



# Personality-dependent passage behaviour of an aquatic invasive species at a barrier to dispersal

J. A. Daniels<sup>\*</sup> , P. S. Kemp

International Centre for Ecohydraulics Research (ICER), University of Southampton, Southampton, U.K.

## ARTICLE INFO

### Article history:

Received 4 March 2022

Initial acceptance 14 April 2022

Final acceptance 29 May 2022

Available online 27 August 2022

MS. number: 22-00124

### Keywords:

alien species  
animal personality  
biodiversity loss  
bold–shy continuum  
gauging weir  
habitat fragmentation  
instream infrastructure  
non-native species  
river engineering  
secondary spread

Intraspecific variation in personality traits is increasingly recognized as an important determinant of invasion success and is associated with the dispersal ability of several invasive species. However, previous studies have focused on the dispersal of invasive species through continuous habitats, despite the high levels of anthropogenic fragmentation in modern environments. This study investigated how personality influences the behaviour of aquatic invasive species at an anthropogenic barrier to dispersal, using the passage behaviour of American signal crayfish, *Pacifastacus leniusculus*, at an experimental Crump weir as a model system. Personality was characterized by determining the repeatability of boldness, activity and sociability, with correlations between traits indicating behavioural syndromes, while passage behaviour was quantified as motivation and subsequent ability to pass the weir. Boldness and activity were repeatable and positively correlated, indicating a boldness–activity syndrome. However, sociability was not repeatable and was therefore not classified as a personality trait, potentially as a result of the confounding effects of social hierarchy formation. Bolder individuals tended to be more motivated to pass the weir, although motivation was not related to activity. Few individuals passed the weir, and personality was not related to passage success. This study evidences the presence of behavioural syndromes in signal crayfish and demonstrates that personality can influence the motivation of invasive species to expand their range in a fragmented habitat. Although no relationship with passage success was observed, the higher levels of motivation in bold individuals may lead to differential passage success in natural situations where the time to attempt passage is not constrained by experimental conditions.

© 2022 The Authors. Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Human translocation of species beyond their native range is a defining feature of the Anthropocene (Ricciardi, 2007). Invasive species have profound impacts on native ecosystem functioning, resulting in substantial biodiversity losses (Blackburn et al., 2019; Simberloff et al., 2013; Vilà et al., 2011), degradation of ecosystem services (Vilà et al., 2010; Vilà & Hulme, 2017) and associated socioeconomic impacts (Diagne et al., 2021). With ever greater globalization, there has been a rapid increase in the rate of invasion and spread of non-native species within recipient ecosystems (Seebens et al., 2017, 2021). This has been further exacerbated by shifts in climate, both through the elimination of thermal barriers to invasion (e.g. Chown et al., 2012; Vilizzi et al., 2021) and the emergence of new pathways for introduction and spread (e.g. Miller & Ruiz, 2014).

Understanding the species level traits associated with invasiveness has been a primary focus in invasion science, with attributes such as high dispersal rates, rapid reproduction and broad physiological tolerance among the key predictors of success (e.g. Liao et al., 2021; Quell et al., 2021). Furthermore, intraspecific variation is increasingly recognized as an important driver of invasion dynamics, with particular attention focused on variation in personality traits (e.g. boldness, sociability, activity, aggression and exploration) and associated behavioural syndromes, i.e. correlations between these traits (Chapple et al., 2012; Juette et al., 2014; Rehage et al., 2016). Personality, defined as individual differences in behaviours that are stable over time and context (Sih et al., 2004), can impact success at any stage of the invasion process (Brand et al., 2021; Juette et al., 2014; Rehage et al., 2016), as traits that maximize the probability of being introduced outside the native range may also promote successful establishment and spread within the recipient ecosystem (Chapple et al., 2012). These traits are also likely to influence interactions with native species and habitats, and

<sup>\*</sup> Corresponding author.

E-mail address: [J.A.Daniels@soton.ac.uk](mailto:J.A.Daniels@soton.ac.uk) (J. A. Daniels).

thus may play an important role in determining the intensity of ecological impacts (Juette et al., 2014).

Intraspecific variation in personality traits can influence dispersal tendency in a wide variety of taxa (e.g. great tits, *Parus major*, Dingemanse et al., 2003; common lizards, *Lacerta vivipara*, Cote & Clobert, 2007; North American red squirrels, *Tamiasciurus hudsonicus*, Cooper et al., 2017; mud crabs, *Panopeus herbstii*, Belgrad & Griffen, 2018; thorn-tailed rayaditos, *Aphrastura spinicauda*, Botero-Delgadillo et al., 2020), suggesting a strong influence on the spread of invasive species (Cote, Clobert, et al., 2010; Rehage et al., 2016; Sih et al., 2012). Indeed, sociability (e.g. negative relationship for mosquitofish, *Gambusia affinis*, Cote, Fogarty, et al., 2010), aggression (e.g. positive relationship for delicate skinks, *Lampropholis delicata*, Michelangeli et al., 2017), activity (e.g. positive relationship for round gobies, *Neogobius melanostomus*, Thorlacius et al., 2015) and certain behavioural syndromes (e.g. boldness–exploration–climbing syndrome in signal crayfish, *Pacifastacus leniusculus*, Galib et al., 2022) are important predictors of invasive dispersal. Furthermore, several studies have demonstrated that behavioural traits vary along the invasion gradient, with individuals at the invasion front showing higher levels of boldness and exploratory behaviour (Gruber et al., 2017; Myles-Gonzalez et al., 2015) and lower levels of aggression (Hudina et al., 2015).

Previous studies exploring the influence of personality on dispersal in invasive species have focused on continuous, uninterrupted environments (e.g. Cote, Fogarty, et al., 2010), but modern habitats are often heavily fragmented by anthropogenic barriers to animal movement (e.g. roads, Shepard et al., 2008; fences, Ito et al., 2013; deforested areas, Feeley & Rehm, 2012; river infrastructure, J. Jones et al., 2019). These barriers can have considerable impacts on native species by preventing access to critical habitat (Sheer & Steel, 2006), increasing levels of human–wildlife conflict (e.g. vehicle collisions; Hill et al., 2019) and reducing gene flow between populations (Dixon et al., 2007). For this reason, considerable effort is directed at removing such barriers (O'Connor et al., 2015), or at least mitigating their adverse effects (Denneboom et al., 2021; Silva et al., 2018). However, there is also increasing recognition that barriers to movement may be both ecologically and economically beneficial if they slow or block the secondary spread of invasive species (Hermoso et al., 2015). For example, fences have been used in New Zealand and Australia to exclude introduced mammalian predators from areas of habitat that are important for native and reintroduced species (Clapperton & Matthews, 1996; Moseby & O'Donnell, 2003; Short & Turner, 2000). Similarly, common river infrastructure such as dams, weirs and culverts (Belletti et al., 2020) can act as a barrier to the spread of invasive species (e.g. Kerby et al., 2005), and in some cases are constructed specifically for this purpose (i.e. exclusion barriers; Jones, Tummers et al., 2021). This trade-off between mitigating the impacts of habitat fragmentation and using discontinuity as a means of invasive species control is described as the 'connectivity conundrum' (Zielinski et al., 2020). The potential for barriers to exclude invasive species may be influenced by personality, with higher levels of boldness and activity, and low levels of sociability, being potential indicators of a greater probability of successful passage (Hirsch et al., 2017). However, despite the use of exclusion barriers in invasive species management, understanding of how personality influences barrier passage behaviour remains limited. This information is important for accurate predictions of the spread of invasive species in fragmented habitats, and for effective implementation of exclusion barriers as a management technique (Hirsch et al., 2017).

This study investigated how personality influences the behaviour and ability of an aquatic invasive species to overcome an impediment to movement. Using the American signal crayfish as a

model, we investigated the role of personality on passage behaviour at a gauging weir, a low-head partial barrier that is a common feature in anthropogenically fragmented fluvial landscapes. Signal crayfish are the most widespread invasive crayfish in Europe (Kouba et al., 2014), and their introduction has an overwhelmingly negative impact on native biodiversity (Crawford et al., 2006; Dunn et al., 2009; Edmonds et al., 2011) and hydromorphology (Faller et al., 2016; Harvey et al., 2014). Repeatable personality traits, including boldness, activity and foraging voracity, have previously been observed in signal crayfish (Galib et al., 2022; Taylor, 2016). Additionally, recent research has demonstrated that behavioural syndromes (namely activity–distance moved and boldness–exploration–climbing syndromes) influence the dispersal of signal crayfish in continuous habitats (Galib et al., 2022). Exclusion barriers limit the movement of invasive crayfish in situ (Rosewarne et al., 2013) and in laboratory conditions (Frings et al., 2013; Kerr et al., 2021), and their intentional use is likely to be an important tool in integrated pest management strategies (Krieg & Zenker, 2020). Understanding the mechanisms that underpin barrier passage behaviour of signal crayfish is vital for effective management.

To understand the relationship between personality and barrier passage behaviour, we characterized the personality of signal crayfish by (1) quantifying the repeatability of boldness (latency to emerge from refuge after simulated danger), activity (distance moved in an open field environment) and sociability (tendency to gravitate towards conspecifics) and (2) identifying the presence of behavioural syndromes based on correlations between personality traits. Thereafter, we determined how personality influenced the behaviour of signal crayfish at a low-head weir by quantifying (1) motivation and (2) passage success under experimental conditions. Following the theoretical predictions proposed by Hirsch et al. (2017), we expected that bolder, more active and less sociable individuals would exhibit higher levels of motivation, and therefore an increased likelihood of successful barrier passage. Bolder individuals may be more likely to interact with novel environments such as the barrier, and boldness is known to be associated with a greater dispersal tendency (Galib et al., 2022). Similarly, Thorlacius et al. (2015) demonstrated that activity is an important predictor of dispersal, and the greater dispersal potential of more active individuals is likely to lead to increased interaction with the barrier and a higher probability of passage success. Less sociable individuals are known to disperse greater distances (Cote, Fogarty, et al., 2010), and in this case may be more motivated to pass the barrier to move into an area with a low density of conspecifics.

