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LETTER

Reproductive benefits associated with dispersal in headwater populations of Trinidadian guppies (*Poecilia reticulata*)

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Abstract

Theory suggests that the evolution of dispersal is balanced by its fitness costs and benefits, yet empirical evidence is sparse due to the difficulties of measuring dispersal and fitness in natural populations. Here, we use spatially explicit data from a multi-generational capture–mark–recapture study of two populations of Trinidadian guppies (*Poecilia reticulata*) along with pedigrees to test whether there are fitness benefits correlated with dispersal. Combining these ecological and molecular data sets allows us to directly measure the relationship between movement and reproduction. Individual dispersal was measured as the total distance moved by a fish during its lifetime. We analysed the effects of dispersal propensity and distance on a variety of reproductive metrics. We found that number of mates and number of offspring were positively correlated to dispersal, especially for males. Our results also reveal individual and environmental variation in dispersal, with sex, size, season, and stream acting as determining factors.

KEYWORDS

capture–mark–recapture, dispersal, fitness, wild pedigree, movement ecology, *Poecilia reticulata*

INTRODUCTION

Dispersal is one of the major processes shaping diversity in the natural world. Broadly defined, dispersal is a departure from a local environment, followed by movement and settlement in a new location (Clobert et al., 2012). Dispersal followed by successful breeding leads to gene flow, which alters the distribution of genotypes across space (Clobert et al., 2012; Ronce, 2007). Dispersal, then, plays a crucial role in determining population structure, patterns of adaptive differentiation, and population dynamics (Bonte & Dahirel, 2017; Kawecki & Holt, 2002; Kubisch et al., 2014; Sexton et al., 2009). The effects of dispersal on these evolutionary and ecological processes crucially depend on the fitness of dispersing individuals, both in terms of their survival and reproduction. Yet, dispersal and fitness are two of the most challenging quantities to empirically measure in wild populations, making our understanding of their relationship tenuous (Doligez & Pärt, 2008).

Theory suggests that the probability and extent of dispersal within a population are shaped by a balance between fitness costs and benefits incurred by dispersing individuals (Holt, 2003). Dispersal costs may manifest though energetic costs of physically moving, and/or increased mortality associated with passing through unsuitable or dangerous environments (Bonte et al., 2012). Benefits may arise through a variety of mechanisms, including a reduction in competition among relatives (Hamilton, 1977; Perrin & Mazalov, 2000; Taylor, 1988), escape from unfavourable natal conditions (Meylan et al., 2002; Venable & Brown, 1988), resource acquisition (Clobert et al., 2012) and inbreeding avoidance (Perrin & Mazalov, 1999; Pusey & Wolf, 1996). Dispersal should evolve when dispersal benefits outweigh costs, yet we expect those benefits to differ between individuals and environments. Given observed variation in dispersal propensity, it is important to understand how fitness benefits of dispersal are distributed across individuals and environments to understand dispersal evolution. The extent to which fitness effects of dispersal depend on individual characteristics such as sex, size and total distance dispersed, as well as environmental factors, remains an open question in most natural systems. Here, we integrate whole-population mark–recapture and pedigree analyses in two natural populations of Trinidadian guppies (*Poecilia reticulata*) to quantify the relationship between dispersal and reproductive fitness at fine spatial and temporal scales.

Poecilia reticulata are live-bearing fish inhabiting streams and rivers throughout Trinidad and Tobago. Decades of research on the guppy mating system have shown that female choice is important (Haskins & Haskins, 1949, 1950; Houde, 1987), often on the basis of phenotypic novelty (Brooks & Endler, 2001; Hughes et al., 2013). Given the genetic basis of *P. reticulata* coloration (Haskins & Haskins, 1951; Houde, 1992), this preference might be a mechanism for females to avoid mating with kin (Daniel & Rodd, 2016; Hughes et al., 1999). *P. reticulata* populations in headwater streams are also strongly regulated by density dependence, with high population density increasing mortality and limiting reproductive success (Reznick et al., 2012). Thus, it is likely that guppy dispersal plays an important role in minimising inbreeding and allowing fish to escape high density pools––potentially providing dispersing individuals with substantial fitness benefits.

To date, it is known that male guppies are more likely to disperse than females (Croft et al., 2003) and that density-dependent dispersal varies with guppy life stage (De Bona et al., 2019). Throughout Trinidad, guppies show strong patterns of population structure associated with drainage (Fraser et al., 2015), distance, and barriers to gene flow (Crispo et al., 2006), suggesting some dispersal limitation at large spatial scales. *P. reticulata* is also a prolific global invader, and its ability to establish new populations following dispersal or artificial introduction greatly impacts freshwater ecosystems worldwide (Deacon et al., 2011). However, no previous study has related dispersal to reproduction in the *P. reticulata* system, or quantified how reproductive benefits of dispersal vary among individuals or environments. As such, the crucial link between dispersal and fitness––and its consequences for dispersal evolution, gene flow, and population structure––remain unknown. Here, we aim to fill this gap with a long-term, multi-generational study to ask the overarching question: **Is dispersal correlated with reproductive success in *P. reticulata*?**

Our hypothesis, based on the natural history of guppy populations in headwater environments, is that dispersal confers a reproductive benefit at this scale, and that these benefits are greater for males than females. That is, guppies that move at all and those that disperse farther experience greater reproductive success than philopatric individuals, and reproductive benefits are higher for males as they compete for access to females. However, we predict that movement is only beneficial at small spatial scales within the low predation environment, as long-distance dispersal into downstream high predation reaches results in high mortality (Weese et al., 2011). These costs associated with local adaptation to heterogeneous predation regimes may lead to the evolution of short dispersal distances over evolutionary time. We also analysed how dispersal behaviour vary with male body size, and across seasons. We hypothesise that smaller fish move more to escape conditions where they are competitively inferior, and all fish move more and in the downstream direction during the wet season due to floods and high stream flow, which facilitate both passive and active movement. Our data allowed us to test for correlations between fine-scale dispersal and fitness for two natural populations, and contributes to the understanding of individual variation in dispersal for a model system in ecology and evolution.

