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Improved performance, within-individual consistency and between-individual differences in the righting behaviour of the Caribbean sea star, *Oreaster reticulatus*

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Abstract

Individuals cope differently to challenging and stressful situations. Being inverted is challenging and stressful for animals, as the position leaves them vulnerable to predators and desiccation. Although sea star self-righting was first studied in the 19th century, efforts to quantify patterns of within-individual consistency and among-individual differences are limited. Here we examined the performance and repeatability of righting behaviour in the Caribbean sea star (*Oreaster reticulatus*). *Oreaster reticulatus* were wild caught and transported to a nearby facility where they were inverted up to five times. Most animals improved their righting times and exhibited within-individual consistency and among individual differences in righting method. We posit that it may be favourable to employ a consistent righting method to effectively achieve an upright position. Predation pressure and stress physiology are hypothesized to shape individual differences in righting behaviour. Moreover, these results provide preliminary evidence of personality in sea stars.

Keywords

personality, starfish, self-righting, stress physiology, invertebrate behaviour.

1. Introduction

Repeatable behaviour (i.e., behaviours that can be quantified to show between-individual variation and within-individual consistency, Sinn et al., 2008; Rudin & Briffa, 2012; Briffa et al., 2013) occurs in an extensive range of animal taxa (Bell et al., 2009). Repeatability broadly refers to the expression of behavioural consistency through time and is an important step for

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assessing behavioural syndromes (Sih et al., 2004), temperament (Reale et al., 2007), personality (Gosling, 2001), and coping styles (Koolhaas et al., 1999). For instance, on a proximate level personality is associated with differences in metabolism and stress physiology (Biro & Stamps, 2010; Wolf & Weissing, 2010). When observed under challenging or stressful conditions, repeatable behaviour can be useful for elucidating the physiological underpinnings of animal personality.

Marine invertebrates are increasingly recognized to perform behaviours that are repeatable (Hirose, 2011; Rudin & Briffa, 2012; Briffa et al., 2013; Toscano et al., 2013). For example, individuals in the phyla Cnideria exhibit repeatable startle responses to external stimuli (Sinn et al., 2008; Briffa & Greenaway, 2011; Rudin & Briffa, 2012; Briffa et al., 2013). There is also evidence that repeatability extends into the behaviours of other marine invertebrates including Echinoderms and Molluscs (Migita, 2012; Laming et al., 2013). Many invertebrate phyla are completely marine, which presents a challenging but nonetheless potentially rewarding opportunity to study the evolution of animal behaviour (Carew & Sahley, 1986; Mather & Logue, 2013).

Sea stars are a diverse taxa of echinoderm with nearly, 1900 extant species (Mah & Blake, 2012). They are recognized as being radially symmetric with multiple arms that extend from a central disk. For Asteroids, locomotion is accomplished by podia (tube feet) that extend in two rows along the centre axis of each arm to the central disk. Podia are a duo-gland system that can secrete an adhesive and de-adhesive protein to allow for temporary yet strong adhesion to surfaces (Flammang et al., 1998; Hennebert et al., 2014). Sea star movement rates are generally slow but may be directed to targets less than 1 m from the animal (e.g., 1.5–3.7 m/day, *Acanthaster planci*, Kurihara, 1999; Garm & Nilsson, 2014). Perhaps one of the most remarkable characteristics is their ability to rapidly transition from a rigid to flexible body (Migita et al., 2005). This is accomplished through collagenous (‘catch’) connective tissue controlled by the nervous system (Motokawa, 1985; Motokawa & Wainwright, 1991). Catch connective tissue likely evolved to facilitate prey capture and handling, as protection from predators, and to achieve an upright position when accidentally inverted (Blake, 1981; Motokawa, 1988; Neumann, 2000).

