

Variation in risk-taking and aggression in morphotypes of the beadlet anemone, *Actinia equina* (L.), and the green anemone, *Actinia prasina* (Gosse)



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ABSTRACT

Anemones exhibit distinct between-individual differences in behaviours such as risk-taking and aggressiveness. The genus of anemone *Actinia* contains numerous morphotypes which occupy different locations on the shore and show different levels of aggressiveness. In this study we explored whether their propensity to take risks likewise differed between three groups of anemones: *Actinia prasina*; a low shore morph of *Actinia equina* characterised by a blue limbus around the pedal disc (described as ring-present, RP); and upper shore morphs of *A. equina* characterised by a lack of such a ring (ring-absent, RA). Risk-taking behaviour was measured using startle-response durations across two trials, separated by two weeks. In-between trials anemones were allowed to engage in pairwise contests with a randomly-selected opponent, during which the number of occurrences of behaviours related to movement of the body, tentacles and acrorhagi were counted and compared between groups to identify systematic variation in potentially offensive and defensive postures. Length of holotrich nematocysts, thought to be linked to aggressiveness, was also measured. Both risk-taking and inflation/deflation of acrorhagi significantly differed between groups: RA anemones were risk-prone and aggressive, RP anemones risk-averse and non-aggressive, *A. prasina* occupying a position in-between. Likewise nematocyst lengths varied between groups, shortest among RP anemones and longest in RA anemones. These data suggest that different morphotypes are associated with differences in risk-taking which may result from a complex interplay of various ecological factors linked to the habitats these morphotypes occupy, and add further credence to theories on speciation within the *Actinia equina* species complex.

1. Introduction

The extent to which individual animals take risks can have implications for their fitness that depend on internal and external factors (Sih et al., 2004). Risk-prone animals are likely to forage regardless of danger whereas risk-averse individuals favour safety above obtaining food (Wilson et al., 1993). This represents a trade-off since time spent avoiding dangers – such as predation, novelty, or periods of poor environmental quality leading to stress or harm – cannot be spent foraging, and successful strategies would limit risk-averse behaviours when not necessary. The relative success of risk-prone and risk-averse strategies largely depends on the environmental pressures to which the population is exposed; for example, risk-prone animals tend to excel where predation risk is low (e.g. Bell, 2005). Risk-taking behaviour is often strongly correlated with intraspecific aggression where risk-prone individuals are also likely to be more aggressive (Rudin and Briffa, 2012; Sih et al., 2004; although c.f. Bell, 2005). The link between (intra-specific) aggression and risk-taking (which, in the context of anti-

predator strategies, is considered inter-specific aggression; Huntingford, 1976) is at least partially driven by internal factors such as hormone or gene expression (Koolhaas et al., 1999). Multiple behaviours linked in such a manner are termed behavioural syndromes, particularly when correlated across contexts (Sih et al., 2004) and, though the evolutionary reasons for the development of behavioural syndromes is still unclear, functionally adaptive relationships are often observed. For instance, the link between risk-taking and aggression may allow for maintaining possession of a resource when under challenge or predation threat (Taylor and Lattanzio, 2016). The syndrome may also represent underlying genetic mechanisms which limit the extent to which these behaviours can evolve independently of the other (Sih et al., 2004).

Variation in behaviour – especially when linked in such a manner – has profound implications for fitness dependent upon the environment to which organisms are exposed. Behavioural plasticity allows individuals to modulate their behaviour (including risk-taking and aggressiveness) in accordance with internal state as well as epigenetic and

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environmental factors (Dall et al., 2004; Frost et al., 2007). However, the extent to which animals can modulate their behaviour is limited (Briffa and Greenaway, 2011; Frost et al., 2007), especially when linked as a behavioural syndrome (Sih et al., 2004; Bell, 2005; Adriaenssens and Johnsson, 2012). Behavioural consistency (or consistent individual differences in behaviour) may be explained by limitations on plasticity or from selection favouring combinations of behaviour adaptive to a particular environment (the constraint and adaptive hypotheses, respectively; Bell, 2005). The net result, however, is that the behavioural profile of a population should be the most appropriate for the challenges present in the habitat (Adriaenssens and Johnsson, 2012; Hensley et al., 2012) and is likely to differ between discrete populations based putatively on differences in environmental challenges and the behavioural responses available (e.g. Bell, 2005; Dingemanse et al., 2007; Endler, 1995). Understanding these behaviours, how they're linked, and the mechanisms driving them may inform theories on how these behaviours evolve, either independently or together. Numerous studies compare populations from isolated patches but, even within a single community, behaviour may vary across an environmental gradient (Hensley et al., 2012) and this information can elucidate the relationship between behaviours within a syndrome.

