



Behavioural type, plasticity and predictability are linked to shell shape in a marsh ecosystem predator–prey interaction



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Animal personality results from a complex interplay between consistent individual differences in behaviour and behavioural plasticity in response to environmental variation and can have significant impacts on intraspecific interactions. *Littoraria irrorata*, the marsh periwinkle, is an important consumer in salt marsh ecosystems and can directly influence marsh health, primarily through its interaction with its main predator, the blue crab, *Callinectes sapidus*. Here we examine the roles of behavioural type, plasticity and predictability in shaping the antipredator responses of *L. irrorata* across environmental contexts (i.e. with and without a predator cue). Specifically, we examine changes in measures of boldness: climbing height and time out of refuge, as well as their association with shell morphology. We found that snails exhibited different behavioural types along a bold–shy continuum and that they were correlated across traits. Snails also differed in the shape of their reaction norm and their degree of predictability, both of which were correlated with behavioural type: shy snails climbed higher, spent more time in the refuge and were less plastic and more predictable. Although shell length and size class did not influence snail behaviour, aperture size was strongly linked to key aspects of snail personality, as snails with larger apertures were less bold, less plastic and more predictable. Personality thus appears to be related to certain features of shell morphology and is consistent with phenotypic compensation, where individuals invest in more pronounced morphological defences to compensate for a riskier lifestyle. Given that personality can often determine an individual's growth, development and probability of predation, understanding its role in various ecological contexts, such as population dynamics and predator–prey relationships, is critical.

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Behaviour in animals can be highly structured, often being consistent within an individual over time (i.e. behavioural type; Bell et al., 2009), and known as animal personality (Gosling, 2001; Wolf & Weissing, 2012). Studies have shown that personality can significantly influence fitness in a variety of species (Bell & Sih, 2007; Biro et al., 2004, 2006; Carter et al., 2010; Dingemanse & Wolf, 2010; Sih et al., 2003; Smith & Blumstein, 2010), although individuals may still exhibit important behavioural differences in how they respond to changing environments (i.e. behavioural plasticity; Dingemanse & Wolf, 2013; Toscano, 2017). Such variation can be quantified using behavioural reaction norms, in which a single trait is measured across several environmental contexts (Mathot et al., 2012).

Constraints on sensory capabilities, cognition, morphology or physiology (Dall et al., 2004; Hazlett, 1995) can vary among individuals and thus create differences in behavioural plasticity (e.g. Briffa et al., 2008; Mitchell & Biro, 2017; Stamps, 2016; Toscano, 2017).

Moreover, differences in life history strategies may also explain both individual variation in behavioural types as well as individual variation in plasticity (Snell-Rood, 2013; Stamps & Biro, 2016). For example, fast-growing individuals might be more active, exploratory and risk prone to sustain their growth trajectory; conversely, individuals with higher residual reproductive potential might be more risk averse to protect their resources (Clark, 1994; Edenbrow & Croft, 2011; Wolf et al., 2007). Such trade-offs may also vary with individual state or across ontogeny (Cornwell et al., 2019; Edenbrow & Croft, 2011). Finally, the degree of behavioural consistency itself (i.e. predictability; Biro & Adriaenssens, 2013) can vary among individuals (Stamps, 2016). While some variation in predictability might be nonfunctional, such as in response to fluctuating hormone levels triggered by hunger status (Tolkamp et al., 1998), individuals may differ in predictability in response to varying perceived predation risk. For example, unpredictable behaviour may be more efficient in reducing vulnerability to predation (Bednekoff & Lima, 1998, 2002). It is therefore important to evaluate how consistency, plasticity and predictability shape behavioural responses within and across different environments.

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The marsh periwinkle, *Littoraria irrorata*, is an abundant mollusc in salt marshes along the southeastern Atlantic and Gulf coasts of the United States (Crist & Banta, 1983). Salt marshes provide a multitude of ecosystem services, acting as sinks for excess nitrogen, buffering coastlines and serving as critical habitat for ecologically and commercially important species (Boesch & Turner, 1984; Davidson-Arnott et al., 2002; Gordon et al., 1985; King & Lester, 1995; Moeller et al., 1996). In recent years, mounting evidence indicating that salt marshes function under top-down, rather than bottom-up, control has sparked a newfound interest in the roles that consumers play in these systems (Bertness et al., 2014; Johnson et al., 2009; Silliman & Bertness, 2002; Silliman et al., 2004; Silliman & Newell, 2003; Silliman & Zieman, 2001). When densities are not controlled by predation, *L. irrorata* can decimate large areas of emergent salt marsh vegetation, typically the smooth cordgrass, *Spartina alterniflora*, via grazing and fungal farming (Silliman & Bertness, 2002; Silliman & Zieman, 2001). The blue crab, *Callinectes sapidus*, exerts top-down control on estuarine food webs, thus indirectly sustaining salt marshes by preying upon herbivores such as periwinkles (Silliman & Bertness, 2002). The trophic cascade imposed by such predators plays an important role in regulating *Spartina* productivity (Silliman & Bertness, 2002).

Littoraria irrorata use predator avoidance behaviour by climbing *S. alterniflora* before the high tide to remain out of reach of neritic predators (Dix & Hamilton, 1993; Warren, 1985), which significantly decreases snail mortality (Silliman & Bertness, 2002; Warren, 1985). *Littoraria irrorata* have relatively few morphological antipredation adaptations, other than differentially modifying their aperture opening to decrease predation success when exposed to high densities of blue crabs (Moody & Aronson, 2012; Vermeij, 1973). Yet this morphological adaptation cannot completely deter predation as its effectiveness is dependent on overall snail size (Moody & Aronson, 2012). Climbing behaviour is thus critical for reducing predation rates. In natural populations, variation among individuals in their climbing behaviour, and to a lesser extent refuge use, has been observed, suggesting potentially important trait heterogeneity (Stanhope et al., 1982). While previous studies have explored the effect of chemical cues and environmental conditions on behavioural responses (Carroll et al., 2018; Dix & Hamilton, 1993; Duval et al., 1994; Henry et al., 1993), these studies did not consider that behavioural differences among individuals might be the mechanism generating intraspecific variation in predator avoidance displays (but see Cornwell et al., 2019).

Here we vary the presence of a predator cue to directly test whether marsh periwinkles exhibit consistent behaviours within contexts (behavioural types) and across environments (behavioural plasticity) in two key antipredator traits: climbing height and refuge use. Both traits are related to boldness, an individual's propensity to take risks, which is a key axis of animal personality and can have significant impacts on survival (Johnson & Sih, 2005; Sih et al., 2003; Wilson et al., 1993). We used olfactory cues from blue crabs to simulate predation risk as they have been shown to elicit strong antipredator behaviour in marsh periwinkles (Duval et al., 1994). We predicted that climbing height and refuge use would increase in the presence of the predator cue (reflecting decreased boldness), but we asked whether (1) mean behavioural expression and (2) response to risk would vary among individuals, and (3) whether trait correlations would emerge, with some individuals consistently bolder than others across several behaviours (behavioural syndrome: Sih et al., 2004). We also asked whether behavioural plasticity is correlated with individual predictability, which could reflect differences in internal state (Biro & Stamps, 2008; Dorset et al., 2017). Among-individual variation in predictability can also be

evolutionarily adaptive: under predation threat, animals must hide and so would be more predictable under predation risk.

Finally, we asked how personality relates to shell morphology. We predicted that large snails would be less responsive to predation risk as they are more likely to experience size refuges given the known size-structured predation relationship between blue crabs and snails, leading to differences in the slopes of the reaction norms (Schindler et al., 1994). Additionally, we predicted that snails with smaller apertures would be less responsive to risk as trait compensation between morphological and behavioural adaptations has been observed in other snail species, also leading to differences in the slopes of the reaction norms (Cotton et al., 2004; DeWitt et al., 1999; Rundle & Bronmark, 2001).

