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Context-dependent individual behavioral consistency in *Daphnia*

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Abstract. The understanding of consistent individual differences in behavior, often termed “personality,” for adapting and coping with threats and novel environmental conditions has advanced considerably during the last decade. However, advancements are almost exclusively associated with higher-order animals, whereas studies focusing on smaller aquatic organisms are still rare. Here, we show individual differences in the swimming behavior of *Daphnia magna*, a clonal freshwater invertebrate, before, during, and after being exposed to a lethal threat, ultraviolet radiation (UVR). We show consistency in swimming velocity among both mothers and daughters of *D. magna* in a neutral environment, whereas this pattern breaks down when exposed to UVR. Our study also, for the first time, illustrates how the ontogenetic development in swimming and refuge-seeking behavior of young individuals eventually approaches that of adults. Overall, we show that aquatic invertebrates are far from being identical robots, but instead they show considerable individual differences in behavior that can be attributed to both ontogenetic development and individual consistency. Our study also demonstrates, for the first time, that behavioral consistency and repeatability, that is, something resembling “personality,” is context and state dependent in this zooplankton taxa.

Key words: animal personality; behavioral type; *Daphnia*; UV radiation; zooplankton.

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INTRODUCTION

Individual behavior plays a key role in the interaction between an organism and its environment, since behavioral changes are generally the first responses to an alteration in environmental conditions. It also affects, and is affected by, physiology, habitat choice, and ecological and evolutionary feedbacks (Chapman et al. 2011). The swimming behavior and the resulting spatial distribution of individuals are often driven by the (perceived) risk in different areas of the habitat and influenced by the individual state (e.g., age,

energy levels, hormonal levels). These consistent behavioral differences among individuals within and between contexts are important for the dynamics of animal populations (Smith and Blumstein 2008) and are sometimes termed behavioral types (Sih et al. 2004). They allow for novel traits to become established, and help species to adapt to new and challenging conditions (Dall et al. 2004, Sih et al. 2004, Zuk et al. 2014). Knowledge about state-dependent and inter-individual differences is thus needed to understand and predict the distribution patterns we observe in nature.

Most studies so far have addressed higher organisms, such as mammals, birds, and fish (Bell et al. 2009), but fewer have focused on invertebrates (Kralj-Fiser and Schuett 2014). Although consistent behavioral differences between individuals are likely more pronounced among higher-order organisms, there are numerous reasons why this should also be addressed among lower-order organisms, such as invertebrates. There are already several invertebrate studies showing consistent behavioral types (Sih and Watters 2005, Reaney and Backwell 2007, Briffa and Greenaway 2011, Schuett et al. 2011), although a recent review highlighting the discrepancy between personality research in vertebrates and invertebrates lists only few studies concerning larger aquatic invertebrates, such as mollusks, large crustaceans, and cnidarians (Kralj-Fiser and Schuett 2014). These studies found consistent individual differences in several aspects of behavior for sea anemones (*Condylactis gigantean*; Briffa and Greenaway 2011), hermit crabs (*Pagurus bernhardus*, reviewed by Kralj-Fiser and Schuett 2014), and aquatic isopods (*Idotea balthica*, Jormalainen and Tuomi 1989, Yli-Renko et al. 2015). This shows that consistent individual differences in behavior in aquatic invertebrates are likely a widespread and critical phenomenon. Small, rapidly reproducing organisms also allow for studies on possible ontogenetic changes in personality (Groothuis and Trillmich 2011) on time scales of days or weeks rather than months or years; especially in the field of plankton biology, such consistent behavioral differences between individuals have been neglected. Planktonic crustaceans occur in very high abundance and constitute an important link in marine and limnic food webs. To our knowledge, only one study has focused on consistent behavioral differences in a planktonic organism, showing individual differences in consumptive rates in marine copepods (Morozov et al. 2013). There have, however, been several studies on clonal variation in *Daphnia* showing that differences in swimming velocity and vertical distribution could be attributed to a large part to clonal diversity (Boeing et al. 2006, Sereni and Einum 2015).

