Biological Journal of the Linnean Society, 2024, **143**, blae113
https://doi.org/10.1093/biolinnean/blae113
Advance access publication 23 December 2024
Original Article

OXFORD

Original Article

Genetics and resource availability shape divergence in life history and behaviour between locally adapted populations of Atlantic mollies (*Poecilia mexicana*, Poeciliidae)

John L. Coffin[1,5], Bethany L. Williams[2,3], Michael Tobler[2,3,4,*]

[1]Division of Biology, Kansas State University, Manhattan, KS 66506, USA
[2]Department of Biology, University of Missouri—St. Louis, St. Louis, MO 63121, USA
[3]WildCare Institute, St. Louis Zoo, St. Louis, MO 63110, USA
[4]Whitney R. Harris World Ecology Center, University of Missouri—St. Louis, St. Louis, MO, USA
[5]Present address: Washburn Rural High School, Topeka, KS 66619, USA

[*]Corresponding author. Department of Biology, University of Missouri—St. Louis, 1 University Blvd., St. Louis, MO 63121, USA. E-mail: tobler@umsl.edu

ABSTRACT

Phenotypic variation is common along environmental gradients, but it is often not known to what extent it results from genetic differentiation between populations or phenotypic plasticity. We studied populations of a livebearing fish that have colonized streams rich in toxic hydrogen sulphide (H_2S). There is strong phenotypic differentiation between adjacent sulphidic and non-sulphidic populations. In this study, we varied food availability to pregnant mothers from different populations to induce maternal effects, a form of plasticity, and repeatedly measured life-history and behavioural traits throughout the ontogeny of the offspring. Genetic differentiation affected most of the traits we measured, in that sulphidic offspring tended to be born larger, mature later, have lower burst swimming performance, be more exploratory, and feed less effectively. In contrast, maternal effects impacted few traits and at a smaller magnitude, although offspring from poorly provisioned mothers tended to be born larger and be more exploratory. Population differences and maternal effects (when both were present) acted additively, and there was no evidence for population differences in plasticity. Overall, our study suggests that phenotypic divergence between these populations in nature is caused primarily by genetic differentiation and that plasticity mediated by maternal effects accentuates but does not cause differences between populations.

Keywords: adaptation; extreme environment; hydrogen sulphide; maternal effects

INTRODUCTION

Phenotypic variation is at the heart of evolutionary analyses because it links the cause (natural selection) to the consequence (genotypic change) of adaptive evolution (Lande and Arnold 1983). We have known how inheritance causes resemblance between parents and their offspring for well over a century, reflecting a genetic component to phenotypic variation (Stenseth *et al.* 2022). However, trait variation can also be influenced by phenotypic plasticity, whereby a single genotype can give rise to alternative phenotypes in response to internal or environmental cues (West-Eberhard 1989, Pigliucci 2001). In addition, the environment experienced by parents can affect phenotypes of their offspring (i.e. parental effects; Uller 2008, Badyaev and Uller 2009), representing a case of plasticity that spans generational boundaries. Phenotypic variation in nature can therefore arise from genetic differences among individuals, plasticity induced by individual exposure to different environmental conditions, plasticity induced by parental effects, and their interactions (Scheiner 1993, Dingemanse and Araya-Ajoy 2015). For many natural systems, we know little about the origins of phenotypic variation, although it critically shapes our inference of adaptation in natural populations.

Plasticity induced by parental effects is particularly strong from mothers owing to their higher reproductive investment and, in viviparous species, the physically intimate relationship with their developing young (Lindholm *et al.* 2006, Wolf and Wade 2009). Such maternal effects are widespread in nature (Mousseau and Fox 1998) and can impact trait expression and evolution (Rossiter 1996, Wilson *et al.* 2005, Beckerman *et al.* 2006). Maternal effects can be adaptive if the expression of

Received 16 July 2024; revised 24 September 2024; accepted 26 November 2024

offspring traits is biased to match the environment experienced by the mother (Marshall and Uller 2007) or if mothers in good condition are able to endow phenotypes that provide a competitive advantage to their offspring in any environment (Grafen 1988, Monaghan 2008, Van Allen *et al.* 2021). However, maternal effects can also be maladaptive and produce mismatches between offspring phenotype and environment, as documented in some organisms responding to anthropogenic climate change that reduces the reliability of environmental cues (Schuler and Orrock 2012, Leonard and Lancaster 2020). Maladaptive maternal effects can also be related to stress, whereby physiological stress responses in mothers have unintended negative side effects on offspring (MacLeod *et al.* 2021). Regardless of whether maternal effects are adaptive, they are important biological phenomena that warrant careful attention and explicit accounting in evolutionary analyses owing to the non-genetic effects on phenotypic expression.

Phenotypic variation in nature is common along environmental gradients, but it is often unclear whether it is caused by genetic differentiation among populations or plastic effects that arise from population-specific environmental exposure histories experienced by mothers or directly by their offspring. For example, freshwater springs rich in toxic hydrogen sulphide (H_2S) in the Grijalva River basin of southern Mexico are extreme environments that are connected to adjacent non-toxic streams, and stark phenotypic gradients can be observed in fish occupying these habitats in as little as a few metres. Sulphide springs are complex ecosystems, with several correlated sources of selection (Tobler *et al.* 2016b). Hydrogen sulphide is toxic because it disrupts aerobic ATP production (Cooper and Brown 2008, Tobler *et al.* 2016b), but habitats rich in H_2S also differ from non-sulphidic habitats in other physical and chemical water parameters (e.g. lower dissolved oxygen concentrations, lower pH, and higher salinity) (Riesch *et al.* 2010a, Tobler *et al.* 2011, Greenway *et al.* 2014). Additionally, the communities of competitors and predators differ between habitat types. Sulphidic environments are generally characterized by low species richness but high population densities (Greenway *et al.* 2014). In addition, predatory fish are largely absent in sulphidic environments, whereas insect and avian predators can be more abundant (Tobler *et al.* 2007, Riesch *et al.* 2010a, Greenway *et al.* 2014). Resource availability also differs greatly between habitat types; fish in non-sulphidic environments eat primarily algae and detritus, whereas fish in sulphidic environments have shifted to eating primarily sulphide bacteria and invertebrates (Tobler *et al.* 2015).

Populations of Atlantic mollies (*Poecilia mexicana*), a species of livebearing fish of the family Poeciliidae, have independently colonized and adapted to sulphidic streams across multiple river drainages, and previous studies have documented that colonization of sulphide springs has been associated with convergent changes in morphology, locomotion, and respiration (Tobler and Hastings 2011, Camarillo *et al.* 2020), behaviour (Plath *et al.* 2007a, Lukas *et al.* 2021, Doran *et al.* 2022), physiology (Tobler *et al.* 2011, Barts *et al.* 2018, Greenway *et al.* 2020), and life-history traits (Riesch *et al.* 2011a, b, 2014). Phenotypic divergence between sulphidic and non-sulphidic mollies is likely to have a significant genetic component, because it coincides with strong genetic differentiation between populations, although there are no physical barriers separating populations in the different habitat types (Palacios *et al.* 2013, Plath *et al.* 2013, Riesch *et al.* 2016). However, trait variation between populations is also likely to have an environmental component; although population differentiation persists in captive populations reared in common-garden conditions in the laboratory (Tobler *et al.* 2016a, Greenway *et al.* 2020), there is also evidence for plasticity caused by short-term exposure to different environmental conditions (Bierbach *et al.* 2011, Passow *et al.* 2017a, Nobrega *et al.* 2024). In addition, the impact of maternal effects on offspring trait expression remains to be investigated in these livebearing fish.

Hence, we tested how genetic differentiation, maternal effects, and their interactions shape phenotypic expression in *P. mexicana* populations from sulphidic and non-sulphidic habitats. To induce maternal effects, we manipulated the availability of resources to pregnant mothers, because natural populations vary substantially in nutritional state. Fish in sulphidic habitats are consistently under food stress, exhibiting significantly reduced body condition (when inferred through both length–weight regression and body fat content analysis; Plath *et al.* 2005, Tobler *et al.* 2006, Tobler 2008). Food stress arises as a consequence of constraints associated with resource acquisition; because H_2S coincides with and exacerbates hypoxia, fish from sulphidic habitats have to trade off performing aquatic surface respiration, a compensatory behaviour to access better-oxygenated surface waters, with benthic foraging (Tobler *et al.* 2009). Accordingly, populations in sulphide springs have adaptations to low resource availability, including reductions in routine metabolic rates and energetically expensive tissues, such as the brain (Schulz-Mirbach *et al.* 2016, Passow *et al.* 2017b). In other species, including some poeciliids, resource availability experienced by mothers has been shown to impact trait expression in their offspring (Reznick *et al.* 1996, Altmann and Alberts 2005, Boots and Roberts 2012), and different population histories in terms of exposure to food stress in *P. mexicana* might have caused changes in resource-induced maternal effects.

To quantify the effects of genetic differentiation and maternal effects in populations of *P. mexicana*, we followed families of offspring from birth to the onset of maturation and repeatedly quantified a host of complex phenotypic traits. Focal traits included brood size, size at birth, and age at maturity, in addition to ontogenetic trajectories in growth rates, burst swimming, exploratory behaviour, and feeding rate. We chose these traits because they likely affect fitness, and we have prior knowledge for many of them from natural populations, providing us with a framework to make *a priori* predictions. Specifically, our experiments sought to address four specific questions. First, is there evidence for differences in phenotypic traits between populations from sulphidic and non-sulphidic habitats that persist in fish reared in a common-garden environment for multiple generations? Divergence in phenotypic traits between populations regardless of maternal food treatments would indicate that trait differentiation is attributable to genetic variation between populations. Second, is there evidence for maternal effects in response to resource availability? Differences in offspring traits between maternal food treatments, irrespective of population of origin, would suggest resource-induced maternal effects. Third, how do

functional traits vary throughout ontogeny, and how do population differences and maternal effects interact with ontogeny? Age is a major determinant in the expression of many traits (Hegyi *et al.* 2006, Zhang *et al.* 2015), but how population differences and maternal effects impact trait expression through ontogeny is less clear. In other poeciliids, maternal effects tend to be present at birth and decline with age (Lindholm *et al.* 2006). In contrast, population differences between sulphidic and non-sulphidic *P. mexicana* are stark in adults, suggesting that differences might emerge early in life and even increase throughout ontogeny (Riesch *et al.* 2011a). Accordingly, we predicted that age would impact most of the traits measured, that population differentiation would increase with age, and that maternal effects would diminish with age. Fourth, how do population differences interact with maternal effects? A difference in how each population responds to variation in maternal resource availability would indicate genotype-by-environment interactions. Fish from sulphidic habitats generally face constraints in resource levels, whereas those from non-sulphidic habitats have access to more abundant resources (Tobler *et al.* 2006, 2009, Tobler 2008). Hence, we predicted that trait variation induced by the low-food treatment would occur in the same direction as trait variation produced by differences between the non-sulphidic and sulphidic populations (i.e. maternal effects would be aligned with population differences). In this case, maternal effects would accentuate divergence between populations that resembles patterns of variation found in the wild. Alternatively, low-resource traits might be canalized in the sulphidic population because sulphidic individuals are constantly food stressed in nature. In this case, maternal effects might be weaker in the sulphidic population.

