

## RESEARCH ARTICLE

## Mechanisms and Consequences of Infection-induced Phenotypes

# Predation cues amplify the effects of parasites on the personality of a keystone grazer

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**Abstract**

1. Parasites can alter species interactions either by modifying infected host behaviour or by influencing behavioural responses in uninfected individuals. Salt marsh ecosystems are characterized by a predator–prey interaction between the keystone grazer, *Littoraria irrorata*, and its main predator, *Callinectes sapidus*, both integral players in mediating the productivity of these habitats.
2. *Littoraria* also acts as the first intermediate host for at least four species of digenetic trematode. Parasite infection has been shown to decrease grazing and climbing in populations of *Littoraria*, although effects on infected host response to predators have not been investigated. Moreover, how infection might increase or decrease among-individual variation in behaviour (i.e. animal personality) is still unknown. Here we ask how trematode infection affects the expression of boldness in the anti-predator responses of *L. irrorata* in both the absence and presence of a predator cue.
3. We find that individual boldness varies substantially, and repeatability tends to increase as the number of stressors increases, with infected individuals exposed to a predator cue showing the strongest expression of behavioural types.
4. Parasitism amplifies this effect, although the parasite itself does not appear to directly induce behavioural changes: infected snails show no evidence of decreased climbing or differences in refuge use as compared to their uninfected counterparts. Infection might therefore drive the expression of condition-dependent personality differences evident only under high-risk conditions.
5. Group infection status strongly influenced behavioural reaction norms: uninfected individuals grouped with an infected snail were more responsive to predation risk, exhibiting increased climbing behaviour and spending less time in the water. Here parasites are influencing personality indirectly by inducing avoidance behaviours in healthy individuals, although only in high-risk environments.
6. The potential for exposure to parasites and predators fluctuates greatly across marsh ecosystems. Given the ecological importance of this predator–prey relationship, trematode infection can act as an important, although indirect, determinant of overall salt marsh community structure, health and function.

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## KEYWORDS

animal personality, behavioural plasticity, keystone grazer, *Littoraria irrorata*, parasite infection, predator–prey relationships

## 1 | INTRODUCTION

Animals within populations can exhibit important among-individual differences in behavioural traits that remain consistent over time, often known as animal personalities or behavioural types (Bell et al., 2009; Gosling, 2001; Wolf & Weissing, 2012). Such traits typically include activity, exploration and boldness, wherein animals with bold, aggressive personalities are prone to taking risks, and those with shy, docile personalities tend to be more cautious (Sih et al., 2004; Wilson et al., 1993), although individuals may still exhibit important behavioural differences in how they respond to changing environments (i.e. behavioural plasticity; Dingemanse & Wolf, 2013; Toscano, 2017).

A number of ecological factors have been shown to shape animal personality, including resource competition (Cote et al., 2008; Dingemanse et al., 2004) and predation regimes (Bell & Sih, 2007; Reale et al., 2007). Predation is often a major source of mortality for bold individuals and the benefits of risk taking are thus tightly linked to spatial and temporal variation in predation dynamics (Sih et al., 2004; Toscano, 2017). Differences in life-history strategies may also explain individual variation in behavioural types (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). Similarly, animal personalities may arise from variation in individual states, such as energy reserves or body size which can play a large role in determining individual behavioural types as they often limit the actions that can be performed (Dall et al., 2004; McElreath & Strimling, 2006). In addition to such factors, parasitic infection also has the potential to markedly change host state (Barber & Dingemanse, 2010; Richardson et al., 2022).

*Littoraria irrorata*, the marsh periwinkle, is an important consumer in salt marsh ecosystems along the Southeastern Atlantic and Gulf coasts of the United States and can directly influence marsh health, notably through its interaction with its main predator, the blue crab, *Callinectes sapidus*. When their densities are not controlled by predation, *L. irrorata* can decimate large areas of emergent salt marsh vegetation, typically the smooth cordgrass, *Sporobolus alterniflorus* (formerly *Spartina alterniflora*), via grazing and fungal farming (Silliman & Bertness, 2002; Silliman & Zieman, 2001). *C. sapidus*, exerts top-down control on the estuarine food web, thus indirectly sustaining salt marshes by preying upon grazers such as periwinkles (Silliman & Bertness, 2002). The trophic cascade imposed by this predator–prey interaction plays an important role in regulating *Sporobolus* productivity (Silliman & Bertness, 2002).

*L. irrorata* is also the first intermediate host to at least four species of digenetic trematodes, most commonly *Parorchis acanthus* (Coil & Heard, 1966; Heard, 1968, 1970; Holliman, 1961). Digenetic trematodes rely on several hosts to complete their life cycles. Typically, the first intermediate host is a mollusc in which asexual reproduction occurs, producing free-swimming cercaria that infect the second intermediate host, which then pass the infection (via trophic transmission) to the definitive host in which the parasite reaches sexual maturity (Esch et al., 2002) and lays eggs that pass into the environment. For some trematode species, the eggs are infectious to snails if eaten; for others, a free-swimming miracidium larva hatches from the egg to penetrate a snail (Buck et al., 2017). In aquatic systems, digenetic trematode parasites have been shown to induce a range of behavioural changes in their hosts (Bernot, 2003; O'Dwyer et al., 2014; Swartz et al., 2015). Previous work in *L. irrorata* has shown that trematode-infected snails climb and graze less than uninfected individuals, leading to changes in the interaction between snails and cordgrass (Morton, 2018; Morton & Silliman, 2020). Many gastropod species maintain ecologically important niches and influence ecosystems via grazing and other activities. Therefore, such behavioural shifts can indirectly affect ecosystem structure and function (Kuris et al., 2008; Wood et al., 2007).

Parasitism, like predation, can thus impose fitness costs on individuals and is increasingly recognized as a major evolutionary force that can shape animal personalities (Barber & Dingemanse, 2010; Behringer et al., 2018; Belgrad & Smith, 2014). Moreover, parasitism, like predation, can prompt individuals to adopt defensive tactics, with costs including reduced energy intake, decreased reproductive success and increased vulnerability to other predators (Buck et al., 2018; Clinchy et al., 2013). For example, individuals can avoid interacting with conspecifics with whom they are likely to share parasites, especially if they show signs of infection (Behringer et al., 2006; Dugatkin et al., 1994). Individuals could also identify signals of infection associated with noncontagious infections and alter their behaviour (Behringer et al., 2018; Krause et al., 1999). For instance, *Littorina littorea* do not follow infected snails when cercaria are present in their mucus trails (Davies & Knowles, 2001). While these infections cannot be passed directly between hosts, individuals can use these cues to not only differentiate between infected and uninfected conspecifics, but also to assess trade-offs regarding infection risk in their environment.

