



Shifting the focus from species to individuals in invasion biology: individual differences in jumping behaviour

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Dispersal is critical to population persistence, colonization and connectivity which are all critical components of invasive success. While individual propensity to disperse varies within populations, the underlying mechanisms promoting individual dispersal remain unclear. Collectively, dispersal is influenced by the environment and individual phenotype. Here we investigated individual dispersal propensity in the Trinidadian guppy, *Poecilia reticulata*, and related individual variation in dispersal behaviour to phenotype and social/environmental conditions. Namely, we addressed the effect of sex ratio (social/environmental factor) on the tendency for individuals to disperse across physical barriers via jumping behaviour. Jumping is vital for the dispersal of many aquatic species and has been anecdotally linked to the guppy's global invasive success. We found similar jumping behaviour for males and females, with population sex ratio not influencing the magnitude of male or female dispersal. Further, we found consistent among-individual variation in jumping probability; individual differences explained 17.46% and 7.92% of total variation in jumping probability for males and females, respectively. These results strongly indicate that sex ratio does not influence jumping behaviour, suggesting that species invasions are mediated by a nonrandom subset of individuals with greater dispersal tendencies. Overall, this study stresses the need to move the focus of invasion biology from the species level to incorporate information on individual variation in behaviour.

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The abundance of freshwater vertebrate populations has declined, on average, by 84% since 1970 (WWF, 2020). Invasive species are considered a primary threat to these highly diverse ecosystems (Albert et al., 2021; Reid et al., 2019). As species introductions become more frequent in the future, the impacts of invasive species are likely to increase (Hulme, 2009; Reid et al., 2019). It is therefore important that key factors contributing to invasive success are identified. A critical step in the invasion process is the increase in the invader's non-native distribution via dispersal (Deacon & Magurran, 2016). In ecology, dispersal can be defined as the movement of individuals into previously unoccupied areas (Ronce, 2007). For freshwater fish, jumping is vital for increasing non-native distribution and underlies the success of several aquatic species invasions (Deacon & Magurran, 2016; Jones et al., 2021). However, dispersal via jumping is an energetically

costly and potentially risky behaviour (Howard, 1960; Sulak et al., 2002). It may therefore be advantageous for individuals to disperse only when exposed to unfavourable abiotic or biotic conditions (Railsback et al., 1999). Here, we examined the role of phenotype and social context in driving the dispersal of the widely invasive Trinidadian guppy, *Poecilia reticulata*.

Within a population, certain individuals are more likely to disperse than others (Clobert et al., 2012; Comte & Olden, 2018; Galib et al., 2022). The possession of particular phenotypic traits can predispose individuals to disperse independently of environmental stimuli (innate dispersal; Belthoff & Dufty, 1998; Ritchison et al., 1992). Other aspects of an individual's phenotype can also contribute to dispersal indirectly (Clobert et al., 2012; Dobson, 1982; Trochet et al., 2016). For example, in mating systems where females control mating, but males are more abundant, intense male-male competition is likely to be predominant and male-biased dispersal is expected (Dobson, 1982; Trochet et al., 2016). Although an accurate, predictive understanding of dispersal is vital to the effective management of invasive species (Chapple et al.,

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2012), the extent to which dispersal is driven by phenotype or the environment remains poorly understood (Chapple et al., 2012; Comte & Olden, 2018; Ritchison et al., 1992).

Individual variation in behaviour is increasingly recognized as a key driver of group dynamics (Webster & Ward, 2011). In the three-spined stickleback, *Gasterosteus aculeatus*, relatively shy individuals are more strongly influenced by the presence of bold conspecifics in terms of sheltering, foraging and shoaling behaviour than vice versa (Harcourt, Ang, et al., 2009; Harcourt, Sweetman, et al., 2009). Similarly, in the barnacle goose, *Branta leucopsis*, individuals with greater exploratory responses to novel objects are more likely to lead a paired individual to a food patch (Kurvers et al., 2009). As shy individuals are more likely to conform to the behaviour of bold conspecifics, the presence of bold individuals within a group can disproportionately shift the mean value of a behaviour observed within a group (Webster & Ward, 2011). Accordingly, if individuals differ in dispersal propensity, the composition of individuals within a population can affect the broader patterns of dispersal observed for the population.