Sea stars move with their oral side to the substratum, however individuals may be accidentally overturned by falling from vertical surfaces or by wave action (Blake, 1981). Righting behaviour in sea stars has been studied since the late 19th century when research focused mainly on the stimuli that invoked righting and nervous system activities (Jennings, 1907; Kleitman, 1941; Pollis & Gonor, 1975). More recently, sea star righting behaviour has been investigated in response to environmental change and as an indication of stress (Watts & Lawrence, 1990; Lawrence & Cowell, 1996; Held & Harley, 2009). Migita (2012) suggested that sea stars are capable of complex righting behaviour including the ability to learn to complete the action in a shorter amount of time. Despite the long history of sea star research and suggestions that sea star righting behaviour is complex and repeatable, contemporary research on this topic remains scant. Furthermore, no investigations have analysed righting behaviour while statistically controlling for important confounding factors (e.g., body size and temperature).

For shelled animals, survival may depend on the ability to quickly and effectively attain an upright position when inverted (e.g., snapping turtle, *Chelydra serpentina*, Steyermark & Spotila, 2001; steppe tortoises, *Testudo horsfieldii*, Bonnet et al., 2001; horseshoe crabs, *Limulus polyphemus*, Penn & Brockmann, 1995). In sea stars, the stress associated with self-righting (Lawrence & Cowell, 1996; Held & Harley, 2009) may affect performance (i.e., the time to attain and upright position). Given that inverted sea stars are known to use more than one method to attain an upright position (Pollis & Gonor, 1975), it is plausible that these animals perform the manoeuver with individual consistency. Here we conducted a study to investigate individual performance and repeatability in the righting behaviour of the Caribbean sea star (*Oreaster reticulatus*, Linnaeus, 1758). *Oreaster reticulatus* is an Asteroid (i.e., sea star or starfish) that inhabits fringing reefs and coastal waters of the Caribbean Sea (Clark & Downey, 1992; Metaxas et al., 2008). In the current study, animals were wild caught and moved to a nearby facility. Prior to testing we predicted: (1) The time to achieve an upright position improves, independent of body size and temperature, as *O. reticulatus* are repeatedly challenged with inversion and; (2) individual *O. reticulatus* consistently rely on a single righting-method to attain an upright position following inversion.

2. Methods

The study occurred at the Cape Eleuthera Institute on Eleuthera, The Bahamas (24°49′10.2″N, 76°18′25.2″W) from 20 January 2014 to 26 January

2015. *Oreaster reticulatus* were collected indiscriminately (adults (orange to red) and juveniles (olive green to brown); Clark & Downey, 1992) by snorkelling in shallow nearshore areas with mixed sand and coral rubble substrate. Animals ($N = 20$) were captured by hand in groups of five, placed in a plastic tote (50 × 70 cm) filled with sea water, and transported less than 100 m to the holding facility. All sea stars were first held overnight to allow time to recover from any potential stress endured during capture and transport. The five sea stars were placed at marked locations (1–5) an equal distance apart around a circular tank (1.55 m diameter) filled with 40 cm of water regulated by a centrally-located stand pipe (approx. 300 l/h flow). Sea star arms were numbered such that the left side of arm one included the madreporite (a calcareous opening to filter water and regulate water pressure), and the remaining arms were numbered successively in a counter clockwise direction from arm one. For all animals and during the first trial, arm one was pointed at the wall of the circular tank. To track the animals, individuals were placed around the tank in order of body size. Animals were then inverted and the behaviours recorded by a video camera (GoPro Hero 3, Woodman Labs, San Mateo, CA, USA) suspended above the tank. If an individual failed to right itself in 30 min, the trial for that animal was terminated, and the animal was immediately returned to the ocean ($N = 3$). A sea star was considered in the normal position when the full oral surface faced down. Between trials we allowed animals approx. 20 min without disturbance to provide them with a rest period while in the normal position. Individuals were re-inverted underwater and rotated both in tank position (clockwise) and by the arm that pointed to the circular tank wall (counter-clockwise) for up to five trials (due to technical issues, sea stars ID6, ID7, ID8, ID9 and ID10 were assessed across four trials). This procedure was performed to reduce the stress associated with immersion and re-immersion (Lawrence & Cowell, 1996) and to eliminate any influence of within- tank location and sea star orientation.