One such gradient occurs across the rocky shore, which is naturally exposed to temporal and spatial variations in submergence with knock-on effects to the ecology of littoral organisms (such as on feeding regimes, desiccation and predation risk). Community structure on the shore is considered to be driven by an interaction of biotic and abiotic challenges: upper limits of species are defined by their physiological tolerance to emersion whilst lower limits are defined by their ability to compete for space, avoid predators and obtain sufficient food (Southward, 1958). Differences in competitiveness and responses to risk may, therefore, directly influence the distributions of animals and the potential for individuals of a particular behavioural type to aggregate (Hensley et al., 2012; Wolf and Weissing, 2012). Animals without the requisite physiology or behavioural repertoire for a set of environmental conditions are likely to move or are otherwise unlikely to survive within that habitat (Huey, 1991). On rocky shores, in particular, this has resulted in the formation of discrete zones containing particular assemblages of organisms most suited to (and best capable of competing for) that shore height. However, the distribution of particular species across these vertical gradients is likely to reflect intraspecific behavioural and physiological variation (Hensley et al., 2012). Risk-taking animals trade off safety for greater opportunities to utilise available resources, which may manifest as a more rapid recovery from a disturbance (Réale et al., 2010). At the top of the shore, where submersion time is already limited, risk-taking behaviour may be a more appropriate strategy to minimise time lost after a disturbance; in contrast, on the lower shore where organisms are expected to spend the majority of their time submerged and predators may be more abundant, time lost to protection is less important. Aggressiveness, however, is more likely to increase towards the lower shore where competition for space is a significant component of community structure (Southward, 1958). Potentially, where the distribution of animals is enforced through behavioural and physiological limitations relative to their environment, reproductive isolation may occur between individuals with one likely outcome being sympatric speciation (Hensley et al., 2012).

Though morphologically simple, cnidarians are capable of exhibiting behaviours which consistently differ between individuals i.e. are not random responses to environmental challenges (e.g. Ayre and Grosberg, 1995; Briffa and Greenaway, 2011). In *Actinia* a common and cosmopolitan intertidal anemone, interclonal contests are commonplace and involve individuals fighting off unrelated anemones using specialised tentacles, acrorhagi, containing high densities of nematocysts (Turner et al., 2003; Williams, 1991). During contests acrorhagi are inflated and brought down on an opponent in a process called overtopping; in the most aggressive interactions acrorhagial tissue, termed a peel, is left behind on the opponent (Turner et al., 2003). The

purpose of aggression appears linked to territoriality, as anemones do not attack clonemates (Turner et al., 2003); instead, aggression appears most prevalent in high density aggregations, often arising as individuals migrate to suitable microhabitats during colder seasons (Brace and Quicke, 1986; Brace and Reynolds, 1989). Individual *Actinia* also appear to consistently differ in their response to perceived predation threat; termed startled responses, feeding tentacles are withdrawn when disturbed and only re-extended after a certain period of time (Briffa and Greenaway, 2011).

The species *Actinia equina* is known for its numerous morphotypes, varying in colour and pattern of the column wall and in the colour of the pedal disc (Quicke and Brace, 1984; Watts and Thorpe, 1998). Some of these morphotypes have been reclassified as new species based on genetic evidence, such as the strawberry anemone *Actinia fragacea* (Carter and Thorpe, 1981). More recently a green-coloured morphotype was putatively described as heterospecific and described as the green anemone *Actinia prasina* (Solé-Cava and Thorpe, 1987). However, among the remaining morphotypes of *A. equina* there remains debate over whether the morphotypes constitute multiple variants of a single species or numerous separate species (Watts et al., 2000; Perrin et al., 1999) and to what extent they are capable of interbreeding (Perrin et al., 1999). Three morphotypes have been previously described and are found in discrete zones on the intertidal: the Low (L) morph, Mid (M) morph and Upper (U) morph, each named after the zone on the shore in which they are usually found. U and M morphs are indistinguishable by gross morphology and only reliably separated through genetic analysis (Perrin, 1993). Whilst these morphs are often identified by colour this may not always be appropriate since colour is likely assimilated from the diet and therefore environmentally determined (Watts et al., 2000); however, lower shore varieties have a blue ring around the limbus of the pedal disc, which is absent in higher shore varieties. The genetic relationship between these morphotypes is, furthermore, unclear; sexual reproduction among *A. equina* appears limited with most offspring produced asexually, and young brooded within the enteron are most frequently of the same morphotype (Perrin et al., 1999). Thus, though these morphotypes overlap in distribution (with the magnitude of overlap defined largely by shore topography) the degree of gene flow between the morphs is not known. Distributional differences may be a result of individual differences in behaviour, with those morphotypes positioned higher on the shore tending to exhibit high levels of aggression (Brace and Reynolds, 1989). In contrast, low shore morphs tend to show very little aggression, often not even attempting to attack their opponent (Brace et al., 1979; Brace and Reynolds, 1989). *A. equina* are able to adjust their behaviour dependent on their environment (e.g. Brace & Quicke, 1986) but the extent to which their distribution relies on evolved responses to their environment rather than phenotypic plasticity are unclear (Briffa and Greenaway, 2011). Furthermore, even after being held under laboratory conditions for up to 6 months behavioural differences in aggressiveness are maintained (Brace et al., 1979). Lengths of holotrich nematocysts within the acrorhagi also differ between morphs (Watts et al., 2000), and may be important in determining contest winners and losers (Rudin and Briffa, 2011). Further understanding of the distribution and behaviour of these morphotypes has been cited as key in understanding both their ecology and their relatedness (Perrin et al., 1999).

Whilst variation in aggressiveness across morphotypes is well characterised, as yet no studies have attempted to determine whether this behavioural response to an environmental challenge likewise varies between morphotype/with shore height. Linking discrete behavioural types to the different morphotypes may help explain why the morphs aggregate at particular shore heights, and may provide evidence that explains speciation among the *Actinia* group based on habitat-derived reproductive isolation (Ingleby and Johnson, 2014). Furthermore, evidence for the presence of a risk taking-aggressiveness behavioural syndrome has been found within this species overall (Rudin and Briffa, 2012) but how this relationship varies with ecological factors

associated with shore height (essentially through morphotype) is unclear. The aims of this study were therefore to examine how risk-taking varies between morphotypes of *Actinia* and determine the extent to which these responses were related to aggressiveness. Specifically, we aimed to (1) determine whether startle responses varied between morphotypes; (2) determine whether engaging in agonistic contests caused changes in startle response durations, and whether the magnitude of change varied dependent on morphotype; and, (3) characterise the behavioural processes involved in agonistic encounters and assess whether contest behaviours differed between morphotypes. Within this study we use the term morphotype to describe three discrete varieties: *A. equina* without a blue ring around the limbus (Ring Absent), composed of U and M varieties; *A. equina* with a blue ring around the limbus, a red column and a green pedal disc (Ring Present), ostensibly the L morph; and *A. prasina*, with a green column and green pedal disc and a blue limbus.