Just as individual behaviour can influence group dynamics, individual behavioural responses are also shaped by the environment (Gilliam & Fraser, 2001). Individuals should only disperse when the expected benefits of dispersal exceed the benefits of site fidelity; however, both biotic and abiotic conditions influence the costs and benefits of dispersal (Gilliam & Fraser, 2001; Railsback et al., 1999). For example, if the temperature range of an occupied habitat is harmful, dispersal is beneficial (Aparicio & Sostoa, 1999).

Sex-biased dispersal is predicted to occur when the costs and benefits of dispersal are not equally divided between the sexes (Greenwood, 1980) but even among individuals of the same sex, the benefits of dispersal are unlikely to be equally divided (Ritchison et al., 1992). For example, more sexually attractive males will not suffer the same costs of intense male-male competition as their less attractive competitors (Atwell & Wagner, 2014; Lawrence, 1987). Thus, individual phenotype and social context can mould the probability of dispersal.

The aim of this study was to identify the relative importance of individual traits and environmental/social conditions in driving dispersal. Namely, we investigated the effect of variation in sex ratio on individual propensity to disperse in the Trinidadian guppy. The guppy utilizes a well-characterized and potentially risky jumping behaviour to disperse over physical barriers, such as riffles and waterfalls, present throughout their native and non-native habitats (Soares & Bierman, 2013). This jumping behaviour has been observed frequently in both wild (Magurran, 2005; Seghers, 1973) and captive populations, with fish frequently jumping over 6 cm high (approximately three times the body length; Soares & Bierman, 2013). In this study, we manipulated the sex ratio to test three competing hypotheses regarding individual tendency for guppies to jump: (1) dispersal is dependent on the sex ratio; (2) a subset of individuals are predisposed to disperse independently of the sex ratio; (3) dispersal is dependent on a combination of phenotypic traits (including sex and other traits, e.g. size, pigmentation) and sex ratio. Under hypothesis 1, we predicted that males would disperse more often when the sex ratio is male biased and that no sex differences in dispersal will be observed at even or female-biased sex ratios (Croft et al., 2003). Under hypothesis 2, we predicted that some individuals would disperse significantly more often than others and that dispersal behaviour would not be affected by sex or sex ratio (Belthoff & Dufty, 1998; Ritchison et al., 1992). Under hypothesis 3, we expected male-biased dispersal exclusively in male-dominated sex ratios, but also expected to see strong individual variation in jumping probability (Clobert et al., 2012; Dobson, 1982; Trochet et al., 2016).

METHODS

Fish Selection

All individuals used in this experiment ($N = 160$) were descendants of wild-caught guppies from the lower Tacarigua River in Trinidad. Individuals were randomly selected from stock tanks and moved to individual tanks for subsequent treatment allocation. All individuals were photographed, and their phenotype quantified using ImageJ (Rueden et al., 2017), which facilitated later photo-identification. For all individuals, standard length, tail length and body depth were measured to the nearest millimetre (Rueden et al., 2017). In addition, for all males the percentage of surface area covered by each of three major colour components was calculated: melanic pigments (black spots and lines), structural iridescent colours and carotenoids (red, orange and yellow). These traits were selected as they influence female mate choice and male courtship behaviour and previous research suggests that dispersal is related to mating system (Croft et al., 2003; Greenwood, 1980; Magurran, 2005). To confirm sexual maturity, only male guppies displaying body coloration and fully developed gonopodium and females measuring over 15 mm were included in the study (Evans et al., 2002; Shahjahan et al., 2013).

Treatment Allocation

Individual males ($N = 60$) and females ($N = 100$) were haphazardly allocated to one of four treatment groups representative of sex ratios most commonly observed in wild guppy populations (Pettersson et al., 2004): even (five females to five males), female (10 females), female biased (seven females to three males) and male biased (three females to seven males). Each treatment was replicated four times, giving a total of 16 unique replicates.