METHODS

Sample Collection

We collected marsh periwinkles from two salt marshes dominated by cord grass (*S. alterniflora*) outside of Wilmington, North Carolina, U.S.A. The first location (NC1) at Fort Fisher Recreation Center (33°57'27.1"N 77°55'35.9"W) borders a small tidal creek that drains into a larger system of creeks. The second location (NC2) at Carolina Beach State Park (34°02'51.9"N 77°55'15.6"W) is part of a salt marsh that runs adjacent to the brackish Cape Fear River and is separated from NC1 by 13 km. Both locations have similar predators, primarily *C. sapidus*, and tidal cycles. In May 2019, we haphazardly collected *L. irrorata* at each location from each of three size classes: small (<15 mm), medium (15–20 mm) and large (>20 mm). Size classes were chosen to represent a range of snail ages, from young subadults to adults older than 2 years (Bingham, 1972; Stiven & Hunter, 1976; Zengel et al., 2016). Locations were sampled at low tide and 15 snails from each size class were collected at each location. Snails were transported to the Center for Marine Science at the University of North Carolina, Wilmington, where they were individually marked with coloured paint. Snails were housed in groups of 15 in mesh containers that sat on a platform in a 37.8-litre aquarium at a height that allowed each container to have access to both 3 cm of sea water and 6 cm of air. Aquaria were filled with high-quality filtered sea water; salinity ranged from 25 to 30 ppt, temperature ranged from 75 to 80 °F, and the system maintained a 12:12 h light:dark cycle. Snails were fed a mixture of standing dead and fresh *S. alterniflora* ad libitum for the entirety of the experiments (Bärlocher & Newell, 1994). Snails were allowed to acclimate for a minimum of 48 h prior to experimentation.

Shell Shape Assessments

Snails were blotted dry and weighed to the nearest 0.01 g using a portable electronic balance (VWR International, Radnor, PA, U.S.A.). Shell length was measured from the top of the apex to the tip of the aperture, shell width was measured at the widest part of the shell, and inner aperture length was measured at the widest part of the inside of the aperture opening as illustrated by Moody and Aronson (2012). All morphological features were measured to the nearest 0.01 mm using digital callipers (TESA Brown & Sharpe TWIN-CAL IP67).

Personality Assessments

Behaviour was assessed both in the presence and absence of a predator chemical cue. Crab chemical cues were used instead of live crabs to minimize snail mortality and ensure that enough data would be collected for each individual. Predator cue water was generated by holding five *C. sapidus*, fed crushed marsh periwinkles ad libitum, in

separate stagnant 10-gallon (37.85-litre) tanks for 1 week prior to the start of trials. The predator cue water used for each trial was randomly selected from among the five tanks and high-quality filtered sea water was used for the control trials. Boldness represents one of the five major personality axes (Réale et al., 2007) and was quantified here using (1) climbing height and (2) proportion of time spent out of refuge.

Climbing height was measured by placing five snails of the same size class in a 11.4-litre bucket (diameter = 18.5 cm, height = 29 cm), with walls vertically protracted and marked every 1 cm, and filled with 3 cm of high-quality filtered sea water. Snails were placed equidistant from one another and from the edge of the bucket and were allowed to acclimate for 5 min. Then, after a 10 min trial, behaviour was measured as the maximal height climbed by each snail to the nearest 1 cm (individuals not breaching the water were given a height of 0 cm and the maximum climbing height was 29 cm). Bold snails were those that climbed short distances and remained close to the water. For the refuge trials, two hollow hemispheres with a 3×3 cm opening were placed in the bottom of the bucket, which allowed snails to freely crawl in and out. Snails were arranged in the same manner as in the climbing height trials. Behaviour was observed every 2 min during the 10 min trial, and here boldness was calculated as the proportion of observations where snails were outside the refuge. Individuals remained in the same groups for all personality assessments. They were tested three times for each behaviour in both the presence and absence of cues, for a total of 12 trials per snail. All tests occurred on different days.

Ethical Note

The number of *L. irrorata* collected was far below the naturally occurring densities at each site (NC1: 107 snails/m²; NC2: 60 snails/m²). Snails were also collected haphazardly over several metres to ensure no one area was oversampled. Snails were collected with permission and in accordance with permit number 2018_0288 from the North Carolina Division of Parks and Recreation. Snails were housed in ambient conditions and in a system that was pre-established to have long-term success in housing this species. Snails were fed and tanks cleaned regularly. Snails were dissected at the end of the study to screen for parasites and to collect tissue for a subsequent study.

Statistical Analyses

All data were analysed using R version 3.6.3 (R Core Team, 2020) and RStudio version 1.3.1093 (RStudio Team, 2020). Bayesian models were created in 'Stan' computational framework and accessed using the 'brms' package (Bürkner, 2017, 2018). Four chains were generated with 4000 iterations in each chain, discarding the first 500 iterations. Convergence was verified by the \hat{R} values, where values close to 1 indicate good convergence (Gelman & Rubin, 1992). The adjustment process generates a posteriori distributions of the parameters with respective credible intervals (CI). In all cases, the 95% credible interval (95% CI) for the posterior probability distribution of the effect is reported. Fixed effects and correlation parameters with credible intervals not overlapping zero are considered significant (Beveridge et al., 2022; Bürkner, 2017; Roth & Sterck, 2020).

Climbing height and time out of refuge values were log-transformed to achieve normality within and among individuals and stabilize variance. Refuge use was treated as a continuous variable, since residual variance models require a Gaussian distribution and in cases where categories are greater than 5 (here we have 6), likelihood models and categorical least squares models perform similarly and either method is acceptable (Rhemtulla et al., 2012). Shell measurements were square root-transformed to improve

normality of residuals and intercepts. Shell and aperture length, climbing height and refuge data were additionally z-transformed to yield a mean of zero and variance of one to aid in model convergence and prior specification (Beveridge et al., 2022). An initial analysis of size differences showed snails did not differ significantly in length ($F_{1,88} = 0.26$, $P = 0.61$) or width ($F_{1,88} = 1.24$, $P = 0.27$) between locations. However, snails differed significantly in aperture length ($F_{1,88} = 7.87$, $P = 0.006$), with snails from NC1 having narrower apertures than snails from NC2. Moreover, in our univariate exploratory models, only aperture length influenced both height climbed and refuge use and was the only morphological trait retained in subsequent analyses (see [Supplementary material](#) for model outputs).

A multivariate double hierarchical mixed model was fitted to quantify the among- and within-individual covariances between climbing height, refuge use and aperture length, containing random intercept and slope effects on both height climbed and refuge use with respect to time and context. Predictability, which is measured as the spread of the residuals around an individual's reaction norm, was also evaluated by imposing structure onto the residual part of the variance and then partitioning it among individuals (Cleasby et al., 2015; Hertel et al., 2020). We assessed all among-individual covariances of these effects (i.e. a 9×9 unstructured variance–covariance matrix). Given that the model was parameter heavy, only the correlations of interest are highlighted (see [Supplementary material](#) for model structure, code and full results). The covariance between individual predicted mean values of each trait (the intercept–intercept covariance) evaluates the extent of a behavioural syndrome as well as whether aperture length is related to behavioural type. The covariance between random slope effects for context on each trait evaluates whether the degree of behavioural plasticity across the environmental gradient varies among individuals. The covariance between random slope effects for trial on each trait evaluates whether individuals become bolder (or shyer) over time. We also evaluated covariance between residual variances and random intercept and slope effects across traits to test whether predictability varied with behaviour or morphology. Predictors in the model included location, context (presence versus absence of a predator cue) and trial. The latter two were mean centred, such that the random intercept variance represents among-individual differences in predicted mean values in the average context and midpoint in time during the sampling.

Finally, a linear mixed model with the fixed effects of location, aperture length and trial and with individual and testing group as random effects was fitted to test for individual differences in mean level boldness in both the absence and presence of a predator cue. Given the large differences in variances between these contexts (see below), repeatability (R) was calculated as a context-specific R . Credible intervals for the repeatability estimates were calculated by simulating the data 1000 times to get a posterior distribution for all variance components.