Here, we investigate, for the first time, whether small clonal planktonic organisms, *Daphnia magna*, show repeatability in their normal swimming behavior and in their reaction to a naturally occurring lethal threat: exposure to ultraviolet

radiation (UVR). Ultraviolet radiation affects mortality rates and reproduction in several crustacean zooplankton species (Williamson et al. 1994), and *Daphnia* shows natural avoidance behavior when exposed to UVR, by swimming deeper into the water column adding to the phenomenon of diel vertical migration (Rhode et al. 2001). Individuals therefore face a trade-off between remaining in food-rich surface waters and being harmed by UVR (Hansson 2000, Hylander et al. 2014).

In order to assess the extent of individual behavioral consistency and whether this consistency is transferred to the coming generation, we quantified the inter-individual differences in swimming activity and UVR avoidance behavior three times during a mother's life time. Moreover, we also performed similar behavioral studies on two of her daughters, allowing us to estimate the individual consistency, plasticity, and the respective correlation between mother and daughter trait values.

METHODS

Study organism

Daphnia magna, originating from cultures collected in Lake Bysjön, southern Sweden (55.6753 lat, 13.5452 long), was used as study organism. Three cultures were kept in 12-L plastic aquaria and fed ad libitum two times per week with an algal suspension dominated by *Scenedesmus* spp. One week prior to the start of the experiments, we isolated 18 individuals, which were each transferred to a 200-mL glass jar containing a medium composed of 150 mL of tap water and 50 mL of the *Scenedesmus* sp. algal suspension. We added new food every second day by removing 50 mL of media and adding 50 mL of the *Scenedesmus* sp. algal suspension. Of these individuals, 11 survived the whole experimental phase, and from each of them, we chose two randomly selected offspring, which were also tested for repeatable UVR avoidance behavior. Hence, we tested 33 individuals in total, from 11 families originating from one population.

Behavioral assay

Each *Daphnia* was individually assayed for UVR response. We labeled the *Daphnia* using fluorescent nanoparticles (quantum dots) according to Ekvall et al. (2013). Behavioral assays were

performed in an aquarium ($0.15 \times 0.15 \times 0.6$ m) with four top-mounted blue light-emitting diode (LED) arrays as excitation lights for the fluorescent nanoparticles (655 ITK Carboxyl quantum dot, fluorescent at 655 nm; Life Technologies, Carlsbad, California, USA, Prod. Nr.: Q21321MP). The UVR threat was simulated using an UVR LED (250 mW/cm^2) positioned centrally at the top of the aquarium. All behavioral assays were recorded on videos and later analyzed using ImageJ (Abràmoff 2004) and OpenCV C++ library (<http://opencv.org>). For more detailed information regarding labeling and the experimental system, see Bianco et al. (2013) and Ekvall et al. (2013).

After labeling, each *Daphnia* was individually transferred to the aquarium for behavioral assays. It was left there to acclimatize for at least 20 min with the blue excitation light turned on. We terminated and postponed the experiment if the individual did not swim up to the upper 10 cm within 1 h. This was done in order to standardize the initial UVR stimulus among trials. After acclimatization, we recorded 3 minutes of video for three consecutive phases: without UVR, with UVR, and a final period without UVR, 9 minutes of recording in total. From these videos, we extracted the three-dimensional position of the individual two times per second. We then calculated the swimming velocity and the depth in the water column. We used a cumulative measure—the refuge demand—to assess the consistent behavioral differences in UVR avoidance between the individuals (Hansson et al. 2016). Refuge demand is the integral of the water depth of the individual over time, so that larger values are associated with animals that stay deep in the water column for a longer time (Fig. 1). We chose this measure over simple depth measurements before and during the exposure, as it includes the “reluctance” of re-emerging to the surface. The initial generation (“mothers”) was assayed once per day for three consecutive days. They were then placed back into glass jars where they reproduced. After a week, two juveniles from each mother were isolated and tested once per week for three consecutive weeks during their ontogeny following the same protocol as for their mothers. After the last assay, all individuals were photographed and their body size was measured using ImageJ.