Experimental Set-up

The experimental tank (90 × 30 cm and 30 cm high) was divided in half by an opaque Perspex barrier (Fig. 1). The barrier prevented horizontal movement between the two sections of each tank. The barrier between the two sections reached only 3 cm above the water level, thus allowing guppies to move between the two sections by jumping (Soares & Bierman, 2013). The experimental tank utilized an external water filter to generate a realistic flow of water from section 2 to section 1. The flow rate (surface velocity) was 9.1 cm/s. Foliage was placed adjacent to and extending above the height of the barrier to distort the flow of water between sections. The tank had gravel on the bottom, and within each section was a large plastic plant for cover and a filter for aeration. High walls (>15 cm above the water level) prevented fish escape. No lid was used because this may have affected jumping behaviour. All individuals were introduced simultaneously to one section of each tank (section 1; Fig. 1) and were fed daily using a constant amount of Aquarian Complete Nutrition fish flake food. Tanks were monitored hourly from 0900 to 1700 over 48 h. Each overnight period was recorded as one trial. As time of day was recorded for each trial, differences in jumping behaviour overnight were accounted for in our model. As soon as individuals were observed in section 2, they were photographed and returned to section 1. It was necessary to reintroduce individuals to maintain the sex ratio and population size of the treatment and to measure individual repeatability. As all 'jumpers' were photographed, photo-identification using ImageJ (Rueden et al., 2017) was possible and both the number of unique jumpers and the number of jumps each one made could be recorded.

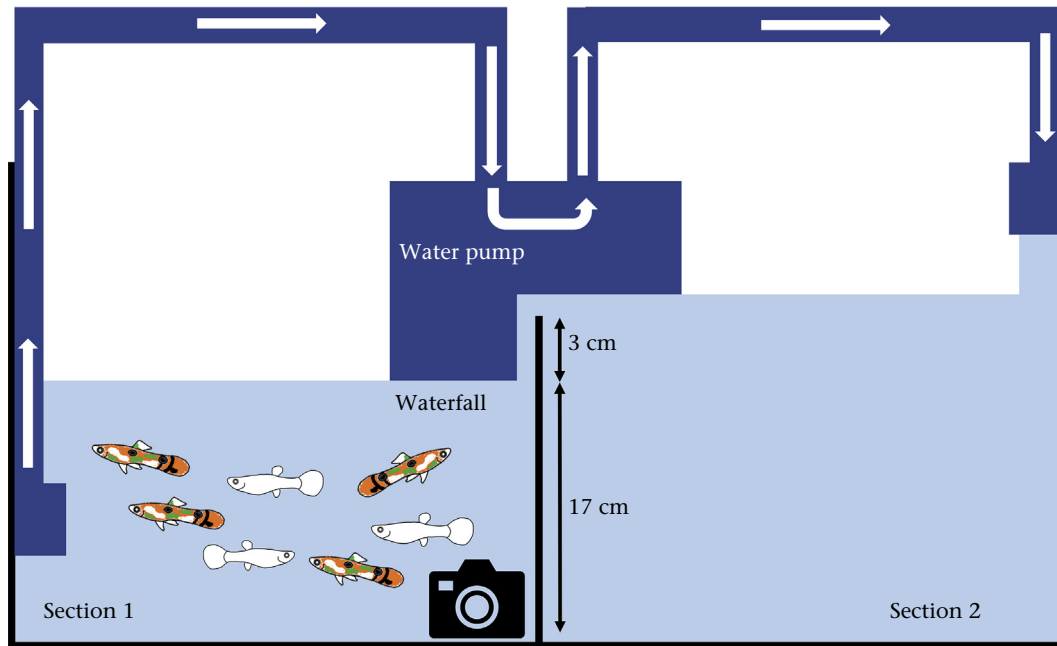


Figure 1. The experimental tank design used in this study. Foliage was included in the experimental tank to distort the flow of water over the barrier, but for clarity this has not been illustrated.

Six jumps were recorded by a GoPro camera. From the orientation of fish, and movements made immediately prior to jumping, all recorded jumps were inferred to be intentional attempts to disperse over the barrier. Other jumps were either not recorded or were not visible in the recordings due to GoPro battery life, fast movement of the fish or visual obstruction.