2. Methods

2.1. Experimental animals

Anemones (*Actinia equina*: Ring present $n = 13$, Ring Absent $n = 32$; *Actinia prasina* $n = 15$) were collected from a rocky shore to the north-west of the pier at Llandudno (North Wales, UK; OS grid reference SH7881). Individuals were prised from the rock using a flathead screwdriver, which results in no tissue damage and leaves anemones fully capable of reattaching to a substrate. A minimum of a 2 m gap was left between any individuals that were collected to ensure that no clonemates were incorporated into the study (Watts et al., 2000). Anemones were placed individually into sealable plastic bags, with enough seawater to cover them, and brought back to the labs at the University of Liverpool on the same day where they were immediately placed into individual transparent plastic cups and allowed to settle onto dry pebbles previously collected from the shore at Llandudno. Once they were attached (after ~1–2 h) the anemones were provided with seawater collected from the docks in Liverpool and placed into a constant-temperature room maintained at 10 °C. Anemones were initially fed to satiation on mussel flesh (*Mytilus edulis*) collected for this purpose and fed once weekly on the same diet. The water in each cup was replaced three times per week with seawater collected from the docks around Liverpool. This was sufficient to maintain a clean environment and sufficient oxygenated water without the need for aeration. Anemones were maintained under these conditions for 1–2 months prior to experimentation.

2.2. Anatomy

Prior to the behavioural trials the lengths of holotrich nematocysts from the acrorhagi of individual anemones were measured. Anemones were placed into a large tank containing fresh seawater and a small amount of tissue (1–2 mm³) was excised from acrorhagi and stained using 0.1% methylene blue solution. The nematocysts were examined under a compound light microscope (Leitz HM-LUX, Germany); ten undischarged nematocysts were measured for each individual and the average length recorded. Anemones were then allowed at least one week to recover before behavioural trials began.

2.3. Behaviour

Startle responses, which may simulate activity of a predator or a sudden, unexpected change in environmental conditions (Briffa and Greenaway, 2011; Hensley et al., 2012), were used in this study as a measure of the propensity for individuals to take risks. Anemones were placed, along with their pebbles, into a tank of fresh sea-water and allowed time to fully unfurl their feeding tentacles. At this point, a 50 ml syringe of sea-water was discharged into the oral disc from a

distance of approximately 2 cm, resulting in the anemone retracting its tentacles. The time taken from the moment of discharge until the anemone had fully reopened its tentacles was measured; those anemones which had not reopened within 1 h were assigned a value of 3660.01 s.

One week after the startle response trial, pairwise agonistic contests were performed. In each case, two anemones (with their pebbles) were placed into a test tank identical to those used in previous trials. Anemones were randomly allocated an opponent (irrespective of morphotype), ensuring that individuals were size-matched (since relative size is a potential influence on contest behaviour and outcome; Brace and Pavey, 1978; Brace et al., 1979) and the two individuals pushed together until the tentacles were in contact. Whilst theoretically any combination of two morphotypes (the same morph or different morphs) could have been paired, here this method resulted in RA morphs paired with isomorphic and allomorphic anemones, but neither RP nor *A. prasina* were paired with individuals of the same morph. The contest was then allowed to proceed until either one anemone had retreated or 1 h had passed, whichever was the longer. Movements among anemones are otherwise infrequent and usually induced as an escape response from adverse conditions, such as agonistic encounters (Ottaway, 1978) and thus retreating behaviour is a good indicator of a loss in an agonistic encounter (Rudin and Briffa, 2011). Fifty-five of the fifty-eight contests (94.8%) resulted in a clear winner or loser, indicating that anemones had sufficient time to compete and 1 h was an appropriate cut-off. During the contests, the behaviour of individuals of each morph was characterised (in a similar manner to Rudin and Briffa, 2011) and the number of incidences of each of the following behaviours recorded: (1) movement of tentacles towards an opponent; (2) movement of tentacles away from the opponent; (3) retraction of the tentacles (as per startle response); (4) movement of body/pedal disc towards the opponent; (5) movement of body/pedal disc away from the opponent; (6) number of attacks made overall; (7) inflation of the acrorhagi; (8) deflation of acrorhagi; (9) number of peels left on an opponent. These behaviours were selected to encompass a range of movements that may potentially indicate aggressive (intending to cause damage or to attack the opponent: 1, 4, 6, 7 and 9) and non-aggressive or defensive (intending to avoid being damaged: 2, 3, 5 and 8) actions. Additionally, the number of individual anemones making at least one attack was recorded. No individual anemone was utilised in more than one encounter.

One week after the contest, boldness was measured for a second time using the same startle response duration method previously described.

2.4. Analysis

Of the 60 anemones, two were discarded from analysis since they did not recover from the pairwise contests.