Data treatment and statistics

All statistical analyses were performed using the statistical software R v 3.2.2 (R Core Team 2015). We used the lme function for linear mixed-effect models (Pinheiro et al. 2014). If not otherwise indicated, we always corrected for the repeated measurements of individuals during the three assays by including the individual’s ID as random factor and allowed for interactions between all independent factors in the initial models and used stepwise backward deletion selection. The reliability of the chosen test was confirmed by examining the distribution of the residuals. If unreliable, we used correlations instead. We transformed the swimming velocity measurements by square root transformation to normalize the data while preventing the scaling of the variances with the mean.

The general ontogenetic differences in swimming velocity between generations were assessed using a mixed-effect model with generation, assay, and UVR phase as independent factors and swimming velocity as dependent factor. Refuge demand is a cumulative measure over all three UVR phases and was therefore also analyzed with a mixed model with assay and generation as independent variables. In all three analyses, we included individual ID as random factor.

We analyzed the repeatability of the different behaviors by calculating the intraclass correlation coefficient (ICC) using the R package ICC (Wolak et al. 2012). For swimming velocity, we analyzed repeatability for each UVR phase (before, during, and after UVR exposure) over three consecutive assays, whereas refuge demand provided one repeatability measure over the three assays. The reliability of the chosen test was confirmed by visually inspecting the distribution of the residuals of a linear model with the individual ID as independent factor and the respective variable as dependent factor.

We tested the influence of body size on swimming velocity during the different UVR phases using data of mothers of the first assay and daughters in the third assay when they reached adult size and were closest in age. We used a mixed-effect model with body size of the animal and the UVR phase as independent variables and the swimming velocity as dependent variable, as well as individual ID as random variable. We calculated the relationship between mother and daughter trait values in swimming velocity, refuge