Statistics

The experimental tank was checked at hourly intervals. Each interval was considered a ‘trial’ for each individual in each experimental tank. For every trial, each individual fish was scored as having jumped the barrier or not (binomial distribution). To test whether sex ratio affects jumping behaviour and whether individuals differ in the probability of jumping, we used binomial generalized linear mixed models (GLMMs). Models were constructed with jumping as a response variable (yes or no), sex ratio treatment (number of males divided by total number of individuals), time of day, number of previous trials (to control for habituation), standard length (as both a linear and a quadratic term), relative tail length (tail length/standard length), relative body depth (body depth/standard length) and percentage cover of each colour component, as well as individual ID and tank ID, as random effects. Standard length was included as a quadratic term as jumping propensity was expected to be maximized at a certain length and not increase indefinitely with size. Models were fitted in a Bayesian framework using MCMCglmm (Hadfield, 2010). We used standard diffuse gamma priors on estimable variance components. The residual variance, which is unobservable in a binomial model with one trial for each observation, was fixed at one. This fixed residual variance was subsequently used in repeatability calculations following Morrissey et al. (2014) and de Villemereuil et al. (2016). For the male model, 1000 samples were retained with a thinning interval of 5000 iterations, following a burn-in of 3000000 iterations. For the female model, 1250 samples were retained with a thinning interval of 20000, following a burn-in of 15000000. Convergence was checked using trace plots and posterior distribution densities. To account for the different scales of

explanatory variables, all values were mean centred. Given that one treatment contained only females, and the behaviour of males and females was expected to differ, separate models were created for each sex. Comparison of 95% highest posterior density (HPD) intervals was used to determine whether there were sex-specific differences.

Ethical Note

All animal experimentation carried out during this project was approved by the University of St Andrews Animal Welfare and Ethics Committee in January 2022. All fish were kept in mixed-sex

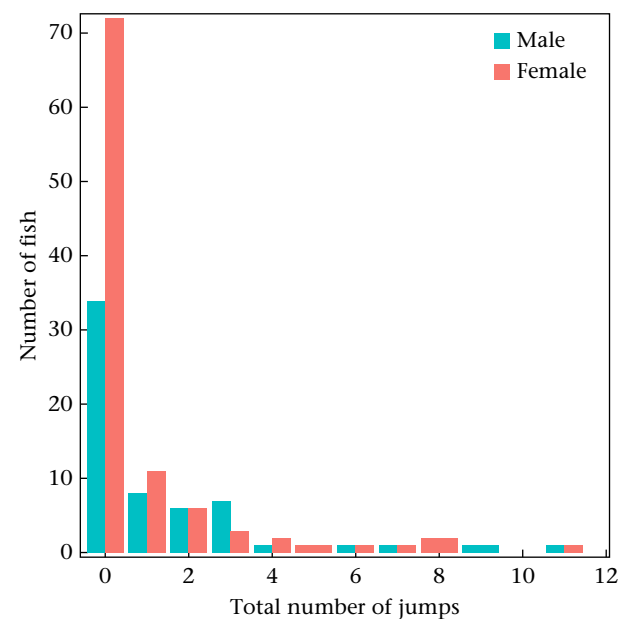


Figure 2. The total number of times each fish jumped over the barrier within the 48 h study period. As the experimental tank was checked hourly between 0900 and 1700, the maximum possible number of jumps was 19.

stock tanks ($N = 20$, 60×40 cm and 30 cm high), in densities that are representative of natural conditions in Trinidad. All fish were returned to stock tanks after the experiments. To mimic natural conditions, all stock tanks contain gravel and plastic plants. Aeration is provided by small filters connected to a central air compressor. Fish were fed once per day (0900) with Aquarian Complete Nutrition fish flake food. Light (12:12 h light:dark) and

temperature (26°C) were controlled and maintained by the technical staff at the University. Fish welfare was supervised by the university NACWCO. Experimental tanks were divided in half and each section contained gravel, plastic plants and a filter for aeration. To minimize impacts, the sex ratios, group sizes and experimental tank dimensions mimicked natural habitats. All experimental tanks were checked daily to ensure all fish were in good health.

