

RESEARCH ARTICLE

American eel personality and body length influence passage success in an experimental fishway

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Funding information

Nature Conservancy; National Science Foundation, Grant/Award Number: IIA-1539071

Handling Editor: Paulo S. Pompeu

Abstract

1. Millions of dams impair watershed connectivity across the globe and have severely affected migratory fish populations. Fishways offer upstream passage opportunities, but artificial selection may be imposed by these structures. Using juvenile American eel *Anguilla rostrata* as a model species, we consider whether individual differences in behaviour (i.e. personality) and fish size can predict passage success.
2. We evaluated the expression of bold and exploratory behaviours using open field and emergence assays in the laboratory. Then we assessed the propensity for individuals to volitionally climb through an experimental fishway to understand if personality and fish size could predict climbing success.
3. We demonstrate personality in juvenile eels, and swimming speed in the open field was negatively associated with climbing propensity. Slower swimmers were up to 60% more likely to use the passage device suggesting that more exploratory eels incurred greater passage success. For successful climbers, climbing time was negatively associated with fish length.
4. *Synthesis and applications.* Our results suggest fish may segregate at barriers based on personality and size. Preventing a subset of individuals from accessing upstream habitat is likely to have negative consequences for fish populations and aquatic ecosystems. Selection may be alleviated by increasing passage opportunities, maximizing fishway attraction and avoiding inefficient passage solutions.

KEYWORDS

American eel, animal personality, artificial selection, dam passage, eel ladder, fish passage, fishway, watershed connectivity

1 | INTRODUCTION

There are 16.7 million dams distributed across the globe (Lehner et al., 2011). Though often beneficial to humans, dams modify the environment by altering flows, disrupting connectivity and changing ecological communities living within and along impounded watersheds (Graf, 2006; Perkin et al., 2015; Poff et al., 2007). Habitat

loss associated with hydropower dams is considered a leading cause of migratory fish decline world-wide (Harris et al., 2017; Limburg & Waldman, 2009). In the United States alone, over 200 fishways have been installed at hydropower projects to offer upstream passage opportunities (Pringle et al., 2000).

Migratory species are the target of many passage systems which are challenged with accommodating ontogenetic, temporal and

life-history variation among individuals and populations (Zydlewski & Wilkie, 2012). However, fishway performance is highly variable (0%–100%), and on average, <50% of individuals pass successfully (Bunt et al., 2016; Noonan et al., 2012). While some studies have estimated passage rates for fish populations, little is known about their selectivity on individuals. Poor fishway performance invokes high selective potential, as research suggests selection may be imposed on behaviour, morphology, sex and physiology (Haugen et al., 2008; Jones et al., 2021; Maynard et al., 2017; Volpato et al., 2009). Given such high variation in performance we consider whether personality, in addition to fish size, may also influence passage success, especially when passage efficiencies are low.

'Personality' refers to behavioural differences among individuals that are consistent through time and across contexts (Carere & Maestripietri, 2013; Wolf et al., 2007). This inherent behavioural variation has ecological and evolutionary consequences (Wolf & Weissing, 2012), and some personalities have a higher adaptive capacity to respond to anthropogenic change (Sih et al., 2011) leading to a selective shift in behaviours within populations (Miranda et al., 2013; Pamela Delarue et al., 2015; Smith & Blumstein, 2013). Therefore, certain individuals may be better adapted to navigate fishways and experience greater passage success. Previous research on fish behaviour demonstrates a link between personality and fish movement, where bolder, more exploratory phenotypes have higher movement and dispersal rates (Chapman et al., 2011; Jones et al., 2021; Myles-Gonzalez et al., 2015; Zavorcka et al., 2015). We expect these same individuals to have a higher propensity to use fishways.

Because animal personalities are partially heritable (Dingemans et al., 2002; Kortet et al., 2014; Mazue et al., 2015), excluding some behavioural types from rearing or spawning habitat may reduce genetic diversity within fish populations. Further, research shows that modifying the personality composition of a population may affect demographic parameters (via the link between personality and fitness Moiron et al., 2020; Smith & Blumstein, 2008), reproductive strategies (Dammhahn et al., 2018) and growth rates (Mittelbach et al., 2014). Ultimately, investigating behavioural-mediated selectivity against certain personality types is a critical next step in fish passage research as evidence of phenotypic filtering would underscore the need to incorporate mitigation strategies that consider behavioural variation.

