Born this way: individuality is seeded before birth and robust to environmental stress

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Abstract

Consistent individual differences in behavior, known as behavioral individuality, are pervasive across the animal world and have major ecological and evolutionary consequences. Nevertheless, we still have a limited understanding of what drives individuality and how it emerges during ontogeny. Here, we subjected clonal individuals to a ubiquitous yet critical environmental challenge—the threat of predation—to disentangle the developmental mechanisms of individuality. Under such a salient environmental stressor, among-individual differences may collapse or expand depending on whether there is a single or multiple optimal strategies, demonstrating that individuality itself is a developmentally plastic trait. If, however, the environment does not impact among-individual variation, this suggests that individuality is determined before birth. We continuously tracked the behavior of genetically identical fish (Amazon mollies, *Poecilia formosa*), reared with or without predation stress, from birth through their first month of life. Predation shifted mean-level behaviors, with predator-exposed individuals swimming more slowly and spending more time near their refuges. However, the magnitude of individuality (as evidenced by repeatability) increased similarly over development in both treatments, indicating that individuality crystallizes robustly over time, even under stress and in a vacuum of genetic variation. Predator-reared fish also exhibited greater within-individual variability in refuge use, suggesting increased behavioral flexibility or disrupted developmental canalization in response to stress. Surprisingly, maternal identity, but not maternal behavior, was the strongest predictor of swimming speed, pointing to non-behavioral maternal effects as a key pre-birth source of behavioral variation. Refuge use however was not at all predicted by maternal identity, indicating that major fitness-related behaviors can have entirely different developmental mechanisms. Collectively, we show that individuality persists despite environmental stress and is seeded before birth through non-genetic factors. Even in the face of a shared environmental challenge, the behavioral trajectories of individuals are unique.

Introduction

Understanding what shapes individuality has been a long-standing, fundamental question in the field of biology that has permeated many aspects of culture, from philosophy to science fiction. Individuality, or consistent differences in behavior among individuals, is ubiquitous across the animal kingdom [1–5], can have important fitness implications for individuals [6–11], and can shape the evolutionary trajectories of populations [12–14], even driving speciation [15,16]. Where do individual differences in behavior come from? While this question has been historically posed as the “nature vs nurture” debate, this framing is now widely regarded as a false dichotomy, as both genetic and environmental variation will almost always interact to influence an individual's behavior. Considerable effort has been spent controlling for these two factors in order to pinpoint the drivers of behavioral individuality. Nevertheless, there is a growing body of work indicating that even when genetic and environmental variation is minimized, individuals still exhibit consistent differences in their behaviors [17–20], even at birth [21,22]. Some of this variation may be due to variation in pre-birth influences, such as maternal effects or developmental stochasticity, which may play an underappreciated role in generating variation among individuals [5,20,23–27]. This type of non-genetic variation may help set the seed around which further behavioral individuality crystallizes. Regardless of where such initial differences arise, the continued persistence of individuality despite our best efforts to minimize it suggests that we still lack a full understanding of the key mechanisms underlying its emergence. To identify these mechanisms, we must consider not only *what* shapes behavior, but also *how* behavioral differences emerge over the course of life.

Development is an iterative, path-dependent process, where early experiences may lead to lasting behavioral differences [28,29]. Thus, tracking how individuals respond to environmental challenges during development can reveal the processes that shape their behaviors. One predominant environmental feature that individuals must contend with is that of risk, most notably in the form of predation. Because most animals are subject to predation risk, their behavioral responses to this risk can heavily impact their fitness. Across taxa, predation stress during development has been shown to have profound effects on individual behavior, brain function, and personality [30–41], making predation a salient environmental candidate for shaping behavioral individuality. However, we still do not understand how predation shapes the *emergence* of individuality from birth throughout ontogeny. This is an important knowledge gap, because exposure to predation stress may impact patterns of individual behavioral variation in different ways. On the one hand, predation stress may collapse variation attributed to among-individual differences, making individuals behave more similar to each other, if there is an optimal behavioral strategy for survival in a predator-rich environment [42]. On the other hand, predation stress could instead expand among-individual differences [31], as there may be many strategies to mitigate risk in the face of predation. A final possibility is that individual differences may not be impacted by predation stress during development, implying a predominant role for pre-birth factors in driving behavioral individuality. Disentangling these possibilities requires closely tracking individual behavior from birth throughout development, across different developmental environments.

Studying the emergence of individuality over development can be very challenging due to the presence of confounding genetic variation in animals, as well as an inability to reliably measure behavior of individuals from birth in standardized conditions throughout ontogeny, either due to study species (e.g., some species require parental care introducing uncontrolled variation in experience among offspring) or technological limitations in following individuals at such early points in their lives. To fully understand the processes that shape behavioral variation, we must be able to solve these challenges and intimately track the details of the timing and rate that behaviors emerge in individuals [43].