In a conceptual model developed by Kortet et al. (2010), animal personalities were most likely to emerge in environments with high infection and predation risks. *L. irrorata* exhibit key individual differences in response to predation risk in both shell emergence (Cornwell et al., 2020) and climbing behaviour (Salerno & Kamel, 2023). These traits are related to boldness, an individual's propensity to take risks, which can have important impacts on survival (Johnson & Sih, 2005;

Sih et al., 2003), as bold snails spent more time in the water and less time hiding in refuges, increasing the risk of encountering a predator (Salerno & Kamel, 2023). Moreover, shy snails displayed less behavioural plasticity and high predictability in response to predation cues, suggesting a consistently risk-averse lifestyle. While *P. acanthus* does not directly kill *L. irrorata*, it may manipulate its host such that it becomes more susceptible to predation, perhaps to increase its own transmission rates, resulting in direct alterations to the snail's behaviour (e.g. Seppälä & Jokela, 2008). How infection status and the presence of infected individuals shape individual differences in behaviour thus has the potential to markedly affect responses to predators.

Here we ask how trematode infection interacts with predation risk to influence the expression of personality in *L. irrorata* with respect to three anti-predator behavioural traits: climbing height, time out of water and refuge use. We use olfactory cues from blue crabs to simulate predation risk as they have been shown to elicit strong anti-predation behaviour in marsh periwinkles (Duval et al., 1994). We predict that boldness will decrease in the presence of the predator cue but ask whether (a) mean behavioural expression and (b) response to risk will vary among individuals as a direct result of infection status. We also ask whether the presence of an infected individual will modify the behavioural responses of uninfected conspecifics.

## 2 | MATERIALS AND METHODS

### 2.1 | Sample collection

In September 2021, 240 marsh periwinkles (mean length =  $18.39 \pm 1.3$  mm) were collected from a cord grass *S. alterniflorus* dominated salt marsh adjacent to the Bogue Sound in Atlantic Beach, North Carolina ( $34^{\circ}42'23.5''\text{N}$   $76^{\circ}45'06.7''\text{W}$ ). This location was chosen because previous work showed high trematode prevalence in *L. irrorata*, ranging from ~0.5% to 14%, which can depend on marsh health (Morton & Silliman, 2020). Snails were haphazardly collected during low tide and were then 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 L aquarium at a height which allowed snails in each container to have access to both 3 cm of seawater and 6 cm of air. Aquaria were filled with high-quality filtered seawater; salinity ranged from 25 to 30 ppt, temperature ranged from 21 to 24°C, and the system maintained a 12L:12D photoperiod. Snails were fed a mixture of standing dead and fresh *S. alterniflorus* ad lib for the entirety of the behavioural trials (Barlocher & Newell, 1994). Snails were allowed to acclimate for a minimum of 48 h prior to the trials to break their tidal circadian rhythm (Hovel et al., 2001). Seven individuals died before all behavioural trials could be completed and these individuals were excluded from analyses ( $n = 233$ ). Of 233 snails, 41.2% had scars on their shells, indicative of past unsuccessful predation attempts

by their main predator, the blue crab and confirming the presence of predation risk at this location. This study did not require ethical approval.

### 2.2 | Morphological measurements

Previous work found that personality in marsh periwinkles was strongly correlated with shell shape (Salerno & Kamel, 2023), thus several morphometric features were measured here. Snails were blotted dry and weighed to the nearest 0.01 gram using a portable electronic balance (VWR International). Shell length was measured from the top of the apex to the tip of the aperture and inner aperture length was measured at the widest part of the inside of the aperture opening as illustrated by Moody and Aronson (2012). Morphological traits were measured to the nearest 0.01 mm using digital callipers (TESA Brown & Sharpe TWIN-CAL IP67).

### 2.3 | Personality assessments

Individual behaviour was assessed both in the presence and absence of a predator chemical cue from *L. irrorata*'s main predator, the blue crab, *C. sapidus*. Olfactory cues were generated by holding three *C. sapidus*, fed crushed marsh periwinkles ad lib, in separate stagnant 37.85 L tanks for 1 week prior to the start of trials. To standardize the olfactory cue across crabs, individuals were size matched, held in the same conditions and fed the same diet on the same schedule. The water used for each trial was randomly selected from among the tanks and high-quality filtered seawater was used for the control trials. The behaviours under consideration were linked to boldness, one of the five major personality axes (Reale et al., 2007), and were measured as (a) maximal climbing height, (b) time spent out of water and (c) time spent out of refuge. *L. irrorata*'s main predators are neritic, thus bold, risk-taking individuals would be those staying in or close to the water and facing increased risk of a predator encounter.

Climbing height and time spent out of water were measured by placing five snails in a 11.4 L bucket ( $d = 18.5$  cm,  $h = 29$  cm), with walls vertically protracted and marked every 1 cm, and filled with 3 cm of high-quality filtered seawater. 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 (a) the maximal height climbed by each snail to the nearest centimetre (individuals not breaching the water were given a height of 0 and the maximum climbing height was 29 cm), and (b) time out of the water measured as the latency to emerge from the water (snails were observed every minute during the 10-min trial and latency was calculated as time in minutes where snails were above the water line). In a separate set of trials testing refuge use, two hollow hemispheres with a 3 cm  $\times$  3 cm opening were placed in the bottom of the bucket which allowed snails to freely crawl in and out. This experiment tested whether, given the option, snails chose to use the refuge. Although not quantified, snails tended to stay in the water

or use the refuge and climbed little (Salerno, pers. obs.). Snails were arranged in the same manner as in the previously described trials. Behaviour was observed every minute during the 10-min trial and here boldness was calculated as the time in minutes where snails were outside the refuge. Individuals remained in the same groups for all personality assessments. Snails were tested three times for each behaviour in each treatment. All tests occurred within the same 2-h window on subsequent days to standardize potential differences in cercarial influence on behaviour based on time of day.