## METHODS

### *Crayfish Collection and Husbandry*

Signal crayfish ( $N = 90$ ) were collected from the River Barle, Somerset, U.K. (51°10'67.3"N, 3°65'77.7"W), between 11 August and 1 September 2020 using a combination of artificial refuge traps (ARTs) and hand surveying. ART catches tend to be less sex- and size-biased than traditional baited traps (Green et al., 2018) and ARTs have been used seasonally to control signal crayfish populations on the River Barle since 2015. Hand surveys were conducted in an upstream direction, focusing on areas of low flow (glides or pools), by overturning cobbles and small boulders and searching the exposed area for crayfish. Once captured, crayfish were held in cooled transport tanks with water from the source site, before being transported to the International Centre for Eco-hydraulics Research Facility, University of Southampton Boldrewood Campus. On arrival in the laboratory, each crayfish was weighed, and the carapace and chela length were recorded. The sex of each crayfish was ascertained, after which each individual was

marked with three unique identifiers to enable them to be tracked during the study: (1) number written on the carapace using an oil-based permanent marker (as described in [Ramalho et al., 2010](#)); (2) pattern punctured in the uropods using a needle (as described in [Guan, 1997](#)); and (3) a passive integrated transponder (PIT) tag attached to the carapace using cyanoacrylate glue (as in [Kerr et al., 2021](#)). Crayfish were then held for at least 24 h prior to use in behavioural assays. To reduce the risk of aggressive interactions crayfish were separated by sex and held together in two 1000-litre holding tanks (aerated and filtered with 75% weekly water change) with an excess of shelters (PVC pipes) at a mean temperature of 16.1 °C (SD = 1.4).

### Personality Characterization

Between 14 August and 8 September 2020, crayfish were subjected to three different behavioural assays designed to quantify individual boldness, activity and sociability. To assess the repeatability of these behaviours, each crayfish was tested twice (as in [Cote, Clobert, et al., 2010](#); [Taylor, 2016](#)), with a minimum of 24 h between assays of the same type. Boldness and activity assays were conducted consecutively and were not conducted within 24 h of the separate sociability tests. Assays were conducted overnight (1900–0600) in glass tanks (650 × 180 mm and 290 mm high) containing water from the holding tanks ([Fig. 1](#)) that was changed between each test. To prevent visual disturbance during the trials, the arena was surrounded by black plastic sheeting and crayfish were observed remotely using infrared security cameras.

As crayfish behaviour is known to change both pre- and post-moult ([Bacqué-Cazenave et al., 2019](#); [Chang, 1995](#)), any individual tested within 1 week of moulting was excluded from further testing and analysis. Crayfish that moulted early in the experiment ( $N = 8$ ) were separated from the main population for at least 1 week or until the carapace had completely hardened, at which point they were returned to the main population and subjected to the behavioural assays as described. Thirty-four individuals moulted during the experiment, resulting in a final sample size of 56 individuals (25 males and 31 females; mean  $\pm$  SD mass =  $14.98 \pm 4.49$  g, carapace length =  $36.52 \pm 3.36$  mm, chela length =  $27.45 \pm 4.71$  mm).

### Boldness

Crayfish were placed in a submerged shelter (PVC pipe with diameter 65 mm) positioned at one end of the experimental arena ([Fig. 1a](#)). The open end of the shelter was sealed using a piece of 12 mm thick plywood, secured by a bucket containing several large rocks. The individual was allowed to acclimate for 5 min, after which the seal was removed by lifting the plywood and the bucket vertically. A stimulus simulating danger was presented immediately after unsealing the shelter by rattling a pair of stainless steel tongs (length = 360 mm) against the open end (opposite sides of the shelter hit five times each in quick succession). Boldness was measured as the time taken for the entire carapace to emerge from the shelter (s), with shorter latencies reflecting higher levels of boldness.

### Activity

Activity was measured using an open-field test, whereby crayfish were allowed to move freely throughout the arena for 15 min once they had emerged from the shelter in the boldness assay. The arena was divided laterally into 50 mm sections ([Fig. 1a](#)), and activity was recorded as the number of times the individual moved between sections. A single movement between sections was recorded each time the joint of the carapace and the abdomen fully crossed a line on the base of the arena. It is possible that this measure of activity may have been influenced by exploratory

behaviour, as crayfish were tested in a novel environment ([Réale et al., 2007](#)). However, [Perals et al. \(2017\)](#) demonstrated that activity is not correlated with exploratory behaviours in open-field tests, and numerous studies have successfully measured activity using this approach ([Cote, Fogarty, et al., 2010](#); [Hirsch et al., 2017](#); [Taylor, 2016](#)), suggesting this measure accurately reflects activity.

### Sociability

Crayfish sociability was assessed using the methods established by [Taylor \(2016\)](#). The focal crayfish was placed in the centre of the experimental arena and held in an upturned PVC pipe. A companion crayfish was then placed into a perforated plastic container (120 × 120 mm and 150 mm high) at one end of the arena, and a rock of similar shape and size was placed in an identical container at the opposite end ([Fig. 1b](#)). Companions were randomly selected from the group of individuals that matched the sex and length (carapace length within 10%) of the focal individual, as both factors are known to influence the likelihood of antagonistic interactions ([Ahvenharju & Ruohonen, 2007](#); [Sippel et al., 1995](#)). Given that personality traits should be consistent over time and context ([Sih et al., 2004](#)), the order in which crayfish experienced the trials (i.e. either as a companion or focal first) was not controlled. The locations of the companion and rock relative to the focal individual were randomized between trials. After a 5 min acclimation period, the focal individual was released and allowed to move freely through the experimental arena for 10 min. A 100 mm neutral zone was established in the centre of the tank, and the time spent on each side of the neutral zone was recorded during the trial. Sociability was then calculated as log (time spent with companion crayfish/time spent with rock).

### Passage Behaviour

#### Experimental set-up and procedure

To assess crayfish passage behaviour, a model Crump weir (2.38 × 0.60 m and 0.34 m high) was installed in a recirculating flume (16 × 0.60 m and 0.80 m high) at the International Centre for Ecohydraulics Research Facility, University of Southampton Boldrewood Campus ([Fig. 2a](#)). A Crump weir was selected as an example of a low-head structure commonly installed in the U.K. to gauge river flow ([National River Flow Archive, 2022](#)) and known to impede the movement of native aquatic species ([Russon et al., 2011](#); [Vowles et al., 2015](#)). The experimental area was delineated by screens placed 1 m upstream and downstream of the leading edge and foot of the weir, respectively. The base of the flume was covered with gravel to provide a seminatural substrate to a depth of approximately 25 mm.

Flow velocity at the weir crest (mean = 0.68 m/s; [Fig. 2b](#)) was maintained at a constant discharge of 0.071 m<sup>3</sup>/s, and a sloped overshot weir at the downstream end of the flume was used to flood the weir and maintain a water depth of 570 mm throughout the flume. These conditions resembled those in a previous experiment in which partial barrier passage of crayfish was observed ([Kerr et al., 2021](#)). Flow velocity was measured 25 mm above the substrate at 95 locations in the experimental area using an electromagnetic flowmeter (Valeport Model 801; measurements averaged over 10 s).

The movements of crayfish within the experimental area were monitored using four PIT antennas (two coils of 2.5 mm<sup>2</sup> stranded copper wire) positioned laterally in the flume ([Fig. 2a](#)). Each antenna was connected to a detection system consisting of four external tuning units (Oregon RFID) and a single multiantenna half duplex (HDX) reader powered by a 12 V leisure battery. The PIT system was tuned and tested daily, with longitudinal detection distances ranging from 80 to 150 mm.

