

Social decision-making in a freshwater gastropod

Denis Meuthen^{*1,2}, Dustin Raeke², Jannis Bednarzik², Mauricio Bravo Soldevilla²,
Niclas Kuper^{1,3} & Melanie Dammhahn^{1,4}

¹Joint Institute for Individualisation in a Changing Environment (JICE), University of Münster and
Bielefeld University, Münster and Bielefeld, Germany

²Evolutionary Biology, Bielefeld University, Konsequenz 45, D-33615 Bielefeld, Germany

³Department of Psychology, University of Münster, Fliegerstr. 21, D-48149 Münster, Germany

⁴Institute for Neurobiology and Behavioural Biology, University of Münster, Badestraße 9, D-48149
Münster, Münster, Germany

AUTHOR CONTRIBUTIONS (CRediT Taxonomy):

Denis Meuthen: Conceptualization, Data Curation, Formal Analysis, Funding acquisition, Investigation,
Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization,
Writing – original draft, Writing – review & editing.

Dustin Raeke: Investigation.

Jannis Bednarzik: Investigation.

Mauricio Bravo Soldevilla: Investigation.

Niclas Kuper: Writing – review & editing.

Melanie Dammhahn: Writing – review & editing.

FUNDING: This work was supported by a Freigeist Fellowship of the VolkswagenStiftung to Denis
Meuthen.

DATA AVAILABILITY STATEMENT: Data and R code is available at <https://uni-bielefeld.sciebo.de/s/36WamX8qQnozxs> and will be submitted to a permanent repository (e.g. Dryad/Zenodo) after acceptance of the manuscript.

CONFLICT OF INTEREST: We have no conflict of interest to declare.

^{*}Corresponding author: Denis Meuthen, denis.meuthen@uni-bielefeld.de, Evolutionary Biology,
Bielefeld University, Konsequenz 45, D-33615 Bielefeld, Germany. Tel.: ++49 521 106 28 20. Fax: ++49
521 106 64 26

Abstract

Animals are hypothesized to plastically adjust their social behaviour expression dependent on their environment and their phenotype to ensure that its benefits outweigh its costs. There is a strong research bias towards socially complex vertebrates and eusocial insects. Thus, here we study mollusks, a taxon whose social behaviour is less well studied. As predation is one of the strongest drivers of sociality, we study antipredator plasticity in the freshwater gastropod *Physella acuta*. Using a split-clutch design, we raised individuals from birth onwards until adulthood under either perceived high or low (control) predation risk conditions. In a first experiment, we investigated differences in social association preferences with conspecific groups whereas in a second experiment we studied interindividual interactions within groups. In line with expected antipredator benefits of collective defences, snails raised in high-risk conditions displayed greater social preferences and engaged in more interindividual interactions (sociability) than controls. In snails raised under high-risk, thick-shelled individuals (i.e., individually defended snails) showed lower social preferences, suggesting that for them, the costs associated with sociality outweigh fitness benefits of collective defences. Counterintuitively, the opposite pattern emerged in low-risk snails. However, larger studies show that even when raised under low-risk conditions, thick-shelled individuals are generally larger. This makes them better competitors, which favours maximization of resource-related benefits from joining conspecifics. Lastly, snails raised in high-risk conditions displayed lower competitiveness towards conspecifics, likely to reduce conspicuousness to predators. Altogether, even in a gastropod species, social behaviour expression is plastically adjusted to both developmental environments and individual phenotypes.

Introduction

Sociobiology, the systematic study of the biological basis of all social behaviour, has been a steadily growing field due to the ubiquity of social life across taxa (Traniello et al., 2026; Traniello and Bakker, 2026). This research has given us a wealth of knowledge on explaining why animals do not always maximize sociality. This is because sociality confers both costs and benefits. Costs of social behaviour include increased competition over resources and mates alongside increased risk of disease transmission whereas benefits of social behaviour include, but are not limited to, indirect fitness benefits, increased access to information which can translate into increased foraging efficiency, and increased protection from predation (Krause and Ruxton, 2002; Ward and Webster, 2016). As costs and benefits from sociality vary dependent on both the environment and individual phenotype, both social behaviour expression as well as the underlying mechanisms have evolved to be phenotypically plastic (Cardoso et al., 2015; Froemke and Young, 2021; Oliveira, 2012, 2009). Like other instances of behavioural plasticity, this manifests either as developmental and/or contextual plasticity (Stamps, 2015). For plasticity in social behaviour to be adaptive, the fitness benefits of social interactions need to outweigh its costs. At the same time, both benefits and costs of social behaviours are a function of the available information about both the own phenotype and the environment. For example, social animals are known to base social preference and avoidance on both their individual immune-related physiology such as the level of cytokines (Dantzer et al., 1996) as well as on the level of disease in a social group (Kavaliers and Choleris, 2018). Unfortunately, our knowledge on the ubiquity of the factors that modulate social plasticity is limited due to a bias in empirical research in this field towards taxa known to be socially complex such as vertebrates and eusocial insects (Dochtermann et al., 2026; Rosenthal et al., 2017). However, to achieve generalization of hypotheses relating to social behaviour,

we require more research on so far neglected animal taxa (e.g., Aquiloni and Tricarico, 2015) alongside the further development of methods that allow for comparing social behaviour across taxa, which is challenging due to the difficulty of operationalizing social behaviours similarly across species (Kuper et al., 2025). A powerful solution to this challenge may be the use of the interpersonal circumplex, an organizational framework derived from human psychology (Zeigler-Hill and Highfill, 2017). This framework was originally developed with the goal of decoding interpersonal events, which are human interindividual dyadic interactions that have social and emotional consequences for both participants. Based on the three facets directionality, object and resource, this framework conceptualizes and empirically cross-validates eight interpersonal variables that are intercorrelated with each other in a way that forms a perfect equally spaced circumplex containing a vertical dominance axis and a horizontal warmth axis (Wiggins, 1979). Essentially, any meaningful interindividual social behaviour is believed to be representable as a vector originating from the centre of this circumplex. Here, we aim to operationalize animal social behaviour alongside the sociability and competitiveness axes of the circumplex, which are rotated by 45° compared to the major axes and can be directly linked to fitness consequences in non-human animals. Furthermore, here we aim to study and operationalize social behaviour and its plasticity in an understudied diverse phylum, the mollusks (Rosenberg, 2014), as research on mollusk social behaviour is believed to “reveal great surprises” (Aquiloni and Tricarico, 2015).

To this end, the antipredator context appears promising as predator-related fitness benefits are considered to be one of the main benefits of sociality (Krause and Ruxton, 2002) and predation is one of the most common and widespread explanations for group living across taxa (e.g., Rieucau et al., 2015). Antipredator plasticity is also among the most convincing and best-studied instances of adaptive phenotypic

plasticity (Hoverman, 2010). Defences against predation can be collective (i.e., social), e.g. the many-eyes effect where group size is correlated with predator detection and avoidance probability due to increased vigilance (Treherne and Foster, 1980), the dilution effect where the probability to be attacked by predators is lower with larger group sizes (Wrona and Dixon, 1991), and the confusion effect where predators increasingly struggle with singling out individual prey with increasing group size (Krakauer, 1995; Neill and Cullen, 1974). Defences can also be individual-based such as predator-induced morphological defences which arise during development and effectively increase individual survival in the presence of predators (Hoverman, 2010). Shifting between individual-based and collective defences drives predator-prey dynamics (de la Cruz Barron et al., 2023). Furthermore, both defence types are developmentally plastic and individuals raised under high predation risk become more social in risky situations (Meuthen et al., 2016, but see Meuthen et al., 2019) and develop greater morphological defences in adulthood (Tollrian and Harvell, 1999). Thus, the antipredator context appears to be well-suited to test the overarching hypothesis that social behaviour is affected by both developmental environments and individual phenotypes.

As study system, we use *Physella acuta*, a member of the by far largest mollusk group, the gastropods (Lydeard and Lindberg, 2003). This ~1 cm large invasive species with global distribution (Vinarski, 2017) is well-established in the research of individual-based antipredator responses. When predation risk is perceived to be high, individuals crawl out of the water to reach a safe refuge (Meuthen, 2025; Meuthen and Mutingwende, 2025). In the longer term, risk-exposed individuals also develop morphological defences such as a thicker shell which increases predator handling times and thereby benefits survival (Auld and Relyea, 2011; DeWitt, 1998; Meuthen and Reinhold, 2023; Meuthen and Mutingwende, 2025). Here, in split-clutch

experiments, we raise individual *P. acuta* under either high or low perceived predation risk as communicated by exposure to conspecific alarm cues or a water control treatment. Then, we assess both their phenotype and social behaviour in adulthood within two different experiments. In the first experiment, we measure social association preferences with groups of conspecifics whereas in the second experiment, we investigate interindividual social interactions within groups to operationalize social behaviour along the sociability and competitiveness axes of the interpersonal circumplex.

