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Variation in personality shaped by evolutionary history, genotype and developmental plasticity in response to feeding modalities in the Arctic charr

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Animal personality has been shown to be influenced by both genetic and environmental factors and shaped by natural selection. Currently, little is known about mechanisms influencing the development of personality traits. This study examines the extent to which personality development is genetically influenced and/or environmentally responsive (plastic). We also investigated the role of evolutionary history, assessing whether personality traits could be canalized along a genetic and ecological divergence gradient. We tested the plastic potential of boldness in juveniles of five Icelandic Arctic charr morphs (*Salvelinus alpinus*), including two pairs of sympatric morphs, displaying various degrees of genetic and ecological divergence from the ancestral anadromous charr, split between treatments mimicking benthic versus pelagic feeding modalities. We show that differences in mean boldness are mostly affected by genetics. While the benthic treatment led to bolder individuals overall, the environmental effect was rather weak, suggesting that boldness lies under strong genetic influence with reduced plastic potential. Finally, we found hints of differences by morphs in boldness canalization through reduced variance and plasticity, and higher consistency in boldness within morphs. These findings provide new insights on how behavioural development may impact adaptive diversification.

1. Introduction

Animal personality is defined as among-individual behavioural differences that are consistent across time and/or contexts [1,2]. Variation in personality traits within populations has been shown to be subjected to natural selection due to ecological conditions [3], with heritability estimated between 0.32 [1] and 0.52 [4] in various species. Personality can also be plastic, as individuals' behaviour can respond to environmental factors, while remaining consistent among individuals (e.g. the most active individual being less active around predators, but still being the most active relative to other individuals [5]). Such behavioural plasticity may influence biological diversification and speciation [6]. Indeed, phylogenetic clades with greater behavioural plasticity display higher species richness [7,8]. Several theoretical models suggest how different personality traits appear and coexist among individuals within and between populations (reviewed in [9,10]): personality differences could arise from individual differences in life-history strategies [11], from individual differences in state that can be either directly due to heterogeneous environmental factors or indirectly due

to differences in parental contributions [12], or even from stochastic chaos dynamics [13,14]. Those personality differences could be further maintained if they lead to similar fitness pay-offs or through frequency-dependent selection [15]. Stamps & Groothuis [16] posited that variations in personality could be at the origin of differential niche-picking or niche construction between individuals (see also [10]), leading to separation of personalities into sympatric distinct niches for which they are more fitted, which we hypothesize promotes sympatric divergence between personalities within species.

Comparative study of personality variations between species, or between populations occupying different niches within a species, can allow identification of ecological factors driving the evolution of personality. Nevertheless, some pitfalls may hamper the use of this approach: intrinsic interspecies differences in behaviour, and geographical confounding effect as ecological conditions differ between sites. In this project, we aimed at partly bypassing those issues by using different morphs of the same species, the Arctic charr (*Salvelinus alpinus*), a fish of the Salmonid family found in sympatry in Icelandic freshwater lakes and rivers. In order to simultaneously disentangle genetic and environmental effects on the development of personality, these morphs were raised in a common garden design where a key environmental variable was manipulated: benthic versus pelagic modality of food distribution.

In many freshwater fishes, utilization of benthic versus pelagic habitats has driven ecological specialization and evolutionary divergence within species, leading to the repeated evolution of coexisting sympatric ecomorphs within lakes [17–19]. This high evolvability is believed to be due to a high plastic potential, notably in morphology of feeding apparatus structures linked with different diets [20]. Such plastic changes are suspected to be initiated by behavioural differences [21]. As behaviour is the most immediate adaptive mechanism available for animals against environmental change [22–26], Wilson & McLaughlin [27] posited that studying populations exhibiting behavioural divergence, yet low morphological divergence, is relevant to understand the initial stages of resource polymorphism [28].

In Iceland, Arctic charr morphs tend to be either benthic, i.e. feeding on the bottom with stocky dark-brown bodies and subterminal lower jaw seemingly adapted to benthic prey exploitation, or pelagic, i.e. feeding in the water column with fusiform silvery bodies and pointy snouts with terminal mouth seemingly adapted to plankton filtration or even to piscivory [29–31]. The morphs studied here (electronic supplementary material, figure S1) display various degrees of genetic, ecological and morphological divergence in the wild, due to partial reproductive isolation and differential niche-use in lakes [29,32,33]. The large benthic (LB, benthic) and the planktivorous (PL, pelagic) sympatric morphs from Lake Þingvallavatn are an extreme example of such divergence, with obvious morphological differences, distinct specialized diets and spatio-temporally separated reproduction [30–32,34–36]. The brown (VB) and the silver (VS) sympatric morphs from Lake Vatnshlíðarvatn display more subtle morphological and ecological differences: while VB are closer to the previous description of a benthic morph and VS are closer to the description of a pelagic morph, morphological divergence is not as pronounced as between LB and PL [37].

These morphs are thought to descend from the same ancestral population [38,39], this ancestor probably represented

contemporarily by extant anadromous populations retaining higher genetic diversity [37]. Ancestral Arctic charr were landlocked in lakes formed at different geological times after the last glaciation. Although the specific events during colonization and early divergence are unknown, it is assumed that the time since separation from the ancestral population translates into a gradient of evolutionary divergence from the common ancestor between Arctic charr populations throughout Iceland [37,40]. Although broader sampling and more genetic data are needed to estimate the origin and history of each population, we use the monomorphic anadromous population in Fljótaá River (AN) to represent the putative ancestral form, sympatric VS and VB morphs from Lake Vatnshlíðarvatn as moderately diverged from the ancestor (landlocked 6000–8000 years ago [41]), and sympatric LB and PL morphs from Lake Þingvallavatn as highly diverged forms (landlocked approx. 10 000 years ago [42]). Consistently, genetic analyses show strong genetic divergence between Lake Þingvallavatn sympatric morphs (LB and PL, in advanced divergence state), but weaker genetic separation between Lake Vatnshlíðarvatn sympatric morphs (VB and VS, in early state of divergence) [29,33,37,43,44].

Developmental plasticity is the property of a given genotype to produce different phenotypes depending on the environmental conditions under which development takes place [45], observed as differences in means by conditions (reaction norms). Canalization refers to the capacity of organisms to produce standard phenotypes despite genetic and environmental perturbations, reducing variance around reaction norms [46,47]. Diet treatment where the same food items are either provided as floating (pelagic) or on the bottom (benthic) has been shown to elicit plastic response in growth, body shape and craniofacial/skeletal features in the Arctic charr morphs studied here [20,48–50]. The data suggest differences in morphological plasticity, where morphs from Lake Þingvallavatn (LB and PL, more diverged) were less plastic over ontogeny with a more canalized development than morphs from Lake Vatnshlíðarvatn (VS and VB, moderately diverged), and where LB and VB morphs were more morphologically canalized than their respective sympatric counterparts [49,50]. The 'plasticity-first hypothesis' states that ancestral phenotypic plasticity induced by environmental perturbations leads to developmental reorganization and uncovers cryptic genetic variation, producing novel trait variants on which selection can act, and that undergo phenotypic accommodation and ultimately genetic accommodation [51]. In this sense, genetic fixation of new behavioural accommodations acquired through ancestral behavioural plasticity and decanalization when the environment changes or when invading a new environment, i.e. Baldwin effect [22,52,53], could allow individuals to survive until genetic assimilation [54]. The costs of maintaining behavioural plasticity could then be reduced over evolutionary time, when the optimal behavioural trait value for the new conditions has been reached, by genetically fixing and canalizing this phenotype in the population. To our knowledge, whether this mechanism could be happening concerning personality traits has not been addressed.

In the present study, we examined what roles genotype, plasticity and canalization play in the development of personality in the Arctic charr. We focused on a widely studied aspect of animal personality, boldness—the individual propensity to take risks [1]—that has recently been reported in the Arctic

charr [55–57]. We hypothesized that (a) differences in ecological backgrounds lead to the evolution of different personality profiles between morphs (genotype), (b) the early environment influences the developmental trajectories of personality traits (developmental plasticity of personality) within morphs, and (c) the degree of evolutionary divergence influences the degree of developmental plasticity of personality and the magnitude of personality range between morphs, potentially via canalization.

