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Research Article

Evidence for dispersal personality in the guppy across ecological conditions, with a minor effect of relative brain size

Gilles De Meester[1,2], **Mirjam Amcoff**[1], **Arezo Shamsgovara**[1], **Alessandro Devigili**[1,3], **Alexander Kotrschal**[4], **John L. Fitzpatrick**[1] and **Niclas Kolm**[1]

[1]Department of Zoology, Stockholm University, Stockholm, Sweden
[2]CREAF, Centre for Ecological Research and Forestry Applications, Bellaterra, Spain
[3]Department of Biology, University of Padova, Padova, Italy
[4]Behavioural Ecology, Wageningen University and Research, Wageningen, the Netherlands

Correspondence: Gilles De Meester (gilles.demeester@gmail.com)

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Individuals that disperse typically exhibit specific phenotypical traits that facilitate dispersal and settlement success, known as 'dispersal syndromes'. Consequentially, characterizing dispersers is crucial to understand other processes such as metapopulation dynamics and biological invasions. One trait that may play a major, yet overlooked, role in dispersal is relative brain size. Larger brains, through enhanced cognition and behavioural flexibility, could both increase and decrease the costs of dispersal, depending on the ecological context. However, barely any effort has been made to investigate the link between brain size and dispersal, especially so at the individual level. Here, we tested the impact of brain size on dispersal behaviour, in both a stable and unpredictable environment. We used Trinidadian guppies *Poecilia reticulata* from lines artificially bred for large and small relative brain size. Fish were placed in a laboratory set-up of interconnected tanks, where we quantified how likely and how fast they were to disperse between tanks under two ecologically relevant conditions: a stable (control) and unpredictable environment (experimental drought). Surprisingly, there was only limited evidence that large- and small-brained guppies differed in dispersal behaviour in either ecological context. While we found no differences in dispersal behaviour between the large- and small-brained lines, both overall dispersal speed and dispersal likelihood correlated negatively with individual relative brain size, but only during the first opportunity fish had to disperse. Generally, guppies reduced dispersal after experiencing an environmental drought. Regardless of brain size or ecological context, they exhibited consistent interindividual variation in their decision to disperse or to stay, indicating the existence of a dispersal personality trait. Our results are valuable in the current context of invasive alien species. Understanding what traits influence the success during the various steps of the invasion process is of major importance from both a fundamental and conservation perspective.

Keywords: cognitive buffer hypothesis, dispersal syndrome, environmental variability, personality, *Poecilia reticulata*, relative brain size

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Introduction

Whether or not to disperse is a crucial question within the life of many animals, bearing important fitness consequences (Clobert et al. 2012, Borges et al. 2022). Dispersal, here defined as the departure from the current habitat to move to and settle in a new one (Clobert et al. 2012, Borges et al. 2022), is a fundamental determinant of gene flow, (meta) population dynamics and ecosystem functioning (Ronce 2007, Gonzalez et al. 2009, Clobert et al. 2012, Crosby et al. 2023). Furthermore, dispersal ability is considered a key factor in the success of invasive species (Rehage and Sih 2004, Gruber et al. 2017). For these reasons, there has been great interest in determining the proximate and ultimate causes of dispersal.

Dispersion is costly and risky (Bonte et al. 2012), hence, the decision to disperse will depend on both extrinsic and intrinsic factors. Extrinsic triggers for dispersal could be deteriorating local conditions (Matthysen 2012), when the risks of staying outweigh the potential risks of leaving, such as increased local predation (Bestion et al. 2014) or environmental disturbances (Bates et al. 2006, Matthysen 2012). For example, fish often disperse to refugia on the onset of droughts (Davey et al. 2006, Goss et al. 2013, Driver and Hoeinghaus 2016). Dispersers are not just a random subset of the population; they are often characterized by specific morphological, physiological and behavioural traits, known as 'dispersal syndromes', predicted to increase successful dispersal and/or settlement in a new patch (Clobert et al. 2009, Ronce and Clobert 2012, Michelangeli et al. 2017, Cote et al. 2022). For example, dispersing individuals are often more active, larger and in possession of specific morphological adaptations for movement (Cote et al. 2022). Extrinsic and intrinsic factors will interact to determine the decision to disperse, as different phenotypes may vary in their ability to deal with specific extrinsic triggers (Matthysen 2012). For instance, in common lizards *Zootoca vivipara*, individuals preferring low body temperatures are more likely to disperse under warmer conditions, while 'hot' phenotypes show the opposite trend (Bestion et al. 2015). Conversely, some extrinsic triggers could motivate a large proportion of the population to disperse regardless of their intrinsic traits, e.g. predation negates personality-dependent dispersal in mosquitofish *Gambusia affinis* (Cote et al. 2013).

One key biological trait that could be part of a 'dispersal syndrome', but has received surprisingly little attention in this regard, is relative brain size. As larger brains are often coinciding with higher cognitive abilities and increased behavioural flexibility (Sol 2009), they may theoretically either reduce or increase the costs of dispersal: Dispersal should be less risky for large-brained animals as higher behavioural flexibility should allow rapid adjustment to novel environments (Sol et al. 2005, Sol 2009, Herczeg et al. 2019), and more efficient information gathering while prospecting potential new patches should lead to more 'informed dispersal', all of which could help to avoid or minimize the costs of settling in a suboptimal habitat (Clobert et al. 2009, Liedtke and Fromhage 2021a, Crosby et al. 2023). Thus, a positive correlation between relative brain size and dispersal propensity would be expected. However, large-brained animals also stand to lose more when leaving a familiar patch, as they may have invested considerable time and effort in learning about their environment, whereas small-brained animals may only possess superficial knowledge. The higher cost of losing familiarity could then discourage large-brained animals from dispersing (Bonte et al. 2012, Liedtke and Fromhage 2021a, 2021b, Crosby et al. 2023). Additionally, larger brains are known to be metabolically expensive (Aiello and Wheeler 1995, Kotrschal et al. 2013, 2016, 2019), and this could lead to tradeoffs with other morphological and physiological adaptations for dispersal (Zhang et al. 2025).

Moreover, the exact relationship between brain size and dispersal could depend on the specific ecological context (Clobert et al. 2009). While animals ought to be more likely to disperse under environmental disturbances (Goss et al. 2013) and in unpredictable habitats (Cayuela et al. 2016), large- and small-brained individuals may differ in their response. Large-brained animals could be less inclined to give up their cognitive investment under good local conditions, but may be more perceptive of detrimental environmental changes and therefore react faster by dispersing (Crosby et al. 2023). Conversely, larger brains should facilitate survival during environmental disturbances and in unpredictable habitats via enhanced behavioural flexibility, resulting in a lower need to 'escape' (Kotrschal et al. 2015b, Sonnenberg et al. 2019, Wagnon and Brown 2020).

Currently, the link between dispersal and relative brain size remains enigmatic, as data is scarce and conflicting. Indirect evidence comes from comparative studies which show higher invasiveness in large-brained species in some taxa (birds: Sol et al. 2002, mammals: Sol et al. 2008, reptiles and amphibians: Amiel et al. 2011) but not in others (fish: Drake 2007). Bird species with relative larger brains have lower hand-wing indices, which is associated with reduced flight performance and dispersal ability (Zhang et al. 2025). Only a single study has documented a direct positive relationship between relative brain size and natal, but not adult, dispersal rate across seabird species (Crosby et al. 2023). Noteworthy, these studies have focused exclusively at the interspecific level, yet recent research has acknowledged that within a population, particular individuals are more likely to disperse than others (Rehage and Sih 2004, Cote et al. 2010, Michelangeli et al. 2017, Jessop et al. 2024). It is thus critical, from both a fundamental and conservation perspective, to understand which biological traits drive dispersal propensity at the individual level (Rehage and Sih 2004, Jessop et al. 2024). Finally, how individual phenotype and environment interact during dispersal has rarely been considered in these studies on relative brain size.

Here, we provide the first study on the relationship between brain size and dispersal propensity at the individual level under different ecologically relevant contexts. We used Trinidadian guppies *Poecilia reticulata* from a unique artificial breeding experiment. The Trinidadian guppy is almost

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ubiquitous across the streams and rivers of Trinidad, a likely consequence of its high tendency to disperse and colonize new patches (Deacon and Magurran 2016, De Bona et al. 2019, Borges et al. 2022). It is known to frequently disperse upstream, across physical barriers like waterfalls and riffles, helped by (but not limited to) its remarkable areal jumping behaviour (Soares and Bierman 2013, De Waele et al. 2022, Jessop et al. 2024). The guppy is also a widespread invasive species, which has been attributed at least partially to its high dispersal propensity (Deacon and Magurran 2016). Within their native range, guppies inhabit environments exposed to strong seasonal fluctuations in weather conditions. During the dry season, rivers often shrink to a collection of isolated pools. Dispersal in response to changing or unstable environmental conditions may thus be an essential strategy for guppies to avoid getting trapped in shallow pools with suboptimal conditions and a high risk of complete desiccation (Deacon and Magurran 2016, De Waele et al. 2022). Experiments confirmed that wild guppies react to being trapped in shallow or small water bodies by jumping to deeper areas (De Waele et al. 2022). For our study, we used male guppies belonging to artificial breeding lines with well-documented differences in relative brain size (~15.4%) and corresponding changes in neuron numbers and cognitive abilities (Kotrschal et al. 2013, 2015a, 2017, Buechel et al. 2018, Marhounová et al. 2019). We tested large- and small-brained guppies on their propensity to disperse from a familiar to a novel environment in both a stable control condition and in response to environmental unpredictability (simulated by an experimental drought). Although the link between dispersal and brain size can go both ways, we predicted that large-brained guppies would be faster and more likely to disperse, and that this effect would be the strongest in the face of environmental unpredictability. Alternatively, large-brained guppies may be less inclined to disperse if the cost of losing familiarity is too high.