First, in line with previous research across taxa and in *P. acuta* in specific, we expect individuals raised in high-risk conditions to plastically develop greater individual-based (i.e., thicker shells) and collective antipredator defences (i.e., greater association with conspecifics) than low-risk conspecifics. Second, because the presence of individual-based defences may reduce the benefits of collective defences, in high-risk individuals where defences confer fitness benefits, we expect better-defended individuals to plastically develop lower social preferences than less-defended ones. Third, due to the fitness benefits of being social (see above) and the costs of oddity (Landeau and Terborgh, 1986) in a risky environment, we expect high-risk individuals to have developed greater sociability (which increases the benefits of grouping) and lower competitiveness (which frequently decreases oddity and therefore predation risk across taxa) than low-risk ones.

Material and Methods

Experiment 1

The first experiment ran from January to April 2025. We used an outbred lab population at Bielefeld University that was generated from 10 wild populations collected across

Europe (more details on the population in Meuthen, 2025) and since then kept in 10 replicate tanks within the lab. For breeding, we isolated 50 adult snails (5 snails per replicate tank, mean $\pm$ SD shell height: 7.49 ± 0.74 mm, shell width: 4.31 ± 0.46 mm, weight: 0.050 ± 0.012 g) within 60 x 45 x 50mm tanks (Boite LAB 1, Multiroir, Périgny-sur-Yerres, France) containing 50 ml of remineralized osmosis water (SaltyShrimp ShrimpMineral GH/KH+, Garnelenhaus, Barsbüttel, Germany; target conductivity: 500 ± 10 μ S) and a 2 x 2 cm piece of polystyrene for egg deposition. Snails were kept at 25 ± 1 °C, and illuminated with daylight LED strips (LFL-40W2-004, Bioledex, Augsburg, Germany; dimmed to 25% of output) positioned 27 cm above the waterline provided light in a 12:12 cycle (from 0800 am to 0800 pm). Every day, we changed 100% of the water and provided each snail with 0.027 ± 0.004 g (mean $\pm$ SD) crushed algae tabs (Spirulina Tabs Nature, sera, Heinsberg) and 0.044 ± 0.006 g crushed sepia shells. The breeding period concluded at the fifth day; infertile clutches were removed. One day prior to hatching, we split each clutch in two equally sized halves and moved each half into a new tank containing only 50 ml of remineralized water and 0.044 ± 0.006 g crushed sepia shells; temperature and light conditions remained the same. After hatching, each of the two tanks was then assigned to either a high-risk condition (i.e., with conspecific alarm cues), or a low-risk condition (i.e., a water control); details on alarm cue production are given in the following paragraph. Three times per week, with at least one intermission day, we changed 100% of the water, added an age-adjusted amount of food (0-6 days of age: 0.003 ± 0.002 g; 7-14 days of age: 0.007 ± 0.001 g; 14-20 days of age: 0.027 ± 0.004 g; 21-28 days of age: 0.072 ± 0.008 g), 0.044 ± 0.006 g sepia shells, and 12.5 μ l of their assigned treatment. Given that the *P. acuta* alarm cue induces antipredator responses for 41 h before degrading (Turner & Montgomery, 2003), our high-risk condition ensured exposure to alarm cues on 6 days per week, which is an established level of high-risk across earlier studies (Auld & Relyea, 2011,

Auld & Relyea, 2010b, Meuthen & Reinhold, 2023). To avoid density effects on growth and morphology (Beaty et al., 2016, Goepfner et al., 2020), we separated individuals into groups of six at 28 days age. At 54-55 days age, we placed ID tags on each individual. To this end, we removed individuals from their home tank, blotted them dry, and then glued a bee number tag (model FC075, Ickowicz Apiculture, Bollene, France) on each shell using cyanoacrylate (UHU Sekundenkleber, UHU GmbH, Germany). Snails were returned to their tanks only after the glue has dried. These tags have a low tag-loss rate and do not impact life history in *P. acuta* (Henry and Jarne, 2007). In total, we raised 124 individuals from nine different families and 28 tanks (54 high-risk and 70 low-risk individuals) and used them to run social trials in which animals could choose to associate with either a tank containing conspecifics or an empty tank (details see below) at 69-89 days age.

Alarm cues used in this study were shared with a larger batch prepared for a different study, and thus were derived from 395 adult donor individuals of the same population (mean $\pm$ SD shell height 10.34 ± 0.74 mm, shell width 5.47 ± 0.37 mm, weight 0.119 ± 0.023 g), which were crushed using a glass mortar and pestle and filtered through filter floss. The resulting extract was diluted to a total volume of 395 ml of water and stored at -20°C , which retains alarm cue efficacy (Meuthen and Mutingwende, 2025). Water controls were prepared and stored the same way. During application of treatments, we added 12.5 μl of the respective thawed treatment. For the alarm cue treatment, this corresponds to a final concentration of 1 snail/4L water, which is established to induce behavioural and morphological plasticity in our model system (Meuthen, 2025; Meuthen and Reinhold, 2023; Taniel et al., 2020).

Trials were conducted within 20 x 30 x 20 cm tanks filled with 3.4 L of water. On each short side of the tank, we placed 46 mm x 62 mm x 52 mm (LxWxH) cages

whose sides (except for the bottom) were – outside of 8 mm acrylic borders on each side - covered with ultrafine stainless steel gauze mesh that was impermeable for snails but permeable to odors; preliminary dye tests showcased that odors can freely spread from these cages into the middle of the trial tank within 1 min. As the cages were located on opposite ends of the tank, the half of the tank that each cage was positioned in was determined to be its respective association zone.

To start a trial, we first selected three full-sibling individuals that were unrelated to the focal animal but received the same treatment during development and placed them into one cage, the other one was left empty. After placing these cages inside the experimental tank, we used a featherweight forceps to place the focal animal in the centre of the tank. Afterwards, for 30 min, we recorded the focal animal's position from above at 1920 x 1080 pixel resolution using a camera (C922 Pro HD Stream, Logitech, China). After the trial concluded, all animals were returned to their home tanks. All focal animals were tested twice at subsequent days with the position of the cages reversed (i.e., stimulus snails were now located on the opposite side of the tank) and with different stimulus animals. The day after their second trial, we assessed the phenotype of focal animals by removing them from the tank, and blotting them dry. Afterwards, we assessed shell length, shell width, and shell thickness (three times: at the top, at the centre and at the bottom of the aperture) with a digital caliper (Model ABS-AOS 500-181-30, Mitutoyo, Kawasaki, Japan) and finally weighed them, including the shell, to an accuracy of 0.1 mg on a digital scale (Quintix 124-1S, Sartorius, Göttingen, Germany). Individuals whose shell was damaged by this procedure were excluded from further trials whereas those with intact shells were still used as stimulus animals. Stimulus animals were also never used more than once per day in each trial, and no animal was used more than 9 times as stimulus. Between trials, we washed tanks, cages and forceps with 3% hydrogen peroxide to remove residual odours and then

carefully rinsed them with fresh water before re-using them. In total, we completed 216 trials (108 high-risk testing 54 individuals, 108 low-risk trials testing 54 individuals). In five trials, air bubbles were trapped inside the stimulus cage, causing it to float away from its original position during the trial. In one trial, a technical issue interrupted video-recording. Individual snails may display strong tank side preferences independent of stimulus position and statistically controlling for this fact is not possible in the absence of an experiment where the side with the stimulus is swapped for the same snail. Thus, we had to remove not only these trials but also the respective first/second trial of the same individuals from our dataset. Thus, our final dataset consisted of 202 trials (102 high-risk trials on 51 individuals and 100 low-risk trials on 50 individuals).

We estimated social preferences by assessing the time that the focal individual spent in the association zone of the cage containing stimulus snails (i.e., the half of the tank that the cage was located in). To be noted as being within a specific association zone, each individual had to have more than 50% of its body within that zone. As established in mate choice trials across taxa, we measured association times only after each individual entered both association zones and then re-entered another association zone (which ensures that the individual had the opportunity to inspect both stimulus cages). This did not happen in nine trials (five high-risk trials and four low-risk trials, i.e., 4.5% of all trials), which were thus excluded from analysis. Hence, our final sample size consisted of 193 trials (97 high-risk trials on 51 individuals and 96 low-risk trials on 50 individuals). As a measure of individual defence, for each focal individual, also we calculated an average shell thickness value from the three shell thickness measurements obtained across the aperture.