RESULTS

Height Climbed

At the level of the average individual, height climbed did not change across the trials (estimate = 0.08, 95% CI = −0.08, 0.09). As expected, it did increase when snails were exposed to a predator cue, with animals climbing less when tested in the absence of a cue (estimate = 0.94, 95% CI = 0.93, 0.96). Height climbed did not differ between locations (estimate = −0.00, 95% CI = −0.01, 0.00). Individuals differed from one another in mean height climbed (intercept SD = 0.38, 95% CI = 0.38, 0.39; Fig. 1a) and substantially differed in their responses to a changing environment (SD = 0.77, 95% CI = 0.75, 0.78; Fig. 2a). There was a strong relationship between individual intercepts and slopes with respect to context (correlation

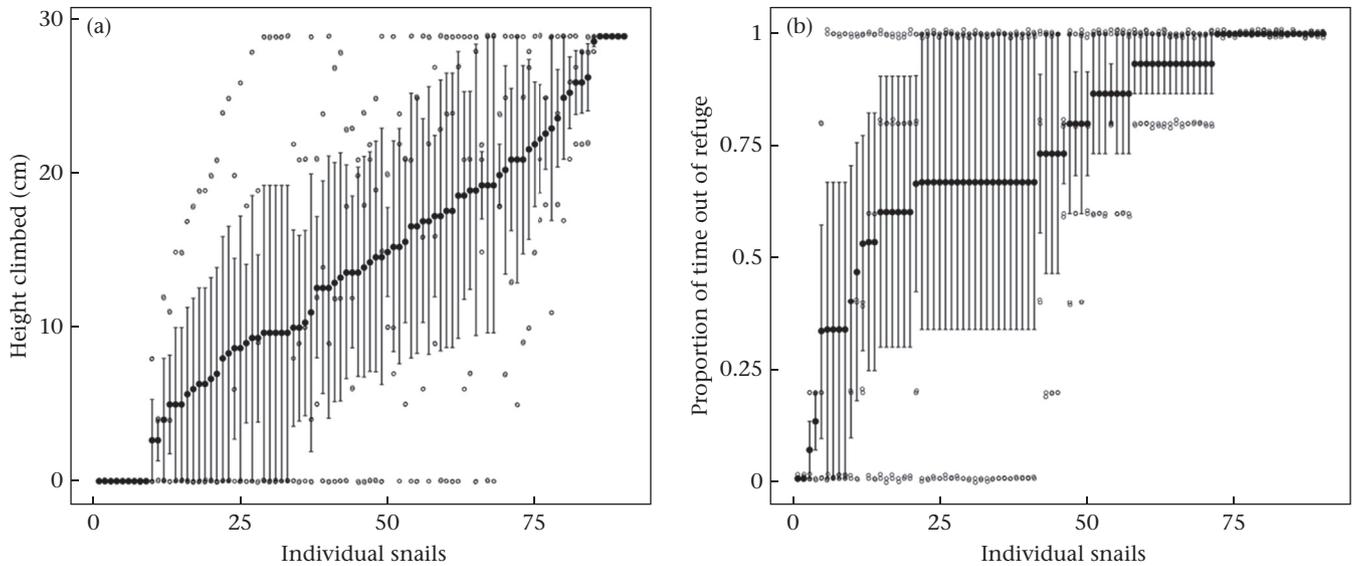


Figure 1. Mean \pm SE (a) height climbed and (b) proportion of time out of refuge for 90 snails in the absence of a predator cue. Each snail was tested three times. Raw data points are included and offset by the jitter function in R.

($r = -0.75$, 95% CI = $-0.85, -0.68$): snails that climbed higher in the absence of a predator cue showed less behavioural plasticity and so tended to climb higher in the presence of a predator cue, whereas individuals who climbed less in the absence of a predator cue increased their climbing height more when a predator cue was present. Residual variance also differed among individuals (intercept SD = 3.51, 95% CI = 3.31, 3.68). Behavioural type and predictability were negatively correlated (intercept–slope covariance: $r = -0.24$, 95% CI = $-0.38, -0.11$; Fig. 3c), indicating that snails that climbed higher (i.e. were shyer) were more predictable. The positive correlation between behavioural plasticity and predictability (intercept–slope covariance: $r = 0.23$, 95% CI = 0.10, 0.37) was also strong, meaning that more responsive snails had higher residual variance and were less predictable. Trait repeatability (R) of height climbed using the linear mixed model was 0.25 (95% CI = 0.11, 0.37) in the absence of a predator cue and 0.24 (95% CI = 0.08, 0.37) in the presence of one.

Refuge Use

Unlike height climbed, refuge use changed slightly across trials (estimate = -0.12 , 95% CI = $-0.19, -0.04$), with individuals becoming shyer over time. When exposed to a predator cue, refuge use increased (estimate = -0.67 , 95% CI = $-0.75, -0.55$), with snails becoming less bold. Refuge use did differ between locations, with bolder snails at NC1 (estimate = 0.23, 95% CI = 0.16, 0.31). Individuals differed from one another in mean refuge use (intercept SD = 0.15, 95% CI = 0.10, 0.22; Fig. 1b) and differed in their responses to a changing environment (SD = 0.20, 95% CI = 0.08, 0.33; Fig. 2b). There was a similar relationship between individual intercepts and slopes with respect to context ($r = 0.35$, 95% CI = 0.08, 0.61): snails that used the refuge in the absence of a predator cue showed less behavioural plasticity, whereas bolder individuals, which did not use the refuge in the absence of a predator cue, increased their refuge use when a

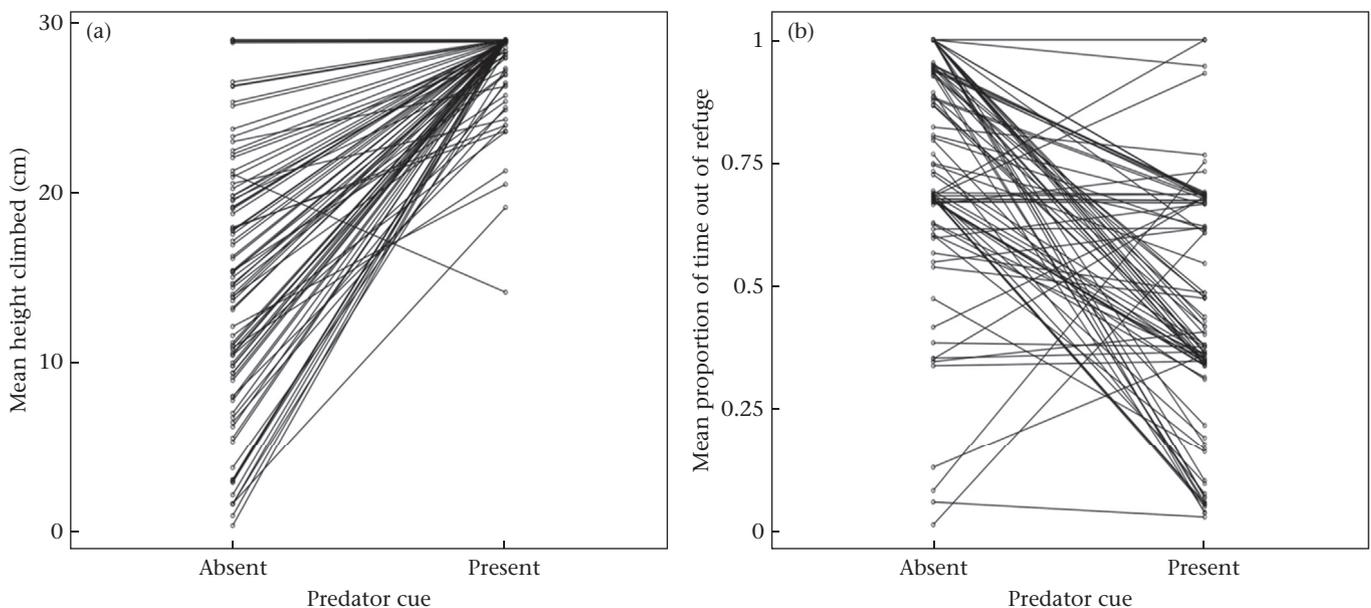


Figure 2. Mean \pm SE (a) height climbed and (b) proportion of time out of refuge for 90 snails across the environmental gradient of a predator cue. Each line represents an individual's reaction norm.