Nematocyst lengths were compared between morphotypes using ANCOVA with pedal disc diameter included as a covariate, since the length of some cnidocysts may vary with size of the anemone (Francis, 2004). *Post-hoc* Tukey tests were utilised to discriminate between morphotypes.

For boldness, log startle response duration was compared between morphotypes for both trial 1 and trial 2; for trial 2 the outcome of the agonistic encounter (win, lose or draw) was also included as a main effect and a *morphotype* × *outcome* interaction term included in the model. Where boldness significantly differed between morphotypes *post-hoc* Tukey tests were utilised to discriminate between groups. A two-way repeated-measures ANOVA was used to compare boldness across the trials (before and after the agonistic encounter) with a *trial* × *morphotype* interaction term included.

For aggression, each behaviour was analysed using a negative binomial GLM (to account for overdispersion) with morphotype, pedal disc diameter (of both the individual and its opponent, and their interaction) and nematocyst length (likewise, of both the individual and

its opponent, and their interaction) as predictor variables. Assumptions of these tests were checked by visual analysis of normal probability plots of the residual and residuals versus fits plots. Where significant effects were observed, to account for unequal sample sizes between the morphotypes, we used a resampling procedure to improve our confidence in the calculated coefficients. Data were randomly sampled from the largest group (RA) and the models recomputed 100 times with equal sample sizes across morphotype. Mean z scores were calculated for each significant factor across the 100 computations and used to determine p at $\alpha = 0.05$ (Supplementary Material). Number of peels left on the opponent and number of attacks were not analysed using this method due to very low number of occurrences of these behaviours.

Analyses of nematocyst length and boldness were conducted in Minitab (ver. 17.1.0), and those of aggression were conducted in R (ver. 3.1.1; R Core Team, 2015) using the MASS package (Venables and Ripley, 2002).

3. Results

3.1. Anatomy

Undischarged holotrich nematocysts extracted from acrorhagi significantly differed between morphotypes ($F_{2,57} = 4.77$, $p = 0.012$). Nematocysts were significantly longer in the RA anemones compared to the RP anemones, whereas length of nematocysts in *A. prasina* did not significantly differ from either (Fig. 1). There was little evidence of a relationship between nematocyst length and pedal disc diameter ($F_{1,57} = 0.18$, $p = 0.674$).

3.2. Behaviour

In the first boldness trial RP anemones took significantly longer to recover than both RA anemones and *A. prasina* ($F_{2,49} = 5.87$, $p = 0.005$; Fig. 2a). In the second trial, measured after the agonistic encounter, no difference was observed in boldness between morphotypes ($F_{2,49} = 0.17$, $p = 0.844$; Fig. 2b). Likewise, the outcome of the contest did not influence boldness ($F_{2,49} = 0.90$, $p = 0.414$), and there was no interaction between the morphotype and contest outcome ($F_{4,49} = 0.65$, $p = 0.630$). However, overall behaviour significantly shifted towards a generally shyer phenotype after the agonistic encounter compared to before ($F_{1,55} = 7.28$, $p = 0.009$; Fig. 3) regardless of morphotype ($F_{2,55} = 1.99$, $p = 0.146$) and with a non-significant interaction between trial and morphotype ($F_{2,55} = 1.80$, $p = 0.174$).

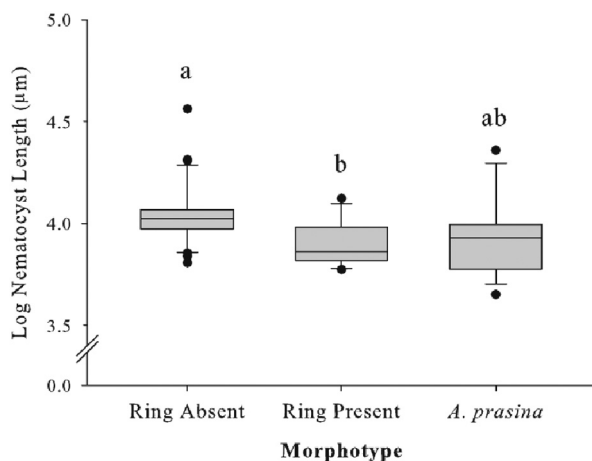


Fig. 1. Median log-transformed length of undischarged holotrich nematocysts extracted from the acrorhagi of three types of anemone: Ring Absent *Actinia equina* (Ring Absent, $n = 31$), Ring Present *A. equina* ($n = 13$), and *A. prasina* ($n = 14$). Boxes represent 25th and 75th percentiles, whiskers represent 10th and 90th percentiles, points represent outliers. Boxes sharing a common letter were not significantly different.

Three of the behaviours involved in aggressive interactions could be, at least partially, explained by the factors under study (Table 1). Differences in movements of the acrorhagi were observed between morphotypes (Fig. 4), with RP *A. equina* showing significantly reduced acrorhagial activity compared to RA anemones in both inflation ($z = -2.74$, $p = 0.006$) and deflation ($z = -2.05$, $p = 0.041$), with *Actinia prasina* exhibiting an intermediate level of behaviour for each. The larger an individual relative to its opponent the more frequently it move its pedal disc towards the opponent (individual vs opponent size interaction: $z = -1.98$, $p = 0.048$), but this was not reflected in any tendencies to move away from an opponent. Despite moderate evidence of relationships between size or nematocyst length on tentacle movement away from an opponent, these were not confirmed with resampled analyses (Supplementary Material). However, there was no effect of the interaction of focal-individual size with opponent size.