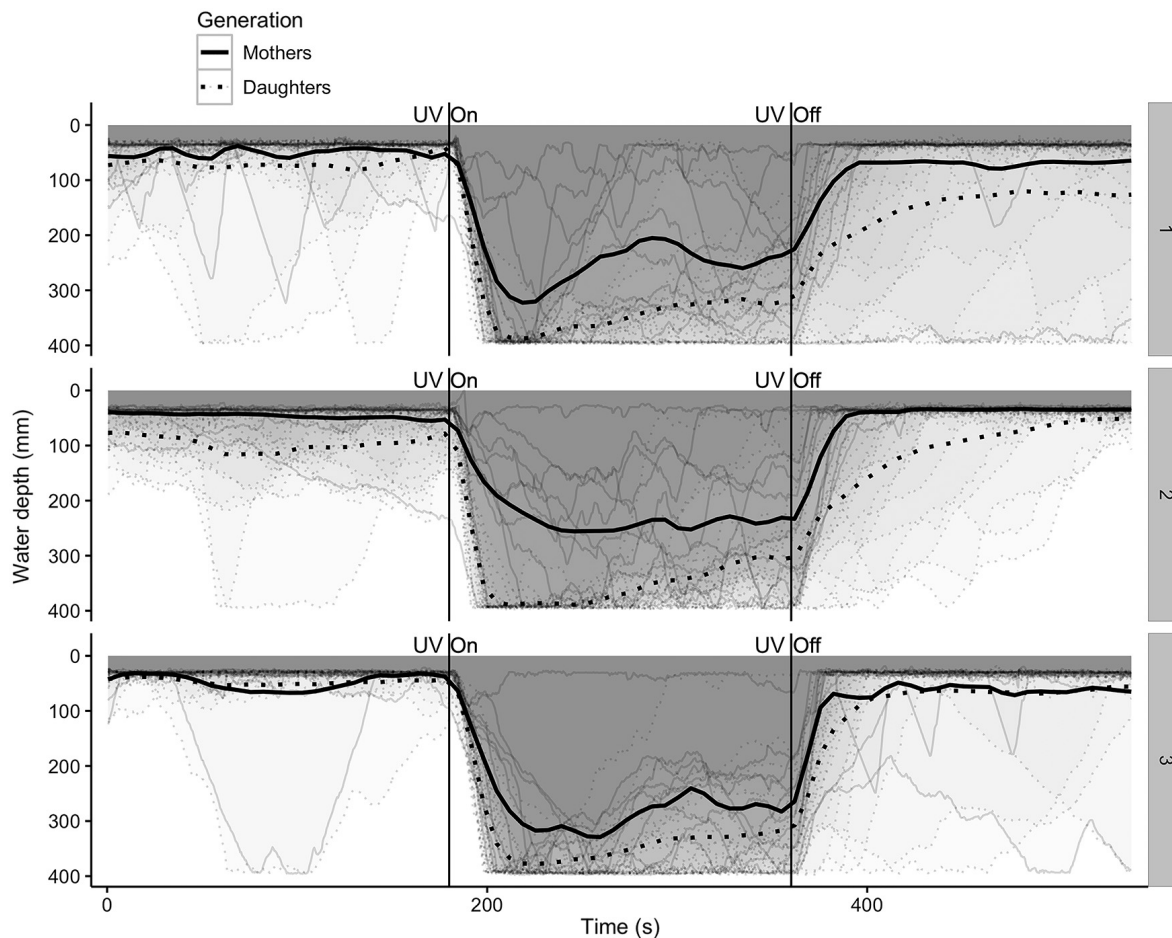


Fig. 1. The average (smoothed using local regression, thick lines) and individual depth and refuge demand at which individual daphnids (11 mothers [solid lines], 22 daughters [dashed lines]) were spotted during the three consecutive experimental assays and three UV phases.

demand, and water depth using Spearman's rank order correlation and a linear model for body length. For these comparisons, we used the averaged daughter response from assay 3 and the response of mothers from assay 3 to test approximately similar-aged individuals and individuals that had been tested three consecutive times.

RESULTS

The swimming velocity of individual *Daphnia* was repeatable between assays before they were exposed to UVR; that is, individuals that were fast in the first trial were generally also fast in the two consecutive trials, and likewise, slow ones remained slower (Table 1, Fig. 2). This was independent of whether all individuals, mothers, or

daughters were analyzed. The swimming velocity was not consistent within individual *Daphnia* during and after the exposure over the three assays (Table 1). Swimming velocity was explained by two significant interactions: generation and UV phase as well as generation and assay (see Appendix S1: Fig. S1; Table 2). While daughters were generally faster than the mothers in the first assay, this pattern reversed in the third assay (Appendix S1: Fig. S1). More interestingly, mothers swam faster than daughters during UVR exposure, but the opposite was true before and after exposure (Appendix S1: Fig. S1). Once adult, larger-sized animals generally swam slower than smaller ones (mean $5.04 \text{ mm/s} \pm 2.76 \text{ SD}$; estimate = -2.77 SE = 0.72 ; $F_{1,30} = 14.59$, $P = 0.0006$).

Table 1. Repeatability (R) values, that is, the proportion of the total variation that is reproducible among repeated measurements of the same individual, for refuge demand and swimming velocity.