MATERIALS AND METHODS

Experimental overview

For our experiments, we used two laboratory-reared populations of *Poecilia mexicana* originating from wild-caught relatives in the Tacotalpa River drainage of Tabasco, southern Mexico (Supporting Information, Fig. S1). One population originated from a sulphide spring complex called El Azufre I (according to Plath *et al.* 2013; hereafter referred to as the sulphidic population or ecotype), and the other population was from a non-sulphidic stream 4.1 km away, connected to the mainstem of the Tacotalpa River, called Arroyo Bonita (Plath *et al.* 2010, 2013; hereafter referred to as the non-sulphidic population or ecotype). The sulphidic population shows strong genetic differentiation from nearby non-sulphidic populations, and there are very low rates of gene flow between habitat types (Plath *et al.* 2007b, 2010, Tobler *et al.* 2008).

Both populations were reared in 680 L stock tanks filled with filtered tap water. Tanks were fed *ad libitum* twice daily with commercial dry fish food (Purina), and ~50% of the water was exchanged weekly. Mothers used in this experiment were raised in common-garden conditions for at least three generations (i.e. they were at least great-grandchildren from individuals originally collected in the wild, but we did not track pedigree beyond the first three generations).

From each tank, 30 females were caught with a dipnet and isolated in a 20 L tank with an aerating filter and a bundle of plastic mesh as shelter for newborn fry. Female *P. mexicana* can store sperm (Torres-Martínez *et al.* 2017), hence paternal identity is unknown. However, given the density in stock tanks (200–300 fish), it is unlikely that one male sired all broods. Females were fed twice daily, once with aquatic gel diet for omnivorous fish (Mazuri) and once with freshly hatched *Artemia* nauplii (Brine Shrimp Direct). Females were randomly assigned to either a 'high-food' diet, which approximated *ad libitum* feeding (0.32 mL per feeding), or a 'low-food' diet (0.08 mL per feeding). The diet treatments were based on the results of past experiments, which showed that reduced food availability significantly impacts metabolic rates (Passow *et al.* 2015) and body condition (Greenway *et al.* 2016) in *P. mexicana*. The specific amounts of food were then determined using a pilot experiment that showed that the low-food diet reduced fish body condition. Fifteen females from each population were assigned to each group (Fig. 1). Each tank was checked daily for newborn fry.

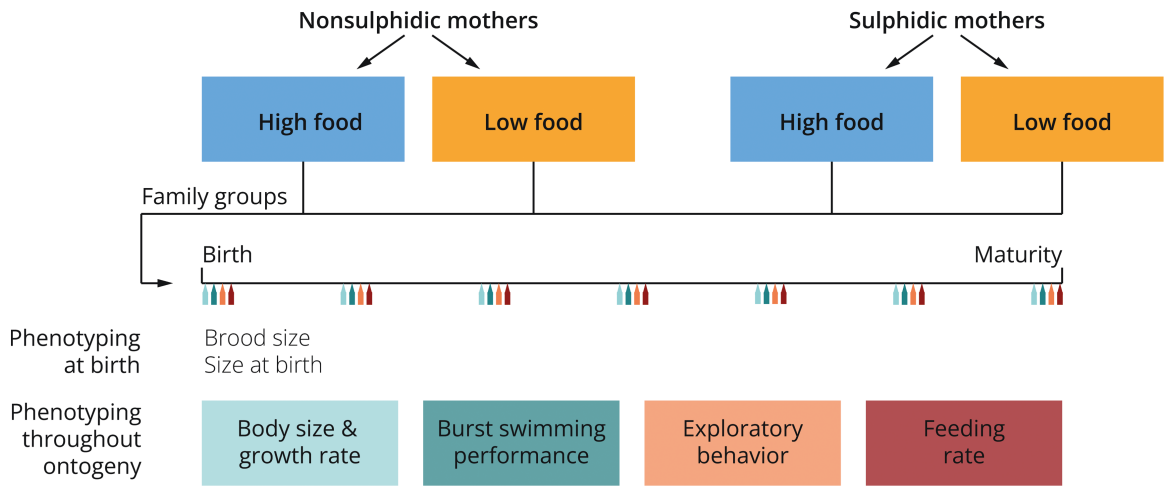

Figure 1. Overview of our experimental design. We subjected pregnant sulphidic and non-sulphidic mothers to either a high- or a low-food treatment and measured seven traits in their offspring throughout their development. These traits include four life-history traits (birth size, brood size, growth rate, and age at maturity) and three behavioural traits (burst swimming, exploratory behaviour, and feeding rate).

By the end of the experiment, 19 sulphidic broods (13 from the high-food treatment and 6 from the low-food treatment) and 24 non-sulphidic broods (13 from the high-food treatment and 11 from the low-food treatment) were collected and used for quantification of life-history and behavioural traits. Three females were reused as mothers. The amount of time each female was in the food treatment before giving birth varied (mean 26.9 days, range 0–99 days). Given that some females gave birth during the acclimation period or immediately after beginning the food treatments, we included treatment length as a potential covariate in all analytical models. Additionally, for a subset of models we tested whether using females that were in the treatment for ≥7 days would affect the resulting top models (Supporting Information, Table S1). Because the models were largely unaffected, we chose to include all broods to increase statistical power to detect population differences throughout ontogeny.

Whenever a brood was born, we recorded the brood size, date of birth for each family, the number of days that the female was in the food treatment, and the standard length of the mother (distance from the anterior tip of the snout to the posterior end of the caudal peduncle, in millimetres). Mothers were then removed from the tanks, and we randomly selected 15 newborn fry (if available; brood sizes ranged from 3 to 72) from each family to remain in the experimental tanks to minimize density-dependent effects.

From that point on, we followed the developing families through ontogeny. All fry, irrespective of the food treatment of the mother, received the same amount of food; they were fed *ad libitum* twice daily with a mixture of decapsulated brine shrimp eggs (Brine Shrimp Direct) and dry food. We assessed offspring phenotypes at approximately weekly intervals by measuring life-history traits (size at birth, weekly growth rate, and age at maturity) and behavioural traits (burst swimming, exploratory behaviour, and feeding rate; see Fig. 1). Fry were too small to tag and track individually, hence fry were chosen haphazardly for quantification of behavioural traits. We tested specifically whether there were differences in these phenotypes between maternal food treatments (i.e. maternal effects), between populations (i.e. sulphidic vs. non-sulphidic, indicating effects of evolved population differences), or their interaction. All analyses were conducted in R v.4.0.5 (R Core Team 2023). Code and data to reproduce all analyses can be found on GitHub (https://github.com/michitobler/common-garden). Experimental protocols were approved by the Institutional Animal Care and Use Committee of Kansas State University (#4856 and #4586)

Size at birth and growth rate

To measure size at birth, we photographed each family from above on the day of their birth with a Nikon D90 digital camera fitted with an AF-S Micro NIKKOR 105 mm f/2.8 lens. A ruler was included in the background of each image. Images were imported to ImageJ v.1.53 (Schneider *et al.* 2012) and calibrated by setting the scale. We measured the standard length (in millimetres) of each offspring in the family. These measurements were averaged across all individuals to obtain a single mean size at birth for each family. This measurement was completed weekly, and the measurement for each family was subtracted from the measurement of that family from the week before to obtain an average growth rate (in millmetres per week). To account for allometric differences in growth rate, we converted the average weekly growth rates to a proportional growth rate by dividing the average weekly growth rate by the mean body size measured the week before.

Age at maturity

We estimated the minimum age at maturity for each family using morphological characteristics of male sexual maturity. Although the sexes of juvenile livebearers are difficult to distinguish, at the onset of sexual maturity the male anal fin is modified into an intromittent organ (gonopodium), whereas it remains unmodified in females (Rosen and Gordon 1953, Chambers 1987). We therefore measured the minimum age at maturity (in days) as the time it took to for the first male in a group to develop its complete gonopodium as judged by the presence of a fleshy palp on anal fin ray 3.

Burst swimming

Most fish avoid predation with a highly conserved, reflexive escape response that causes the head to move away from the stimulus, bending the body into a 'C' shape (Eaton *et al.* 1977). Then, a strong stroke of the caudal fin starts the movement away from the stimulus (Domenici and Blake 1997). This process is known as a C-start response and is frequently used as a metric of escape performance in fish (Walker 1997, Ghalambor *et al.* 2004, Langerhans *et al.* 2004, Camarillo *et al.* 2020). To quantify this burst swimming behaviour, we adopted the methods and metrics used by prior studies (Langerhans *et al.* 2004, Ingley *et al.* 2016, Camarillo *et al.* 2020). We placed a haphazardly chosen individual from each family in a glass Petri dish (9 cm in diameter, containing 2 cm of water) with opaque sides, suspended above an angled mirror, providing a ventral view of each fish. After 5 min of acclimation, we struck the surface of the water within a body length of the fish with a probe and recorded the movement of the fish from below with a Sony NEX-FS700R camcorder at 60 frames/s and 1080 × 1920 pixel resolution. We converted the resulting .mts files into .mp4 files (to enhance compatibility with downstream applications) with FFmpeg (Tomar 2006).

We used DLTdv8 (Hedrick 2008) to digitize the two-dimensional (2D) location of the isthmus (i.e. the area on the ventral surface of the head where the opercula converge) of the fish in each frame. Digitized points were then used to calculate the maximum velocity (v_{max}, in millimetres per second), maximum acceleration (a_{max}, in millimetres per second squared), and net distance travelled (d_{net}, in millimetres of displacement within 1/12th of a second after the C-start). To calculate v_{max}, we calculated the straight-line distance between each pair of successive digitized points, divided this distance by the inverse of the frame rate (60 frames/s), and found the maximum value between any two points. The value of a_{max} was calculated by subtracting the value of velocity at each point from the value of velocity at the point immediately preceding it and finding the maximum value. The value of d_{net} was calculated by recording the 2D position immediately after the fish ended the C-start with a single stroke of the caudal fin, then recording the 2D position 1/12th of a second later (five frames later) and calculating the straight-line distance between the two points. To reduce the dimensionality

of this dataset, we conducted a principal component analysis (PCA) using the prcomp() function with a correlation matrix. There was one principal component (PC) with an eigenvalue greater than one (explaining 85.6% of the total variance), which was retained as a compound metric of burst swimming performance. Positive scores along this PC axis were associated with higher velocity, acceleration, and distance travelled (Supporting Information, Table S2A). All mathematical operations were conducted using packages contained in the base distribution of R.

Exploratory behaviour

We used an open field test to quantify the exploratory tendencies of fry. We filled a Styrofoam cup (9 cm in diameter) with 3 cm of water and covered the arena with a sheet of glass. We haphazardly selected one individual from each family and placed it in the arena undisturbed for a 5 min acclimation period, after which we recorded 5 min of video from above with a GoPro Hero 4 (1080 × 1920 pixel resolution, linear field of view, 30 frames/s).

We used idTracker (v.2.1, bundled with 64-bit Matlab Compiler Runtime 8.3; Pérez-Escudero *et al.* 2014) to track the 2D location of the fish automatically for the entire 5 min recording. We set the number of individuals to one and manually determined the intensity threshold (.5–.8) and minimum size (40–250 pixels) for each video. We also imported a still frame from each video into ImageJ to measure the centroid coordinates and arena radius.