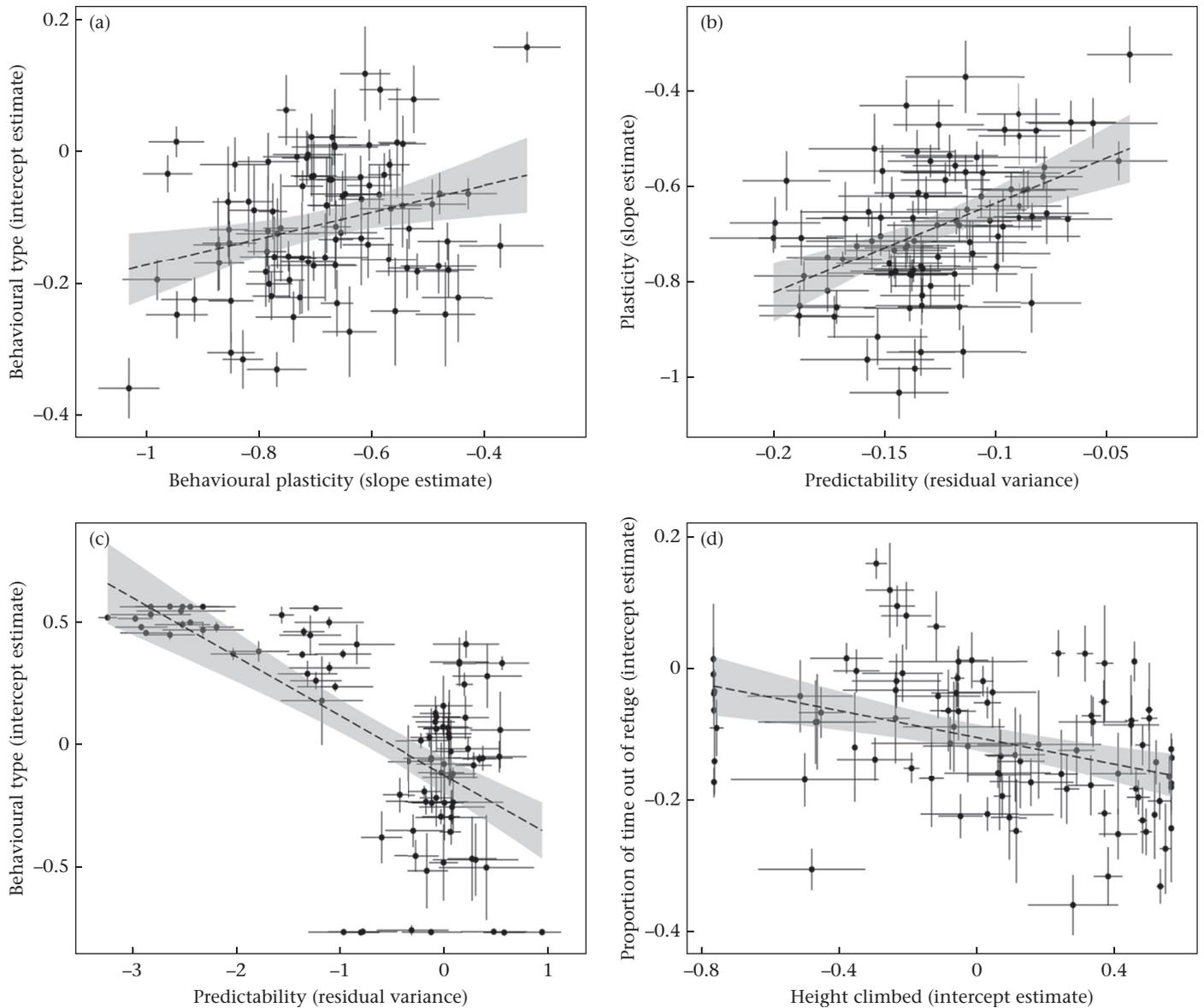


Figure 3. Estimates of individual slopes and intercepts with respect to height climbed and proportion of time out of refuge across the environmental gradient of a predator cue. Error bars denote the standard error of the predicted values. Correlations were estimated from mixed models. Refuge use: (a) behavioural type versus behavioural plasticity; (b) behavioural plasticity versus predictability. Height climbed: (c) behavioural type versus predictability; (d) between behavioural types. The lines represent the smoothed conditional means to aid in visualization.

predator cue was present (Fig. 3a). Residual variance minimally differed among individuals (intercept SD = 0.03, 95% CI = 0.00, 0.08) and there was weak evidence for a relationship between predictability and individual intercepts ($r = 0.14$, 95% CI = -0.21, 0.45). However, the positive correlation between behavioural plasticity and predictability ($r = 0.42$, 95% CI = 0.27, 0.60) again indicates that more responsive snails were less predictable (Fig. 3b). Trait repeatability of refuge use using the linear mixed model was 0.18 (95% CI = 0.05, 0.30) in the absence of a predator cue and 0.08 (95% CI = 0.01, 0.20) in the presence of one.

Correlations Among Behaviour and Morphology

The among-individual correlation between mean height climbed and mean refuge use (intercept*intercept correlation: $r = -0.22$, 95% CI = -0.36, -0.07) suggests individuals displayed shy phenotypes across traits (Fig. 3d). Changes in height climbed

were correlated with changes in refuge use over time as well (slope–slope covariance: $r = 0.43$, 95% CI = 0.15, 0.55).

There was also strong evidence that aperture length was related to key aspects of personality (Fig. 4). Snails with wide apertures climbed higher (intercept*intercept correlation: $r = 0.16$, 95% CI = 0.11, 0.21) and spent more time in the refuge ($r = -0.14$, 95% CI = -0.53, 0.17), although this correlation was less certain. Snails with wider apertures were also less plastic (height climbed: $r = -0.16$, 95% CI = -0.21, -0.12 (Fig. 5); refuge use: $r = -0.28$, 95% CI = -0.75, -0.05) and more predictable (height climbed: $r = -0.02$, 95% CI = -0.05, 0.02; refuge use: $r = -0.31$, 95% CI = -0.56, -0.01). Overall, snails with larger apertures were less bold, less plastic and more predictable.

DISCUSSION

Individual snails consistently differed in their mean level boldness, their responsiveness to environmental variation and their

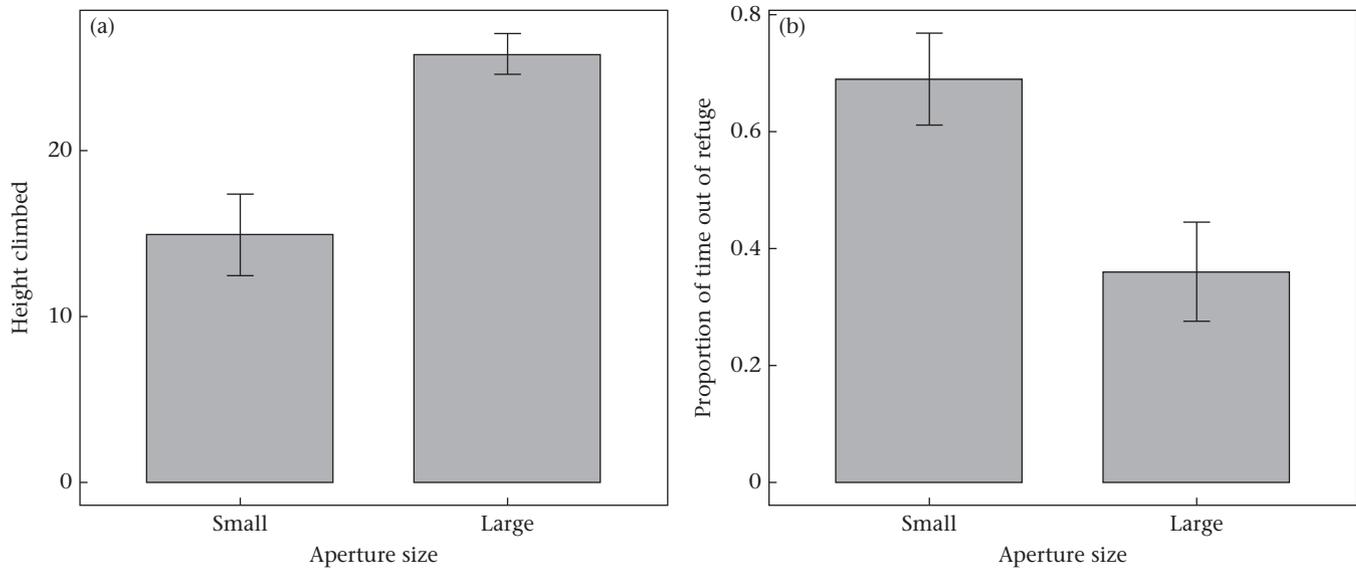


Figure 4. Mean \pm SE (a) height climbed and (b) proportion of time out of refuge for a subset of snails with the smallest and largest aperture openings ($N = 10$ snails per group).

