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RESEARCH ARTICLE

Heritable intraspecific variation among prey in size and movement interact to shape predation risk and potential natural selection

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Abstract

1. Predator and prey traits are important determinants of the outcomes of trophic interactions. In turn, the outcomes of trophic interactions shape predator and prey trait evolution. How species' traits respond to selection from trophic interactions depends crucially on whether and how heritable species' traits are and their genetic correlations. Of the many traits influencing the outcomes of trophic interactions, body size and movement traits have emerged as key traits. Yet, how these traits shape and are shaped by trophic interactions is unclear, as few studies have simultaneously measured the impacts of these traits on the outcomes of trophic interactions, their heritability, and their correlations within the same system.
2. We used outcrossed lines of the ciliate protist *Paramecium caudatum* from natural populations to examine variation in morphology and movement behaviour, the heritability of that variation, and its effects on *Paramecium* susceptibility to predation by the copepod *Macrocyclops albidus*.
3. We found that the *Paramecium* lines exhibited heritable variation in body size and movement traits. In contrast to expectations from allometric relationships, body size and movement speed showed little covariance among clonal lines. The proportion of *Paramecium* consumed by copepods was positively associated with *Paramecium* body size and velocity but with an interaction such that greater velocities led to greater predation risk for large body-sized paramecia but did not alter predation risk for smaller paramecia. The proportion of paramecia consumed was not related to copepod body size. These patterns of predation risk and heritable trait variation in paramecia suggest that copepod predation may act as a selective force operating independently on movement and body size and generating the strongest selection against large, high-velocity paramecia.

4. Our results illustrate how ecology and genetics can shape potential natural selection on prey traits through the outcomes of trophic interactions. Further simultaneous measures of predation outcomes, traits, and their quantitative genetics will provide insights into the evolutionary ecology of species interactions and their eco-evolutionary consequences.

KEYWORDS
allometry, body size, consumer-resource, copepod, foraging, intraspecific variation, *paramecium*, predator–prey

1 | INTRODUCTION

Predator and prey traits shape, and are shaped by, the outcomes of trophic interactions (Abrams, 2000; DeLong, 2021; Pimentel, 1961; Schaffer & Rosenzweig, 1978). Predator and prey traits shape the outcome of trophic interactions because they partially determine the results of each step in the foraging process (DeLong, 2021; Jeschke et al., 2002; Wootton et al., 2023). Foraging outcomes, in turn, shape predator and prey traits because, all else equal, predators with traits leading to greater predation success will have higher fitness whereas prey with traits leading to greater predation avoidance will have higher fitness (Abrams, 2000; DeLong, 2021; Pimentel, 1961; Schaffer & Rosenzweig, 1978). Thus, intraspecific variation in predator and prey traits plays a key eco-evolutionary role by determining the outcomes of trophic interactions while providing the raw material necessary for predators or prey traits to evolve in response to trophic interactions.

Many traits influence the outcomes of trophic interactions such as prey crypsis and defences and predator foraging behaviour (Endler, 1978; Greene, 1986; Tollrian & Harvell, 1999), and intraspecific variation in these traits alters the likelihood of predation between predator and prey individuals. Among the traits influencing trophic interactions, predator–prey body sizes and movement have emerged as key traits universally influencing trophic interactions (Aljetlawi et al., 2004; Pawar et al., 2012; Vucic-Pestic et al., 2010; Yodzis & Innes, 1992). Predator–prey body sizes have direct effects on predator–prey interactions by determining, for example, whether a predator can physically consume a given prey item (Paine, 1976), the energetic demand of predators (Kleiber, 1932; Yodzis & Innes, 1992), and the total amount of energy contained in an individual prey (Charnov, 1976; Yodzis & Innes, 1992). Predator and prey movement also play a key role because movement behaviour determines predator–prey encounter rates. In general, greater predator or prey velocities lead to more encounters among predators and prey, leading to more opportunities for predation events (Aljetlawi et al., 2004; Pawar et al., 2012). Furthermore, body size and movement are inextricably linked in many species. Specifically, a common pattern within and among species is a positive allometric relationship in which larger body sizes are associated with greater movement speeds (Cloyed et al., 2021; Hirt et al., 2017). In general, for a given prey size, increasing predator size should increase feeding rates through greater encounter rates and/or shorter handling times on prey (Coblentz et al., 2023; Pawar et al., 2012; Rall et al., 2012; Uiterwaal & DeLong, 2020). For a given predator body size, increasing prey size could lead to higher predator feeding rates by increasing the predator–prey encounter rates or decrease feeding rates by lengthening prey handling times (Coblentz et al., 2023; Pawar et al., 2012; Rall et al., 2012; Uiterwaal & DeLong, 2020). Prior studies also have found unimodal relationships between feeding rates and predator–prey size ratios (Brose et al., 2008; Kratina et al., 2022; Rall et al., 2012; Vucic-Pestic et al., 2010). However, these unimodal relationships often occur over orders of magnitude of variation in predator–prey body size ratios.