Here, we used an ideal animal study system in conjunction with high-resolution tracking to bypass historical experimental limitations and deeply study the emergence of behavioral individuality over ontogeny. The Amazon molly (*Poecilia formosa*) is an all-female freshwater fish that reproduces via gynogenesis, resulting in genetically identical individuals [44–47], allowing us to minimize the effects of confounding genetic variation, analogous to twin studies in humans [48]. They are also live-bearing without any parental care, so individuals can be isolated from birth with minimal consequence to standardize life experience from day one. We combined this optimal study species with custom tracking technology (using cameras connected to individual Raspberry Pi computers [21,49]) to record and extract behaviors from individuals (N=107) at high temporal resolution (1s resolution for 10 hours every day) over the first 28 days of their lives. These fish were placed in one of two environmental conditions, with or without exposure to predator cues, to determine how stress shapes behavior and the magnitude of individuality across development. We also standardized the environments that these individuals' mothers experienced (none ever faced predation stress) and used the same tracking approach to measure the behavior of all mothers before they gave birth (N=15, for seven days) to test whether maternal behavior and/or identity explain offspring behavior (Figure 1). This resulted in over 30,000 hours of data-rich recordings (>100 million data points) that we then quantified using a convolutional neural network-based pipeline to track the position of each individual all day, every day. Using these data we extracted ecologically relevant behavioral metrics, such as swimming velocity and time spent near a refuge in the tank, that are likely to be affected by predation threat [50–54].

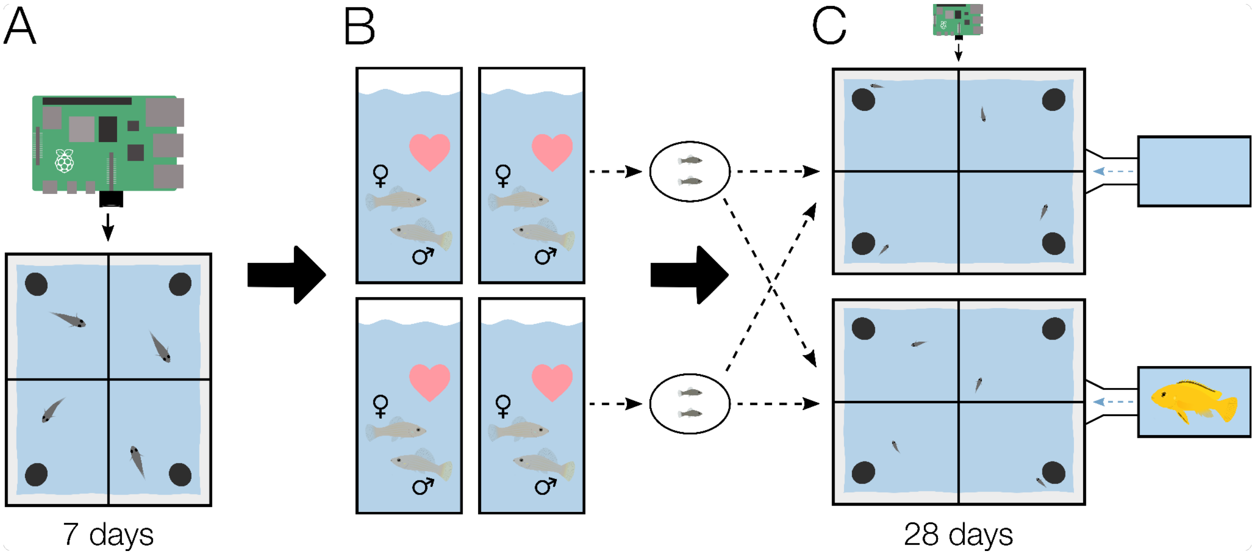

Figure 1. Experimental design. A) Adult Amazon mollies were each placed in identical individual tanks in our custom tracking system and recorded using cameras attached to Raspberry Pi computers for 12 hours each day over one week. B) Fish were then placed in individual tanks with a male Atlantic molly to initiate reproduction. C) Offspring born from the breeding tanks were split evenly by brood and placed into individual tanks in one of two closed-water tracking systems—with and without water containing predator cues—and continuously recorded for four weeks.

In our study, we asked a series of questions to disentangle the developmental drivers of behavioral variation. First, we asked how average behavior shifts over ontogeny in the face of a significant environmental challenge (threat of predation). Predator-exposed fish may adjust fitness-relevant behaviors, such as swimming velocity and time spent near their shelter, and/or show different behavioral developmental trajectories from control fish. Second, and of prime interest here, we tested whether and how predation may alter the magnitude of individuality, quantified as the relative magnitude of variance among individuals, across time compared to animals that are reared under benign conditions. This will reveal whether individuality itself is developmentally plastic or seeded before birth through non-genetic factors. Finally, we looked for evidence of such pre-birth influences in the form of maternal effects, across developmental environments and behaviors, as a potential explanation for what may drive individual differences in behavior, even in the absence of genetic and environmental variation. Our powerful study system, large individual sample sizes, and high temporal resolution tracking provides a uniquely comprehensive understanding of the fundamental yet elusive processes that generate individuality.

Results

Predation stress during development impacts mean-level behavior

We used generalized linear mixed models to test for behavioral differences between treatments by including treatment, time, and their interaction as our fixed effects of interest. A significant interaction would indicate that behavioral change over ontogeny occurs differently in each treatment. Indeed, we found evidence for significant treatment x time interactions in both velocity (treatment x time: post.mean = 0.005 [95% CI: 0.002, 0.007]; *pd* = 0.999; Figure 2A) and refuge use (treatment x time: post.mean = 0.01 [95% CI: 0.004, 0.009]; *pd* > 0.999; Figure 2B). Even in the face of these significant interactions, there were still overall main effects of treatment for both swimming velocity (control: post.mean = 1.83 scaled pixels per second [95% CI: 1.04, 2.61]; predator: post.mean = 1.62 scaled pps [95% CI: 0.83, 2.41]; probability of direction (*pd*) = 0.999) and refuge use (control: post.mean = -0.04 scaled proportion [95% CI: -1.87, 0.11]; predator: post.mean = 0.18 scaled proportion [95% CI: 0.03, 0.32]; *pd* = 0.987), with predator-reared fish moving more slowly and spending more time near their refuge (Figure 2). For velocity, these differences between the two treatments appeared small, but were present on the first day of life (control: post.mean = 1.19 scaled pps [95% CI: 0.62, 1.73]; predator: post.mean = 0.75 scaled pps [95% CI: 0.30, 1.18]; *pd* = 0.985). Unlike velocity, there were no differences in refuge use on day one (control: post.mean = 0.22 scaled proportion [95% CI: -0.01, 0.44]; predator: post.mean = 0.25 scaled proportion [95% CI: -0.01, 0.48]; *pd* = 0.44). Neither velocity nor refuge use were predicted by body size (Table S1), and body size was not predicted by rearing environment (length: post.mean = -0.057 [95% CI: -1.712, 1.669]; width: post.mean = -0.160 [95% CI: -0.446, 0.099]).