To address this, juvenile full sibs of AN, VS, VB, LB and PL morphs were reared in common garden in benthic versus pelagic feeding modality treatments. We tested for differences in boldness repeatability, averages and variances across morphs and treatments to characterize personality profiles. If personality development is under genetic influence (a), we expected mean boldness to be morph-specific, or at least population-specific (between lakes/rivers). If personality development responds to environmental conditions, i.e. is plastic (b), we expected differences in mean boldness between treatments, either overall or within morphs. If a longer time since divergence leads to canalization of personality traits (c), we expected reduced plasticity, lower variance and higher consistency in boldness in more diverged morphs. Note that these predictions are not mutually exclusive. To our knowledge, this study is the first empirical attempt to simultaneously assess the role of evolutionary history, genetic and environmental influences, and in particular the influence of feeding modalities, in shaping personality during early life.

2. Material and methods

(a) Biological material

This study used offspring of wild-caught Arctic charr morphs: AN from Fljótaá River; VS and VB sympatric morphs from Lake Vatnshlíðarvatn; LB and PL sympatric morphs from Lake Þingvallavatn. For each morph, three male and three female wild adults were captured with gill nets or electrofishing during spawning season: AN on the 22 October 2018 (65.999641°, −19.004670°); VS on the 17 September 2018 (65.510907°, −19.666710°); VB on the 3 September 2018 (65.516883°, −19.612980°); LB on the 9 August 2018 (64.234195°, −21.047049°); PL from 7 October 2018 to 14 October 2018 (64.190976°, −21.093420°). Each fish was stripped of gametes, and pure crosses were made on site, creating three families within each morph. Eggs from each family were kept separated and raised in common garden. Incubation conditions were complete darkness at $4.3 \pm 0.14°C$, pH 7.3 ± 0.15, dissolved O_2 saturation $101.4 \pm 1.8\%$ and eggs were checked daily.

(b) Housing conditions

One week before anticipated hatching date, families were transferred to separate 20 l cylindrical tanks (water renewal kept above 200% per hour (40–50 l h^{-1}) to maintain oxygen saturation; 12 h/12 h light/dark photoperiod at 80 lux). Fish were fed ground commercial aquaculture start food (INICO 0.4 mm) three times a day. Before first feeding, the water temperature was maintained at $4.0 \pm 0.3°C$ matching Þingvallavatn spawning beds temperatures [58], then progressively increased to $7.6 \pm 1.1°C$ between 50 and 90 degree days (daily temperature × age in days) after first feeding to match more typical groundwater temperatures [58] and to increase growth rates during feeding treatment. At 1226.3 ± 20.7 degree days after hatching, individuals within families were individually tagged with Visible Implants Elastomer (VIE, Northwest Marine Technology, 2008), and half was randomly assigned to a benthic feeding treatment,

the other half to a pelagic feeding treatment (see next paragraph). Hence, we had 10 different batches (5 morphs × 2 treatments). Specificities regarding number of tank replicates, fish density and families' distribution over replicate tanks are detailed in electronic supplementary material, table S1.

(c) Feeding treatments

Feeding treatments, following Parsons et al. [49,50], started 16 days after tagging and lasted for 120 days. Fish from both treatments received the same food quantity (4% of overall biomass) and quality: from day 1 to day 30, they received a 60 : 40% mixture, respectively, of INICO commercial aquaculture pellets (to ensure complete nutrition) and bloodworms (to expose individuals to a prey item foraged by juveniles in the wild), then a 50 : 50% mixture from day 31 to day 120. Pellets were distributed manually five times a day and bloodworms once a day. Pellet granulometry was 0.8 mm from day 1 to day 60, and 1.1 mm from day 61 to day 120, to adapt to fish growth. Only the distribution modality differed between treatments, mimicking prey shape and accessibility in natural habitats. In the benthic treatment, food was accessible exclusively at the bottom of the tank: whole pellets were distributed through a funnel and whole bloodworms were distributed in a food trap placed at the bottom to encourage scrapping of food from the substrate like benthic-feeders would in the wild. In the pelagic treatment, ground pellets and chopped bloodworms were spread evenly at the water surface and distributed homogeneously through the water column with water flow. A mesh placed 2–3 cm above the bottom of pelagic tanks prevented benthic feeding, forcing the fish to catch or filter drifting items like pelagic-feeders would.

(d) Open field test

After the completion of the feeding experiment on day 120, and throughout the behavioural testing, fish were maintained on pellets only, using the same distribution modality as the feeding experiment. Bloodworms were no longer provided because behavioural testing would take entire days, and provisioning bloodworms only once a day, as during the feeding experiment, could bias behaviour between fish that had access to it prior to being tested and fish that had not. After 3 days of adjustment to this diet, at day 124, 18 individually tagged fish per family per batch, equally distributed across replicate tanks (AN, LB: 6 individuals per replicate; PL, VB, VS: 9 individuals per replicate to compensate for lesser replicate tanks per family, see electronic supplementary material, table S1 for details), were chosen to be submitted twice to an open field test (OFT) with shelter, with a 7-day interval between each replication, to assess boldness personality trait (18 individuals × 3 families = 54 fish per batch, i.e. 108 fish per morph, i.e. $N = 540$, electronic supplementary material, table S1). These fish were semi-randomly chosen in order to cover a size gradient to account for possible influence of body size on behaviour [59] as notable size variations existed between and within replicate tanks, morphs and families. Individuals from each family within each tank were divided in three size classes, small, medium and large, corresponding, respectively, to the first, second and third quantiles of the body size distribution of family within tank. Two fish per size class were picked at random for each family and tank. For technical reasons, the test started on day 131 instead of day 124 for the AN. All morphs started OFT trials at 276–292 days old from hatching, well before maturity. The OFT arena [55] consisted of an opaque white rectangle tank (39.7 × 29.5 × 25 cm) filled with 6 cm water depth at home tanks' temperature, with a shelter in a corner (14 × 6 × 6 cm) provided with a removable door. The set-up was placed on a white LED backlight (Noldus Information Technology) set at 70 lux to increase contrast. A Basler Ace acA1920-150um camera placed 110 cm above the arena recorded

each test at 30 frames per second. At the beginning of the test, the fish was placed in the closed shelter. After a 5 min acclimation, the shelter door was opened, and the fish was free to explore the arena for 20 min. Once the 20 min were completed, the fish was gently netted, anaesthetized in a 300 ppm phenoxyethanol solution, weighed, and fork length and total length were measured. Water in the arena was replaced between each trial.

(e) Boldness score assessment

The fish were tracked from the obtained videos with Ethovision XT v. 14 (Noldus Information Technology). The arena was divided into four virtual zones: the shelter zone covering the shelter area, overlapping with an entry zone extended 3 cm from the shelter door; the border zone corresponding to a buffer of 3.5 cm along the edges of the arena; the centre zone being the remaining part of the arena and corresponding to the riskiest area since thigmotaxis (tendency to remain close to the enclosure walls) is commonly associated with shyness [60,61]. The fish barycentre was used to calculate the latency to first exit the shelter (s), frequency of visits in each zone, cumulative time spent in each zone (duration, s), mean velocity (corrected by body length, s^{-1}), absolute angular velocity (degrees s^{-1}) and the total distance travelled (cm). If an individual did not exit the shelter (head and trunk not visible) after 20 min in either replication, it was considered not to have responded to the test and was excluded from the subsequent principal component analysis (PCA) (justification in electronic supplementary material, figure S2). Eventually, a total of $N = 463$ fish were included in the PCA analyses (details in electronic supplementary material, table S1).

We can consider that the first OFT replication is the most accurate assessment of boldness, as all individuals are completely naive to the test at that point [57,62]. Hence, we reduced all behavioural variables recorded during the first OFT replication into a primary axis of behavioural variation with a PCA, removing variables showing high correlation with others on the factor map. We retained total distance travelled, absolute angular velocity, entry frequency and shelter, centre and entry durations. The first axis of this PCA (PC1) explained 58.0% of the variance in the data, to which the variables with strongest contributions were total distance travelled, shelter duration and entry frequency (respective PC1 loadings: 0.941, −0.935 and 0.839; see electronic supplementary material, figure S2 and accompanying R script [63]). Consequently, PC1 represents a gradient from shyest (negative values) to boldest individuals (positive values), as high PC1 coordinates indicate that the fish explored the arena instead of spending time in the shelter and re-entered the entry zone numerous times. We then used this PCA as a template applied to the whole dataset. Each individual was hence assigned a boldness score for each replication, corresponding to its coordinate on PC1, the boldness scores at the second OFT replication being predicted based on the PCA parameters calculated with the first replication, consequently taking repeated measures into account while conserving the multiple-behaviours complexity of risk-taking.