Despite general expectations for body size and movement effects on trophic interactions, whether and how these traits might evolve in response to selection through trophic interactions depends critically on how heritable they are. For a quantitative trait to evolve, some proportion of intraspecific variation in that trait must be heritable (Lande & Arnold, 1983; Lush, 1937). Furthermore, how responsive a trait is to selection depends on how heritable that trait is (Lande & Arnold, 1983; Lush, 1937). If a trait is only weakly heritable, its response to selection will be weak for a given amount of phenotypic trait variation within the population, whereas traits with high heritability will respond more strongly. When traits influencing predator–prey interactions are heritable, they can have important ecological consequences. For example, heritable prey defence traits can generate unique eco-evolutionary predator–prey cycles (Yoshida et al., 2003) or structure predator communities when predators differ in their susceptibility to prey defences (Lenhart et al., 2018). Regarding body sizes and movement, these traits are likely to be heritable to some extent in most organisms with heritability of both traits being found across a variety of taxa from microbes to vertebrates (Charmantier et al., 2011; Dochtermann et al., 2019; Gervais et al., 2020; Hertel et al., 2020; Mousseau & Roff, 1987; Stirling et al., 2002).

Beyond heritability, trait responses to selection also depend on the genetic correlations among traits (Arnold, 1992; Lande & Arnold, 1983). For example, genetic correlations can constrain evolutionary responses of traits or lead to evolutionary changes in traits that are not under selection if they are correlated with traits that are under selection (Arnold, 1992). Allometric relationships between

body size and movement suggest that these traits should be positively correlated (Cloyed et al., 2021; Hirt et al., 2017). In this case, selection occurring in the same direction on both traits or directional selection on either trait alone should lead to a directional evolutionary response in both traits (Arnold, 1992; Lande & Arnold, 1983). However, if selection operates in different directions on the two traits, evolution may be constrained and dependent on the quantitative genetic details of the system (Arnold, 1992). If body size and movement traits are not genetically correlated, then selection should be able to operate independently on each trait. Thus, different potential genetic correlations and selection pressures create different expectations for how natural selection through predation might operate.

Previous studies on body size and movement variation (e.g. Cloyed et al., 2021; Hirt et al., 2017), their effects on trophic interactions (e.g. Aljetlawi et al., 2004; Vucic-Pestic et al., 2010), and their heritability and potential genetic correlations (e.g. Hertel et al., 2020; Mousseau & Roff, 1987) provide us with a set of expectations on the interactions between predator and prey traits, predation, and evolution. However, it is unclear how these processes interact generally, as we are unaware of studies simultaneously measuring body size and movement heritability, correlations, and their impacts on predation. We do so by taking advantage of a laboratory system consisting of a protist prey *Paramecium caudatum* and its copepod predator *Macrocyclops albidus*. We examined how outcrossed and then clonally propagated lines of *P. caudatum* varied in morphology and movement, the heritability of those traits, and how intraspecific variation in *Paramecium* morphology and movement and body size in the *M. albidus* related to *Paramecium* predation risk. From the literature outlined above, we first hypothesized that *Paramecium* body size and movement speed variation would be heritable and positively correlated. Second, we hypothesized that *Paramecium* body size and movement speed would be positively correlated with predation rates due to increased encounter rates and a minimal effect of handling times given copepod sizes relative to *Paramecium*. Third, we hypothesized that copepod body size would be positively correlated with predation rates on paramecia because larger copepod size should increase encounter rates with the paramecia and potentially lower their handling times.

2 | MATERIALS AND METHODS

2.1 | Study system

We collected *Paramecium caudatum*, from three sites near Lincoln, Nebraska, USA: Spring Creek Prairie Audubon Center (40°41′24″ N, 96°51′0″ W), Conestoga Lake State Recreation Area (40°45′36″ N, 96°51′0″ W), and Wildwood Lake State Wildlife Management Area (41°2′24″ N, 96°50′24″ W) in June and July of 2023. We focused collections on shallow, nearshore waters with emergent or floating vegetation. After isolating individual cells, we then washed them four times with autoclaved pond water from the Spring Creek Prairie site by pipetting the cell in as small a volume as possible, placing the cell into 1 mL of autoclaved pond water, and repeating the process three more times. We then placed the washed cells alone in separate test tubes. In total, we isolated over one hundred lineages. We reared isolated lineages in lettuce media inoculated with bacteria from the Spring Creek Prairie site. We made lettuce media using 15 g of organic romaine lettuce autoclaved in 1 L of filtered pond water with 0.7 g of ground-dried autoclaved pond mud. We maintained the bacterial flora by transferring inoculated media into new jars of uninoculated media every other day or so.