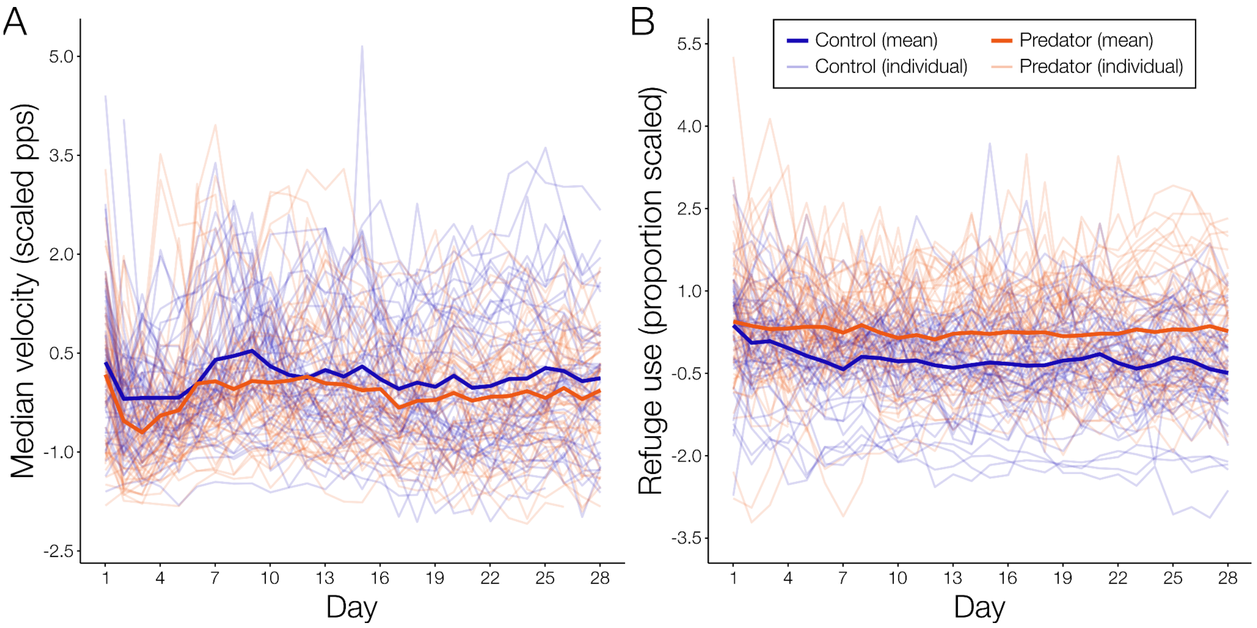

Figure 2. Average-level behaviors (velocity (A), in scaled pixels per second, and refuge use (B), in proportion scaled) of individuals over developmental time, reared with (orange) and without (blue) predation threat. Thin lines represent the behaviors of individuals over time, while thick lines represent mean behaviors of individuals in a given developmental treatment. Note that for median velocity (A), a single individual's day one data is not shown (but are included in analysis) due to its unusually high value (10.12 scaled pps) that would hinder visual clarity of the plot if included.

Individuality persists despite predation stress during development

We used generalized linear mixed models to explore patterns of individual behavioral variation, estimating variance components at each day (among- and within-individual) to then calculate repeatability of behavior over developmental time, our proxy for individuality. We found that for both velocity and refuge use, individuality persisted, regardless of environmental treatment (Figure 3A-B). In both treatments, individuals began life with low repeatability, which gradually increased over the next four weeks, resulting in individuals with highly repeatable behaviors by the time they were one month old. Notably, repeatability and among-individual variance did not differ by developmental treatment, as indicated by overlapping confidence intervals. However, for refuge use, within-individual variance was greater in predator-reared individuals (Figure 3D), indicating that predator-reared fish behave less consistently, or alternatively, exhibit greater flexibility in this behavior, within any given day compared to control-reared fish.