Experiment 2

263 The second experiment ran from April to July 2025. In this study, we used a lab
264 population at Bielefeld University derived from 50 individuals collected from a natural
265 lake in Bielefeld (52°03'11.5"N 8°33'28.6"E) in 2020 and since then kept in the lab
266 within 20 x 30 x 20 cm tanks. We randomly selected 120 snails (mean $\pm$ SD shell
267 height: 6.40 ± 1.04 mm, shell width: 3.69 ± 0.56 mm, weight: 0.04 ± 0.017 g) from this
268 population and set them up for breeding within plastic cylinders ($\varnothing$ 5 cm, 10 cm high)
269 that contained 50 ml of water, a $2 \times 2 \times 1$ cm polystyrene rectangle to aid egg deposition
270 and were closed with air-permeable foam stoppers. These tanks were kept at $25 \pm 1^\circ\text{C}$
271 under a 12:12 hour light/dark cycle. Every day, we removed deposited eggs, performed
272 a full water change, and added 0.024 ± 0.008 g (mean $\pm$ SE, $n=10$) crushed cuttlefish
273 shells alongside 0.013 ± 0.004 g crushed algae tabs (Spirulina Tabs Nature, sera,
274 Heinsberg, Germany). Breeding concluded after five days, and collected clutches were
275 individually transferred to $\varnothing$ 3.5 cm, 1.8 cm high petri dishes containing 4 ml water.
276 Immediately after hatching, offspring were, in groups of up to 6 individuals transferred
277 into new containers as before. After assigning containers randomly to the two treatment
278 groups, treatments, water change and feeding schedules were the same as in the first
279 experiment. All containers were kept at 21°C within temperature-controlled incubators
280 (KB E4, Binder, Germany) that were illuminated by LED light bars 5.2 cm above snail
281 tanks (LED Light Bars with Control Unit, Binder, Germany). At two months age, to allow
282 us to differentiate between individuals, snails were blotted dry and tagged using six
283 different colors of nail polish, which is an established method that does not impact life
284 history in our model system (Henry and Jarne, 2007). The social behavior of individuals
285 was sampled after adulthood was reached, at 49-77 days age. In total, we raised 56
286 individuals (26 high-risk and 30 low-risk) from 17 different families, raised in 27 different
287 tanks.

As we did not have remaining alarm cues from the same batch used in the first experiment, we generated an additional batch of alarm cues specifically for this study. To this end, we sacrificed 10 additional donor individuals of the same population (mean $\pm$ SD shell height 7.71 ± 1.11 mm, shell width 4.56 ± 0.50 mm, weight 0.061 ± 0.022 g). Alarm cues and water controls were prepared, handled, stored and applied in the same way as described in Experiment 1.

Concurrently, we also prepared snail groups to be used as stimuli during social trials. These were directly taken from the stock tanks of the same lab population that we obtained parental individuals from. We randomly selected 64 adult snails (mean $\pm$ SD shell height: 5.91 ± 0.44 mm, shell width: 3.04 ± 0.27 mm, weight: 0.04 ± 0.01 g) from these tanks and then formed eight groups of eight snails each within plastic tanks ($15.2 \times 10 \times 8.5$ cm) containing 500 ml of water. These tanks were housed under the same conditions as the experimental individuals. Every week, we provided 0.013 ± 0.004 g crushed algae tabs and 0.024 ± 0.008 g cuttlefish shell as food. These stimulus snails were always assigned to be used as stimuli for a fixed treatment group (either high-risk or low-risk) to avoid them communicating a different level of risk to focal individuals during trials.

Social trials were run in $15.2 \times 10 \times 8.5$ cm plastic tanks containing 150 ml of water at $25 \pm 1^\circ\text{C}$. Containers containing focal and stimulus animals were acclimated to this temperature for at least 30 min before trials were started. To start a trial, we introduced first one of the groups containing eight stimulus individuals, and thereafter two randomly selected focal individuals that were unrelated to each other but from the same risk treatment. Afterwards, snail social behavior was recorded for 30 minutes using an overhead camera at 1920×1080 pixel resolution using a camera (C922 Pro HD Stream, Logitech, China). After the trial, snails were returned to their respective

tanks and on the following day, focal snails were re-tested in the same way using a different focal partner and a different stimulus snail group. Immediately after finishing its second trial, we phenotyped every focal snail the same way as described for Experiment 1. Stimulus snails always got at least one day intermission for recovery after being used as stimuli for two days in a row. Between trials, we washed tanks and forceps with 3% hydrogen peroxide to remove residual odours and then carefully rinsed them with fresh water before re-using them. In total, we completed 63 trials with 10 snails each to repeatedly assess the social behaviour of 56 individuals (26 high-risk and 30 low-risk).

Video records were used to classify social interactions as instances where individuals display either sociability and/or competitiveness. We define sociability as the number of social interactions where two snails come into physical contact with each other, with the end being defined as both individuals being farther than one focal body size apart. This is in accordance with previous research which has determined that the active space of gastropods is roughly equivalent to the snail diameter (Simpson et al., 1973). If a focal snail concurrently encountered two or more other snails that were next to each other, we recorded this as a single social interaction that terminated when the focal snail reached the specified distance from the outermost stimulus snail. Competitiveness was assessed by calculating the proportion of competitive interactions of all social interactions. A competitive interaction was defined as the act of one snail mounting another snail, i.e., where the mounting snail's foot is only in contact with the other snail's shell and no other surface. This is because competitive individuals mount subordinate ones across diverse animal taxa to exert dominance (e.g., Huang et al., 2017). Second, in gastropods, mounting occurs in the context of reproduction (Koene and Ter Maat, 2007). In simultaneous hermaphrodites such as *P. acuta*, each individual can assume both male and female functions during

reproduction. As the male function is less resource-limited, assuming it benefits individual fitness, which is why conspecifics actively compete over assuming this function. Individuals actively mounting a conspecific are assuming the male function and at the same time, the mounting act defends against intrasexual competition over the male function by other individuals (Koene and Ter Maat, 2007).

To reliably estimate whether sociability (i.e., count data) and competitiveness (i.e., proportion data) are repeatable, or in other words, show personality (sensu Réale et al., 2026), we require substantial sample sizes (Stoffel et al., 2017). Thus, we repeated the same social trials for an additional 74 times using 37 different individual snails. These additional snails for repeatability testing were siblings from the same families with similar age during testing but did not receive the same pre-treatment as described above. This generated a larger dataset containing 186 trials from 93 animals that were each tested twice solely for repeatability testing.

Statistical analysis

Experiment 1

Data was analysed with R 4.6.0 (R Core Team, 2026) using a Bayesian approach with BRMS v. 2.23.0 (Bürkner, 2017). As the dependent variable, we entered the proportion of time that the focal snail associated with the stimulus side of the tank (e.g., the side containing the caged conspecific group) relative to the remaining total experimental time (i.e., after both association areas were visited). As fixed effects, we entered focal treatment (high-risk/low-risk), focal average shell thickness (as individual defence expression), focal body mass (in our model system, individual defence expression is relative to body mass, see Meuthen and Mutingwende, 2025) and focal

363 tank snail density (as rearing density affects social development across taxa, see e.g.,
364 Hesse et al. 2015) as well as a focal treatment $\times$ focal average shell thickness
365 interaction. We also entered two crossed random effect structures: first to control for
366 variation in stimulus attractiveness, we included stimulus individual ID nested in
367 stimulus family ID as a random intercept. Second, to control for variation in focal
368 behaviour, we entered trial order as random slope alongside focal ID nested in focal
369 tank ID nested in focal family ID as random intercepts. As appropriate preliminary data
370 for this study is absent, we first attempted to run this model with default improper flat
371 priors, i.e. uniform distributions over the declared bounds of the parameters. However,
372 these attempts did not lead to successful model convergence. Follow-up attempts to
373 simplify the model to allow convergence massively inflated the effective number of
374 parameters (p_{loo}), hence we fit weakly informative priors on random effects while
375 retaining improper flat priors for the fixed effects. Following common practice in
376 Bayesian modelling, we fit normal distributions with a mean of zero and a standard
377 deviation of one for most random effects to provide weakly informative regularization
378 which aims to avoid extreme estimates and overfitting. The only exception was the
379 focal ID nested in focal tank ID nested in focal family ID random intercept. Here, while
380 retaining the same mean value, we increased prior standard deviation to six to account
381 for the higher complexity and variability of this random effect and additionally fit a
382 weakly informative Lewandowski-Kurowicka-Joe correlation prior containing a shape
383 parameter of 1. Sampling from the posterior distribution was done using Hamiltonian
384 Monte Carlo, with four Markov chains each run for 25,000 warmup iterations and
385 25,000 sampling iterations. We first ran these models with different appropriate families
386 (binomial, zero-inflated binomial and zero-inflated beta-binomial) and used leave one-
387 out cross-validation to determine the respective model that fit the data best. The
388 appropriateness of the best fitting model was further verified using predictive posterior

checks, autocorrelation checks, the Gelman-Rubin Diagnostic ($R_{\text{hat}} = 1$) and an effective sample size check ($\text{ESS} > 1000$). We discuss our results in language that is loosely based on the suggestion from Dushoff et al. (2019): When credibility intervals (CrI) or highest posterior intervals (HPD) do not overlap zero, for the 90% CrI/HPD, we consider statistical support for an effect to be weak, for the 95% CrI/HPD moderate and for the 99% CrI/HPD strong. Due to our treatment-specific research question (i.e., that in individuals raised under high-risk conditions, we expect a negative correlation between inducible defence expression and the degree of sociality), we aim to disentangle the included interaction independent of statistical significance using EMMEANS v.2.0.3 (Lenth et al., 2026).

Experiment 2

To estimate whether sociability and competitiveness consistently differ among individuals, with our extended larger dataset, we first estimated repeatability using the rptR v. 0.9.23 R package (Stoffel et al., 2017). To this end, we fit two models with either sociability (i.e., the number of social interactions, poisson data) or competitiveness (i.e., the proportion of dominant interactions, proportion data) as dependent variables and individual ID as random intercept. Repeatability (R) estimates were based on 1000 bootstrapping runs and we report 90%, 95% and 99% confidence intervals (CIs) on the original scale.