Material and methods

Study species

Guppies in this study belonged to the ninth generation of an artificial selection experiment for relative brain size. The protocol for the establishment and maintenance of these lines has been previously described in great detail in Kotrschal et al. 2013. In summary, up- and down-selected lines for relative brain size were created by setting up breeding pairs and quantifying the brain weight of parents via dissection after offspring production. Only the offspring of the parents with the largest and smallest brains corrected for body size (upper and lower 20%) were retained. A similar procedure was then followed for the next generations, where each time the offspring of the parents with the upper and lower 50% relative brain sizes were kept. This was repeated in three independent stocks (i.e. replicates). By the fifth generation, up- and down-selected lines differed ~15.4% in relative brain size. We selected 188 adult male guppies (age: 16 to 24 months), the result of five generations of artificial selection in total, interspersed with four generations of random breeding. As there is no sexual dimorphism in relative brain size in our selection lines (Kotrschal et al. 2013), we focused on males due to their higher dispersal rate in the wild (Croft et al. 2003, De Bona et al. 2019, Borges et al. 2022). Animals were experimentally naïve, except for a subset of 58 individuals which were used in a social foraging experiment nine months earlier. Carry-over effects are unlikely due to the timespan between both experiments and the briefness of these social foraging trials (two times one hour).

Fish were sorted in 29 groups of five to six individuals from the same replicate and line. Where possible, groups consisted of both familiar and unfamiliar, and experimentally naïve and previously used individuals. However, perfect standardization in group composition and size was not possible due to the limited number of fish available for some replicates (Supporting information).

Prior to the experiment, all fish were tagged with visible implant elastomers (VIE) in their dorsal epidermis (Northwest Marine Technology). Fish were anesthetized by placing them in a benzocaine bath (0.067 g l^{-1}). They then received one tag on each body side in a different colour (red, green, yellow or blue), thus giving each individual within a group a unique colour code. Groups were then transferred to 7-l tanks, and allowed to recover for at least 24 h. Individuals with clear signs of distress (e.g. abnormal swimming behaviour or posture) were euthanized and replaced (n = 6).

Experimental set-up

Each group was transferred to a separate experimental unit, which consisted of two adjacent 50-l glass tanks. Both tanks contained a layer of white-brown gravel, a plastic plant and an overflow pipe. In one tank (i.e. the 'start tank') we placed an internal filter (Claro 300, Diversa) with a transparent hose attached to the water output (Fig. 1A). Guppies could not see groups in neighbouring experimental units. Fish were fed six times per week with commercial flakes or freshly hatched *Artemia* sp., and subjected to a 25% water change three times per week, both carried out at consistent times. During trials, both tanks in a unit were fed, regardless of fish presence. Room and water temperature were maintained at approximately 26°C and fish were subjected to a 12:12 light:dark cycle.

All fish were tested on their dispersal tendency in both a stable (control) and unpredictable environment. To induce environmental unpredictability, we exposed the fish to a single short drought (below). To account for order and memory effects, 14 groups started with the control treatment and 15 groups with the drought. Due to space constraints, fish were tested in two batches. All experiments took place from June to August 2024 at Stockholm University. Observers were always blind to the origin of the groups.

Dispersal experiment

An experimental round consisted of a habituation, treatment and dispersal phase. As a first step, fish were placed in the

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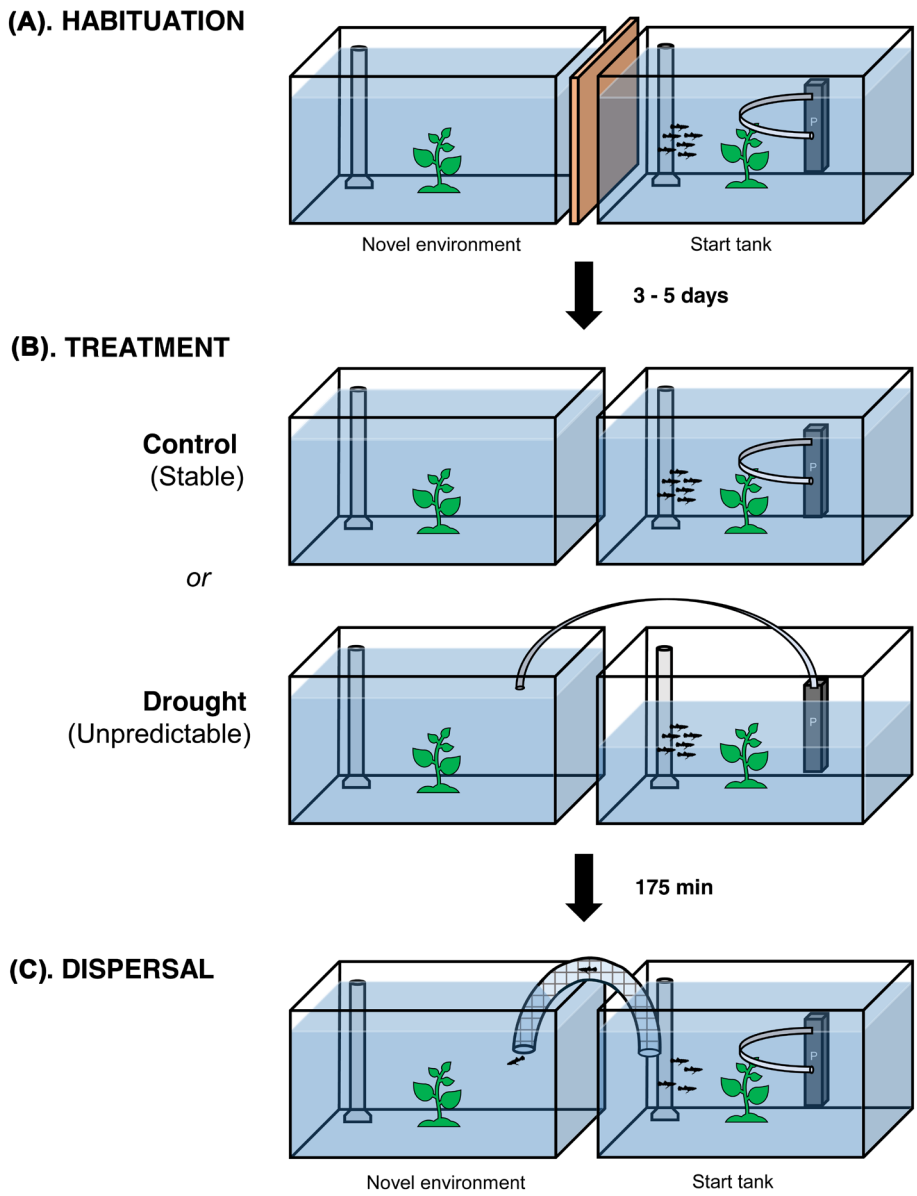


Figure 1. Experimental set up. The experiment consisted of a habitation phase (A) during which fish were allowed to move freely in the start tank; a treatment phase (B) in which fish were exposed to a control treatment and a drought treatment to create a stable and an unpredictable environment respectively; and finally, a dispersal phase (C) in which they were given the opportunity to move (i.e. disperse) to the novel environment. Main text for a full description of the experiment. P = aquatic filter used to pump the water out from the start tank. The novel environment was always on the left.

start tank of their experimental unit and allowed to habituate for five days (Fig. 1A). During this habituation phase, a cardboard divider was placed between the two tanks so fish could not see the novel environment yet.

On the morning of the sixth day, fish were exposed to the experimental treatment. A drought was simulated by connecting the hose of the internal filter to the 'novel environment' tank (Fig. 1B). This way, water was pumped out of the start tank until it had been reduced to half of its original level (Fig. 1B). Fish were exposed to this 'drought' for 175 minutes, thereafter tanks were refilled to their original level. For technical reasons, we were unable to maintain a difference in water levels between start tank and novel environment during the actual dispersal phase, meaning that fish could not disperse during the drought as in nature (De Waele et al. 2022). However, we would argue that witnessing a short change in water levels would still lower the quality of the initial 'habitat' even after water levels are restored, as pools experiencing drastic droughts in nature will likely again be at risk of desiccation in the future. Such environmental unpredictability might prompt fish to disperse, as seen in other species (Cayuela et al. 2016). To account for the stress that quickly adding water could cause (e.g. loud noise and mixing of gravel), an equivalent amount of water was pumped into the

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start tanks of the control groups, yet water levels were maintained here via the overflow pipes. In addition, we poured 0.9 l of water from the start tank to the novel tank in the control groups, so that both treatments could receive chemical information of conspecifics through the tube. During the treatment, cardboard dividers between start tanks and novel environments were removed.