Water temperature (°C) and dissolved oxygen (mg/l) were recorded at the beginning of each trial. Average water temperature ± SD during the test period was 25.4 ± 1.2°C. Dissolved oxygen averaged 7.94 ± 0.2 mg/l and was not further considered in the study. While righting, *O. reticulatus* were noted to perform one of the two distinct methods described by Pollis & Gonor (1975). The first method (M1), involved reaching and twisting 4–5 arms aborally to grasp the substratum, then releasing with 1–2 arms and effectively somersaulting into the normal position (Figure 1A). For the second method (M2), sea stars first reached 2–5 arms orally. With this technique, the remaining arms may twist orally to grasp the substratum. Several of the upwards extending arms may then swing over, causing a change in the centre of gravity and the animal to tip over. The sea star then reached its leading arms aborally and used its tube feet to grip the tank floor and pull itself over into the normal position (Figure 1B). These methods were distinct from one another. At the completion of five trials, sea star radius (RAD) was measured as the distance (cm) from the tip of an arm to the centre of the body. No animals had signs of previous autotomy or other trauma.

2.1. Analyses

Data were first explored for collinearity, linear and non-linear relationships, and influential observations using various visual techniques including Cleveland dot plots, correlations, and box and whisker plots. Plots were generated using the R package 'ggplot2' (Wickham, 2009). Following data exploration, potential explanatory variables for righting duration in a typical sea star were determined to include arm radius (RAD), water temperature (TEMP) and trial (TRIAL: 1-5) (Migita, 2012; Montgomery & Palmer, 2012; Montgomery, 2014). Due to collinearity with arm radius, life stage (adult/juvenile) was not considered in the analyses. To check for an effect of resting period length on righting duration (i.e., the effect of the previous trial resting period length on the current trial righting duration), we used a linear mixed effects model where sea star ID was a random intercept. To evaluate whether the time to achieve an upright position would improve, independent of body size and temperature, as *O. reticulatus* were repeatedly challenged with the presumed stress of inversion (P_1), we examined the effects of arm radius, temperature, and trial using a linear mixed model and a random intercept (sea star ID to indicate the response of a typical animal). Model validation indicated heterogeneity of variance for TRIAL, thus as an alternative to data transformation we included a covariance structure to correct for unequal variance (Zuur et al., 2009). Models were fitted with restricted maximum likelihood estimation (REML, R package 'nlme'; Pinheiro et al., 2014) and validated by examining the normalized residuals against the fitted values and each explanatory variable including those not included in the models (Zuur et al., 2009). Statistical significance was considered at $p < 0.05$.

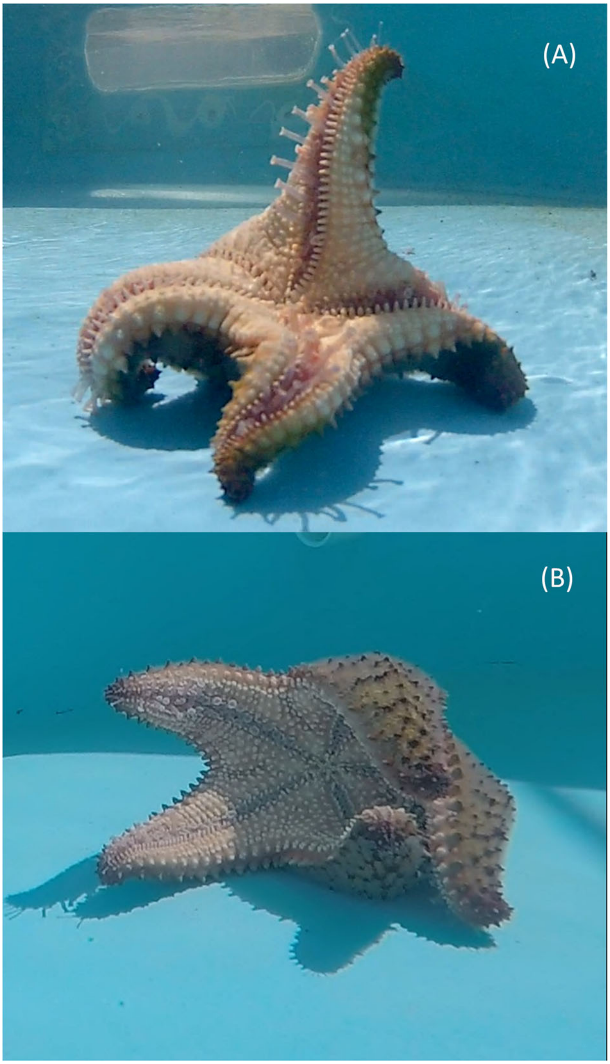

Figure 1. Righting methods 1 (A) and 2 (B) used by the Caribbean sea star *O. reticulatus*. In method 1, the animal reaches aborally with 4 arms whereas in method 2 all five arms reach orally before the animal tips over. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