Using the 2D coordinates in each frame, we calculated several metrics of motion that we used as proxies for exploratory behaviour. We calculated distance travelled between each pair of successive points, the velocity, the acceleration, and the total cumulative distance travelled (d_{total}, in millimetres), as described above. We also calculated average velocity (v_{avg}, in millimetres per second), maximum velocity (v_{max}, in millimetres per second), and maximum acceleration (a_{max}, in millimetres per second squared) by finding the means and maxima of all velocity and acceleration values. Finally, we calculated the proportional average distance from the centre of the arena (d_{centre}, dimensionless) by calculating the distance from the location of the fish to the centroid of the arena across all time points and locations and dividing this value by the arena radius. Videos were excluded if the fish was completely still in all frames. To reduce the dimensionality of the correlation structure and observe it within this dataset, we ran a PCA on v_{avg}, v_{max}, a_{max}, d_{total}, and d_{centre} with a correlation matrix. We retained scores along the first PC axis (explaining 56.9% of the total variance) as a composite exploratory behaviour score. As shown in Supporting Information, Table S2B, higher PC1 scores were associated with more exploratory behaviour (positive loadings for all variables).

Feeding rate

To measure feeding rate, we withheld food from individuals of each tank for 24 h prior to the experiment and placed one haphazardly selected fry in a viewing tank for a 5 min acclimation period. We custom-built a glass aquarium with the dimensions 10 cm × 10 cm × 1 cm, and the rear wall of the viewing tank was covered with a black sheet of plastic to enhance contrast between the background and the fish in the tank. The feeding solution consisted of 1 g of freshly hatched, live *Artemia* nauplii diluted into 100 mL of filtered tap water. After 5 min of acclimation, we added 0.08 mL of the feeding solution to the viewing tank and recorded 5 min of video with the camcorder. We analysed the video frame by frame using BORIS v.7.13 (Friard and Gamba 2016) and recorded the number of successful strikes (a feeding strike that ends in consumption of the food item).

Statistical analyses of individual traits

There were many potential sources of variation in our experiment. Other than the effects of interest for our study (population, maternal food treatment and their interaction), the observed variation in traits could also have arisen from differences in fry age, maternal body size (standard length), the duration of her food treatment, and brood size. Consequently, we used a model selection approach to find the models that were best supported by our data for each experiment separately. For each phenotype, we created a global model that contained all possible effects. For phenotypes that were measured only once for each family (size at birth, brood size, and age at maturity), we used a general linear model using the lm() function from the stats package v.3.6.2. For phenotypes that were measured repeatedly through development (growth rate, burst swimming, exploratory behaviour, and feeding rate), we used a linear mixed model implemented with the lmer() function from the lme4 package v.1.1-26 (Bates *et al.* 2015) that included 'family' as a random effect. Additionally, to ensure that signals of population differentiation and maternal effects occurring at birth were not obscured by measurements later in life, we also subset our dataset for each phenotype to analyse only the earliest data point for each family (referred to as 'at birth' analyses as opposed to 'overall' in sections below). We then used the dredge() function from the MuMIn package v.1.47.1 (Bartón 2009) to create a model selection table based on the effects contained in the global model, with different models ranked and weighted based on the Akaike information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002, Johnson and Omland 2004). Full model selection tables are available for each phenotype in Supporting Information, Table S3. To avoid overfitting, we limited the models to a maximum of four terms. We chose the top-supported model for each trait, and quantification and visualization of effects was accomplished by calculating and plotting estimated marginal means for the effects of 'population' and/or 'food treatment', depending on the best-supported model, using the Effect() function from the effects package v.4.2-2 (Fox and Weisberg 2018a, b). To aid in drawing inferences from our models, we generated 95% confidence intervals (CI) for model coefficients in our top models using the confint() function form the base R distribution. Effect sizes were calculated as partial eta-squared (η_p^2), which represents the proportion of variance explained by a particular variable after accounting for the variance explained by all other variables. We calculated η_p^2 with the etasq() function (Fox *et al.* 2021) for general linear models or the eta_squared() function (Ben-Shachar *et al.* 2020) for linear mixed models.

Multivariate analysis

Given that selection ultimately acts on complex, multivariate phenotypes (Lande and Arnold 1983), we sought to understand

Table 1. Model terms in the best-supported model for each dependent variable. Empty cells represent terms that were not present in the best-supported model for that dependent variable. The regression coefficients, 95% confidence intervals, and effect size (η_p^2) statistics are presented for each included model term. The regression coefficients for brood size, treatment duration, standard length of the mother, and age are slopes that represent the effect of each term on each dependent variable. The categorical variables 'population' and 'food treatment' represent the difference between each of the two levels (i.e. non-sulphidic vs. sulphidic and high vs. low). The reference levels for population and food treatment are non-sulphidic and high, respectively. Abbreviation: PC, principal component.

Dependent variable	Brood size	Treatment duration	Standard length of mother	Age	Population	Food treatment
Size at birth	−0.03 (−0.05, −0.02) η_p^2 = 0.34		0.06 (0.03, 0.09) η_p^2 = 0.16		0.90 (0.49, 1.31) η_p^2 = 0.36	0.42 (0.01, 0.84) η_p^2 = 0.02
Brood size		0.24 (0.09, 0.39) η_p^2 = 0.20	1.26 (0.77, 1.76) η_p^2 = 0.40			
Age at maturity					10.54 (0.23, 20.84) η_p^2 = 0.15	
Growth rate at birth					−0.06 (−0.11, −0.01) η_p^2 = 0.12	
Overall growth rate				−0.01 (−0.01, −0.01) η_p^2 = 0.50		
Burst swimming at birth			0.04 (−0.01, 0.09) η_p^2 = 0.06			
Overall burst swimming				0.03 (0.02, 0.05) η_p^2 = 0.16	−0.48 (−0.94, −0.03) η_p^2 = 0.03	
Exploratory behaviour at birth						1.26 (−0.79, 1.20) η_p^2 = 0.08
Overall exploratory behaviour					1.00 (0.30, 1.70) η_p^2 = 0.28	0.73 (0.04, 1.42) η_p^2 = 0.18
Feeding rate at birth						
Overall feeding rate					−6.29 (−11.39, −1.78) η_p^2 = 0.85	−2.55 (−7.76, 2.67) η_p^2 = 0.03
Multivariate trait variation PC1		0.05 (0.03, 0.07) η_p^2 = 0.53			0.76 (−0.07, 1.59) η_p^2 = 0.12	
Multivariate trait variation PC2		−0.02 (0.00, 0.04) η_p^2 = 0.15			−1.98 (−2.80, −1.16) η_p^2 = 0.51	−0.97 (−1.76, −0.19) η_p^2 = 0.22

how the traits measured for our analyses vary and covary to shape multivariate phenotypes jointly. To do so, we averaged each phenotype across all ages for each tank. We selected this approach rather than including age as a covariate and analysing raw phenotypic scores because of timing and logistical constraints that made it impossible to conduct each experiment on offspring that were exactly the same age. We analysed the averaged phenotypes with a PCA (correlation matrix) and used scores along the first two PCs, which had eigenvalues greater than one, as dependent variables. We analysed PC scores along each axis separately because the axes, by definition, were orthogonal. For each axis, we created a global linear model using the 'lm' function in R containing all possible effects (population, treatment, the interaction between population and treatment, standard length of the mother, and treatment length) and selected the best-supported model based on AIC_c, as explained above.

RESULTS

We measured seven functional traits in offspring from a sulphidic and a non-sulphidic population of *P. mexicana* throughout ontogeny. Model selection tables for the analysis of each trait across all ages can be found in Supporting Information, Table S3, and the best-supported models are summarized in Table 1. For brevity, we will present results in the context of our hypotheses outlined in the Introduction, focusing on how all traits vary through ontogeny in terms of population differentiation, maternal effects, and their interaction, rather than presenting the results for each trait separately.

Is there evidence for population differentiation?

We found evidence for population differences in six of the traits measured: size at birth, age at maturity, growth rate at birth, overall burst swimming, overall exploratory behaviour, and overall feeding rate, but not brood size (Fig. 2B) or overall growth rate (Fig. 3A). Age at maturity and overall burst swimming differed between populations, but not between food treatments, whereas there were effects of 'population' and 'food treatment' (but no interactions) on size at birth, overall exploratory behaviour, and overall feeding rate (see Table 1 and below). Sulphidic individuals were born 9.2% larger [estimated marginal mean for sulphidic fish (EMM_S) = 10.03 mm, estimated marginal mean for non-sulphidic fish (EMM_{NS}) = 9.18 mm; $\eta_p^2 = 0.36$; Fig. 2A], matured an average of 10.5 days later (EMM_S = 54.2 days, EMM_{NS} = 43.7 days; $\eta_p^2 = 0.15$; Fig. 2D), had a lower growth rate at birth (EMM_S = 0.065 body lengths/day, EMM_{NS} = 0.074 body lengths/day; Fig. 3B), had lower burst swimming performance (EMM_S = −0.28 PC1, EMM_{NS} = 0.20 PC1; Fig. 3C), were more exploratory (EMM_S = 0.66 PC1, EMM_{NS} = −0.34 PC1; Fig. 4A), and were 36.6% less successful during feeding (EMM_S = 10.9, EMM_{NS} = 17.2; Fig. 4C).

Is there evidence for maternal effects in response to resource availability?

To test whether maternal effects induced by resource availability during pregnancy impact functional traits in offspring, we compared each phenotype between offspring born to mothers who experienced a high-food environment and mothers who experienced a low-food environment. Mothers in low-food treatments produced offspring that were 3.4% larger at birth [estimated marginal mean for fish in the low-food treatment (EMM_{low}) = 9.8 mm; estimated marginal mean for fish in the high-food treatment (EMM_{high}) = 9.4 mm; $\eta_p^2 = 0.11$; Fig. 2A], were more exploratory across all ages (PC1 EMM_{low} = 0.42, PC1 EMM_{high} = −0.31; Fig. 4A) and less successful during feeding across all ages (EMM_{low} = 12.7, EMM_{high} = 15.3; Fig. 4C). For all remaining traits (brood size, age at maturity, overall growth rate, and overall burst swimming), 'food treatment' was not included in the best-supported model (Table 1), suggesting that maternal effects did not affect the expression of those traits.

How do population differences and maternal effects interact with ontogeny?

To determine how traits changed through offspring development, we compared each phenotype across age groups. 'Age' was included in the top models for growth rate and overall burst swimming, indicating that these traits changed throughout ontogeny, whereas the other phenotypes were not affected by age. Across populations and food treatments, fry grew at a slower relative rate (estimate: −0.01, CI: −0.01, 0.01; $\eta_p^2 = 0.50$) and performed better in burst swimming trials (estimate: 0.03, CI: 0.02, 0.049; $\eta_p^2 = 0.16$) as they got older (Table 1). Burst swimming scores were also lower in sulphidic individuals (see above), but the interaction term 'population × age' was not included in the top model, demonstrating that both populations exhibited similar changes in burst swimming throughout ontogeny.

As mentioned above, fry from the sulphidic population and the low-food maternal treatment were larger at birth (Fig. 2A; Table 1). Additionally, size at birth was negatively correlated with brood size (Fig. 2C). However, there were no population differences or maternal effects on brood size, which was higher in larger mothers (mother SL; estimate: 1.26, CI: 0.73, 1.79; $\eta_p^2 = 0.38$) and mothers who spent longer in the food treatment (treatment length; estimate: 0.24, CI: 0.08, 0.40; $\eta_p^2 = 0.19$). Growth rate at birth was lower in sulphidic fry (estimate: −0.06, CI: −0.12, −0.01; $\eta_p^2 = 0.12$; Table 1; Fig. 3B), but there was no evidence for maternal effects on growth rate at birth ('food treatment' was not included in best-supported model). Note that the population difference in growth rate at birth disappeared as fry developed (Fig. 3A). Other traits that were measured throughout ontogeny (burst swimming and feeding rate) did not exhibit population differences or maternal effects at birth (Figs 3D, 4D). The maternal effect that we detected on exploratory behaviour across all ages (see above) was also evident at birth (Fig. 4B). These results collectively demonstrate that, contrary to our hypothesis regarding ontogenetic variation of functional traits, population differentiation did not increase with age, and maternal effects were not always observable at birth, nor did they decline with age.