Next, the dispersal phase started by connecting the start tank and novel environment with a silicone tube filled with water (⌀ = 2 cm, length = 25–35 cm, length varied due to a larger distance between some tanks as a result of their fixed position in the overflow system) (Fig. 1C). The tubes were semi-transparent, to avoid that fish would need to enter a completely dark space. Fish could then move freely between the start tank and novel environment using this pathway. We did not prevent fish from swimming back, as wild animals are known to prospect new sites before settling (Jungwirth et al. 2015) and such sampling behaviour could be directly linked to an individual's cognitive abilities and hence relative brain size. The dispersal phase lasted for 95 h, during which we checked the tanks and recorded the position of each individual fish every hour, from 8:30 to 18:30 daily. Fish that moved at least once to the novel tank were classified as 'dispersers'. Per individual, we recorded its dispersal status (disperser or not), its 'dispersal time' (in hours since the start), whether and how fast it moved back to the start tank ('second dispersal time'), and how many times it moved across the tunnel ('number of transitions'). After 95 h, we captured all fish, and repeated the experiment. Groups were directly transferred to a new experimental unit and allowed to habituate again for three days. Thereafter, the experimental procedure was followed as before, but each group was given the opposite treatment as in their first round.

Brain dissection

As guppies showed considerable inter-individual variation in dispersal behaviour, even within groups, we were interested in whether such variation could be explained by individual differences in relative brain size. Thus, upon completion of the second round, all fish were euthanized with an overdose of benzocaine. Fish were fixated in a 4% paraformaldehyde solution in phosphate-buffered saline (PBS) for one week, washed with PBS for minimal 48 h, and then stored in PBS at 4°C. Prior to dissection, standard length (distance snout-tip to end of the caudal peduncle) was measured using a digital calliper. Brains were removed under a stereo zoom microscope and weighted with a digital scale (precision = 0.001 mg).

During dissections, we also observed that one individual had an elastomer slightly inside the spinal cord. To avoid a potential bias caused by reduced mobility, it was removed from the analyses.

Statistical analyses

A total of 28 groups were tested during both treatments. One group (small-brained) accidentally had the cardboard divider between start tank and novel environment present during the entire dispersal phase, and was therefore removed from the analyses for this phase. For two large-brained groups in the drought treatment and one small-brained group in the control treatment, we only removed the cardboard after the treatment phase. Preliminary analyses revealed that these fish did not differ from other groups in behaviour, and their data was therefore retained.

Group sizes varied between four to six individuals due to insufficient fish in some replicates, and mortality prior to or in between rounds. In the end, we collected data on 159 fish in the stable condition ($N_{large} = 92$, $N_{small} = 67$) and 166 fish in the unpredictable condition ($N_{large} = 91$, $N_{small} = 74$). Fish would sometimes lose one or both VIE tags. In most cases, we could still deduce their original colour code based on those of their group members, or by finding leftover ink within the animal during dissections. In one tank, however, this was not possible, leaving us with two fish in the second round whose original colour code we could not determine. While we were able to track such individuals within a round based on other morphological traits (e.g. natural occurring dots and patterns), we could not compare their performance across rounds. These particular fish were given a new individual code for the second round and treated as new individuals in most analyses, except for the analyses of the dispersal consistency scores (below): as both 'tag-less' individuals dispersed, we could still assign a consistency score to their original colour-code. Because of this, and mortality in between rounds, we only have repeated data for 156 individuals ($N_{large} = 91$, $N_{small} = 65$). Morphological data was missing for three individuals.

We started by verifying that selection lines differed in relative brain size, using a linear mixed effect model (LMER) with brain weight as response variable and standard length as controlling variable, both log-transformed and scaled. Selection line (up versus down) was included as fixed factor. Here, and in most further models, we initially controlled for differences between replicates and batches by including them as predictors, but removed them in case they were non-significant and doing so did not decrease model fit (based on AIC). Group ID was included as random factor.

Then, to test for differences in dispersal time and tendency between selection lines and treatments, we ran a survival analysis using a mixed-effects Cox proportional hazard model ('coxme' package, Therneau 2015) as we were dealing with censored data (i.e. non-dispersers received the maximum dispersal time of 95 h). Survival models simultaneously test the probability of an event (i.e. dispersal of an individual) occurring and the time it requires to happen (i.e. dispersal time). Selection line, treatment and their interaction were included as fixed effects, as were experimental round (first versus second), a round × selection line interaction, standard length (log-transformed and scaled) and group size (less than six fish versus six fish) to account for the effects of memory, body size and population density on dispersal (De Bona et al. 2019, Borges et al. 2022). Batch and replicate were treated as above. Group number, individual identity and tank number were added as random effects. Next, we wanted to estimate the repeatability of dispersal times. Each individual in a treatment received a dispersal rank, with lower ranks indicating

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later dispersal. Due to overdispersion, we calculated the adjusted repeatability with a Poisson additive overdispersion model using the *rptR* function ('rptR' package, Stoffel et al. 2017), with the same random effects and any significant predictors from the aforementioned survival model.

Once dispersed, there was considerable variation among fish in how often they moved back and forth between two tanks. Within this subset of dispersers ($N_{observations}=105$, $N_{individuals}=78$), we subsequently analysed the number of transitions between tanks, using a generalized mixed-effect model (GLMER) with Poisson distribution ('lmerTest' package, Kuznetsova et al. 2017). Two fish were excluded as their first dispersal was at 95 h, and hence they had no opportunity to move back. To ensure model convergence, the 'bobyqa' optimizer was used (Bates et al. 2015). The GLMER had identical predictors and random effects as the survival model, with two exceptions: time until first dispersal was included to account for the fact that earlier dispersers have more opportunity to go back and forth, and group identity had to be removed as a random effect to avoid a singular fit.

In addition, we analysed variation in dispersal behaviour at the individual-level, using similar models as those described above, but with individual brain size and standard length (both log-transformed and scaled) as predictors instead of selection line.

Next, each individual was assigned a 'dispersal consistency' score as follows: (0) never dispersed, (1) only dispersed in one treatment and (2) dispersed in both treatments. To analyse this ordinal categorical data, we constructed a cumulative link mixed model (CLMM) (*clmm2* function in 'ordinal' package, Christensen 2023) with dispersal consistency score as response variable and selection line as fixed effect. Treatment order (control–drought versus drought–control) and its interaction with selection line were also added to the model, as were standard length and batch. Replicate was fitted as a nominal effect as it violated the assumption of proportional odds (Christensen 2015). Group identity was included as random effect.

Finally, we tested whether dispersers and non-dispersers differed in relative brain weight. We used two separate LMERs (one for each phase) with brain weight as response variable, dispersal status (yes versus no), standard length, round, replicate and batch as predictors, and group ID as random effect. Two additional similar LMERs were used to test for differences in relative brain weight between dispersers and non-dispersers in round 1 and round 2 separately. A final similar LMER was used to test whether relative brain weight differed among individuals with different dispersal consistency scores. As we repeatedly tested the same data in five different models here, we corrected for multiple testing using the Benjamini and Hochberg procedure (Benjamini and Hochberg 1995).

All analyses were ran in R ver. 4.2.1 (www.r-project.org). Survival models were checked for the assumption of proportional hazards (Therneau and Lumley 2020), GLMERs for overdispersion (Lüdecke et al. 2021) and CLMMs for the assumption of proportional odds and scale effects (Christensen 2023). Significance was tested using the *Anova* function ('car' package, Fox and Weisberg 2019) except for the CLMMs where stepwise model-comparison with the *anova* function was required. Post hoc pairwise comparisons were ran with the 'emmeans' package (Lenth et al. 2019). In all models, non-significant interactions were removed from the model. All final model structures are reported with the full-results in the Supporting information.

Results

Across treatments, we witnessed a total of 105 dispersal events. More than half of the individuals (54.7% or 87 individuals) never dispersed, while 27.7% (44 individuals) dispersed once and only a minority of fish dispersed in both treatments (17.6% or 28 individuals). Dispersal also varied greatly across groups, with the number of dispersers per tank ranging from zero to five.

First, we confirmed that guppies from the up-selected lines indeed had larger brains, relative to their body size, compared to the down-selected lines ($F_{1,25}=42.55$, $p < 0.001$; Fig. 2). Brain weight was significantly and positively correlated with standard length (estimate ± SE = 0.73 ± 0.05, $F_{1,157}=243.02$, $p < 0.001$, $N=164$). We also detected weak to strong differences in brain size between batches and replicates (Supporting information).