While many fishways are engineered to encourage passage by adult fish during spawning migrations, catadromous eels move upstream as juveniles in pursuit of rearing habitat, and their small size presents a convenient opportunity to evaluate passage performance in the laboratory. Young eels are remarkable climbers, so eel 'ladders' (substrate-lined, irrigated ramps) have been installed at dams to promote passage. Unlike other fishways (e.g. pool and weir, vertical slot, fish elevators), eel ladders are species and ontogenetic specific. If personality affects passage performance at eel ladders, behavioural traits may carry greater influence in other passage systems, making eels an ideal candidate for investigating the link between personality and fish passage.

In this study, we focused on the American eel *Anguilla rostrata*, which has experienced range-wide declines over the last few decades (Haro et al., 2000). After beginning life in the Sargasso Sea, juveniles enter coastal rivers across eastern North America each spring. While some individuals remain in estuarine waters until maturity, many swim upstream to colonize inland freshwater environments (Jessop et al., 2008). Those that continue upriver often encounter dams, which impede eel movement and limit access to rearing habitat where eels may spend decades before maturation (Hitt et al., 2012; Jessop, 2010). Like other fishways, the ability for eel ladders to accommodate among-individual variation is not well-understood. Therefore, we aimed to (a) test for among-individual variation in behaviours known to influence fish movement, (b) assess climbing behaviour through an experimental passage device in the laboratory and (c) model how personalities and body size influence passage time and motivation. We hypothesize that bolder, more exploratory fish will be more likely to use the passage device. Ultimately, demonstrating any relationship between personality and climbing propensity would offer context for behavioural-mediated selection during fish passage and have major implications for migratory fish management.

2 | MATERIALS AND METHODS

2.1 | Fish collection and housing

We dip-netted pigmented (Stage 7; Haro & Krueger, 1988) young-of-year American eels (7.4–13.3 cm) from the Souadabscook Stream in Hampden, Maine, USA (44.76°N, 68.86°W), in June 2019. This life stage falls between the highly migratory 'glass' and resident 'yellow' stages and demonstrates high variation in upstream movement. The capture location was downstream of all major barriers in the watershed, so we assumed that all fish lacked dam passage experience. Eels were housed communally at the Aquaculture Research Center at the University of Maine (Orono, Maine) in a 375-L tank maintained at 16°C ($\pm 1^\circ\text{C}$) with a 12:12 photoperiod and fed frozen bloodworms *ad libitum* daily. After a 3-week acclimation, we tagged fish with a unique colour combination of non-toxic acrylic paint to identify individuals throughout the study. Each fish was anesthetized in MS-222 (100 mg/l, buffered with 3.0 mM NaHCO₃, pH = 7.0), measured and injected with <50 μl of paint subcutaneously in two locations posterior to the anus. After marking, eels recovered for 2 weeks prior to testing. Acclimation times were used to minimize the influence of capture, transport, tagging and acclimation to communal housing tanks in behavioural assays.

2.2 | Personality assays

The personality of each fish was assessed through three repeated observations in two personality assays (outlined below). Within-individual consistency and among-individual variation in behavioural

responses were used to determine if the study group had personality. Each behavioural response was then interpreted in the context of two personality axes (boldness and exploratory activity). Further details about the assays and our interpretations of behaviours are provided in Appendix S1.

2.2.1 | Open field test

Open field assays consisted of square tanks (74×74 cm) with convex bottoms filled to a depth of 5.2 cm along the perimeter (2.5 cm in the centre; Figure 1a). Fish were individually netted from housing tanks and placed into the open field where after a 30-s acclimation, we recorded fish behaviour for 5 min. Videos were analysed post hoc using ANY-maze software, and we measured average speed (*mean speed*) and the proportion of time spent along the edge of the tank (*time along edge*; Figure 1a). Since many individuals exhibited climbing behaviour in the open field (i.e. breaking the water surface in effort to climb tank wall), we also counted the number of independent climbing events (*escape attempts*). Some fish ($n = 12$) were too large for ANY-maze to accurately track movement, so we used

ImageJ 1.52a (Schneider et al., 2012) and JWatcher V0.9 (Blumstein et al., 2000) to measure *mean speed* and *time along edge* respectively. We observed high agreement when comparing ANY-maze to both JWatcher ($R^2 = 0.93$) and ImageJ ($R^2 = 0.99$) outputs.