Response variable Phase	All individuals	Mothers	Daughters
Refuge demand	$R = 0.274$ CI = [0.063, 0.503]	$R = 0.075$ CI = [-0.219, 0.517]	$R = 0.157$ CI = [-0.082, 0.452]
Swimming velocity			
Before	$R = 0.43$ CI = [0.21, 0.63]	$R = 0.744$ CI = [0.451, 0.915]	$R = 0.357$ CI = [0.097, 0.622]
During	$R = 0.164$ CI = [-0.041, 0.404]	$R = 0.177$ CI = [-0.176, 0.614]	$R = 0.090$ CI = [-0.135, 0.387]
After	$R = 0.21$ CI = [-0.004, 0.44]	$R = 0.576$ CI = [0.207, 0.846]	$R = 0.107$ CI = [-0.121, 0.404]

Notes: The upper and lower limits of the confidence interval (CI) are also shown. Significant results are emphasized in boldface.

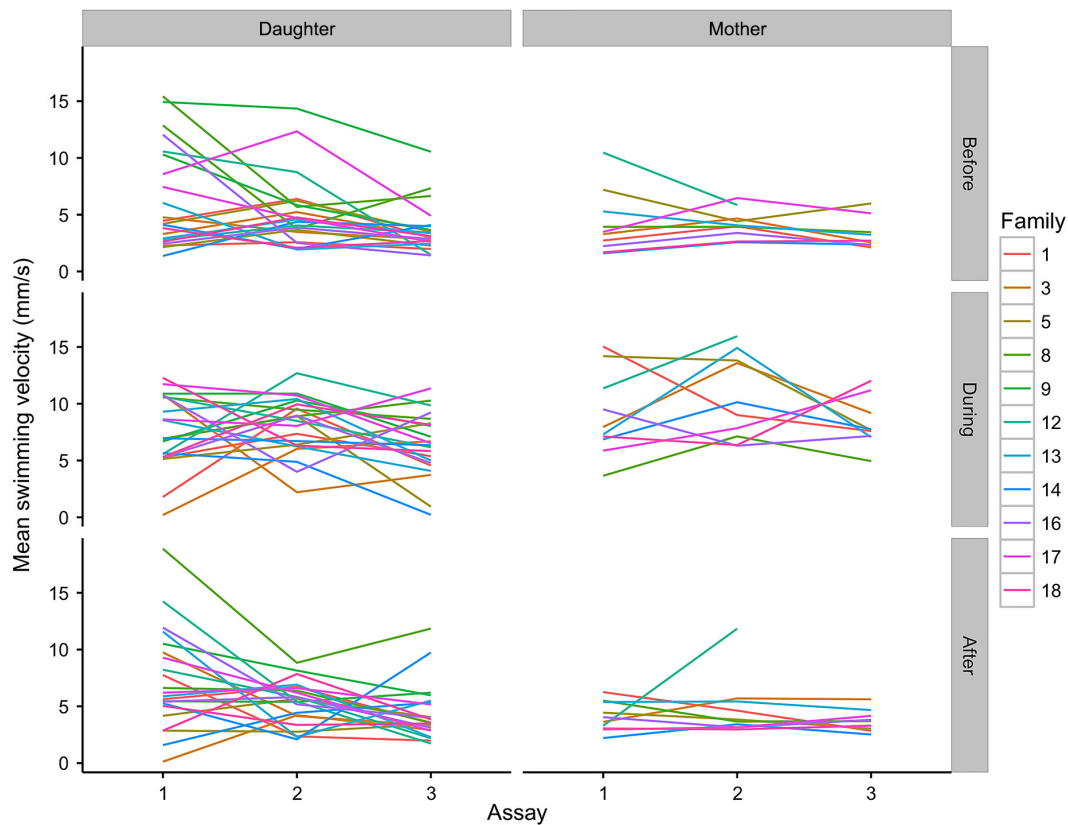


Fig. 2. Individual mean swimming velocity (mm/s) of *Daphnia* mothers and daughters measured over the three assays, before, during, and after exposure to ultraviolet radiation threat. Each line denotes color-coded family identification.

Table 2. Results of the final mixed model results testing the influence of the generation, assay, and ultraviolet radiation (UVR) phase on swimming velocity.