(f) Statistical analyses

As time spent in the shelter was a major component of shyness in the PCA, we considered the proportion of non-responding fish—technically spending the maximum time in the shelter—as a complementary group-level indicator of boldness. The proportion of non-responding individuals was compared between morphs, treatments and batches with χ^2-tests. All other statistics were performed with R v. 4.3.0 software [64] and are provided in the R script accompanying this article [63]. Mean boldness score and proportion of non-responding individuals were compared between morphs to investigate the genetic influence on the development of personality, and between treatments and batches to investigate boldness plasticity. Boldness score repeatability (i.e. consistency) and variances were compared between morphs to assess differences in canalization of boldness. We partitioned the total variance in boldness into among- and within-individual variances for each morph. Among-individual variance (V_{among}) represents the group-level variance in boldness, i.e. how much individuals behaved differently from each other across replications. Within-individual variance (V_{within}) represents the variance in boldness at the data level, i.e. how much an individual behaved differently from itself across replications.

(i) Mean boldness scores

We fitted a linear mixed model predicting z-scaled boldness score in the Bayesian language Stan [65] using the brms package v. 2.19.0 [66]. The model (referred to as model.0, details in accompanying R script [63]), included morph, treatment, their interaction, z-scaled total length of the fish and OFT replication as fixed predictors. Random factors included individual ID, family, tank, time-category (as OFT tests were run over entire days, we attributed a time-category to each trial according to running slots to control for potential differences in diel activity) and date (as one OFT replication would last for 6 days per morph, to account for possible stress accumulation over days). Diagnostics of model.0 were validated by inspecting potential scale reduction factors, effective sample sizes, tails heaviness and lightness, trace plots, densities, autocorrelation plots and trace rank plots for each model parameter. We also verified the robustness of the results by running model.0 again using several different seeds.

We calculated marginal (R2m), conditional (R2c) and inclusive (IR2) R^2-values for model.0, describing the amount of variance in boldness scores explained by the fixed predictors, the whole model and each predictor, respectively (method adapted from [67], details in accompanying R script [63]). We applied the functions emmeans and contrast (package emmeans v. 1.7.8 [68]) under Tukey linear hypothesis to model.0, to perform pairwise *post hoc* comparisons of boldness scores between morphs and between treatments within morphs.

(ii) Boldness repeatability, among- and within-individual variances

Boldness repeatability (R) evaluates the proportion of the total variance that is due to among-individual variance in boldness [4], corresponding to the behavioural consistency at the group level over replications. In other words,

$$R = \frac{V_{among}}{\text{total variance}} = \frac{V_{among}}{(V_{among} + V_{within})}.$$

On the one hand, we extracted the posterior samples corresponding to the standard deviations for the ID random predictor and the residuals of model.0, squared them to obtain V_{among} and V_{within}, respectively, which we used to calculate R. On the other hand, we calculated those three variables for each morph and compared them statistically by following the method proposed by Royauté & Dochtermann [69], fitting a multi-level structure brms model (model.morph), with boldness score as the response variable, the morph as fixed predictor, random effects for both the intercept and the morph-related effect, which were nested within the individual IDs, allowing capture of V_{among} per morph, and finally a sigma term accounting for potential variations in the residual standard deviation among morphs, capturing V_{within} per morph (details in accompanying R script [63]). Diagnostics of model.morph were produced as described in the previous paragraph.

Still using Royauté & Dochtermann's guidelines [69], we examined pairwise differences in the posterior distributions of V_{among}, V_{within} and R between morphs (ΔV_{among}, ΔV_{within} and ΔR, respectively). All estimates are medians of posterior distributions with their 95% credible interval (CI), along with probability of direction (PD), indicating the proportion of samples that are of the estimate's sign, i.e. roughly the probability that the estimate is different from zero. We also calculated the effect sizes for each pairwise comparison to estimate the amplitudes of ΔV_{among}, ΔV_{within} and ΔR between morphs, by calculating the probability of superiority between the posterior distributions of each parameter for each pair of morphs (A statistic [70], package RProbSup v. 3.0 [71]). Finally, we tested whether model.morph detected the correct pattern of differences in variance components among morphs [69], by comparing models similar to model.morph, allowing (m1) neither V_{among} nor V_{within}, (m2) V_{among} only, (m3) V_{within} only or (m4) both V_{among} and V_{within}, to vary by morph (details in accompanying R script [63]).

Note: as a side investigation, we also compared V_{among}, V_{within} and R between treatments within morphs to test the genotype-by-environment influence on the emergence of personality (see accompanying R script [63]). Results are presented and discussed in electronic supplementary material, table S2.

Note: Bayesian statistics do not use frequentist p-values. The significance of an estimate is obtained when its CI or its highest posterior density interval (HPDI) does not overlap zero. We considered a tendency for an estimate when the CI or HPDI overlapped zero no further than 0.09 units with a PD $\geq$ 0.92. Regarding the A statistic, we considered a large effect when A $\in$ [0.00;0.10] $\cap$ [0.90;1.00], a small effect when A $\in$ [0.11;0.20] $\cap$ [0.80;0.89], and a negligible effect otherwise.

3. Results

(a) Mean boldness score

The morph had significant impact on boldness score, the *post hoc* test highlighting gradual increase in mean boldness along the divergence gradient (with AN as a reference: AN = VS < VB < LB < PL) with a tendency for the PL to have a higher mean boldness than LB and VB morphs (table 1 and figure 1a). The treatment itself had no significant impact on boldness score, but the morph-by-treatment interaction had a slight effect within morphs (table 1), VS-benthic fish being significantly bolder compared with VS-pelagic fish, with a similar tendency within PL (table 1 and figure 1b). Larger fish were also significantly bolder (table 1). Model.0 explained 62.0% of the variance in the data (R2c), with 30.9% explained by the fixed effects (R2m). Further examination of R^2-values (table 1) indicated that the morph explained the vast majority of the variance (26.8%) while the morph-by-treatment interaction and the total length had a minute impact (0.7% and 0.5%, respectively). Variation in boldness scores was similar between families within a morph (visual inspection, see electronic supplementary material, figure S3).

(b) Proportions of non-responding individuals

The proportions of non-responding fish (table 2) depended on the morph (χ^2 (4, N = 536) = 21.27, p < 0.001), treatment (χ^2 (1, N = 536) = 4.73, p < 0.05) and batch (χ^2 (9, N = 536) = 28.18, p < 0.001), and broadly followed the same pattern as mean boldness scores: the more diverged the morph, the bolder, with the fewest non-responding fish (except VB and LB standing out of this pattern). With 6.5% more fish coming out compared with the pelagic treatment, fish from the benthic treatment appeared significantly bolder overall. This was also the case within morphs, with the AN showing the largest proportion difference between treatments, but more marginally for the VB in which proportions were almost equal between treatments.

(c) Boldness repeatability, V_{among} and V_{within}

The boldness score was repeatable over the whole dataset—confirming (along with [55–57]) that boldness can be considered a personality trait in the Arctic charr [1]—as well as within each morph. A notable exception was the AN (table 3). Interestingly, repeatability tended to increase along the divergence gradient, with the AN and PL morphs at the two extremes of the gradient showing a significant difference (AN < (VS = VB = LB) < PL, table 3). The A statistics revealed notable differences in repeatability in pairwise comparisons involving AN and PL morphs (table 3). Also, AN had generally lower V_{among} compared with the other morphs, and when considering V_{within}, AN and PL morphs had similar values and were significantly less variable than VS, VB and LB morphs, which were also similar to each other (i.e. the general V_{within} pattern (AN = PL) < (VS = VB = LB), table 3 and figure 1a). The A statistics revealed large differences in pairwise comparisons of V_{among} involving AN, and the only negligible difference in V_{within} was between LB and VS morphs (table 3). Out of the four models compared, m4 was best supported, indicating that both V_{among} and V_{within} varied by morph [69].
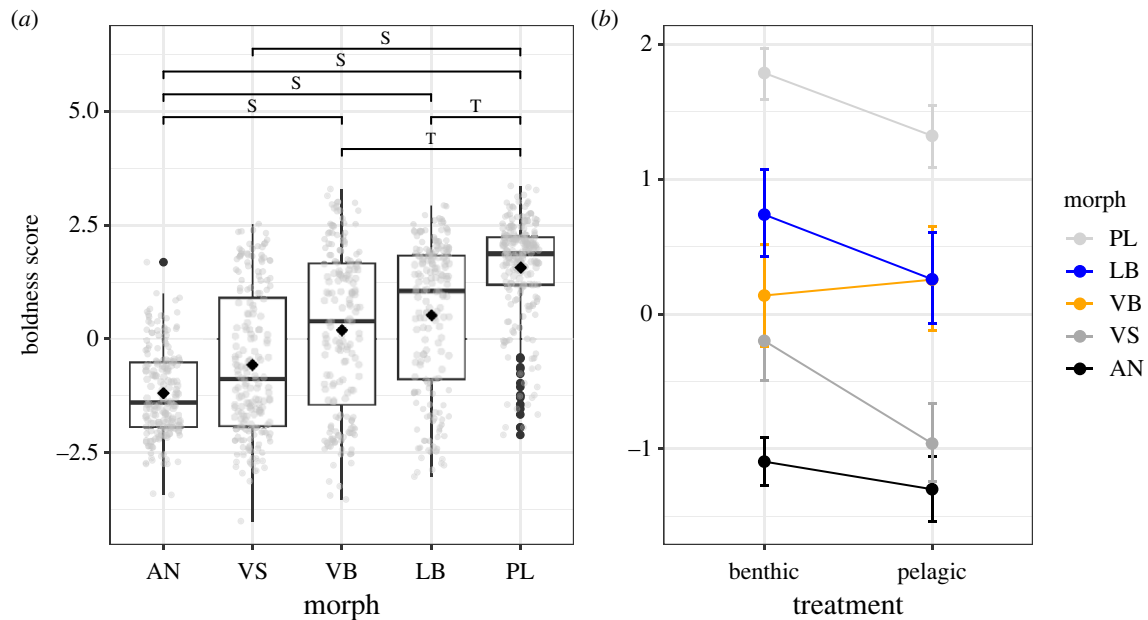
4. Discussion