2.2.2 | Emergence test

Emergence testing started at least 36 hr after the open field test. The emergence assay was performed in a rectangular tank (58×74 cm), and the refuge consisted of a covered, dark plastic cylinder (26 cm diameter), with a gate valve (5 cm diameter; Figure 1b). The tank was filled with enough water to submerge the valve opening, and concrete blocks were arranged 15.7 cm in front of the refuge to provide additional obstacles for exploration. After a 1-min acclimation in the refuge, we opened the valve and allowed each eel 5 min to exit the refuge and explore the tank. During each trial, we recorded whether an individual emerged (*binary emergence*), emergence latency (*emergence time*) and the time to cross the dashed line in Figure 1b (*exploration time*). We performed open field and emergence tests weekly for 3 weeks,

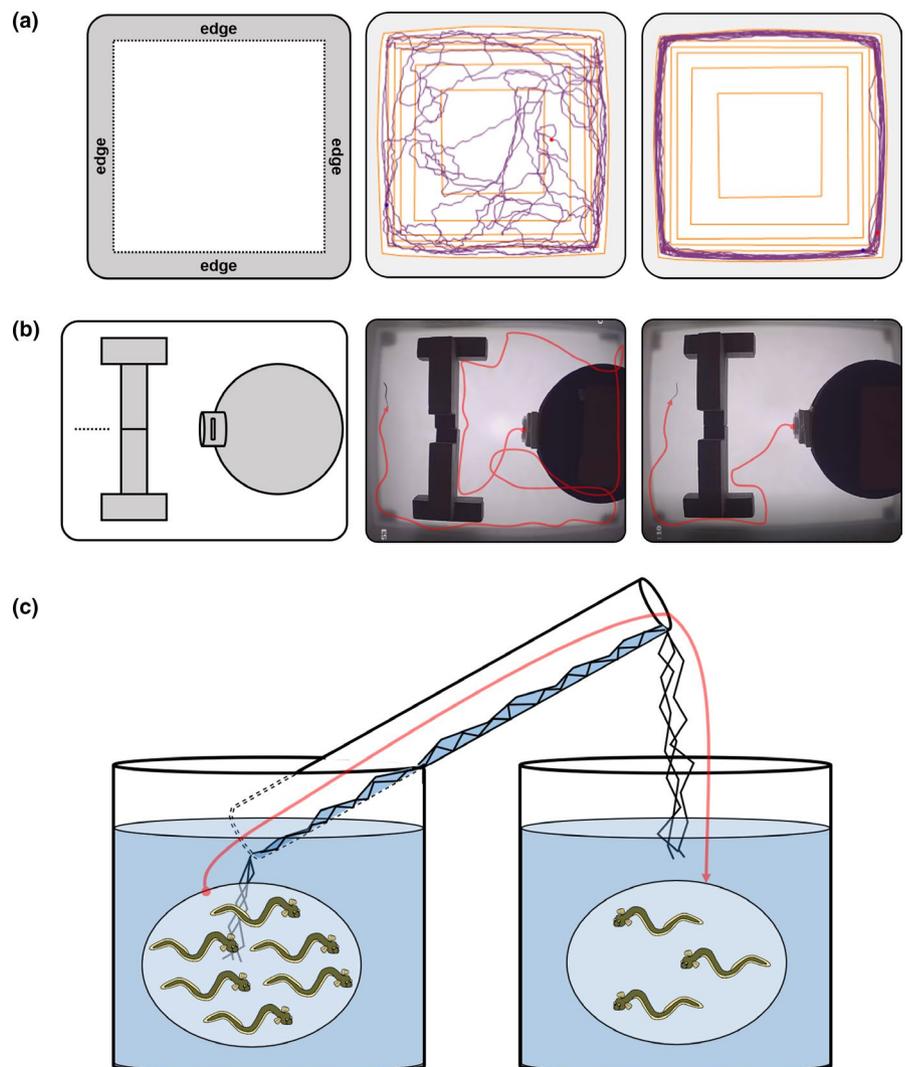


FIGURE 1 Overview of assays used to assess eel behaviour. (a) Open field. Left: Aerial view of assay. Shaded region used to calculate *time along edge*. Middle, Right: Tracks (purple lines) for two fish that responded differently to the open field. (b) Emergence. Left: Aerial view of assay. Circular region represents refuge, and rectangles are concrete blocks used as post-emergence obstacles to prevent fish from immediately crossing dotted line used to calculate *exploration time*. Middle, Right: Tracks (red lines) from two fish show differences in exploratory activity. (c) Cross section of climbing test. All eels were placed in the left tank and afforded the opportunity voluntarily move (red line) through a mesh-lined (jagged lines), irrigated pipe over 8 hr

and individual eels were allowed at least 36 hr to recover between assays (Figure S1).