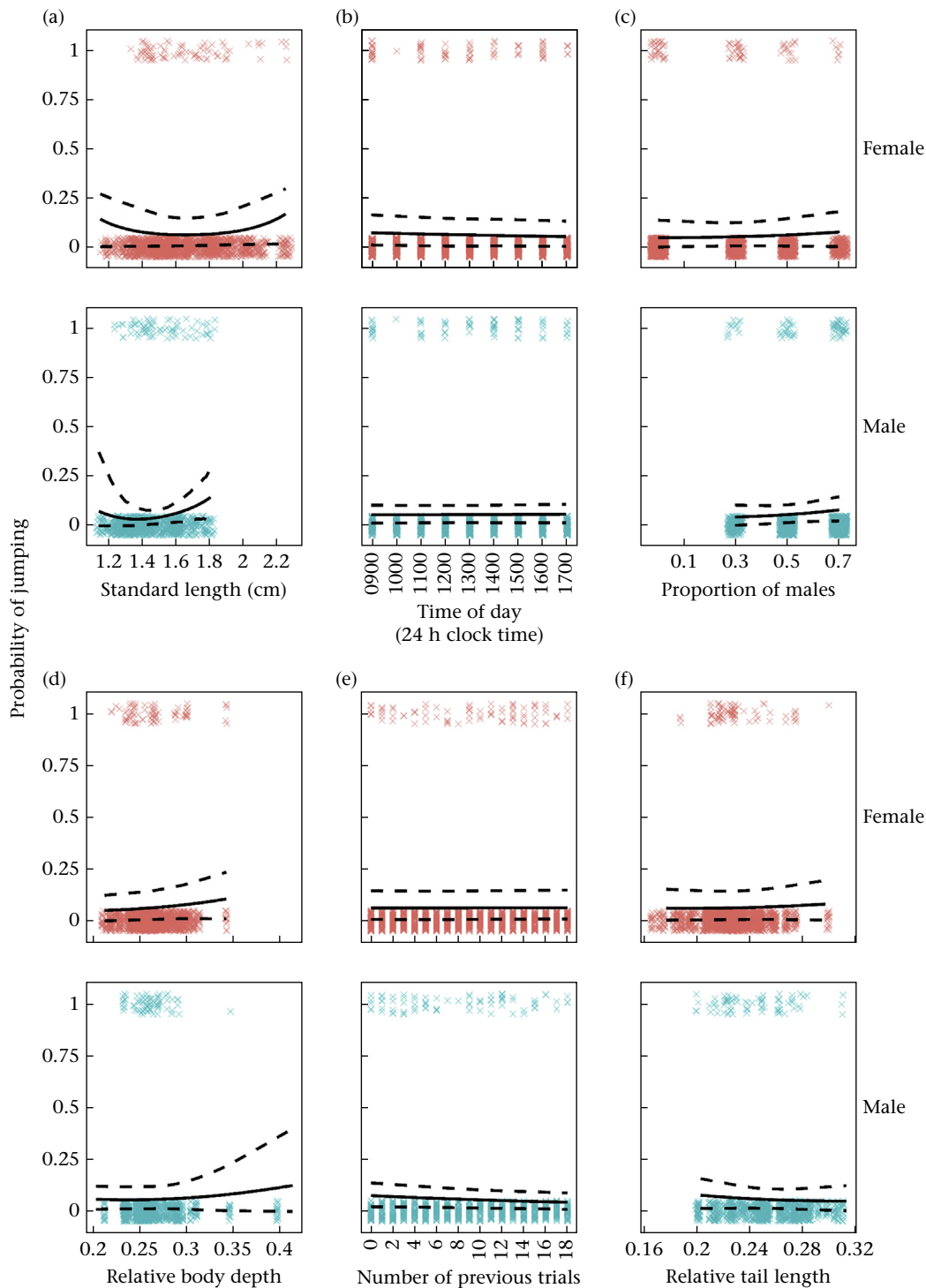


Figure 3. The relationship between probability of jumping over a waterfall for Trinidadian guppy females ($N = 100$) and males ($N = 60$) and: (a) standard length (cm); (b) time of day (24 h clock time); (c) proportion of males in the population; (d) relative body depth (body depth/standard length); (e) the number of previous trials within the study period; and (f) relative tail length (tail length/standard length). Solid lines represent model estimates and dashed lines represent 95% highest posterior density intervals. Points represent the binary outcome of jumping (1) or not jumping (0) for each trial for each fish. To account for overlapping values, all points have been jittered and made partially transparent.

RESULTS

Of 160 individuals, 54 (43% of males, 28% of females) jumped the barrier at least once (Fig. 2). Of these 54 jumpers, nine (four males, five females) jumped the barrier five times or more. The most jumps made by a single individual over the observation period was 11 (this was observed for both a male in the male-biased treatment and a female in the female treatment).

The probability of an average male (in terms of both size and coloration) jumping in a given trial in the even sex ratio treatment was 0.12 (95% HPD interval: 0.03 : 0.24). For an average-sized female in the even treatment the probability of jumping in a given trial was 0.06 (HPD: 0.006 : 0.14). The overlap of HPD intervals suggests that males and females do not differ significantly in terms of dispersive jumping behaviour.