## 2.4 | Infection status

*L. irrorata* are the first intermediate host to at least four species of trematodes, most commonly *Parorchis acanthus* (Morton, 2018). Infected individuals harbour sporocysts and/or rediae (Esch et al., 2002), and infection status can be determined by either dissecting the visceral mass of the snail, or through a nonlethal cercarial shedding method. For this study, we chose the nonlethal cercarial shedding method modified from Buck et al. (2017) and Morton (2018) to establish infection status of each individual, and all individuals were screened for parasites via shedding after the personality assessments were completed.

First, snails were removed from the aquaria and left to dry in a bucket for 24–48 h. This drying process was necessary to ensure that, when re-introduced to seawater, infected snails would always shed cercariae, allowing for the most accurate determination of infection status (Morton, 2018). After the drying period, individual snails were placed in a single 5 mL well within a 12-well non-tissue culture treated plate (Corning Incorporated) and completely submerged in filtered seawater heated to 30°C. Well plates were secured with a plastic lid to ensure each snail was completely submerged and to prevent escape. Well plates were then placed directly under fluorescent lights for >2.5 h after which each well was visually inspected for trematode cercaria using a dissecting microscope and any infected individuals were noted. Individuals were subsequently returned to their containers. To decrease the chances of overlooking an infection, individuals were screened three times over 9 days. Individuals that shed  $\geq 1$  cercaria at least once were classified as infected. Identification of trematode species was not performed, although Morton (2018) found that of 3616 *L. irrorata* collected from Atlantic Beach, 97.7% were infected with a single species of trematode, *P. acanthus*.

Finally, since snails were randomly assigned to groups for the personality assessments before infection status was known, an individual's infection status in relation to the infection status of the group was also defined. Uninfected snails were categorized as uninfected in a group of uninfected snails (UU;  $n = 27$  groups) or uninfected in a group with an infected snail (UI;  $n = 22$  groups). Infected snails were categorized as infected in a group of uninfected snails (IU;  $n = 22$  groups). Of the 22 groups, 20 groups had one infected snail, and two groups had two, corresponding to group prevalence of 20% and 40% respectively.

## 2.5 | 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). Data were examined for outliers and collinearity and residuals were inspected prior to analysis (Zuur et al., 2007). Exploratory univariate linear mixed models with a Gaussian error structure were implemented using lme4 (Bates et al., 2015) and fit to inform model structure for the more complex multivariate (MV) mixed model. The aim was to determine which effects were significant and supported for inclusion into the MV model (c.f. Beveridge et al., 2022). Morphological measurements were strongly collinear and were analysed separately. Weight was the variable that most greatly influenced behaviour and was thus retained (Table S1). Differences in morphology between infected and uninfected snails were tested using linear models. With respect to the behavioural traits, we included predator cue and trial as random slope effects with the fixed effects of weight, predator cue, infection status, group infection status and the random effect of trial. For height climbed and time out of water, the inclusion of predator cue and trial as random slope effects was supported (LR test:  $\chi_9^2 = 144.97$ ,  $p = 0.0002$  and  $\chi_{12}^2 = 10.82$ ,  $p = 0.02$  respectively). For refuge use, inclusion of trial as a random slope was supported ( $\chi_7^2 = 2.78$ ,  $p < 0.001$ ). Inclusion of infection status as a fixed effect was not supported (LR test:  $\chi_8^2 = 1.72$ ,  $p = 0.19$ ), although group infection and its interaction with predator cue were (LR test  $\chi_{11}^2 = 13.56$ ,  $p < 0.008$ ) and retained for subsequent analyses.

We used a Bayesian approach to fit the two models described below. Results are often very similar between frequentist and Bayesian approaches, although an advantage of the latter is that the model gives a posterior distribution for each estimated parameter and hence inherently reflects uncertainty (Hertel et al., 2020). The 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 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).

First, linear mixed models were fit to test for individual differences in mean-level boldness. Among-individual variation in average behavioural expression (i.e. behavioural type) is measured as the variance of a random intercept in a mixed-effects model. The existence and extent of among-individual variation is commonly quantified as repeatability (Hertel et al., 2020), which indicates the proportion of phenotypic behavioural variance in a population that can be attributed to individual differences in behavioural expression (Bell et al., 2009). Repeatability ( $R$ ) was initially assessed for all snails combined, although given the large differences in variances between environments (the presence vs. absence of a predator cue) and group infection (the presence vs. absence of

infected group members), repeatability was also calculated as a context-specific  $R$ , with the model containing the fixed effect of weight and with individual and trial as random effects. Credible intervals for the repeatability estimates were calculated by simulating the data 1000 times to get a posterior distribution for all variance components.

Next, a multivariate double hierarchical mixed model was fit to quantify the among- and within-individual covariances between climbing height, time out of water and refuge use, containing random intercept and slope effects with respect to context (predation and parasitism) and trial. The BRMS package allows the application of this type of model, which is needed to estimate individual variation in predictability (Bürkner, 2017). 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). Individuals with high residual variance ( $R_{IV}$ ) are thus more unpredictable than those with lower residual variance. All among-individual covariances of these effects were assessed. Given that the model is parameter heavy, only the correlations of interest are highlighted (see Supporting Information for model structure, code and full results). The covariance between random slope effects on each trait evaluates whether the degree of behavioural plasticity varies among individuals, and the intercept-slope covariance evaluates whether this behavioural plasticity is correlated with behavioural type. Covariance between residual variances and random intercept and slope effects were also evaluated across traits to test for correlations between an individual's  $R_{IV}$  and (a) its behavioural type and (b) its degree of behavioural plasticity (Hertel et al., 2020). The covariance between individual predicted mean values of each trait (the intercept-intercept covariance) evaluates the extent of a behavioural syndrome. Predictors in the model included weight, predator cue (present/absent), group infection (UU, UI and IU) and its interaction with predator cue, with trial as a random effect.