Conjugation is the sexual stage of paramecia, involving meiosis followed by genetic exchange between individuals of different mating types. To generate outcrossed lines from the isolated Paramecium lineages, in August 2023, we combined cells from all isolates into 100 mm Petri dishes. Cells began conjugating within a day, and we collected adjoined conjugates and isolated them into new tubes. As *Paramecium* exconjugates (cells post conjugation) are genetically identical (Ahsan et al., 2022; Bell, 1989; Hiwatashi, 2001), individuals descended from the conjugating pair are clones that are potentially genetically different from clonal lines descended from other exconjugant pairs through both recombination and genetic differences. We established 132 outcrossed lines and maintained them on lettuce media.

The predator in our foraging experiment, the copepod *Macrocyclops albidus*, also originated from the Spring Creek Prairie in June through August, 2023. We used a combination of wild-collected and lab-reared adults in foraging trials. For the lab-reared individuals, we isolated gravid *M. albidus* in a single Petri dish with *P. caudatum* provided ad libitium as food. Eggs hatched and grew through stages, and we collected new adults from these stocks for the trials.

We reared all paramecia and copepod stocks at room temperature (23°C).

2.2 | Video phenotyping

To examine whether and how the *Paramecium* lines differed in morphological and movement traits, we phenotyped cells from videos. Twenty-four hours prior to taking videos of the *Paramecium*, we placed cells from each outcrossed line into fresh bacterized media in new test tubes at room temperature to create common-garden conditions. For each outcrossed line, we washed approximately 20 *Paramecium* cells three times in 1 mL of 0.2 μm filtered autoclaved pond water. We then placed the *Paramecium* onto a Petri dish in 0.1 mL of filtered autoclaved pond water and covered the drop with a deep-well projection slide cover (Carolina Deep-Well Slides, Model: 60-3730 60-3730E). After placing the slide cover over the *Paramecium*, we took a 25 s video of the *Paramecium* using a stereo microscope (Leica M165C) outfitted with a camera (Leica DMC 4500). Seven outcrossed lines did not have enough cells available on the day of video phenotyping, leaving us with videos for 126 of the 133 outcrossed lines.

To extract morphological and movement data from the videos, we used the R package Bemovi (Behaviour and MOrphology from VIdeo; Pennekamp et al., 2015). Bemovi uses particle tracking software to identify and track individual cells in videos and then extracts information on their morphology and movement. For each video, we took the median of the extracted data from Bemovi across all cells within an outcrossed line to get a single representative set of morphological and movement measurements. The number of identified particle tracks used to obtain the medians ranged from $N = 9$ to 36 per outcrossed line after data processing.

2.3 | Foraging experiment

We housed 58 copepods alone within deep-well projection slides (Carolina Deep-Well Slides, Model: 60-3730 60-3730E) of 2.4 cm diameter and 1.4 mm depth with approximately 0.8 mL of filtered autoclaved pond water. Prior to each foraging trial, we starved the copepods for 24 h to standardize hunger levels. We used only non-gravid copepods. For copepods that became gravid during, we fed them paramecia daily until they dropped their eggs and could be used again after a 24-h starvation period. Before each trial, we washed each copepod twice by removing 0.6 mL of water and replacing it with filtered autoclaved pond water. For each trial, we also washed 40 paramecia three times using 1 mL filtered pond water. After adding the 40 paramecia to the deep-well projection slide arenas, we placed the arenas in an incubator (Percival E30BC8) at 25°C. After 30 min, we removed the arenas and counted the remaining *Paramecium* cells under a stereo microscope. Given the short length of the trials, we did not perform control experiments to account for mortality or growth during the trial. Growth should have been minimal since the trial duration is approximately the time it takes for a *P. caudatum* to divide once showing signs of binary fission and we did not use cells showing signs of division (Hinrichs, 1928). Furthermore, natural mortality was unlikely as we have never observed mortality in healthy paramecium cells in such a short period in autoclaved pond water (Authors, *Personal Observation*).

In total, we conducted 4–7 replicate foraging trials with different *M. albidus* individuals for each of 38 randomly chosen outcrossed *Paramecium* lines. Across trials, the same copepod was never used with the same outcrossed line more than once and was never used more than once in a day. Overall, individual copepods were used in 2–8 total foraging trials, leading to a total of 230 foraging trials.

2.4 | Copepod morphology measurements

We photographed 57 of the 58 *M. albidus* used in the foraging trials using a stereo microscope (Leica M165C) outfitted with a camera (Leica DMC 4500) and measured their lengths and widths in millimetres. The one non-photographed copepod died during the experiment, and its foraging trials were excluded from the analysis.