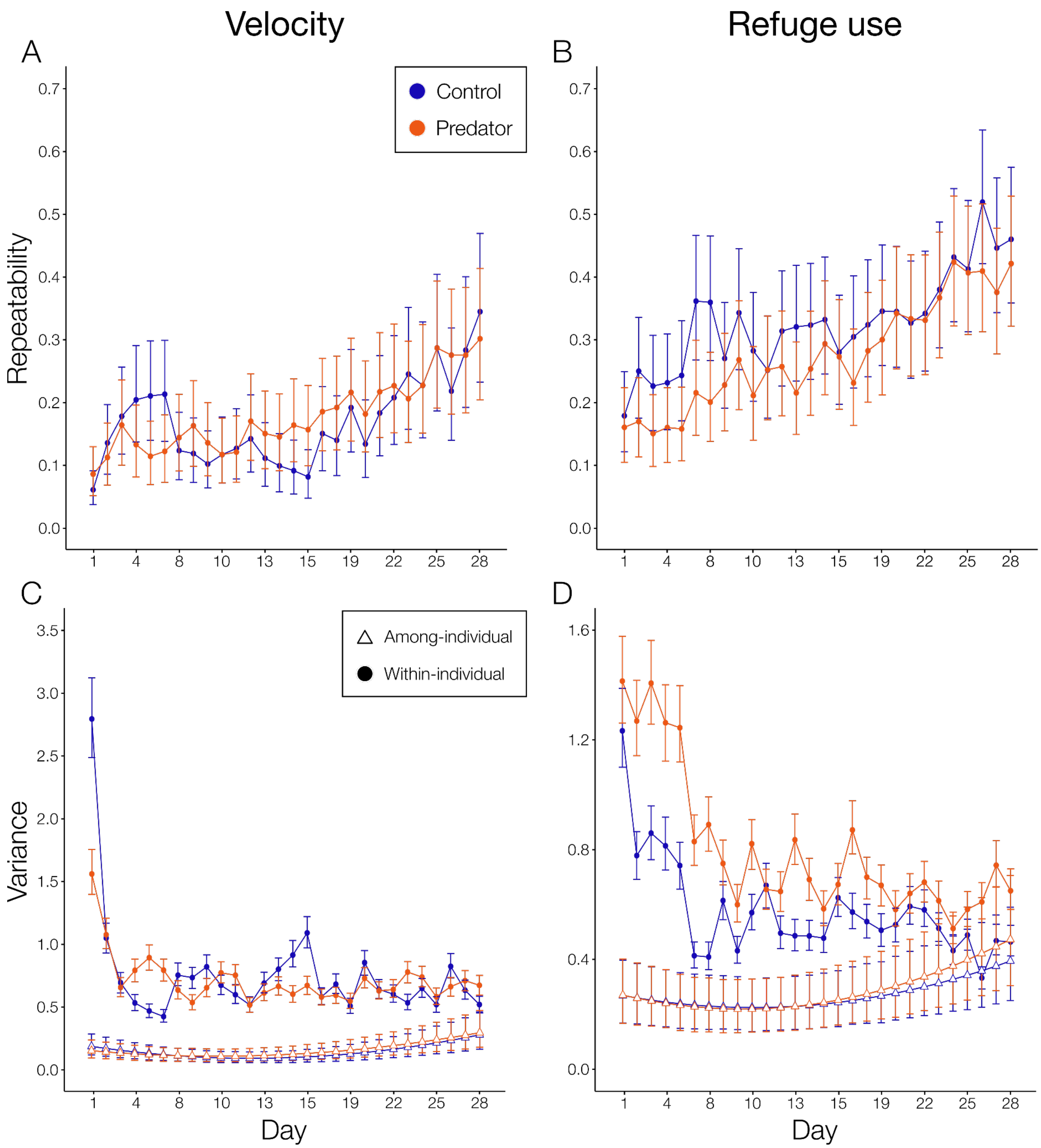

Figure 3. Extracted variance components over developmental time, colored by treatment. Repeatability—the proportion of variance attributed to variation between individuals (the metric of individuality)—increased over the first month of life for velocity (A) and refuge use (B), and this pattern did not differ between treatments, indicating the persistence of individuality in the face of predation stress. C-D show variance components as posterior medians, separated into among- and within-individual (i.e., residual) components. For velocity (C), both among- and within-individual variance did not change over time or between treatments, aside from day one of life, where within-individual variance was much higher, particularly in the control group. For refuge use (D), among-individual variance also did not differ by treatment. Within-individual

variance was highest during the first week of life, followed by a sharp decrease and plateau for the rest of development. However, within-individual variance was consistently greater in predator-reared fish over developmental time. Error bars on all plots indicate 95% confidence intervals.

Maternal identity strongly predicts velocity, but not refuge use

For both velocity and refuge use, maternal behavior did not predict offspring behavior (Figure 4; velocity: post.mean = 0.021 [95% CI: -0.100, 0.150]; refuge use: post.mean = 0.036, [95% CI: -0.162, 0.251]). However, despite this, we did find that maternal identity explained a large proportion of the variance in velocity, and this did not differ by developmental environment (control: ICC = 0.544 [95% CI: 0.303, 0.768]; predator: ICC = 0.546 [95% CI: 0.315, 0.780]; Figure 4A). For refuge use, the proportion of variance attributed to maternal identity was negligible (control: ICC = 0.012 [95% CI: 0.0002, 0.065]; predator: ICC = 0.009 [95% CI: 0.0001, 0.051]), with large amounts of uncertainty for each mother (Figure 4B). Maternal identity did not predict body size (length: post.mean = 0.546 [95% CI: <0.001, 3.926]; width: post.mean = 0 [95% CI: <0.001, 0.021]).