How do population differences interact with maternal effects?

We hypothesized that variation from maternal effects would be aligned with population differences, but that there would be an interaction between population differences and maternal effects (i.e. different magnitudes of maternal effects in each population attributable to different evolutionary histories associated

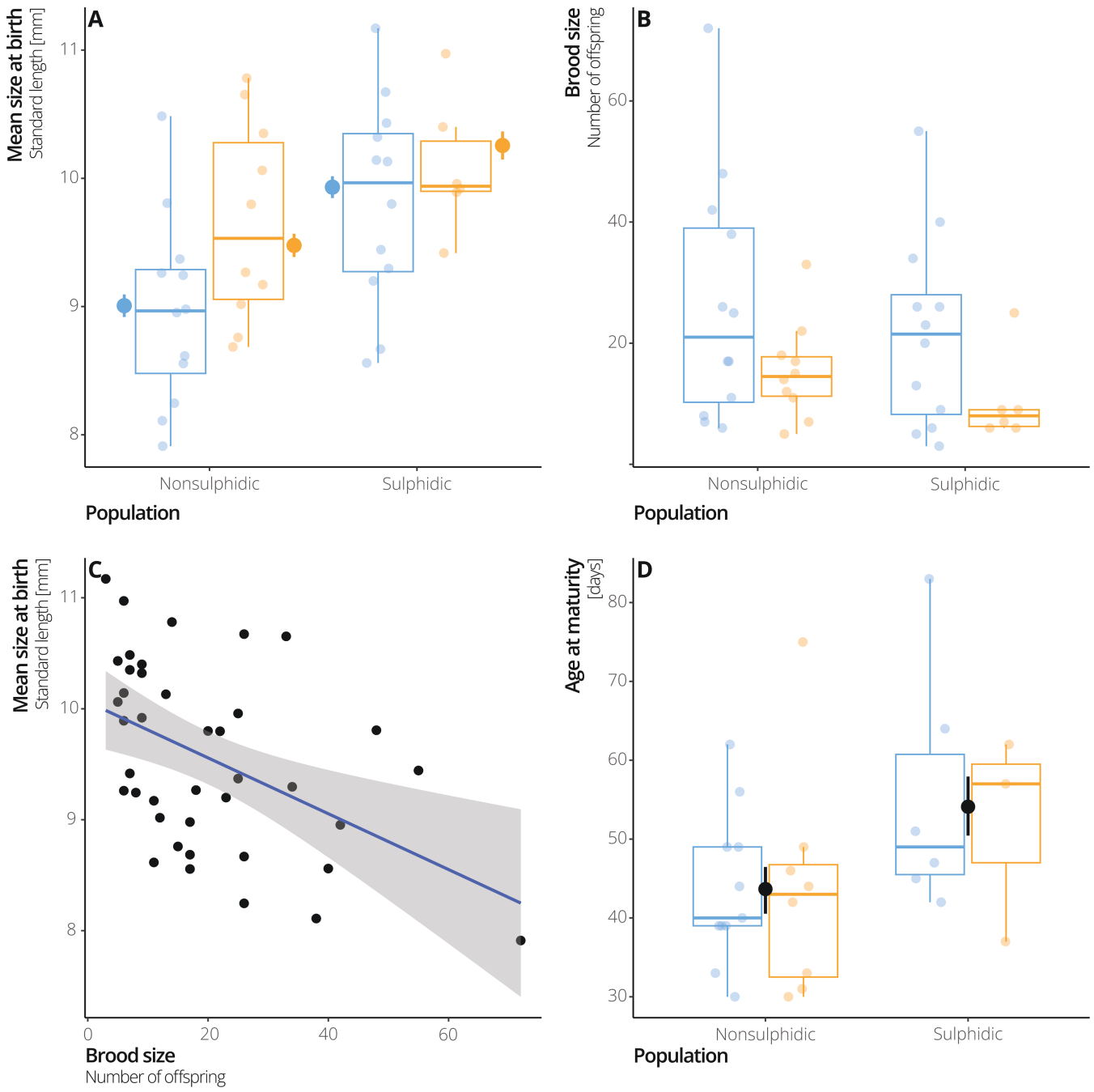

Figure 2. Plots of average standard length (A), brood size (B), their relationship (C), and age at maturity (D) for each family. Data are summarized in boxplots, with raw data points overlaid. In both populations, the high-food treatment is shown in blue and the low-food treatment in orange. When the best-supported model for a phenotype contained the terms 'population' and/or 'food treatment', the estimated marginal means for those effects were visualized as large points (±SE).

with resource stress). Contrary to our predictions, no 'population × food treatment' interactions were included in the best-supported model for any of the traits we measured (Table 1), suggesting a general lack of support for interactions between population differences and maternal effects. Therefore, maternal effects, if present, were similar in direction and magnitude between populations.

To address our hypothesis further, we asked whether population differences and maternal effects were, in fact, aligned, and whether they explained a similar proportion of phenotypic variance when they acted in unison. We compared the signs (positive vs. negative coefficient estimates) and effect sizes (η_p^2) of population differences and maternal effects for the three traits with evidence of both effects simultaneously impacting trait expression: size at birth, overall exploratory behaviour, and overall feeding rate. For all traits, the difference between the non-sulphidic and sulphidic populations occurred in the same direction as the trait shifts between the high- and low-food treatments, indicating that the effects were aligned (Figs 2A, 4A, C). Effect size estimates for 'population' and 'food treatment' for

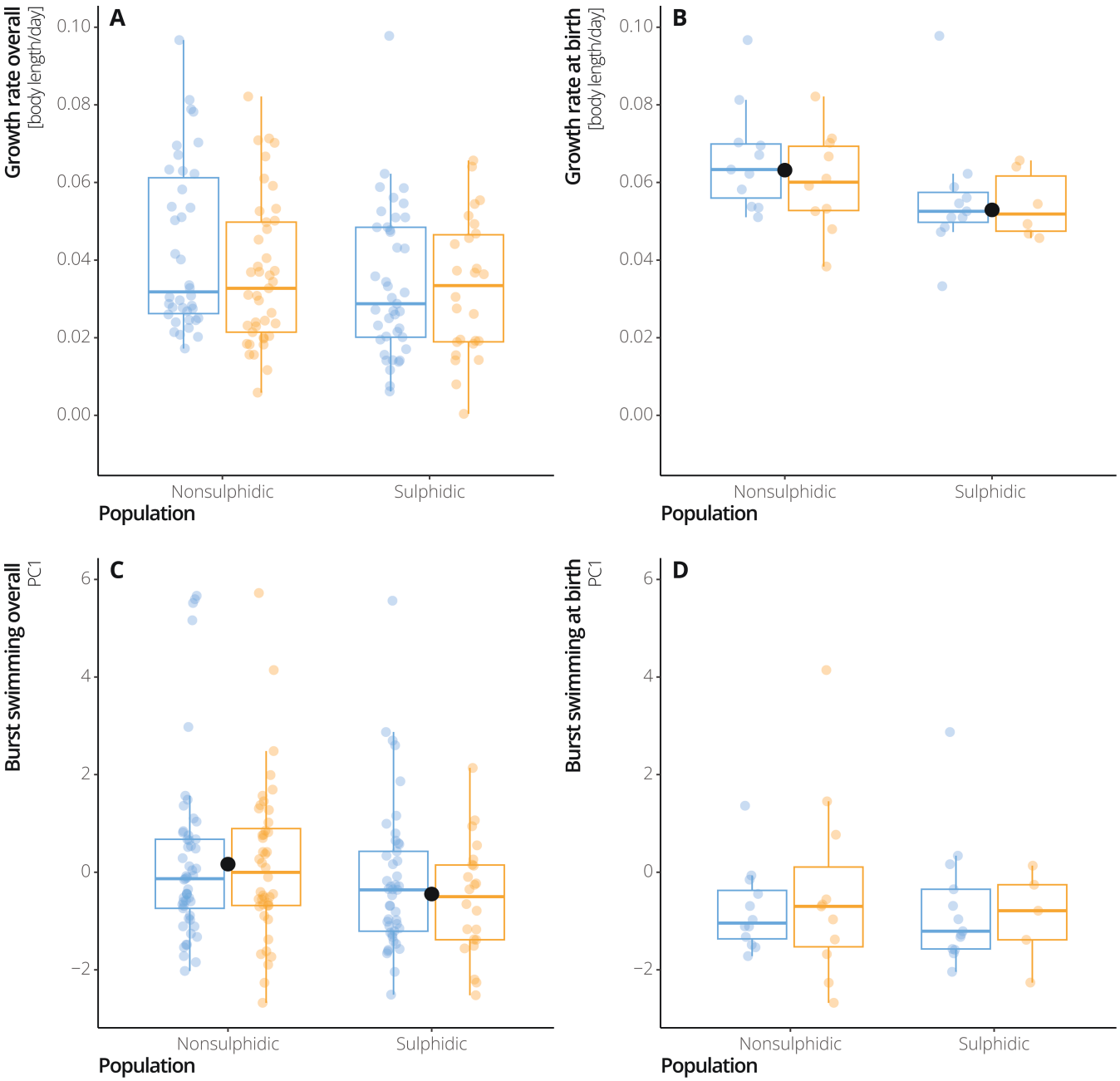

Figure 3. Data for different phenotypes are summarized in boxplots, with raw data points overlaid. In both populations, the high-food treatment is shown in blue and the low-food treatment in orange. When the best-supported model for a phenotype contained the terms 'population' and/or 'food treatment' (see Table 1), the estimated marginal means (EMMs) for those effects were visualized as large points (±SE). A, variation in overall growth rate (neither 'population' nor 'food treatment' in the top model). B, variation in growth rate at birth (EMM for 'population'). C, variation in overall burst swimming (EMM for 'population'). D, variation in burst speed at birth (neither 'population' nor 'food treatment' in the top model). Abbreviation: PC1, principal component 1.

all three traits indicated that 'population' had a larger effect on trait expression than 'food treatment' (η_p^2 = 0.36 vs. 0.02 for size at birth, η_p^2 = 0.28 vs. 0.18 for exploratory behaviour, and η_p^2 = 0.85 vs. 0.03 for feeding rate).