2.2.3 | Climbing test

Three weeks after personality assays, we subjected eels to a climbing test to measure the propensity for individuals to move between tanks under conditions similar to eel ladders. This assay consisted of two 375-L tanks connected by an opaque, PVC tube (1.2 m long, 10 cm diameter) at a 32° incline (Figure 1c). The tube was lined with 2.5-cm polypropylene netting, and some material extended beyond the openings of the tube. A pipe at the apex of the device supplied filtered water to the starting tank at 4 L/min, to create an attractant flow while maintaining a constant water level. All fish were placed in the starting tank simultaneously within 1 hr of first light and allowed to volitionally move to the neighbouring tank over 8 hr. To limit disturbance from observers, the starting tank was screened with dark fabric and successful climbers were identified hourly. Every fish was subjected to the 8-hr climbing test thrice over 10 days, allowing at least 36 hr between trials. After Trials 2 and 3, fish that remained in the starting tank were given an opportunity to climb overnight, and successful climbers were identified the following morning (24 hr after the start of each trial). After each climbing test, fish were returned to communal housing tanks.

2.3 | Data analysis

2.3.1 | Assessment of repeatability

We estimated the repeatability of each response variable in open field and emergence tests. Analyses were conducted in Program R (R Core Team, 2013). We used the *LME4* package (Bates et al., 2015) to create a linear mixed-effect model for each behaviour (dependent variable), and treated fish ID as a random intercept. We controlled for testing order (1–31), open field tank/emergence apparatus and fish length by including these variables as fixed effects in each model. To determine if individuals behaved consistently through time (i.e. personality), we estimated the adjusted repeatability (R), by dividing the among-individual variance by the total variance (between-individual variance combined with marginal variance associated with fixed effects; Dingemans & Dochtermann, 2013). We used the *rptR* package (Stoffel et al., 2017) to generate 95% confidence intervals (CI) around repeatability estimates by performing 1,000 parametric bootstrap iterations. Variables were considered 'highly' repeatable if $R > 0.5$ or 'marginally' repeatable if $R > 0.2$, and the lower bound of the CI was >0.0 (Aplin et al., 2015; Baker et al., 2018; Dzieweczynski & Crovo, 2011). To meet normality assumptions, we applied the optimal Box-Cox power transformation for *time along edge*, *emergence time* and *exploration time* using the *ENVSTATS* package (Millard, 2013). For personality variables that were inherently non-Gaussian (*binary*

emergence, *escape attempts*), we used the link-scale approximation of R (Stoffel et al., 2019).

2.3.2 | Relationship between personality and climbing

Two different climbing outcomes were used to assess passage success. First, we used a GLM with a binomial response to describe whether each fish ever climbed during any of the three 8-hr trials (*climb binary*). For fish that climbed successfully, we assessed climbing speed in a mixed-effect framework by using the time to reach the neighbouring tank (*climbing time*) as the dependent variable with fish ID as a random intercept to control for repeated observations of individuals that climbed over multiple trials (Figure S1). Although we measured climbing time in discrete, 1-hr intervals, a relatively modest sample size ($n = 29$) of climbing observations led to poor model convergence using a Poisson error distribution. Instead, we \log_{10} transformed *climbing time* and assumed a Gaussian error term, which improved model fit and increased homoscedasticity. Since we were most interested in characterizing climbing motivation, and we did not record hourly climbing times for overnight climbers after Trials 2 and 3, only climbing observations that occurred within the 8-hr trials were used in these analyses (Table 1).

To determine if personality was a predictor of climbing behaviour, we incorporated repeatable personality variables as fixed effects in climbing models. For all continuous, repeatable behaviours, we simulated the best linear univariate predictor (BLUP) for each individual (Dingemans et al., 2020; Gharnit et al., 2020). Over multiple personality trials, BLUPs represent a mean behavioural response (or mean Box-Cox transformed response if used to estimate R), for each fish following 1,000 simulations using the *ARM* package (Gelman & Hill, 2007), while controlling for tank, testing order and fish length. Fish length was the only covariate considered in climbing models as all eels were exposed to the assay simultaneously within a single tank. We then tested for correlations between all combinations of BLUPs (*time along edge*, *mean speed*, *exploration time*, *escape attempts*) and fish length. Variables were

TABLE 1 The number of observations per-individual (1, 2 or 3) used to estimate repeatability and BLUP of behaviours in personality assays (open field, emergence), characterize climbing motivation (*climb binary*) or assess *climbing time* in juvenile American eel