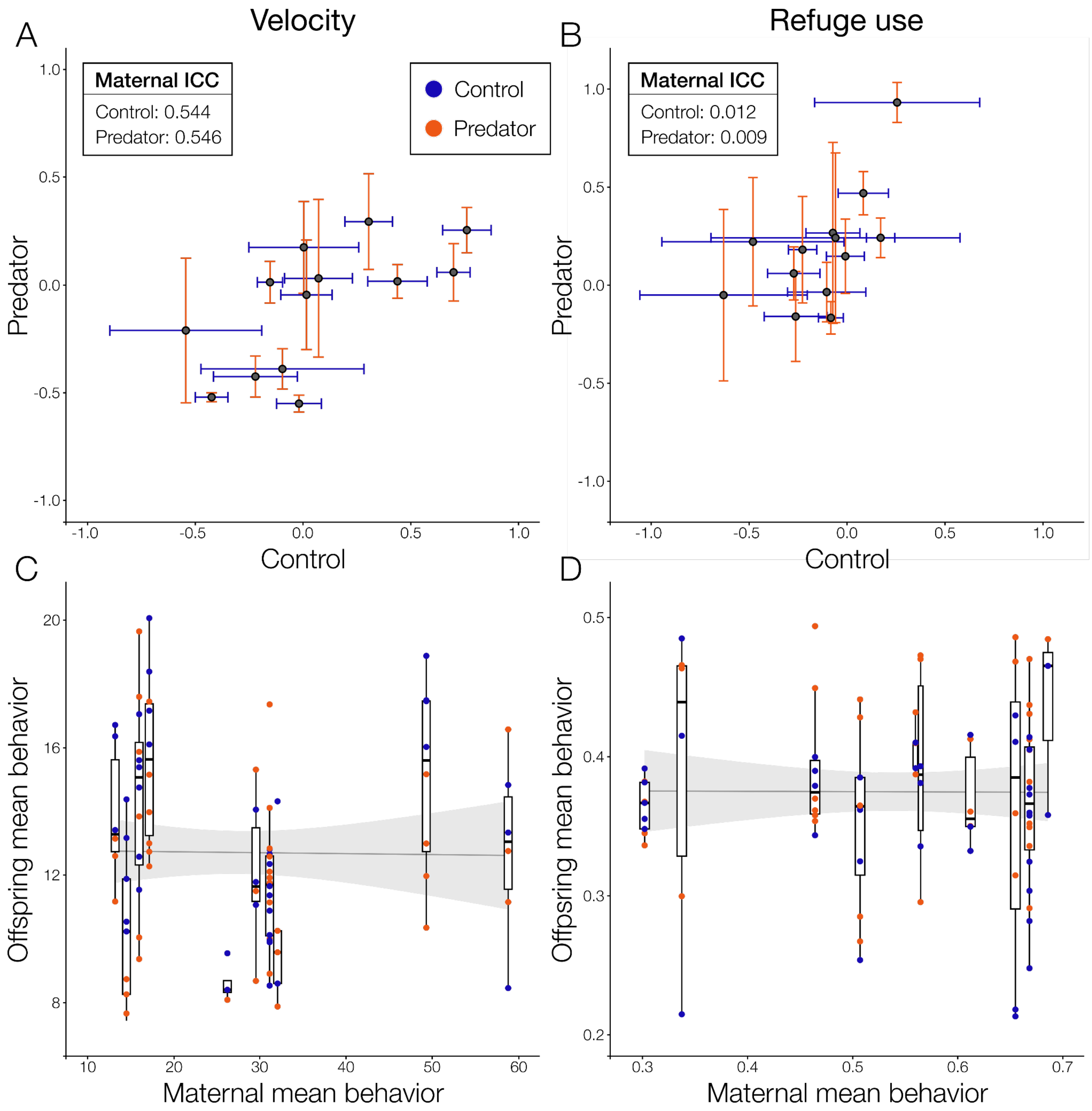

Figure 4. Evidence of maternal effects across behaviors. A-B show the relationship between control and predator siblings from each mother (A=velocity; B=refuge use; units=scaled behavior). Grey dots indicate the mean behavioral values of all offspring from a given mother. Error bars show the standard error of means for control (blue) and predator (orange) offspring of that mother. Maternal identity explains a large proportion of variance in velocity (0.534), but not refuge use (0.012). C-D show the lack of association between maternal behavior and offspring behavior, for both velocity (C) and refuge use (D). Boxplots represent individual mothers, while blue and orange dots show mean behaviors over developmental time for each individual offspring of that mother, reared with (orange) or without (blue) exposure to predator cues.

Discussion

We found that both developmental environment (Figure 2) and maternal identity (Figure 4A) are sufficient to drive mean-level behavioral variation, even in the absence of genetic differences. Perhaps surprisingly though, environmental stress did not disrupt the emergence of behavioral individuality (repeatable differences among individuals) across development, suggesting that individuality is seeded before birth rather than developmentally plastic in response to an individual's environment (Figure 3A-B). However, individuals reared under stress did show greater variability (within-individual variation) in their refuge use behavior, indicating that stress does increase behavioral flexibility or disrupt developmental canalization (Figure 3D).

Exposure to predation during development impacted mean-level behavior, with predator-reared individuals moving more slowly and spending more time near their refuges, showing that our animals responded to the cues of predation stress as we expected (Figure 2). Predation stress also affected the way in which behaviors emerged over time. For velocity, behavioral differences between treatments were immediately apparent on day one (Figure 2A); for refuge use, these differences emerged more slowly over the first week of life (Figure 2B). Considering the clonal nature of Amazon mollies, this reflects pure behavioral plasticity (that may be adaptive), suggesting that stress alone can alter the way in which behaviors emerge over ontogeny. Our comprehensive approach to investigating the effects of predation on the emergence of behavior supports previous work in various non-clonal taxa showing that exposure to predation during development shapes behavior [30–32,34,35,39].