### 3 | RESULTS

Of 233 snails collected and screened, 24 individuals were infected with trematode parasites (10.3%), similar to previous estimates for this location (Morton & Silliman, 2020). Given the unbalanced sample size, a power analysis was conducted using the PWR package in R (Champely et al., 2018). Results indicate that the sample sizes were sufficient to achieve 80% power for detecting a medium to large effect ( $d = 0.62$ ; Cohen, 1988), at a significance criterion of  $\alpha = 0.05$ , between infected and uninfected snails. We found no detectable differences in shell length ( $F_{1,231} = 1.641$ ,  $p = 0.202$ ), aperture length ( $F_{1,231} = 1.36$ ,  $p = 0.245$ ) or weight ( $F_{1,231} = 0.626$ ,  $p = 0.429$ ) between infected and uninfected snails. Across individuals, behaviours were strongly influenced by predator cue and its interaction with group infection status. In response to predator

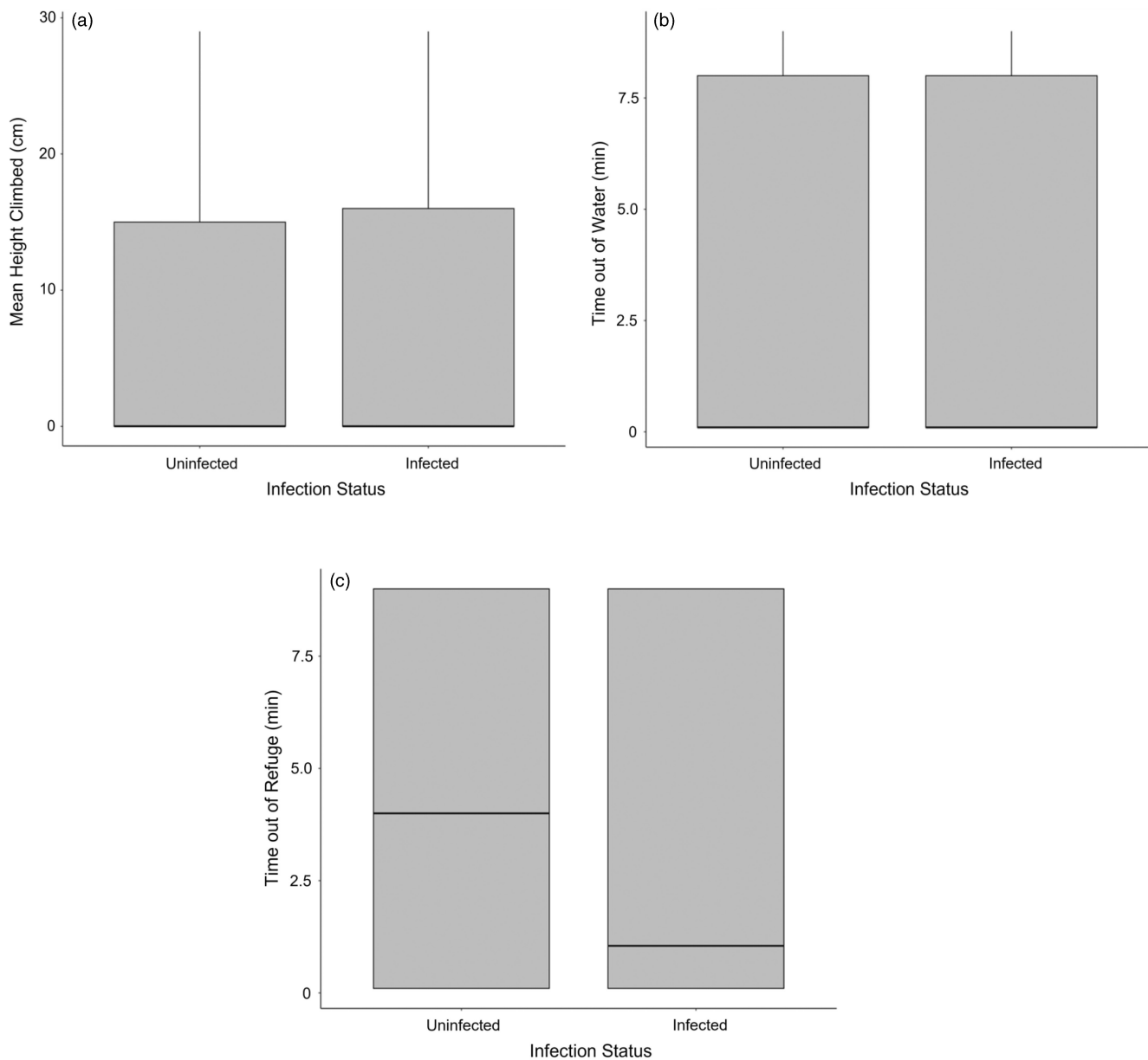
cues, individuals climbed higher (Est = 9.72, 95% CI = 9.20–10.23), spent more time out of water (Est = 3.85, 95% CI = 3.67–4.03) and more time in the refuge (Est = -0.82, 95% CI = -1.11 to -0.49), and this effect was strongest when surrounded by infected conspecifics (height climbed: Est = 2.33, 95% CI = 2.04–2.64 and time out of water: Est = 0.62, 95% CI = 0.36–0.85; Table 1; Table S2e). Behaviour also changed across days with snails spending less time in the refuge in later trials (Est = 0.54, 95% CI = 0.46–0.63; Table 1; Table S2e). Individual infection status did not influence any of the measured behaviours: height climbed (Est = 0.526,  $t$ -value = 0.459,  $p = 0.646$ ), time out of water (Est = 0.243,  $t$ -value = 0.57,  $p = 0.569$ ) and time out of refuge (Est = -0.178,  $t$ -value = -0.383,  $p = 0.702$ ; Figure 1).

#### 3.1 | Repeatability

Snails showed among-individual variation in mean-level behavioural expression, as measured by repeatability. In the absence of a predator cue, repeatability for height climbed, time out of water and time out of refuge were  $R = 0.18$  [0.13–0.21], 0.16 [0.09–0.23]

**TABLE 1** Estimates, errors and 95% CI for the fixed and random effects on all three behavioural traits.  $\hat{R}$  values in the model converged at 1. Effects with credible intervals not overlapping zero are considered significant and are bolded.