Large- and small-brained guppies did not differ in dispersal rate ($\chi^2_1=0.25$, $p=0.62$, proportion of trials in which fish dispersed: $N_{large}=68/183$, $N_{small}=36/138$), neither

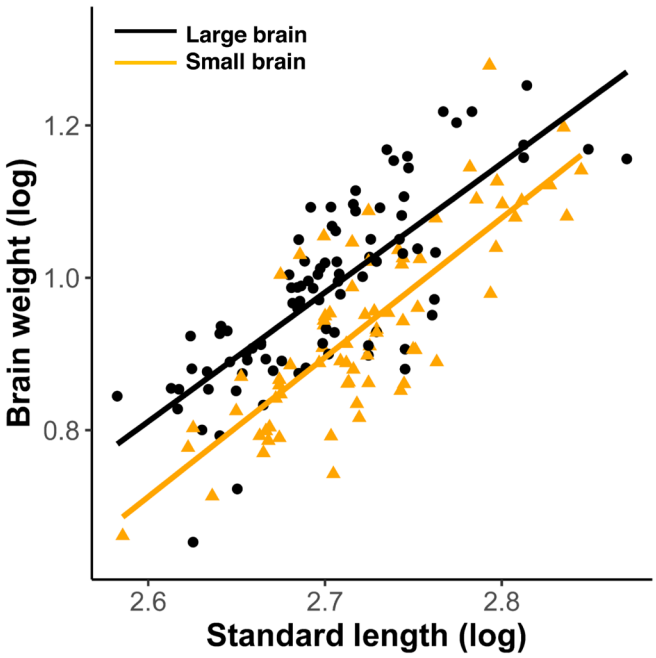


Figure 2. Correlation between brain weight (log-transformed) and standard length (log-transformed) for guppies from both selection lines (large-brained = black dots, small-brained = orange triangles). Sample sizes were as follows: $N_{large}= 91$, $N_{small}=73$.

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under stable- or unpredictable-conditions (line × treatment: $\chi^2_1 = 0.00$, $p = 0.99$) and in neither round (line × round: $\chi^2_1 = 0.04$, $p = 0.83$). However, treatment itself had a strong effect on dispersal ($\chi^2_1 = 10.26$, $p < 0.01$). Fish which had experienced a drought were less likely and slower to disperse compared to the stable treatment (hazard ratio ± 95 % CI = 0.46 [0.29; 0.74], proportion of dispersals: $N_{control} = 62/159$, $N_{drought} = 42/162$; Fig. 3A). Dispersal did not depend on experimental round, group size or standard length (all $p > 0.05$), but there were moderate differences between replicates ($\chi^2_1 = 8.38$, $p = 0.02$, Supporting information). While we found no differences between selection lines at the group-level, the analyses at the individual level showed a moderate effect of relative brain size on dispersal. This effect was independent of treatment (brain size × treatment: $\chi^2_1 = 0.03$, $p = 0.57$) but differed across time (brain size × round: $\chi^2_1 = 4.05$, $p = 0.04$). Specifically, guppies with larger relative brain sizes were less likely and slower to disperse (decreasing risk scores) during the first opportunity for dispersal (round 1 HR ± 95% CI = 0.56 [0.33; 0.93], $p = 0.03$) but not thereafter (round 2: 0.90 [0.54; 1.50], $p = 0.69$) (Fig. 3B).

Individual dispersal ranks were weakly but significantly repeatable across treatments ($R = 0.29$, 95% CI = [0.16; 0.44], link-scale, $p < 0.001$, $N_{ind} = 156$). However, dispersal rank was not repeatable when only considering those individuals that dispersed at least once ($R = 0.04$, 95 % CI = [0; 0.23], link-scale, $p = 0.32$, $N_{ind} = 70$).

In 41 out of the 105 dispersal events, fish moved back to the start tank at least once. Guppies often made multiple transitions between the start tank and novel environment (ranging from 2 to 17 transitions, median of 5). The number of transitions was not explained by selection line ($\chi^2_1 = 1.94$, $p = 0.16$), treatment ($\chi^2_1 = 0.64$, $p = 0.42$), round ($\chi^2_1 = 0.65$, $p = 0.42$) or their interactions (line × treatment: $\chi^2_1 = 0.16$, $p = 0.69$; line × round: $\chi^2_1 = 1.27$, $p = 0.25$). Fish in the second batch had a higher number of transitions (estimate ± SE = 0.83 ± 0.19, $\chi^2_1 = 19.41$, $p < 0.001$), and there was a very strong correlation between first dispersal time and the number of transitions, showing that earlier dispersers made more transitions (slope ± SE = -0.01 ± 0.00, $\chi^2_1 = 14.10$, $p < 0.001$). There was no effect of standard length or experimental round (all $p > 0.05$, Supporting information), but fish in larger groups tended to move more often (0.40 ± 0.22, $\chi^2_1 = 3.19$, $p = 0.07$). Using individual brain size data as predictor instead of selection line yielded similar results (Supporting information).

Next, we found no evidence that large-brained fish were more consistent dispersers than small-brained ones (LRT = 1.88, df = 1, $p = 0.17$; Fig. 4). Treatment order, regardless of brain size, did also not impact dispersal consistency (order: LRT = 0.34, df = 1, $p = 0.56$; line × order: LRT = 1.88, df = 1, $p = 0.17$). Replicate, fitted as a nominal effect, did have a significant impact on dispersal consistency (LRT = 12.22, df = 4, $p = 0.02$). Closer inspection of the data revealed that this was due to replicate 2, where there were more individuals with score 2 (consistent dispersers) than individuals with score 1 (single dispersers). Body size did not impact dispersal consistency (LRT = 0.06, df = 1, $p = 0.81$).

Finally, we found no differences in relative brain size between dispersers and non-dispersers in either the stable- ($F_{1,148} = 0.43$, $p_{adj} = 0.52$) or unpredictable treatment ($F_{1,147} = 2.55$, $p_{adj} = 0.17$), either round 1 ($F_{1,147} = 2.84$, $p_{adj} = 0.14$) or round 2 ($F_{1,150} = 0.11$, $p_{adj} = 0.74$), nor was it related to individual dispersal consistency scores ($F_{2,141} = 0.65$, $p_{adj} = 0.52$) (Fig. 5).

Discussion

Whether and when to disperse is a complicated decision, as both intrinsic traits and environmental conditions will

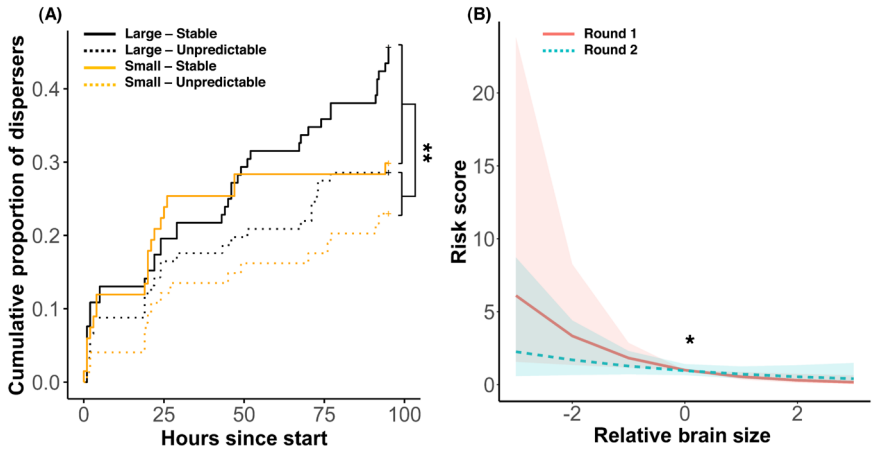


Figure 3. (A) Cumulative proportion of dispersers over time, per selection line (large-brained = black, small-brained = orange) and treatment (stable = solid lines, unpredictable = dashed lines.) ($N_{large\ -stable} = 92$, $N_{large\ -\ unpred} = 91$, $N_{small\ -\ stable} = 67$, $N_{small\ -\ unpred} = 71$). (B) Effect of individual relative brain size on dispersal per experimental round (round 1 = red solid line, round 2 = blue dotted line). Higher risk scores indicate a higher probability of an event (i.e. dispersal) occurring and a shorter time-to-event ($N_{round\ 1} = 157$, $N_{round\ 2} = 164$). Statistical significant differences are indicated as follows: '*" $p < 0.05$, '**' $p < 0.01$.