Multivariate analysis

In addition to the univariate analyses of trait variation, we were also interested in understanding how the traits covaried with one another, and whether and how multivariate phenotypes were impacted by population differences and maternal effects. We averaged each phenotype across ages for each family, conducted a PCA, then analysed PC scores along the first two PC axes. The first PC accounted for 30.8% of variance in multivariate phenotypes, and scores along the first PC were primarily ($|r| > 0.5$) and negatively correlated with feeding rate (see Supporting Information, Table S2C). The second PC explained 28.1% of variance and was positively correlated with growth rate and negatively correlated with size at birth ($|r| > 0.5$; Supporting Information, Table S2C). Overall, PCA indicated variation along two primary axes of phenotypic variation (which were

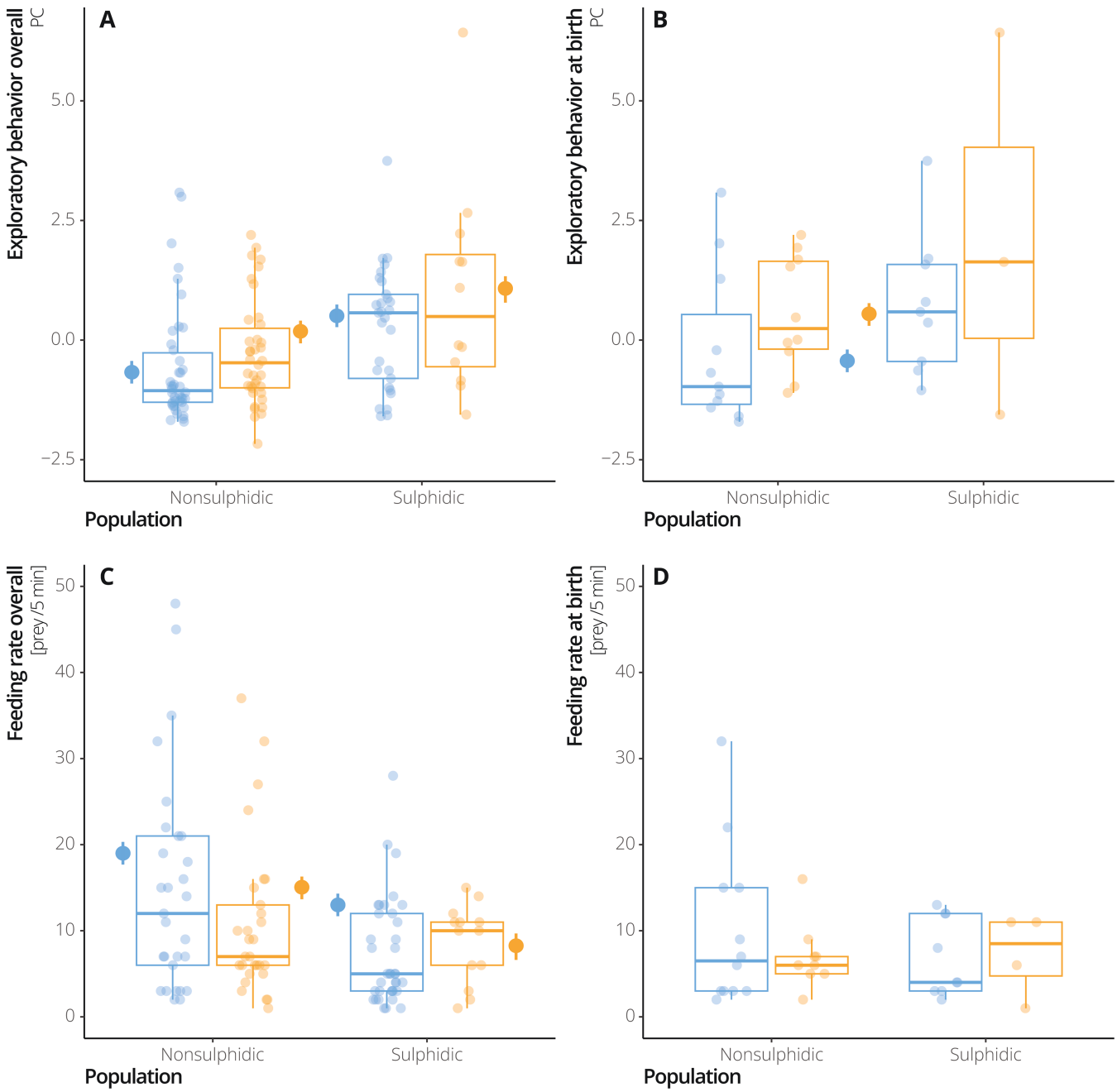

Figure 4. Data for different phenotypes are summarized in boxplots, with raw data points overlaid. In both populations, the high-food treatment is shown in blue and the low-food treatment in orange. When the best-supported model for a phenotype contained the terms 'population' and/or 'food treatment' (see Table 1), the estimated marginal means (EMMs) for those effects were visualized as large points (±SE). A, variation in overall exploratory behaviour (EMM for 'population' and 'food treatment'). B, variation in exploratory behaviour at birth (EMM for 'food treatment'). C, variation in overall feeding rate (EMM for 'population' and 'food treatment'). D, variation in feeding rate at birth (neither 'population' nor 'food treatment' in the top model). Abbreviation: PC, principal component.

not exactly perpendicular to the PC axes) that highlight potential trade-offs in organismal function: there is variation along an axis that trades off high feeding rates at one end of the spectrum with higher exploratory behaviour and a higher age at maturity at the other end of the spectrum (although the correlations of the latter two variables in the PCA were <0.5). In addition, there is variation along an axis that trades off large size at birth at one end of the spectrum with high growth rate at the other end of the spectrum (Fig. 5).

Variation along PC1 was primarily influenced by 'Treatment length' (estimate: 0.05; CI: 0.03, 0.07; $\eta_p^2 = 0.53$) and 'population' (estimate: 0.76; CI: −0.07, 1.59; $\eta_p^2 = 0.12$; Table 1), and fish from the sulphidic population tended to have higher scores than those from non-sulphidic populations (Fig. 5). Variation along PC2 was influenced by 'treatment length' (estimate: 0.02: CI: 0.00, 0.04; $\eta_p^2 = 0.15$), 'population' (estimate: −1.98; CI: −2.80, −1.16; $\eta_p^2 = 0.51$; Table 1), and 'food treatment' (estimate: −0.97; CI: −2.80, −1.16; $\eta_p^2 = 0.51$; Table 1). Experimental groups

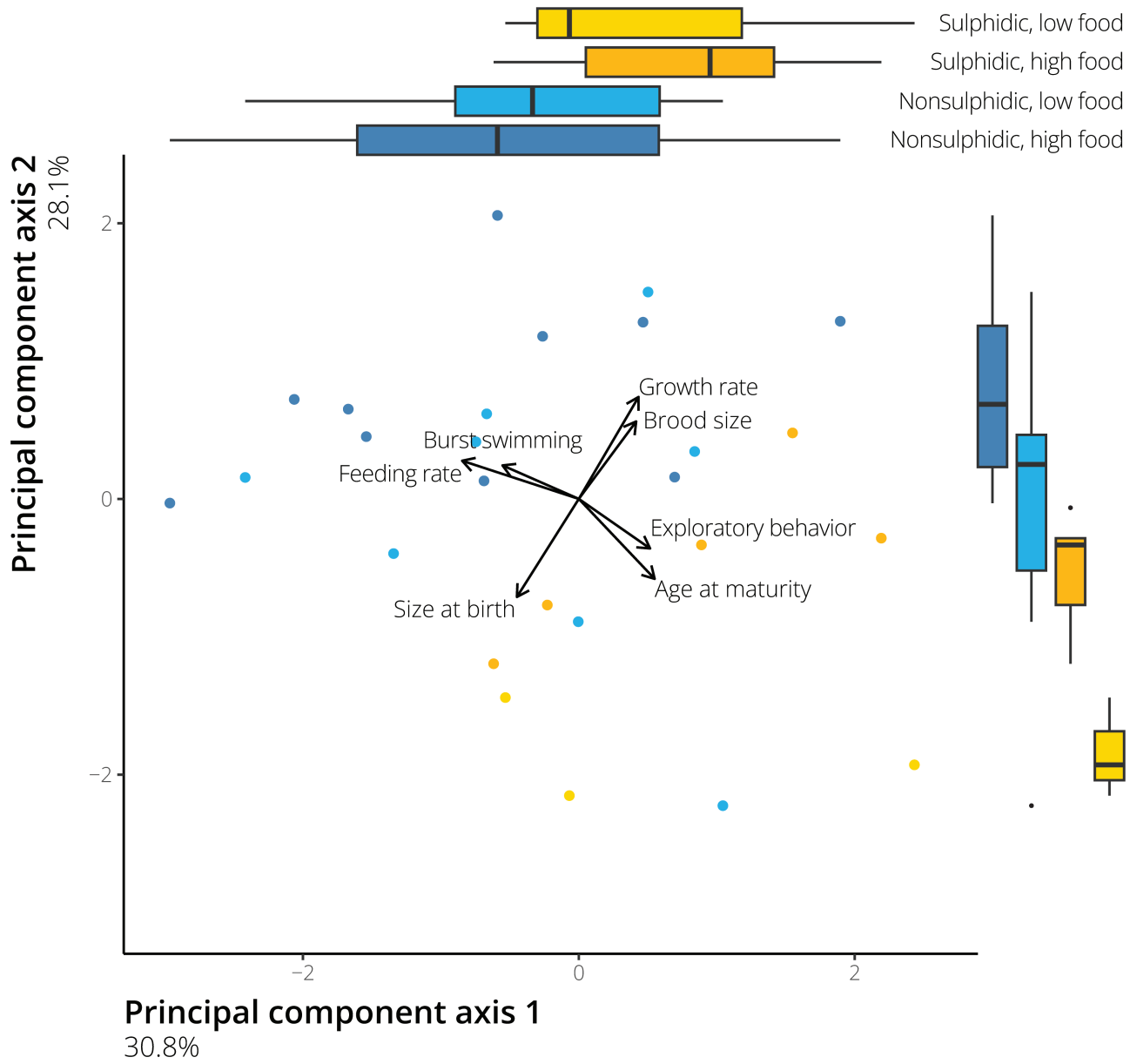

Figure 5. Plot of principal component scores representing linear combinations of all phenotypes in multivariate space. Scores were plotted along the first two principal components. Non-sulphidic families are shown in shades of blue and sulphidic families in shades of yellow. The high-food treatment within each population is shown in the darker shade (i.e. dark blue or dark yellow). Radiating from the origin are arrows that represent the correlation between the principal component scores and each input variable (shown as text at the end of each arrow). Loadings were calculated by multiplying the eigenvector for each input variable by the square root of the eigenvalue for that principal component axis. Boxplots show the distribution of principal component scores along each of the principal component axes.

segregated by population and food treatment, with sulphidic fish having lower scores than non-sulphidic fish, and with fish in the low-food treatment having lower scores than fish in the high-food treatment (Fig. 5). As for the univariate analyses, maternal effects were aligned with population differences in PC2 scores (Fig. 5), and 'population' had a larger effect than 'food treatment', and there was no evidence for a 'population × food treatment' interaction (the term was not included in best-supported models).

DISCUSSION

Phenotypic variation can be shaped by multiple genetic and non-genetic factors, but the interplay of genes and environmental effects is rarely disentangled in natural systems, although it fundamentally impacts our inference of adaptation. We examined how genetic variation (i.e. population differences), phenotypic plasticity mediated by maternal effects, and their interactions shape trait expression in two populations of *P. mexicana* that are exposed to strong divergent selection in nature. We found trait differences between populations despite fish being housed in common-garden conditions in the laboratory for at least three generations, meaning that populations could have adapted to laboratory conditions (Morgan *et al.* 2022). In contrast, exposure of mothers to different food treatments impacted relatively few traits in their offspring and, if they occurred, had weaker effects than the population differences. It is important to note, however,

that treatment durations varied among mothers, and it is possible that maternal effects attributable to food availability could be stronger with longer exposure times. Nevertheless, maternal effects tended to be aligned with population differences and act in the same way across populations. We also found no evidence for interactions between populations and food treatments, suggesting that although populations have diverged in phenotypic traits, they have retained similar maternal influences on those same traits. Overall, we found that the stark phenotypic differences between populations of *P. mexicana* that are evident in nature are largely a consequence of genetic divergence, probably representing local adaptation to the distinct ecological conditions of their habitats. Maternal effects in response to resource availability, although present in some traits, appear to accentuate population differences, but not cause them.