Afterwards, treatment-dependent variation in sociability and dominance in our base dataset was analysed applying the same software as in Experiment 1. However, here, we constructed two models with either sociability (i.e., the number of social interactions) or competitiveness (i.e., the proportion of dominant interactions) as dependent variables. Focal risk treatment (low-risk/high-risk), focal body mass and

focal tank snail density were entered as fixed factors and individual ID nested in tank ID nested in family ID as a random intercept. We did not include a random slope describing the order effects between the two trials of each individual as doing so led to model convergence issues. Priors and posterior sampling procedures were the same as in Experiment 1. We first ran these models with different appropriate families (Poisson, zero-inflated Poisson, negative binomial, and geometric distributions for sociability; binomial, zero-inflated binomial and zero-inflated beta-binomial for competitiveness because non-zero inflated beta-binomial distributions could not be sampled for this dataset by Stan) and selected models the same way as described for Experiment 1. Model results were interpreted the same way as in Experiment 1, with the same rationale expanding to CIs.

Results

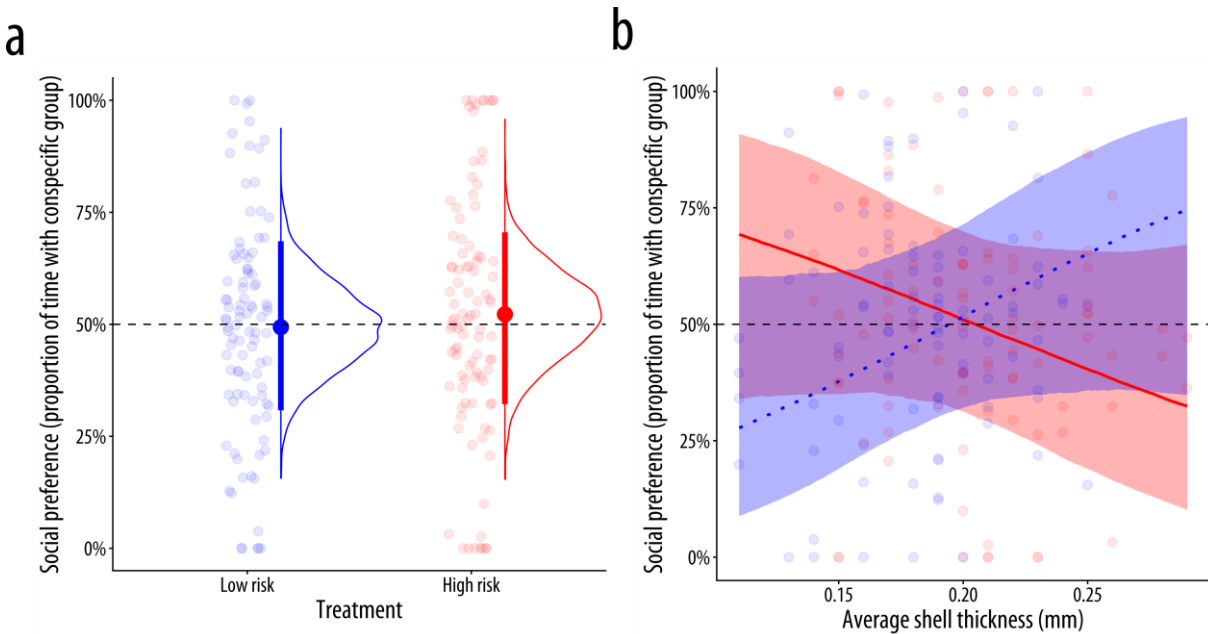
Experiment 1

The explanatory power of our statistical model to explain variation in social preferences was high ($R^2 = 0.998$, 95% CI [0.998, 0.998]) and the part related to the fixed effects alone (R^2_{marginal}) was 0.390 [0.277, 0.473]. Within this model, we found weak statistical support for an interaction between developmental risk environments and individual defence expression (estimate: 20.082 with 90% [3.123, 37.072], 95% [-0.230, 40.488], and 99% CIs [-6.535, 47.102], Fig. 1b). Furthermore, independent of defence expression, we also found weak support for low-risk rearing conditions to decrease association with tanks containing conspecifics (estimate: -3.976 with 90% [-7.312, -0.646], 95% [-7.967, 0.009], and 99% CIs [-9.278, 1.290], Fig. 1a). In contrast, we did not find statistical evidence for social preferences to be affected by either individual defence expression alone (estimate: -8.588 with 90% [-19.802, 2.644], 95% [-21.999,

439 4.912], and 99% CrIs [-26.413, 9.432]), individual body mass (estimate: 5.228 with
440 90% [-3.086, 13.638], 95% [-4.704, 15.304], and 99% CrIs [-7.893, 18.788]), or rearing
441 density (estimate: -0.020 with 90% [-0.250, 0.209], 95% [-0.296, 0.252], and 99% CrIs
442 [-0.389, 0.336]).

443 Despite the absence of statistical support for the following effects, disentangling
444 the interaction suggests that for individuals raised in high-risk conditions, greater
445 individual defence expression was descriptively associated with lower social
446 preferences (estimated slope: -8.610 with 90% [-19.600, 2.850], 95% [-22.000, 4.910],
447 and 99% HPDs [-26.010, 9.760]) whereas the opposite pattern was observable for
448 individuals raised in low-risk conditions (estimated slope: 11.510 with 90% [-1.000,
449 24.010], 95% [-3.430, 26.470], and 99% HPDs [-8.190, 31.540]).

450



451

452 **Figure 1** Variation in social preferences between adult *P. acuta* individuals raised
453 lifelong under either low (blue, n = 96 trials with 50 individuals) or high perceived
454 predation risk conditions (red, n = 97 trials with 51 individuals). Figure (a) shows
455 estimated Bayesian posteriors with their medians and 95% credible intervals (solid
456 dots and lines), posterior distributions (violin plots) and individual raw datapoints

(transparent dots). Figure (b) shows the slope between individual defence expression (average shell thickness) and social preferences as estimated Bayesian posteriors with medians (line) and 95% credible intervals (transparent fill) alongside raw datapoints (transparent dots).

Experiment 2

First, both sociability and competitiveness consistently differed among individuals. Repeatability for sociability was low and statistical support was weak ($R = 0.18$ with 90% [0.010, 0.329], 95% [0.000, 0.366], and 99% CIs [0.000, 0.430], $p=0.048$). While repeatability of competitiveness was even lower, statistical support was strong ($R = 0.032$ with 90% CI [0.013, 0.050], 95% [0.010, 0.053], and 99% CIs [0.005, 0.060], $p=0.001$).

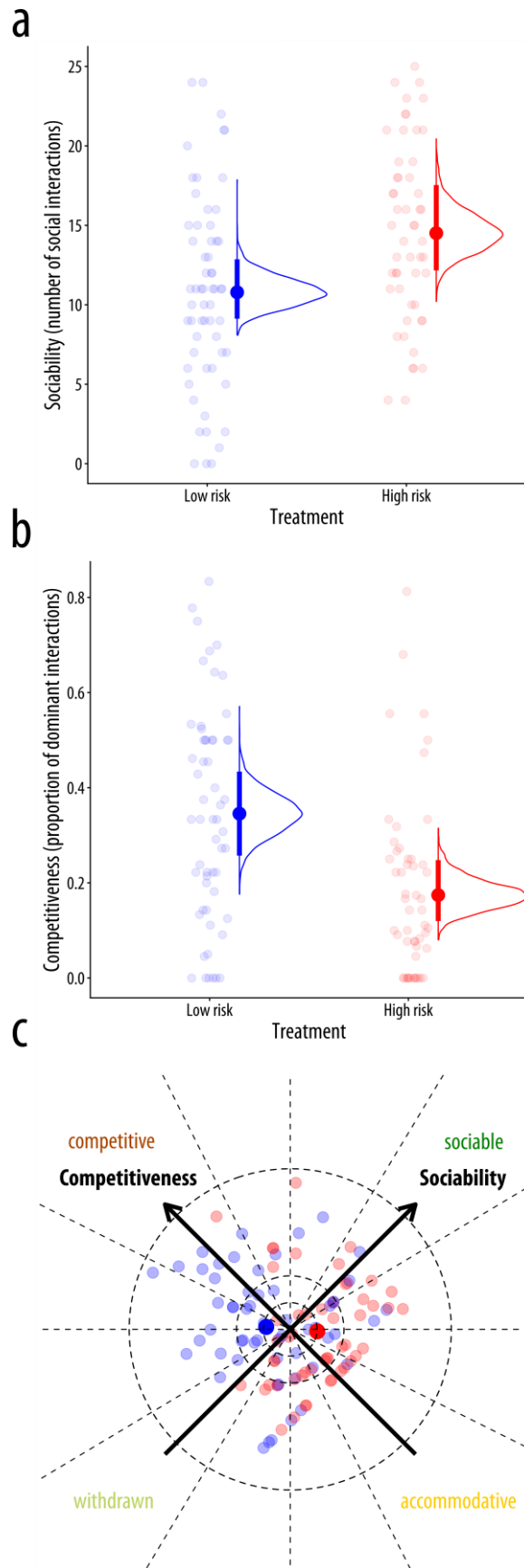
Second, we found statistical evidence for developmental risk environments to impact *P. acuta* sociability and competitiveness.