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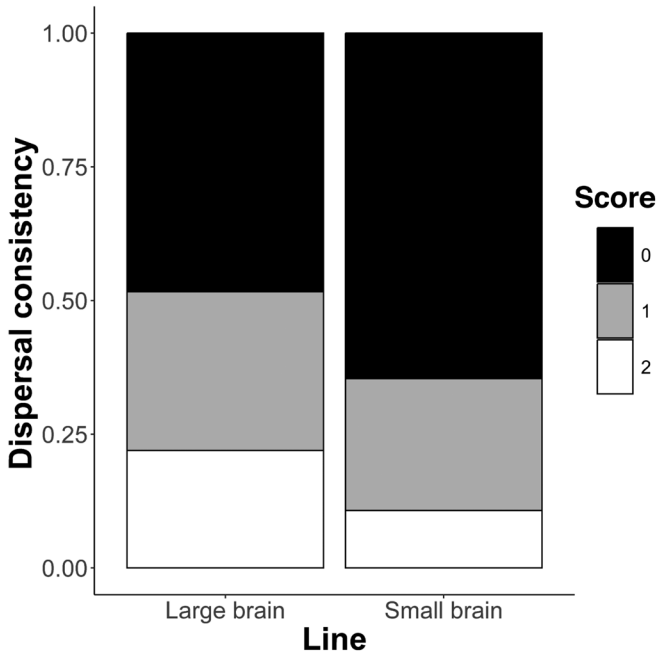


Figure 4. Proportion of individuals that never dispersed (0, black), only dispersed in one treatment (1, grey) and dispersed in both treatments (2, white) per selection line ($N_{large} = 91$, $N_{small} = 65$).

influence the tradeoffs between the costs, risks and benefits of leaving a current patch. Having relatively larger brains can theoretically both increase and decrease the costs of dispersal. Here, we found that guppies exhibit consistent interindividual variation in dispersal behaviour. In addition, we found correlational evidence that dispersal was related to relative brain size, but contrary to our expectations, this was independent of ecological context.

Guppies showed moderate consistent interindividual variation in dispersal rank (i.e. how fast they disperse relative to other individuals in the group) across conditions ($R = 0.29$). However, dispersal rank was not repeatable when only considering the individuals that dispersed at least once ($R = 0.04$), i.e. by leaving out the individuals that consistently had the maximum dispersal rank. This seems to suggest that individuals differ consistently in whether they disperse, rather than in how fast they disperse. Together with previous work (Jessop et al. 2024), this demonstrates the existence of a dispersal personality trait in guppies, cf. the widely used definition of inter-individual behavioural variation consistent across time and context (Réale et al. 2007). It has been suggested that distinct dispersal strategies should especially evolve in unpredictable, dynamic habitats where there is no optimal dispersal strategy (Cote et al. 2016, Coates et al. 2019), such as rivers with frequent droughts as in which our guppies naturally occur (Deacon and Magurran 2016, De Waele et al. 2022). Repeatability in dispersal behaviour has been described in other species as well (e.g. spiders: Bonte et al. 2009, fish: Cote et al. 2010, Moran et al. 2017, Coates et al. 2019, lizards: Michelangeli et al. 2017) and highlights that interindividual variation can have important consequences for metapopulation dynamics (Cote et al. 2010). Especially in the context of biological invasions this is a highly relevant insight, as it is critical to understand both species- and individual traits that contribute to the introduction and spread of

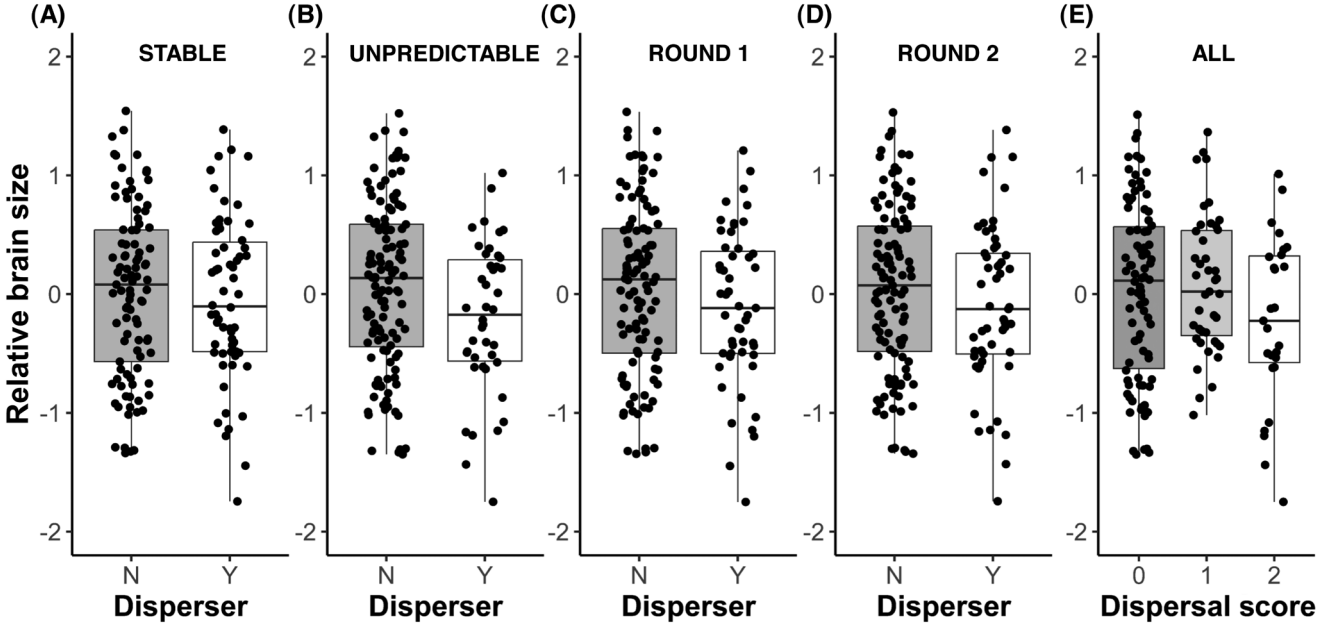


Figure 5. Relative brain size (residuals from a log(brain weight) – log(standard length) regression) of dispersers (Y) and non-dispersers (N) separated per treatment (A–B), per round (C–D) and per dispersal consistency score (E). No significant differences were found. Sample sizes were as follows; stable: $N_N = 97$, $N_Y = 62$; unpredictable: $N_N = 120$, $N_Y = 42$; round 1: $N_N = 106$, $N_Y = 51$; round 2: $N_N = 111$, $N_Y = 53$; all: $N_0 = 86$, $N_1 = 43$, $N_2 = 27$.

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invasive populations (Cote et al. 2010, Chapple et al. 2012, Shine et al. 2021).

Brain size was a promising candidate to be part of a dispersal syndrome, and we initially expected large-brained fish to show higher dispersal, especially in response to environmental unpredictability, as they should have a higher capacity to adapt to novel environments (Drake 2007, Sol 2009, Herczeg et al. 2019), more efficient information-gathering (van der Bijl et al. 2015, Corral-López et al. 2019) and higher alertness for environmental changes (Crosby et al. 2023). Alternatively, large-brained guppies could have been expected to show lower dispersal due to either a higher capacity to deal with environmental changes (Sol 2009) or increased costs associated with the loss of familiarity (Bonte et al. 2012). We indeed found limited support for a link between relative brain size and dispersal in the latter direction. Overall, there were no differences between large- and small-brained lines in how often, how fast, or how consistent they dispersed. At the individual level, however, guppies with relatively large brains were less likely and slower to disperse (decreasing risk scores) than guppies with relatively smaller brains, but only during the first opportunity for dispersal. Conversely, relative brain size did not differ between dispersers and non-dispersers in either treatment or round, suggesting that small-brained guppies are mainly faster to disperse.

The discrepancy between results obtained by comparing selection lines versus correlating individual level measures seems surprising, but may be reconciled by the fact that despite clear differences in average relative brain weight, there is still a considerable overlap between our selection lines (Fig. 2, Supporting information). This could mask behavioural variation caused by more subtle changes in brain size (Triki et al. 2022, Beltran and Tarwater 2024). While the individual-level analyses use the full range of brain size variation, we are cautious in making strong conclusions based on these results. Analyses at the individual level are correlational in nature, and thus possibly confounded, compared to our experimental approach based on selection lines where we have been able to experimentally manipulate relative brain size specifically.

If guppies with relatively smaller brains indeed show faster dispersal, we could explain this in several ways. Firstly, this relationship might reflect a energetic tradeoff between brain size and other dispersal traits, e.g. the negative correlation between relative brain size and hand-wing index in birds (Zhang et al. 2025). But such tradeoffs should be consistent across time and thus experimental rounds. Alternatively, large-brained guppies may exhibit higher levels of neophobia, which could have prevented or delayed their entry into the tunnels in our set-up. Consistent with this interpretation, large-brained guppies have previously been shown to be less inclined to exploit novel food sources (Kotrschal et al. 2014). However, neophobia is expected to decline over time (de Bruijn and Romero 2020), in which case large-brained guppies should become more willing to disperse over consecutive exposures. Yet, the opposite seemed to occur in round 2, with small-brained guppies becoming less likely and slower to disperse than in round 1. We thus consider it unlikely that the observed patterns are driven by differences in neophobia (alone). A third explanation is that guppies with larger brains collect more information about their environment prior to deciding whether or not to disperse, aligning with the observation that wild guppies with smaller telencephalons make hastier decisions (Burns and Rodd 2008). Following on this, it is also possible that large-brained individuals are slower to disperse as their higher cognitive flexibility (Buechel et al. 2018, Boussard et al. 2021) allows them to deal with a broader range of environmental challenges while small-brained guppies must disperse in a gamble to find an optimal habitat. Small-brained guppies by round 2 might have figured out that there was no better habitat available, explaining their reduced dispersal. Finally, one significant cost of dispersal is the loss of familiarity, which would be considerably higher for large-brained individuals who learn more about their environment, thus explaining their reluctance to disperse (Bonte et al. 2012, Liedtke and Fromhage 2021a, 2021b, Crosby et al. 2023). It is possible that this pattern disappeared by the second round as by then even the small-brained guppies had enough time to become familiar with the relatively simple start tank.