An independent t-test was used to compare consistency between the two righting methods. To assess whether one righting method was more consistently used, proportions (dominant method/non-dominant method) were inverse ArcSin transformed. Because righting method is a non-Gaussian response variable and few easily applied methods exist for calculating repeatability from non-Gaussian data, we tested whether individuals consistently rely on a single righting-method to attain an upright position following inversion (P_2) using the R package 'rptR' which can currently estimate group-level repeatability for additive or multiplicative overdispered models (Nakagawa & Schielzeth, 2010; Schielzeth & Nakagawa, 2011). Behaviours are repeatable if they show relatively low within-individual variance compared to high among-individual variance (Bell et al., 2009). For non-Gaussian data the approach uses MCMC bootstrapping to generate within- and between-group variance components at the original scale or link scale, as well as credible intervals and standard errors. For the model, righting method was treated as a binary (i.e., binomial) response with individual ID as a random intercept. Because data visualization indicated no relationships between additional covariates and righting method, only a random intercept model was specified. The p-values are not provided for Bayesian estimation, therefore we considered the behaviour repeatable if the credible interval contained a repeatability value of $\geqslant 0.35$ (Bell et al., 2009). All analyses were carried out in the R statistical environment (R Core Team, 2016).

3. Results

Of the 20 *O. reticulatus* specimens captured ($\text{mean}_{\text{RAD}} \pm \text{SD} = 14.8 \pm 2.6$ cm), 15 were adult ($\text{mean}_{\text{RAD}} = 16.0 \pm 1.8$ cm) and 5 juvenile ($\text{mean}_{\text{RAD}} = 11.3 \pm 1.24$ cm). Of these individuals, 85% ($N = 17$) were able to consecutively right themselves in less than 30 min in each trial of Round 1 (Figure 2). All individuals righted themselves in the first, second, and third trial whereas two individuals were unable to achieve an upright position following the fourth trial. Most animals (70%) improved righting time while others, namely ID6 and ID18, became slower and following the third trial did not right themselves in less than 30 min (Figure 2).

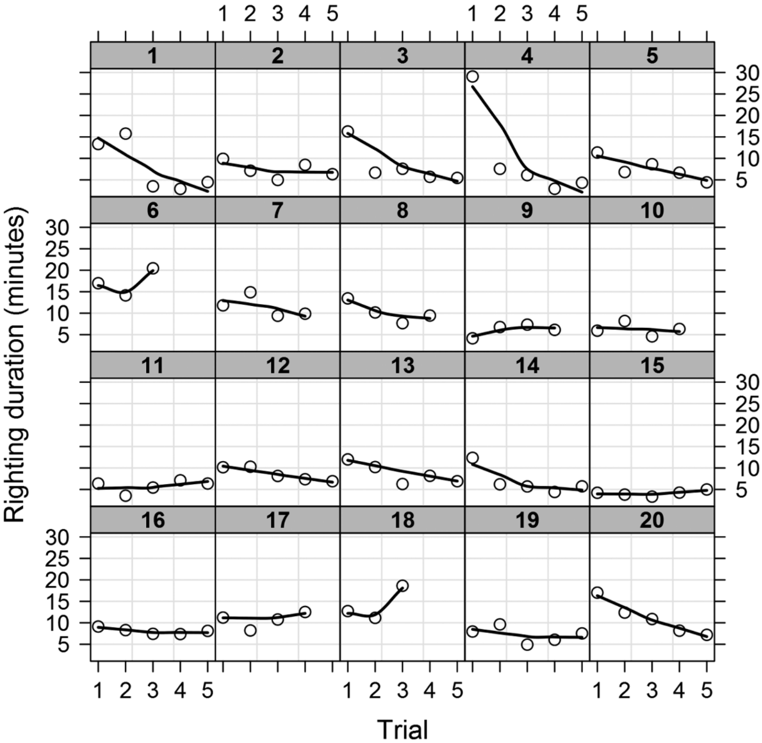

Figure 2. Righting duration (minutes) across consecutive trials for individual *O. reticulatus*. Trends are illustrated by locally weighted regression curves.