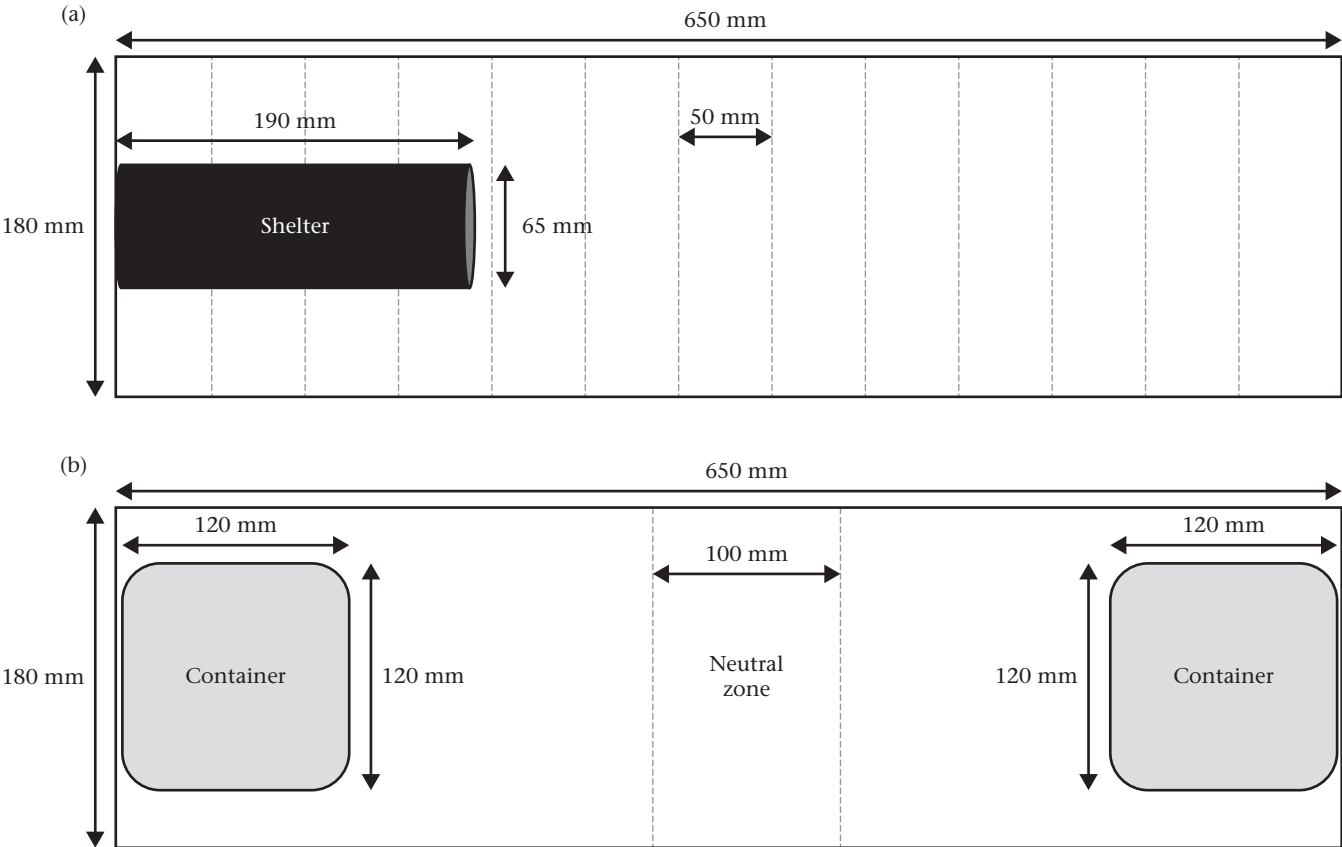


Figure 1. Plan view of experimental arenas used to assess (a) boldness and activity and (b) sociability in American signal crayfish, *Pacifastacus leniusculus*.

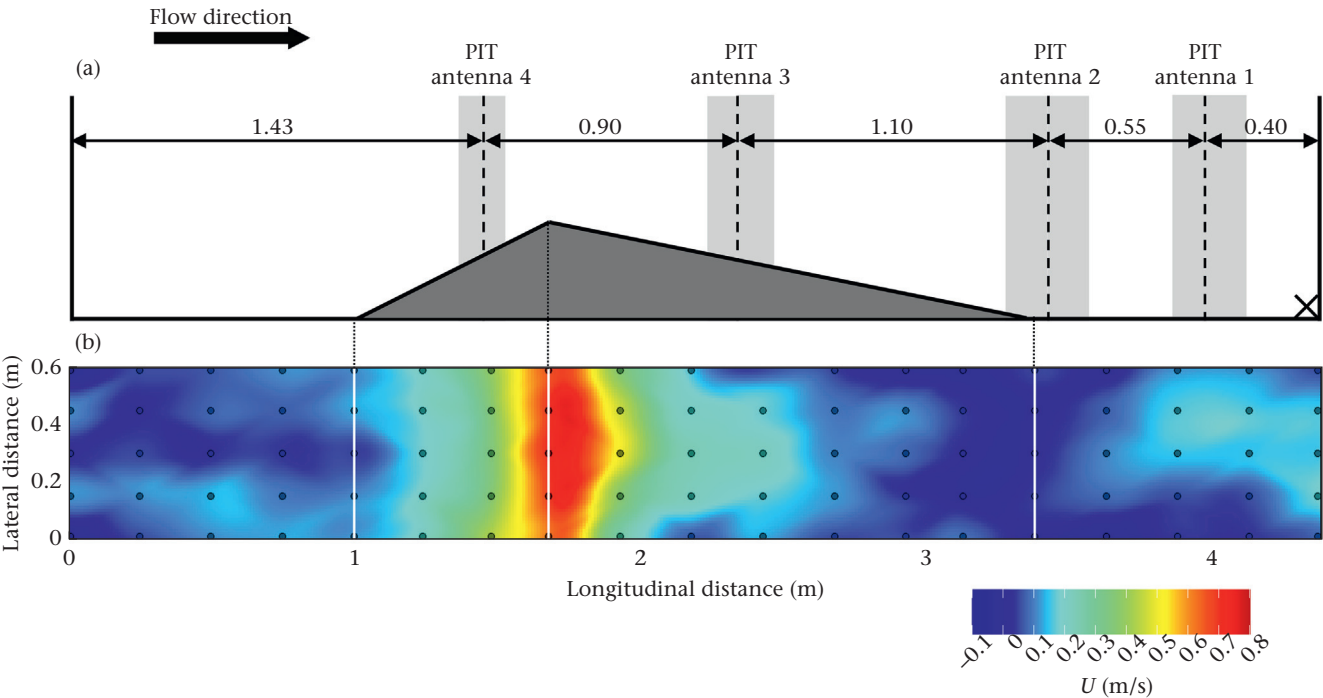


Figure 2. (a) Side view of the experimental area used to assess the behaviour of American signal crayfish at an artificial barrier, showing the model Crump weir (dark grey), PIT antennas (dashed lines), PIT antennas' detection distances (light grey shaded area) and release location of the crayfish (cross). (b) Plan view flow velocity map of the experimental area (grey circles represent locations of flow velocity measurements).



**Table 1**

Metrics used to assess the behaviour of American signal crayfish at a model Crump weir installed in a recirculatory flume at the International Centre for Ecohydraulics Research Facility, University of Southampton Boldrewood Campus

No.	Metric	Definition	Objective	GLM error structure
1	Number of weir entries	The number of times the crayfish progressed onto the weir face	Motivation	Poisson
2	Probability of attempt	Binary measure of whether the crayfish attempted to pass the weir. An attempt was defined as a detection at PIT antenna 3, as this antenna was positioned at the downstream extent of the high-velocity region created by the weir crest	Motivation	Binomial
3	Number of attempts	The number of times the crayfish attempted to pass the weir	Motivation	Quasi-Poisson
4	Time to first attempt	The time interval between the start of the trial and the first attempt to pass the weir (s)	Motivation	Quasi-Poisson
5	Maximum distance of ascent	The maximum distance moved upstream on the weir face (m)	Motivation	Gaussian
6	Passage success	Binary measure of whether the crayfish successfully passed the weir. Successful passage was defined as a detection at PIT antenna 4, as this antenna was located upstream of the weir crest	Passage success	Binomial

Barrier passage trials were conducted no sooner than 24 h after the final personality assays. Individual crayfish were held in a separate 20-litre tank for 0.5–1 h prior to the barrier passage trials, and gradually acclimated to the flume water temperature (mean  $\pm$  SD =  $22.2 \pm 1.38$  °C). Crayfish were placed in a porous container at the downstream end of the flume for an additional 30 min to acclimatize to flow conditions. Following the acclimatization period, crayfish were released at the downstream end of the experimental area (Fig. 2a). Trials were terminated once the crayfish had passed upstream beyond the weir crest or after 1 h if they failed to do so.

#### Assessment of crayfish passage behaviour

Six metrics of crayfish passage behaviour were recorded: (1) number of weir entries, (2) probability of attempt, (3) number of attempts, (4) time to first attempt, (5) maximum distance of ascent and (6) passage success (Table 1). Metrics 1 and 5 were derived from direct observations of the crayfish during the trial under dim red light, with all other metrics calculated from PIT telemetry data. Although observations of barrier passage success were not blinded for personality, each metric was defined objectively prior to the commencement of the trials (Table 1).

#### Ethical Note

This study was sanctioned by the University of Southampton Animal Welfare and Ethical Review Board (submission ID: 57510), and all capture/transport of crayfish was undertaken under licence from the Environment Agency (EP/EW098-H-261/15538/01) and Natural England (IAS permit number 39). To reduce the number of crayfish used in this study, the total to be collected was determined using a power analysis based on a previous study of crayfish passage (Daniels et al., 2022), while also accounting for expected high levels of moulting (based on the work of Taylor, 2016 and previous experience of crayfish husbandry), and uncertainty in the original data set. Given their invasive status in England, returning signal crayfish to the wild is prohibited by law (The Invasive Alien Species (Enforcement and Permitting) Order 2019), and crayfish were dispatched humanely at the end of the study by freezing at  $-14$  °C.

#### Data Analysis

As mass, carapace and chela length were closely correlated, principal components analysis was used to condense these to a single variable. The first principal component (size PC1) explained 86.5% of the variance in these size variables. As this was the only principal component with an eigenvalue greater than 1 it was selected to represent size in further analysis.

To assess the repeatability of the behaviours, adjusted repeatability values ( $R_A$ ) were calculated using the rptR package in R, which estimates  $R_A$  based on variance values extracted from mixed-effects models (Stoffel et al., 2017). Poisson error distributions were used in the mixed-effects models for boldness and activity, and a Gaussian error distribution was used for sociability. Ninety-five per cent confidence intervals (CI) were determined through parametric bootstrapping ( $N = 1000$ ) and  $P$  values were calculated through likelihood ratio tests. To identify confounding variables to be accounted for in repeatability analysis, generalized linear mixed models (GLMMs) incorporating size PC1, sex and water temperature as fixed effects, alongside the individual crayfish as a random effect, were constructed for each of the personality traits. Only one relationship between these factors and a personality trait was observed (water temperature and boldness; coefficient =  $-0.151$ , SE =  $0.055$ ,  $P = 0.006$ ), and therefore temperature was added as a fixed effect to the mixed model used to calculate the repeatability of boldness. For behaviours that were found to be repeatable, the average value for the personality trait across the two trials was used for further analysis. Conversely, behaviours that were not repeatable were not classified as personality traits and were therefore excluded from further analysis.