	Num df	Den df	F-value	P-value
Intercept	1	250	217.81	<0.0001
Generation	1	31	1.12	0.3
Assay	2	250	13.2	<0.0001
UVR phase	2	250	14.97	<0.0001
Generation:assay	2	250	3.17	0.044
Generation:UVR phase	2	250	8.64	0.0002

Note: The conditional R^2 of the model is 0.48.

Almost all individuals gathered at shallow depths before and after the UVR treatment, while they escaped into deep water when exposed to UVR (Fig. 1). The refuge demand of mothers was generally smaller than that of their daughters ($F_{1,31} = 24.53$, $P < 0.0001$), but once daughters became adult, the differences evened out (Fig. 3). The refuge demand, that is, the overall escape behavior, showed individual consistency when considering all individuals together, although

when analyzing each generation separately, it was not (Table 1).

There was no correlation between mother and daughter values in swimming velocity (Spearman's rank order correlations: before UVR: $S = 74$, $\rho = 0.55$, $P = 0.10$; during UVR: $S = 184$, $\rho = -0.12$, $P = 0.76$; after UVR: $S = 160$, $\rho = 0.03$, $P = 0.95$), refuge demand (Spearman's rank order correlation $S = 212$, $\rho = 0.036$, $P = 0.92$), and depth positioning behavior ($S = 190$, $\rho = -0.15$, $P = 0.68$). However, there was a relationship between the body size of mothers and that of daughters (slope = 0.37, SE = 0.14, $F_{1,9} = 6.91$, $P = 0.027$).

DISCUSSION

Here, we show that, despite being a clonal organism, *Daphnia magna* individuals are far from behaving like identical robots. Instead, they show individual repeatability in swimming velocity especially before exposed to the UVR threat. This was independent of ontogenetic

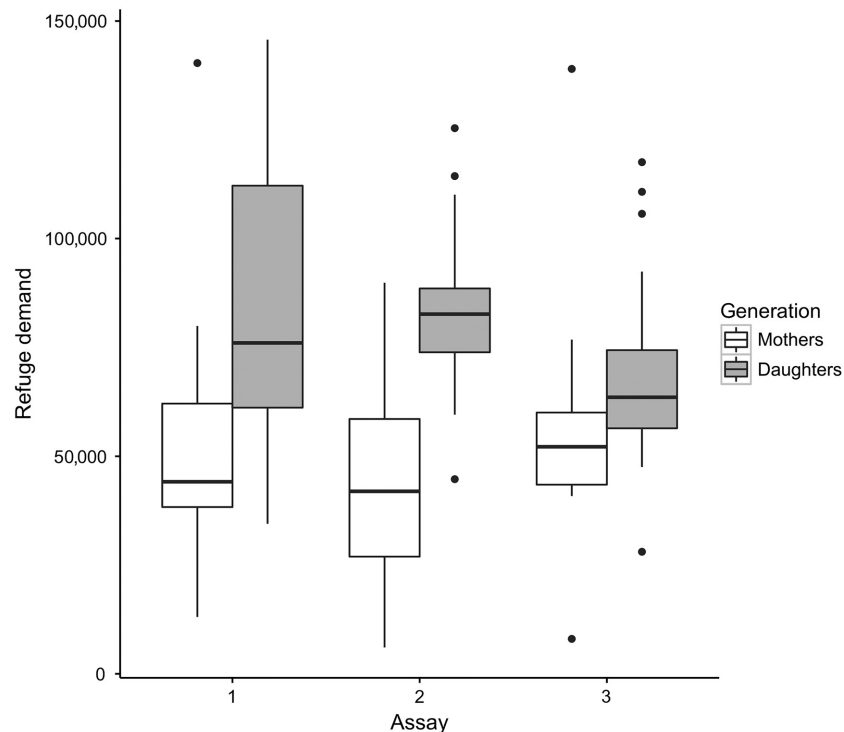


Fig. 3. Boxplot showing the median differences in refuge demand (mm*s) between mothers and daughters. It shows that mothers can generally be found higher in the water column than their daughters. This difference diminishes once the daughters become adults themselves.