In both environmental conditions, repeatability, and hence the magnitude of individuality, increased over ontogeny, suggesting that individuality crystallizes over time potentially through self-reinforcing behavioral patterns or internal feedback loops [21,55]. Perhaps surprisingly, this strengthening of individuality over time was not impacted by predation, with repeatability increasing similarly over development in both treatments (Figure 3A-B). This indicates that the seeds for individuality may be set before birth, and suggests that there may be many optimal behavioral strategies to overcome environmental challenges. While our results are contrary to other studies where exposure to predation either suppressed or expanded among-individual variance (e.g., [35–37]), our work measured behavior continuously over development, rather than at set intervals which can only provide snapshots of behavior. This temporally rich approach allowed us to estimate individual variance components daily, improving the accuracy of our repeatability calculations and revealing additional insights into how behavioral variation emerges throughout ontogeny [43]. One example of this can be seen in our estimates of behavioral variability. Although among-individual variance did not differ between experimental treatments, we did uncover temporal and treatment-level changes in within-individual variation by allowing residual variance to fluctuate over time in our model (heterogeneous residual variance; see methods for more information on our statistical approach). This revealed that while individuals in both treatments became less behaviorally variable (more consistent) as they aged, predator-reared fish showed greater variation in refuge use within a given day throughout development (Figure 3D). Greater behavioral variability in predator-reared individuals may reflect either an adaptive increase in behavioral flexibility, or a disruption of developmental canalization, in response to risk (see more on this below). We encourage others to account for heterogeneous residual variance over time, as this not only provides useful insights into the often underappreciated yet important within-individual variation [56–60], but also directly impacts the calculation of repeatability (which is dependent on correctly estimating residual variance at a given time point).

If individuality remains robust throughout environmental stress during development, what then drives it? We found that despite attempting to minimize potential maternal effects, for activity-related behavior (i.e., velocity), maternal identity predicted offspring behavior more so than any other component (including variance attributed to individual identity; Figure 4A). While this study was not designed to fully test for the effects of differential maternal experience (e.g., if the mothers themselves experienced predation stress or not) on offspring behavior because the mothers used in this experiment were all reared in similar conditions, our results suggest that maternal effects may play a notable role in shaping behavior and may be a key candidate for setting the seeds of individuality before birth. Despite this strong evidence of maternal effects, we did not see any association between maternal and offspring behavior (Figure 4C-D), indicating that the influence of mothers was not mediated by what they did, but rather by who they were (although maternal behavior was collected when fish were adults rather than during early development). This points to non-behavioral maternal effects, such as maternal provisioning, physiological state, and/or inherited epigenetic variation through changes in DNA methylation or maternal hormone transfer [21,23,24,61,62], as mechanisms through which behavioral variation emerges, even in the absence of genetic or environmental variation. Individuality may initiate through cryptic differences among mothers that bias developmental trajectories from the very start of life.

Interestingly, our two representative behaviors, velocity and refuge use, emerged differently over ontogeny and appeared driven by different factors. Variation in velocity was best explained by maternal identity (ICC=0.528; Figure 4A), while variation in refuge use was not explained by maternal identity at all (ICC=0.012; Figure 4B). As for developmental environment, differences between treatments were more apparent from the beginning of life for velocity, but not for refuge use, which emerged over the first week of life. Additionally, predation stress increased behavioral variability (within-individual variance) throughout development for refuge use, but not velocity. These differences in how behavioral traits arise during ontogeny and what drives their variation suggests that major suites of ecologically relevant behaviors can have different mechanisms of emergence. Behaviors relating to space or refuge use may be far more context-dependent than swimming speed. For example, while humans have highly consistent walking speeds [63], decisions about where and when to move, such as crossing a street, vary much more with context (e.g., how much traffic is present). Even fully understanding the developmental processes underlying one suite of behaviors may not inform others, and we should be careful to not generalize across traits when studying the mechanisms of animal behaviors.

Because our study focused on isolating the effects of the environment on behavioral development, we minimized genetic variation and carefully controlled experimental environments. However, it is impossible to eliminate all factors that could contribute to variation in behavior. Small genetic differences between individuals could still arise even among individuals within the same clonal lineage (e.g., either germ-line or somatic mutations [64]), and individual experiences, particularly of the mothers, are impossible to fully standardize from the first second of life.

One hallmark of sexual reproduction is its ability to generate variation among individuals. Yet here (and in other recent work [21,22]) we found a striking degree of among-individual variation even when genetic differences were minimized. Future work could reintroduce genetic variation in a fully standardized environment to better understand the contribution of allelic variation (or lack thereof) to the onset of individuality (e.g., comparing clonal Amazon mollies to their parental species, which naturally contain more genetic variation via sexual reproduction). Other ecologically important environmental factors, such as temperature [65–67] or resource availability [68], could also be systematically manipulated to further assess their impact on individuality. Given our evidence for maternal effects without behavioral transmission, a key next step is to explore how maternal environment shapes offspring behavior using a multigenerational design that investigates the impacts of maternal experience on mechanisms that canalize individual behavioral trajectories.

In this study, we disentangled the developmental drivers of individuality to understand the mechanisms that make individuals unique. Despite facing a strong environmental stressor that affected mean-level behaviors, individuality persisted, suggesting that development does not result in a single dominant phenotype, but rather an acceptable range. Even though mean values may be shifted up or down, the magnitude of variation among individuals does not change—behavioral individuality appears to be a robust and intrinsic feature of animal life.