3.1. Prediction 1: the time to achieve an upright position improves, independent of body size and temperature, as O. reticulatus are repeatedly challenged with inversion

There was no effect of resting period length on righting duration ($t_{51} = 1.42$, $p = 0.16$). In the LMM to explain righting duration, neither body size nor temperature explained sea star righting duration whereas trial was highly significant (Table 1). At mean water temperature (25.4°C) and arm radius (14.8 cm), righting duration decreased significantly with each successive trial from a predicted maximum time of 9.8 min (8.2, 11.4, 95% CI) during the first trial to a predicted minimum time of 6.7 min during the final trial (5.6, 7.8, 95% CI). This relationship was apparent despite that several individuals maintained a relatively short righting time across all trials (Figure 2). Upon successive experiences being inverted, a typical sea star was able to improve the time in which to return to the normal position by 3 min (Figure 3).

Table 1.
Linear mixed model effect sizes, direction and statistical significance for righting duration of *O. reticulatus*.

Model term	Value	SE	df	*t*	*p*
Intercept	−70.0	105	68	−0.66	0.51
TRIAL	−0.77	0.18	68	−4.20	<0.001
TEMP	3.03	4.09	68	0.74	0.46
RAD	5.73	6.72	18	0.85	0.40
TEMP × RAD	−0.22	0.26	68	−0.83	0.41

The variance components for the random effects are: $\sigma^2_{\text{intercept}} = 5.18$, $\sigma^2_{\text{residual}} = 35.96$.

3.2. Prediction 2: individual O. reticulatus consistently rely on a single righting-method to attain an upright position following inversion.

Of the 91 occasions when sea stars used a particular righting method, 64% ($N = 58$) were Method 2. When Method 1 was the dominant mode of righting for an individual, an average ± SD of 76 ± 0.12% of the trials were completed with this technique. Similarly, 78 ± 0.16% of the trials were completed using method 2 when it was the dominant technique

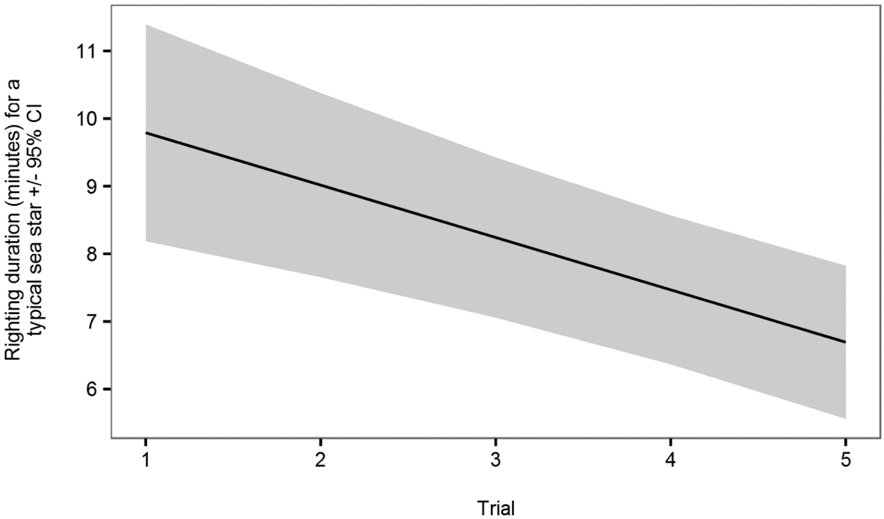

Figure 3. Fitted values (± 95% CI) from a linear mixed model for the righting duration of a typical *O. reticulatus* across five trials. Estimates were generated by holding body size and water temperature at their means ($\bar{x}_{\text{body size}} = 14.8$ cm; $\bar{x}_{\text{Temp}} = 25.4$°C).