It is hard to discern which of the last two explanations (enhanced cognitive flexibility versus a higher cost of losing familiarity) is the main cause for lower dispersal in large-brained individuals. This should be more explicitly tested in follow-up studies. For instance, the cost of losing familiarity could be experimentally manipulated, e.g. by varying the time fish spent in the start tank (Liedtke and Fromhage 2021a) or increasing its spatial complexity (DePasquale et al. 2016). The cognitive flexibility explanation could be tested by adjusting the quality of the start tank. While our study tried to do this by simulating environmental unpredictability, another possibility would be to measure brain size-dependent dispersal under varying levels of predation risk (Kotrschal et al. 2015b).

Nonetheless, the overall evidence for a link between dispersal and relative brain size was rather limited. Perhaps this indicates that our set-up was not entirely suitable to measure natural dispersal tendencies. Wild guppies often disperse upstream, swimming through or jumping over riffles and waterfalls (Soares and Bierman 2013, Deacon and Magurran 2016, De Waele et al. 2022), while here they had to move through an artificial tunnel without any flow. However, wild guppies disperse in various ways, both up- and downstream (Croft et al. 2003, Borges et al. 2022), and our interest lies in understanding variation in the motivation to leave a familiar habitat rather than to disperse via a specific pathway.

One could argue that our experimental design was more of a test for explorative behaviour rather than dispersal. Given that exploration might be a strong driver of dispersal in the first place (Dingemanse et al. 2002, Gruber et al. 2017, Botero-Delgadillo et al. 2020, Cote et al. 2022), it would be difficult to rule out an effect of explorative behaviour in any potential dispersal experiment. Even so, we believe that dispersal required more than just being explorative in our study.

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Exploration tests typically measure how animals behave once in a new environment, while here we tested how likely animals were to leave a familiar environment. These behaviours might be regulated by different motivational processes. This is supported by the fact that our selection lines are known to differ in explorative behaviour (Kotrschal et al. 2014) yet only showed limited differences in dispersal, and in the opposite direction than the aforementioned differences in exploration. In addition, our dispersal rate (45%) is very similar to the one observed by Jessop et al. (2024) (43%) who quantified guppy dispersal over artificial waterfalls, and both experiments found dispersal in guppies to be repeatable ($R = 0.29$ versus $R = 0.17$). We thus believe that dispersal measured in our experiment is an adequate reflection of guppies' inclination to leave a familiar habitat and of natural dispersal tendencies. We nonetheless admit that the experimental design could be improved upon to more robustly measure dispersal behaviour, e.g. by introducing a flow – mimicking natural riffles and waterfalls (Jessop et al. 2024), having multiple interconnected tanks, or by increasing the length of the tunnels to exceed daily movement distances of guppies (Cote et al. 2010, 2013, Bestion et al. 2015). This could have allowed us to find more profound differences between selection lines.

The general lack of differences could also relate to the fact that we only tested adult males. Simulations suggest that dispersers should only invest in higher cognition when they disperse either very early or very late in life, as to maximize the time spent in one habitat and profit optimally from the cognitive investment they will make there (Liedtke and Fromhage 2021a). In seabirds, brain size indeed predicts natal but not adult dispersal (Crosby et al. 2023). In addition, previous research has demonstrated that differences in cognitive flexibility (reversal learning) between large- and small-brained guppies are mostly apparent at younger ages (< 12 months) and disappear due to cognitive ageing later in life (Boussard et al. 2021). Due to a low availability of young individuals at the time of the experiment, we were only able to use guppies older than that (16–24 months). Cognitive ageing, however, rarely means a decline in all cognitive domains (Boussard et al. 2021), and dispersers would theoretically benefit from a broader range of cognitive processes than just reversal learning. Admittedly, we cannot exclude the possibility that cognitive ageing might have equalized cognitive flexibility, and therefore the cost-benefit trade-offs of dispersing, between our selection lines. Hence, it is possible that differences in dispersal between large- and small-brained guppies would have been more explicit at a younger age. This would be an interesting hypothesis to explore in future experiments.

Independent of their brain size, guppies dispersed more often during the control treatment than after an experimental drought. This was surprising, as dispersal is often assumed to be triggered by environmental disturbances (Bates et al. 2006, Matthysen 2012) and should be higher in unpredictable environments (Cayuela et al. 2016). Several fish species, including guppies, are known to move out of shallow areas in response to drought (Davey et al. 2006, Goss et al. 2013, Driver and Hoeinghaus 2016, De Waele et al. 2022). The most likely explanation is that stress inflicted by the drought lead to lower mobility. While wild guppies certainly experience stress during droughts, they will also have access to more cues (e.g. temperature changes) that indicate the start of a drought and can react accordingly. In the absence of such cues, they may have simply reverted to a general stress response. Nonetheless, we would have expected stress-levels to subside over the 95 h, yet the effect of treatment seemed consistent across time (as treatment did not violate the assumption of proportional hazards in our models). Alternatively, due to practical limitations, fish were unable to disperse during the actual, but relatively short, period of drought. Perhaps fish would have responded differently if they had been able to do so. On the other hand, as argued above, in nature pools that already experienced strong fluctuations in water levels would likely be at risk of desiccation again in the future. This unpredictability would have made the start tank a suboptimal habitat from which fish should have been keen to disperse. It is possible that a single short drought was insufficient to induce the intended environmental unpredictability. Finally, selection is also predicted to act against dispersal in cases of extreme habitat fragmentation, due to higher movement costs and an increased risk of mortality (Bonte et al. 2012). For guppies, a lower dispersal rate during a period of drought might be an adaptive strategy if they are unfamiliar with their direct surroundings and cannot guarantee whether or not deeper areas are reachable in their environment. Such caveats may also explain why there was no interaction between treatment and brain size.

Our results are interesting in the context of the contemporary global problem of invasive alien species. Even though not evident in our data set, the literature seems to show a clear link between brain size and/or cognition and invasive success. For instance, large-brained vertebrate species are generally shown to be more successful invaders (Sol et al. 2002, 2005, 2008, Drake 2007, Amiel et al. 2011), and invasive species often outperform local natives on various cognitive tasks (Hazlett et al. 2002, Roudez et al. 2007, Griffin and Diquelou 2015, Chow et al. 2018). However, biological invasions are complicated, multi-staged processes (Chapple et al. 2012), and when and how the link between brain size/cognition and invasive success arises remains unclear (Szabo et al. 2020, Chow et al. 2021). One possibility could be that large-brained species or individuals are simply more likely to end up in new environments. Alternatively, once established at their point of introduction, the expansion towards further new areas, i.e. the actual invasion stage, could be driven by large-brained individuals (Chapple et al. 2012). Our results, however, may indicate that, at least in guppies, that relative larger brains do not increase the probability to end up in or spread across new environments. This would suggest that if brain size facilitates invasive success, it is most likely during the establishment phase after arrival, when increased behavioural flexibility would help individuals to rapidly adjust to new environmental conditions (Szabo et al. 2020). However, this warrants further investigation, especially since older research reported that relative brain size is not a determinant

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of establishment success in invasive fish species either (Drake 2007). Studying which particular biological traits help invasive species to overcome the consecutive stages of the invasion process is of major importance, both from a fundamental and conservation perspective, and can be highly valuable to design and implement more informed prevention and management strategies against invasive species (Rehage and Sih 2004, Cote et al. 2010, Chapple et al. 2012, Daniels and Kemp 2022).

Conclusion

The decision whether or when to disperse is a complicated challenge in the life of many animals. In this study, we demonstrated how dispersal is affected by both external conditions (i.e. unpredictable environment) and intrinsic traits, as indicated by the consistent interindividual variation in the decision of whether or not to disperse across treatments. This interindividual variation was, however, largely unrelated to relative brain size. While selection lines did not differ in dispersal behaviour, we observed a negative correlation at the individual level between relative brain size and dispersal speed during the initial dispersal. We suggest that these patterns could be either due to brain size-dependent costs in giving up a familiar environment or differences in cognitive flexibility leading to a differential need to disperse. We suggest for future studies to specifically test how the age of animals, the quality and spatial complexity of the environment and the time spent in the start tank would affect the relationship between relative brain size and dispersal. Such factors will likely influence the tradeoffs between the loss of cognitive investment in the current environment and the benefits of behavioural flexibility in a new habitat. We are convinced that such controlled experiments will reveal much about the role of cognition in dispersal, a question that is highly relevant with regards to the current challenge of invasive alien species.

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Conflict of interest – The authors declare no conflict of interest.
Permits – This study was approved by the Stockholm Animal Research Ethical Permit Board (permit no. 16124-2023). Ten fish died during the VIE tagging, and six individuals had to be euthanized due to visible distress. Five additional fish died during the habituation prior to experimental round 1, due to natural causes or by jumping out of the tank. One other fish died in between experimental round 1 and 2, and another fish had to be euthanized due to an infection.