The explanatory power of our sociability model was small ($R^2 = 0.243$, 95% CI [0.091, 0.400]) and the part related to the fixed effects alone (R^2_{marginal}) was 0.138 [0.018, 0.274]. This model provides moderate statistical support for individuals raised in high-risk conditions to display ~30% more sociability than low-risk ones (estimate: -0.296 with 90% [-0.501, -0.092], 95% [-0.540, -0.051], and 99% CrIs [-0.627, 0.033], Fig. 2a). In contrast, we found no statistical support for either individual body mass (estimate: -0.271 with 90% [-3.764, 4.281], 95% [-4.554, 5.075], and 99% CrIs [-6.133, 6.619] or rearing density (estimate: 0.067 with 90% [-0.022, 0.155], 95% [-0.039, 0.173], and 99% CrIs [-0.076, 0.210]) to affect sociability.

Our competitiveness model explained more variance in the data than the sociability model as R^2 was 0.403 [0.280, 0.536] and $R^2_{\text{marginal}} = 0.297$ [0.197, 0.393]. This model provides strong statistical support for snails raised in high-risk conditions

483 to show ~50% lower competitiveness than low-risk ones (estimate: 0.926 with 90%
484 [0.439, 1.407], 95% [0.341, 1.506], and 99% Crls [0.133, 1.703], Fig. 2b). Meanwhile,
485 we found no statistical support for competitiveness to be affected by either body mass
486 (estimate: 6.967 with 90% [-2.348, 16.225], 95% [-4.226, 18.078], and 99% Crls [-
487 7.935, 21.815]) or rearing density (estimate: 0.131 with 90% [-0.071, 0.336], 95% [-
488 0.112, 0.379], and 99% Crls [-0.194, 0.467]).

489 We also observe clear separation between social behavioural types alongside
490 the sociability and competitiveness axes of the interpersonal circumplex, a framework
491 from human psychology that allows operationalizing interindividual social behaviour as
492 vectors originating from the centre of the circumplex (Fig. 2c).



493

494 **Figure 2** Variation in social personality between adult *P. acuta* individuals raised
 495 lifelong under either low (blue, n = 52 trials with 26 individuals) or high perceived

predation risk conditions (red, n = 60 trials with 30 individuals). Figures (a) and (b) show estimated Bayesian posteriors with their medians and 95% credible intervals (solid dots and lines), posterior distributions (violin plots) and individual raw datapoints (transparent dots). Figure (c) shows z-transformed raw data to showcase social personality as vectors within the interpersonal circumplex framework that can be used to operationalize interindividual social behaviour. Here, large opaque dots showcase means alongside standard errors (which are smaller than dot size and are thus not recognizable) whereas small transparent dots showcase average individual values across trials.

Discussion

In our study, we first found that lifelong exposure to conspecific alarm cues - indicating high perceived predation risk - induced greater social preferences to associate with conspecific groups in *P. acuta*. Second, under high perceived risk, individuals with thicker shells descriptively showed lower social preferences whereas the opposite pattern appeared to emerge under low risk. Third, individuals raised in high-risk conditions display greater sociability and lower competitiveness towards conspecifics. Taken together, the present study provides evidence that in the gastropod *P. acuta*, social behaviour expression is affected by both developmental environments and individual phenotypes.

Our first finding is that the freshwater gastropod *P. acuta* increases their preference to join a group of conspecifics as well as the number of social interactions when raised under high perceived predation risk. This result is consistent with findings in vertebrate taxa where grouping has been found to be a proactive response to the use of dangerous habitats (ungulates: Creel et al. (2014), birds: Beauchamp (2004), fish: Seghers (1974)) and where tighter grouping results from developmental plasticity in high-risk environments (Meuthen et al., 2016, but see Meuthen et al., 2019). It is

also in line with the knowledge that group formation leads to survival benefits for individual group members in predatory encounters and is thus an adaptive strategy to enhance fitness (Foster and Treherne, 1981; Neill and Cullen, 1974; Rieucou et al., 2015; Turner and Pitcher, 1986).

Our second finding is that in snails raised in high-risk conditions, individual defence expression descriptively predicts the extent of social preference with well-defended individuals being less social in *P. acuta*. This result is in line with other studies showing across non-gastropod taxa that individual phenotypes often shape social preferences. For example, in fish, body size is incorporated into shoaling decisions to balance between dilution and oddity effects (Rodgers et al., 2011). More generally, condition-dependent mate preferences are also widespread (Cotton et al., 2006). In the specific context, where both individual defences (Hoverman, 2010) as well as collective defences (Krause and Ruxton, 2002) are suggested to reduce predation risk, our result also suggests that in the presence of individual defences, the costs associated with sociality such as competition over resources including mates or risks of pathogen transmission (Krause and Ruxton, 2002; Ward and Webster, 2016) may outweigh the predation-related additional fitness benefits of sociality. At the same time, our result suggests that developmental (morphological) plasticity, which has a long lag time and is thus not always adaptive (Padilla and Adolph, 1996), is effectively combined with behavioural flexibility to maximize fitness.

Interestingly, our results also suggest that in low-risk individuals, well-defended individuals descriptively show greater social preferences. While this result appears counterintuitive at first, an explanation may be that individual defence expression (i.e., shell thickness) is not independent from body size (which can be predicted from body mass) due to mechanistic constraints on individual ability of developing different

aspects of the shell independently. While this fact is not well-supported for low-risk animals in our dataset due to limited sample sizes causing large confidence intervals that include both positive and negative slopes (Figure S1), a previous study with large sample sizes on the same species suggests that body mass reliably predicts shell thickness even in low-risk environments despite the slope being shallower than in high-risk environments (Meuthen and Mutingwende, 2025). This ultimately suggests that within low-risk individuals, the larger individuals may have been the ones who showed greater social preferences. Large size is usually positively correlated with interspecific competitive ability (Arnott and Elwood, 2009), and joining a group allows competitive individuals to outcompete conspecifics, by which in turn they gain increased access to resources including mating opportunities. In contrast, smaller, non-competitive individuals would theoretically only suffer the costs from joining a social group and should avoid competition, which is also in line with our results. Past studies in other taxa have also suggested social preferences to depend on individual competitive ability such as in fish where individuals with higher maximum metabolic rate, linked to competitive ability, are more social (Killen et al., 2021) and shoaling with poor competitors is a preferred strategy (Metcalf and Thomson, 1995).

Our third result arising from a study focusing on interindividual social interactions first suggests increased sociality in individuals from a high-risk environment, confirming the abovementioned preference to associate with conspecifics when cues of predation are perceived during development due to the protective benefits of collective defences such as the many-eyes effect (Treherne and Foster, 1980), the dilution effect (Wrona and Dixon, 1991) and the confusion effect (Krakauer, 1995; Neill and Cullen, 1974). Furthermore, our results also suggest lower competitiveness in individuals growing up in high-risk conditions. Competitive behaviours are often conspicuous, which attracts predators (Jakobsson et al., 1995),

and anti-predator vigilance is usually decreased during competitive encounters (Dunn et al., 2004; Ota, 2018). Hence, to reduce predation risk, in a high-risk environment, engaging into fewer or shorter competitive bouts is an adaptive strategy (Lange and Leimar, 2001; Ukegbu and Huntingford, 1988), which is in line with the decreased competitiveness that we observed.

Applying the interpersonal circumplex framework from human psychology that is suggested to be useful for operationalizing interindividual social behaviour indeed allows us to describe *P. acuta* social behaviour in a more unified manner. This allows comparison across taxa, which is helpful to determine differences and similarities in social behaviours and predictors thereof (Kuper et al., 2025).

Taken together, our study suggests that *P. acuta* has evolved plasticity in its social behaviour that depends on both environments and phenotypes so as to balance costs and benefits of sociality. However, our observed effect sizes were frequently small, causing us unable to find strong statistical support in most cases despite using a reasonably large sample size. Hence, there is a clear need for replication studies with larger sample sizes to verify our observations. Nevertheless, following the suggestion by Aquiloni and Tricarico (2015) that “research on mollusk social behavior will reveal great surprises”, our study opens up multiple new avenues for follow-up research since our findings clearly extend earlier research which suggests that mucus trail following behaviour is one of the main drivers of gastropod sociality (Ng et al., 2013). Instead, our results suggest that *P. acuta* social behaviour may at least in some aspects be comparable in complexity to vertebrate or mammal social behaviours. Supporting this idea is the observation that social isolation has negative effects on long-term memory in the great pond snail *Lymnaea stagnalis* (Dalesman and Lukowiak, 2011). Despite the proximate pathways underlying social behaviour being

evolutionarily conserved (Robinson et al., 2008), social behaviour is known to be primarily a product of convergent evolution due to shared selective pressures (e.g., Duffy et al., 2000; Brady et al., 2006; Kapheim et al., 2015). Considering the possibility of convergent evolution, the first open question is to what extent this finding is specific to *P. acuta* or generalizable to other gastropod or mollusk species that have a shared evolutionary history. Furthermore, to be able to use gastropod species for cross-taxon comparisons of social behaviour as required for generalization studies, we also need to investigate their social network structure, another important tool for the study of animal sociality (Wey et al., 2008). This need is particularly highlighted by the fact that not a single mollusk social network is included in public social network databases (Sah et al., 2019). These networks can help us to gain a better understanding of the degree of individualisation of their social relationships (Kuper et al., 2025), i.e., whether social behaviours result from random association or from preferences to socialize with specific individuals. Another challenge that will aid cross-species comparison of social behaviour is to find equivalents for other important interpersonal circumplex axes such as the warm-cold axis (Wiggins, 1979) in gastropods, requiring future research to focus on improving our understanding of gastropod interindividual social behaviour and its long-term consequences. Lastly, it will be interesting to elucidate to what extent the observed differences in social preferences have an epigenetic origin, and to what extent changes in social preferences, a type of social niche construction, predict future epigenetic change (Meuthen et al., 2026).