(a) Boldness under strong genetic influence

The results show that the development of boldness in this species is predominantly influenced by genetic background and less so by the environment (feeding modality) (see also [55,57]). We and previous studies found no differences in mean boldness score between sympatric morphs (e.g. VS-VB, LB-PL, SB-PL, [56,57]). This suggests that genetic differences between closely related sympatric morphs are too subtle to engender detectable differences in boldness. However, PL and LB sympatric morphs, which are also more genetically, ecologically and morphologically diverged from each other than VB from VS, tended to differ in mean boldness score (table 1 and figure 1a). This indicates genetic influence on boldness may be more easily discovered in more diverged populations between lakes and rivers and suggests that differences in average boldness could widen as sympatric morphs further diverge from each other.

An increase in boldness with the morph's degree of divergence from the common ancestor was observed (roughly, AN < VS < VB < LB < PL; table 1 and figure 1a). Similar ranking of boldness by morph was seen in independently reared offspring (same morphs sampled three years prior in [57]; 1–2 years later in Dellinger *et al*. [72]). Such consistency within morphs across years further suggests that boldness patterns are heritable, with stable selective pressures maintaining them in the wild. The boldness gradient among the five morphs also appears to be consistent over social rearing contexts, as individuals raised in isolation [57] responded similarly to our individuals raised in high-density groups. This corroborates previous studies showing no effect of

Table 1. Left: output of model.0, Bayesian brms linear mixed model predicting z-scaled boldness score including the morph (AN from Fjlótaá River taken as reference, sympatric VS and VB from Vatnshlíðarvatn, and sympatric LB and PL from Þingvallavatn), treatment (benthic or pelagic, benthic being taken as reference) and their interaction (AN morph and benthic treatments taken as references), z-scaled total length of the fish and OFT replication (first replication taken as reference) as fixed predictors, and individual ID, family, tank, date and time-categories as random predictors. **Middle:** variance explained (IR2) by each predictor of model.0. **Right:** results of the Tukey post hoc pairwise comparisons of boldness scores between morphs, and between treatments within morphs, carried out on model.0, with significant estimates highlighted in bold font, while tendencies are highlighted in italic font. Estimate: median of posterior distribution for each variable or contrast; s.e., standard error; CI, credible interval; HPDI, 95% highest posterior density intervals.

Model.0

predictor	estimate	s.e.	CI
intercept	−0.81	0.31	[−1.43; −0.18]
VS	0.67	0.41	[−0.14; 1.47]
VB	0.82	0.41	[0.00; 1.63]
LB	0.97	0.41	[0.17; 1.77]
PL	1.72	0.41	[0.91; 2.52]
treatment pelagic	−0.04	0.15	[−0.34; 0.25]
total length	0.12	0.04	[0.05; 0.19]
OFT replication 2	−0.01	0.08	[−0.17; 0.14]
VS pelagic	−0.35	0.21	[−0.75; 0.06]
VB pelagic	0.13	0.22	[−0.30; 0.56]
LB pelagic	−0.10	0.21	[−0.51; 0.30]
PL pelagic	−0.18	0.21	[−0.58; 0.23]
ID	0.30	0.05	[0.20; 0.39]
family	0.43	0.12	[0.26; 0.73]
tank	0.08	0.05	[0.00; 0.20]
date	0.19	0.04	[0.12; 0.28]
time-categories	0.20	0.15	[0.06; 0.59]
sigma	0.67	0.02	[0.63; 0.72]

variance explained

predictor	IR2	HPDI
morph	0.268	[0.10; 0.43]
treatment	0.008	[0.00; 0.02]
total length	0.005	[0.00; 0.02]
OFT replication	0.001	[0.00; 0.00]
morph-by-treatment interaction	0.007	[0.00; 0.06]
ID	0.094	[0.04; 0.15]
family	0.167	[0.05; 0.44]
tank	0.006	[0.00; 0.03]
date	0.035	[0.01; 0.07]
time-categories	0.035	[0.01; 0.07]

post hoc

comparison	pair	estimate	HPDI
between morphs	VS–AN	0.49	[−0.31; 1.26]
	VB–AN	**0.89**	[0.12; 1.68]
	LB–AN	**0.92**	[0.13; 1.69]
	PL–AN	**1.63**	[0.85; 2.43]
	VB–VS	0.39	[−0.39; 1.15]
	LB–VS	0.43	[−0.32; 1.22]
	PL–VS	**1.15**	[0.37; 1.92]
	LB–VB	0.03	[−0.76; 0.80]
	PL–VB	*0.75*	[−0.04; 1.52]
	PL–LB	*0.72*	[−0.05; 1.49]
between treatments	AN	0.04	[−0.25; 0.33]
within morphs	VS	**0.39**	[0.11; 0.67]
(benthic–pelagic)	VB	−0.09	[−0.39; 0.23]
	LB	0.15	[−0.16; 0.43]
	PL	*0.22*	[−0.06; 0.51]

Figure 1. Boldness scores across the five morphs of Arctic charr, from the least to the most diverged: AN from Fljótaá River, sympatric VS and VB from Vatnsh-líðarvatn, and sympatric LB and PL from Þingvallavatn. (a) Boxplots of boldness scores for each morph: the rhombus represents the mean, grey dots are scattered individual values, the central line indicates the median, ends of the boxes denote upper and lower quartiles, whiskers cover 95% of values. Significance levels from Tukey *post hoc* pairwise comparisons of boldness scores between morphs, carried out on model.0: S, significant; T, tendency (see also table 1). (b) Reaction norms of boldness scores across treatments (benthic and pelagic) for each morph: the dot represents the mean, vertical bars indicate 1 s.e., the slope of the line across treatments indicates the direction and amplitude of boldness plasticity. The benthic fish were significantly bolder than the pelagic fish within the VS, and tended to be within the PL (see also table 1).

Table 2. Proportion of non-responding individuals, i.e. fish that did not exit the OFT shelter after 20 min, per morph, per treatment and per batch ($N = 73$ out of 540 fish tested).

	morph	AN	VS	VB	LB	PL
	all treatments considered	19.4%	13.0%	19.6%	15.1%	0.9%
treatment	all morphs considered					
benthic	10.4%	13.0%	9.3%	19.2%	10.9%	0.0%
pelagic	16.9%	25.9%	16.7%	20.0%	19.6%	1.9%

direct early-life social exposure on mean personality trait [13], or on repeatability of behaviour [73], unlike the highly influential effect of social contexts on personality usually described in other taxa [74]. All these observations constitute even more clues in favour of a strong and heritable genetic effect on Arctic charr boldness development.