Due to extremely low frequencies, neither number of attacks made nor number of peels was analysed statistically. RP morphs of *A. equina* left no peels at all compared to two individuals of the RA morph leaving at least one peel. *A. prasina* left seven peels in total but all were made by a single individual. The same individual was also responsible for the majority of attacks made by *A. prasina*. RA anemones were the most aggressive according to number of attacks, with eight individuals performing at least one attack for a total of 16 attacks made on opponents.

4. Discussion

Previous studies have indicated that aggressiveness differs between morphotypes of *Actinia equina* (e.g. Brace et al., 1979; Brace and Reynolds, 1989) and, whilst consistent individual differences in risk-taking have also been observed (Briffa and Greenaway, 2011), as yet no differences in such behaviour between morphotypes have been studied or described within the literature. Here we demonstrated that startle response durations, a measure of risk-taking, may also differ between morphotypes of *Actinia equina* and the congener *Actinia prasina*. Furthermore, those morphs which were more likely to engage their acrorhagi in contests (i.e. were ostensibly more aggressive) were also more likely to be risk-taking, suggesting risk-taking and aggressiveness are linked as a behavioural syndrome within this species. Variation in aggressiveness could also be partially explained by size differences between contestants or by the length of nematocysts, consistent with previous studies (e.g. Allcock et al., 1998; Rudin and Briffa, 2011).

The behaviours exhibited by the different morphotypes may be related to ecological factors associated with the different parts of the shore these morphs inhabit (Hensley et al., 2012). The posture adopted by anemones when startled or emersed, with tentacles retracted, provides protection for the tentacles from predation or deleterious changes to the local environment but at the cost of the ability to feed or to engage in contests with other Anthozoans, and minimises oxygen delivery for respiration (Shick et al., 1979); thus re-exposing the tentacles and oral disc to be able to take part in these activities as soon as possible must be weighed against the potential danger of persistent predators or exposure to poor environmental quality. Since these differences were expressed under consistent laboratory conditions, between-group variation in risk-taking may represent evolutionary responses to the different ecological requirements at various shore heights. The opportunity to feed is limited to submergence time and will, for mid-shore morphs (represented here by the RA group), be limited compared to low shore types, such as *A. prasina* and the RP group of *A. equina*. Likewise, maximal respiration rates can only be achieved for shorter periods of time. Thus life on the higher shore may engender a less cautious approach with quicker recovery from such a defensive posture to ensure that the reduced submergence time is fully utilised. Conversely, on the lower shore, where anemones spend most of the time submerged, time to feed is greater but it also follows that there are likely more marine predators of anemones (Bell et al., 2006; Edmunds et al., 1974; Mauzey et al., 1968; Wyer and King, 1974), including those

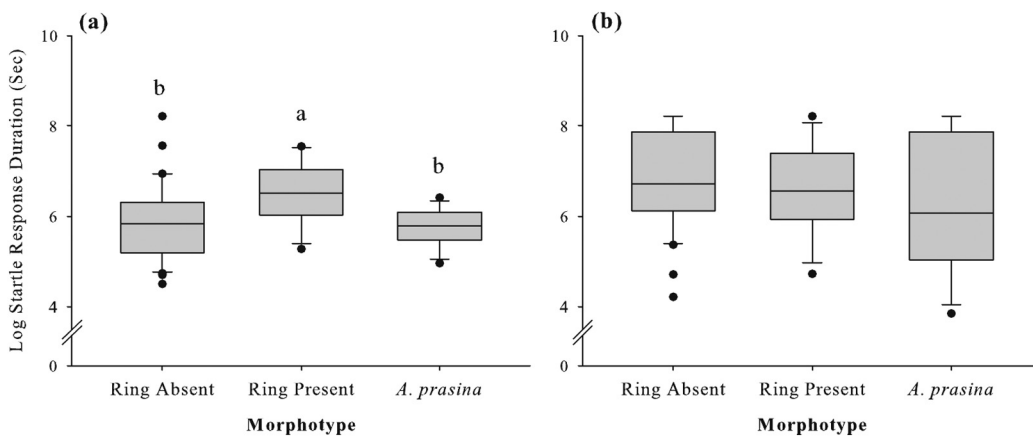


Fig. 2. Median log-transformed startle-response durations for anemones (a) before an agonistic contest and (b) one week after an agonistic contest. Anemones were of three types: *Actinia equina* without a blue limbus around the pedal disc (Ring Absent, $n = 31$), *A. equina* with a blue limbus (Ring Present, $n = 13$), and green anemones *A. prasina* ($n = 14$). Boxes represent 25th and 75th percentiles, whiskers represent 10th and 90th percentiles, points represent outliers. Boxes sharing a common letter were not significantly different.

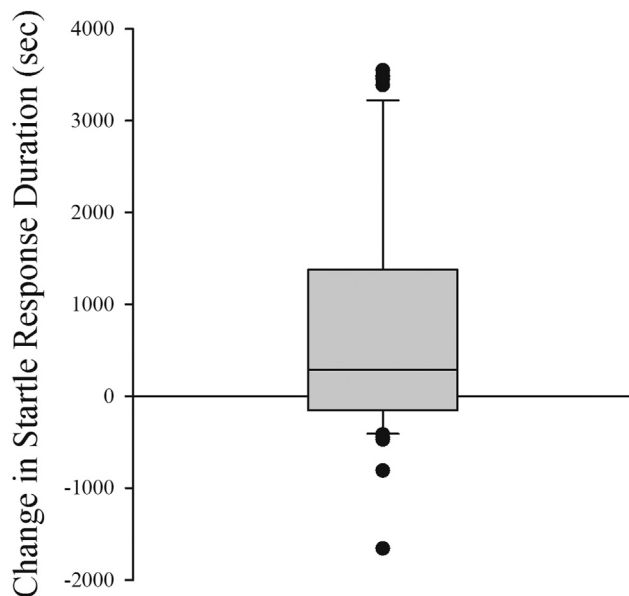


Fig. 3. Median change in individual startle-response durations across all anemones ($n = 58$), *Actinia equina* (with and without a blue limbus around the pedal disc) and *A. prasina*. Startle responses were measured as trials before and after an agonistic encounter. Box represents 25th and 75th percentiles, whiskers represent 10th and 90th percentiles, points represent outliers.