Author contributions

Gilles De Meester: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Mirjam Amcoff**: Conceptualization (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – review and editing (equal). **Arezo Shamsgovara**: Investigation (equal); Methodology (supporting); Writing – review and editing (equal). **Alessandro Devigili**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Alexander Kotrschal**: Conceptualization (equal); Methodology (equal); Resources (equal); Writing – review and editing (equal). **John L. Fitzpatrick**: Conceptualization (equal); Methodology (equal); Resources (equal); Writing – review and editing (equal). **Niclas Kolm**: Conceptualization (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.c.7738874 (De Meester et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Aiello, L. C. and Wheeler, P. 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. – Curr. Anthropol. 36: 199–221.
Amiel, J. J., Tingley R. and Shine, R. 2011. Smart moves: effects of relative brain size on establishment success of invasive amphibians and reptiles. – PLoS One 6: e18277.
Bates, A. J., Sadler, J. P. and Fowles, A. P. 2006. Condition-dependent dispersal of a patchily distributed riparian ground beetle in response to disturbance. – Oecologia 150: 50–60.
Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.
Beltran, R. S. and Tarwater, C. E. 2024. Overcoming the pitfalls of categorizing continuous variables in ecology, evolution and behaviour. – Proc. R. Soc. B 291: 20241640.
Benjamini, Y. and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. – J. R. Stat. Soc. Ser. B Methodol. 57: 289–300.
Bestion, E., Teyssier, A., Aubret, F., Clobert, J. and Cote, J. 2014. Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. – Proc. R. Soc. B 281: 20140701.
Bestion, E., Clobert, J., Cote, J. and Gaillard, J. M. 2015. Dispersal response to climate change: scaling down to intraspecific variation. – Ecol. Lett. 18: 1226–1233.

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Bonte, D., Clercq, N. D., Zwertvaegher, I. and Lens, L. 2009. Repeatability of dispersal behaviour in a common dwarf spider: evidence for different mechanisms behind short- and long-distance dispersal. – Ecol. Entomol. 34: 271–276.
Bonte, D. et al. 2012. Costs of dispersal. – Biol. Rev. Camb. Philos. Soc. 87: 290–312.
Borges, I. L., Dangerfield, J. C., Angeloni, L. M., Funk, W. C. and Fitzpatrick, S. W. 2022. Reproductive benefits associated with dispersal in headwater populations of Trinidadian guppies (*Poecilia reticulata*). – Ecol. Lett. 25: 344–354.
Botero-Delgadillo, E., Quirici, V., Poblete, Y., Poulin, E., Kempenaers, B. and Vásquez, R. A. 2020. Exploratory behavior, but not aggressiveness, is correlated with breeding dispersal propensity in the highly philopatric thorn-tailed rayadito. – J. Avian Biol. 51: e02262.
Boussard, A., Amcoff, M., Buechel, S. D., Kotrschal, A. and Kolm, N. 2021. The link between relative brain size and cognitive ageing in female guppies (*Poecilia reticulata*) artificially selected for variation in brain size. – Exp. Gerontol. 146: 111218.
Buechel, S. D., Boussard, A., Kotrschal, A., van der Bijl, W. and Kolm, N. 2018. Brain size affects performance in a reversal-learning test. – Proc. R. Soc. B 285: 20172031.
Burns, J. G. and Rodd, F. H. 2008. Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. – Anim. Beh. 76: 911–922.
Cayuela, H., Boualit, L., Arsovski, D., Bonnaire, E., Pichenot, J., Bellec, A., Miaud, C., Lena, J. P., Joly, P. and Besnard, A. 2016. Does habitat unpredictability promote the evolution of a colonizer syndrome in amphibian metapopulations? – Ecology 97: 2658–2670.
Chapple, D. G., Simmonds, S. M. and Wong, B. B. 2012. Can behavioral and personality traits influence the success of unintentional species introductions? – Trends Ecol. Evol. 27: 57–64.
Chow, P. K. Y., Lurz, P. W. W. and Lea, S. E. G. 2018. A battle of wits? Problem-solving abilities in invasive eastern grey squirrels and native Eurasian red squirrels. – Anim. Behav. 137: 11–20.
Chow, P. K. Y., Clayton, N. S. and Steele, M. A. 2021. Cognitive performance of wild eastern gray squirrels (*Sciurus carolinensis*) in rural and urban, native and non-native environments. – Front. Ecol. Evol. 9: 615899.
Christensen, R. H. B. 2015. A tutorial on fitting cumulative link models with the ordinal package. – http://cran.nexr.com/web/packages/ordinal/vignettes/clm_tutorial.pdf.
Christensen, R. 2023. ordinal – Regression models for ordinal data. R package ver. 2023.12-4.1. – https://CRAN.R-project.org/package=ordinal.
Clobert, J., Le Galliard, J. F., Cote, J., Meylan, S. and Massot, M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. – Ecol. Lett. 12: 197–209.
Clobert, J., Baguette, M., Benton, T. G. and Bullock, J. M. 2012. Dispersal ecology and evolution. – Oxford Univ. Press.
Coates, W. D., Hale, R. and Morrongiello, J. R. 2019. Dispersal decisions and personality in a freshwater fish. – Anim. Behav. 157: 209–218.
Corral-López, A., Romensky, M., Kotrschal, A., Buechel, S. D. and Kolm, N. 2019. Brain size affects responsiveness in mating behaviour to variation in predation pressure and sex ratio. – J. Evol. Biol. 33: 165–177.
Cote, J., Fogarty, S., Weinersmith, K., Brodin, T. and Sih, A. 2010. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). – Proc. R. Soc. B 277: 1571–1579.
Cote, J., Fogarty, S., Tymen, B., Sih, A. and Brodin, T. 2013. Personality-dependent dispersal cancelled under predation risk. – Proc. R. Soc. B 280: 20132349.
Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D. and Baguette, M. 2016. Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. – Ecography 40: 56–73.
Cote, J. et al. 2022. Dispersal syndromes in challenging environments: a cross-species experiment. – Ecol. Lett. 25: 2675–2687.
Croft, D. P., Albanese, B., Arrowsmith, B. J., Botham, M., Webster, M. and Krause, J. 2003. Sex-biased movement in the guppy (*Poecilia reticulata*). – Oecologia 137: 62–68.
Crosby, C., Sayol, F. abd Horswill, C. 2023. Relative brain size is associated with natal dispersal rate and species' vulnerability to climate change in seabirds. – Oikos 2023: e09698.
Daniels, J. A. and Kemp, P. S. 2022. Personality-dependent passage behaviour of an aquatic invasive species at a barrier to dispersal. – Anim. Behav. 192: 63–74.
Davey, A. J. H., Kelly, D. J. and Biggs, B. J. F. 2006. Refuge-use strategies of stream fishes in response to extreme low flows. – J. Fish Biol. 69: 1047–1059.
De Bona, S., Bruneaux, M., Lee, A. E .G., Reznick, D. N., Bentzen, P. and Lopez-Sepulcre, A. 2019. Spatio-temporal dynamics of density-dependent dispersal during a population colonisation. – Ecol. Lett. 22: 634–644.
de Bruijn, R. and Romero, L. 2020. Prior restraint stress inhibits habituation to novel objects in the European starlings (*Sturnus vulgaris*). – J. Exp. Zool. A. Ecol. Integr. Physiol. 333: 88–95.
De Meester, G., Amcoff, M., Shamsgovara, A., Devigili, A., Kotrschal, A., Fitzpatrick, J. L. and Kolm, N. 2026. Data from: Evidence for dispersal personality in the guppy across ecological conditions, with a minor effect of relative brain size. – Figshare, https://doi.org/10.6084/m9.figshare.c.7738874.
De Waele, H., Vila Pouca, C., van Boerdonk, D., Luiten, E., Leenheer, L. M., Mitchell, D. J., Vega-Trejo, R. and Kotrschal, A. 2022. Jumping out of trouble: evidence for a cognitive map in guppies (*Poecilia reticulata*). – Behav. Ecol. 33: 1161–1169.
Deacon, A. E. and Magurran, A. E. 2016. How behaviour contributes to the success of an invasive poeciliid fish: the Trinidadian guppy (*Poecilia reticulata*) as a model species. – In: Weis, J. S. and Sol, D. (eds), Biological invasions and animal behaviour. Cambridge Univ. Press, pp. 266–290.
DePasquale, C., Neuberger, T., Hirrlinger, A. M. and Braithwaite, V. A. 2016. The influence of complex and threatening environments in early life on brain size and behaviour. – Proc. R. Soc. B 283: 20152564.
Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K. and van Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. – Anim. Behav. 64: 929–938.
Drake, J. M. 2007. Parental investment and fecundity, but not brain size, are associated with establishment success in introduced fishes. – Funct. Ecol. 21: 963–968.
Driver, L. J. and Hoeinghaus, D. J. 2016. Fish metacommunity responses to experimental drought are determined by habitat heterogeneity and connectivity. – Freshw. Biol. 61: 533–548.
Fox, J. and Weisberg, S. 2019. An R companion to applied regression. – Sage.

