



## Personality and habitat segregation in giant sea anemones (*Condylactis gigantea*)

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### ABSTRACT

Animal personality is described as consistent differences in individual behavior across time or context, and may vary spatially. Bolder animals are more likely to migrate, grow slowly, or explore than shyer animals. Personality types within a population can also differ between discrete habitats or continuously across an environmental gradient. We examined the distribution of giant sea anemone (*Condylactis gigantea*) responses to disturbance across a continuous habitat gradient to determine whether anemones' habitat selection is explained by individual variation. On four different occasions we induced individual anemones to retract their tentacles by touching them with a model blue crab (*Callinectes sapidus*) and recorded the time for their tentacles to relax into their original state. We also recorded several environmental variables associated with each anemone. We found that individual anemones behaved in consistently different ways and that a combination of seagrass measurements and the number of close conspecifics, as well as their tentacle color, significantly explained this variation. This indicates that personality may either influence habitat choice, or that habitats favor certain personalities. Ultimately, personality types are segregated by habitat type, which suggests that such variation could lead to reproductive isolation.

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### 1. Introduction

Non-human animals from many taxa exhibit “personality” (Briffa and Greenaway, 2011; Briffa et al., 2008; Huntingford, 1976; Schuett et al., 2011), or consistent individual differences in behavioral responses through time or across contexts (Réale et al., 2007; Sih et al., 2004). Contexts are functional categories such as feeding, courtship, or competitive encounters (Briffa and Weiss, 2010), and when multiple behaviors are correlated across contexts they are referred to as a “behavioral syndrome.”

Recent evidence suggests that personality may often be adaptive (Brydges et al., 2008; Dingemanse et al., 2007), but could also reduce fitness by limiting potentially adaptive behavioral plasticity (Sih et al., 2004). In instances where personality is adaptive, fitness may be enhanced because certain habitats favor specific behaviors (Adriaenssens and Johnsson, 2011). Past studies have demonstrated that behavioral syndromes are related to, and even induced by, environmental and predation pressures during ontogeny, (Dingemanse et al., 2007; Dziewczynski and Crovo, 2011), which suggests that habitat variables play a differential role in the fitness of certain personality types.

One dimension of personality has been labeled the shy–bold continuum (Bell, 2007; Biro and Stamps, 2008; Dingemanse and Wolf,

2010; Wilson et al., 1994). Boldness is measured by an animal's reaction to a potentially dangerous situation, such as time spent foraging in the presence of a predator (Réale et al., 2007; Wilson et al., 1994). A bold individual would be more likely to forage in dangerous environments and have shorter reaction times to predatory stimuli. Boldness has been studied in various taxa (Briffa et al., 2008; Dingemanse et al., 2007; Höjesjö et al., 2011), and has far reaching consequences for an animal's life history. Bolder individuals from several studies have been shown to be more likely to migrate (Chapman et al., 2011), disperse (Armitage and Van Vuren, 2003; Cote et al., 2011; Fogarty et al., 2011), grow more slowly (Adriaenssens and Johnsson, 2011), or explore more widely (van Oers et al., 2004) than their shyer conspecifics. Collectively, these studies indicate that the boldness may have long-term effects on survival and fitness.

Previous studies concluded that personality might differ among populations in discrete habitats (Bell and Stamps, 2004; Brydges et al., 2008; Dingemanse et al., 2007; Herczeg et al., 2009; Martin and Réale, 2008a), but these studies focused specifically on discrete habitats such as different ponds and rivers. A shortcoming of this focus is that there may be other factors that covary with these isolated populations. To properly determine whether habitat and personality covary, one should study them along a continuous gradient at a single location. This would also allow for the possibility of habitat choice within a population, because animals have been shown to have preferences for a certain habitat type based on morphology and life history factors (Huey, 1991). By segregating according to preference for different habitats, personality groups within a population may aggregate and, over time, become

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reproductively isolated. Such reproductive isolation could ultimately lead to sympatric speciation (Dieckmann and Doebeli, 1999).