Traits and predictors	Estimate	Error	Lower 95% CI	Upper 95% CI
Climbing height				
Weight	0.05	0.06	-0.02	0.12
Predator cue	<b>9.72</b>	<b>0.50</b>	<b>9.20</b>	<b>10.23</b>
Predator: Group Infection (UI)	<b>2.33</b>	<b>0.29</b>	<b>2.04</b>	<b>2.64</b>
Predator: Group Infection (IU)	<b>1.90</b>	<b>0.90</b>	<b>0.96</b>	<b>2.83</b>
Trial	0.07	0.07	0.00	0.14
Time out of water				
Weight	-0.00	0.00	-0.01	0.00
Predator cue	<b>3.85</b>	<b>0.16</b>	<b>3.67</b>	<b>4.03</b>
Predator: Group Infection (UI)	<b>0.62</b>	<b>0.22</b>	<b>0.36</b>	<b>0.85</b>
Predator: Group Infection (IU)	0.36	0.50	-0.16	0.87
Trial	0.01	0.00	0.00	0.03
Time out of refuge				
Weight	<b>1.45</b>	<b>0.14</b>	<b>1.27</b>	<b>1.60</b>
Predator cue	<b>-0.82</b>	<b>0.25</b>	<b>-1.11</b>	<b>-0.49</b>
Predator: Group Infection (UI)	<b>0.48</b>	<b>0.12</b>	<b>0.30</b>	<b>0.61</b>
Predator: Group Infection (IU)	<b>0.61</b>	<b>0.19</b>	<b>0.36</b>	<b>0.83</b>
Trial	<b>0.54</b>	<b>0.08</b>	<b>0.46</b>	<b>0.63</b>

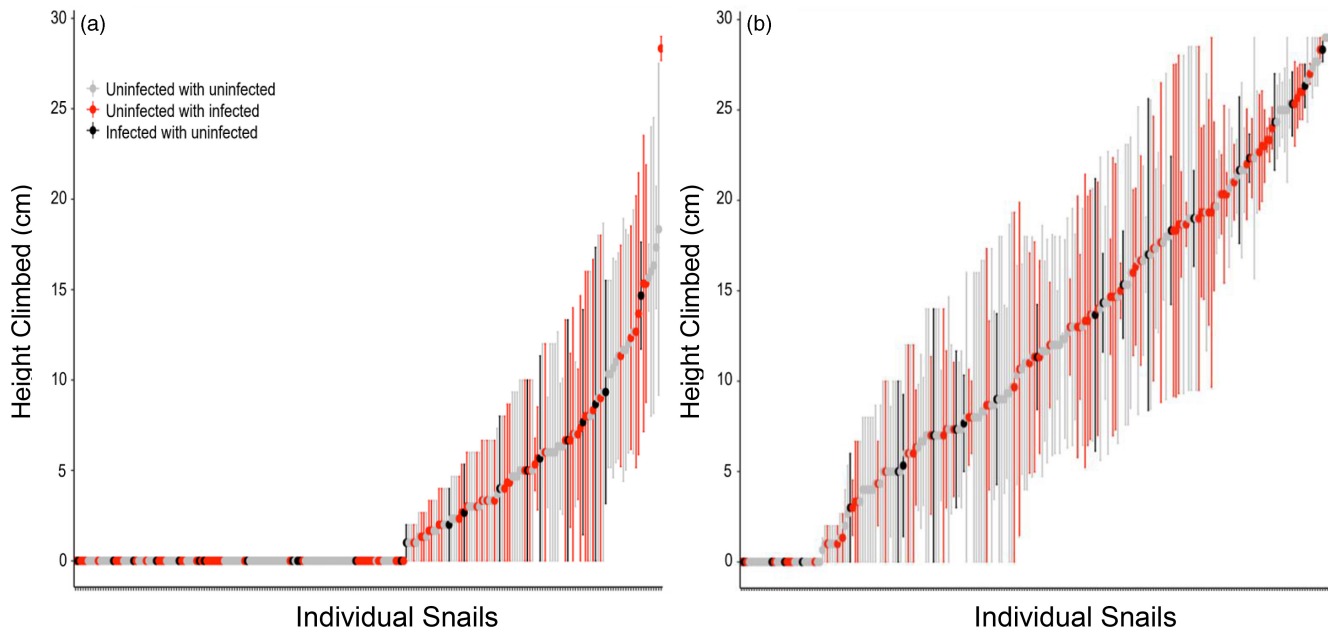


**FIGURE 1** Box plots of (a) height climbed, (b) time out of water and (c) time out of refuge in infected ( $n = 24$ ) and uninfected snails ( $n = 209$ ).

and 0.15 [0.11–0.17] respectively, when all snails were considered (Figure 2a). In the presence of a predator cue, values for height climbed and time out of water doubled to  $R = 0.41$  [0.25–0.50] and 0.33 [0.22–0.34] (Figure 2b). Repeatability for refuge use remained similar at  $R = 0.12$  [0.05–0.16]. Indeed, when groups of snails were analysed separately, repeatability tended to increase as the exposure to potential stressors increased, from (a) predator cue only (UU), to (b) predator cue + infected conspecific (UI), finally to (c) predator cue + individual infection (IU) (Table 2). For height climbed, repeatability varied from  $R = 0.13$  for UU individuals in the absence of a predator cue to  $R = 0.61$  for IU individuals exposed to a predator cue. This pattern was similar for time out of water (UU:  $R = 0.11$ ; IU:  $R = 0.52$ ) and refuge use (UU:  $R = 0.07$ ; IU:  $R = 0.20$ , Table 2).

### 3.2 | Behavioural plasticity and predictability

Individual snails differed substantially in their responses to a changing environment (i.e. their reaction norms) with UI snails showing greater responsiveness (height: SD estimate = 1.28, 95% CI: 0.52–2.10; time out of water: SD estimate = 0.07, 95% CI = 0.01–0.15) to the predator cue, as compared to UU snails (Table S2d; Figure 3). IU snails did not differ from UU snails (height: SD estimate = 0.46, 95% CI: 0.00–0.99; time out of water: SD estimate = 0.13, 95% CI = 0.00–0.17). Moreover, for height climbed, bold snails in the UI group showed higher plasticity than bold snails in the other groups, as evidenced by the negative correlation between behavioural type and behavioural plasticity (intercept–slope covariance:  $r = -0.17$ , 95% CI =  $-0.22$  to  $-0.12$ ). Individuals did not vary in their



**FIGURE 2** Mean  $\pm$  SE of height climbed for all snails in (a) the absence of a predator cue and (b) the presence of a predator cue. Colours indicate snails from each group infection category. Snails were categorized as uninfected grouped with uninfected conspecifics (UU: grey), uninfected grouped with an infected conspecific (UI: red), or infected grouped with uninfected conspecifics (IU: black).