To identify the presence of behavioural syndromes, pairwise Kendall's correlations were conducted for each combination of personality traits. Given the non-normal distributions of the personality data, Kendall's correlations were an appropriate method of identifying relationships between personality traits. To account for multiple testing, a Bonferroni correction was applied to the critical  $P$  value.

To determine how personality traits influenced behaviour at an artificial barrier, generalized linear models (GLMs) were created for each of the key metrics. Initial GLMs contained the three personality traits, size PC1, sex and flume temperature, as predictor variables, and the error structure was varied according to the structure of the response variable (Table 1). Variance inflation factors (VIFs) were calculated for each model to assess multicollinearity between predictor variables, with values  $>5$  indicating problematic amounts of collinearity (James et al., 2013). All VIF scores were less than 2.52, suggesting the GLMs were unlikely to be affected by multicollinearity. Manual backwards selection of the initial GLMs was conducted by removing variables in descending order of significance until only significant variables remained, or Akaike's information criterion was minimized (i.e. the minimum adequate model, MAM, was identified). For all models, the assumptions of normality of residuals and homoscedasticity were assessed through visual inspection of diagnostic plots (normal Q–Q and residuals versus fitted, respectively), and no violations were found. A single outlier was removed from the activity variable (number of lines

crossed = 351,  $z$  score = 4.04), but the remaining data for this individual were retained.

## RESULTS

### Personality Characterization

#### Repeatability of behaviours

Individuals exhibited repeatable boldness (i.e. latency to emerge from shelter;  $N = 56$ ,  $R_A = 0.286$ , 95% CI = [0.071, 0.476],  $P = 0.002$ ; Fig. A1a) and activity ( $N = 56$ ,  $R_A = 0.701$ ,  $P < 0.001$ , 95% CI = [0.546, 0.806]; Fig. A1b), indicating that these behaviours were personality traits. Conversely, sociability was not repeatable over time ( $N = 56$ ,  $R_A = 0.133$ , 95% CI = [0, 0.367],  $P = 0.176$ ; Fig. A1c), and was therefore not considered a personality trait in this case.

#### Behavioural syndromes

Higher boldness (shorter emergence latency) was associated with greater activity ( $\tau = -0.281$ ,  $P = 0.002$ ; Fig. A2), demonstrating the presence of a boldness–activity syndrome.

### Passage Behaviour

#### Motivation

Aspects of crayfish motivation were associated with boldness, but not activity (Table 2). Bolder individuals were more likely to attempt to pass the weir (Fig. 3a), made more attempts (Fig. 3b), attempted more quickly (Fig. 3c) and progressed further up the weir (Fig. 3d). Activity was included in the MAM as a predictor of time to first attempt (Fig. 4) but no association was observed.

#### Passage success

Only three crayfish (5.4%) successfully passed the barrier in the study, meaning no relationship between personality and passage success was observed under the experimental conditions described (i.e. no variables retained in MAM).

## DISCUSSION

Although personality is known to influence the secondary spread of invasive species, its effects on dispersal in fragmented habitats remain poorly understood. This study quantified personality traits exhibited by American signal crayfish, an important aquatic invasive species in the U.K. (Holdich et al., 2014) and Europe (Vaeßen & Hollert, 2015), and investigated the influence of personality on passage behaviour at a low-head weir under experimental conditions. Measures of boldness and activity were repeatable over time and positively correlated, indicative of a

boldness–activity syndrome. Conversely, sociability was not repeatable and was therefore not classified as a personality trait, potentially as a result of the formation of social hierarchies in the holding tanks. Bolder individuals were more motivated to pass the experimental weir, as indicated by positive relationships between boldness and the probability of attempting to pass the weir, the number of attempts, the time to first attempt and the distance progressed up the weir face, although this did not result in higher passage success. Activity was not associated with either motivation or passage success. This study provides empirical evidence that personality influences the motivation of an invasive species to pass an anthropogenic dispersal barrier, but further work is recommended to determine how this may affect passage success in natural conditions.

The initial phase of this study quantified aspects of personality in American signal crayfish and identified the presence of behavioural syndromes in which traits are correlated. Measures of both boldness and activity were repeatable over time, indicating personality traits, while sociability was not. Although the estimate of repeatability ( $R$ ) for boldness of 0.286 is within the range of that published for other crayfish species ( $R = 0.16$ – $0.49$ ; noble crayfish, *Astacus astacus*, Vainikka et al., 2011; yabby, *Cherax destructor*, Biro et al., 2014; red swamp crayfish, *Procambarus clarkii*, Raffard et al., 2017), it was much lower than that for activity ( $R = 0.701$ ). Variation in repeatability between traits is common, and likely driven by differences in the extent to which the trait is influenced by other intrinsic and extrinsic factors (e.g. sex, age and experimental conditions; Bell et al., 2009). Indeed, Taylor (2016) found that the repeatability of activity and boldness in signal crayfish varies between populations, experimental protocol and position along the invasion gradient. Furthermore, in this study relatively low variation in water temperature (between 14.5 and 18.6 °C) influenced boldness, but not activity.

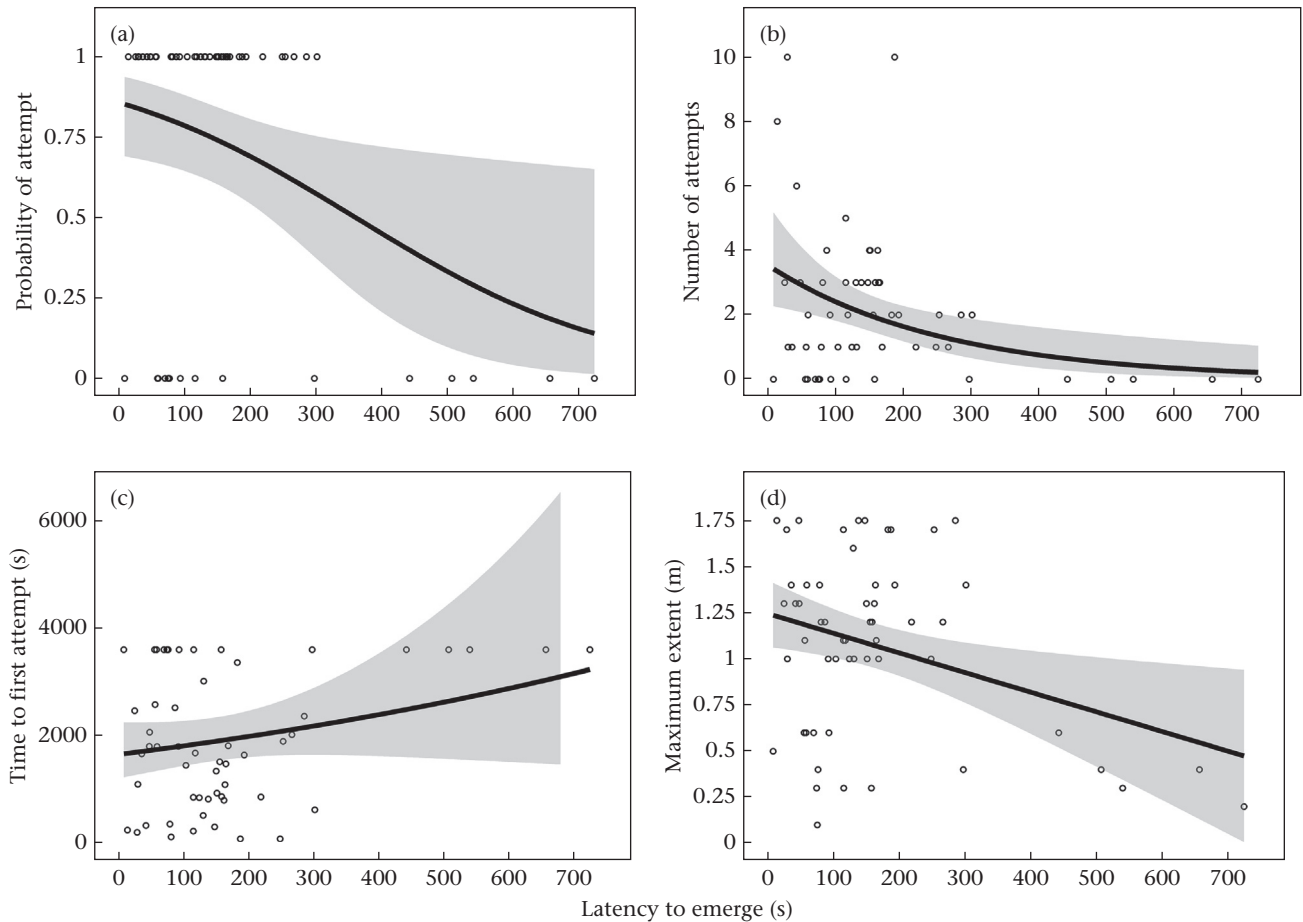
This study found no evidence for repeatability of sociability in signal crayfish. This finding is in line with Taylor (2016), but note that crayfish were kept in communal tanks prior to sociability testing in both studies. Signal crayfish are known to form social dominance hierarchies (Ahvenharju & Ruohonen, 2006, 2007), and their establishment in the holding tanks may have confounded the results of the sociability tests, with less dominant individuals avoiding potentially agonistic interactions and therefore being classified as asocial. Future research is recommended to determine the influence of social hierarchy on estimates of sociability.