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ele.11966 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [05/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Gonzalez, A., Mouquet, N. and Loreau, M. 2009. Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning. – In: Naeem, D., Bunker, D., Hector, A., Loreau, M. and Perrings, C. (eds), Biodiversity, ecosystem functioning and ecosystem services. Oxford Univ. Press, pp. 134–146.
Goss, C. W., Loftus, W. F. and Trexler, J. C. 2013. Seasonal fish dispersal in ephemeral wetlands of the Florida Everglades. – Wetlands 34: 147–157.
Griffin, A. S. and Diquelou, M. C. 2015. Innovative problem solving in birds: a cross-species comparison of two highly successful passerines. – Anim. Behav. 100: 84–94.
Gruber, J., Brown, G., Whiting, M. J. and Shine, R. 2017. Geographic divergence in dispersal-related behaviour in cane toads from range-front versus range-core populations in Australia. – Behav. Ecol. Sociobiol. 71: 38.
Hazlett, B. A., Acquistapace, P. and Gherardi, F. 2002. Differences in memory capabilities in invasive and native crayfish. – J. Crustac. Biol. 22: 493–448.
Herczeg, G., Urszan, T. J., Orf, S., Nagy, G., Kotrschal, A. and Kolm, N. 2019. Brain size predicts behavioural plasticity in guppies (*Poecilia reticulata*): an experiment. – J. Evol. Biol. 32: 218–226.
Jessop, A., Morrissey, M. and Barbosa, M. 2024. Shifting the focus from species to individuals in invasion biology: individual differences in jumping behaviour. – Anim. Behav. 212: 93–100.
Jungwirth, A., Walker, J. and Taborsky, M. 2015. Prospecting precedes dispersal and increases survival chances in cooperatively breeding cichlids. – Anim. Behav. 106: 107–114.
Kotrschal, A., Rogell, B., Bundsen, A., Svensson, B., Zajitschek, S., Brännström, I., Immler, S., Maklakov, A. A. and Kolm, N. 2013. Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. – Curr. Biol. 23: 168–171.
Kotrschal, A., Lievens, E. J. P., Dahlbom, J., Bundsen, J., Semenova, S., Sundvik, M., Maklakov, A. A., Winberg, S., Panula, P. and Kolm, N. 2014. Artificial selection on relative brain size reveals a positive genetic correlation between brain size and proactive personality in the guppy. – Evolution 68: 1139–1149.
Kotrschal, A., Corral-Lopez, A., Amcoff, M. and Kolm, N. 2015a. A larger brain confers a benefit in a spatial mate search learning task in male guppies. – Behav. Ecol. 26: 527–532.
Kotrschal, A., Buechel, S. D., Zala, S. M., Corral-Lopez, A., Penn, D. J. and Kolm, N. 2015b. Brain size affects female but not male survival under predation threat. – Ecol. Lett. 18: 646–652.
Kotrschal, A., Kolm, N. and Penn, D. J. 2016. Selection for brain size impairs innate, but not adaptive immune responses. – Proc. R. Soc. B 283: 20152857.
Kotrschal, A., Zeng, H. L., van der Bijl, W., Ohman-Magi, C., Kotrschal, K., Pelckmans, K. and Kolm, N. 2017. Evolution of brain region volumes during artificial selection for relative brain size. – Evolution 71: 2942–2951.
Kotrschal, A., Corral-Lopez, A. and Kolm, N. 2019. Large brains, short life: selection on brain size impacts intrinsic lifespan. – Biol. Lett. 15: 20190137.
Kuznetsova, A., Brockhoff, P. B. and Christensen, R. H. B. 2017. lmerTest package: tests in linear mixed effects models. – J. Stat. Softw. 82: 1–26.
Lenth, R., Singmann, H., Love, J., Buerkner, P. and Herve, M. 2019. emmeans: estimated marginal means, aka least-squares means. – R package ver. 1.4.3.01. https://rvlenth.github.io/emmeans/.
Liedtke, J. and Fromhage, L. 2021a. Should dispersers be fast learners? Modeling the role of cognition in dispersal syndromes. – Ecol. Evol. 11: 14293–14302.
Liedtke, J. and Fromhage, L. 2021b. The joint evolution of learning and dispersal maintains intraspecific diversity in metapopulations. – Oikos 130: 808–818.
Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P. and Makowski, D. 2021. performance: an R package for assessment, comparison and testing of statistical models. – J. Open Source Softw. 6: 3139.
Marhounová, L., Kotrschal, A., Kverková, K., Kolm, N. and Němec, P. 2019. Artificial selection on brain size leads to matching changes in overall number of neurons. – Evolution 73: 2003–2012.
Matthysen, E. 2012. Multicausality of dispersal: a review. – In: Clobert, J., Baguette, M., Benton, T. G. and Bullock, J. M. (eds), Dispersal ecology and evolution. Oxford Univ. Press, pp. 3–18.
Michelangeli, M., Smith, C. R., Wong, B. B. M. and Chapple, D. G. 2017. Aggression mediates dispersal tendency in an invasive lizard. – Anim. Behav. 133: 29–34.
Moran, N. P., Mossop, K. D., Thompson, R. M., Chapple, D. G. and Wong, 2017. Rapid divergence of animal personality and syndrome structure across an arid–aquatic habitat matrix. – Oecologia 185: 55–67.
Réale, D., Reader, S. M., Sol, D., McDougall, P. T. and Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. – Biol. Rev. 82: 291–318.
Rehage, J. S. and Sih, A. 2004. Dispersal behavior, boldness, and the link to invasiveness: a comparison of four *Gambusia* species. – Biol. Invas. 6: 379–391.
Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. – Annu. Rev. Ecol. Evol. Syst. 38: 231–253.
Ronce, O. and Clobert, J. 2012. Dispersal syndromes. – In: Clobert, J., Baguette, M., Benton, T. G. and Bullock, J. M. (eds), Dispersal ecology and evolution. Oxford Univ. Press, pp. 119–138.
Roudez, R. J., Glover, T. and Weis, J. S. 2007. Learning in an invasive and a native predatory crab. – Biol. Invas. 10: 1191–1196.
Shine, R., Alford, R. A., Blennerhasset, R., Brown, G. P., DeVore, J. L., Ducatez, S., Finnerty, P., Greenlees, M., Kaiser, S. W., McCann, S., Pettit, L., Pizzatto, L., Schwarzkopf, L., Ward-Fear, G. and Phillips, B. L. 2021. Increased rates of dispersal of free-ranging cane toads (*Rhinella marina*) during their global invasion. – Sci. Rep. 11: 23574.
Soares, D. and Bierman, H. S. 2013. Aerial jumping in the Trinidadian guppy (*Poecilia reticulata*). – PLoS One 8: e61617.
Sol, D. 2009. Revisiting the cognitive buffer hypothesis for the evolution of large brains. – Biol. Lett. 5: 130–133.
Sol, D., Timmermans, S. and Lefebvre, L. 2002. Behavioural flexibility and invasion success in birds. – Anim. Behav. 63: 495–502.
Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. and Lefebvre, L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. – Proc. Natl Acad. Sci. USA 102: 5461–5465.
Sol, D., Bacher, S., Reader, S. M. and Lefebvre, L. 2008. Brain size predicts the success of mammal species introduced into novel environments. – Am. Nat. 172: S63–71.

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ele.11966 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [05/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Sonnenberg, B. R., Branch, C. L., Pitera, A. M., Bridge, E. and Pravosudov, V. V. 2019. Natural selection and spatial cognition in wild food-caching mountain chickadees. – Curr. Biol. 29: 670–676.

Stoffel, M. A., Nakagawa, S., Schielzeth, H. and Goslee, S. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. – Methods Ecol. Evol. 8: 1639–1644.

Szabo, B., Damas-Moreira, I. and Whiting, M. J. 2020. Can cognitive ability give invasive species the means to succeed? A review of the evidence. – Front. Ecol. Evol. 8: 187.

Therneau, T. 2015. coxme: mixed effects Cox models. – R package ver. 2.2-3, https://cran.r-project.org/package=coxme.

Therneau, T. M. and Lumley, T. 2020. "survival": survival analyses. – R package ver. 3.2-7, https://cran.r-project.org/package=survival.

Triki, Z., Granell-Ruiz, M., Fong, S., Amcoff, M. and Kolm, N. 2022. Brain morphology correlates of learning and cognitive flexibility in a fish species (*Poecilia reticulata*). – Proc. R. Soc. B 289: 20220844.

van der Bijl, W., Thyselius, M., Kotrschal, A. and Kolm, N. 2015. Brain size affects the behavioural response to predators in female guppies (*Poecilia reticulata*). – Proc. R. Soc. B 282: 20151132.

Wagnon, G. S. and Brown, C. R. 2020. Smaller brained cliff swallows are more likely to die during harsh weather. – Biol. Lett. 16: 20200264.

Zhang, Y., He, L., Yao, Y., Xu, H., Ji, Y., Lei, F., Fan, L. and Xiong, Y. 2025. Predictable evolution towards larger brains and lower hand-wing indices in long-tailed birds. – Funct. Ecol. 40: 191–202.

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ele.11966 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [05/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License