The Caribbean giant sea anemone (*Condylactis gigantea*) is an ideal model organism to study the relationship between personality and habitat selection. Each organism is a non-clonal individual (Shick, 1991), which may segregate across microhabitats based on differing color morphologies (Stoletzki and Schierwater, 2005). As pelagic larvae, these anemones disperse over a wide range to choose their habitat, and even though they are highly sedentary as adults, they possess the ability to move across short distances by means of a pedal disk, allowing them some degree of habitat selection following larval dispersal (Jennison, 1981; Shick, 1991). Studies conducted on clonal anemones have found consistent differences in aggressive behavior, as well as habituation rates (Ayre and Grosberg, 1995), and a recent study reported *in situ* personality in the intertidal clonal anemone *Actinia equina* (Briffa and Greenaway, 2011).

Our aim was to determine whether there was a covariation between individual behavior and microhabitat structure. While habitat preference is mediated by a variety of intrinsic factors, it may also play a role in personality development. Conversely, if personality is an individual intrinsic attribute, we would also expect an association between habitat and personality as a result of personality driving habitat selection. In either scenario, we expect personality type to be associated with habitat.

## 2. Methods

### 2.1. Study site

We studied the giant sea anemone found in a seagrass bed outside the Calabash Caye Field Research Station in Belize (17°16'N, 87°48'W) from 6 to 24 October 2011. The bed was comprised of mainly *Thalassia testudinum*, a thin, wide-bladed seagrass, and *Syringodium filiforme*, which have tall, thin shoots. Both species occurred in varying densities and blade heights, resulting in a gradient of habitat conditions. Depth also varied across the bed. A total of 135 anemones were labeled with numbered conch shells to ensure that we could relocate individuals through time. The shells' naturally fusiform shape and heavy weight made them resistant to potential tidal action, and being locally abundant, they were ideal as place markers. Shells were marked with waterproof ink on their smooth sides and placed roughly within 10 cm of the anemones' tentacle mass with the numbers clearly visible.

### 2.2. Data collection

We quantified the reaction of the anemones to being touched with a 15.2 × 10 cm plastic blue crab (*Callinectes sapidus*) every other day for a total of 4 tests per subject. The blue crab was an appropriate model because it is a common co-existing species throughout the Caribbean (Millikin and Williams, 1984). The model was placed randomly amongst available tentacles, without contacting the oral disk, and shaken laterally. Vigorous stimulation for 3 seconds induced a visible tensing and partial retraction of stimulated tentacles. We timed the latency for the last of the focal tentacles to return to a relaxed state. Physical stimulation was assumed to be the primary source of sensory input during trials because of the anemones' biology (Shick, 1991). If chemosensation did play a role in the trials, the plastic of the model crabs was novel but remained consistent in all tests. On each experimental day, the numbered anemones were randomly located across the site and tested to avoid potential order effects.

A variety of environmental variables associated with each anemone's location were measured. Water temperature was recorded at the time of each test. The number of conspecifics within a 1 m radius was also recorded. To characterize the variation of the seagrass

bed, total shoot density (number of shoots per quadrat) and average shoot height (in cm) were counted for *T. testudinum* and *S. filiforme* within a 25 × 25 cm square quadrat around each anemone. We recorded depth using a measuring tape and corrected for tidal cycle variation using a tide chart (Toy, 2011). Depths were normalized by removing the change in height between low tide and the nearest tide point to the time of measurement.

We measured individual physical characteristics of each anemone as well. Specifically, we noted tentacle color and tentacle tip color, and scored them 0 (for green) and 1 (for purple) in both measures. The diameter of each anemone was measured by averaging five haphazardly placed diameter measurements of the tentacle body. We noted contact with conspecifics by scoring individuals with 0 (for no) and 1 (for yes).

All behavioral measurements were taken under snorkel by two observers. We practiced tests on anemones not included in the study to standardize both the stimulation protocol and the latency measurements. We did this until both observers consistently performed the stimulus test and recorded the same time independently at least three times. Number of conspecifics, depth, and physical characteristics were also measured under snorkel. All seagrass measurements were taken while SCUBA diving.

### 2.3. Statistical analysis

Latency was square root transformed to normalize times to more-closely reflect a normal distribution. We performed a principal component analysis (varimax rotation, Kaiser normalization, eigenvalues > 1.00 extracted) and used loading scores ≥ |0.60| to interpret factors and to reduce the set of measured variables to a set of uncorrelated factors for subsequent analyses.