Assessment	Observations per fish			Total fish ^a
	3	2	1	
Open field	59	2	0	61
Emergence	60	1	0	61
<i>Climb binary</i>	59	0	0	59
<i>Climbing time</i>	2	6	11	19

^aThe initial sample size was 63 fish, but two were excluded from our analysis because they could not be consistently identified between trials. Two open field observations and one emergence observation were removed due to protocol errors. Two fish were removed from the climbing analysis because they died before trials were completed.

not highly correlated ($|r| < 0.3$) except for *time along edge* and *exploration time* which were marginally correlated ($r = -0.46$). Since both behaviours were significantly repeatable and measured in different assays, we included both in the climbing analysis. Variables were z-standardized to directly compare effect sizes among independent variables.

For each climbing outcome, we used Akaike's information criterion adjusted for small sample size (AICc) to evaluate the relative support for competing models using $\Delta\text{AICc} < 2.00$ as a threshold for model support. We first evaluated the support for fish length, which was retained if it improved by >2.00 AICc against the null model. Each repeated behaviour was then incorporated into the climbing model in a univariate framework (or with fish length, if supported), and we retained personality variables if they improved support by >2.00 AICc (Burnham & Anderson, 2002). We also tested for nonlinear responses (quadratic, exponential, logarithmic) for each behaviour, which we considered to be more supported if they outperformed the linear response by >2.00 AICc. Supported models were validated by analysing the effect sizes for each behaviour (β) and those with 95% CI not overlapping zero were considered to significantly influence the climbing outcome.

2.3.3 | Distribution of personality traits

Finally, to assess whether the distribution of personality traits differed between the sample of individuals that climbed in the experimental fishway and the sample of individuals that did not climb, we calculated the phenotypic distance between the two samples using the Δp method. This nonparametric distance measure is calculated based on a joint cumulative distribution function and can be used to assess trait divergence between populations (Brehm et al., 2019; Safran et al., 2012). We performed this analysis on any personality trait that significantly influenced a climbing outcome in MATLAB R2020a (MathWorks Inc.).

3 | RESULTS

3.1 | Assessment of personality

We found evidence of repeatable behaviours in both open field and emergence trials which demonstrated personality in juvenile eels (Table 2). All variables measured in the open field showed

significant repeatability and *mean speed* was highly repeatable ($R = 0.53 \pm 0.07$ SE). *Exploration time* was significantly repeatable ($R = 0.30 \pm 0.13$ SE) in the emergence test. Substantially more fish left the refuge during Trials 2 and 3, compared to Trial 1. This suggests that fish may have become acclimated to the apparatus after initial exposure which is likely why *binary emergence* and *emergence time* were not repeatable.

3.2 | Assessment of climbing and personality

Personality was a predictor of climbing motivation as *mean speed* was the most supported variable in the *climb binary* assessment (Table 3). Model predictions show that less exploratory fish (i.e. high *mean speed*) were less likely to climb. While a linear effect of *mean speed* on this outcome was supported against the null model (Table S1), quadratic ($\beta = -1.24 \pm 0.65$ SE) and exponential effects ($\beta = -1.11 \pm 0.52$ SE) were the highest ranking models (Table 3). These models also predicted less exploratory fish to have little to no climbing propensity (Figure 2). While other models suggest that bolder fish (i.e. low *time along edge*) were more likely to climb (Table S1), they did not meet our model selection criteria and CI included zero.

For successful climbers ($n = 19$), fish length predicted the time taken to ascend the passage device. The most supported *climbing time* model suggests that larger fish ascended the passage device sooner than smaller individuals ($\beta = -0.17 \pm 0.06$ SE; Figure 2) and including a linear effect of fish length improved model support by >5.00 AICc against the baseline (Table S1). Adding personality variables to the fish length model did not improve model support, which suggests that while some behaviours were predictive of passage motivation, they were not reliable predictors of climbing time. The lack of support for fish length in the *climb binary* assessment suggests that larger fish may not have a greater motivation to climb but were faster climbers relative to smaller conspecifics.

