred within individual) were factors that had support for varying LR (Table 1). Holding the other effects constant (i.e., considering other factors at mean value, since factors were centred), larger crabs took longer than smaller ones to re-emerge from their burrows after disruption ($\beta = 0.209$, 95% CI [0.106, 0.339]; ΔDIC = 2.18). In contrast, crabs that were further from the disruption ($\beta = -0.001$, 95% CI [-0.001, 7.56×10^{-5}]; ΔDIC = 2.22) and from their burrows ($\beta = -0.002$, 95% CI [-0.003, -4.10×10^{-4}]; ΔDIC = 5.83) took less time to re-emerge after disruption.

3.2. Personality and individual variation in plasticity

We found strong support that *D. wichmanni* showed repeatable individual differences in all behavioural tests (Table 1: $r_{adj.}$ ranged between 0.203–0.658, 95% CI [lower: 0.106–0.481, higher: 0.444–0.755]; ΔDIC ranged between 30.44–131.12; Fig. 3). This was true even though the variances of MFD between individuals differed with accumulating disruption—i.e., MFD showed individual variation in plasticity (Table 2: $\sigma^2_{slope} = 4.971$, 95% CI [0.197, 88.657]; ΔDIC = 3.69; Fig. 4). The conditional repeatability for MFD was not much different from its adjusted repeatability (Table 1: $r_{adj.} = 0.458$, 95% CI [0.328, 0.626]; Table 2: $r_{cond.} = 0.477$, CI [0.237, 0.657]. Evidence of individual variation in plasticity with accumulating disruption was not found in other behavioural measures (Table 2, ΔDIC

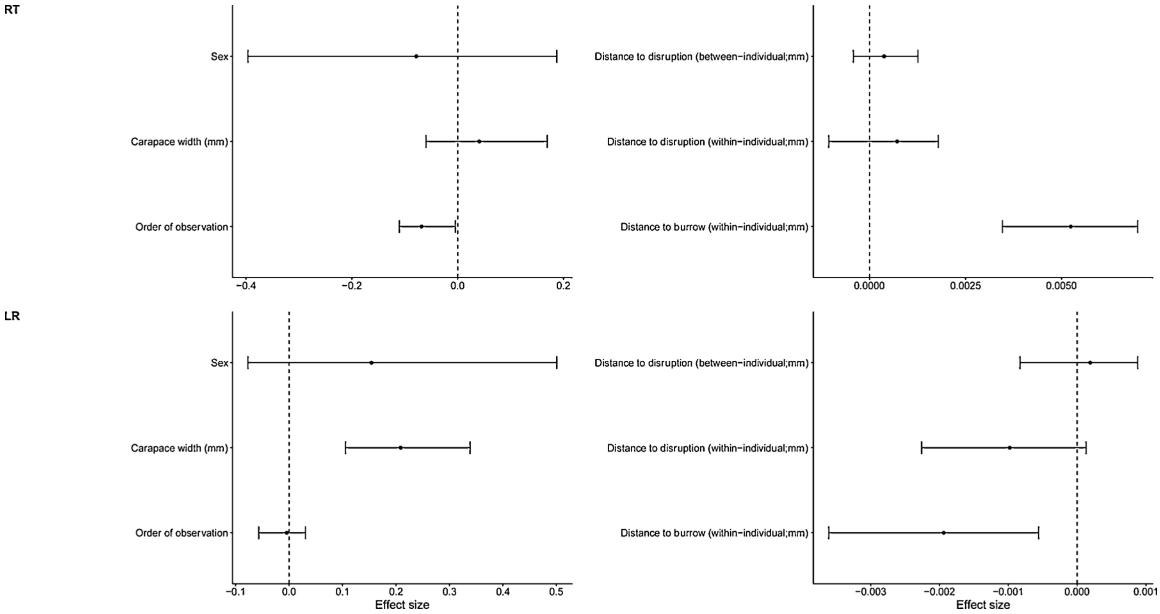

Fig. 2. The estimated effect size and corresponding 95% credible interval of factors influencing behavioural measures RT and LR (Risk-taking behaviours).