(b) Boldness plasticity

The treatment engendered a plastic response in boldness, with significantly fewer non-responding fish in the benthic treatment compared with the pelagic treatment (table 2). Although we did not detect this relationship between bold-ness score and benthic treatment in the fish that responded to the OFT, such a pattern can be perceived (figure 1b) as all morphs except the VB show lower boldness scores in pela-gic treatment (significant for VS, tendency for PL), the morph-by-treatment interaction weakly but significantly influencing boldness scores (table 1). If non-responding indi-viduals could have been attributed a (most likely low) boldness score (discussed in electronic supplementary material, figure S2), one can imagine stronger boldness score differences between treatments within morphs, hence

the detection of higher plasticity levels. This would be especially apparent within the AN, showing a rather flat boldness score reaction norm, but the largest difference in proportions of non-responding fish, between treatments. These elements considered parallelly indicate that the devel-opment of boldness is plastic, and that the degree of plasticity differs by genotypes. Higher boldness in benthic treatment may be due to competitive access to localized food. Agonistic behaviours towards conspecifics are well known in the Arctic charr, with dominance typically established through a high degree of aggressiveness by larger fish monopolizing access to food [75]. A positive correlation between boldness and dominance has already been demonstrated in salmonids [76] which parallels our results showing a significant positive effect of size on boldness. Hence, interindividual competition in our benthic treatment may have fuelled higher levels of boldness to fight for first access to the resource. Competition was probably much lower in the pelagic treatment, where food was equally accessible by all through the water column. In this case, further work is necessary to assess whether these observed behavioural patterns relate to devel-opmental plasticity (long-term effect) or temporal plasticity (or flexibility) in boldness [77].

Table 3. Estimates per morph (AN from Fljótaá River, sympatric VS and VB from Vatnshlíðarvatn, and sympatric LB and PL from Þingvallavatn), pairwise differences in the posterior distributions between morphs (Δ) and their effect sizes, of boldness score repeatability (R), among-individual variance (V_{among}) and within-individual variance (V_{within}). Significant Δ estimates and large effect sizes are highlighted in bold font, while tendencies for Δ and small effect sizes are highlighted in italic font. Estimates & Δ: all estimates are medians of posterior distributions with their 95% credible interval (CI), along with probability of direction (PD) of the Δ, indicating the proportion of samples that are of the estimate's sign, i.e. roughly the probability that the estimate is different from zero. Effect size: probability of superiority (A) with its standard error (s.e.) and 95% confidence interval (CI), between the posterior distributions of each variable for each pair of morphs. The A statistic is a probability-based measure of effect size, indicating the probability that a randomly chosen member of group 1 scores higher on the response variable than a randomly chosen member of group 2, i.e. in our case if A < 0.5, morph 2 outscores morph 1 and vice versa.

variable	morph	estimates estimate	lower CI	upper CI	pairwise comparison	Δ estimate	lower CI	upper CI	PD	effect size A	s.e.	lower CI	upper CI
R	AN	0.03	0.00	0.18	VS–AN	*0.21*	−0.03	0.41	0.95	**0.95**	0.00	0.95	0.96
	VS	0.25	0.03	0.44	VB–AN	*0.18*	−0.06	0.40	0.92	**0.92**	0.00	0.92	0.93
	VB	0.22	0.01	0.42	LB–AN	*0.24*	0.00	0.45	0.98	**0.98**	0.00	0.97	0.98
	LB	0.28	0.08	0.47	PL–AN	**0.40**	0.19	0.56	1.00	**1.00**	0.00	1.00	1.00
	PL	0.44	0.27	0.58	VB–VS	−0.03	−0.32	0.26	0.58	0.42	0.01	0.41	0.43
					LB–VS	0.03	−0.25	0.31	0.58	0.58	0.01	0.57	0.59
					PL–VS	*0.19*	−0.06	0.44	0.93	**0.93**	0.00	0.92	0.93
					LB–VB	0.06	−0.22	0.34	0.65	0.66	0.01	0.65	0.67
					PL–VB	*0.22*	−0.04	0.47	0.94	**0.95**	0.00	0.94	0.95
					PL–LB	0.16	−0.09	0.40	0.89	*0.89*	0.00	0.89	0.90
V_{among}	AN	0.03	0.00	0.19	VS–AN	**0.60**	0.03	1.25	0.98	**0.98**	0.00	0.98	0.99
	VS	0.65	0.08	1.27	VB–AN	0.66	0.00	1.51	0.98	**0.98**	0.00	0.97	0.98
	VB	0.71	0.04	1.55	LB–AN	**0.72**	0.15	1.40	0.99	**1.00**	0.00	0.99	1.00
	LB	0.76	0.21	1.44	PL–AN	**0.52**	0.23	0.83	1.00	**1.00**	0.00	1.00	1.00
	PL	0.56	0.32	0.87	VB–VS	0.06	−0.86	1.05	0.55	0.55	0.01	0.54	0.56
					LB–VS	0.12	−0.74	0.99	0.61	0.61	0.01	0.59	0.62
					PL–VS	−0.09	−0.76	0.53	0.61	0.40	0.01	0.39	0.41
					LB–VB	0.05	−0.93	1.03	0.54	0.55	0.01	0.53	0.56
					PL–VB	−0.14	−1.01	0.58	0.64	0.36	0.01	0.34	0.37
					PL–LB	−0.20	−0.92	0.43	0.73	0.27	0.01	0.26	0.29
V_{within}	AN	0.91	0.73	1.14	VS–AN	**1.00**	0.48	1.77	1.00	**1.00**	0.00	1.00	1.00
	VS	1.91	1.44	2.67	VB–AN	**1.57**	0.88	2.54	1.00	**1.00**	0.00	1.00	1.00
	VB	2.49	1.83	3.43	LB–AN	**1.02**	0.49	1.76	1.00	**1.00**	0.00	1.00	1.00
	LB	1.94	1.45	2.64	PL–AN	*−0.21*	−0.48	0.08	0.92	**0.08**	0.00	0.07	0.09
	PL	0.71	0.54	0.94	VB–VS	0.57	−0.40	1.62	0.88	*0.87*	0.00	0.87	0.88
					LB–VS	0.01	−0.87	0.88	0.51	0.52	0.01	0.51	0.53
					PL–VS	**−1.20**	−1.97	−0.69	1.00	**0.00**	0.00	0.00	0.00
					LB–VB	−0.54	−1.60	0.41	0.86	*0.13*	0.00	0.12	0.14
					PL–VB	**−1.77**	−2.71	−1.06	1.00	**0.00**	0.00	0.00	0.00
					PL–LB	**−1.23**	−1.94	−0.69	1.00	**0.00**	0.00	0.00	0.00

Two explanations could be mentioned for the overall low plasticity level we found. Firstly, the treatment used may not elicit strong plastic changes in this species, or was not administered long enough. Exposure to the same feeding modalities only elicited minimal plastic response in morphological traits among these morphs [49]. Additionally, environmental enrichment administered from hatching had no detectable effect on boldness in an Arctic charr aquaculture strain [55]. This suggests that weak plastic response may not necessarily reflect insensibility to a particular treatment, but rather a lack of environmental responsiveness of boldness in the species. Secondly, environmental canalization might have evolved rapidly, and only small amounts of remaining plasticity are detectable, like Parsons *et al.* [49] suggested about Arctic charr morphology.

(c) Potential effects of evolutionary history on variation in personality

If a longer time since divergence leads to canalization of personality traits, we expected reduced plasticity, overall lower boldness variance and higher boldness consistency in more diverged morphs. Following our predictions, boldness consistency showed a tendency to increase with divergence degree. A higher sample size and/or more numerous OFT replications would most likely have turned this tendency into significant increase [78], given the notable effect sizes detected between morphs in terms of repeatability (table 3). The ancestral proxy AN showed an extremely low repeatability, which can be explained by this morph's general behaviour in the OFT: consistent with AN's low mean boldness score, almost all AN individuals actually spent most of their time hiding in the shelter (median of 89% of the time, for a dataset median of 56%). Therefore, AN's low boldness repeatability was not due to individuals not behaving consistently over replications, but rather because they all behaved the same [1]. AN also had significantly lower boldness variance components. A current extremely canalized state of boldness in the AN, as it is the morph with the longest adaptation time to its habitat, would explain the apparent lack of boldness variability in this morph, despite their higher genetic diversity [37]. Nevertheless, AN morph still showed substantial plastic potential, as it had the largest difference in percentage of non-responding fish between treatments. The 'plasticity-first hypothesis' [51] suggests plasticity in ancestral populations provides opportunity for adaptive divergence when colonizing a new environment, describing ancestral plasticity as a key for rapid evolution, predicted to be reduced after acclimation to the new habitat. Our data do not support this model [51], as (i) even though boldness plasticity differed to some extent between morphs, submitting our ancestral proxy to 'derived' conditions (treatments) (ii) did not trigger the expression of boldness levels found in diverged morphs and (iii) did not uncover ancestral cryptic genetic variation as boldness variance components in the AN were among the lowest. However, it is worth noting that in another study in which no differential treatments were applied to the same morphs [57], the AN was (i) the only morph showing temporal plasticity in boldness over multiple OFT replications, with a boldness score increasing and ultimately reaching both (ii) a boldness mean equivalent to the most diverged morphs and (iii) boldness variance equivalent to the most variable morph.