We fitted a linear mixed effects model in RStudio (v0.94.110) using the nlme package (v 3.1-102). We used transformed latency time with trial number and the five extracted PCA factors as fixed effects, and sea anemone identity as a random effect. We tested for the significance of between-individual differences by comparing (using a log-likelihood ratio test) a model that does not contain anemone identity as a random effect, with one that does (Martin and Réale, 2008b). To estimate the total variance explained by the model with identity, we divided the residual variance by the total variance and subtracted this quotient from one.

## 3. Results

We extracted five factors that we named total contact, substantial contact, temperature/depth, tip color, and tentacle color, which together explained 66% of the variance in the initial observations (Table 1). The first factor, total contact, was explained by the number of *Syringodium* shoots, *Syringodium* height, and total number of seagrass shoots. The second factor, substantial contact, was explained by *Thalassia* shoot density and the number of conspecifics within 1 m. The third factor, temperature/depth, was explained by temperature and depth. The fourth factor, tip color, was loaded only with tip color, while the fifth factor, tentacle color, was loaded with tentacle color. For subsequent analysis, we transformed factor tentacle color with a  $\log(x+2)$  transformation.

Anemones exhibited significantly repeatable differences in their response to our stimulus (log-likelihood ratio test;  $P=0.024$ ), suggesting that individuals explained a significant amount of the variance, i.e. they show distinct personalities. The linear mixed effect model explained 10.8% of the total variance. The proportion of variance in latencies explained by individuality (termed repeatability) was 8.57%. Two PCA factors, substantial contact and tentacle color, significantly explained variation in emergence time (Table 2). Individuals with shorter latency times were located in areas with sparser *Thalassia* density and less conspecifics (Fig. 1A). Individuals with

**Table 1**

Results from a principal component analysis that produced 5 composite factors. Bolded scores indicate variables that were used in naming factors.

Measures	Factors				
	Total contact	Substantial contact	Temperature/depth	Tentacle color	Tip color
Diameter (cm)	-0.076	-0.040	-0.366	-0.489	0.483
Temperature (°C)	0.001	0.147	<b>0.743</b>	0.062	0.038
Contact with conspecifics	-0.381	0.342	-0.173	0.556	-0.032
<i>Sarangodinium</i> density (shoots/quadrat)	<b>0.873</b>	0.016	-0.058	0.025	-0.051
<i>Sarangodinium</i> height (cm)	<b>0.812</b>	0.045	-0.108	-0.070	-0.050
<i>Thalassia</i> density (shoots/quadrat)	0.556	<b>0.652</b>	0.076	-0.019	0.124
<i>Thalassia</i> height (cm)	0.312	0.539	-0.116	0.067	0.183
Total shoot density (shoots/quadrat)	<b>0.837</b>	0.463	0.023	0.000	0.060
Depth (cm)	-0.117	-0.170	<b>0.688</b>	-0.123	-0.006
Number of conspecifics	-0.051	<b>0.752</b>	0.054	-0.129	-0.266
Tentacle color	0.051	-0.185	-0.033	<b>0.770</b>	0.085
Tip color	-0.015	-0.020	0.092	0.067	<b>0.882</b>

purple tentacles had shorter latencies than green individuals, while smaller individuals tended to have longer latencies (Fig. 1B).

**4. Discussion**

Our results indicate an association between habitat and personality in anemones. Importantly, this result differs from past studies that have only looked at personality in the context of discretely different habitats (Bell and Stamps, 2004; Brydges et al., 2008; Dingemane et al., 2007; Herczeg et al., 2009; Martin and Réale, 2008a) because we measured habitat continuously. Thus, our result illustrates the potential for finer-scale relationships between habitat and personality.

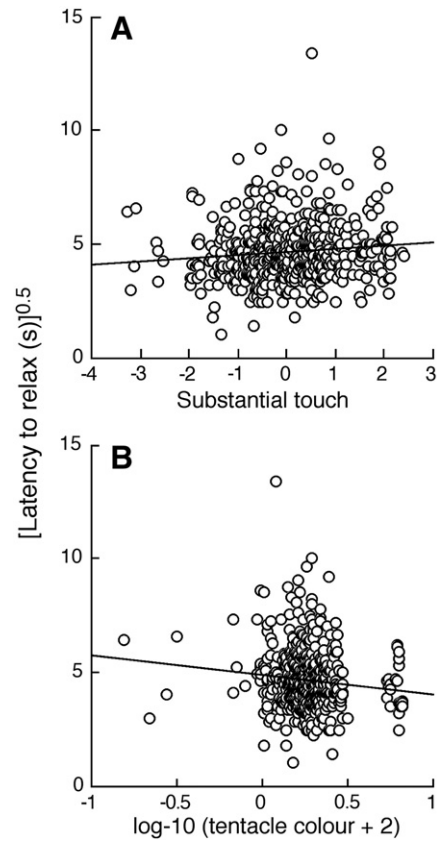
These associations between personality and habitat in anemones may emerge via two alternative pathways. First, the height of *Thalassia* and the number of surrounding conspecifics may induce consistent behaviors, and therefore personality, in resident anemones. Second, anemones may select their environment based on individual preferences.