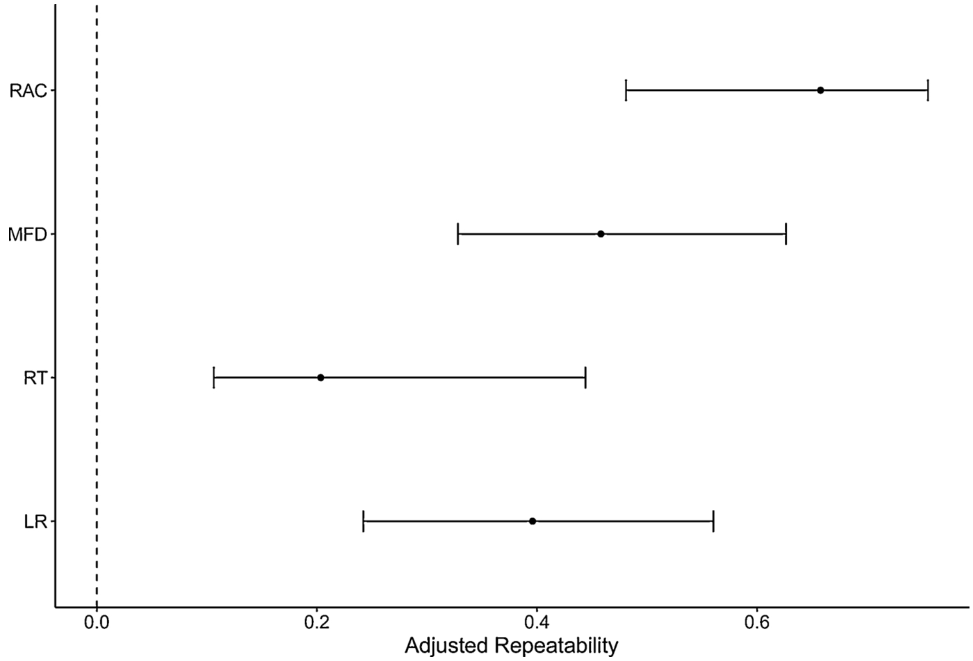

Fig. 3. Estimated adjusted repeatability and corresponding 95% credible interval of behavioural measures RAC, MFD, RT and LR.