2.5 | Replication statement for foraging trials

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Outcrossed line	Outcrossed line	4–7
Individual copepod	Individual copepod	2–8

2.6 | Statistical analyses

2.6.1 | Analysis of phenotype data

The Bemovi video analysis provided a suite of variables describing the morphological and movement phenotypes of the *Paramecium* outcrossed lines. To reduce the dimensionality of the phenotypes, we first excluded variables given by Bemovi that have an unclear meaning in terms of the *Paramecium* phenotypes such as the 'greyness' of the paramecia. Next, we examined a correlation matrix of the remaining variables using the medians across individuals within outcrossed lines to determine which variables were highly correlated with one another and thus may be providing similar information (see Appendix S1). For the variables that were highly correlated, we chose the most easily interpretable variable to include as a measure of the phenotype. This process resulted in the following variables describing the *Paramecium* phenotypes: length, width, aspect ratio, mean turning angle, standard deviation of the turning angle, gross speed, net displacement, and standard deviation of gross speed (for definitions of the variables see Appendix S2). After selecting these variables to describe *Paramecium* phenotypes, we further reduced the dimensionality by performing a Principal Components Analysis after centering and standardizing each variable.

We estimated the broad-sense heritability (H^2) of each of the selected *Paramecium* variables using the trait variation among outcrossed clonal lines (Lynch & Walsh, 1998). To estimate the heritability of traits using clonal lines, one can use an analysis of variance with the trait of interest measured for each cell in the videos as the response and genotype (or clonal line, in this case) as a fixed effect (Lynch & Walsh, 1998). Broad-sense heritability is then estimated as the amount of variation explained by genotype divided by the total variation (Lynch & Walsh, 1998), with the caveat that maternal effects are not factored out of this estimate of H^2.

2.6.2 | Analysis of copepod foraging data

To analyse the copepod foraging data, we used a generalized linear mixed effects model. To allow for over/under-dispersion in the data, we modelled the response (the proportion of paramecia consumed in the foraging trial) as beta-binomially distributed using a logit link function. To account for non-independence due to the repeated use of outcrossed lines and individual copepods, we included

random intercepts for *Paramecium* outcrossed line and individual copepod. As our questions were about how *Paramecium* phenotypes and copepod size influenced the proportion of paramecia consumed, we included the first and second principal component analysis axes from the analysis of the *Paramecium* phenotypes, their interaction, and copepod length as fixed effects. Copepod length and width were correlated and using width rather than length had no qualitative effect on our results (Appendix S3). We performed the regression in a Bayesian framework using the R package 'brms' (Bürkner, 2017). For model details, see Appendix S4. Last, we used the model predictions to visualize a fitness surface where fitness is defined as the predicted proportion of paramecia surviving the foraging trial.

All analyses were performed using R v. 4.3.1 (R Core Team, 2023). This work did not require licences or permits for field work and did not require ethical approval.

3 | RESULTS

3.1 | Paramecium phenotypes

The first two Principal Components Analysis axes explained 60.2% of the total variation in median phenotypes across all the outcrossed lines (Figure 1; Appendix S5). The first axis was positively associated with measures of speed and displacement (i.e. gross speed, its standard deviation, and net displacement) and *Paramecium* aspect ratio and negatively associated with mean turning angle of the paramecia. The second axis was positively associated with *Paramecium* size (length, width) and had a slight negative association with the standard deviation in turning angle. Thus, we interpret the first axis as representing movement speed and lack of turning and the second axis as a measure of size. We also note that size and speed loading on separate axes reflects a lack of strong correlation between size and speed (absolute values of the correlations between the size and movement traits considered ranged from 0.02 to 0.36; mean = 0.14; Appendix S1).

Estimates of the broad-sense heritability of the *Paramecium* morphological and movement traits ranged from 0.14 to 0.73 (Table 1). The heritability estimates of the size traits were 0.64 for length, 0.59 for width, and 0.44 for the aspect ratio. The heritability for movement traits of the paramecia were lower on average than the morphological traits but had greater variation ranging from 0.14 for net displacement to 0.73 for gross speed (Table 1).

3.2 | Prey and predator traits and foraging rates

We estimated a positive effect of size, speed, and their interaction on the proportion of *Paramecium* cells eaten by copepods (Figure 2; Table 2). The interactive effect was such that small paramecium had relatively constant risk of predation by copepods whereas large paramecium had greater risk of predation when they were fast (Figures 2 and 3). We found no statistically clear relationship between copepod