Methods

Maternal behavior and breeding

To track the behavior of potential mothers of experimental fish, we placed adult Amazon mollies in individual tanks and monitored them for one week (Figure 1A). All adult fish were of similar age, from the same clonal lineage, and were reared in the same conditions. Experimental tanks were made of white acrylic (Perspex) and had identical environments (dimensions = 15x19x15 cm), each containing white gravel along two of the four sides of the tank, as well as a standpipe covered in a sponge filter that fish could also use as a refuge. All fish experienced the same feeding schedule (fed a standard amount of Tetra-Min flake fish food and brine shrimp twice per day), daily light cycle (12:12 light:dark), water temperature (26±2 °C), and water depth (10 cm). The experimental tank area was also surrounded by white curtains to reduce potential disturbance from external stimuli. Above each set of four tanks was a mounted camera attached to a Raspberry Pi 3B+ computer that recorded individual behaviors (see "Tracking behavior" below).

After one week, we transferred each adult fish to an individual 5-gallon glass tank containing an artificial plant for shelter and a male Atlantic molly (*Poecilia mexicana*) to initiate breeding (Figure 1B). Amazon mollies are gynogenetic, meaning that while all individuals are genetically identical to their mother, they still require mating with a male from a closely related species to trigger embryogenesis (his genetic material is unused in the offspring [44,46]). One week later, we removed males from the tanks. Throughout the breeding period, all fish experienced the same conditions (including temperature, light cycle, and food access). This resulted in 13 mothers that gave birth to offspring used in the rest of the study.

Offspring experimental setup

When fish were born in the breeding tanks, we transferred them that day (the first day of their lives) to their experimental tanks in the tracking system (Figure 1C). We transferred all newborn fish in a standardized way, by first moving them by net to a small container of water, then moving them to their respective individual tanks, limiting air exposure. We took individuals from each brood and distributed them evenly between individual tanks that were part of two closed circulating water systems: one containing a live electric yellow lab cichlid (*Labidochromis caeruleus*), and one without (control). Each closed water system was connected to a sump tank below the experimental tanks; in the predator system, this sump tank contained the cichlid, which was fed whole Tetra-Min flake food, blood worms, and brine shrimp daily. All tanks in a given filtration system shared water, so fish in the predator system were consistently receiving chemical (but not visual) cues from the cichlid (cues from this cichlid elicit anti-predator behavior in adult Amazon mollies [69]). To deliver alarm cues to experimental fish, which are released from the skin following mechanical damage [70–74], we fed the cichlid an anesthetized small black molly (*Poecilia sphenops*) twice per week—once between Monday and Wednesday, and once between Thursday and Friday—on random days during those two windows and at random times of day to reduce habituation. Experimental conditions for offspring were identical to those used for tracking the behavior of the adults (mothers), except fish were fed powdered instead of whole Tetra-Min flake fish food. Tanks contained aquarium gravel along the walls to help promote natural foraging behaviors, and each group of tanks was surrounded by curtains to reduce outside disturbance. There were always multiple individuals in a given shared water system, so fish did not perceive complete social isolation [21,22], which can lead to altered behaviors in some fish [75]. We allowed fish to develop in their individual tanks undisturbed for four weeks, resulting in data from 107 individuals.

Tracking behavior

For efficiency and reproducibility, all videos were processed within one of two snakemake pipelines (see supplemental code [76]), specialized either for adults or for juveniles. All videos were first cropped to exclude adjacent tanks using ffmpeg (version 6.1.1, FFmpeg Developers), based on manually labeled points. We also used labeled center-points to assign the (up to) four tracks in each video to specific individuals. For tracking adults, we used a neural network (efficientNet b3 [89]), trained and implemented using SLEAP [78]. For tracking babies, we similarly began with a neural network (LEAP [77]) using SLEAP [78], which was generally accurate, but struggled when small fish were above gravel. To address this, we also used a custom tracker based on a mixture of gaussians background subtractor [80], implemented using openCV [79] in python. Because this takes advantage of frame-to-frame differences, it was successful tracking fish over gravel. Both sets of tracks were filtered to remove extremely high density pixels (which likely represent false detections of stationary objects). To combine these two streams, we used a custom implementation of the Viterbi algorithm [81], which seeks to estimate the most likely path of some unknown value (in this case, the location of fish) based on probabilistic observed values (the two parallel detections of fish). From these post-processed tracks we calculated the median velocity, proportion of frames "active" (defined as moving > 5 pixels/second), median velocity when "active," and proportion of frames detected in the corner with the standpipe (which acts as a refuge). Videos were manually inspected by an expert observer (JHG) for major issues that would result in inaccurate tracking (i.e., missing or moved fish, camera movement).

Measuring body size

To estimate individual body size of offspring at the end of the experiment, we used a custom python script to extract crops of each individual (based on their detected position) on day 27 and manually labeled the head, tail-peduncle, and body width (at its widest point) using

Supervisely, a web-based computer vision platform [82]. The identity and treatment of fish in these crops were blinded during labeling.