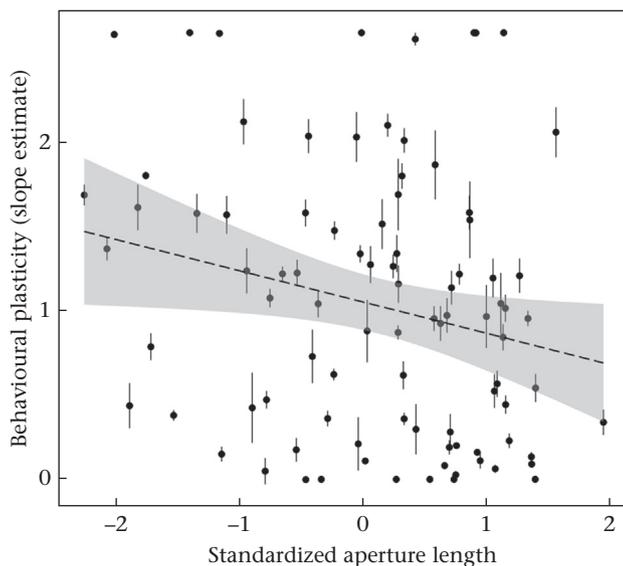


Figure 5. Relationship between aperture length and behavioural plasticity for height climbed. Error bars denote the standard error of the predicted values. Correlations were estimated from mixed models. The line represents the smoothed conditional mean to aid in visualization.

predictability of behaviour. Height climbed changed little across trials, and refuge use tended to decrease, but the slopes of the temporal reaction norms did not differ substantially among individuals. This pattern potentially suggests some sensitization to protocols, although this was largely restricted to trials in which the predator cue was present. Importantly, aperture size was strongly correlated with multiple measures of personality, suggesting that this aspect of shell shape critically influences the expression of personality.

Contrary to predictions, shell length did not influence any of the behavioural measures in this study, even though selection pressures can vary across ontogeny and different behaviours can be advantageous at different life stages (Dahirel et al., 2017; Wolf et al., 2007). For example, smaller snails are inherently more vulnerable to predation than larger snails due to the known size-structured predation relationship between *C. sapidus* and *L. irrorata*. Although *C. sapidus* are aggressive predators, the size ratio that is

most advantageous for successful predation is ≥ 6 (crab width:snail length); thus, as crab size increases, smaller snails become increasingly vulnerable to predation while larger snails can enter a size refuge (Hamilton, 1976; Schindler et al., 1994). The lack of correlation between personality and either shell length or size class (small, medium, large), coupled with a strong effect of aperture length, suggests a more complex relationship between boldness and shell morphology than simple size differences.

Snails with wider apertures climbed consistently higher and were less bold than those with narrow apertures. Differences in aperture size may be a result of local predation pressures: when exposed to extended predator cues, *L. irrorata* will decrease their aperture opening by increasing their apertural lip thickness, thereby reducing the success of predation (Hulthen et al., 2014; Moody & Aronson, 2012). Predation pressures can vary on a fine spatial scale, thus predator-induced morphological adaptations can also vary spatially (Moody & Aronson, 2012). Indeed, aperture length differed significantly between sites, with NC1 snails having narrower apertures, and increased boldness, compared to snails at NC2. Greenfield et al. (2002) found that *Littoraria* inhabiting an area regularly accessible to *C. sapidus* had narrower apertures relative to individuals inhabiting the high marsh, and induction of aperture lip thickness by water-borne predatory cues has been demonstrated in *Littorina obtusata* (Trussell, 1996). Such morphological compensation has been seen in other species as well. In freshwater snails, species with thinner shells are more likely to climb out of the water in the presence of a predator compared to thick-shelled species, which tend to hide under a refuge (Rundle & Bronmark, 2001), and smaller snails show increased antipredation behaviour (DeWitt et al., 1999). Across marine snails, species with taller spires and higher shell aspect ratios exhibit increased behavioural responses when exposed to predator cues (Cotton et al., 2004).

Interestingly, indirect estimates of predation, as measured by counting the proportion of scarred snails, showed that NC1 had a lower percentage of scarred individuals (15.6%) as compared to NC2 (28.9%), despite those snails being better defended (i.e. narrower apertures). However, the lack of a relationship between sublethal injuries and shell morphology across sites does not necessarily discount crab presence as a factor shaping morphological characteristics. Water-borne predatory cues are known to rapidly induce morphological changes regardless of predation attempts (Moody & Aronson, 2012). The apertural differences seen here may indicate a populationwide response of shell

thickening to water-borne predatory cues rather than individual responses to sublethal attacks. Further research is necessary to distinguish whether morphological differences between sites arise from selective predation, the occurrence of past experiences with predators or induction by water-borne predatory cues (Moody & Aronson, 2007; Trussell, 1996). It should also be noted that morphological variation in intertidal snails can be driven by differences in wave energy (Trussell, 1997). Snails inhabiting wave-exposed shores typically have larger apertures when compared to conspecifics in protected areas, a trait that helps reduce the threat of dislodgement in areas with high wave energy (Trussell, 1997). Although salt marshes are generally more protected from wave energy when compared to rocky shorelines, differences in wave exposure between sites, rather than predation pressure, may also explain the variation in aperture size observed.

Boldness traits were also correlated and varied among individuals, with some individuals climbing high in each trial and spending most of their time in the refuge. Fluctuating selection or trade-offs over space and time could help explain the maintenance of these different behavioural types within a population. For example, bolder male agamas (*Agama planiceps*) have larger home ranges and increased consumption but suffer higher levels of predation attempts when compared to shyer conspecifics (Carter et al., 2010). Bolder mud crabs (*Panopeus herbstii*) also suffer higher mortality due to predation by blue crabs compared to shy conspecifics (Belgrad & Griffen, 2016). In such scenarios, spatial or temporal variation in predation intensity ensure that neither behavioural type performs consistently better across contexts, thereby equalizing fitness (Toscano, 2017). In addition to predator avoidance, *L. irrorata* rely on behavioural adaptations to thermoregulate and avoid desiccation (Henry et al., 1993). Internal snail temperature was found to be positively correlated with substratum temperature when snails were close to the marsh floor and negatively correlated with height climbed on *Spartina* stems, suggesting that climbing behaviour may be a thermoregulation tactic allowing snails to reduce body temperature and avoid mortality due to thermal stress (Williams & Appel, 1989). However, although climbing decreases internal body temperature, increased wind speeds associated with greater heights in the canopy can result in higher levels of desiccation. For example, snails have been observed at low heights on days of potentially lethal temperatures, presumably to avoid desiccation (Iacarella & Helmuth, 2012). Thus, the varying physiological trade-off between avoiding desiccation versus thermal stress may also explain the maintenance of different behavioural types in this species.

The slopes of the reaction norms also differed among individuals: snails with wider apertures were shyer overall and were less plastic in their response to predation risk. Shell shape is highly variable within species, and previous studies have related shell shape to predation vulnerability (Hoverman & Relyea, 2009). Wider apertures in *L. irrorata* decrease predator handling time, significantly increasing predation success (Moody & Aronson, 2012). The correlations in climbing height and refuge use between contexts might be the result of behavioural tendencies that carry over across situations (Sih et al., 2003), although the magnitude of these tendencies is clearly influenced by shell shape. Shy individuals were found to have less behavioural plasticity and wider apertures, suggesting trait compensation: that is, bold individuals compensate for their increased exploratory and bold behaviours by expressing phenotypic traits that reduce risk (Kuo et al., 2015). For example, in the aquatic snail, *Radix balthica*, bold snails exhibit a more defended shell type than shy snails (Ahlgren et al., 2015), although in a previous study on *L. irrorata*, bold individuals were less plastic overall (Cornwell et al., 2020). However, boldness in the latter case was measured by shell opening latency and was not linked to shell morphology. These differences suggest a certain degree of independence among various measures of boldness and, more generally, personality potentially reflecting their relative ecological importance.