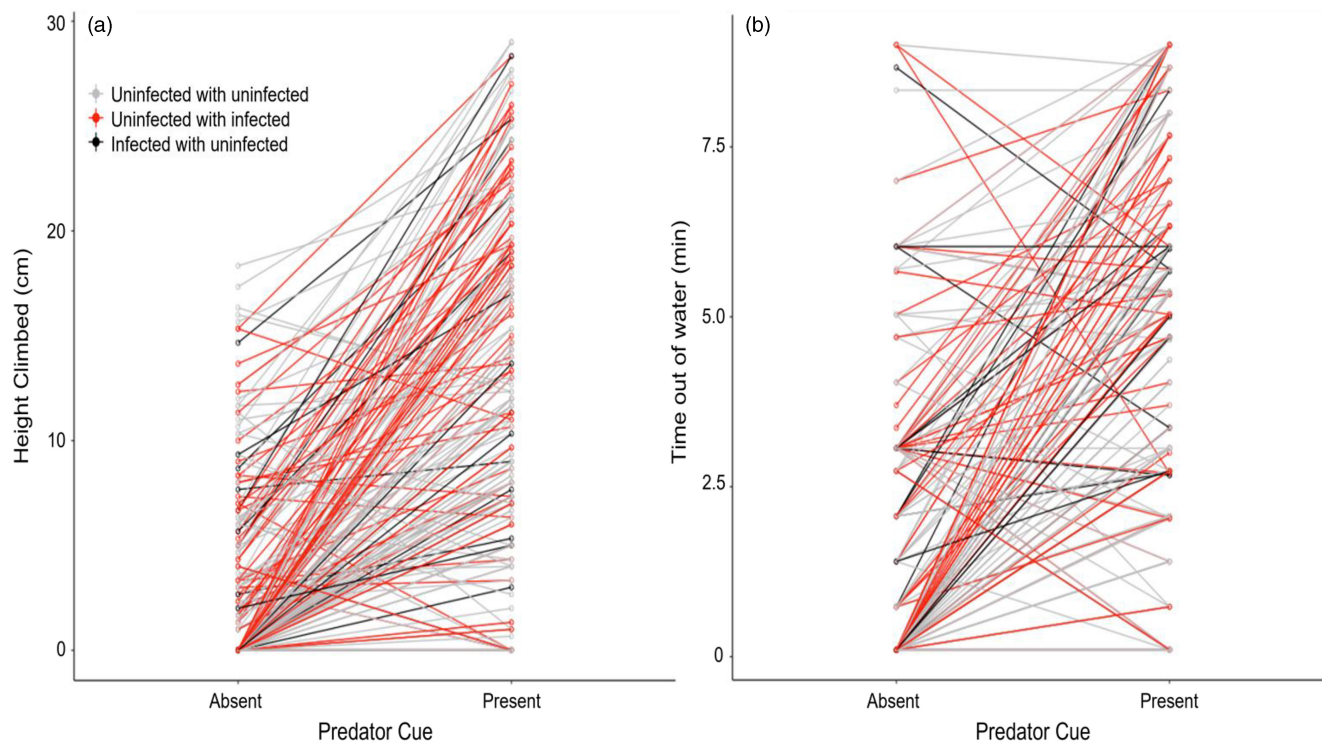
**TABLE 2** Repeatability estimates and 95% credible intervals for snail behaviour in the absence and presence of a predator cue. Snails were analysed separately by group infection status. Differences in individual behavioural expression (i.e. personality) were stronger as the number of stressors increased; infected snails exposed to a predator cue had the highest repeatability.

Traits and group infection status	Repeatability [ $\pm$ 95% CI]	
	Predator Cue absent	Predator Cue present
<b>Climbing height</b>		
UU: uninfected grouped with uninfected conspecifics	0.13 [0.10–0.16]	0.23 [0.20–0.25]
UI: uninfected grouped with an infected conspecific	0.19 [0.17–0.22]	0.38 [0.35–0.43]
IU: infected grouped with uninfected conspecifics	0.12 [0.10–0.14]	0.61 [0.57–0.74]
<b>Time out of water</b>		
UU: uninfected grouped with uninfected conspecifics	0.11 [0.05–0.14]	0.18 [0.13–0.23]
UI: uninfected grouped with an infected conspecific	0.08 [0.07–0.19]	0.28 [0.22–0.35]
IU: infected grouped with uninfected conspecifics	0.19 [0.10–0.34]	0.52 [0.46–0.61]
<b>Time out of refuge</b>		
UU: uninfected grouped with uninfected conspecifics	0.07 [0.01–0.24]	0.19 [0.10–0.28]
UI: uninfected grouped with an infected conspecific	0.12 [0.03–0.19]	0.06 [0.01–0.12]
IU: infected grouped with uninfected conspecifics	0.13 [0.05–0.21]	0.20 [0.15–0.23]

behavioural plasticity with respect to refuge use, as predator cue was not supported as a slope effect in the original models (LR test:  $\chi^2_7 = 4.27, p = 0.12$ ).

Residual variance also differed among individuals (height climbed  $\omega = 1.44$ , 95% CI: 1.31–1.58, time out of water  $\omega = 2.40$ , 95% CI:

2.14–2.65, refuge use:  $\omega = 0.02$ , 95% CI: 0.02–0.03). Behavioural type and predictability were strongly correlated (intercept-slope covariance: height climbed:  $r = 0.72$ , 95% CI = 0.71–0.74, time out of water:  $r = 0.50$ , 95% CI = 0.30–0.70, time out of refuge:  $r = -0.27$ , 95% CI = -0.54 to -0.03) indicating that bold snails (those who climbed



**FIGURE 3** Reaction norms for (a) height climbed and (b) time out of water across a predation cue gradient. Snails were categorized as uninfected grouped with uninfected conspecifics (UU: grey), uninfected grouped with an infected conspecific (UI: red) or infected grouped with uninfected conspecifics (IU: black). UI snails (red) showed greater behavioural plasticity than UU (grey) and IU (black) snails.

less and spent more time in the water) had lower residual variance and were more predictable. Predictability and plasticity were also positively correlated (height climbed:  $r = 0.46$ , 95% CI = 0.36–0.57, time out of water:  $r = 0.35$ , 95% CI = 0.27–0.43) indicating that snails with higher residual variance (i.e. more unpredictable) were more responsive (Table S2d). This pattern was not evident for refuge use since individuals did not vary in their degree of plasticity.