3.3 | Distribution of personality traits

The distribution of the supported personality trait *mean speed* differed significantly between the sample of eels that chose to climb in

TABLE 2 Repeatability of behaviours measured in the open field and emergence assays. *R* = repeatability; moderately repeatable behaviours are italicized, and highly repeatable behaviours are bolded and italicized. Range = range of values observed for each behaviour

Behaviour	Assay	Personality axis	<i>R</i>	SE	95% CI	Range
<i>mean speed</i>	Open field	Exploratory activity	0.533	0.073	(0.379–0.669)	0.04–0.15 m/s
<i>time along edge</i>	Open field	Boldness	0.438	0.080	(0.282–0.591)	0.50–1.00
<i>escape attempts</i>	Open field	Boldness	0.297	0.102	(0.069–0.464)	0–44
<i>binary emergence</i>	Emergence	Boldness	0.234	0.114	(0.000–0.436)	0,1
<i>emergence time</i>	Emergence	Boldness	0.185	0.133	(0.000–0.476)	6–290 s
<i>exploration time</i>	Emergence	Exploratory activity	0.295	0.132	(0.032–0.570)	6–75 s

TABLE 3 Relative performance of models used to assess climbing propensity of juvenile eels. Climbing outcome = response variable in climbing model^a. Model = independent variables used in climbing model^b. ΔAIC_c = difference in Akaike's information criterion (adjusted for small sample size) from the most supported model. R^2_m = marginal R^2 (only calculated for mixed-effect models). $R^2 = R^2$ for the entire model (i.e. conditional R^2 for mixed-effect models). β = effect size of the univariate effect. For quadratic models, β = quadratic effect, for models that included fish length and personality, β = effect size of behaviour. SE = standard error of effect size

Climbing outcome	Model	ΔAIC_c	R^2_m	R^2	β	SE	95% CI
Climb binary	$(mean\ speed)^2$	0.00	–	0.19	-1.24	0.65	(-2.51 to 0.03)
	$\exp(mean\ speed)$	0.28	–	0.14	-1.11	0.52	(-2.13 to -0.09)
Climbing time	length	0.00	0.29	0.46	-0.17	0.06	(-0.29 to -0.06)
	$(time\ along\ edge)^2 + length$	0.05	0.44	0.45	0.10	0.04	(0.02 to 0.18)
	$\log(length)$	0.84	0.28	0.40	-0.34	0.12	(-0.57 to -0.11)
	$\exp(escape\ attempts) + length$	0.93	0.33	0.49	-0.06	0.05	(-0.16 to 0.03)
	$\exp(time\ along\ edge) + length$	1.24	0.34	0.44	0.05	0.04	(-0.03 to 0.13)
	$\exp(length)$	1.82	0.20	0.49	-0.05	0.02	(-0.09 to -0.01)
	$\exp(mean\ speed) + length$	1.83	0.33	0.45	-0.04	0.04	(-0.11 to 0.04)
	$\log(exploration\ time) + length$	1.90	0.31	0.47	-0.15	0.16	(-0.47 to 0.16)

^aClimb binary = a binary response that describes if a fish climbed at least once during the test. Climbing time = mixed-effect model that describes the time (\log_{10} hr) to climb through a passage device with fish ID as a random intercept

^bmean speed = the average swimming speed in the open field, time along edge = the proportion of time spent along the edge of the open field (Figure 1a), escape attempts = number of wall-climbing attempts in the open field, exploration time = time to fully explore emergence tank (Figure 1b).

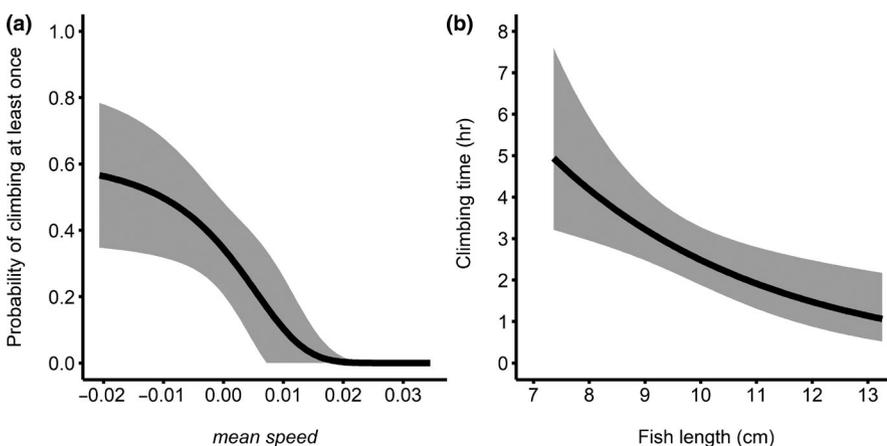


FIGURE 2 Predictions from most supported model for each climbing assessment for juvenile eels. (a) Climb binary assessment. Horizontal axis represents BLUP for mean speed in the open field. (b) Climbing time assessment. This analysis was performed in a mixed-effect framework with a random intercept. The mean intercept is represented here. Shaded areas represent 95% CI for each prediction

the experimental fishway and those that did not ($\Delta p = 30.92$, $CI = [12.76, 42.43]$, $p = 0.01$; Figure 3).