The data may fit better with a scenario where mean, plasticity and variances of a trait can evolve independently (e.g. [79]). In this view, the trait is canalized in the ancestral environment, and a transient boost in plasticity and its potential further maintenance after drastic environmental change is contingent on multiple factors, such as the difference in mean, variance and predictability of the new environmental conditions for instance. Independent evolution of boldness mean, plasticity, variances and consistency could explain discrepancies in boldness components observed here between sympatric morphs.

The trend for increasing boldness repeatability with divergence across morphs—that is, more pronounced personalities in more diverged morphs—suggests an initial decanalization of boldness upon ancestral colonization, followed by progressive recanalization of this trait over time [80]. This is consistent with higher boldness variability found in more recently diverged VS and VB, possibly representing a state of decanalization or weak canalization [49,50]. Also, the fact that AN and VS had the highest plasticity, respectively, in proportions of non-responding fish (table 2) and in boldness score reaction norm (figure 1b and table 1) between treatments, also supports a possible boost in boldness plasticity in colonizing ancestors. Indeed, the recently diverged VS has retained numerous ancestral features: body and head morphology, colorations, migration [41], resource use [37] and even mean boldness (as seen here and in [57]), hence probably also its seemingly high remnant plasticity. The loss of plasticity in VB could be attributed to ecological divergence among these sympatric morphs. VB specialize on one prey-type and spend their whole life cycle within the lake, while generalist VS alternate prey according to seasonal abundance and migrate to adjacent streams to spawn [37,41]. VS's generalist lifestyle might promote plasticity persistence to be able to juggle with those seasonal changes. Highly diverged LB and PL both showed high consistency and somewhat equal levels of plasticity, but differed in boldness within-individual variance. Low variability and high consistency in boldness in the PL is probably attributed to narrow specialization in a 'simple' open-water environment where they shoal in small groups [34]. This probably favours predictable and consistent behaviours for better coordination necessary for shoal formation, hence a high degree of behavioural canalization, also allowed by their longer divergence time. PL residual degree of boldness plasticity (tendency, table 1) might be maintained to allow for behavioural adjustments to a pelagic lifestyle after ontogenetic shift from spawning grounds. In contrast, its sympatric counterpart LB dwells solitarily in a highly complex habitat amidst lava rocks and crevasses [21] probably equally favouring the use of multiple behavioural sub-niches (multiple behavioural optima), leading to an array of coexisting consistent boldness profiles: bold individuals actively defending territories, intermediate fish searching for food in unoccupied spots, and shy individuals hiding from predators/conspecifics between crevasses. The higher within-individual variance in boldness may additionally grant LB individuals the flexibility to exploit those different behavioural sub-niches when needed (e.g. a shy fish sometimes risking exiting its crevasse to find food). Consequently, despite the common evolutionary history of Þingvallavatn morphs, major ecological differences between them could explain the hampering of boldness canalization towards a single boldness profile in the LB, as

opposed to the highly canalized PL. In both sympatric pairs, the more specialized morph tended to be bolder, consistent with specialist lifestyle favouring plasticity loss and fixation of inflexible behavioural routine often associated with higher boldness [81].

Interestingly, boldness seems to follow a canalization fashion similar to morphological canalization among these morphs [49]. This hints towards potential genetic correlation between these morphological and behavioural traits, hence selection acting on personality traits could lead to correlated changes in morphology [25,82,83]. However, LB was found to be more morphologically canalized than PL [49] when we found the contrary for boldness, suggesting that evolution of canalization can be trait-specific. All in all, these interpretations should be taken with caution, as this fully laboratory-based design focuses on only one aspect of foraging, still far from mimicking all potential selective and developmental cues available in nature, and as expression of boldness in the lab might not necessarily fully reflect natural behaviours. An experimental design including more families would be beneficial to confirm our conclusions.

5. Conclusion and implication for sympatric diversification and adaptability

This study contributed to partly unveil the roles of genetic influence, environmental responsiveness (developmental plasticity) and evolutionary history in shaping boldness as a personality trait. We showed that the level of boldness was dependent mostly on genetic influence (morph-dependent and heritable), little influenced by environmental inputs (low plasticity). We also found clues of boldness canalization by showing a tendency to greater boldness consistency and a reduction in plasticity along the evolutionary gradient, and lower boldness variance in morphs harbouring the longest evolutionary history in their habitat. These findings suggest strong evolutionary implications for species diversification, as change in behaviour is indeed the first adaptive response of organisms facing environmental changes [22–26]. Radical environmental changes (in this case, from anadromous migration to lake residency) impose behavioural shifts to cope with new environmental features. Developmental plasticity in personality grants higher adaptability via the potential to quickly reach new adaptive peaks [84,85], by rapid formation of environmentally induced new consistent behavioural phenotypes at the population level [22,52,53]. In low productivity systems, lowering intraspecific competition by exploiting different resources in the new environment optimizes resource availability. Hence, personality shifts favouring the use of different resources, parallelly create niche shifts as well [10,16]. Differential selective pressures in newly colonized niches can sort out these environmentally induced personalities in potentially opposite directions [6]. Eventually, the best-fitted personality patterns selected for in respective niches might become fixed over time. Ultimately, divergence between individuals in the separate behaviourally constructed niches could occur [24]. As behavioural traits are often genetically correlated with morphological or physiological traits, selection acting on personality traits could also apply indirect selection on the other correlated traits [25,82,83], eventually leading to polymorphic or polyphenic species (resource polymorphism [28,86,87]). To date, it is still very unclear whether the emergence of personality could be a cause or a by-product of species diversification. A key challenge to test this scheme would be to define whether more plastic populations in terms of personality evolve more rapidly under new selective pressures than populations with low personality plasticity. This would for sure provide outstanding new insights on how such a diversity of personality traits can appear and be maintained within and between populations over the course of evolution.

References

1. Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007 Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318. (doi:10.1111/j.1469-185X.2007.00010.x)

2. Sih A, Bell A, Chadwick Johnson J. 2004 Behavioral syndromes: an ecological and evolutionary overview.

Trends Ecol. Evol. **19**, 372–378. (doi:10.1016/j.tree.2004.04.009)

3. Dingemanse NJ, Réale D. 2005 Natural selection and animal personality. *Behaviour* **142**, 1159–1184. (doi:10.1163/156853905774539445)

4. Dochtermann NA, Schwab T, Sih A. 2015 The contribution of additive genetic variation to personality variation: heritability of personality. *Proc. R. Soc. B* **282**, 20142201. (doi:10.1098/rspb.2014.2201)

5. Sih A, Kats LB, Maurer EF. 2003 Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Anim. Behav.* **65**, 29–44. (doi:10.1006/anbe.2002.2025)

6. Pfennig DW, Wund MA, Snell-Rood EC, Cruickshank T, Schlichting CD, Moczek AP. 2010 Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol. Evol.* **25**, 459–467. (doi:10.1016/j.tree.2010.05.006)

7. Nicolakakis N, Sol D, Lefebvre L. 2003 Behavioural flexibility predicts species richness in birds, but not extinction risk. *Anim. Behav.* **65**, 445–452. (doi:10.1006/anbe.2003.2085)

8. Sol D, Stirling DG, Lefebvre L. 2005 Behavioral drive or behavioral inhibition in evolution: subspecific diversification in holarctic passerines. *Evolution (N Y)* **59**, 2669–2677. (doi:10.1554/05-196.1)

9. Dingemanse NJ, Wolf M. 2010 Recent models for adaptive personality differences: a review. *Phil. Trans. R. Soc. B.* **365**, 3947–3958. (doi:10.1098/rstb.2010.0221)

10. Wolf M, Weissing FJ. 2010 An explanatory framework for adaptive personality differences. *Phil. Trans. R. Soc. B.* **365**, 3959–3968. (doi:10.1098/rstb.2010.0215)

11. Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio PO. 2010 Personality and the emergence of the pace-of-life syndrome concept at the population level. *Phil. Trans. R. Soc. B.* **365**, 4051–4063. (doi:10.1098/rstb.2010.0208)

12. Reddon AR. 2012 Parental effects on animal personality. *Behav. Ecol.* **23**, 242–245. (doi:10.1093/beheco/arr210)

13. Bierbach D, Laskowski KL, Wolf M. 2017 Behavioural individuality in clonal fish arises despite near-identical rearing conditions. *Nat. Commun.* **8**, 15361. (doi:10.1038/ncomms15361)