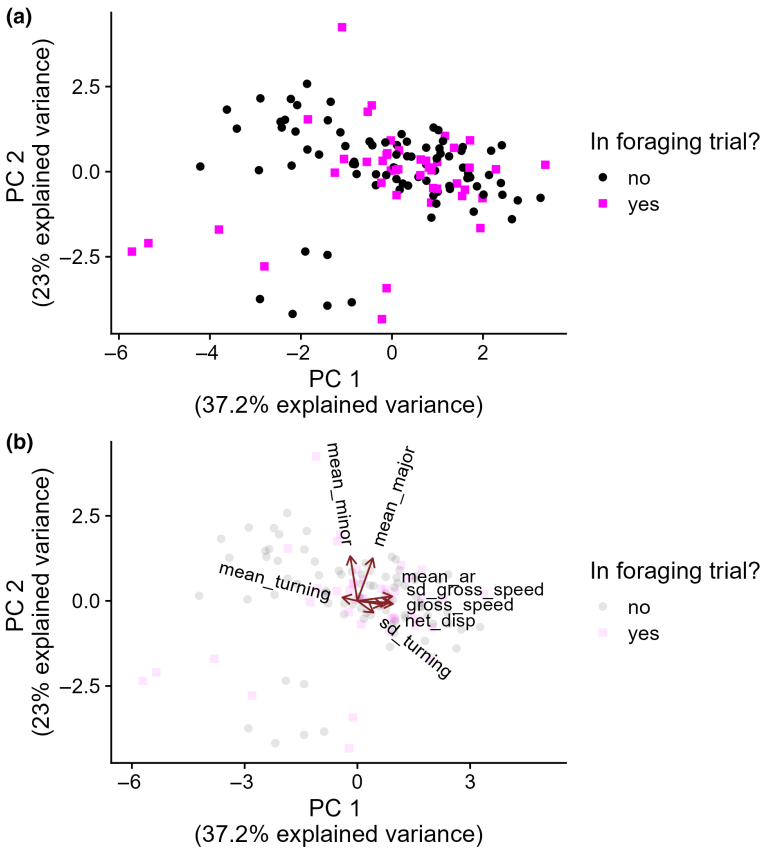

FIGURE 1 The first two components of a principal components analysis of the mean phenotypes of *Paramecium caudatum* outcrossed lines explained 60.2% of the total variation (a). The first principal component was positively associated with the mean aspect ratio of the paramecia (mean_ar) and several speed-related phenotypes (e.g. gross speed (gross_speed) and net displacement (net_disp)) and negatively associated with the mean turning angle (mean_turning; b). The second principal component was positively associated with the mean length and width of the paramecia (mean_major, mean_minor; b). Definitions of the phenotypic traits are in Appendices S2 and S5. The black circles in A and B represent outcrossed lines that were phenotyped but not included in the foraging trials whereas the magenta squares represent the outcrossed lines that were phenotyped and included in the foraging trials.

TABLE 1 Summary of the heritability of *Paramecium caudatum* traits.

Trait	Trait sum of squares	Total variance	Broad-sense heritability
Major axis (length)	1.4×10^{6}	2.2×10^{6}	0.64
Minor axis (width)	2.0×10^{5}	3.4×10^{5}	0.59
Aspect ratio (length/width)	133.3	239.3	0.44
Mean turning	2.1	13.9	0.15
SD turning	42.9	111.9	0.38
Gross speed	3.7×10^{8}	5.1×10^{8}	0.73
Net displacement	2.2×10^{9}	15.3×10^{9}	0.14
SD gross speed	4×10^{7}	6.5×10^{7}	0.62

Abbreviation: SD, standard deviation.