effects, as the results are robust also when analyzing mothers and daughters separately. Hence, a fast-swimming individual in trial one was generally also fast in consecutive trials, and vice versa (Table 1, Fig. 2). However, once they were exposed to the UVR threat, the consistent differences in swimming velocity between individuals disappeared. As expected, swimming velocities were highest during their escape to deeper waters, suggesting that it is adaptive among *Daphnia* to avoid UVR (Hansson and Hylander 2009, Williamson et al. 1994).

Interestingly, adult individuals were slower than younger ones in a neutral environment, but had a higher swimming velocity during UVR exposure (Appendix S1: Fig. S1). However, in contrast to previous studies (Hansson and Hylander 2009, Hylander et al. 2014), daughters responded more strongly to the UVR threat than mothers. Accordingly, daughters had a higher refuge demand and remained closer to the bottom, while mothers occurred at different depths during the UVR exposure (Fig. 1). This could be due to the more severe UVR effects on dividing cells in the offspring (Zellmer 1995) or a generally more explorative behavior of older individuals. The refuge demand, that is, the overall escape behavior, was highly repeatable within individuals when analyzing mothers and daughters together (Table 1), suggesting individual consistency, that is, that some individuals are more risk taking than others over consecutive exposures. However, this behavioral consistency does not remain when separating mothers and daughters. This indicates that these repeatability estimates were confounded by ontogenetic differences. The daughters' refuge demand eventually approached the one of the mother generation over time (Fig. 3), illustrating the influence of ontogenetic and morphological state on personality and behavior (Groothuis and Trillmich 2011, Wilson and Krause 2012).

Combining the results of refuge demand and swimming velocity suggests that behavioral consistency in *Daphnia* depends on the environmental context and the considered traits. Undisturbed individuals, that is, before the UVR exposure, showed consistent behavioral differences in swimming behavior, suggesting an "optimal" behavior that is state specific and can differ between individuals. The adaptive value of these differences, however, remains to be tested.

There was no relationship between the swimming velocity and refuge demand of mothers and daughters. Taken together, each new generation is therefore likely to express a new suite of behavioral types for refuge demand independent of the mother generation. With regard to swimming velocity, a similar variation within individuals of the same clone has been previously observed in daphnids (Dodson et al. 1997). A strategy that allows for phenotypic variation in each generation should be especially favorable in an unpredictable environment, such as small ponds and tidal pools, which are the natural habitats of daphnids.

In a broader context, our results imply that some zooplankton distribution patterns in time and space can emerge from individual behavioral types and state-dependent decisions and are not just the average behavior of the whole population. Although low sample size and ontogenetic changes can influence repeatability of results (Wolak et al. 2012, Biro and Stamps 2015), our study suggests that consistency in behavior is important and prevalent in *Daphnia*. However, we encourage future studies using *Daphnia*, but also other planktonic organisms, to include large sample size and also to monitor the ontogenetic stage of the organisms. These should also aim at linking different personality traits directly to life-history traits such as fecundity or reproductive strategy (size at birth vs. the number of offspring), which would give insight into the evolutionary and ecological importance of the observed pattern; especially when our approach is combined with elaborate and repeated heritability studies that take into account several different populations (De Meester 1991), the eco-evolutionary consequences will become clearer. Based on our findings, we conclude that *D. magna* shows consistent individual intra-clonal differences and repeatability in swimming activity. This suggests that individual behavioral consistency, resembling personality, exists even at such low phylogenetic levels as planktonic zooplankters; however, more research is needed to assess its importance and prevalence in this important group.

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Jan Heuschele and Mikael T. Ekvall contributed equally to the paper.

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