which consume tentacles (Hall et al., 1982). Thus more risk-averse anemones, with slower recovery times, may be selectively favoured since they will be more defensive and any time lost for feeding will not have a large impact because submergence time is not, or only very partially, restricted. Risk-prone, more quickly-recovering anemones may therefore be more successful higher up the shore where feeding opportunities are constrained and predation pressure is ostensibly low. However, on the low shore RP anemones are sympatric with *A. prasina* which exhibits a slightly more risk-prone phenotype. This distribution makes little sense since, if the risk-prone strategy were adaptive across the shore, the RA group of *A. equina* would dominate throughout since they are much more aggressive than either RP *A. equina* or *A. prasina* (Brace et al., 1979). *A. prasina* appears to utilise different habitats than either form of *A. equina*, preferring cryptic environments compared to the exposed surfaces of *A. equina* (Haylor et al., 1984). Thus, although they are more risk-prone and ostensibly may face more predators, their choice of habitat provides improved protection in a low shore environment; the influence of habitat choice on vulnerability to predators, though, is deserving of further study. Furthermore, whether behaviour influences survival rates of anemones at different shore heights, or individuals of different behavioural type seek appropriate habitats,

remains to be explored (Hensley et al., 2012). We must also be cautious about interpreting laboratory-based results: behaviour exhibited under field conditions may differ from lab conditions (Osborn and Briffa, 2017) although aggressiveness remains consistent over time in the lab. Nevertheless, the apparent association of habitat preference with morphotype seems likely to explain the divergent behaviours observed in these animals, though it does require further testing under field conditions.

Morphotype, relative body size, and length of holotrich nematocysts within the acrorhagi are known factors influencing aggressiveness (or, at least, likelihood of winning agonistic contests) within *Actinia*. Here, there was some evidence that three of the nine behavioural measurements taken during agonistic interactions appeared to vary systematically based on these three factors (despite attempts to constrain size differences within the study): relative size appeared linked primarily to movement of the body whereas morphotype was linked to movement of the acrorhagi themselves. Larger anemones are considered more likely to win in an encounter (Brace et al., 1979; although c.f. Brace, 1981) though this seems to be due to a more rapid coordination of integrated nervous conducting systems resulting in faster induction of agonistic behaviour (Jackson and McFarlane, 1976; Brace and Pavey, 1978), and this may explain the relationship with body movement. Acrorhagial activity was, however, more closely aligned with morphotype: RP anemones were significantly less likely to inflate or deflate these tentacles than RA anemones, which reflects accepted differences in aggressiveness between morphs (Brace et al., 1979; Brace and Reynolds, 1989). Acrorhagial movement within *A. prasina* sat in-between that of the two *A. equina* morphotypes; previous evidence indicates *A. prasina* are less aggressive than higher shore anemones (Brace et al., 1979) but differences between *A. prasina* and low shore *A. equina* have not previously been confirmed. Surprisingly, none of the morphological features were significantly related to movement of feeding tentacles; these are known to be withdrawn during encounters (Rudin and Briffa, 2011) but perhaps this is a result of contest outcome directly and not related to the morphological features examined. Thus, it seems that the coordination of body movements, perhaps in general but also within contests, differs dependent on anemone size, and may have some role in positioning within contests, but the ability to cause harm to an opponent (through use of acrorhagi, longer nematocysts, or a combination of the two) is more strongly defined by morphotype. The combination of the two may be important since size selection on shores will also be based on exposure and shore height, where limited feeding opportunities and space on the upper shore often result in smaller anemones (Francis, 1988). Among *A. elegantissima* reduced size is not a disadvantage as smaller anemones form an aggressive periphery around clonal groups and successfully compete against larger individuals due to having more numerous acrorhagi (Ayre and Grosberg, 1996). In contrast, *A. equina* clones tend to be scattered rather than clustered (Brace and Quicke,