624 **References**

- 625 Aquiloni, L., Tricarico, E. (Eds.), 2015. Social Recognition in Invertebrates: The
626 Knowns and the Unknowns. Springer International Publishing, Cham.
627 <https://doi.org/10.1007/978-3-319-17599-7>
- 628 Arnott, G., Elwood, R.W., 2009. Assessment of fighting ability in animal contests.
629 *Animal Behaviour* 77, 991–1004.
630 <https://doi.org/10.1016/j.anbehav.2009.02.010>
- 631 Auld, J.R., Relyea, R.A., 2011. Adaptive plasticity in predator-induced defenses in a
632 common freshwater snail: altered selection and mode of predation due to prey
633 phenotype. *Evol Ecol Evol Ecol* 25, 189–202. [https://doi.org/10.1007/s10682-](https://doi.org/10.1007/s10682-010-9394-1)
634 [010-9394-1](https://doi.org/10.1007/s10682-010-9394-1)
- 635 Beauchamp, G., 2004. Reduced flocking by birds on islands with relaxed predation.
636 *Proc. R. Soc. Lond. B* 271, 1039–1042. <https://doi.org/10.1098/rspb.2004.2703>
- 637 Brady, S.G., Sipes, S., Pearson, A., Danforth, B.N., 2006. Recent and simultaneous
638 origins of eusociality in halictid bees. *Proc Biol Sci* 273, 1643–1649.
639 <https://doi.org/10.1098/rspb.2006.3496>
- 640 Bürkner, P.-C., 2017. brms: An R Package for Bayesian Multilevel Models Using Stan.
641 *Journal of Statistical Software* 80, 1–28. <https://doi.org/10.18637/jss.v080.i01>
- 642 Cardoso, S.D., Teles, M.C., Oliveira, R.F., 2015. Neurogenomic mechanisms of social
643 plasticity. *Journal of Experimental Biology* 218, 140–149.
644 <https://doi.org/10.1242/jeb.106997>
- 645 Cotton, S., Small, J., Pomiankowski, A., 2006. Sexual Selection and Condition-
646 Dependent Mate Preferences. *Current Biology* 16, R755–R765.
647 <https://doi.org/10.1016/j.cub.2006.08.022>

648 Creel, S., Schuette, P., Christianson, D., 2014. Effects of predation risk on group size,
649 vigilance, and foraging behavior in an African ungulate community. *Behavioral*
650 *Ecology* 25, 773–784. <https://doi.org/10.1093/beheco/aru050>

651 Dalesman, S., Lukowiak, K., 2011. Social snails: the effect of social isolation on
652 cognition is dependent on environmental context. *Journal of Experimental*
653 *Biology* 214, 4179–4185. <https://doi.org/10.1242/jeb.064857>

654 Dantzer, R., Bluthé, R.-M., Aubert, A., Goodall, G., Bret-Dibat, J.-L., Kent, S., Goujon,
655 E., Layé, S., Parnet, P., Kelley, K.W., 1996. Cytokine Actions on Behavior, in:
656 Rothwell, N.J. (Ed.), *Cytokines in the Nervous System*. Springer US, Boston,
657 MA, pp. 117–144. https://doi.org/10.1007/978-1-4615-9695-0_7

658 de la Cruz Barron, M., van Velzen, E., Klümper, U., Weitere, M., Berendonk, T.U.,
659 Kneis, D., 2023. Shifts from cooperative to individual-based predation defense
660 determine microbial predator-prey dynamics. *ISME J* 17, 775–785.
661 <https://doi.org/10.1038/s41396-023-01381-5>

662 DeWitt, T.J., 1998. Costs and limits of phenotypic plasticity: Tests with predator-
663 induced morphology and life history in a freshwater snail. *Journal of*
664 *Evolutionary Biology* 11, 465–480. [https://doi.org/10.1046/j.1420-](https://doi.org/10.1046/j.1420-9101.1998.11040465.x)
665 [9101.1998.11040465.x](https://doi.org/10.1046/j.1420-9101.1998.11040465.x)

666 Dochtermann, N.A., Sekhar, M.A., Nakagawa, S., 2026. Ungeneralizable
667 generalizations? A meta-meta-analysis of the influence of taxonomic bias on the
668 study of behaviour. *Animal Behaviour* 236, 123542.
669 <https://doi.org/10.1016/j.anbehav.2026.123542>

670 Duffy, J.E., Morrison, C.L., Ríos, R., 2000. Multiple Origins of Eusociality Among
671 Sponge-Dwelling Shrimps (synalpheus). *Evolution* 54, 503–516.
672 <https://doi.org/10.1111/j.0014-3820.2000.tb00053.x>

673 Dunn, M., Copelston, M., Workman, L., 2004. Trade-offs and seasonal variation in
674 territorial defence and predator evasion in the European Robin *Erithacus*
675 *rubecula*. *Ibis* 146, 77–84. <https://doi.org/10.1111/j.1474-919X.2004.00221.x>

676 Dushoff, J., Kain, M.P., Bolker, B.M., 2019. I can see clearly now: Reinterpreting
677 statistical significance. *Methods in Ecology and Evolution* 10, 756–759.
678 <https://doi.org/10.1111/2041-210X.13159>

679 Foster, W.A., Treherne, J.E., 1981. Evidence for the dilution effect in the selfish herd
680 from fish predation on a marine insect. *Nature* 293, 466–467.
681 <https://doi.org/10.1038/293466a0>

682 Froemke, R.C., Young, L.J., 2021. Oxytocin, Neural Plasticity, and Social Behavior.
683 *Annu. Rev. Neurosci.* 44, 359–381. [https://doi.org/10.1146/annurev-neuro-](https://doi.org/10.1146/annurev-neuro-102320-102847)
684 [102320-102847](https://doi.org/10.1146/annurev-neuro-102320-102847)

685 Henry, P.Y., Jarne, P., 2007. Marking hard-shelled gastropods: tag loss, impact on life-
686 history traits, and perspectives in biology. *Invertebrate Biology* 126, 138–153.
687 <https://doi.org/10.1111/j.1744-7410.2007.00084.x>

688 Hesse, S., Anaya-Rojas, J.M., Frommen, J.G., Thünken, T., 2015. Social deprivation
689 affects cooperative predator inspection in a cichlid fish. *R. Soc. open sci.* 2,
690 140451. <https://doi.org/10.1098/rsos.140451>

691 Hoverman, J.T., 2010. Predator-induced plasticity, in: *Encyclopedia of Life Sciences*
692 (ELS). John Wiley & Sons, Chichester.
693 <https://doi.org/10.1002/9780470015902.a0003305.pub2>

694 Huang, P., He, X., Zhang, E., Chen, M., 2017. Do same-sex mounts function as
695 dominance assertion in male golden snub-nosed monkeys (*Rhinopithecus*
696 *roxellana*)? *American J Primatol* 79, e22636. <https://doi.org/10.1002/ajp.22636>

697 Jakobsson, S., Brick, O., Kullberg, C., 1995. Escalated fighting behaviour incurs
 698 increased predation risk. *Animal Behaviour* 49, 235–239.
 699 [https://doi.org/10.1016/0003-3472\(95\)80172-3](https://doi.org/10.1016/0003-3472(95)80172-3)

700 Kapheim, K.M., Pan, H., Li, C., Salzberg, S.L., Puiu, D., Magoc, T., Robertson, H.M.,
 701 Hudson, M.E., Venkat, A., Fischman, B.J., Hernandez, A., Yandell, M., Ence, D.,
 702 Holt, C., Yocum, G.D., Kemp, W.P., Bosch, J., Waterhouse, R.M., Zdobnov,
 703 E.M., Stolle, E., Kraus, F.B., Helbing, S., Moritz, R.F.A., Glastad, K.M., Hunt,
 704 B.G., Goodisman, M.A.D., Hauser, F., Grimmelikhuijzen, C.J.P., Pinheiro, D.G.,
 705 Nunes, F.M.F., Soares, M.P.M., Tanaka, É.D., Simões, Z.L.P., Hartfelder, K.,
 706 Evans, J.D., Barribeau, S.M., Johnson, R.M., Massey, J.H., Southey, B.R.,
 707 Hasselmann, M., Hamacher, D., Biewer, M., Kent, C.F., Zayed, A., Blatti, C.,
 708 Sinha, S., Johnston, J.S., Hanrahan, S.J., Kocher, S.D., Wang, J., Robinson,
 709 G.E., Zhang, G., 2015. Genomic signatures of evolutionary transitions from
 710 solitary to group living. *Science* 348, 1139–1143.
 711 <https://doi.org/10.1126/science.aaa4788>