For both sexes, we found no evidence for an effect of treatment (sex ratio), relative tail length, number of previous trials or time of day on jumping probability for either sex (Fig. 3). For both males and females, jumping probability was minimized around mean values of standard length (Fig. 3). Nevertheless, the magnitude of the effect of standard length on jumping probability was negligible and there is a lot of uncertainty around these estimates. To illustrate, an increase in standard length of 2 mm relative to the mean gives an estimated increase in male jumping probability of 0.007 (HPD: -0.008 : 0.17). For females, increasing the mean value of standard length by 2 mm increased jumping probability by 0.004 (HPD: -0.008 : 0.02). We found similar results for the effect of relative body depth. Increasing relative body depth by 0.05 (approximately 25% of the range of values for this trait) gave an

estimated increase in jumping probability of 0.01 (HPD: -0.04 : 0.08) for males and 0.02 (HPD: -0.02 : 0.07) for females.

For males, jumping probability decreased slightly with increasing percentage cover of melanic pigments (Fig. 4a). A male with 10% cover of melanic pigments has an estimated 0.06 (HPD: 0.004 : 0.12) reduction in jumping probability relative to a male with 5% melanic pigment cover. However, no biologically significant effect of carotenoid or structural iridescent pigments on male jumping probability was detected (Fig. 4b, c).

There was consistent among-individual variation in jumping probability for both males and females (Fig. 5). For males, consistent individual differences explained approximately 17.46% (HPD: 2.65 : 34.68%) of total observed variation. For females, consistent individual differences explained 7.92% (HPD: 1.44 : 16.12%) of total observed variation. For males there was no consistent effect of tank ID on jumping probability (tank ID explained only 3.43% of total variation; HPD: <0.001 : 13.32%). Conversely, for females, tank ID explained 21.66% (HPD: 1.6 : 44.71%) of total observed variation.

DISCUSSION

We found little evidence for an effect of social context (i.e. sex ratio) on dispersal behaviour. Morphological traits also had negligible effects on jumping probability. Instead, we saw that individual guppies varied in their tendency to disperse via jumping behaviour.

Previous studies have found that male and female guppies differ in movement patterns (Borges et al., 2022; Croft et al., 2003; De Bona et al., 2019). Males have been shown to swim further within a section of homogeneous stream (Borges et al., 2022; Croft et al.,