Snails also differed in their degree of predictability, a measure of within-individual variation, which can have important implications for fitness (Stamps et al., 2012). Recent behavioural studies have linked individual state to variation in predictability, with particular emphasis on differences in average resting metabolic rate (RMR). RMR is a major component of the total daily energy expenditure and may be related to the capacity to engage in energetically costly physical activities that are sustained over time (Biro et al., 2018; Briffa et al., 2013). Existing theory predicts generally positive correlations between individual mean level activity and mean level RMR (Biro & Stamps, 2008). Most recently, Biro et al. (2018) showed that mice with higher aerobic scope were less predictable in their behaviour as compared to those with a lower aerobic scope. Similarly, bold snails had the greatest behavioural plasticity in climbing height and refuge use and were the least predictable.

This greater variability may be in response to varying perceived predation risk and might be mediated by the life history trade-off between growth and mortality (Biro & Stamps, 2008; Mangel & Stamps, 2001; Wolf & Weissing, 2012). For instance, traits related to food acquisition are expected to be expressed differently over an individual's lifetime (Biro & Stamps, 2008). If, for example, juvenile growth rate correlates positively with adult size and fecundity, younger snails should prioritize feeding and tolerate a higher risk of predation, while adults would prioritize reproduction and be more risk averse (Roff, 1992; Stamps, 2007). While this type of asset protection theory predicts a decrease in risky behaviour as an individual accumulates resources and increases in size (Beveridge et al., 2022; Clark, 1994), this pattern was not observed here. In *L. irrorata* from Virginia, bolder individuals have higher RMR and grow faster (Cornwell et al., 2020). The greater unpredictability seen in bold snails here might reflect the necessity to forage more often to satisfy their higher energy demands. It has been suggested that snails may conserve energy by affixing themselves to stalks if feeding at each low tide is not required to replenish reserves, thus explaining why shy snails, which consistently climbed high and were more predictable, might have lower RMR (Hovel et al., 2001).

Individual differences in behaviour provide the raw material upon which selection can act, and behaviour itself has the most immediate effects on feeding, mating and survival rates (Careau & Garland, 2012; Sih et al., 2003). Here we show that *L. irrorata* exhibits both consistent differences in behaviour and consistent differences in the plasticity and predictability of that behaviour, key axes of the expression of animal personality. Moreover, personality varies with morphology, with boldness being strongly dependent on aperture size. Indeed, boldness and unpredictability in snails with narrower apertures might reflect phenotypic compensation: they invest in more pronounced morphological defences to compensate for their riskier lifestyle. Personality here seems less dictated by the ontogenetic trade-off between growth and mortality since shell length (an indirect measure of age) was not a significant predictor of personality. Nevertheless, recent work has illuminated the central role that *C. sapidus* plays in regulating the densities of *L. irrorata*, thus indirectly releasing *Spartina* from potentially intense grazing pressures (Silliman & Bertness, 2002; Silliman & Zieman, 2001). How personality ultimately affects the outcome of interactions between predator and prey can thus have significant effects on the health of salt marshes, ecosystems that are both ecologically and economically important (Boesch & Turner, 1984; Silliman & Bertness, 2002).

Author Contributions

Christina Salerno: Conceptualization, Methodology, Validation, Investigation, Resources, Data curation, Formal analysis, Writing – Original draft, Writing – Review & Editing, Project administration.
Stephanie Kamel: Conceptualization, Methodology, Formal

analysis, Resources, Data curation, Writing – Original draft, Writing – Review & Editing, Visualization, Supervision, Funding acquisition.

Data Availability

Data will be made available on request.

Declaration of Interest

None.