Finally, the among-individual correlations between height climbed–time out of water (intercept–intercept covariance;  $r = 0.65$ , 95% CI = 0.25–0.77), height climbed–time out of refuge (intercept–intercept covariance;  $r = -0.11$ , 95% CI = -0.42 to -0.06) and time out of water–time out of refuge (intercept–intercept covariance;  $r = -0.19$ , 95% CI = -0.44 to -0.09) were all supported, although the correlations with refuge use were weaker. In general, snails that climbed higher spent more time out of the water and less time out of the refuge, displaying characteristics of a shy personality, while the opposite was true for snails displaying a bold personality.

## 4 | DISCUSSION

The effects of parasitism on marsh periwinkle personality reflect a complex interplay between individual infection, infection environment and predation risk. Across all measured behaviours, boldness decreased in the presence of a predator cue, although the magnitude of differences in mean behavioural expression varied as a function of infection status and predation risk, with infected individuals exposed

to a predator cue showing the strongest expression of behavioural types, and highest repeatability estimates. In low-risk environments, behavioural variation among individuals was minimal and was not affected by infection status, reflected in the low repeatability values (Figure 2a). Many individuals did not climb and spent most of their time in the water, potentially to avoid additional costs of emersion. In fact, increased wind speeds associated with greater heights in the canopy can result in higher levels of desiccation and snails have been observed near the substrate despite the higher temperatures, presumably to avoid desiccation (Iacarella & Helmuth, 2012).

However, in high-risk environments, inherent differences among individuals were revealed as among-individual variation increased, and personality differences became more apparent (Figure 2b). Overall, boldness decreased with snails climbing more and spending more time out of the water, although the magnitude varied across individuals. Exposure to predation risk might thus reveal state-dependent personality, where state can include energy reserves, reproductive value, physiology or, in this case, parasite infection (Dingemanse & Wolf, 2010; Houston & McNamara, 1999; Sih et al., 2015; Wolf & Weissing, 2010). When exposed to a predator cue, individual infection status further increased the expression of individual behavioural differences, with the highest repeatability values observed in these trials (height climbed ( $R = 0.61$ ), time out of water ( $R = 0.52$ ) and time out of refuge ( $R = 0.20$ ); Table 2). In other words, parasitism induced greater among-individual variation in average boldness, although the parasite itself does not appear to be altering population-level responses: infected snails showed



no evidence of decreased climbing, or differences in time out of water and refuge use as compared to their uninfected counterparts (Figure 1).

Given that snails are castrated and therefore have zero fitness, it is difficult to posit how personality differences are of adaptive value to the host (Lafferty & Kuris, 2009). The interactive effects of predation risk and parasite infection suggest that personality may be condition dependent, with boldness now varying along a continuum of 'sickness' (Dantzer, 2001). Trematode infection can impart scaling physiological effects ('sickness') based on the intensity of infestation and the characteristics of the specific species, thus leading to variation in the extent of behavioural changes observed (Clausen et al., 2008; Curtis, 1985; Lauckner & Kinne, 1980; Levri & Lively, 1996; McCurdy et al., 2000; Morton, 2018; Wood et al., 2007). In mature trematode infections, larvae extend throughout the visceral mass of the individual, potentially causing tissue destruction (Fretter & Graham, 1963; Lauckner & Kinne, 1980; Smyth & Halton, 1983). Thus, the degree of infection, and extent of tissue destruction, may be drivers behind the observed variation in boldness. Previous studies on the same population found that on average, infected *L. irrorata* were less likely to climb and feed (Morton, 2018; Morton & Silliman, 2020), which might again reflect differences in 'sickness'. Similarly, Seaman and Briffa (2015) found that infected *Littorina littorea* had a higher repeatability of operculum re-opening time, and thus greater variation in behavioural type, when compared to uninfected conspecifics ( $R = 0.50$  and  $0.35$  respectively), although this difference was not statistically significant. This suggests that parasitic infection alone is not a driver of behavioural diversification but that, as seen here, the additive effects of stressors may lead to enhanced expression of personality. This is further supported by the observation that, in uninfected individuals, repeatability in the high-risk environment increased when an infected conspecific was present. While these snails would not experience a continuum of sickness, the exposure to multiple stressors may nonetheless reveal other condition-dependent trade-offs which influence personality in this species.

Individuals also showed substantial variation in behavioural plasticity in response to a predation cue, with the magnitude of this plasticity strongly influenced by group infection. We found that uninfected individuals grouped with an infected individual (UI) were the most responsive to predation risk, exhibiting increased climbing behaviour and spending less time in the water as compared to UU or IU snails (Figure 3). Here, parasites are interacting with the host population by influencing the behaviour of uninfected conspecifics, likely by inducing avoidance behaviours (Buck et al., 2018). Moreover, within the UI snails, bold individuals showed the highest degree of plasticity, suggesting that their propensity to stay in the water and not climb was strongly overridden by the presence of an infected conspecific. Indeed, Kortet et al. (2010) predicted that high risks of predation and parasitism would favour low levels of boldness when animals have little means to compensate for the high costs of predation and parasitism. Apart from climbing behaviour, *L. irrorata* have limited mechanisms to protect themselves from predation and

even fewer mechanisms to resist parasite infection. Therefore, increased responsiveness in the face of multiple stressors may be the optimal strategy for avoiding predation and infection.

Gathering the information needed to avoid infected conspecifics is achieved through visual, chemical and mechanosensory cues, which are then used to inform behavioural decisions (Behringer et al., 2018). For example, one of the first visually based parasite avoidance behaviours was described in three-spined sticklebacks, in which uninfected individuals avoid shoaling with infected conspecifics based on their display of abnormal behaviour (Dugatkin et al., 1994), which leads to spatial differences in parasitized versus unparasitized individuals (Barber et al., 1998). In trematode-infected rainbow trout, chemical alarm substances are released that alert healthy conspecifics nearby, resulting in increased activity of uninfected conspecifics (Poulin et al., 1999). *L. irrorata* have the ability to detect and respond to crushed conspecifics (Duval et al., 1994), and to the chemical cues of predators present in air, water and mucus (Carroll et al., 2018; Dix & Hamilton, 1993; Duval et al., 1994). *L. irrorata* also possess the ability to detect cues from the mucus trails produced by conspecifics (Ng et al., 2013); therefore it is possible that they utilize them as a source of information about the presence of parasitized conspecifics. Indeed, other species of *Littorina* can detect trematode cercariae in the mucus trails of conspecifics and avoid associating with those infected individuals (Davies & Knowles, 2001).