Trait variation across populations and maternal food treatments

There is a rich history integrating field-based studies that quantify trait variation of poeciliid fishes in nature with laboratory-based studies that isolate causative environmental factors (Endler 1980, 1995, Reznick and Bryga 1987, Reznick *et al.* 1990, Langerhans *et al.* 2007, Tobler *et al.* 2008, Ghalambor *et al.* 2015, Ingley and Johnson 2016). Although most studies focus on single traits or a few related traits and take a snapshot at a single ontogenetic stage, our study demonstrated that multiple complex trait differences quantified in common-garden conditions, across food treatments and across ontogeny, closely mirror differences in traits between populations in nature.

First, our study corroborates a genetic basis for population divergence in reproductive life-history traits. We documented population divergence in size at birth, with sulphidic mollies giving birth to larger offspring (see Figs 2A, 5). This finding is consistent with life-history studies of sulphide spring populations in *P. mexicana* and other poeciliid species (Riesch *et al.* 2010b, c, 2014). Our multivariate results (Fig. 5) indicated that, like other poeciliids, the non-sulphidic population of *P. mexicana* closely resembles an opportunistic life-history strategy (Winemiller and Rose 1992), which places a premium on earlier maturity and higher fecundity at the expense of lower juvenile survivorship. The differences in life history we found in the sulphidic population might represent a shift from an opportunistic life-history strategy towards an equilibrium life-history strategy, in which parents produce fewer but larger offspring, which is energetically costly to parents but should ultimately benefit offspring competitive ability (Winemiller and Rose 1992). In natural populations, maternal effects induced by variation in resource availability probably accentuate genetic differences in offspring size across sulphidic and non-sulphidic habitats. This pattern was also evident across a plethora of life-history traits in guppies; in all 10 life-history traits with evidence for significant genetic divergence and maternal effects, these effects always occurred in the same direction (Felmy *et al.* 2022).

Second, we found both matching and conflicting patterns of population differentiation in age and size at maturity in comparison to previous work in livebearing fishes. Prior studies have demonstrated that guppies in streams with high predation pressure on adults mature earlier than conspecifics from low-predation populations (Reznick and Endler 1982). Likewise, in this study *P. mexicana* from the non-sulphidic habitat, which experience higher predation by fish (Riesch *et al.* 2009, Greenway *et al.* 2014), matured earlier than those from the sulphidic habitats where fish predators are absent. This finding contrasts with a previous study that found fish from sulphidic populations reaching maturity at a significantly smaller size than individuals from non-sulphidic populations (Riesch *et al.* 2011b). This discrepancy between our findings and those of previous studies suggests that plasticity in size at maturity might be strong and that variation in experimental design and rearing conditions matters.

Third, we found behavioural differences between populations from sulphidic and non-sulphidic habitats, including exploratory behaviour, feeding rate, and burst swimming. Previous work has shown that non-sulphidic mollies and ones that were better fed were bolder in their natural habitat, but behavioural differences also disappeared in the laboratory (Riesch *et al.* 2009). Although we did not measure boldness *per se*, exploratory behaviour as measured in our experiment (i.e. activity levels in a novel arena) is often characterized as part of a behavioural syndrome that is correlated with boldness (Conrad *et al.* 2011). Unlike previous work, our study found that individuals from the sulphidic population and the low-food treatment were more exploratory (Table 1; Fig. 3E). These results support that the maternal resource environment affects exploratory behaviour, but also imply heritable differences between populations. Similar heritable population differences were also found for feeding rate and burst swimming but without any evidence for maternal effects. At least for burst swimming, the pattern of population differentiation in our experiment again mirrors findings from adult fish in natural habitats (Camarillo *et al.* 2020).

Trait variation and adaptive function

Sulphide springs and adjacent non-sulphidic habitats not only differ in the presence and absence of H_2S, but they also vary in numerous abiotic and biotic factors that are often not addressed in studies of adaptation. Sulphidic habitats have lower dissolved oxygen concentrations, higher temperature, higher specific conductivity, and lower pH (Tobler *et al.* 2011), which, in turn, affect the biotic communities (Greenway *et al.* 2014) and selection associated with resource exploitation, competition, predation, and parasites (Riesch *et al.* 2010a, Tobler *et al.* 2014, 2015). Adaptation in sulphide springs is therefore not solely in response to selection from H_2S but is instead in response to a multifarious selective regimen that has caused multivariate phenotypic differentiation between populations (Tobler *et al.* 2018). The complexity of selective regimens and evolutionary responses makes disentangling cause-and-effect relationships difficult, especially because theoretical predictions for the effects of different, covarying sources of selection are not mutually exclusive. For example, the evolution of large offspring size at birth could be explained by: (i) selection from H_2S, which should favour larger offspring with a lower surface-to-volume ratio to reduce the influx of toxic H_2S (Riesch *et al.* 2014); (ii) selection from resource constraints, which favours larger offspring with higher energy stores (Reznick *et al.* 1996); or (iii) relaxation of selection from predation, which also favours larger offspring (Reznick and Endler 1982, Johnson and Belk 2001, Jennions *et al.* 2006). Likewise, resource constraints and low predation also favour more exploratory individuals that are better able to locate and

exploit resources in those conditions (Teska *et al.* 1990, Kaun *et al.* 2007, Huang *et al.* 2012). Assessing the adaptive value of trait differences between sulphidic and non-sulphidic populations is consequently non-trivial and remains a work in progress.

Variation in some traits investigated in our study might also be the consequence of genetic, developmental, or functional trade-offs with other traits. Such trade-offs are common in organisms inhabiting contrasting environments, because divergent selection acting to optimize one trait can inadvertently influence other traits owing to constraints (Ghalambor *et al.* 2004, Kawecki and Ebert 2004, Garland *et al.* 2022). For example, reductions in burst swimming performance, as documented in our study for fish from the sulphidic population, might arise as a consequence of selection for increased steady swimming efficiency, because different body shapes are associated with optimization of steady vs. unsteady swimming (Langerhans 2007, 2009, Tokić and Yue 2012). Indeed, a trade-off between burst speed and sustained swimming performance has been documented in adult fish from the same populations we studied here (Camarillo *et al.* 2020). The trade-off is likely to be balanced by the need for energy-efficient swimming in sulphidic habitats with resource constraints (but low predation) and selection for efficient predator avoidance in non-sulphidic habitats with high abundances of natural enemies (but abundant resources) (Camarillo *et al.* 2020). Our study found a similar reduction in burst swimming performance in the sulphidic population, even among individuals that had not yet reached maturity, suggesting that population differences in burst swimming arise early in ontogeny.

Our results also matched *a priori* predictions regarding potential trade-offs between respiration and feeding. Habitats rich in H_2S also experience rampant hypoxia, which has selected for the evolution of craniofacial traits (larger heads and jaws and longer gill filaments) that increase ventilation efficiency (Camarillo *et al.* 2020). In addition to changes in morphology, sulphidic individuals also exhibit decreased foraging efficiency compared with non-sulphidic individuals (Tobler *et al.* 2009), which was supported by our findings related to feeding rate (Fig. 4C). The decreases in feeding rates noted in this and other studies might therefore be a consequence of the craniofacial modifications that accompany colonization of sulphidic habitats.

Plasticity accentuates genetic trait differentiation in natural populations

Phenotypes in nature are the sum of genetic and environmental effects, but, surprisingly, we found no evidence for canalization or the evolution of plasticity by genotype × environment interactions. Our work demonstrated that maternal effects were aligned with population differences, accentuating trait divergence between populations, and that the trait shifts induced by maternal effects were of a similar magnitude in both populations. For two of the traits in which we observed population differentiation and maternal effects (size at birth and exploratory behaviour), the lowest phenotypic scores were found in non-sulphidic fry from high-food mothers, and the highest scores were found in sulphidic fry from low-food mothers (Figs 2A, 3E). Because sulphidic mollies exhibit reduced foraging efficiency and body condition as a consequence of hypoxia (Tobler 2008, Tobler *et al.* 2009), sulphidic habitats are naturally analogous to our low-food treatment, and non-sulphidic habitats are similar to the high-food treatment. If maternal effects enhance population differences in natural populations in a similar manner to our experiments, this could explain why stronger trait divergence is typically observed in nature than in common-garden-reared fish (Tobler *et al.* 2008, Passow *et al.* 2015). Likewise, it is important to note that our experiments captured only a small aspect of phenotypic plasticity, i.e. the portion controlled by the mother. Future work needs to address genetic effects, maternal effects, and plasticity in response to variation in environmental factors directly experienced by the offspring to gain a better understanding of the forces driving trait variation in nature. We also caution that inferences in our study were based on comparisons of a single population pair, and leveraging replicated populations pairs of sulphidic and non-sulphidic *P. mexicana* in the future will help to uncover general patterns about the role of maternal effects and genetic divergence in shaping trait variation in this system (Nobrega *et al.* 2024).

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

ACKNOWLEDGEMENTS

We would like to thank the members of the community in Tapijulapa, Tabasco for access to field sites and for their hospitality. We also would like to thank the Mexican government for issuing permits for past field collections, in addition to Lenin Arias Rodriguez at the Universidad Juárez Autónoma de Tabasco and the staff at the Centro de Investigación E Innovación Para la Enseñanza y El Aprendizaje for support of research expeditions to obtain the specimens that gave rise to the populations used in this study. The assistance provided by J. Onnen and Q. La Fon was essential for processing our diverse datasets.

CONFLICT OF INTEREST

None declared.

FUNDING

Funding for this research was provided by grants from the National Science Foundation (IOS-1931657), the U.S. Army Research Office (W911NF-15-1-0175), and the Des Lee Collaborative Vision in Zoological Studies to M.T., and by a Graduate Assistance in Areas of National Need (GAANN) fellowship from the U.S. Department of Education to J.L.C.

DATA AVAILABILITY

All datasets and R scripts used to analyse the data, with associated documentation, have been archived on GitHub (https://github.com/michitobler/common-garden).

REFERENCES

Altmann J, Alberts SC. Growth rates in a wild primate population: ecological influences and maternal effects. *Behavioral Ecology*

and Sociobiology 2005;**57**:490–501. https://doi.org/10.1007/s00265-004-0870-x

Badyaev AV, Uller T. Parental effects in ecology and evolution: mechanisms, processes and implications. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2009;**364**:1169–77. https://doi.org/10.1098/rstb.2008.0302

Bartón K. MuMIn: multi-model inference. *Comprehensive R Archive Network (CRAN)* 2009.

Barts N, Greenway R, Passow CN *et al.* Molecular evolution and expression of oxygen transport genes in livebearing fishes (Poeciliidae) from hydrogen sulfide rich springs. *Genome* 2018;**61**:273–86. https://doi.org/10.1139/gen-2017-0051

Bates D, Mächler M, Bolker B *et al.* Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 2015;**67**:1–48.