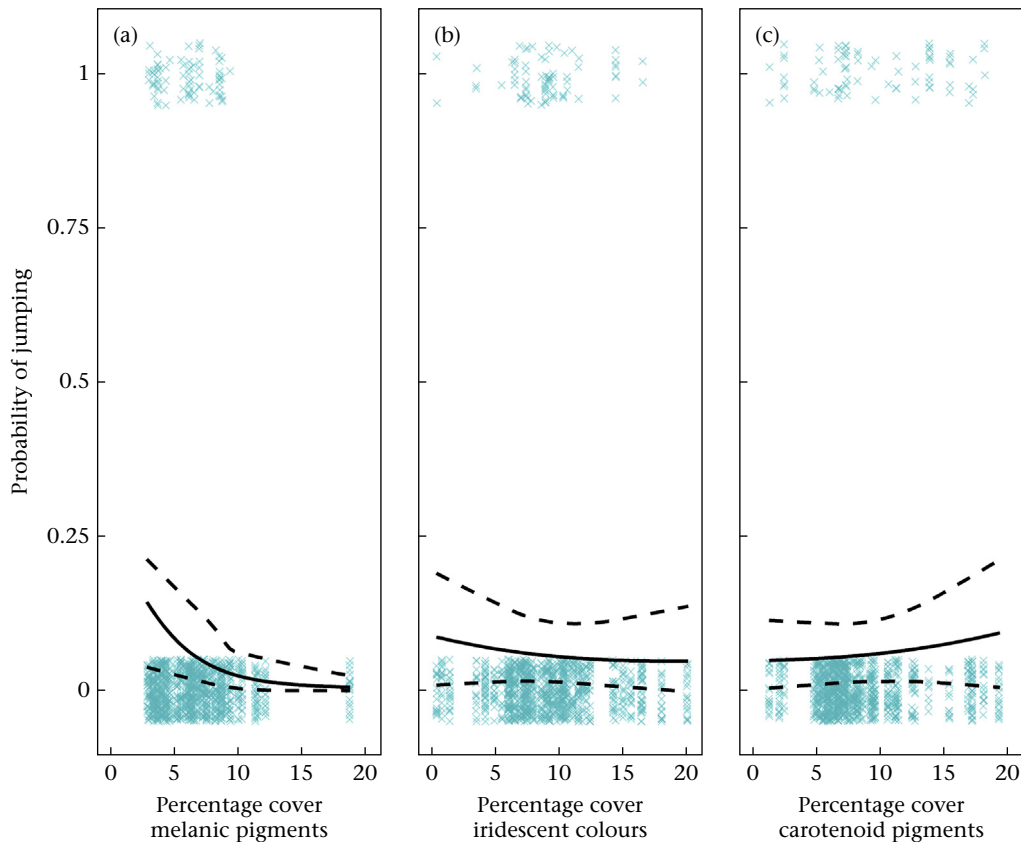


Figure 4. The relationship between probability of jumping over a waterfall and percentage cover of three major colour components in male Trinidadian guppies ($N = 60$). (a) Melanic pigments; (b) structural iridescent colours; and (c) carotenoid pigments. Solid lines represent model estimates and dashed lines represent 95% highest posterior density intervals. Points represent the binary outcome of jumping (1) or not jumping (0) for each trial for each fish. To account for overlapping values, all points have been jittered and made partially transparent.

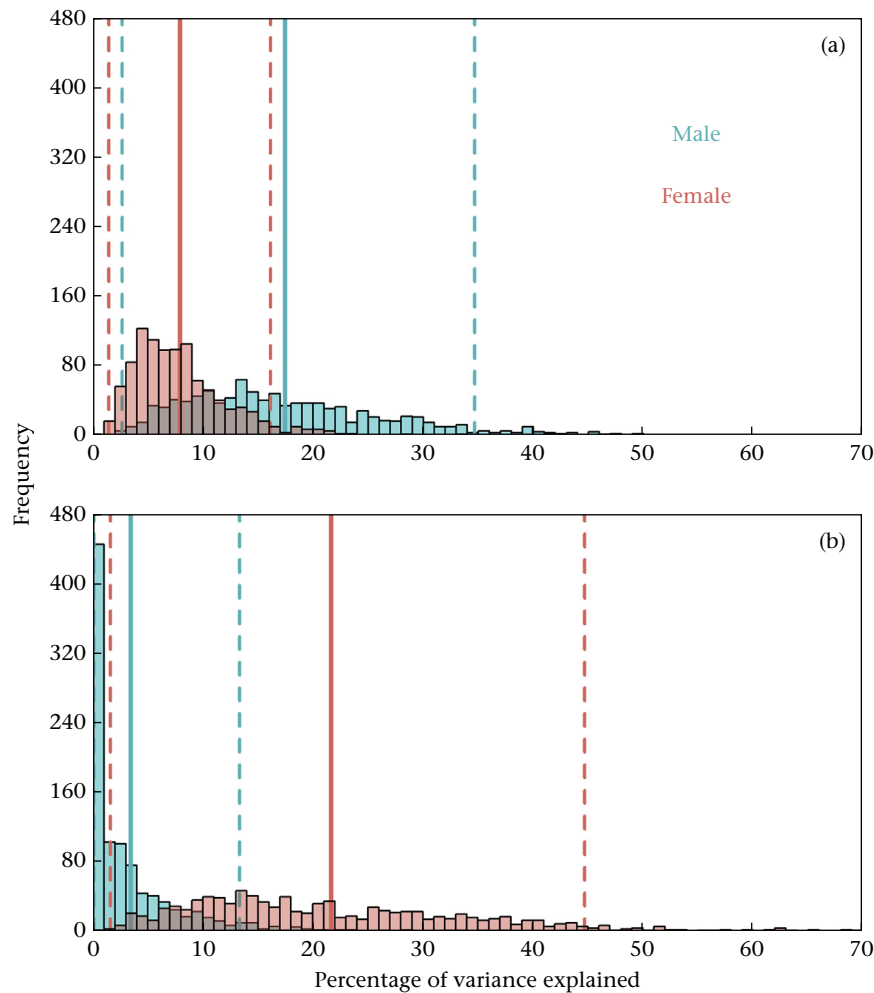


Figure 5. The proportion of total variance in the jumping probability of Trinidadian guppies explained by the random effect of (a) individual ID and (b) tank ID, as calculated from 1000 posterior samples of generalized linear mixed models constructed separately for males and females. Solid vertical lines represent the mean proportion of variance explained by the respective random effect. Dashed lines represent upper and lower bounds of 95% highest posterior density intervals.