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Supplementary Material

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References

- Ahlgren, J., Chapman, B. B., Nilsson, P. A., & Bronmark, C. (2015). Individual boldness is linked to protective shell shape in aquatic snails. *Biology Letters*, *11*(4), Article 20150029. <https://doi.org/10.1098/rsbl.2015.0029>
- Bärlocher, F., & Newell, S. Y. (1994). Growth of the salt marsh periwinkle *Littoraria irrorata* on fungal and cordgrass diets. *Marine Biology*, *118*(1), 109–114. <https://doi.org/10.1007/bf00699224>
- Bednekoff, P. A., & Lima, S. L. (1998). Randomness, chaos and confusion in the study of antipredator vigilance. *Trends in Ecology & Evolution*, *13*(7), 284–287. [https://doi.org/10.1016/s0169-5347\(98\)01327-5](https://doi.org/10.1016/s0169-5347(98)01327-5)
- Bednekoff, P. A., & Lima, S. L. (2002). Why are scanning patterns so variable? An overlooked question in the study of anti-predator vigilance. *Journal of Avian Biology*, *33*(2), 143–149. <https://doi.org/10.1034/j.1600-048X.2002.330204.x>
- Belgrad, B. A., & Griffen, B. D. (2016). Predator–prey interactions mediated by prey personality and predator hunting mode. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1828), Article 20160408. <https://doi.org/10.1098/rspb.2016.0408>
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*(4), 771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>
- Bell, A. M., & Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, *10*(9), 828–834. <https://doi.org/10.1111/j.1461-0248.2007.01081.x>
- Bertness, M. D., Brisson, C. P., Bevil, M. C., & Crotty, S. M. (2014). Herbivory drives the spread of salt marsh die-off. *PLoS One*, *9*(3), Article e92916. <https://doi.org/10.1371/journal.pone.0092916>
- Beveridge, D., Mitchell, D. J., Beckmann, C., & Biro, P. A. (2022). Weak evidence that asset protection underlies temporal or contextual consistency in boldness of a terrestrial crustacean. *Behavioral Ecology and Sociobiology*, *76*, 94. <https://doi.org/10.1007/s00265-022-03198-2>
- Bingham, F. O. (1972). Shell growth in the gastropod *Littorina irrorata*. *Nautilus*, *85*(4), 136–141.
- Biro, P. A., Abrahams, M. V., Post, J. R., & Parkinson, E. A. (2004). Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1554), 2233–2237. <https://doi.org/10.1098/rspb.2004.2861>
- Biro, P. A., Abrahams, M. V., Post, J. R., & Parkinson, E. A. (2006). Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *Journal of Animal Ecology*, *75*(5), 1165–1171. <https://doi.org/10.1111/j.1365-2656.2006.01137.x>
- Biro, P. A., & Adriaenssens, B. (2013). Predictability as a personality trait: Consistent differences in intraindividual behavioral variation. *American Naturalist*, *182*(5), 621–629. <https://doi.org/10.1086/673213>
- Biro, P. A., Garland, T., Beckmann, C., Ujvari, B., Thomas, F., & Post, J. R. (2018). Metabolic scope as a proximate constraint on individual behavioral variation: Effects on personality, plasticity, and predictability. *American Naturalist*, *192*(2), 142–154. <https://doi.org/10.1086/697963>
- Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, *23*(7), 361–368. <https://doi.org/10.1016/j.tree.2008.04.003>
- Boesch, D. F., & Turner, R. E. (1984). Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries*, *7*, 460–468. <https://doi.org/10.2307/1351627>
- Briffa, M., Bridger, D., & Biro, P. A. (2013). How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. *Animal Behaviour*, *86*(1), 47–54. <https://doi.org/10.1016/j.anbehav.2013.04.009>
- Briffa, M., Rundle, S. D., & Fryer, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: Animal personalities in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1640), 1305–1311. <https://doi.org/10.1098/rspb.2008.0025>
- Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*(1), 1–28. <https://doi.org/10.18637/jss.v080.i01>
- Bürkner, P.-C. (2018). Advanced Bayesian multilevel modeling with the R package brms. *R Journal*, *10*(1), 395–411.
- Careau, V., & Garland, T. (2012). Performance, personality, and energetics: Correlation, causation, and mechanism. *Physiological and Biochemical Zoology*, *85*(6), 543–571. <https://doi.org/10.1086/666970>
- Carroll, J. M., Church, M. B., & Finelli, C. M. (2018). Periwinkle climbing response to water- and airborne predator chemical cues may depend on home-marsh geography. *PeerJ*, *6*, Article e5744. <https://doi.org/10.7717/peerj.5744>
- Carter, A. J., Goldizen, A. W., & Tromp, S. A. (2010). Agamas exhibit behavioral syndromes: Bolder males bask and feed more but may suffer higher predation. *Behavioral Ecology*, *21*(3), 655–661. <https://doi.org/10.1093/beheco/arg036>
- Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, *5*(2), 159–170. <https://doi.org/10.1093/beheco/5.2.159>
- Cleasby, I. R., Nakagawa, S., & Schielzeth, H. (2015). Quantifying the predictability of behaviour: Statistical approaches for the study of between-individual variation in the within-individual variance. *Methods in Ecology and Evolution*, *6*(1), 27–37.
- Cornwell, T. O., McCarthy, I. D., & Biro, P. A. (2020). Integration of physiology, behaviour and life history traits: Personality and pace of life in a marine gastropod. *Animal Behaviour*, *163*, 155–162.
- Cornwell, T. O., McCarthy, I. D., Snyder, C. R. A., & Biro, P. A. (2019). The influence of environmental gradients on individual behaviour: Individual plasticity is consistent across risk and temperature gradients. *Journal of Animal Ecology*, *88*(4), 511–520. <https://doi.org/10.1111/1365-2656.12935>
- Cotton, P. A., Rundle, S. D., & Smith, K. E. (2004). Trait compensation in marine gastropods: Shell shape, avoidance behavior, and susceptibility to predation. *Ecology*, *85*(6), 1581–1584. <https://doi.org/10.1890/03-3104>
- Crist, R. W., & Banta, W. C. (1983). Distribution of the marsh periwinkle *Littorina irrorata* (Say) in a Virginia salt marsh. *Gulf Research Reports*, *7*(3), 225–235.
- Dahirel, M., Vong, A., Ansart, A., & Madec, L. (2017). Individual boldness is life stage-dependent and linked to dispersal in a hermaphrodite land snail. *Ecological Research*, *32*(5), 751–755. <https://doi.org/10.1007/s11284-017-1484-x>
- Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, *7*(8), 734–739. <https://doi.org/10.1111/j.1461-0248.2004.00618.x>
- Davidson-Arnott, R. G. D., van Proosdij, D., Ollerhead, J., & Schostak, L. (2002). Hydrodynamics and sedimentation in salt marshes: Examples from a macrotidal marsh, Bay of Fundy. *Geomorphology*, *48*(1–3), 209–231. [https://doi.org/10.1016/s0169-555x\(02\)00182-4](https://doi.org/10.1016/s0169-555x(02)00182-4)
- DeWitt, T. J., Sih, A., & Hucko, J. A. (1999). Trait compensation and cospecialization in a freshwater snail: Size, shape and antipredator behaviour. *Animal Behaviour*, *58*, 397–407. <https://doi.org/10.1006/anie.1999.1158>
- Dingemanse, N. J., & Wolf, M. (2010). Recent models for adaptive personality differences: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 3947–3958. <https://doi.org/10.1098/rstb.2010.0221>
- Dingemanse, N. J., & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: Causes and consequences. *Animal Behaviour*, *85*(5), 1031–1039. <https://doi.org/10.1016/j.anbehav.2012.12.032>
- Dix, T. L., & Hamilton, P. V. (1993). Chemically mediated escape behavior in the marsh periwinkle *Littoraria irrorata* Say. *Journal of Experimental Marine Biology and Ecology*, *166*(1), 135–149. [https://doi.org/10.1016/0022-0981\(93\)90082-y](https://doi.org/10.1016/0022-0981(93)90082-y)
- Dorset, E. E., Sakaluk, S. K., & Thompson, C. F. (2017). Behavioral plasticity in response to perceived predation risk in breeding house wrens. *Evolutionary Biology*, *44*(2), 227–239.
- Duval, M. A., Calzetta, A. M., & Rittschof, D. (1994). Behavioral responses of *Littoraria irrorata* (Say) to water-borne odors. *Journal of Chemical Ecology*, *20*(12), 3321–3334. <https://doi.org/10.1007/bf02033729>
- Edenbrow, M., & Croft, D. P. (2011). Behavioural types and life history strategies during ontogeny in the mangrove killifish, *Kryptolebias marmoratus*. *Animal Behaviour*, *82*(4), 731–741. <https://doi.org/10.1016/j.anbehav.2011.07.003>
- Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–472. <https://doi.org/10.1214/ss/1177011136>
- Gordon, D. C., Cranford, P. J., & Desplanque, C. (1985). Observations on the ecological importance of salt marshes in the Cumberland Basin, a macrotidal estuary in the Bay of Fundy. *Estuarine, Coastal and Shelf Science*, *20*(2), 205–227. [https://doi.org/10.1016/0272-7714\(85\)90038-1](https://doi.org/10.1016/0272-7714(85)90038-1)
- Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, *127*(1), 45–86. <https://doi.org/10.1037/0033-2909.127.1.45>
- Greenfield, B. K., Lewis, D. B., & Hinke, J. T. (2002). Shell damage in salt marsh periwinkles (*Littoraria irrorata* Say, 1822) and resistance to future attacks by blue crabs (*Callinectes sapidus* Rathbun, 1896). *American Malacological Bulletin*, *17*(1–2), 141–146.
- Hamilton, P. V. (1976). Predation on *Littoraria irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea: Portunidae). *Bulletin of Marine Science*, *26*(3), 403–409.