Beckerman AP, Benton TG, Lapsley CT *et al.* How effective are maternal effects at having effects? *Proceedings Biological Sciences* 2006;**273**:485–93. https://doi.org/10.1098/rspb.2005.3315

Ben-Shachar M, Lüdecke D, Makowski D. Effectsize: estimation of effect size indices and standardized parameters. *Journal of Open Source Software* 2020;**5**:2815. https://doi.org/10.21105/joss.02815

Bierbach D, Schulte M, Herrmann N *et al.* Predator-induced changes of female mating preferences: innate and experiential effects. *BMC Evolutionary Biology* 2011;**11**:190. https://doi.org/10.1186/1471-2148-11-190

Boots M, Roberts KE. Maternal effects in disease resistance: poor maternal environment increases offspring resistance to an insect virus. *Proceedings Biological Sciences* 2012;**279**:4009–14. https://doi.org/10.1098/rspb.2012.1073

Burnham KP, Anderson DR. 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*. New York, NY: Springer.

Camarillo H, Arias Rodriguez L, Tobler M. Functional consequences of phenotypic variation between locally adapted populations: swimming performance and ventilation in extremophile fish. *Journal of Evolutionary Biology* 2020;**33**:512–23. https://doi.org/10.1111/jeb.13586

Chambers J. The cyprinodontiform gonopodium, with an atlas of the gonopodia of the fishes of the genus *Limia*. *Journal of Fish Biology* 1987;**30**:389–418. https://doi.org/10.1111/j.1095-8649.1987.tb05764.x

Conrad JL, Weinersmith KL, Brodin T *et al.* Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *Journal of Fish Biology* 2011;**78**:395–435. https://doi.org/10.1111/j.1095-8649.2010.02874.x

Cooper CE, Brown GC. The inhibition of mitochondrial cytochrome oxidase by the gases carbon monoxide, nitric oxide, hydrogen cyanide and hydrogen sulfide: chemical mechanism and physiological significance. *Journal of Bioenergetics and Biomembranes* 2008;**40**:533–9. https://doi.org/10.1007/s10863-008-9166-6

Dingemanse NJ, Araya-Ajoy YG. Interacting personalities: behavioural ecology meets quantitative genetics. *Trends in Ecology & Evolution* 2015;**30**:88–97. https://doi.org/10.1016/j.tree.2014.12.002

Domenici P, Blake RW. The kinematics and performance of fish fast-start swimming. *The Journal of Experimental Biology* 1997;**200**:1165–78. https://doi.org/10.1242/jeb.200.8.1165

Doran C, Bierbach D, Lukas J *et al.* Fish waves as emergent collective antipredator behavior. *Current Biology* 2022;**32**:708–14.e4. https://doi.org/10.1016/j.cub.2021.11.068

Eaton RC, Bombardieri RA, Meyer DL. The Mauthner-initiated startle response in teleost fish. *The Journal of Experimental Biology* 1977;**66**:65–81. https://doi.org/10.1242/jeb.66.1.65

Endler JA. Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 1980;**34**:76–91. https://doi.org/10.1111/j.1558-5646.1980.tb04790.x

Endler JA. Multiple-trait coevolution and environmental gradients in guppies. *Trends in Ecology & Evolution* 1995;**10**:22–9. https://doi.org/10.1016/s0169-5347(00)88956-9

Felmy A, Reznick DN, Travis J *et al.* Life histories as mosaics: plastic and genetic components differ among traits that underpin life-history strategies. *Evolution* 2022;**76**:585–604. https://doi.org/10.1111/evo.14440

Fox J, Friendly M, Monette G. Heplots: visualizing hypothesis tests in multivariate linear models. *Comprehensive R Archive Network (CRAN)* 2021.

Fox J, Weisberg S. Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. *Journal of Statistical Software* 2018a;**87**:1–27.

Fox J, Weisberg S. 2018b. *An R Companion to Applied Regression*. Thousand Oaks, CA: SAGE Publications.

Friard O, Gamba M. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution* 2016;**7**:1325–30. https://doi.org/10.1111/2041-210x.12584

Garland T Jr, Downs CJ, Ives AR. Trade-offs (and constraints) in organismal biology. *Physiological and Biochemical Zoology* 2022;**95**:82–112. https://doi.org/10.1086/717897

Ghalambor CK, Hoke KL, Ruell EW *et al.* Non-adaptive plasticity potentiates rapid adaptive evolution of gene expression in nature. *Nature* 2015;**525**:372–5. https://doi.org/10.1038/nature15256

Ghalambor CK, Reznick DN, Walker JA. Constraints on adaptive evolution: the functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). *The American Naturalist* 2004;**164**:38–50. https://doi.org/10.1086/421412

Grafen A. On the uses of data on lifetime reproductive success. In: Clutton-Brock TH (ed.), *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. Chicago, IL: University of Chicago Press, 1988, 454–85.

Greenway R, Arias-Rodriguez L, Diaz P *et al.* Patterns of macroinvertebrate and fish diversity in freshwater sulphide springs. *Diversity* 2014;**6**:597–632. https://doi.org/10.3390/d6030597

Greenway R, Barts N, Henpita C *et al.* Convergent evolution of conserved mitochondrial pathways underlies repeated adaptation to extreme environments. *Proceedings of the National Academy of Sciences of the United States of America* 2020;**117**:16424–30. https://doi.org/10.1073/pnas.2004223117

Greenway R, Drexler S, Arias-Rodriguez L *et al.* Adaptive, but not condition-dependent, body shape differences contribute to assortative mating preferences during ecological speciation. *Evolution; International Journal of Organic Evolution* 2016;**70**:2809–22. https://doi.org/10.1111/evo.13087

Hedrick TL. Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspiration & Biomimetics* 2008;**3**:034001. https://doi.org/10.1088/1748-3182/3/3/034001

Hegyi G, Török J, Tóth L *et al.* Rapid temporal change in the expression and age-related information content of a sexually selected trait. *Journal of Evolutionary Biology* 2006;**19**:228–38. https://doi.org/10.1111/j.1420-9101.2005.00970.x

Huang P, Sieving KE, Mary CMS. Heterospecific information about predation risk influences exploratory behavior. *Behavioral Ecology* 2012;**23**:463–72. https://doi.org/10.1093/beheco/arr212

Ingley SJ, Camarillo H, Willis H *et al.* Repeated evolution of local adaptation in swimming performance: population-level trade-offs between burst and endurance swimming in *Brachyrhaphis* freshwater fish. *Biological Journal of the Linnean Society* 2016;**119**:1011–26. https://doi.org/10.1111/bij.12852

Ingley SJ, Johnson JB. Divergent natural selection promotes immigrant inviability at early and late stages of evolutionary divergence. *Evolution* 2016;**70**:600–16. https://doi.org/10.1111/evo.12872

Jennions MD, Wong BBM, Cowling A *et al.* Life-history phenotypes in a live-bearing fish *Brachyrhaphis episcopi* living under different predator regimes: seasonal effects? *Environmental Biology of Fishes* 2006;**76**:211–9. https://doi.org/10.1007/s10641-006-9022-7

Johnson JB, Belk MC. Predation environment predicts divergent life-history phenotypes among populations of the livebearing fish *Brachyrhaphis rhabdophora*. *Oecologia* 2001;**126**:142–9. https://doi.org/10.1007/s004420000504

Johnson JB, Omland KS. Model selection in ecology and evolution. *Trends in Ecology & Evolution* 2004;**19**:101–8. https://doi.org/10.1016/j.tree.2003.10.013

Kaun KR, Riedl CAL, Chakaborty-Chatterjee M *et al.* Natural variation in food acquisition mediated via a *Drosophila* cGMP-dependent protein kinase. *The Journal of Experimental Biology* 2007;**210**:3547–58. https://doi.org/10.1242/jeb.006924

Kawecki TJ, Ebert D. Conceptual issues in local adaptation. *Ecology Letters* 2004;**7**:1225–41. https://doi.org/10.1111/j.1461-0248.2004.00684.x

Lande R, Arnold SJ. The measurement of selection on correlated characters. *Evolution* 1983;**37**:1210–26. https://doi.org/10.1111/j.1558-5646.1983.tb00236.x

Langerhans RB. Evolutionary consequences of predation: avoidance, escape, reproduction, and diversification. In: Elewa AMT (ed.), *Predation in Organisms*. Berlin: Springer, 2007, 177–220.

Langerhans RB. Trade-off between steady and unsteady swimming underlies predator-driven divergence in *Gambusia affinis*. *Journal of Evolutionary Biology* 2009;**22**:1057–75. https://doi.org/10.1111/j.1420-9101.2009.01716.x

Langerhans RB, Gifford ME, Joseph EO. Ecological speciation in *Gambusia* fishes. *Evolution* 2007;**61**:2056–74. https://doi.org/10.1111/j.1558-5646.2007.00171.x

Langerhans RB, Layman CA, Shokrollahi AM *et al.* Predator-driven phenotypic diversification in *Gambusia affinis*. *Evolution* 2004;**58**:2305–18. https://doi.org/10.1111/j.0014-3820.2004.tb01605.x

Leonard AM, Lancaster LT. Maladaptive plasticity facilitates evolution of thermal tolerance during an experimental range shift. *BMC Evolutionary Biology* 2020;**20**:47. https://doi.org/10.1186/s12862-020-1589-7

Lindholm AK, Hunt J, Brooks R. Where do all the maternal effects go? Variation in offspring body size through ontogeny in the live-bearing fish *Poecilia parae*. *Biology Letters* 2006;**2**:586–9. https://doi.org/10.1098/rsbl.2006.0546

Lukas J, Auer F, Goldhammer T *et al.* Diurnal changes in hypoxia shape predator-prey interaction in a bird-fish system. *Frontiers in Ecology and Evolution* 2021;**9**:151.

MacLeod KJ, While GM, Uller T. Viviparous mothers impose stronger glucocorticoid-mediated maternal stress effects on their offspring than oviparous mothers. *Ecology and Evolution* 2021;**11**:17238–59. https://doi.org/10.1002/ece3.8360

Marshall DJ, Uller T. When is a maternal effect adaptive? *Oikos* 2007;**116**:1957–63.

Monaghan P. Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2008;**363**:1635–45. https://doi.org/10.1098/rstb.2007.0011

Morgan R, Andreassen AH, Åsheim ER *et al.* Reduced physiological plasticity in a fish adapted to stable temperatures. *Proceedings of the National Academy of Sciences of the United States of America* 2022;**119**:e2201919119. https://doi.org/10.1073/pnas.2201919119

Mousseau T, Fox C (eds.). *Maternal Effects as Adaptations*. New York, NY: Oxford University Press, 1998.

Nobrega M, Greenway R, Passow CN *et al.* Effects of plasticity and genetic divergence in phenotypic trait expression of sulfide spring fishes. *Environmental Biology of Fishes* 2024;**107**:611–29. https://doi.org/10.1007/s10641-024-01555-w

Palacios M, Arias-Rodriguez L, Plath M *et al.* The rediscovery of a long described species reveals additional complexity in speciation patterns of poeciliid fishes in sulfide springs. *PLoS One* 2013;**8**:e71069. https://doi.org/10.1371/journal.pone.0071069

Passow CN, Arias-Rodriguez L, Tobler M. Convergent evolution of reduced energy demands in extremophile fish. *PLoS One* 2017b;**12**:e0186935. https://doi.org/10.1371/journal.pone.0186935

Passow C, Greenway R, Arias-Rodriguez L *et al.* Reduction of energetic demands through modification of body size and metabolic rates in locally adapted extremophile fishes. *Physiological and Biochemical Zoology* 2015;**88**:371–83.

Passow CN, Henpita C, Shaw JH *et al.* The roles of plasticity and evolutionary change in shaping gene expression variation in natural populations of extremophile fish. *Molecular Ecology* 2017a;**26**:6384–99. https://doi.org/10.1111/mec.14360

Pérez-Escudero A, Vicente-Page J, Hinz RC *et al.* idTracker: tracking individuals in a group by automatic identification of unmarked animals. *Nature Methods* 2014;**11**:743–8. https://doi.org/10.1038/nmeth.2994

Pigliucci M. *Phenotypic Plasticity: Beyond Nature and Nuture*. Baltimore, MD: The Johns Hopkins University Press, 2001.