The observation of a boldness–activity behavioural syndrome, as indicated by a positive correlation between the two personality traits, has not been widely documented in signal crayfish. Galib et al. (2022) found that activity (measured as time in motion) and the distance moved during the trial were not associated with boldness, although this may be because personality assays were conducted during the day in field conditions. Additionally, boldness was assessed using a direct stimulus (pressure applied to the tail) and was calculated differently for individuals classified as ‘bold’ or ‘shy’. Identification of behavioural syndromes may help predict the invasiveness of a non-native species, particularly the success of dispersal (Cote, Clobert, et al., 2010) and range expansion. For example, the co-occurrence of high boldness and activity in a behavioural syndrome may increase the likelihood of encountering anthropogenic transport vectors, and subsequently increase the probability of locating and exploiting novel resources and mates within the non-native range (Chapple et al., 2012). Furthermore, boldness and activity are associated with increased aggression and foraging voracity in signal crayfish (Pintor et al., 2008, 2009), increasing the potential to outcompete and prey on native species within the recipient ecosystems. Note that although similar designs have been used in multiple studies (e.g. Cote, Fogarty, et al., 2010;

**Table 2**  
Variables associated with the motivation of signal crayfish ( $N = 56$ ) to pass an experimental weir

Metric	Predictor variable	Coefficient	SE	$P$
Number of weir entries Probability of attempt	—	—	—	—
	Boldness	−0.007	0.003	<b>0.014</b>
	Size PC1	−0.664	0.283	<b>0.019</b>
Number of attempts Time to first attempt	Sex (male)	−1.971	0.801	<b>0.014</b>
	Boldness	−0.004	0.001	<b>0.004</b>
	Boldness	0.002	0.001	<b>0.031</b>
Maximum distance of ascent	Activity	0.005	0.002	0.069
	Boldness	−0.001	0.000	<b>0.012</b>

Variables present in the table are those retained in minimum adequate models (MAMs) derived from full GLMs. Dashes indicate that none of the predictor variables were retained in the MAM, and bold represents significant associations.



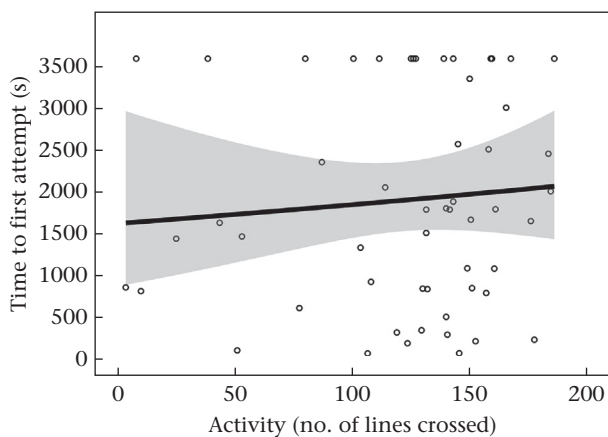
**Figure 3.** Relationships between the boldness of American signal crayfish and (a) probability of attempting to pass an experimental Crump weir, (b) the number of attempts, (c) the time to first attempt and (d) the maximum distance of ascent. Black lines show GLM predictions and grey shading denotes 95% confidence intervals.

Lothian & Lucas, 2021), boldness and activity assays conducted consecutively may not be truly independent. This may increase the likelihood of observing boldness–activity syndromes, and future research is encouraged to separate these assays fully.

The second element of this study investigated the relationship between personality and the behaviour of an invasive species at a low-head anthropogenic barrier that commonly fragments aquatic habitats. As predicted, bolder individuals were more likely to

attempt to pass, attempted to pass more quickly and more frequently, and progressed further up the weir face. As such, it is intuitive to predict that bolder and more motivated individuals are more likely to negotiate barriers in the wild. Indeed, recent studies have demonstrated that higher levels of boldness and exploratory behaviour are associated with increased passage success in brown trout, *Salmo trutta*, and American eels, *Anguilla rostrata*, respectively (Lothian & Lucas, 2021; Mensinger et al., 2021). Similar relationships have been considered for invasive fish, but only in speculative terms, with a positive relationship being predicted (e.g. mosquitofish, Cote, Fogarty, et al., 2010; round gobies, Hirsch et al., 2017). Although not observed directly in this study, the relationship between personality and motivation suggests that personality may influence passage success in crayfish as well as in teleosts, although further work is needed to confirm this relationship.

The lack of relationship between personality and passage success in this study may result from the very low number of crayfish that passed the experimental weir (5.4% of those tested). Passage in this study was substantially lower than observed in previous experiments conducted at the same laboratory with comparable weir designs and set-ups (e.g. 14% in Kerr et al., 2021 and 38.1% in Daniels et al., 2022). The source population for this study has been subjected to a consistent trapping regime since 2015 and, although the ARTs used are known to be less sex- and size-specific than conventional baited traps, this may have led to selective removal of bolder individuals, and subsequently an underrepresentation of these individuals in this experiment. Given that bolder individuals were more motivated to pass the barrier, this potential



**Figure 4.** Relationship between the activity of American signal crayfish and the time to the first attempt. Black lines show GLM predictions and grey shading denotes 95% confidence intervals.

underrepresentation may have driven the low rates of passage success. Additionally, numerous factors including interpopulation differences, environmental factors (e.g. water temperature) and variation in study design (e.g. water temperature) may drive variation in crayfish passage success (Frings et al., 2013; Rosewarne et al., 2013). Not only should intraspecific variation in behaviour, such as that associated with personality, be considered in invasive species management, but so should the range of intrinsic, extrinsic and spatiotemporal factors, such as stage of development or range expansion, population, habitat and season.

From the perspective of invasive species management, there are several important implications of this study. Mitigating the negative impacts of anthropogenic barriers on the movement of aquatic organisms represents a substantial conservation challenge, but also provides a means to limit the spread of aquatic invasive species (P. E. Jones et al., 2021b). In cases where river infrastructure presents partial barriers, they may act as ecological filters that segregate populations based on physiological (e.g. locomotory performance) and behavioural (e.g. personality) characteristics (Jones, Champneys et al., 2021). Evidence from this experimental study illustrates how elevated motivation in bolder individuals may increase the probability of negotiating low-head barriers in fragmented river systems, potentially leading to more bold individuals at the expanding edge of an invasion front compared to the invasion core. This spatial sorting of personality traits has been observed in numerous species, including round gobies (Myles-Gonzalez et al., 2015), cane toads (Gruber et al., 2017), common mynas, *Acridotheres tristis* (Burstal et al., 2020; Magory Cohen et al., 2020) and orb-weaving spiders, *Cyrtophora citricola* (Chuang & Riechert, 2022), although evidence for this phenomenon in signal crayfish is mixed (Pintor et al., 2008; Taylor, 2016). Should barrier passage contribute to spatial sorting of personality traits in signal crayfish, this may provide opportunities for the selective removal of bolder individuals (e.g. by trapping), effectively creating an evolutionary trap for individuals at the invasion front (Hale et al., 2016). This could apply a strong selective pressure against boldness, potentially reducing associated impacts (e.g. predation and competition) and rates of range expansion. Avenues of future invasive species research include further consideration of the impacts of personality-biased barrier passage at larger spatiotemporal scales, and the inclusion of personality in dispersal models (Hirsch et al., 2017).

## Author Contributions

**J.A. Daniels:** conceptualization, methodology, investigation, data curation, formal analysis, visualisation, writing—original draft, writing—review and editing; **P.S. Kemp:** conceptualization, methodology, funding acquisition, supervision, writing—review and editing. Both authors gave final approval for publication and agree to be held accountable for the work performed therein.

## Data Availability

Data published in this article are available from the University of Southampton repository at <https://doi.org/10.5258/SOTON/D2123>.

## Declaration of Interest

The authors declare they have no competing interests.

## Acknowledgments

The project was funded by the Engineering and Physical Sciences Research Council Centre for Doctoral Training in Sustainable

Infrastructure Systems (EP/L01582X/1). We thank Nicky Green for her invaluable help with collecting crayfish and advice on crayfish husbandry.