Statistical analysis

All statistical analysis was conducted using R accessed through R Studio (R Studio version 2023.12.1, R version 4.3.3). We selected which behaviors we would investigate by eliminating highly correlated behaviors. This resulted in two behaviors, median velocity (swimming speed) and proportion of time spent near the standpipe (refuge use), that we used for analysis. In order to understand the effect of rearing environment on mean-level behaviors, whether behaviors changed over time, and whether maternal identity explained offspring behavior, we ran Bayesian bivariate mixed models using the MCMCglmm package [83] separately for each behavior (velocity and refuge use). All models included the behavior as our dependent variable, treatment (with or without predator exposure), day, hour, and the interaction between treatment and day as fixed effects, and individual and maternal ID as random effects because these were both of primary interest to our research question. We first conducted model selection to determine the additional random effects structure of our models (i.e. inclusion of random intercepts and slopes for individual and/or mother), choosing the least complex model within 2 of the lowest DIC value. To account for differences in behavior due to time of year (not all fish were reared at the same time), we next compared our models with and without a time of year variable as a fixed effect. We performed hierarchical clustering using the stats package to translate the time of year variable into batches; this revealed four primary clusters, which we used for our time of year batch variable. We also compared our models to one that allowed for heterogeneous residual variance over time, as this could impact repeatability calculations and reveal cryptic yet relevant information about the effects of the developmental environment on behavioral variability. For both behaviors, heterogeneous residual variance improved the models’ fit. The final model for velocity included treatment, day, their interaction, hour, and time of year as fixed effects, and random intercepts for individual and maternal ID (family = gaussian). For refuge use, the final model included treatment, day, their interaction, and hour as fixed effects (time of year did not improve the model fit), and random intercepts for individual and maternal ID (family = gaussian). All models were validated by ensuring variables of interest had low autocorrelation values (<0.1) and high effective sample sizes (>2500), and by visually inspecting trace and density plots. To aid with statistical interpretation of differences between treatment groups, we calculated probability of direction (*pd*) using the package bayestestR (a *pd* value > 0.975 is equivalent to a frequentist p-value of < 0.05 [84-85]).

To test for the effects of body size on behavior, we ran the full models described above with and without the inclusion of individual length and width as fixed effects. Because body size data was collected at the end of the experiment (day 27), any individuals that were not recorded through the end of the experiment could not have their body size measured, so we ran the models on a subset of the data that only included individuals with body size measurements (N = 90 individuals).

To test for differences in mean behaviors between treatments on day one of life, we ran bivariate mixed models on a subset of the data (day one) but excluded day as a fixed effect. We again conducted model selection to determine which other fixed effects should be included for the day one comparison (time of year and hour). Our final model for velocity included treatment and hour as fixed effects, and random intercepts for individual and maternal ID (family = gaussian), and for refuge use included treatment as a fixed effect, and random intercepts for individual and maternal ID (family = gaussian).

To estimate the proportion of variance explained by maternal identity, we calculated the intraclass correlation (ICC) by dividing the variance attributed to maternal ID by the total variance (maternal ID variance / (maternal ID variance + individual ID + residual variance)), separately for control and predator-exposed fish. To determine whether maternal behavior predicted offspring behavior, we ran our full bivariate mixed model (as above), this time with the inclusion of maternal behavior (separately for velocity and refuge use) on a subset of individuals that had data for their own and their mother's behavior (N = 86 individuals).

To partition variance components (among- versus within-individual variance) and estimate behavioral repeatability, our proxy for individuality, we ran separate Bayesian univariate mixed models for each treatment (control, predator) and each behavior. As for the previous models, we also conducted model selection to determine their random and fixed effects structure. Because our goal was to compare control and predator models directly, we chose the most complex model structure that was the best fit for either treatment group, then used this structure for both models to ensure that important sources of variation were not excluded. The best supported model structure for velocity included behavior as our dependent variable, developmental day, hour, and time of year as fixed effects, random intercepts and slopes for individual ID (across day), and random intercepts and slopes for maternal ID (across day). For refuge use, the best supported models included behavior as our dependent variable, developmental day and hour as fixed effects, random intercepts and slopes for individual ID, and random intercepts for maternal ID. Models were again validated by ensuring variables of interest had low autocorrelation and high effective sample sizes.

Estimating variance components and repeatability across time series data is challenging. When random slopes are present, meaning individuals are changing rank-order over time, conditional repeatability can be used to estimate the magnitude of among-individual variance at any given time point [86-87]; however, in these models, residual (i.e., within-individual) variance is typically described by a single component regardless of time. However, with growing evidence of the importance of within-individual behavioral variance [56-60,88], we chose to use heterogeneous residual models that can estimate within-individual variance at a given time point. Indeed, in our study, the best supported models (as described above) included both random slopes and heterogeneous residual variance. Therefore, we expanded the calculations of conditional repeatability proposed by [86] and [87] to also account for heterogeneous residual variance, estimated separately for each day. Our final repeatability equation included the variance attributable to individual intercepts ($\sigma^2_{\alpha 0}$), slopes ($\sigma^2_{\alpha 1}(x^*_1)^2$), their covariance ($2\rho\sigma_{\alpha 0}\sigma_{\alpha 1}x^*_1$), and time-specific heterogeneous residual variance ($\sigma^2_{\epsilon_{x^*}}$):

$$R_{c_{x^*}} = \frac{\sigma^2_{\alpha 0} + \sigma^2_{\alpha 1}(x^*_1)^2 + 2\rho\sigma_{\alpha 0}\sigma_{\alpha 1}x^*_1}{\sigma^2_{\alpha 0} + \sigma^2_{\alpha 1}(x^*_1)^2 + 2\rho\sigma_{\alpha 0}\sigma_{\alpha 1}x^*_1 + \sigma^2_{\epsilon_{x^*}}}$$

For all the models above, we used parameter-expanded priors from similar studies [21,57]; we also verified that these expanded priors were not biasing our data (using MCMCglmm default priors did not change results). To investigate the effects of treatment and maternal identity on offspring body size, we ran Bayesian mixed models (separately for length and width) with body size as our dependent variable, treatment and time of year as fixed effects, and maternal ID as a random effect (family = gaussian).

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Declaration of interests

The authors declare no competing interests.

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