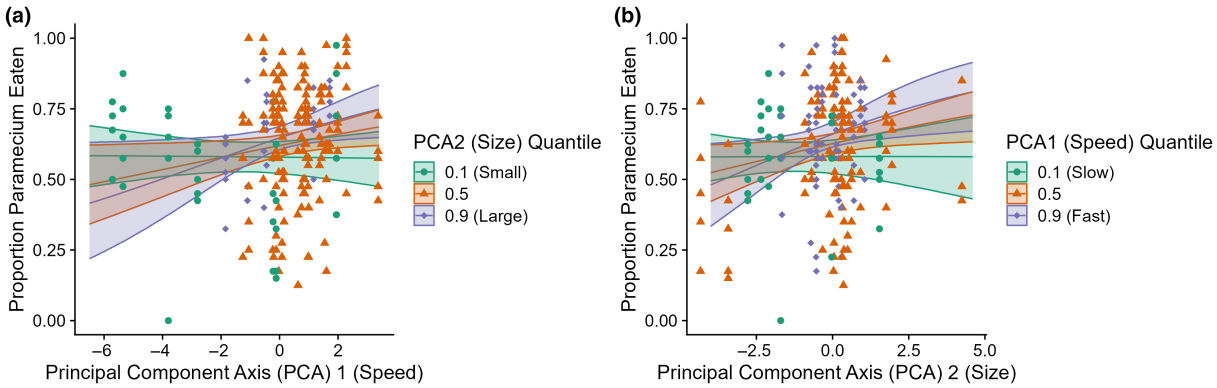

FIGURE 2 The proportion of paramecium eaten increased with paramecium speed (PCA1) and paramecium size (PCA2). However, there was an interaction in which the effect of speed was dependent on size such that larger, faster individuals were at greater predation risk whereas small individuals had similar risk regardless of speed. Coloured lines and shaded areas represent the means and 90% Credible intervals for the relationship between the principal component values and the proportion of *Paramecium* consumed by copepods for different quantiles of the principal component not on the *x*-axis (PCA2 in panel a and PCA1 in panel b). Points are coloured such that the green dots are for outcrossed lines from the 0.15 quantile or less of the principal component not on the *x*-axis, purple dots are for outcrossed lines from the 0.85 quantile or greater of the principal component not on the *x*-axis, and the remaining points are orange.

size and the proportion of *Paramecium* eaten by copepods (Table 2; Appendix S6).

4 | DISCUSSION

Intraspecific trait variation plays a critical role in the ecology and evolution of predator–prey interactions. First, predator and prey traits determine the outcomes of trophic interactions and, thus, their strengths and ecological consequences (DeLong, 2021; Wootton et al., 2023). Second, heritable variation in these traits provides the raw material for selection and the evolution and co-evolution of predator–prey interactions (Abrams, 2000; DeLong, 2021; Pimentel, 1961). Using outcrossed and then clonally propagated lines of *Paramecium caudatum*, we measured the structure and heritability of intraspecific variation in two key sets of traits for determining the outcomes of predator–prey interactions—body size and movement—and determined how these traits were related to the predation risk by copepods. Our study revealed some clear differences between hypotheses generated from studies of interspecific patterns in movement and morphological traits and their relationships with predation and our results. Furthermore, by simultaneously examining the structure and heritability of variation in *Paramecium* movement and body size traits along with their relationships to predator risk, our analyses also revealed how selection through copepod foraging might operate on *Paramecium*.

Allometric scaling studies have generally shown increasing movement speeds with increasing body size across a wide variety of organisms (e.g. Cloyed et al., 2021; Hirt et al., 2017). Although these studies largely focus on multicellular organisms, positive relationships between body size and speed have also been found within species in another ciliate protist (Pennekamp et al., 2019). Thus, we hypothesized that movement speed and body size would be correlated with one another across our outcrossed lines of *Paramecium*. Our analysis of the *Paramecium* phenotypes, however, showed low correlations between speed and body size. Instead, the morphological trait most correlated with speed was *Paramecium* aspect ratio. A previous study on flagellate protists that also showed no relationship between body size and speed may provide a potential explanation (Nielsen & Kiørboe, 2021). Nielsen and Kiørboe (2021) found that flagellates with smaller widths and flagellar characteristics that generated greater force had increased speeds. These results suggest

TABLE 2 Generalized linear mixed effects model results examining the relationships between *Paramecium caudatum* traits (PCA 1 and 2), their interaction, and copepod size with the proportion of *P. caudatum* consumed by copepods.

Parameter	Estimate	90% credible interval	Probability of direction
Fixed effects			
Intercept	−0.1	−2.1, 1.7	0.54
PCA 1 (speed)	0.09	0.01, 0.18	0.96
PCA 2 (size)	0.1	0.01, 0.19	0.97
PCA 1 and 2 interaction	0.05	−0.003, 0.11	0.944
Copepod length	0.52	−1.03, 2.2	0.7
Random effects			
SD copepod ID	0.5	0.38,0.65	
SD paramecium line	0.2	0.06,0.38	
Distributional parameters			
Beta-binomial phi	10.51	8.1,13.6	

Abbreviation: SD, standard deviation.

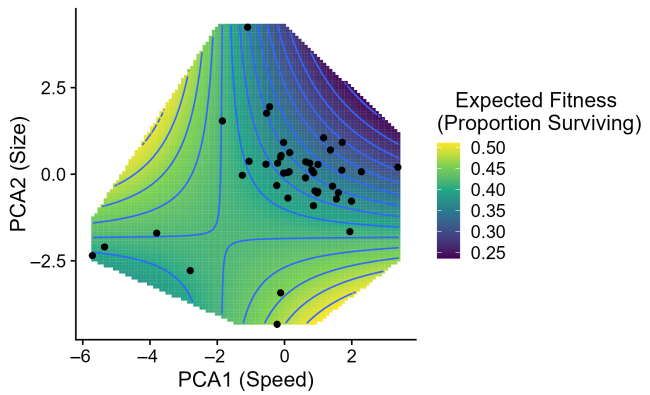

FIGURE 3 A predicted fitness surface using the expected proportion of paramecia surviving copepod foraging trials shows that expected fitness is lowest for paramecia that are fast and large. Points denote the principal component values for the outcrossed lines included in the foraging experiments combinations and the blue lines are contours.

that the relationship between the aspect ratio of the paramecia and swimming speed may be due to a decreased cell radius coupled with greater ability to generate force for a given width by having a greater number of cilia along the length of the cell. Regardless of the cause of the general independence between size and speed, its existence plays a potentially important role in how paramecia might respond to selection from copepod foraging. Specifically, the independence of size and speed suggests a lack of genetic correlation between the traits that can potentially allow the paramecia to separately respond to selection on each trait (Lande & Arnold, 1983). Coupled with predation risk from copepods being highest on fast and large paramecia, the independence of speed and size suggests that selection due to copepod predation could operate to reduce size, speed, or both with similar fitness results.