## References

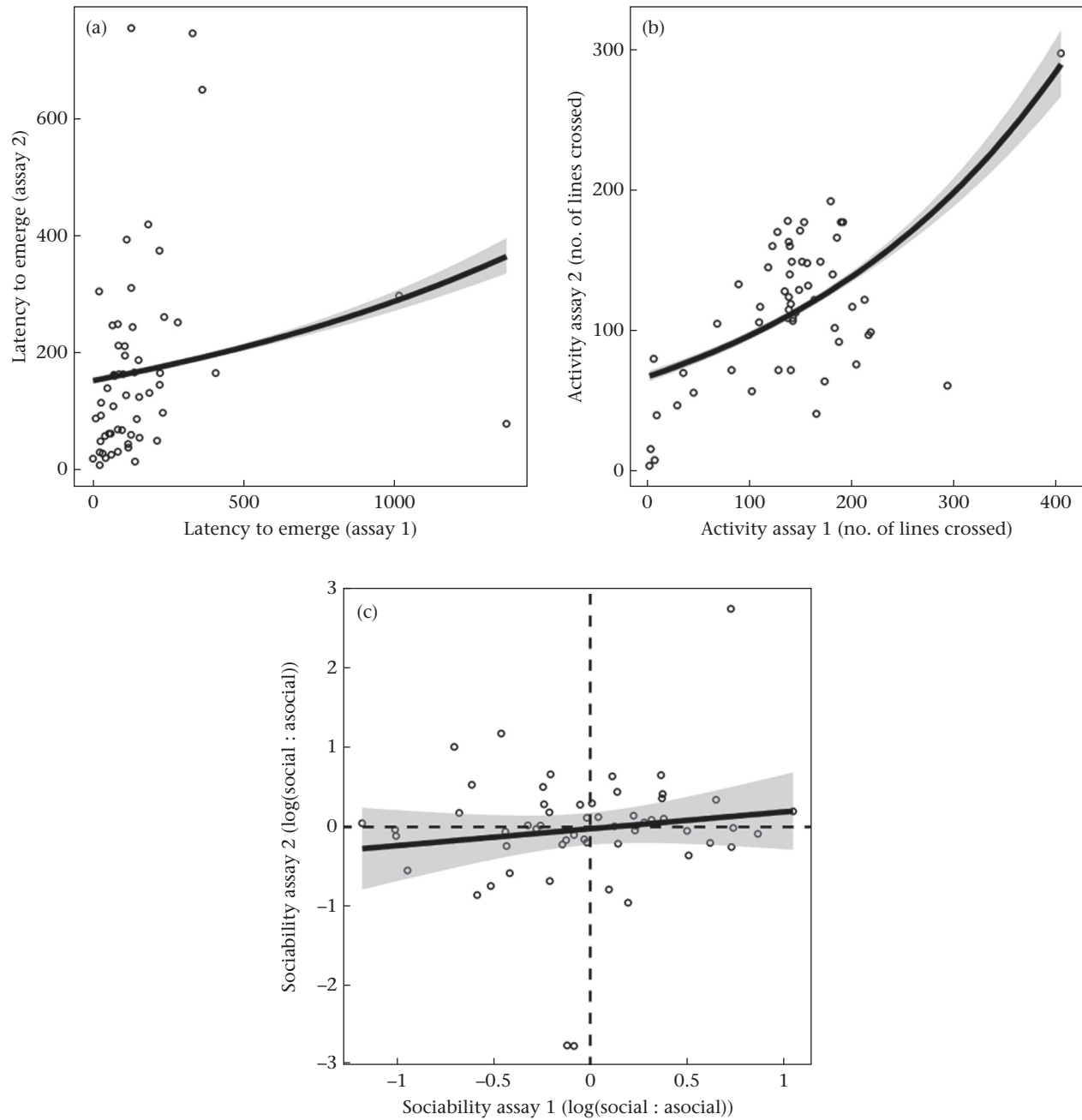
- Ahvenharju, T., & Ruohonen, K. (2006). Unequal division of food resources suggests feeding hierarchy of signal crayfish (*Pacifastacus leniusculus*) juveniles. *Aquaculture*, 259(1), 181–189. <https://doi.org/10.1016/j.aquaculture.2006.05.006>
- Ahvenharju, T., & Ruohonen, K. (2007). Agonistic behaviour of signal crayfish (*Pacifastacus leniusculus* Dana) in different social environments: Effect of size heterogeneity on growth and food intake. *Aquaculture*, 271(1), 307–318. <https://doi.org/10.1016/j.aquaculture.2007.05.004>
- Bacqu -Cazenave, J., Berthomieu, M., Cattaert, D., Fossat, P., & Delbecq, J. P. (2019). Do arthropods feel anxious during molts? *Journal of Experimental Biology*, 222(2), jeb186999. <https://doi.org/10.1242/jeb.186999>
- Belgrad, B. A., & Griffen, B. D. (2018). Personality interacts with habitat quality to govern individual mortality and dispersal patterns. *Ecology and Evolution*, 8(14), 7216–7227. <https://doi.org/10.1002/ece3.4257>
- Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., B rger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussetini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fern ndez, S., ... Zalewski, M. (2020). More than one million barriers fragment Europe's rivers. *Nature*, 588(7838), 436–441. <https://doi.org/10.1038/s41586-020-3005-2>
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, 77(4), 771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>
- Biro, P. A., Adriaenssens, B., & Sampson, P. (2014). Individual and sex-specific differences in intrinsic growth rate covary with consistent individual differences in behaviour. *Journal of Animal Ecology*, 83(5), 1186–1195. <https://doi.org/10.1111/1365-2656.12210>
- Blackburn, T. M., Bellard, C., & Ricciardi, A. (2019). Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment*, 17(4), 203–207. <https://doi.org/10.1002/fee.2020>
- Botero-Delgadillo, E., Quirici, V., Poblete, Y., Poulin, E., Kempenaers, B., & V squez, R. A. (2020). Exploratory behavior, but not aggressiveness, is correlated with breeding dispersal propensity in the highly philopatric thorn-tailed rayadito. *Journal of Avian Biology*, 51(2), Article e02262. <https://doi.org/10.1111/jav.02262>
- Brand, J. A., Martin, J. M., Tan, H., Mason, R. T., Orford, J. T., Hammer, M. P., Chapple, D. G., & Wong, B. B. M. (2021). Rapid shifts in behavioural traits during a recent fish invasion. *Behavioral Ecology and Sociobiology*, 75(9), 134. <https://doi.org/10.1007/s00265-021-03077-2>
- Burstal, J., Clulow, S., Colyvas, K., Kark, S., & Griffin, A. S. (2020). Radiotracking invasive spread: Are common mynas more active and exploratory on the invasion front? *Biological Invasions*, 22(8), 2525–2543. <https://doi.org/10.1007/s10530-020-02269-7>
- Chang, E. S. (1995). Physiological and biochemical changes during the molt cycle in decapod crustaceans: An overview. *Journal of Experimental Marine Biology and Ecology*, 193(1), 1–14. [https://doi.org/10.1016/0022-0981\(95\)00106-9](https://doi.org/10.1016/0022-0981(95)00106-9)
- Chapple, D. G., Simmonds, S. M., & Wong, B. B. M. (2012). Can behavioral and personality traits influence the success of unintentional species introductions? *Trends in Ecology & Evolution*, 27(1), 57–64. <https://doi.org/10.1016/j.tree.2011.09.010>
- Chown, S. L., Huiskes, A. H. L., Gremmen, N. J. M., Lee, J. E., Terauds, A., Crosbie, K., Frenot, Y., Hughes, K. A., Imura, S., Kiefer, K., Lebouvier, M., Raymond, B., Tsujimoto, M., Ware, C., Van de Vijver, B., & Bergstrom, D. M. (2012). Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. *Proceedings of the National Academy of Sciences*, 109(13), 4938. <https://doi.org/10.1073/pnas.1119787109>
- Chuang, A., & Riechert, S. E. (2022). Does spatial sorting explain leading edge personality types in a spider's non-native range? *Ethology*, 128(4), 317–330. <https://doi.org/10.1111/eth.13265>
- Clapperton, B. K., & Matthews, L. R. (1996). Trials of electric fencing for restricting movements of common brushtail possums, *Trichosurus vulpecula* Kerr. *Wildlife Research*, 23(5), 571–579. <https://doi.org/10.1071/WR9960571>
- Cooper, E. B., Taylor, R. W., Kelley, A. D., Marting, A. R., Boutin, S., Humphries, M. M., Dantzer, B., Lane, J. E., & McAdam, A. G. (2017). Personality is correlated with natal dispersal in North American red squirrels (*Tamiasciurus hudsonicus*). *Behaviour*, 154(9–10), 939–961. <https://doi.org/10.1163/1568539X-00003450>
- Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 383–390. <https://doi.org/10.1098/rspb.2006.3734>
- Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4065–4076. <https://doi.org/10.1098/rstb.2010.0176>
- Cote, J., Fogarty, S., Weinersmith, K., Brodin, T., & Sih, A. (2010). Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society B: Biological Sciences*, 277(1687), 1571–1579. <https://doi.org/10.1098/rspb.2009.2128>