712 Kavaliers, M., Choleris, E., 2018. The role of social cognition in parasite and pathogen
 713 avoidance. *Philos Trans R Soc Lond B Biol Sci* 373, 20170206.
 714 <https://doi.org/10.1098/rstb.2017.0206>

715 Killen, S.S., Nadler, L.E., Grazioso, K., Cox, A., McCormick, M.I., 2021. The effect of
 716 metabolic phenotype on sociability and social group size preference in a coral
 717 reef fish. *Ecology and Evolution* 11, 8585–8594.
 718 <https://doi.org/10.1002/ece3.7672>

719 Koene, J.M., Ter Maat, A., 2007. Coolidge effect in pond snails: male motivation in a
 720 simultaneous hermaphrodite. *BMC Evol Biol* 7, 212.
 721 <https://doi.org/10.1186/1471-2148-7-212>

722 Krakauer, D.C., 1995. Groups confuse predators by exploiting perceptual bottlenecks:
 723 A connectionist model of the confusion effect. *Behavioral Ecology and*
 724 *Sociobiology* 36, 421–429. <https://doi.org/10.1007/Bf00177338>
 725 Krause, J., Ruxton, G.D., 2002. *Living in groups*, Oxford series in ecology and
 726 evolution. Oxford University press, Oxford.
 727 Kuper, N., Breitmoser, Y., Caspers, B., Dammhahn, M., Gadau, J., Kaiser, M.I.,
 728 Kandler, C., Kroh, M., Krüger, O., Kurtz, J., Lemola, S., Rauthmann, J.F.,
 729 Richter, S.H., Voelcker-Rehage, C., Back, M.D., 2025. An interdisciplinary
 730 linked-lives approach to individual differences in social behaviour. *Nature*
 731 *Human Behaviour* 9, 2012–2026. <https://doi.org/10.1038/s41562-025-02301-7>
 732 Landeau, L., Terborgh, J., 1986. Oddity and the confusion effect in predation. *Animal*
 733 *Behaviour* 34, 1372–1380. [https://doi.org/10.1016/S0003-3472\(86\)80208-1](https://doi.org/10.1016/S0003-3472(86)80208-1)
 734 Lange, H., Leimar, O., 2001. The influence of predation risk on threat display in great
 735 tits. *Behav Ecol* 12, 375–380. <https://doi.org/10.1093/beheco/12.4.375>
 736 Lenth, R.V., Piaskowski, J., Banfai, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung,
 737 M., Love, J., Miguez, F., Riebl, H., Singmann, H., 2026. Emmeans: estimated
 738 marginal means, aka least-squares means. R package version 1.11.2.
 739 Lydeard, C., Lindberg, D.R. (Eds.), 2003. *Molecular systematics and phylogeography*
 740 *of mollusks*, Smithsonian series in comparative evolutionary biology.
 741 Smithsonian Books, Washington.
 742 Metcalfe, N.B., Thomson, B.C., 1995. Fish recognize and prefer to shoal with poor
 743 competitors. *Proc Biol Sci* 259, 207–210.
 744 <https://doi.org/10.1098/rspb.1995.0030>
 745 Meuthen, D., 2025. Risk allocation in a freshwater gastropod. *Behavioral Ecology* 36,
 746 araf078. <https://doi.org/10.1093/beheco/araf078>

747 Meuthen, D., Baldauf, S.A., Bakker, T.C.M., Thünken, T., 2016. Predator-induced
748 neophobia in juvenile cichlids. *Oecologia* 181, 947–958.
749 <https://doi.org/10.1007/s00442-015-3478-0>

750 Meuthen, D., Ferrari, M.C.O., Lane, T., Chivers, D.P., 2019. High background risk
751 induces risk allocation rather than generalized neophobia in the fathead
752 minnow. *Behavioral Ecology* 30, 1416–1424.
753 <https://doi.org/10.1093/beheco/arz094>

754 Meuthen, D., Hoffman, J.I., Kurtz, J., Berthelsen, A.L., Chakarov, N., Chen, R.S.,
755 Coculla, A., Gadau, J.R., Gossmann, T.I., Mühlenhaupt, M., Chavarria-Pizarro,
756 T., Rapp, T.M., Sepers, B., Vellnow, N., Xu, S., Vendrami, D.L.J., 2026. Exploring
757 the interplay of epigenetics and individualization. *Trends in Ecology & Evolution*
758 41, 318–328. <https://doi.org/10.1016/j.tree.2025.12.010>

759 Meuthen, D., Mutingwende, N., 2025. Chilled but potent: validating the ability of frozen
760 alarm cues to induce antipredator defences in a freshwater gastropod. *Animal*
761 *Behaviour* 226, 123252. <https://doi.org/10.1016/j.anbehav.2025.123252>

762 Meuthen, D., Reinhold, K., 2023. On the use of antibiotics in plasticity research:
763 gastropod shells unveil a tale of caution. *Journal of Animal Ecology* 92, 1055–
764 1064. <https://doi.org/10.1111/1365-2656.13909>

765 Neill, S.R.J., Cullen, J.M., 1974. Experiments on whether schooling by their prey
766 affects the hunting behaviour of cephalopods and fish predators. *Journal of*
767 *Zoology* 172, 549–569. <https://doi.org/10.1111/j.1469-7998.1974.tb04385.x>

768 Ng, T.P.T., Saltin, S.H., Davies, M.S., Johannesson, K., Stafford, R., Williams, G.A.,
769 2013. Snails and their trails: the multiple functions of trail-following in
770 gastropods. *Biological Reviews* 88, 683–700. <https://doi.org/10.1111/brv.12023>

771 Oliveira, R.F., 2012. Social plasticity in fish: integrating mechanisms and function.
772 Journal of Fish Biology 81, 2127–2150. <https://doi.org/10.1111/j.1095->
773 8649.2012.03477.x

774 Oliveira, R.F., 2009. Social behavior in context: Hormonal modulation of behavioral
775 plasticity and social competence. Integrative and Comparative Biology 49, 423–
776 440. <https://doi.org/10.1093/icb/icp055>

777 Ota, K., 2018. Fight, fatigue and flight: narrowing of attention to a threat compensates
778 for decreased anti-predator vigilance. J Exp Biol 221, jeb168047.
779 <https://doi.org/10.1242/jeb.168047>

780 Padilla, D.K., Adolph, S.C., 1996. Plastic inducible morphologies are not always
781 adaptive: the importance of time delays in a stochastic environment.
782 Evolutionary Ecology 10, 105–117. <https://doi.org/10.1007/BF01239351>

783 R Core Team, 2026. R: A language and environment for statistical computing.

784 Réale, D., Dall, S.R.X., Dingemanse, N.J., 2026. Animal personality is a class of
785 variation not a set of traits. Animal Behaviour 237, 123622.
786 <https://doi.org/10.1016/j.anbehav.2026.123622>

787 Rieucou, G., Fernö, A., Ioannou, C.C., Handegard, N.O., 2015. Towards of a firmer
788 explanation of large shoal formation, maintenance and collective reactions in
789 marine fish. Rev Fish Biol Fisheries 25, 21–37. <https://doi.org/10.1007/s11160->
790 014-9367-5

791 Robinson, G.E., Fernald, R.D., Clayton, D.F., 2008. Genes and Social Behavior.
792 Science 322, 896–900. <https://doi.org/10.1126/science.1159277>

793 Rodgers, G.M., Ward, J.R., Askwith, B., Morrell, L.J., 2011. Balancing the Dilution and
794 Oddity Effects: Decisions Depend on Body Size. PLOS ONE 6, e14819.
795 <https://doi.org/10.1371/journal.pone.0014819>

796 Rosenberg, G., 2014. A New Critical Estimate of Named Species-Level Diversity of the
 797 Recent Mollusca*. American Malacological Bulletin 32, 308.
 798 <https://doi.org/10.4003/006.032.0204>

799 Rosenthal, M.F., Gertler, M., Hamilton, A.D., Prasad, S., Andrade, M.C.B., 2017.
 800 Taxonomic bias in animal behaviour publications. Animal Behaviour 127, 83–
 801 89. <https://doi.org/10.1016/j.anbehav.2017.02.017>

802 Sah, P., Méndez, J.D., Bansal, S., 2019. A multi-species repository of social networks.
 803 Sci Data 6, 44. <https://doi.org/10.1038/s41597-019-0056-z>

804 Seghers, B.H., 1974. Schooling Behavior in the Guppy (*Poecilia reticulata*): An
 805 Evolutionary Response to Predation. Evolution 28, 486.
 806 <https://doi.org/10.2307/2407174>

807 Simpson, A.W., Thomas, J.D., Townsend, C.R., 1973. Social behavior in the freshwater
 808 pulmonate snail *Biomphalaria glabrata* (Say). Behavioral Biology 9, 731–740.
 809 [https://doi.org/10.1016/S0091-6773\(73\)80133-6](https://doi.org/10.1016/S0091-6773(73)80133-6)

810 Stamps, J.A., 2015. Individual differences in behavioural plasticities. Biological
 811 Reviews 91, 534–567. <https://doi.org/10.1111/brv.12186>

812 Stoffel, M.A., Nakagawa, S., Schielzeth, H., 2017. rptR: repeatability estimation and
 813 variance decomposition by generalized linear mixed-effects models. Methods in
 814 Ecology and Evolution 8, 1639–1644. <https://doi.org/10.1111/2041-210X.12797>

815 Tariel, J., Plénet, S., Luquet, E., 2020. How do developmental and parental exposures
 816 to predation affect personality and immediate behavioural plasticity in the snail
 817 *Physa acuta*? Proceedings of the Royal Society Series B 287, 20201761.
 818 <https://doi.org/10.1098/rspb.2020.1761>

819 Tollrian, R., Harvell, C.D., 1999. The ecology and evolution of inducible defenses.
 820 Princeton University Press, Princeton.