		Coefficient	SE	z	p
A: Tentacle Movement (towards opp.)					
Intercept		-1.09	7.19	-0.15	0.88
Morphotype	<i>A. prasina</i>	-0.04	0.33	-0.13	0.90
--	RP	-0.23	0.30	-0.77	0.44
NL		0.01	0.13	0.11	0.91
NL (Opponent)		0.02	0.13	0.13	0.90
PDD		0.10	0.08	1.29	0.20
PDD (Opponent)		0.10	0.08	1.25	0.21
NL x NL (Opponent)		<0.001	<0.001	-0.31	0.75
PDD x PDD (Opponent)		<0.001	<0.001	-1.20	0.23
B: Tentacle Movement (away from opp.)					
Intercept		11.46	8.15	1.41	0.16
Morphotype	<i>A. prasina</i>	0.21	0.34	0.61	0.54
--	RP	-0.14	0.32	-0.44	0.66
NL		-0.24	0.15	-1.65	0.10
NL (Opponent)		-0.30	0.15	-1.96	0.050
PDD		0.19	0.09	2.26	0.024
PDD (Opponent)		0.17	0.08	1.99	0.047
NL x NL (Opponent)		<0.001	<0.001	1.65	0.10
PDD x PDD (Opponent)		-0.01	<0.001	-1.87	0.06
C: Tentacle Retraction					
Intercept		-3.06	8.21	-0.37	0.71
Morphotype	<i>A. prasina</i>	0.29	0.41	0.69	0.49
--	RP	0.19	0.40	0.47	0.64
NL		0.03	0.14	0.19	0.85
NL (Opponent)		0.03	0.15	0.20	0.84
PDD		0.04	0.11	0.41	0.68
PDD (Opponent)		0.05	0.10	0.51	0.61
NL x NL (Opponent)		<0.001	<0.001	-0.14	0.89
PDD x PDD (Opponent)		<0.001	<0.001	-0.32	0.75
D: Pedal Movement (towards opp.)					
Intercept		6.34	10.19	0.62	0.53
Morphotype	<i>A. prasina</i>	0.04	0.38	0.12	0.91
--	RP	-0.67	0.38	-1.77	0.08
NL		-0.18	0.18	-0.99	0.32
NL (Opponent)		-0.16	0.19	-0.88	0.38
PDD		0.22	0.09	2.29	0.022
PDD (Opponent)		0.20	0.09	2.13	0.034
NL x NL (Opponent)		<0.001	<0.001	0.78	0.44
PDD x PDD (Opponent)		-0.01	<0.001	-1.98	0.048
E: Pedal movement (away from opp.)					
Intercept		-1.49	9.17	-0.16	0.87
Morphotype	<i>A. prasina</i>	0.22	0.46	0.48	0.63
--	RP	0.00	0.45	0.01	0.99
NL		0.01	0.16	0.06	0.95
NL (Opponent)		0.00	0.17	-0.01	0.99
PDD		0.06	0.12	0.47	0.63
PDD (Opponent)		0.08	0.12	0.72	0.47
NL x NL (Opponent)		<0.001	<0.001	-0.03	0.98
PDD x PDD (Opponent)		<0.001	<0.001	-0.43	0.67
F: Acrorhagial Inflation					
Intercept		2.40	10.99	0.22	0.83
Morphotype	<i>A. prasina</i>	-0.59	0.48	-1.21	0.23
--	RP	-1.57	0.57	-2.74	0.006
NL		-0.11	0.19	-0.56	0.57
NL (Opponent)		-0.11	0.20	-0.52	0.60
PDD		0.15	0.13	1.18	0.24
PDD (Opponent)		0.19	0.12	1.58	0.11
NL x NL (Opponent)		0.00	0.00	0.46	0.64
PDD x PDD (Opponent)		-0.01	0.01	-1.13	0.26
G: Acrorhagial Deflation					
Intercept		-1.77	13.46	-0.13	0.90
Morphotype	<i>A. prasina</i>	-0.28	0.55	-0.51	0.61
--	RP	-1.28	0.63	-2.05	0.041
NL		-0.11	0.24	-0.45	0.66
NL (Opponent)		-0.09	0.24	-0.38	0.70
PDD		0.26	0.15	1.76	0.08
PDD (Opponent)		0.30	0.14	2.14	0.033
NL x NL (Opponent)		0.00	0.00	0.37	0.72
PDD x PDD (Opponent)		-0.01	0.01	-1.64	0.10

Table 1

Coefficient estimates (\pm SE) with associated z and p values for all terms in negative binomial models for (A) tentacle movement towards an opponent; (B) tentacle movement away from an opponent; (C) retraction of the tentacles; (D) movement of the pedal disc towards an opponent; (E) movement of the pedal disc away from an opponent; (F) inflation of acrorhagi; and, (G) deflation of acrorhagi. Significant terms (where $p \leq 0.05$ after resampling; see Supplemental Material) are shaded. NL = nematocyst length (μm , of the individual and its opponent) and PDD = pedal disc diameter (mm, of the individual and its opponent). Morphotype refers to the type of the anemone where *Actinia prasina* and RP (ring present) *A. equina* are compared against RA (ring absent) *A. equina*.

1985) and territorial behaviour seems most beneficial when individuals aggregate in protected habitats during winter conditions. Unfortunately we do not have data on number of holotrich nematocysts within these anemones, and this may be an important determinant of contest success. Whilst our data is limited by a relatively small sample size, it adds to a body of evidence suggesting that both morphology (body size, nematocyst size and quantity) and movement (latency to attack, use of acrorhagi) are important in anemone contests (Ayre and Grosberg, 1996; Rudin and Briffa, 2011); however, their relative contribution to contest success (and, indeed, that of other factors including residency/strength of attachment) remains to be fully explored (although see Rudin and Briffa, 2011).