Plath M, Hauswaldt JS, Moll K *et al.* Local adaptation and pronounced genetic differentiation in an extremophile fish, *Poecilia mexicana*, inhabiting a Mexican cave with toxic hydrogen sulphide. *Molecular Ecology* 2007b;**16**:967–76. https://doi.org/10.1111/j.1365-294X.2006.03212.x

Plath M, Hermann B, Schröder C *et al.* Locally adapted fish populations maintain small-scale genetic differentiation despite perturbation by a catastrophic flood event. *BMC Evolutionary Biology* 2010;**10**:256. https://doi.org/10.1186/1471-2148-10-256

Plath M, Heubel KU, De León FJG *et al.* Cave molly females (*Poecilia mexicana*, Poeciliidae, Teleostei) like well-fed males. *Behavioral Ecology and Sociobiology* 2005;**58**:144–51.

Plath M, Pfenninger M, Lerp H *et al.* Genetic differentiation and selection against migrants in evolutionarily replicated extreme environments. *Evolution* 2013;**67**:2647–61. https://doi.org/10.1111/evo.12133

Plath M, Tobler M, Riesch R *et al.* Survival in an extreme habitat: the role of behaviour and energy limitation. *Naturwissenschaften* 2007a;**94**:991–6. https://doi.org/10.1007/s00114-007-0279-2

R Core Team. *R: a Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing, 2023.

Reznick DN, Bryga H. Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. *Evolution* 1987;**41**:1370–85. https://doi.org/10.1111/j.1558-5646.1987.tb02474.x

Reznick DN, Bryga HA, Endler JA. Experimentally induced life-history evolution in a natural population. *Nature* 1990;**346**:357–9.

Reznick D, Callahan H, Llauredo R. Maternal effects on offspring quality in poeciliid fishes. *American Zoologist* 1996;**36**:147–56. https://doi.org/10.1093/icb/36.2.147

Reznick D, Endler JA. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* 1982;**36**:160–77. https://doi.org/10.1111/j.1558-5646.1982.tb05021.x

Riesch R, Duwe V, Herrmann N *et al.* Variation along the shy–bold continuum in extremophile fishes (*Poecilia mexicana*, *Poecilia sulphuraria*). *Behavioral Ecology and Sociobiology* 2009;**63**:1515–26.

Riesch R, Oranth A, Dzienko J *et al.* Extreme habitats are not refuges: poeciliids suffer from increased aerial predation risk in sulphidic southern Mexican habitats. *Biological Journal of the Linnean Society* 2010a;**101**:417–26. https://doi.org/10.1111/j.1095-8312.2010.01522.x

Riesch R, Plath M, Garcia de Leon FJ *et al.* Convergent life-history shifts: toxic environments result in big babies in two clades of poeciliids. *Naturwissenschaften* 2010b;**97**:133–41. https://doi.org/10.1007/s00114-009-0613-y

Riesch R, Plath M, Schlupp I. Toxic hydrogen sulfide and dark caves: life-history adaptations in a livebearing fish (*Poecilia mexicana*, Poeciliidae). *Ecology* 2010c;**91**:1494–505. https://doi.org/10.1890/09-1008.1

Riesch R, Plath M, Schlupp I. Toxic hydrogen sulphide and dark caves: pronounced male life-history divergence among locally adapted *Poecilia mexicana* (Poeciliidae). *Journal of Evolutionary Biology* 2011b;**24**:596–606. https://doi.org/10.1111/j.1420-9101.2010.02194.x

Riesch R, Plath M, Schlupp I *et al.* Colonization of toxic springs drives predictable life-history shift in livebearing fishes (Poeciliidae). *Ecology Letters* 2014;**17**:65–71.

Riesch R, Schlupp I, Langerhans RB *et al.* Shared and unique patterns of embryo development in extremophile poeciliids. *PLoS One* 2011a;**6**:e27377. https://doi.org/10.1371/journal.pone.0027377

Riesch R, Tobler M, Lerp H *et al.* Extremophile Poeciliidae: multivariate insights into the complexity of speciation along replicated ecological

gradients. *BMC Evolutionary Biology* 2016;**16**:136. https://doi.org/10.1186/s12862-016-0705-1

Rosen DE, Gordon MS. Functional anatomy and evolution of male genitalia in Poeciliid fishes. *Zoologica : scientific contributions of the New York Zoological Society* 1953;**38**:1–47. https://doi.org/10.5962/p.203441

Rossiter M. Incidence and consequences of inherited environmental effects. *Annual Review of Ecology and Systematics* 1996;**27**:451–76. https://doi.org/10.1146/annurev.ecolsys.27.1.451

Scheiner SM. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* 1993;**24**:35–68. https://doi.org/10.1146/annurev.ecolsys.24.1.35

Schneider CA, Rasband WS, Eliceiri KW. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 2012;**9**:671–5. https://doi.org/10.1038/nmeth.2089

Schuler MS, Orrock JL. The maladaptive significance of maternal effects for plants in anthropogenically modified environments. *Evolutionary Ecology* 2012;**26**:475–81. https://doi.org/10.1007/s10682-011-9499-1

Schulz-Mirbach T, Eifert C, Riesch R *et al.* Toxic hydrogen sulphide shapes brain anatomy: a comparative study of sulphide-adapted ecotypes in the *Poecilia mexicana* complex. *Journal of Zoology* 2016;**300**:163–76.

Stenseth NC, Andersson L, Hoekstra HE. Gregor Johann Mendel and the development of modern evolutionary biology. *Proceedings of the National Academy of Sciences of the United States of America* 2022;**119**:e2201327119. https://doi.org/10.1073/pnas.2201327119

Teska WR, Smith MH, Novak JM. Food quality, heterozygosity, and fitness correlates in *Peromyscus polionotus*. *Evolution* 1990;**44**:1318–25. https://doi.org/10.1111/j.1558-5646.1990.tb05234.x

Tobler M. Divergence in trophic ecology characterizes colonization of extreme habitats. *Biological Journal of the Linnean Society* 2008;**95**:517–28. https://doi.org/10.1111/j.1095-8312.2008.01063.x

Tobler M, Alba DM, Arias-Rodríguez L *et al.* Using replicated evolution in extremophile fish to understand diversification in elemental composition and nutrient excretion. *Freshwater Biology* 2016a;**61**:158–71.

Tobler M, DeWitt TJ, Schlupp I *et al.* Toxic hydrogen sulfide and dark caves: phenotypic and genetic divergence across two abiotic environmental gradients in *Poecilia mexicana*. *Evolution* 2008;**62**:2643–59. https://doi.org/10.1111/j.1558-5646.2008.00466.x

Tobler M, Hastings L. Convergent patterns of body shape differentiation in four different clades of poeciliid fishes inhabiting sulfide springs. *Evolutionary Biology* 2011;**38**:412–21. https://doi.org/10.1007/s11692-011-9129-4

Tobler M, Kelley JL, Plath M *et al.* Extreme environments and the origins of biodiversity: adaptation and speciation in sulphide spring fishes. *Molecular Ecology* 2018;**27**:843–59. https://doi.org/10.1111/mec.14497

Tobler M, Palacios M, Chapman LJ *et al.* Evolution in extreme environments: replicated phenotypic differentiation in livebearing fish inhabiting sulfidic springs. *Evolution* 2011;**65**:2213–28. https://doi.org/10.1111/j.1558-5646.2011.01298.x

Tobler M, Passow CN, Greenway R *et al.* The evolutionary ecology of animals inhabiting hydrogen sulfide-rich environments. *Annual Review of Ecology, Evolution, and Systematics* 2016b;**47**:239–62. https://doi.org/10.1146/annurev-ecolsys-121415-032418

Tobler M, Plath M, Riesch R *et al.* Selection from parasites favours immunogenetic diversity but not divergence among locally adapted host populations. *Journal of Evolutionary Biology* 2014;**27**:960–74. https://doi.org/10.1111/jeb.12370

Tobler M, Riesch R, Tobler CM *et al.* Compensatory behaviour in response to sulfide-induced hypoxia affects time budgets, feeding efficiency, and predation risk. *Evolutionary Ecology Research* 2009;**11**:935–48.

Tobler M, Scharnweber K, Greenway R *et al.* Convergent changes in the trophic ecology of extremophile fish along replicated environmental gradients. *Freshwater Biology* 2015;**60**:768–80. https://doi.org/10.1111/fwb.12530

Tobler M, Schlupp I, Heubel KU *et al.* Life on the edge: hydrogen sulfide and the fish communities of a Mexican cave and surrounding waters. *Extremophiles* 2006;**10**:577–85. https://doi.org/10.1007/s00792-006-0531-2

Tobler M, Schlupp I, Plath M. Predation of a cave fish (*Poecilia mexicana*, Poeciliidae) by a giant water-bug (*Belostoma*, Belostomatidae) in a Mexican sulphur cave. *Ecological Entomology* 2007;**32**:492–5. https://doi.org/10.1111/j.1365-2311.2007.00892.x

Tokić G, Yue DKP. Optimal shape and motion of undulatory swimming organisms. *Proceedings Biological Sciences* 2012;**279**:3065–74. https://doi.org/10.1098/rspb.2012.0057

Tomar S. Converting video formats with FFmpeg. *Linux Journal* 2006;**146**:10.

Torres-Martínez A, Hernández-Franyutti A, Uribe MC *et al.* Ovarian structure and oogenesis of the extremophile viviparous teleost *Poecilia mexicana* (Poeciliidae) from an active sulfur spring cave in Southern Mexico. *Journal of Morphology* 2017;**278**:1667–81. https://doi.org/10.1002/jmor.20740

Uller T. Developmental plasticity and the evolution of parental effects. *Trends in Ecology & Evolution* 2008;**23**:432–8. https://doi.org/10.1016/j.tree.2008.04.005

Van Allen B, Jones N, Gilbert B *et al.* Maternal effects and the outcome of interspecific competition. *Ecology and Evolution* 2021;**11**:7544–56. https://doi.org/10.1002/ece3.7586

Walker JA. Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L. (Gasterosteidae) body shape. *Biological Journal of the Linnean Society* 1997;**61**:3–50. https://doi.org/10.1111/j.1095-8312.1997.tb01777.x

West-Eberhard MJ. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* 1989;**20**:249–78. https://doi.org/10.1146/annurev.ecolsys.20.1.249

Wilson AJ, Coltman DW, Pemberton JM *et al.* Maternal genetic effects set the potential for evolution in a free-living vertebrate population. *Journal of Evolutionary Biology* 2005;**18**:405–14. https://doi.org/10.1111/j.1420-9101.2004.00824.x

Winemiller KO, Rose KA. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 1992;**49**:2196–218. https://doi.org/10.1139/f92-242

Wolf JB, Wade MJ. What are maternal effects (and what are they not)? *Philosophical Transactions of the Royal Society B: Biological Sciences* 2009;**364**:1107–15. https://doi.org/10.1098/rstb.2008.0238

Zhang H, Vedder O, Becker PH *et al.* Age-dependent trait variation: the relative contribution of within-individual change, selective appearance and disappearance in a long-lived seabird. *The Journal of Animal Ecology* 2015;**84**:797–807. https://doi.org/10.1111/1365-2656.12321