821 Traniello, J.F.A., Bakker, T.C.M., 2026. Sociobiology and the transformation of
822 evolutionary behavioral biology. *Behav Ecol Sociobiol* 80, 33, s00265-026-
823 03706–8. <https://doi.org/10.1007/s00265-026-03706-8>

824 Traniello, J.F.A., Bakker, T.C.M., Bednekoff, P.A., Cully, S.M., Festa-Bianchet, M.,
825 Gabor, C.R., Hosken, D.J., Johnson, M.A., Knörnschild, M., Voelkl, B.,
826 Wilkinson, G.S., 2026. Behavioral ecology and sociobiology since 1975: The
827 growth and diversification of the biology of adaptive social behavior. *Behav Ecol*
828 *Sociobiol* 80, 34, s00265-026-03707–7. [https://doi.org/10.1007/s00265-026-](https://doi.org/10.1007/s00265-026-03707-7)
829 [03707-7](https://doi.org/10.1007/s00265-026-03707-7)

830 Treherne, J.E., Foster, W.A., 1980. The effects of group size on predator avoidance in
831 a marine insect. *Animal Behaviour* 28, 1119–1122.
832 [https://doi.org/10.1016/S0003-3472\(80\)80100-X](https://doi.org/10.1016/S0003-3472(80)80100-X)

833 Turner, G.F., Pitcher, T.J., 1986. Attack abatement - a model for group protection by
834 combined avoidance and dilution. *American Naturalist* 128, 228–240.
835 <https://doi.org/10.1086/284556>

836 Ukegbu, A.A., Huntingford, F.A., 1988. Brood Value and Life Expectancy as
837 Determinants of Parental Investment in Male Three-spined Sticklebacks,
838 *Gasterosteus aculeatus*. *Ethology* 78, 72–82. [https://doi.org/10.1111/j.1439-](https://doi.org/10.1111/j.1439-0310.1988.tb00220.x)
839 [0310.1988.tb00220.x](https://doi.org/10.1111/j.1439-0310.1988.tb00220.x)

840 Vinarski, M.V., 2017. The history of an invasion: phases of the explosive spread of the
841 physid snail *Physella acuta* through Europe, Transcaucasia and Central Asia.
842 *Biological Invasions* 19, 1299–1314. [https://doi.org/10.1007/s10530-016-1339-](https://doi.org/10.1007/s10530-016-1339-3)
843 [3](https://doi.org/10.1007/s10530-016-1339-3)

844 Ward, A., Webster, M., 2016. *Sociality: The Behaviour of Group-Living Animals*.
845 Springer International Publishing, Cham. [https://doi.org/10.1007/978-3-319-](https://doi.org/10.1007/978-3-319-28585-6)
846 [28585-6](https://doi.org/10.1007/978-3-319-28585-6)

- Wey, T., Blumstein, D.T., Shen, W., Jordán, F., 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour* 75, 333–344. <https://doi.org/10.1016/j.anbehav.2007.06.020>
- Wiggins, J.S., 1979. A psychological taxonomy of trait-descriptive terms: The interpersonal domain. *Journal of Personality and Social Psychology* 37, 395–412. <https://doi.org/10.1037/0022-3514.37.3.395>
- Wrona, F.J., Dixon, R.W.J., 1991. Group size and predation risk: A field analysis of encounter and dilution effects. *American Naturalist* 137, 186–201. <https://doi.org/10.1086/285153>
- Zeigler-Hill, V., Highfill, L., 2017. The Interpersonal Circumplex: A Complementary Approach for Understanding Animal Personality, in: Vonk, J., Weiss, A., Kuczaj, S.A. (Eds.), *Personality in Nonhuman Animals*. Springer International Publishing, Cham, pp. 39–53. https://doi.org/10.1007/978-3-319-59300-5_3

Denis Meuthen, Dustin Raeke, Jannis Bednarzik, Mauricio Bravo Soldevilla, Niclas Kuper & Melanie Dammhahn

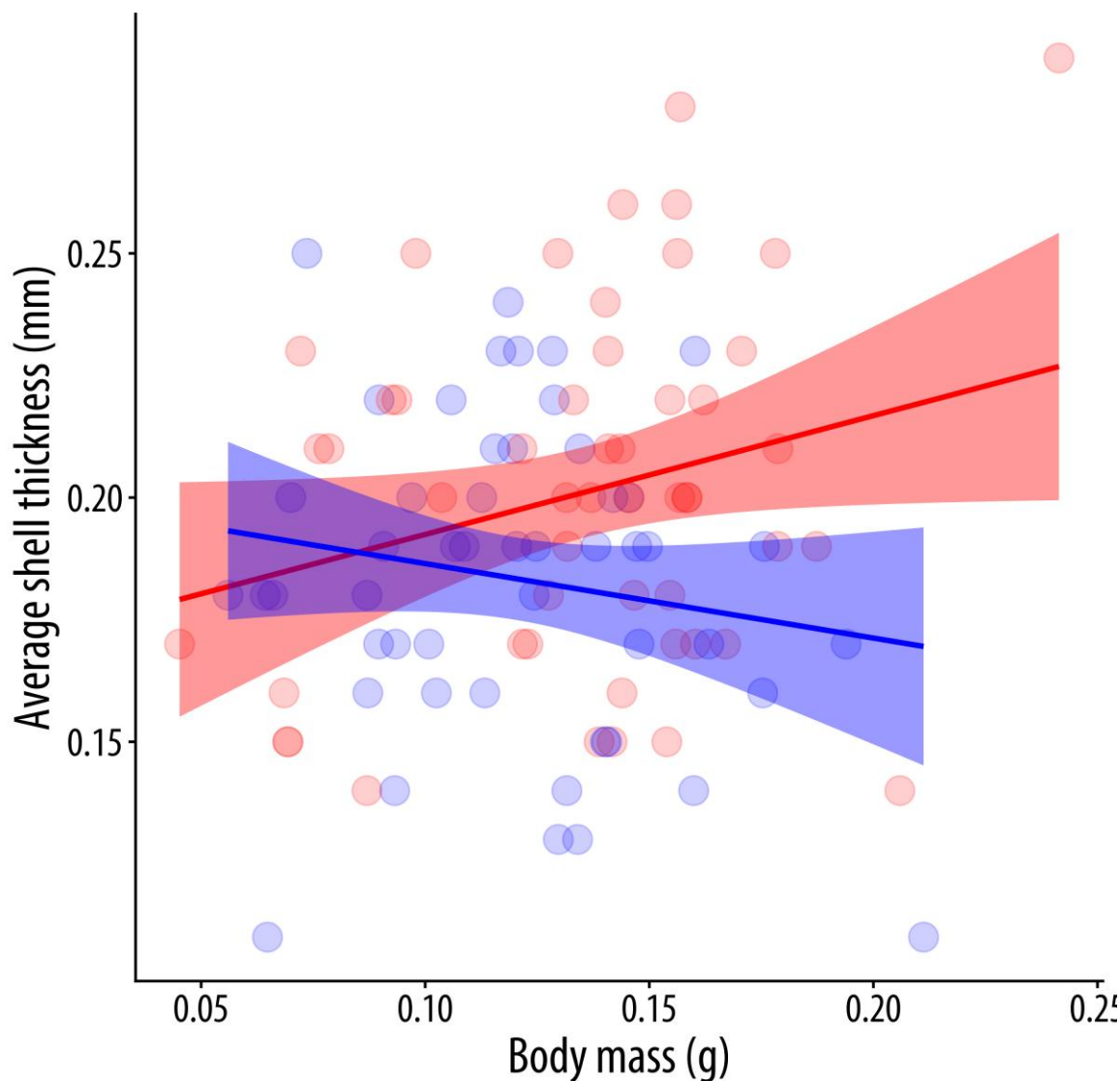


Figure S1. Relationship between average shell thickness and body mass in 69-89-day-old *Physella acuta* of Experiment 1 (for details see main manuscript) that were three times per week with 1 intermission day each exposed from hatching onwards to either conspecific alarm cues (red dots, lines and areas, n = 51) or fresh water (blue dots, lines and areas, n = 50). Least-square regression lines with 95% confidence intervals are shown for each treatment.