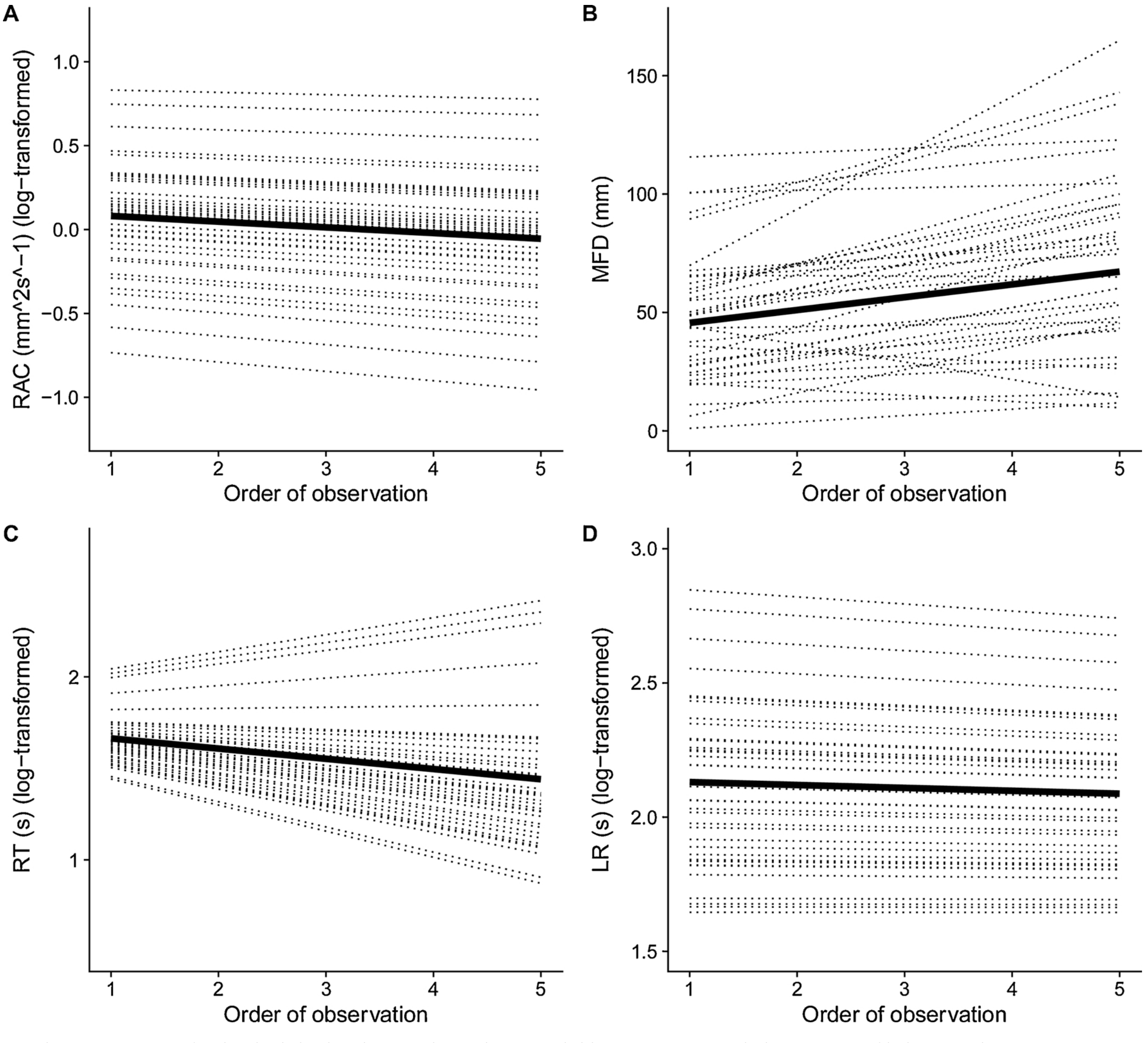

Fig. 4. Behavioural reaction norm of individual (broken line) and population (solid line) over repeated observations of behavioural measures RAC (A), MFD (B), RT (C) and LR (D).

ranged between -37.96 and -14.09; Fig. 4).

3.3. Behavioural syndrome and validity of measures

At the phenotypic level, only measures of foraging behaviour were correlated (Table 3: $Cor_{phenotypic}$ (RAC, MFD) = 0.344, CI [0.213, 0.544]). While at the between-individual level we found good support for the positive correlation of measures for both foraging and risk-taking behaviours (Table 3). Individuals that processed sediment surface area at a greater rate also travelled further from their burrows to feed ($Cor_{between\text{-}individual}$ (RAC, MFD) = 0.558, CI [0.506, 0.721]; Δ DIC = 5.16). Conversely, individuals that were quicker in responding to disruption also took longer to re-emerge after disruption ($Cor_{between\text{-}individual}$ (RT, LR) = 0.443, CI [0.064, 0.578]; Δ DIC = 5.36). However, aside from these, we found no further support for the other correlations (Table 3).

4. Discussion

4.1. Repeated disruption on the behavioural responses of D. wichmanni

Our results do not support our prediction about the response of foraging behaviour to repeated disruption—i.e., individuals will feed faster and further in response to repeated disruption. Nevertheless, they corroborate with our hypothesis that *D. wichmanni* can adapt to repeated disruption by showing resilience in its foraging behaviour. With each repeated observation, RAC decreased, while MFD increased. *Prima facie*, the decrease in RAC indicates that crabs were negatively affected by repeated disruption. However, this explanation seems incongruent with the coupled increase in MFD. Should individuals be negatively affected, we would expect both measures to decrease with each observation. Hence, more plausibly, the decreased in RAC is the result of satiation over time. Nonetheless, sand bubblers were affected by repeated interference. Results of risk propensity measures suggest that sand bubblers responded to the repeated disruptions (elaborated more below). Thus, our results more likely demonstrate the resilience of *D. wichmanni*'s foraging behaviour despite the negative influence of repeated disruption, though we are uncertain of the degree of influence.