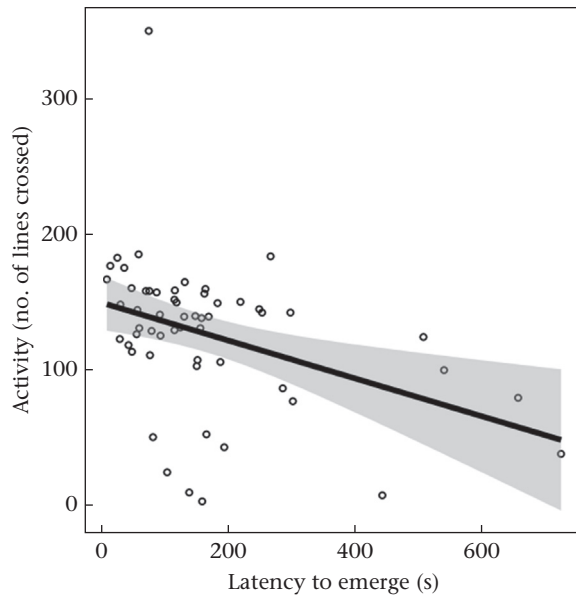
- Crawford, L., Yeomans, W. E., & Adams, C. E. (2006). The impact of introduced signal crayfish *Pacifastacus leniusculus* on stream invertebrate communities. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 16(6), 611–621. <https://doi.org/10.1002/aqc.761>
- Daniels, J. A., Kerr, J. R., & Kemp, P. S. (2022). *River infrastructure and the spread of freshwater invasive species: inferences from an experimentally-parameterised individual-based model* [Submitted manuscript].
- Denneboom, D., Bar-Massada, A., & Schwartz, A. (2021). Factors affecting usage of crossing structures by wildlife – a systematic review and meta-analysis. *Science of the Total Environment*, 777, Article 146061. <https://doi.org/10.1016/j.scitotenv.2021.146061>
- Diagne, C., Leroy, B., Vaissière, A.-C., Gozlan, R. E., Roiz, D., Jarić, I., Salles, J.-M., Bradshaw, C. J. A., & Courchamp, F. (2021). High and rising economic costs of biological invasions worldwide. *Nature*, 592(7855), 571–576. <https://doi.org/10.1038/s41586-021-03405-6>
- Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society Series B: Biological Sciences*, 270(1516), 741–747. <https://doi.org/10.1098/rspb.2002.2300>
- Dixon, J. D., Oli, M. K., Wooten, M. C., Eason, T. H., McCown, J. W., & Cunningham, M. W. (2007). Genetic consequences of habitat fragmentation and loss: The case of the Florida black bear (*Ursus americanus floridanus*). *Conservation Genetics*, 8(2), 455–464. <https://doi.org/10.1007/s10592-006-9184-z>
- Dunn, J. C., McClymont, H. E., Christmas, M., & Dunn, A. M. (2009). Competition and parasitism in the native white clawed crayfish *Austropotamobius pallipes* and the invasive signal crayfish *Pacifastacus leniusculus* in the UK. *Biological Invasions*, 11(2), 315–324. <https://doi.org/10.1007/s10530-008-9249-7>
- Edmonds, N. J., Riley, W. D., & Maxwell, D. L. (2011). Predation by *Pacifastacus leniusculus* on the intra-gravel embryos and emerging fry of *Salmo salar*. *Fisheries Management and Ecology*, 18(6), 521–524. <https://doi.org/10.1111/j.1365-2400.2011.00797.x>
- Faller, M., Harvey, G. L., Henshaw, A. J., Bertoldi, W., Bruno, M. C., & England, J. (2016). River bank burrowing by invasive crayfish: Spatial distribution, biophysical controls and geomorphic significance. *Science of the Total Environment*, 569–570, 1190–1200. <https://doi.org/10.1016/j.scitotenv.2016.06.194>
- Feeley, K. J., & Rehm, E. M. (2012). Amazon's vulnerability to climate change heightened by deforestation and man-made dispersal barriers. *Global Change Biology*, 18(12), 3606–3614. <https://doi.org/10.1111/gcb.12012>
- Frings, R. M., Vaeßen, S. C. K., Groß, H., Roger, S., Schütttrumpf, H., & Hollert, H. (2013). A fish-passable barrier to stop the invasion of non-indigenous crayfish. *Biological Conservation*, 159, 521–529. <https://doi.org/10.1016/j.biocon.2012.12.014>
- Galib, S. M., Sun, J., Twiss, S. D., & Lucas, M. C. (2022). Personality, density and habitat drive the dispersal of invasive crayfish. *Scientific Reports*, 12(1), 1114. <https://doi.org/10.1038/s41598-021-04228-1>
- Green, N., Bentley, M., Stebbing, P., Andreou, D., & Britton, R. (2018). Trapping for invasive crayfish: Comparisons of efficacy and selectivity of baited traps versus novel artificial refuge traps. *Knowledge and Management of Aquatic Ecosystems*, 2018, 15. <https://doi.org/10.1051/kmae/2018007>
- Gruber, J., Brown, G., Whiting, M. J., & Shine, R. (2017). Geographic divergence in dispersal-related behaviour in cane toads from range-front versus range-core populations in Australia. *Behavioral Ecology and Sociobiology*, 71(2), 38. <https://doi.org/10.1007/s00265-017-2266-8>
- Guan, R. Z. (1997). An improved method for marking crayfish. *Crustaceana*, 70(6), 641–652. <https://doi.org/10.1163/156854097X00104>
- Hale, R., Morrongiello, J. R., & Sweater, S. E. (2016). Evolutionary traps and range shifts in a rapidly changing world. *Biology Letters*, 12(6), Article 20160003. <https://doi.org/10.1098/rsbl.2016.0003>
- Harvey, G. L., Henshaw, A. J., Moorhouse, T. P., Clifford, N. J., Holah, N., Grey, J., & Macdonald, D. W. (2014). Invasive crayfish as drivers of fine sediment dynamics in rivers: Field and laboratory evidence. *Earth Surface Processes and Landforms*, 39(2), 259–271. <https://doi.org/10.1002/esp.3486>
- Hermoso, V., Januchowski-Hartley, S. R., & Linke, S. (2015). Systematic planning of disconnection to enhance conservation success in a modified world. *Science of the Total Environment*, 536, 1038–1044. <https://doi.org/10.1016/j.scitotenv.2015.07.120>
- Hill, J. E., DeVault, T. L., & Belant, J. L. (2019). Cause-specific mortality of the world's terrestrial vertebrates. *Global Ecology and Biogeography*, 28(5), 680–689. <https://doi.org/10.1111/geb.12881>
- Hirsch, P. E., Thorlacius, M., Brodin, T., & Burkhardt-Holm, P. (2017). An approach to incorporate individual personality in modeling fish dispersal across in-stream barriers. *Ecology and Evolution*, 7(2), 720–732. <https://doi.org/10.1002/ece3.2629>
- Holdich, D. M., James, J., Jackson, C., & Peay, S. (2014). The North American signal crayfish, with particular reference to its success as an invasive species in Great Britain. *Ethology Ecology & Evolution*, 26(2–3), 232–262. <https://doi.org/10.1080/03949370.2014.903380>
- Hudina, S., Zganec, K., & Hock, K. (2015). Differences in aggressive behaviour along the expanding range of an invasive crayfish: An important component of invasion dynamics. *Biological Invasions*, 17(11), 3101–3112. <https://doi.org/10.1007/s10530-015-0936-x>
- Ito, T. Y., Lhagvasuren, B., Tsunekawa, A., Shinoda, M., Takatsuki, S., Buuveibaatar, B., & Chimeddorj, B. (2013). Fragmentation of the habitat of wild ungulates by anthropogenic barriers in Mongolia. *PLoS One*, 8(2), Article e56995. <https://doi.org/10.1371/journal.pone.0056995>
- James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). *An introduction to statistical learning: with applications in R*. Springer.
- Jones, J., Börger, L., Tummars, J., Jones, P., Lucas, M., Kerr, J., Kemp, P., Bizzi, S., Consuegra, S., Marcello, L., Vowles, A., Belletti, B., Verspoor, E., Van de Bund, W., Gough, P., & García de Leaniz, C. (2019). A comprehensive assessment of stream fragmentation in Great Britain. *Science of the Total Environment*, 673, 756–762. <https://doi.org/10.1016/j.scitotenv.2019.04.125>
- Jones, P. E., Champneys, T., Vevers, J., Börger, L., Svendsen, J. C., Consuegra, S., Jones, J., & García de Leaniz, C. (2021). Selective effects of small barriers on river-resident fish. *Journal of Applied Ecology*, 58(7), 1487–1498. <https://doi.org/10.1111/1365-2664.13875>
- Jones, P. E., Tummars, J. S., Galib, S. M., Woodford, D. J., Hume, J. B., Silva, L. G. M., Braga, R. R., García de Leaniz, C., Vitale, J. R. S., Herder, J. E., & Lucas, M. C. (2021). The use of barriers to limit the spread of aquatic invasive animal species: A global review. *Frontiers in Ecology and Evolution*, 9, 43. <https://doi.org/10.3389/fevo.2021.611631>
- Juette, T., Cucherousset, J., & Cote, J. (2014). Animal personality and the ecological impacts of freshwater non-native species. *Current Zoology*, 60(3), 417–427. <https://doi.org/10.1093/czoolo/60.3.417>
- Kerby, J. L., Riley, S. P. D., Kats, L. B., & Wilson, P. (2005). Barriers and flow as limiting factors in the spread of an invasive crayfish (*Procambarus clarkii*) in southern California streams. *Biological Conservation*, 126(3), 402–409. <https://doi.org/10.1016/j.biocon.2005.06.020>
- Kerr, J. R., Vowles, A. S., Crabb, M. C., & Kemp, P. S. (2021). Selective fish passage: Restoring habitat connectivity without facilitating the spread of a non-native species. *Journal of Environmental Management*, 279, Article 110908. <https://doi.org/10.1016/j.jenvman.2020.110908>
- Kouba, A., Petrussek, A., & Kozák, P. (2014). Continental-wide distribution of crayfish species in Europe: Update and maps. *Knowledge and Management of Aquatic Ecosystems*, 413, 5. <https://doi.org/10.1051/kmae/2014007>
- Krieg, R., & Zenker, A. K. (2020). A review of the use of physical barriers to stop the spread of non-indigenous crayfish species. *Reviews in Fish Biology and Fisheries*, 1–13. <https://doi.org/10.1007/s11160-020-09606-y>
- Liao, H., Pal, R. W., Niinemets, Ü., Bahn, M., Cerabolini, B. E. L., & Peng, S. (2021). Different functional characteristics can explain different dimensions of plant invasion success. *Journal of Ecology*, 109(3), 1524–1536. <https://doi.org/10.1111/1365-2745.13575>
- Lothian, A. J., & Lucas, M. C. (2021). The role of individual behavioral traits on fishway passage attempt behavior. *Ecology and Evolution*, 11(17), 11974–11990. <https://doi.org/10.1002/ece3.7964>
- Magory Cohen, T., Kumar, R. S., Nair, M., Hauber, M. E., & Dor, R. (2020). Innovation and decreased neophobia drive invasion success in a widespread avian invader. *Animal Behaviour*, 163, 61–72. <https://doi.org/10.1016/j.anbehav.2020.02.012>
- 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*, 58(12), 2760–2769. <https://doi.org/10.1111/1365-2664.14009>
- Michelangeli, M., Smith, C. R., Wong, B. B. M., & Chapple, D. G. (2017). Aggression mediates dispersal tendency in an invasive lizard. *Animal Behaviour*, 133, 29–34. <https://doi.org/10.1016/j.anbehav.2017.08.027>
- Miller, A. W., & Ruiz, G. M. (2014). Arctic shipping and marine invaders. *Nature Climate Change*, 4(6), 413–416. <https://doi.org/10.1038/nclimate2244>
- Moseby, K. E., & O'Donnell, E. (2003). Reintroduction of the greater bilby, *Macrotis lagotis* (Reid) (Marsupialia: Thylacomyidae), to northern South Australia: Survival, ecology and notes on reintroduction protocols. *Wildlife Research*, 30(1), 15–27. <https://doi.org/10.1071/WR02012>
- Myles-Gonzalez, E., Burness, G., Yavno, S., Rooke, A., & Fox, M. G. (2015). To boldly go where no goby has gone before: Boldness, dispersal tendency, and metabolism at the invasion front. *Behavioral Ecology*, 26(4), 1083–1090. <https://doi.org/10.1093/beheco/arv050>
- National River Flow Archive. (2022). Search Data—National River Flow Archive. <https://nrfa.ceh.ac.uk/data/search>
- O'Connor, J. E., Duda, J. J., & Grant, G. E. (2015). 1000 dams down and counting. *Science*, 348(6234), 496–497. <https://doi.org/10.1126/science.aaa9204>
- Perals, D., Griffin, A. S., Bartomeus, I., & Sol, D. (2017). Revisiting the open-field test: What does it really tell us about animal personality? *Animal Behaviour*, 123, 69–79. <https://doi.org/10.1016/j.anbehav.2016.10.006>
- Pintor, L. M., Sih, A., & Bauer, M. L. (2008). Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. *Oikos*, 117(11), 1629–1636. <https://doi.org/10.1111/j.1600-0706.2008.16578.x>
- Pintor, L. M., Sih, A., & Kerby, J. L. (2009). Behavioral correlations provide a mechanism for explaining high invader densities and increased impacts on native prey. *Ecology*, 90(3), 581–587. <https://doi.org/10.1890/08-0552.1>
- Quell, F., Schratzberger, M., Beauchard, O., Bruggeman, J., & Webb, T. (2021). Biological trait profiles discriminate between native and non-indigenous marine invertebrates. *Aquatic Invasions*, 16(4), 571–600. <https://doi.org/10.3391/ai.2021.16.4.01>
- Raffard, A., Lecerf, A., Cote, J., Buoro, M., Lassus, R., & Cucherousset, J. (2017). The functional syndrome: Linking individual trait variability to ecosystem functioning. *Proceedings of the Royal Society B: Biological Sciences*, 284(1868), Article 20171893. <https://doi.org/10.1098/rspb.2017.1893>
- Ramalho, R., McClain, R., & Anastácio, P. (2010). An effective and simple method of temporarily marking crayfish. *Freshwater Crayfish*, 17, 57–60. <https://doi.org/10.5869/fc.2010.v17.57>

- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
- Rehage, J. S., Cote, J., & Sih, A. (2016). The role of dispersal behaviour and personality in post-establishment spread. In D. Sol, & J. S. Weis (Eds.), *Biological invasions and animal behaviour* (pp. 96–116). Cambridge University Press. <https://doi.org/10.1017/CBO9781139939492.008>
- Ricciardi, A. (2007). Are modern biological invasions an unprecedented form of global change? *Conservation Biology*, 21(2), 329–336. <https://doi.org/10.1111/j.1523-1739.2006.00615.x>
- Rosewarne, P., Piper, A., Wright, R., & Dunn, A. (2013). Do lowhead riverine structures hinder the spread of invasive crayfish? Case study of signal crayfish (*Pacifastacus leniusculus*) movements at a flow gauging weir. *Management of Biological Invasions*, 4, 273–282. <https://doi.org/10.3391/mbi.2013.4.4.02>
- Russon, I. J., Kemp, P. S., & Lucas, M. C. (2011). Gauging weirs impede the upstream migration of adult river lamprey *Lampetra fluviatilis*. *Fisheries Management and Ecology*, 18(3), 201–210. <https://doi.org/10.1111/j.1365-2400.2010.00778.x>
- Seebens, H., Bacher, S., Blackburn, T. M., Capinha, C., Dawson, W., Dullinger, S., Genovesi, P., Hulme, P. E., van Kleunen, M., Kühn, I., Jeschke, J. M., Lenzner, B., Liebhold, A. M., Pattison, Z., Pergl, J., Pyšek, P., Winter, M., & Essl, F. (2021). Projecting the continental accumulation of alien species through to 2050. *Global Change Biology*, 27(5), 970–982. <https://doi.org/10.1111/gcb.15333>
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grappow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., ... Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8(1), Article 14435. <https://doi.org/10.1038/ncomms14435>
- Sheer, M. B., & Steel, E. A. (2006). Lost watersheds: Barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and lower Columbia river basins. *Transactions of the American Fisheries Society*, 135(6), 1654–1669. <https://doi.org/10.1577/T05-221.1>
- Shepard, D. B., Kuhns, A. R., Dreslik, M. J., & Phillips, C. A. (2008). Roads as barriers to animal movement in fragmented landscapes. *Animal Conservation*, 11(4), 288–296. <https://doi.org/10.1111/j.1469-1795.2008.00183.x>
- Short, J., & Turner, B. (2000). Reintroduction of the burrowing bettong *Bettongia lesueur* (Marsupialia: Potoroidae) to mainland Australia. *Biological Conservation*, 96(2), 185–196. [https://doi.org/10.1016/S0006-3207\(00\)00067-7](https://doi.org/10.1016/S0006-3207(00)00067-7)
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378. <https://doi.org/10.1016/j.tree.2004.04.009>
- Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15(3), 278–289. <https://doi.org/10.1111/j.1461-0248.2011.01731.x>
- Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., Aarestrup, K., Pompeu, P. S., O'Brien, G. C., Braun, D. C., Burnett, N. J., Zhu, D. Z., Fjeldstad, H.-P., Forseth, T., Rajaratnam, N., Williams, J. G., & Cooke, S. J. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, 19(2), 340–362. <https://doi.org/10.1111/faf.12258>
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, 28(1), 58–66. <https://doi.org/10.1016/j.tree.2012.07.013>
- Sippel, J., Figler, M. H., & Peeke, H. V. S. (1995). Prior residence effects in shelter defense in adult signal crayfish (*Pacifastacus leniusculus* (Dana)): Results in same- and mixed-sex Dyads. *Crustaceana*, 68(8), 873–881. <https://doi.org/10.1163/156854095X02078>
- Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8(11), 1639–1644. <https://doi.org/10.1111/2041-210X.12797>
- Taylor, N. G. (2016). *Why are invaders invasive? Development of tools to understand the success and impact of invasive species* (Ph.D. thesis). University of Leeds <https://etheses.whiterose.ac.uk/15633/>
- Thorlacius, M., Hellström, G., & Brodin, T. (2015). Behavioral dependent dispersal in the invasive round goby *Neogobius melanostomus* depends on population age. *Current Zoology*, 61(3), 529–542. <https://doi.org/10.1093/czoolo/61.3.529>
- Vaeßen, S., & Hollert, H. (2015). Impacts of the North American signal crayfish (*Pacifastacus leniusculus*) on European ecosystems. *Environmental Sciences Europe*, 27(1), 33. <https://doi.org/10.1186/s12302-015-0065-2>
- Vainikka, A., Rantala, M. J., Niemelä, P., Hirvonen, H., & Kortet, R. (2011). Boldness as a consistent personality trait in the noble crayfish, *Astacus astacus*. *Acta Ethologica*, 14(1), 17–25. <https://doi.org/10.1007/s10211-010-0086-1>
- Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P. E., & partners, D. (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, 8(3), 135–144. <https://doi.org/10.1890/080083>
- Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14(7), 702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Vilà, M., & Hulme, P. E. (2017). Non-native species, ecosystem services, and human well-being. In M. Vilà, & P. E. Hulme (Eds.), *Impact of Biological Invasions on Ecosystem Services* (pp. 1–14). Springer International Publishing. [https://doi.org/10.1007/978-3-319-45121-3\\_1](https://doi.org/10.1007/978-3-319-45121-3_1)
- Vilizzi, L., Copp, G. H., Hill, J. E., Adamovich, B., Aislabie, L., Akin, D., Al-Faisal, A. J., Almeida, D., Azmai, M. N. A., Bakiu, R., Bellati, A., Bernier, R., Bies, J. M., Bilge, G., Branco, P., Bui, T. D., Canning-Clode, J., Cardoso Ramos, H. A., Castellanos-Galindo, G. A., ... Clarke, S. (2021). A global-scale screening of non-native aquatic organisms to identify potentially invasive species under current and future climate conditions. *Science of the Total Environment*, 788, Article 147868. <https://doi.org/10.1016/j.scitotenv.2021.147868>
- Vowles, A. S., Don, A. M., Karageorgopoulos, P., Worthington, T. A., & Kemp, P. S. (2015). Efficiency of a dual density studded fish pass designed to mitigate for impeded upstream passage of juvenile European eels (*Anguilla anguilla*) at a model Crump weir. *Fisheries Management and Ecology*, 22(4), 307–316. <https://doi.org/10.1111/fme.12128>
- Zielinski, D. P., McLaughlin, R. L., Pratt, T. C., Goodwin, R. A., & Muir, A. M. (2020). Single-Stream recycling inspires selective fish passage solutions for the connectivity conundrum in aquatic ecosystems. *BioScience*, 70(10), 871–886. <https://doi.org/10.1093/biosci/biaa090>

## Appendix



**Figure A1.** Repeatability of (a) boldness, (b) activity and (c) sociability in American signal crayfish, displayed as the relationship between trait values in the first and second assays. Black lines represent GLM predictions, with grey shaded areas representing 95% confidence intervals.



**Figure A2.** Relationship between boldness and activity of American signal crayfish, indicating the presence of a boldness - activity syndrome. The black line represents GLM predictions, with grey shaded areas representing 95% confidence intervals.