Many studies have shown how individual differences can lead to differences in interactions with other species including predation risk (e.g. Cuthbert et al., 2020; Morgan et al., 2016; Pretorius et al., 2019). Although many of the quantitative traits considered in these studies are likely to be heritable, this assumption is rarely tested because studies often use ontogenetic differences between individuals to examine effects of intraspecific variation or do not take the extra step to determine whether differences have a genetic basis. In our study, there is both ontogenetic variation within outcrossed lines due to differences among individuals in time since cell division and variation due to genetic differences among outcrossed lines. Our analyses show that the *Paramecium* traits we considered show significant heritability despite ontogenetic variation. We also find that some traits are more heritable than others. For example, the size-related traits we examined showed a moderate amount of heritability, whereas the movement-related traits showed greater variation in heritability. Previous studies have found that morphological traits, in general, have greater heritability than behavioural or physiological traits (Dochtermann et al., 2019; Mousseau & Roff, 1987; Stirling et al., 2002). Our results are consistent with these meta-analyses even though they were largely based on multicellular organisms and biased towards vertebrates. Given the high heritability estimates for gross speed and its standard deviation that exceed those of the morphological traits, we also hypothesize that there may be a tight link between these movement traits and ciliary morphology or density (Funfak et al., 2014; Osterman & Vilfan, 2011). Overall, the heritability of morphological and movement traits suggests that although certain traits may be able to respond more readily to selection, the paramecia should be capable of evolving in both size- and movement-related traits.

Predator and prey body sizes and velocities in cross-species comparisons show clear relationships with predator feeding rates (Coblentz et al., 2023; Pawar et al., 2012; Uiterwaal & DeLong, 2020; Vucic-Pestic et al., 2010). In general, these studies show that predator feeding rates increase with increasing predator size and with higher movement velocities in either species. Further, cross-species allometries between size and velocities suggest higher feeding rates of predators on larger prey due to greater encounter rates (although this could be counteracted by longer handling times). These patterns led us to hypothesize that: (1) predation risk for the paramecia would increase with *Paramecium* body size and velocity, and (2) predation risk for the paramecia would increase with copepod body size. In contrast, we found evidence of an interaction through which predation risk was highest for large, fast paramecia and was nearly constant for small paramecia regardless of speed. We hypothesize that the reason for this is that smaller paramecia may be harder to detect and capture than larger paramecia, leading to similar predation rates on

smaller paramecia regardless of their velocity and encounter rates. Larger paramecia may be easier to detect and capture, leading to a dependence of predation risk on velocities and encounter rates. These hypotheses are supported by studies of the mechanosensory mechanisms of prey detection in copepods showing larger prey have a greater detection distance than smaller prey (Almeda et al., 2018; Jonsson & Tiselius, 1990; Kiørboe & Visser, 1999). An alternative hypothesis from optimal foraging theory is that the copepods fed more so on larger paramecia due to their higher energy content and ate more of the faster, large paramecia due to higher encounter rates (Charnov, 1976). A reduction in protist size in response to predation has been noted in several predation experiments (Fyda et al., 2005; Griffiths et al., 2018; Kratina et al., 2010; terHorst et al., 2010). Furthermore, although some previous studies have also found unimodal relationships between predation rates and prey size, an analysis of our model residuals showed no evidence of a unimodal relationship (Appendix S7). We suspect there is no unimodal relationship in our study because studies that do show unimodal relationships between predation rates and prey sizes typically span orders of magnitude in predator–prey body mass ratios whereas predator–prey length ratios in our system only ranged from 5 to 13 (Kratina et al., 2022; Rall et al., 2012; Vucic-Pestic et al., 2010). Additional experiments may be able to tease apart the causes of the interaction between paramecia size and speed in determining *Paramecium* predation risk, but our main takeaway is that copepod foraging generates correlational selection—selection on a trait that depends on the value of another trait—on the paramecia in size and movement (Brodie III, 1992; Lande & Arnold, 1983).