In contrast, our analyses show that *D. wichmanni* could habituate its risk-taking behaviours to repeated disruptions only to some extent, supporting both our prediction and hypothesis, though only in part. With each repeated interference, individuals were slower in initiating burrow retreat (decreased in RT). This remained true even after holding constant the effect of individuals' distance (i.e., considering the mean distance of individuals) from their respective burrows. The ability of *D. wichmanni* to habituate to human-induced disruptions was also shared by congeneric *D. fenestrata* (see Gherardi et al., 1999). In addition, individuals that were further away from their refuges generally initiated burrow retreat earlier than individuals that were nearer, when threatened. This suggests that RT might be state-dependent (i.e., dependent on how far individuals are from their refuge).

However, LR did not vary with repeated disruption (i.e., no evidence of habituation). Instead, size, distance to refuge and proximity to disruption played more important roles. Larger individuals generally took longer than smaller individuals to re-emerge from their burrows after a disruption. Individuals that were further away from their burrows (i.e., higher $x_{B_{ij}}$) and from the disruption (i.e., higher $x_{D_{ij}}$) took shorter time to re-emerge from their refuge. These together suggest that sand bubblers could alter their re-emergence response with respect to the relative risk of each disruption. These also suggest that re-emergence response, like RT, might be state-dependent (i.e., dependent on individual size, distance to refuge and danger). The lack of habituation in the LR after repeated disruptions is contrary to the observations of *Scopimera inflata* (see Fielder, 1970) and *Uca annulipes* (see Walker, 1972). Our findings of RT and LR, taken together, suggest that *D. wichmanni* while able to habituate in its risk-taking behaviour to successive interference, will inevitably lose time for surface activities.

4.2. Personality, individual variation in plasticity and behavioural syndrome in D. wichmanni

In concordance with our prediction, we found strong support for repeatable individual differences in all measured behaviours. This lends support to our hypothesis that *D. wichmanni* exhibits personality. Although, the long-term stability of these traits remains uncertain due to the relatively short intervals (10 min) used between observations. Having longer intervals (e.g., 1 day) between observations could help in this regard. However, difficulties encountered in tagging them in the field generate serious concern over the misidentification of individuals when longer intervals are used. Further constrained by tidal influence, we therefore had to compromise with shorter interval periods. Since personality traits may change over the lifetime of an animal (Stamps and Groothuis, 2010), the uncertainty in the long-term stability of these traits does not detract the support for the presence of personality in *D. wichmanni*. Nevertheless, future work should consider examining how stable these repeatable individual behavioural differences are.

Individual variation in behaviour or personality has long been recognised in animals (Sih and Bell, 2008). However, it was only about a decade ago that interest in animal personality surged (Sih et al., 2004). While the reports of personality in animals have increased steadily, those in crustaceans have remained relatively scant (e.g. Vainikka et al., 2011; Mowles et al., 2012; Briffa et al., 2016). This disparity could be the result of its rarity in crustaceans or the lack of research in this area (Gherardi et al., 2012). Our results, thus, contribute to the growing evidence that crustaceans do exhibit personality (e.g., Reaney and Backwell, 2007; Briffa et al., 2008; Vainikka et al., 2011; Mowles et al., 2012; Briffa et al., 2016).

While the support for personality is strong, there was little evidence for individual variation in plasticity. Behavioural plasticity greatly influences a species' ability to cope with changing levels of threats. Not only does it enable for better predator evasion (e.g., Toscano, 2017), it also aids in habituation to low-risk threats (e.g., Rodríguez-Prieto et al., 2010). Hence, individuals that exhibit a greater amount of plasticity are likely to cope better with interference than those with lower amount of plasticity. In *D. wichmanni*, however, only in MFD did the increase in the behavioural response (random slope) vary between individuals as interference accrued. Even so, the degree of increase in MFD over time did not associate with the maximum distance individuals initially foraged from their burrow on the first observation (i.e., no evidence for covariance between random intercept and random slope). These together demonstrate that *D. wichmanni*, as a whole, has limited ability to respond to changes in environmental interference.