4 | DISCUSSION

We show that the individual phenotype (personality and length) influenced passage time and motivation in an experimental fishway, where smaller, less exploratory individuals experienced lower passage success. Our results suggest high potential for artificial selection on behaviour and size during dam passage. Considering that >90% of global river volume will be impacted by impoundments by 2030 (Grill et al., 2015), selection imposed by passage systems may bear severe consequences for fish species and aquatic ecosystems. Our findings add novel perspective to the complexity of fish passage research, and merit attention when mitigation is considered at new and existing dams. Fishways that can accommodate behavioural heterogeneity, by improving

attraction or navigability, could help improve watershed connectivity for fish populations.

4.1 | Behavioural-mediated selection

Our results suggest that personality may predict passage motivation. More exploratory fish (i.e. slow open field swimmers) demonstrated the highest propensity to use the experimental fishway. These findings are supported by research that show positive relationships between exploratory activity and fish movement (Rasmussen & Belk, 2012; Villegas-Ríos et al., 2018). Additionally, we did not observe a statistically significant relationship between boldness and passage motivation, which was unexpected given other studies linking boldness to fish movement (Chapman et al., 2011; Jones et al., 2021; Myles-Gonzalez et al., 2015). However, mean speed was positively correlated with the time along edge ($r = 0.30$), which suggests that more exploratory fish were bolder on average. A larger

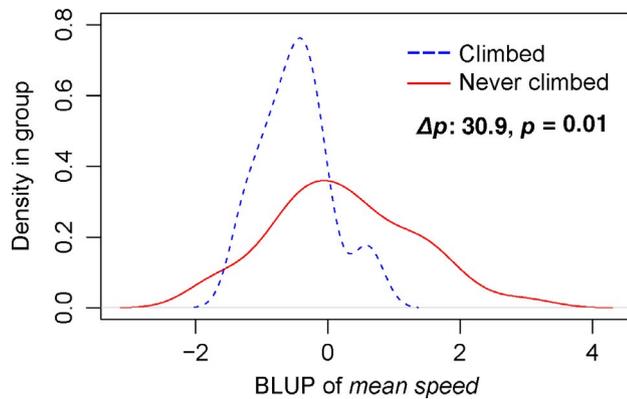


FIGURE 3 Probability density plot showing the distribution of the personality trait 'mean speed' between eels that climbed ($n = 19$) or did not climb ($n = 40$) through an experimental fishway at least once during the three climbing trials. Δp values and associated p -values were used to calculate the distance between the trait distribution for each climbing group

sample size or more discrete assessment of climbing propensity may have revealed such a relationship.

In addition to behaviours discussed above, the development of social structures within the housing tank during the 8 weeks before climbing trials may have also influenced passage motivation. Asocial fish are more likely to disperse (Cote et al., 2010), and Geffroy et al. (2014) showed high sociability in captive juvenile European eels *Anguilla anguilla*. Therefore, sociability may help inform a proximate mechanism for climbing motivation. Presumably, similar social dynamics develop in rivers, though a field-based passage assessment that considers multiple personality axes could help validate our findings. Such 'behavioural syndromes' are well-documented in fish populations (Conrad et al., 2011), where multiple personality traits may influence vulnerability and response to anthropogenic stressors (Sih et al., 2011). We demonstrated a link between personality and passage motivation, and showed significant differences in trait distribution between groups, using a relatively small number of eels ($n = 59$) from a single stream when all individuals started within 1 m of the fishway. When scaling both behavioural variation and fishway conditions to the field, there is potential for extreme behavioural-mediated selection during fish passage. Therefore, upstream rearing habitat may only be available for phenotypes that are motivated to use passage systems.

4.2 | Evidence for size selection

For successful climbers, larger eels climbed faster than smaller fish. This result offers further evidence of size selectivity during fish passage (Haugen et al., 2008; Maynard et al., 2017; Volpato et al., 2009), and is corroborated by Podgorniak et al. (2017), who found the largest juvenile European eels were found upstream of multiple eel ladders. Because most barriers are higher than our experimental device (0.6 m), we expect functional fishways to impose greater size selectivity on passage time.