There is no current evidence to definitively evaluate these hypotheses. However, prior research has determined that habitat differences can induce personality variation within a population of three-spined sticklebacks (*Gasterosteus aculeatus*) (Bell and Sih, 2007; Dingemane et al., 2007), and that behavioral syndromes can be altered by manipulating predation, indicating that personality can be changed ontogenetically (Smith and Blumstein, 2012). Amongst the anemones, we found that individuals who lived in

**Table 2**

A linear mixed effect model explained 10.8% of the variation in individual latency times. Bolded values indicate significant factors.

Variance standard deviation					
Random effects	Individual anemone	0.145	0.381		
	Residual	1.546	1.243		
		Value	Standard error	t Value	P
Fixed effects	Trial	-0.073	0.056	-1.292	0.197
	Total contact	-0.038	0.063	0.551	0.551
	Substantial contact	0.149	0.063	2.355	<b>0.019</b>
	Temperature/depth	0.058	0.069	0.830	0.407
	Tip color	-0.044	0.063	-0.700	0.484
	Tentacle color	-0.426	0.158	-2.698	<b>0.007</b>



**Fig. 1.** The relationship between significant factors (see text) and the latency to relax (in seconds) for individual anemones responding to being touched by a model crab (details in text). Plotted are results of all four tests on all 135 anemones.

areas of higher *Thalassia* density and were surrounded by more conspecifics were shyer than those in more open areas. Because anemones are highly tactile organisms (Shick, 1991), it stands to reason that the contact environment surrounding an individual is relevant to the behavioral responses: *Thalassia* has a wide blade and can grow to be quite tall relative to the anemone's height, while conspecifics share the same gross anatomy in the tentacle body.

Alternatively, personality variation may result in spatial heterogeneity. This could be happening one of two ways. Different personality types may have differential survival rates across a habitat gradient. Personality types that have low survival rates in a certain habitat may be outcompeted and eventually go extinct in that particular habitat. Conversely, personalities that allow individuals to be more successful in competitive encounters (Rudin and Briffa, 2012) and have a higher survival rate in a certain habitat may be able to outnumber inferior conspecifics. Many studies have shown the importance of intraspecific competition and aggression on the structure of anemone populations (Ayre, 1983; Francis, 1973; Ottaway, 1978; Purcell and Kitting, 1982). Personality could also be directly driving habitat choice. Individuals would choose where they settle according to their personality type. In this case, an animal's inherent personality would be a factor in what type of habitat they preferred.

Other habitat measures such as depth or *Syngodium* density were not significantly related to personality variation, indicating that certain environmental variables are more important than others in explaining individual variation in behavior. Whether personality is induced by, or a factor of, habitat segregation is still unknown and future research should be directed toward breaking apart this confound. Studies may also address the extent, or lack thereof, that certain environmental factors have in animal personality. In either

case, the correlation between personality and small-scale habitat differences has larger potential ramifications.

If habitat causes personality, it implies that personality is an induced aspect of an organism's behavior, possibly reflecting behavioral plasticity and adaptation. However, if personality is the driver behind habitat selection, then it may be a heritable characteristic that could be acted upon by natural selection. Studies have already suggested that personality has a genetic component (Gosling, 2001; van Oers et al., 2004), making the latter hypothesis likely. Additionally, anemones are sorting themselves by color morph, a genetically correlated trait, and demonstrate some genetic isolation between variants (Stoletzki and Schierwater, 2005). Our study showed an association between tentacle color and personality, providing further evidence towards a genetic connection. If true, personality based habitat segregation could cause reproductive isolation between personality types, and in the long term, the formation of new species by sympatric speciation (Eroukhanoff et al., 2011).

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