Overall, these data suggest that more aggressive anemones (at least those that engage their acrorhagi more frequently in contests) also tend to be more risk-taking whilst, conversely, those less engaged in agonistic activity are more risk-prone, at least under lab conditions. This may suggest the presence of a behavioural syndrome in these animals (Sih et al., 2004), although whether there is a molecular link between risk-taking and aggression or whether success at different shore heights requires a particular combination of the two behaviours remains to be determined. Anemones must compete for space and it is likely that the number of rewarding positions on the higher shore, where submersion time is limited, is lower than at the low shore where they are submerged the majority of the time. Therefore, on the high shore where both space and time to feed/respire are at a premium, it makes sense for animals to be both risk-taking and aggressive (i.e. intra-specifically and interspecifically aggressive; Huntingford, 1976). If this is evidence of a behavioural syndrome, then selection for a risky-aggressive syndrome may explain why more aggressive anemones are found higher up the shore in contrast to the general ecology of shore habitats where aggressiveness is usually associated with competition for locations lower on the shore. One must however, exercise caution in interpreting these results since not all combinations of morphs competed against each other, and we likely missed some pertinent information regarding the number and intensity of attacks (as observed by Brace and Reynolds, 1989). A more comprehensive analysis of this contest behaviour using all combinations (isomorphic and allomorphic) of pairs may further elucidate the relationship between morphotype and the link between aggression and risk-taking.

After agonistic contests all anemones exhibited a similar level of risk-taking which was, overall, significantly more risk-averse than before the contest but which was not appear to be influenced by the outcome of the fight nor the morphotype. Rudin and Briffa (2012) also demonstrated that post-fight startle response durations tended to be longer than pre-fight response durations, but this was particularly true of those individuals which had lost a fight. Whilst such effects weren't accounted for here it seems clear that the reduction in risk-taking appears to be an important post-fight response; after sustaining damage during the contest anemones may be more defensive to limit the likelihood of further injury (Rudin and Briffa, 2012). Fighting is energetically-demanding (Briffa and Sneddon, 2007) and the reduction in risk-taking may also represent a period of metabolic recovery or is associated with the costs of stress (Earley et al., 2013). The recovery of anemones from contests does need further study (Rudin and Briffa, 2012) but the ecological reasons behind behavioural change may be elucidated by exploring whether change in behaviour occurs

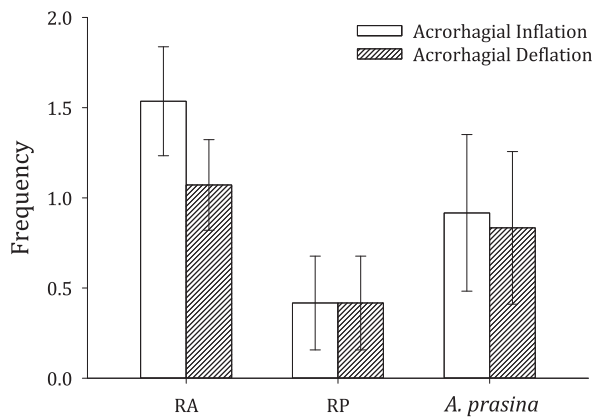


Fig. 4. Mean (\pm SE) frequency of acrorhagial inflation (white bars) and deflation (hatched bars) among anemones of three morphotypes: *Actinia equina* without a blue limbus around the pedal disc (Ring Absent, $n = 31$), *A. equina* with a blue limbus (Ring Present, $n = 13$), and green anemones *A. prasina* ($n = 14$).

simultaneously across other contexts. Importantly, these data indicate a degree of behavioural plasticity among anemones and certainly suggest that risk-taking is modified, at least temporarily, after exposure to environmental challenge.

The lengths of holotrich nematocysts within this study differ between morphs in a manner expected given differences in their behaviour (Rudin and Briffa, 2011, 2012). However, the RA group was composed ostensibly of Upper (U) and Mid (M) morphs together since differentiating the two is difficult without molecular techniques, and since they are thought to exhibit similar behavioural profiles high aggressiveness; (Brace et al., 1979; Brace and Reynolds, 1989). Previous studies indicate that these morphs differ in the length of holotrich nematocysts, with U anemones having short nematocysts and M morphs having the longest. However, the nematocyst length within the RA group was not only the longest in this study but also had low variance, suggesting this group did not contain anemones with disparate nematocyst lengths. U morphs were likely therefore to have been poorly represented within our sample; this may, however, reflect their rarity on some shores (Perrin, 1993; Watts et al., 2000) rather than sampling error. Median nematocyst length in *A. prasina* fell between that of RA and RP *A. equina*, which matches their apparent intermediate behaviour compared to the *A. equina* morphs, but also had somewhat larger variance. Previous studies have found contrasting results when comparing the length of *A. prasina* nematocysts to those of *A. equina* morphs (e.g. Solé-Cava and Thorpe, 1987 and c.f. Watts et al., 2000). Nematocyst length among *A. prasina* seems highly variable and may reflect differences between and within shores reflecting variation in ecology or even genotype within this anemone group. We cannot exclude the possibility that green-columned individuals of other morphs have been included within our *A. prasina* sample; whilst this seems unlikely, given that anemone colour is derived from their diet this remains a potential difficulty in effectively identifying morphotypes through morphology (Watts et al., 2000).

In conclusion, we've built on previous studies on the behaviour in *Actinia* to demonstrate that different members of the species complex exhibit different levels of risk-taking and aggression that may occur as a result of the ecological conditions to which they are exposed. Those anemones with reduced optimal habitat and either reduced opportunities to feed or other methods of protection tend to be more aggressive and take more risks. These data also therefore suggest the existence of a behavioural syndrome in this group of organisms, although much more study is required to uncover the strength of the relationship between risk-taking and aggression in Cnidaria. Behavioural differentiation is, however, supported by differences in morphology (specifically, the lengths of nematocysts within the acrorhagi). Whilst much remains to be done, hopefully this study can act as a stepping stone in

understanding why the morphs occupy different locations on the shore and whether this represents a reproductive barrier and potential speciation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2017.07.011>.

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