14. Fisher DN, Brachmann M, Burant JB. 2018 Complex dynamics and the development of behavioural individuality. *Anim. Behav.* **138**, e1–e6. (doi:10.1016/j.anbehav.2018.02.015)

15. Dall SRX, Houston AI, McNamara JM. 2004 The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**, 734–739. (doi:10.1111/j.1461-0248.2004.00618.x)

16. Stamps JA, Groothuis TGG. 2010 The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.* **85**, 301–325. (doi:10.1111/j.1469-185X.2009.00103.x)

17. Skúlason S et al. 2019 A way forward with eco evo devo: an extended theory of resource polymorphism with postglacial fishes as model systems. *Biol. Rev.* **94**, 1786–1808. (doi:10.1111/brv.12534)

18. Parsons KJ, McWhinnie K, Pilakouta N, Walker L. 2020 Does phenotypic plasticity initiate developmental bias? *Evol. Dev.* **22**, 56–70. (doi:10.1111/ede.12304)

19. Cooper WJ, Parsons K, McIntyre A, Kern B, McGee-Moore A, Albertson RC. 2010 Bentho-pelagic divergence of cichlid feeding architecture was prodigious and consistent during multiple adaptive radiations within African rift-lakes. *PLoS ONE* **5**, e9551. (doi:10.1371/journal.pone.0009551)

20. Adams CE, Woltering C, Alexander G. 2003 Epigenetic regulation of trophic morphology through feeding behaviour in Arctic charr, *Salvelinus alpinus*. *Biol. J. Linnean Soc.* **78**, 43–49. (doi:10.1046/j.1095-8312.2003.00126.x)

21. Snorrason SS, Skúlason S. 2012 Adaptive speciation in northern freshwater fishes. In *Adaptive speciation* (eds U Dieckmann, M Doebeli, J Metz, D Tautz), pp. 210–228. Cambridge, UK: Cambridge University Press.

22. Bateson P. 2004 The active role of behaviour in evolution. *Biol. Philos.* **19**, 283–298. (doi:10.1023/B:BIPH.0000024468.12161.83)

23. Bogert CM. 1949 Thermoregulation in reptiles, a factor in evolution. *Evolution (N Y)*. **3**, 195–211. (doi:10.2307/2405558)

24. Duckworth RA. 2009 The role of behavior in evolution: a search for mechanism. *Evol. Ecol.* **23**, 513–531. (doi:10.1007/s10682-008-9252-6)

25. Levins R, Lewotin RC. 1985 *The dialectical biologist*. Cambridge, MA: Harvard University Press.

26. Mayr E. 1963 *Animal species and evolution*. Cambridge, MA: Harvard University Press.

27. Wilson ADM, McLaughlin RL. 2010 Foraging behaviour and brain morphology in recently emerged brook charr, *Salvelinus fontinalis*. *Behav. Ecol. Sociobiol.* **64**, 1905–1914. (doi:10.1007/s00265-010-1002-4)

28. Skúlason S, Smith TB. 1995 Resource polymorphism. *Trends Ecol. Evol.* **10**, 366–370. (doi:10.1016/S0169-5347(00)89135-1)

29. Gíslason D, Ferguson MM, Skúlason S, Snorrason SS. 1999 Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic char (*Salvelinus alpinus*). *Can. J. Fish. Aquat. Sci.* **56**, 2229–2234. (doi:10.1139/f99-245)

30. Malmquist HJ, Snorrason SS, Skúlason S, Jonsson B, Sandlund OT, Jónasson PM. 1992 Diet differentiation in polymorphic Arctic charr in Thingvallavatn, Iceland. *J. Anim. Ecol.* **61**, 21–35. (doi:10.2307/5505)

31. Snorrason SS, Skúlason S, Jonsson B, Malmquist HJ, Jónasson PM, Sandlund OT, Lindem T. 1994 Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts. *Biol. J. Linnean Soc.* **52**, 1–18. (doi:10.1111/j.1095-8312.1994.tb00975.x)

32. Skúlason S, Snorrason SS, Noakes DLG, Ferguson MM, Malmquist HJ. 1989 Segregation in spawning and early life history among polymorphic Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. *J. Fish Biol.* **35**, 225–232. (doi:10.1111/j.1095-8649.1989.tb03065.x)

33. Guðbrandsson J, Kapralova KH, Franzdóttir SR, Bergsveinsdóttir ÞM, Hafstað V, Jónsson ZO, Snorrason SS, Pálsson A. 2019 Extensive genetic differentiation between recently evolved sympatric Arctic charr morphs. *Ecol. Evol.* **9**, 10 964–10 983. (doi:10.1002/ece3.5516)

34. Sandlund OT et al. 1992 The Arctic charr *Salvelinus alpinus* in Thingvallavatn. *Oikos* **64**, 305–351. (doi:10.2307/3545056)

35. Sandlund OT, Jonsson B, Malmquist HJ, Gydemo R, Lindem T, Skúlason S, Jónasson PM. 1987 Habitat use of Arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Environ. Biol. Fishes.* **20**, 263–274. (doi:10.1007/BF00005297)

36. Jonsson B, Skúlason S, Snorrason SS, Sandlund OT, Malmquist HJ, Jónasson PM, Cydemo R, Lindem T. 1988 Life history variation of polymorphic Arctic charr (*Salvelinus alpinus*) in Thingvallavatn, Iceland. *Can. J. Fish. Aquat. Sci.* **45**, 1537–1547. (doi:10.1139/f88-182)

37. Brachmann MK, Parsons K, Skúlason S, Ferguson MM. 2021 The interaction of resource use and gene flow on the phenotypic divergence of benthic and pelagic morphs of Icelandic Arctic charr (*Salvelinus alpinus*). *Ecol. Evol.* **11**, 7315–7334. (doi:10.1002/ece3.7563)

38. Brunner PC, Douglas MR, Osinov A, Wilson CC, Bernatchez L. 2001 Holarctic phylogeography of Arctic charr (*Salvelinus alpinus* l.) Inferred from mitochondrial DNA sequences. *Evolution* **55**, 573–586. (doi:10.1111/j.0014-3820.2001.tb00790.x)

39. Wilson AJ, Gíslason D, Skúlason S, Snorrason SS, Adams CE, Alexander G, Danzmann RG, Ferguson MM. 2004 Population genetic structure of Arctic charr, *Salvelinus alpinus* from northwest Europe on large and small spatial scales. *Mol. Ecol.* **13**, 1129–1142. (doi:10.1111/j.1365-294X.2004.02149.x)

40. Brachmann MK, Parsons K, Skúlason S, Gaggiotti O, Ferguson M. 2022 Variation in the genomic basis of parallel phenotypic and ecological divergence in benthic and pelagic morphs of Icelandic Arctic charr (*Salvelinus alpinus*). *Mol. Ecol.* **31**, 4688–4706. (doi:10.1111/mec.16625)

41. Jónsson B, Skúlason S. 2000 Polymorphic segregation in Arctic charr *Salvelinus alpinus* (L.) from Vatnshlíðarvatn, a shallow Icelandic lake. *Biol. J. Linnean Soc.* **69**, 55–74. (doi:10.1006/bijl.1999.0316)

42. Saemundsson K. 1992 Geology of the Thingvallavatn area. *Oikos* **64**, 40–68. (doi:10.2307/3545042)

43. Kapralova KH, Morrissey MB, Kristjánsson BK, Ólafsdóttir GÁ, Snorrason SS, Ferguson MM. 2011 Evolution of adaptive diversity and genetic connectivity in Arctic charr (*Salvelinus alpinus*) in Iceland. *Heredity (Edinb)* **106**, 472–487. (doi:10.1038/hdy.2010.161)

44. Steele SE et al. In preparation. Divergence and developmental plasticity for size in ancestral and derived populations of Arctic charr.