In contrast to *Paramecium* size, we found no evidence of an effect of copepod size on *Paramecium* predation risk. We hypothesize that this may be due to the large body size difference between paramecia and copepods and the relative range of size differences observed in the paramecia versus in the copepods. Again, studies examining the effects of predator and prey body sizes on predator feeding rates, both inter- and intra-specifically, generally measure these effects across orders of magnitude in variation of sizes or predator–prey body size ratios (Coblentz et al., 2023; Englund et al., 2011; Pawar et al., 2012; Rall et al., 2012; Uiterwaal & DeLong, 2020; Vucic-Pestic et al., 2010). In our study, mean paramecium lengths among the outcrossed lines used in the experiment ranged from 95 to 233 μm whereas copepod size ranged from 0.9 to 1.4 mm. It is possible that over a larger range of copepod sizes we would have found an effect of copepod size, but that feeding rates on paramecia are generally similar in the size range occurring among adult copepods. Despite the lack of an effect of copepod body size on *Paramecium* predation risk, our statistical model suggested that there was substantial variation among copepods through the random effect of individual copepod. As the model showed no statistically clear effect of copepod size and copepod hunger was standardized, variation among copepods may have been due to some uncontrolled factor such as age or behavioural differences (Toscano et al., 2016; Toscano & Griffen, 2014). Although our inclusion of copepod identity as a random effect in our statistical model may have masked the effect of copepod size on the proportion of paramecia consumed, we believe this is unlikely as there was no evident relationship between proportion of paramecium consumed and copepod size (Appendix S6). Thus, our results on copepod body size are a case in which intraspecific variation in predator and prey traits need not match those predicted from cross-species comparisons as found in some other predation studies (e.g. DiFiore & Stier, 2023; Gallagher et al., 2016; Gibert et al., 2017).

Altogether, the patterns of heritability and correlations of the paramecia traits coupled with the potential correlational selection from copepod foraging suggest that: (1) a variety of morphological and movement trait combinations can lead to similar fitness values, and (2) areas of similar fitness should be readily accessible by paramecium populations. This suggests there is no single adaptive peak in terms of paramecium morphology and movement in regard to copepod predation. Rather, there is a broad fitness plateau with similarly high fitness values for small paramecium and for large, slow paramecium (Figure 3). Although this fitness plateau may exist in the presence of copepod predation, *Paramecium* morphology and movement are likely to have important effects on many other functions such as competitive ability, dispersal, and their own feeding rates (Gibert et al., 2017; Pennekamp et al., 2019; Tan et al., 2021). In turn, these additional ecological effects of morphology and movement may lead to different fitness landscapes and patterns of selection on the paramecia. Nevertheless, strong copepod predation may act as a filter on *Paramecium* morphology and movement narrowing which combinations of size and speed can lead to high fitness. This reflects the overall challenge of understanding how the genetic structure of predator and prey traits interact with multiple sources of selection to shape predator and prey traits, the resultant strengths of predator–prey interactions given predator and prey traits, and their consequences for populations and communities.

5 | CONCLUSIONS

The reciprocal relationships between predator and prey traits and the outcomes of their interactions are central to the functional ecology and evolution of predator–prey interactions (Abrams, 2000; DeLong, 2021; Pimentel, 1961; Schaffer & Rosenzweig, 1978). Understanding these reciprocal relationships requires simultaneous knowledge of how traits influence the outcomes of trophic interactions and the underlying genetics of the traits involved. Using a laboratory system, we determined the heritability and correlations of morphological and movement traits of a prey species and their relationships to predation risk. Our results revealed mismatches between expectations from cross-species allometric relationships and intraspecific patterns in our prey while also revealing the potential for predators to impose correlational selection on uncorrelated traits. These patterns suggest an ability of the prey to adapt to predation in a diversity of ways leading to similar fitness outcomes and call for a better reconciliation between patterns of inter- and

intraspecific variation. We hope our study inspires future work integrating quantitative genetics and functional predator ecology to provide a more synthetic understanding of the eco-evolutionary processes determining the outcomes of predator–prey interactions and their ecological and evolutionary consequences.

AUTHOR CONTRIBUTIONS

KEC, KLM, and JPD designed the study with input of the other authors, all authors performed the study, KEC performed the statistical analyses and led the writing of the manuscript, all authors helped to write the manuscript or contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and code can be found at https://doi.org/10.5281/zenodo.13314989 (Coblentz et al., 2024).

STATEMENT ON INCLUSION

All authors are currently based in the region where the study was conducted.

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SUPPORTING INFORMATION

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

Appendix S1. *Paramecium* trait correlation matrix.

Appendix S2. Table of *Paramecium* trait definitions.

Appendix S3. Copepod length and width correlation.

Appendix S4. Details of generalized linear mixed effects model.

Appendix S5. Principal Component Analysis results of *Paramecium* phenotypic traits.

Appendix S6. Copepod size and *Paramecium* predation risk.

Appendix S7. Model residuals and nonlinearity in size-predation risk relationships.

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