2003; De Bona et al., 2019). Our results show no evidence for male-biased dispersal. However, our study focused on dispersal in the significantly different context of movement over physical barriers. In addition, in the previous investigations, waterfalls were either reinforced to prevent upstream movement or were not present within the study site (Borges et al., 2022; Croft et al., 2003; De Bona et al., 2019). For other taxa, multiple studies have also described sex-biased dispersal, with the sex competing for access to mates dispersing more readily (Greenwood, 1980; Lawrence, 1987). However, this pattern is not ubiquitous across species or taxa (Greenwood, 1980). For example, natal dispersal in Geoffroy's tamarin, *Saguinus geoffroyi*, is not sex biased despite female-female competition for reproductive opportunities (Díaz-Muñoz & Ribeiro, 2014). Further, there is no evidence of male-biased dispersal in Atlantic salmon, *Salmo salar*, a species with intense male-male competition for mates (Consuegra & García De Leániz, 2007). Our results, in combination with previous studies, suggest that the factors that influence male dispersal are unlikely to be the same as those that favour female dispersal. This is not entirely surprising as the associated costs/benefits of certain behaviours are not equally shared among both sexes (Magurran & Nowak, 1991). For those species where sex-biased dispersal is expected but not observed, spatial and temporal variation in multiple conditions can sometimes favour female dispersal and offset male-biased dispersal

(Consuegra & García De Leániz, 2007). The current results stress that females, as well as males, frequently engage in dispersive jumping behaviour. This is an ecologically important result as the dispersal of females is vital to successful reproduction, the establishment of novel populations and the spread of invasive species (Deacon & Magurran, 2016; Deacon et al., 2011). For the same reason it is particularly noteworthy that a gravid female in our study was able to disperse over the barrier and give birth to two young in the second section of the tank. Future studies should therefore investigate the effect of reproductive status on female dispersal behaviour.

While jumping occurred independently of sex ratio, this behaviour was common (>33% of all individuals jumped). Further, jumping over the barrier occurred despite fish being fed daily. Previous research concluded that jumping in the Trinidadian guppy is linked to a behavioural phenotype that is predisposed to disperse (Soares & Bierman, 2013). Here we utilized an experimental design that is more reflective of natural habitats than that used by Soares and Bierman (2013) and found consistent variation in individual dispersal behaviour. Our results lend support to the innate dispersal hypothesis. Innate dispersal behaviour can also explain the lack of sex-biased dispersal as the trait(s) that predispose individuals to disperse may not be related to sex.

As the continued spread of introduced individuals is key to invasive success, jumping as a means of dispersal is an important behavioural trait of aquatic invaders. We found that jumping behaviour is individually linked, rather than associated with a population trait or with social context. Our result aligns with those of other studies that reported significant individual variation in dispersal behaviour. For example, the signal crayfish, *Pacifastacus leniusculus* (Galib et al., 2022), and the mosquitofish, *Gambusia affinis* (Cote, Clobert, et al., 2010), have both been reported to have intraspecific differences in dispersal behaviour. Our result supports the hypothesis of individual-dependent invasion and demonstrate that not all individuals of an invasive species engage in invasive behaviour. Increased research effort is likely to uncover additional examples of individual-dependent invasion in many more taxa (Chapple et al., 2012).

The finding of intraspecific variation in an invasive trait demonstrates that species invasions can be mediated by a nonrandom subset of individuals. Future studies in invasion and conservation biology must therefore look beyond the species level and address the role of individuals in invasion dynamics.

Author Contributions

Aaron Jessop: Conceptualization, Methodology, Formal analysis, Writing – Original draft; Investigation. **Michael Morrissey:** Formal analysis. **Miguel Barbosa:** Writing – Review & editing, Supervision.

Data Availability

Research data are available via the Zenodo public repository: <https://doi.org/10.5281/zenodo.8169179>.

Declaration of Interest

The authors declare that they have no competing interests.

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