Avoiding parasites does come with trade-offs such as energy and time allocations, although the net effect on host fitness must be positive, or else these behaviours would not be maintained (Buck et al., 2018). Moreover, behaviours that protect against parasites impose other costs, so may only be expected to evolve when parasites pose a threat that outweighs the costs of the behaviour (Lafferty, 1992). Infected periwinkles cannot directly infect other periwinkles [although it might be possible that in another species, *L. littorea*, cercariae can re-infect the snail from which they emerged as well as other snails; M.S Davies (pers. obs.) in Davies & Knowles, 2001]; avoidance might then result from a change in predation risk. The mucus trail of infected snails may contain pheromones from the parasite or chemical products resulting from the destruction of snail tissue by the parasite. When these substances are dissolved in seawater, they may be detectable by predators and thus attract them. If uninfected snails can also detect these substances through mucus trails, they may avoid aggregating with infected conspecifics to decrease the possibility of encountering a predator (Davies & Knowles, 2001).

Uninfected snails surrounded by uninfected conspecifics (UU) showed the lowest responsiveness to predation risk. In certain cases, the benefits of boldness in high-risk conditions override the predation costs of exposure and result in higher feeding and developmental rates overall (Sih et al., 2003). Risk-taking behaviour here might thus be mediated by the life-history trade-off between growth and mortality (Biro & Stamps, 2008; Mangel & Stamps, 2001; Wolf & Weissing, 2012), where boldness leads to increased foraging rates but increased mortality as a result of predation (Biro et al., 2006; Toscano & Griffen, 2014). For example,

in three-spined stickleback, resumption of foraging after a simulated predator attack is positively related to growth rate (Ward et al., 2004), and in *L. irrorata* from Virginia, bolder individuals have higher resting metabolic rates and faster growth (Cornwell et al., 2020). Infected snails also displayed lower levels of responsiveness to predation risk which, while no longer benefitting the host, might still benefit the parasite. By remaining in the water, *L. irrorata* would be more susceptible to predation, accelerating cercarial release and reducing the energy required by the parasite to leave the snail, assuming cercariae can survive the process (Davies & Knowles, 2001). Previous work has found that trematode infection leads to differences in predator avoidance behaviours between infected and uninfected gastropods, potentially as a result of impaired predation detection abilities or host manipulation (Belgrad & Smith, 2014; Bernot, 2003; Kamiya & Poulin, 2012; Morton & Silliman, 2020). Even if predation does not enhance cercarial release, transmission to the second host must occur via cercarial shedding in the water (Bernot, 2003; Esch et al., 2002), as the second host is often a crustacean or fish.

Predictability showed little relationship to infection status and, overall, bold snails tended to be more predictable. Predictable individuals have little residual variance around their behavioural type and reaction norm slope (Hertel et al., 2020). Unpredictable individuals, on the other hand, are characterized by high variability around their average behavioural type and reaction norm slope. Predictability and plasticity were also positively correlated in all individuals regardless of infection status, pointing to domain generality, whereby certain individuals are more responsive, in general, than others (DeWitt et al., 1998; Sih et al., 2012; Sih & Del Giudice, 2012). Individual differences in predictability are thought to be driven by individual differences in state variables, for example, metabolism (Biro et al., 2018). Indeed, resting metabolic rate (RMR) is a major component of 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). It is surprising then that parasite infection, which has the potential to significantly impact host energy reserves, appears to have little effect on behavioural predictability.

Our results highlight important differences between population- and individual-level patterns and underscore the need for studies measuring individual behaviour over time and across environments (Hertel et al., 2020; Mitchell et al., 2021; Stamps & Groothuis, 2010). If differences in responsiveness are domain-general and inherent to individuals regardless of infection status, then we would expect to see differences in personality maintained across contexts. In other words, the bold-shy continuum would exist independent of infection status. It is possible then, that boldness can arise via multiple state-dependent mechanisms: in uninfected individuals via the cost-benefits of enhanced foraging and in infected individuals as a result of host manipulation, leading to a far more nuanced view of behaviour.

Parasites can affect host populations in a variety of ways, for example by modifying the behaviours of the infected hosts,

or by inducing avoidance behaviours in uninfected conspecifics. Moreover, the magnitude and scope of these effects vary across environments. Here we show that, in agreement with previous work, *L. irrorata* exhibit individual variation in boldness, a key axis of animal personality (Cornwell et al., 2019; Salerno & Kamel, 2023), although the magnitude of expression is amplified by the presence of parasitized conspecifics and predator cues. Parasites and predators can thus affect the costs and benefits of important personality traits (Kortet et al., 2010). Southeastern salt marshes are strongly influenced by the relationships between grazers like *L. irrorata*, and predators like *C. sapidus* (Silliman & Bertness, 2002; Silliman & Zieman, 2001). Recent work has illuminated the central role that *C. sapidus* plays in regulating the densities of *L. irrorata* which indirectly alleviates *Sporobolus* from potentially detrimental grazing pressures (Silliman & Bertness, 2002; Silliman & Zieman, 2001). Herbivory has been demonstrated to be powerful enough to quickly reduce thriving marshes to bare mud flats and predators of *L. irrorata* are essential to prevent overgrazing (Silliman & Zieman, 2001). If boldness decreases as a function of parasite prevalence, and snails consistently climb higher and spend more time out of the water, then predation rates might decrease and substantially alter grazing rates. Given the ubiquitous distribution of parasites and their modulating effect on such trophic interactions, trematode infection may act as an important, although underappreciated, determinant of salt marsh structure and function.

#### AUTHOR CONTRIBUTIONS

Christina M. Salerno and Stephanie J. Kamel conceived the ideas, designed the methodology, analysed the data and led the writing of the manuscript. Christina M. Salerno collected the data. All authors contributed critically to the drafts and gave final approval for publication.

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#### CONFLICT OF INTEREST STATEMENT

None.

#### DATA AVAILABILITY STATEMENT

The data are available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.18931zd24> (Salerno et al., 2023).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Table S1:** Generalized linear mixed models on the effect of morphological variables on measured behaviours (climbing height, time out of water, time out of refuge).

**Table S2:** Multivariate double hierarchical mixed model to quantify the among- and within-individual covariances between climbing height, time out of water and refuge use, containing random intercept and slope effects with respect to context (predation and parasitism) and trial.

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