($\pm$ 0.16). The most consistent response occurred when Method 2 was dominant ($t_{14.6} = -12.0$, $p < 0.001$). Mean righting times $\pm$ SD were similar for the two methods (mean$_{M1}$: 8.9 $\pm$ 3.8 min, $N = 35$; mean$_{M2}$: 8.4 $\pm$ 4.6 min, $N = 56$, $t_{82.4} = 0.62$, $p = 0.54$). Overall, individuals tended to select one technique, on average, more than 3 out of 5 times to right themselves. Righting method was repeatable according to MCMC estimation at the response scale ($R = 0.47, 0.26, 0.79$, 95% Credible Interval). Notably, ID17 was the only individual that used both techniques equally and performed poorly (mean$_{DURATION}$ $\pm$ SD: 10.7 $\pm$ 1.80 min) over the four trials in which it managed to attain an upright position.

4. Discussion

O. reticulatus demonstrated complexity in righting behaviours including the ability to improve righting time (Figure 2) and individual consistency and among individual differences in righting method. Here most animals improved righting performance, whereas others were unable to reach a normal position in the allotted time (Figure 2). Righting duration was not different between methods; however Method 2 was most consistent when employed by an individual. Although hypothesized in early literature (Pollis & Gonor, 1975), empirical evidence for repeatability in sea star righting behaviour has so far been elusive.

While righting time is restricted to a minimum threshold where constraints such as physical ability limit further improvement, it remains unclear why many animals improved while others maintained a consistent righting rate (Figure 2). Given that a number of sea stars rapidly and consistently achieved an upright position from the first to final trial (Figure 2), the response was not solely the result of a required 'warm-up' of catch-connective tissue. It is possible that some individuals had previous experience being inverted or were recently exposed to predators, thus eliciting a more rapid and consistent escape response. Such behaviour has been documented in both marine and freshwater invertebrates (Rochette et al., 1998; Dalesman et al., 2006; Turner et al., 2006). While righting duration did not differ between the two methods, Method 2 was most consistent. Employing a particular method to efficiently achieve an upright position may be a short-term adaptive mechanism for predator evasion (Rochette et al., 1998; Dalesman et al., 2006; Turner et al., 2006). This would be of particular importance for juveniles which are most often accidentally inverted by wave action (Metaxas et al., 2008).

During this study we maintained steady environmental conditions, as temperature and salinity can have an effect on sea star activity and stress (Watts & Lawrence, 1990; Held & Harley, 2009). Despite these controls, some animals failed to achieve an upright position in 30 min after only three trials (ID6 and ID18, Figure 2). Lawrence & Cowell (1996) found that righting time of the Asteroid *Stichaster striatus* increased or decreased significantly when immersed and re-immersed in water, respectively. While these animals were immersed for more than 8 h, the animals used in the current study were immersed for less than 1 min. Given that wild sea stars are capable of maintaining a rigid posture for many hours, echinoderm oxygen consumption (i.e., energetic cost) during stiffness changes is very low (Motokawa et al., 2012), and sea stars have been shown to successively achieve a normal position up to 12 times/day for three days (Lawrence & Cowell, 1996), it seems unlikely that inverted *O. reticulatus* were simply becoming fatigued. Given that all sea stars were collected and treated using the same procedures, it follows that individuals differ in their capacity to cope with stress. With the minimal amount of energy required to stiffen and soften collagenous connective tissue, these results may indicate early evidence of an individual-level stress response in an echinoderm.

Caribbean sea stars exhibited between-individual variation and within-individual consistency in righting behaviour, which may be the first evidence of personality in an echinoderm. Both ecological and physiological mechanisms explain repeatability in righting behaviour. Although these mechanisms remain untested, we surmise that patterns observed Caribbean sea star righting behaviour are largely related to predation pressures (Abjörnsson et al., 2004) and stress-physiology (Lawrence & Cowell, 1996; Held & Harley, 2009). Given our findings, animals that must occasionally self-right appear to be tenable models for studying personality across environmental contexts.

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