45. Lafuente E, Beldade P. 2019 Genomics of developmental plasticity in animals. *Front. Genet.* **10**, 720. (doi:10.3389/fgene.2019.00720)

46. Stearns SC. 1989 The evolutionary significance of phenotypic plasticity. *Bioscience* **39**, 436–445. (doi:10.2307/1311135)

47. Loison L. 2019 Canalization and genetic assimilation: reassessing the radicality of the Waddingtonian concept of inheritance of acquired characters. *Semin. Cell Dev. Biol.* **88**, 4–13. (doi:10.1016/j.semcdb.2018.05.009)

48. Küttner E, Parsons KJ, Robinson BW, Skúlason S, Danzmann RG, Ferguson MM. 2013 Effects of population, family, and diet on craniofacial morphology of Icelandic Arctic charr (*Salvelinus alpinus*). *Biol. J. Linnean Soc.* **108**, 702–714. (doi:10.1111/j.1095-8312.2012.02038.x)

49. Parsons KJ, Sheets HD, Skúlason S, Ferguson MM. 2011 Phenotypic plasticity, heterochrony and ontogenetic repatterning during juvenile development of divergent Arctic charr (*Salvelinus alpinus*). *J. Evol. Biol.* **24**, 1640–1652. (doi:10.1111/j.1420-9101.2011.02301.x)

50. Parsons KJ, Skúlason S, Ferguson M. 2010 Morphological variation over ontogeny and environments in resource polymorphic Arctic charr (*Salvelinus alpinus*). *Evol. Dev.* **12**, 246–257. (doi:10.1111/j.1525-142X.2010.00410.x)

51. Levis NA, Pfennig DW. 2016 Evaluating 'plasticity-first' evolution in nature: key criteria and empirical approaches. *Trends Ecol. Evol.* **31**, 563–574. (doi:10.1016/j.tree.2016.03.012)

52. Baldwin JM. 1896 A new factor in evolution. *Am. Nat.* **30**, 441–451. (doi:10.1086/276408)

53. Robinson BW, Dukas R. 1999 The influence of phenotypic modifications on evolution: the Baldwin effect and modern perspectives. *Oikos* **85**, 582–589. (doi:10.2307/3546709)

54. Waddington CH. 1953 Genetic assimilation of an acquired character. *Evolution (N Y)* **7**, 118–126. (doi:10.2307/2405747)

55. Philip J, Dellinger M, Benhaïm D. 2022 Among-individual variation of risk-taking behaviour in group and solitary context is uncorrelated but independently repeatable in a juvenile Arctic charr (*Salvelinus alpinus*) aquaculture strain. *Appl. Anim. Behav. Sci.* **249**, 105596. (doi:10.1016/j.applanim.2022.105596)

56. Horta-Lacueva QJ, Benhaïm D, Morrissey MB, Snorrason SS, Kapralova KH. 2021 Animal personality adds complexity to the processes of divergence between sympatric morphs of Arctic charr. *Anim. Behav.* **175**, 57–73. (doi:10.1016/j.anbehav.2021.02.022)

57. Benhaïm D, Vernier L, Leblanc CA. 2023 Personality and temporal plasticity in fish populations along a gradient of evolutionary divergence. *Anim. Behav.* **199**, 23–33. (doi:10.1016/j.anbehav.2023.02.010)

58. Adalsteinsson H, Jónasson PM, Rist S. 1992 Physical characteristics of Thingvallavatn, Iceland. *Oikos.* **64**, 121–135. (doi:10.2307/3545048)

59. Benhaïm D, Skúlason S, Hansen BR. 2003 Behavioural variation in juvenile Arctic charr in relation to body size. *J. Fish Biol.* **62**, 1326–1338. (doi:10.1046/j.1095-8649.2003.00114.x)

60. Simon P, Dupuis R, Costentin J. 1994 Thigmotaxis as an index of anxiety in mice: influence of dopaminergic transmissions. *Behav. Brain Res.* **61**, 59–64. (doi:10.1016/0166-4328(94)90008-6)

61. Dahlbom SJ, Lagman D, Lundstedt-Enkel K, Sundström LF, Winberg S. 2014 Boldness predicts social status in zebrafish (*Danio rerio*). *PLoS ONE* **9**, 2–8. (doi:10.1371/annotation/2fb5edb1-0100-45ef-b8bb-681cc1490295)

62. Brown C. 2001 Familiarity with the test environment improves escape responses in the crimson spotted rainbowfish, *Melanotaenia duboulayi. Anim. Cogn.* **4**, 109–113. (doi:10.1007/s100710100105)

63. Dellinger M, Steele SE, Sprockel E, Philip J, Pálsson A, Benhaïm D. 2023 Data from: Variation in personality shaped by evolutionary history, genotype, and developmental plasticity in response to feeding modalities in the Arctic charr. *Dryad Digital Repository.* (doi:10.5061/dryad.4f4qrfjk2)

64. R Core Team. 2018 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. (https://www.r-project.org/).

65. Carpenter B *et al.* 2017 Stan: A probabilistic programming language. *J. Stat. Softw.* **76**, 11–32. (doi:10.18637/jss.v076.i01)

66. Bürkner PC. 2017 brms: An R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–28. (doi:10.18637/jss.v080.i01)

67. Hertel A *et al*. Submitted. Ontogeny shapes individual specialization. *Res. Sq.* 1–21. Preprint. (doi:10.21203/rs.3.rs-2926801/v1)

68. Lenth R. 2023 *emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 187.* See https://cran.r-project.org/package=emmeans.

69. Royauté R, Dochtermann NA. 2021 Comparing ecological and evolutionary variability within datasets. *Behav. Ecol. Sociobiol.* **75**, 127. (doi:10.1007/s00265-021-03068-3)

70. Ruscio J. 2008 A probability-based measure of effect size: robustness to base rates and other factors. *Psychol. Methods* **13**, 19–30. (doi:10.1037/1082-989X.13.1.19)

71. Ruscio J. 2020 *RProbSup: Calculates Probability of Superiority. R package version 30.* See https://cran.r-project.org/package=RProbSup.

72. Dellinger M, Caperaa M, Le Clech R, Queru J, Benhaïm D. In preparation. Do personality components independently evolve and develop in response to environmental complexity?

73. Edenbrow M, Croft DP. 2013 Environmental and genetic effects shape the development of personality traits in the mangrove killifish *Kryptolebias marmoratus. Oikos* **122**, 667–681. (doi:10.1111/j.1600-0706.2012.20556.x)

74. Webster MM, Ward AJW. 2011 Personality and social context. *Biol. Rev.* **86**, 759–773. (doi:10.1111/j.1469-185X.2010.00169.x)

75. Adams CE, Huntingford FA, Krpal J, Jobling M, Burnett SJ. 1995 Exercise, agonistic behaviour and food acquisition in Arctic charr, *Salvelinus alpinus. Environ. Biol. Fishes.* **43**, 213–218. (doi:10.1007/BF00002494)

76. Sundström LF, Petersson E, Höjesjö J, Johnsson JI, Järvi T. 2004 Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. *Behav. Ecol.* **15**, 192–198. (doi:10.1093/beheco/arg089)

77. Stamps JA. 2016 Individual differences in behavioural plasticities. *Biol. Rev.* **91**, 534–567. (doi:10.1111/brv.12186)

78. Dingemanse NJ, Dochtermann NA. 2013 Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J. Anim. Ecol.* **82**, 39–54. (doi:10.1111/1365-2656.12013)

79. Lande R. 2015 Evolution of phenotypic plasticity in colonizing species. *Mol. Ecol.* **24**, 2038–2045. (doi:10.1111/mec.13037)

80. Bell AM, Hankison SJ, Laskowski KL. 2009 The repeatability of behaviour: a meta-analysis. *Anim. Behav.* **77**, 771–783. (doi:10.1016/j.anbehav.2008.12.022)

81. Coppens CM, de Boer SF, Koolhaas JM. 2010 Coping styles and behavioural flexibility: towards underlying mechanisms. *Phil. Trans. R. Soc. B.* **365**, 4021–4028. (doi:10.1098/rstb.2010.0217)

82. Huey RB, Hertz PE, Sinervo B. 2003 Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* **161**, 357–366. (doi:10.1086/346135)

83. Wolf M, Weissing FJ. 2012 Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.* **27**, 452–461. (doi:10.1016/j.tree.2012.05.001)

84. Rice AM, Pfennig DW. 2007 Character displacement: *in situ* evolution of novel phenotypes or sorting of pre-existing variation? *J. Evol. Biol.* **20**, 448–459. (doi:10.1111/j.1420-9101.2006.01187.x)

85. Snell-Rood EC. 2013 An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim. Behav.* **85**, 1004–1011. (doi:10.1016/j.anbehav.2012.12.031)

86. Levis NA, Pfennig DW. 2019 Phenotypic plasticity, canalization, and the origins of novelty: evidence and mechanisms from amphibians. *Semin. Cell Dev. Biol.* **88**, 80–90. (doi:10.1016/j.semcdb.2018.01.012)

87. Smith TB, Skúlason S. 1996 Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.* **27**, 111–133. (doi:10.1146/annurev.ecolsys.27.1.111)

88. Dellinger M, Steele SE, Sprockel E, Philip J, Pálsson A, Benhaïm D. 2023 Variation in personality shaped by evolutionary history, genotype and developmental plasticity in response to feeding modalities in the Arctic charr. Figshare. (doi:10.6084/m9.figshare.c.6957270)