- Hazlett, B. A. (1995). Behavioral plasticity in crustacea: Why not more? *Journal of Experimental Marine Biology and Ecology*, 193(1–2), 57–66. [https://doi.org/10.1016/0022-0981\(95\)00110-7](https://doi.org/10.1016/0022-0981(95)00110-7)
- Henry, R. P., McBride, C. J., & Williams, A. H. (1993). Responses of the marsh periwinkle, *Littoraria (Littorina) irrorata* to temperature, salinity and desiccation, and the potential physiological relationship to climbing behavior. *Marine Behaviour and Physiology*, 24(1), 45–54. <https://doi.org/10.1080/10236249309378877>
- Hertel, A. G., Niemelä, P. T., Dingemanse, N. J., & Mueller, T. (2020). A guide for studying among-individual behavioral variation from movement data in the wild. *Movement Ecology*, 8, Article 30. <https://doi.org/10.1186/s40462-020-00216-8>
- Hovel, K. A., Bartholomew, A., & Lipcius, R. N. (2001). Rapidly entrainable tidal vertical migrations in the salt marsh snail *Littoraria irrorata*. *Estuaries*, 24, 808–816. <https://doi.org/10.2307/1353172>
- Hoverman, J. T., & Relyea, R. A. (2009). Survival trade-offs associated with inducible defences in snails: The roles of multiple predators and developmental plasticity. *Functional Ecology*, 23(6), 1179–1188. <https://doi.org/10.1111/j.1365-2435.2009.01586.x>
- Hulthen, K., Chapman, B. B., Nilsson, P. A., Hollander, J., & Bronmark, C. (2014). Express yourself: Bold individuals induce enhanced morphological defences. *Proceedings of the Royal Society B: Biological Sciences*, 281(1776), Article 20132703. <https://doi.org/10.1098/rspb.2013.2703>
- Iacarella, J. C., & Helmuth, B. (2012). Body temperature and desiccation constrain the activity of *Littoraria irrorata* within the *Spartina alterniflora* canopy. *Journal of Thermal Biology*, 37(1), 15–22. <https://doi.org/10.1016/j.jtherbio.2011.10.003>
- Johnson, D. S., Fleeger, J. W., & Deegan, L. A. (2009). Large-scale manipulations reveal that top-down and bottom-up controls interact to alter habitat utilization by saltmarsh fauna. *Marine Ecology Progress Series*, 377, 33–41. <https://doi.org/10.3354/meps07849>
- Johnson, J. C., & Sih, A. (2005). Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): A role for behavioral syndromes. *Behavioral Ecology and Sociobiology*, 58(4), 390–396. <https://doi.org/10.1007/s00265-005-0943-5>
- King, S. E., & Lester, J. N. (1995). The value of salt marsh as a sea defence. *Marine Pollution Bulletin*, 30(3), 180–189. [https://doi.org/10.1016/0025-326x\(94\)00173-7](https://doi.org/10.1016/0025-326x(94)00173-7)
- Kuo, C. Y., Irschick, D. J., & Lailvaux, S. P. (2015). Trait compensation between boldness and the propensity for tail autotomy under different food availabilities in similarly aged brown anole lizards. *Functional Ecology*, 29(3), 385–392. <https://doi.org/10.1111/1365-2435.12324>
- Mangel, M., & Stamps, J. (2001). Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research*, 3(5), 583–593.
- Mathot, K. J., Wright, J., Kempnaers, B., & Dingemanse, N. J. (2012). Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*, 121(7), 1009–1020. <https://doi.org/10.1111/j.1600-0706.2012.20339.x>
- Mitchell, D. J., & Biro, P. A. (2017). Is behavioural plasticity consistent across different environmental gradients and through time? *Proceedings of the Royal Society B: Biological Sciences*, 284(1860), Article 20170893. <https://doi.org/10.1098/rspb.2017.0893>
- Moeller, L., Spencert, T., & French, J. R. (1996). Wind wave attenuation over salt-marsh surfaces: Preliminary results from Norfolk, England. *Journal of Coastal Research*, 12, 1009–1016.
- Moody, R. M., & Aronson, R. B. (2007). Trophic heterogeneity in salt marshes of the northern Gulf of Mexico. *Marine Ecology Progress Series*, 331, 49–65. <https://doi.org/10.3354/meps331049>
- Moody, R. M., & Aronson, R. B. (2012). Predator-induced defenses in a salt marsh gastropod. *Journal of Experimental Marine Biology and Ecology*, 413, 78–86. <https://doi.org/10.1016/j.jembe.2011.11.029>
- R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
- Rhemtulla, M., Brosseau-Liard, P.É., & Savalei, V. (2012). When can categorical variables be treated as continuous? A comparison of robust continuous and categorical SEM estimation methods under suboptimal conditions. *Psychological Methods*, 17(3), 354–373. <https://doi.org/10.1037/a0029315>
- Roff, D. (1992). *The evolution of life histories: Theory and analysis*. Chapman & Hall.
- Roth, T. S., & Sterck, E. H. (2020). Social vigilance of friends and foes in western lowland gorillas (*Gorilla gorilla gorilla*). *Animal Behavior and Cognition*, 7(4), 537–555.
- RStudio Team. (2020). *RStudio: Integrated development for R*. Boston: RStudio, PBC. <http://www.rstudio.com/>
- Rundle, S. D., & Bronmark, C. (2001). Inter- and intraspecific trait compensation of defence mechanisms in freshwater snails. *Proceedings of the Royal Society B: Biological Sciences*, 268(1475), 1463–1468. <https://doi.org/10.1098/rspb.2001.1682>
- Schindler, D. E., Johnson, B. M., Mackay, N. A., Bouwes, N., & Kitchell, J. F. (1994). Crab: Snail size-structured interactions and salt marsh predation gradients. *Oecologia*, 97(1), 49–61. <https://doi.org/10.1007/bf00317908>
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378.
- Sih, A., Kats, L. B., & Maurer, E. F. (2003). Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Animal Behaviour*, 65, 29–44. <https://doi.org/10.1006/anbe.2002.2025>
- Silliman, B. R., & Bertness, M. D. (2002). Atrophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences of the United States of America*, 99(16), 10500–10505. <https://doi.org/10.1073/pnas.162366599>
- Silliman, B. R., Layman, C. A., Geyer, K., & Zieman, J. C. (2004). Predation by the black-clawed mud crab, *Panopeus herbstii*, in Mid-Atlantic salt marshes: Further evidence for top-down control of marsh grass production. *Estuaries*, 27(2), 188–196. <https://doi.org/10.1007/bf02803375>
- Silliman, B. R., & Newell, S. Y. (2003). Fungal farming in a snail. *Proceedings of the National Academy of Sciences of the United States of America*, 100(26), 15643–15648. <https://doi.org/10.1073/pnas.2535227100>
- Silliman, B. R., & Zieman, J. C. (2001). Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. *Ecology*, 82(10), 2830–2845. <https://doi.org/10.2307/2679964>
- Smith, B. R., & Blumstein, D. T. (2010). Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*). *Behavioral Ecology*, 21(5), 919–926. <https://doi.org/10.1093/beheco/arq084>
- Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, 85(5), 1004–1011. <https://doi.org/10.1016/j.anbehav.2012.12.031>
- Stamps, J. A. (2007). Growth–mortality tradeoffs and ‘personality traits’ in animals. *Ecology Letters*, 10(5), 355–363. <https://doi.org/10.1111/j.1461-0248.2007.01034.x>
- Stamps, J. A. (2016). Individual differences in behavioural plasticities. *Biological Reviews*, 91(2), 534–567. <https://doi.org/10.1111/brv.12186>
- Stamps, J. A., & Biro, P. A. (2016). Personality and individual differences in plasticity. *Current Opinion in Behavioral Sciences*, 12, 18–23. <https://doi.org/10.1016/j.cobeha.2016.08.008>
- Stamps, J. A., Briffa, M., & Biro, P. A. (2012). Unpredictable animals: Individual differences in intraindividual variability (IIV). *Animal Behaviour*, 83(6), 1325–1334. <https://doi.org/10.1016/j.anbehav.2012.02.017>
- Stanhope, H. S., Banta, W. C., & Temkin, M. H. (1982). Size-specific emergence of the marsh snail, *Littoraria irrorata*: Effect of predation by blue crabs in a Virginia salt marsh. *Gulf Research Reports*, 7(2), 179–182.
- Stiven, A. E., & Hunter, J. T. (1976). Growth and mortality of *Littorina irrorata* Say in three North Carolina marshes. *Chesapeake Science*, 17(3), 168–176.
- Tolkamp, B. J., Allcroft, D. J., Austin, E. J., Nielsen, B. L., & Kyriazakis, I. (1998). Satiety splits feeding behaviour into bouts. *Journal of Theoretical Biology*, 194(2), 235–250. <https://doi.org/10.1006/jtbi.1998.0759>
- Toscano, B. J. (2017). Prey behavioural reaction norms: Response to threat predicts susceptibility to predation. *Animal Behaviour*, 132, 147–153. <https://doi.org/10.1016/j.anbehav.2017.08.014>
- Trussell, G. C. (1996). Phenotypic plasticity in an intertidal snail: The role of a common crab predator. *Evolution*, 50(1), 448–454. <https://doi.org/10.2307/2410815>
- Trussell, G. C. (1997). Phenotypic selection in an intertidal snail: Effects of a catastrophic storm. *Marine Ecology Progress Series*, 151(1–3), 73–79. <https://doi.org/10.3354/meps151073>
- Vermeij, G. J. (1973). Morphological patterns in high-intertidal gastropods: Adaptive strategies and their limitations. *Marine Biology*, 20(4), 319–346. <https://doi.org/10.1007/bf00354275>
- Warren, J. H. (1985). Climbing as an avoidance behavior in the salt marsh periwinkle, *Littoraria irrorata* (Say). *Journal of Experimental Marine Biology and Ecology*, 89(1), 11–28. [https://doi.org/10.1016/0022-0981\(85\)90079-6](https://doi.org/10.1016/0022-0981(85)90079-6)
- Williams, A. H., & Appel, A. G. (1989). Behavioral thermoregulation in *Littoraria irrorata* by climbing. *Marine Behaviour and Physiology*, 16(1), 31–41. <https://doi.org/10.1080/10236248909378739>
- Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy–bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, 107(3), 250–260. <https://doi.org/10.1037/0735-7036.107.3.250>
- Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447(7144), 581–584. <https://doi.org/10.1038/nature05835>
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452–461. <https://doi.org/10.1016/j.tree.2012.05.001>
- Zengel, S., Montague, C. L., Pennings, S. C., Powers, S. P., Steinhoff, M., Fricano, G., Schlemme, C., Zhang, M., Oehreg, J., Nixon, Z., Rouhani, S., & Michel, J. (2016). Impacts of the Deepwater Horizon oil spill on salt marsh periwinkles (*Littoraria irrorata*). *Environmental Science & Technology*, 50(2), 643–652. <https://doi.org/10.1021/acs.est.5b04371>