4.3 | Management implications

Our findings suggest that individual differences in behaviour and size may limit the effectiveness of eel ladders and illustrate the potential for fishways to change the distribution of personality traits during fish passage more broadly. Although catadromous eels can complete their life cycle without moving upriver, limiting upstream movement may have severe consequences for eel populations and aquatic ecosystems. Because upstream movement may be regulated by physiological condition (Edeline et al., 2006), selection at dams may force upstream-bound eels into unfavourable estuarine habitats, reducing fitness and increasing intraspecific competition downstream (Edeline, 2007). Additionally, large female eels are predominantly found in upriver habitats, where low conspecific densities may cue female development (Jessop, 2010; Krueger & Oliveira, 1999). Therefore, dam-imposed selection could reduce the number of females in the population, yielding major consequences for population demographics. American eel also contribute substantial biomass to freshwater environments where they prey on macroinvertebrates and small fish (Hitt et al., 2012; Ogden, 1970). Since predator personalities can control the composition of prey communities (Start & Gilbert, 2017), selection against behavioural types may have consequences for upstream ecosystems beyond reducing the density of top-down regulators.

Despite the potential consequences of selection, eels can access upstream habitat given modest passage improvements. Fishways used by many species may impose greater selection due to greater variation in traits within and among populations. The consequences of segregation are most apparent for anadromous species as the exclusion of mature fish directly removes spawning biomass and the genetic variation contributed by those individuals (Lundqvist et al., 2008; Maynard et al., 2017). Since fish personality and body size are heritable (Kortet et al., 2014; Mazue et al., 2015; Thériault et al., 2007), selection against these traits during dam passage may homogenize fish populations where a lack of genetic variation may reduce resilience to additional stressors. Other sources of artificial selection on fish behavioural types (e.g. fishing, hatchery rearing) demonstrate that such pressure can also lower growth rates and fitness within populations (Mittelbach et al., 2014). For fish that pass dams successfully, some may suffer reduced fitness through fallback, difficulty navigating reservoirs (Pelicice et al., 2015), or 'ecological traps' when individuals encounter unfavourable upstream conditions or experience mortality during downstream dam passage (McLaughlin et al., 2013; Mensinger, Blomberg, et al., 2021; Stich et al., 2014).

Our results add further complexity to fish passage research as we suggest that personality, in addition to size, merits consideration during mitigation. Because fish passage research is species (salmonids) and geographically (Northern Hemisphere) biased, existing strategies may not account for the variation in species, facilities and river systems world-wide (Birnie-Gauvin et al., 2019; Kemp, 2016). Given the prevalence of personality across many fish species, passage solutions that best accommodate behavioural variation may offer more effective and translatable solutions (Birnie-Gauvin et al., 2019). While barrier removal may not be a feasible solution for accommodating

this variation at all dams (Birnie-Gauvin et al., 2019), managers may consider options that maximize fishway attraction and retention in new and existing structures. This may be achieved by (a) increasing the number of passage opportunities at each dam, (b) increasing the size of fishway entrances and limiting attractant flows (i.e. 'spill') elsewhere (Bunt, 2001; Burnett et al., 2014) and (c) avoiding short, steep fishways with high discharges (Bunt et al., 2016; Noonan et al., 2012). Nevertheless, it would be useful to know if these alternatives lead to different types of phenotypic filtering. Until effective mitigation efforts are widely implemented, fishways may continue imposing selection on fish populations and counteract management efforts.

ACKNOWLEDGEMENTS

Financial support for this research was provided by The Nature Conservancy, University of Maine, and the National Science Foundation's Research Infrastructure Improvement NSF #IIA-1539071. In-kind support was provided by the US Geological Survey Maine Cooperative Fish and Wildlife Research Unit. Laboratory support was provided by the University of Maine Aquaculture Research Center. This project was greatly supported by the help of Bobby Harrington, Evan Dunn and many volunteers. The authors thank two anonymous reviewers for providing helpful comments on earlier drafts of the manuscript. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government. This work was conducted under the University of Maine IACUC protocol A2019-02-04. This project was supported by the USDA National Institute of Food and Agriculture, McIntire-Stennis Project number ME041602 through the Maine Agricultural and Forest Experiment Station. Maine Agricultural and Forest Experiment Publication Number 3847.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and methodology; M.A.M. collected and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via Figshare <https://doi.org/10.6084/m9.figshare.16413429> (Mensinger, Brehm, et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Mensinger, M. A., Brehm, A. M., Mortelliti, A., Blomberg, E. J., & Zydlewski, J. D. (2021). American eel personality and body length influence passage success in an experimental fishway. *Journal of Applied Ecology*, 00, 1–10. <https://doi.org/10.1111/1365-2664.14009>