Similarly, there was no evidence of a foraging–risk propensity behavioural syndrome. We found no support for any between-individual correlation between measures of foraging and risk-taking behaviours. Foraging activity often involves some degree of predation risk (see Abram, 1992; Lima, 1998; Carter et al., 2010). Hence, individuals with greater propensity for risks also tend to forage betterBiro and Stamp 2008) since they are more likely to discover and compete for new food resources faster and better respectively (Lima, 1998; Biro et al., 2006). However, individuals may also exhibit greater propensity for risks out of necessity; they are poorer in acquiring and protecting food resources (Maskrey et al., 2018). Regardless, the propensity for risk can correlate—positively or negatively—with foraging performance (e.g. Ólafsdóttir and Magellan, 2016; Maskrey et al., 2018). In other words, foraging and risk-taking behaviours can form part of a behavioural syndrome. However, contrary to our hypotheses and predictions, foraging behaviours were not associated with risk-taking ones in *D. wichmanni*.

The presence of personality in foraging and risk-taking behaviours of *D. wichmanni* suggests that individuals cope with environmental interference, caused either by predatory events or human recreational activities, differently (see Sih et al., 2004, 2012). However, with general fixed plasticity in those behaviours, individuals are unlikely to differ in their ability to respond to changes in the intensity of interference. Yet, the lack of a foraging–risk propensity syndrome points to possible complexities in the coping ability of *D. wichmanni*. Therefore, how and which personality types are more susceptible than others to prolonged or intensified interference requires further examination. Regardless, this study underscores the importance of considering personality traits in understanding how a species might cope with environmental stressors.

4.3. Convergent validity of measures

The study of personality and behavioural syndromes relies extensively on the validity of behavioural tests/measures in quantifying behavioural traits (Burns, 2008; Carter et al., 2013). However, selecting the right measures can be challenging for two reasons. A behavioural trait can be quantified by multiple measures (Carter et al., 2013), but not all measures are suitable. The appropriateness of the measures is contingent on the species and context being studied (Burns, 2008; Gherardi et al., 2012). Conversely, a test could also be measuring several traits. This could result in the same test measuring different personality traits in different contexts (Carter et al., 2012; Magnhagen et al., 2014). Thus, relying on a single measure to quantify a behavioural trait could generate fundamental interpretation issues (Carter et al., 2013).

To circumvent these challenges, the use of multiple measurements to indicate multiple traits is recommended (Carter et al., 2012, 2013). Here we used two behavioural measures to quantify each trait. The correlations found at the between-individual level demonstrate convergent validity for the measures of both traits. In other words, RAC and MFD allowed for the measurement of foraging habit, while RT and LR reliably measured risk propensity. Because these measures showed convergent validity in *D. wichmanni*, they might also be appropriate for quantifying foraging habit and risk propensity of other sand bubblers—owing to their shared behaviours. However, more research is required before this can be ascertained.

5. Conclusions

We observed that the sand bubbler, *D. wichmanni*, possessed limited ability to cope with environmental interference. Not only did it show resilience to disturbance in its foraging behaviour, but it also increased its propensity for risk—being slower in initiating burrow retreat—with each repeated disruption. However, time spent hiding in its burrow did not change after each subsequent disruption. Hence, environmental interference, regardless of intensity, would likely result in time lost for surface activities: placing a limit on its ability to adapt to intense interference, such as those arising from human recreational activities. Because *D. wichmanni* also exhibit repeatable individual differences (personality), individuals likely differ in their ability to cope with disruptions. However, with limited individual variation in plasticity, the population's coping ability is probably limited. That said, the absence of a foraging–risk propensity behavioural syndrome points to possible complexity in its coping ability. Therefore, how intense or prolonged interference will affect *D. wichmanni* would require further work. Nevertheless, this work showed the importance of considering animal personality when exploring a species' ability to cope with environmental stressor.

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