METHODS

Field capture–mark–recapture

We studied low predation populations of *P. reticulata* in neighbouring streams, Taylor and Caigual, in the Guanapo drainage on the south slope of the Northern Range of Trinidad. Data used for this project were collected in a spatially explicit, monthly capture–mark–recapture study that spanned June 2009−July 2011. In April 2009, as part of a separate study (see Travis et al., 2014), guppies from downstream site within the same drainage were translocated upstream of our two focal sites. Translocated individuals eventually reached and bred with the focal resident populations (Fitzpatrick et al., 2016, 2020). However, our goal for this study was to focus on dispersal behaviour of the resident population. Therefore, individuals reported on in this study were fish captured in the first 13 months of the mark-recapture study (June 2009−July 2010), when immigration of translocated individuals into the focal sites was minimal. To account for the presence of few immigrant and hybrids in our data set, we included a hybrid index covariate in all statistical models. This hybrid index varied from 0 (pure resident) to 1 (pure immigrant) and was calculated using genetic data, as described below (see Fitzpatrick et al., 2020). Only 5% of fish in our data set were classified as pure immigrants, suggesting that the vast majority of our data represent the resident populations of Taylor and Caigual prior to the onset of gene flow (Fitzpatrick et al., 2016).

Detailed capture–mark–recapture methods are described in Fitzpatrick et al., (2016). Briefly, we selected a portion of each stream that was the upstream-most extent of wild guppy populations uninterrupted by waterfall barriers. The sampled reach in Taylor was 240 m in length, and 80 m in length in Caigual. Each distinct pool or riffle within focal reaches was uniquely labelled and sampled monthly using a combination of hand nets and mesh traps. All guppies greater than 14 mm were captured, transferred to the lab, and placed in aerated tanks, separated by pool location and sex. Only mature individuals were included in the analyses, as determined by gonopodium morphology for males, and the presence of melanophores at the cloaca for females. These methods are commonly used in capture–mark–recapture studies of Trinidadian guppies, and have been shown to produce low laboratory mortality and high capture probabilities (Reznick et al., 1996). During laboratory processing, individuals were anaesthetised with a dilute solution of MS-222, and new recruits were given a unique subcutaneous elastomer mark (Northwest Marine Technologies, Inc.). Recruits had three scales collected and dried for DNA extraction, and all individuals were weighed and photographed each month. All fish were returned to their exact capture location 1 to 2 days after processing. During their release, fish were acclimated to stream water and released into the lowest flow region of their capture location to minimise accidental passive downstream movement.

Quantifying dispersal variation

The exact pool locations of initial capture and subsequent recaptures were recorded every sampling event for all individuals. Although sizes and locations of pools and riffles change based on seasonal dynamics, they are always noted by the number of meters from the upstream extent of the reach. *P. reticulata* were considered philopatric (non-dispersing) if they were consistently captured less than 10 m from their initial capture location, the approximate length of the maximum pool size. Individuals were considered dispersers if at any point in the study they were captured 10 m or more from the pool where they were first captured, regardless of how many sampling occasions it took for that movement to occur.

We use the threshold of 10 m because that is the length of the largest pool in our study, such that any movement beyond it reflects that an individual departed its initial pool and settled at a new location for a period of time. Given that most guppy daily activity takes place at the within-pool scale and movement between pools places an individual in a new, non-local environment, this threshold matches our definition of dispersal as a ‘a departure from a local environment, followed by movement and eventual settlement in a new location.’ A potential source of error in our estimate of distance could stem from individuals moving and backtracking between sampling occasions, such that total movement would be underestimated. Thus, we are only able to estimate *minimum* distance moved.

In addition to the categorical classification of philopatric or dispersing, we quantified the total distance travelled for all individuals as the cumulative distance moved during our study (Figure 1). This estimate considers upstream and downstream movement equally. For example, a fish that moved upstream from 0 m to 10 m to 20 m would have the same dispersal distance (10 + 10 =20 m) as a fish that moved upstream from 0 m to 10 m, then back downstream from 10 m to 0 m (10 – 0 + 10 = 20 m). Finally, we calculated the range of all dispersing fish, defined as the minimum noncumulative distance spanning all of its locations across the study—in the example above, the first fish has a range of 20 m, and the second fish has a range of 10 m.

Analyses of dispersal patterns

Total estimated dispersal distances showed an excess of zero values, as 47.5% of fish did not disperse at all. As such, we modelled dispersal distance using zero-inflated negative binomial distributions, which accommodates separate analyses of zeros and total counts. We found this to be the most biologically appropriate model to understand both the probability of moving (zero vs. non-zero) as well as total distance moved. For all models described below, we used Akaike information criterion (AIC) for model selection (Johnson & Omland, 2004) to choose between models including different independent variables and distributional assumptions, in addition to using the R package DHARMa (Hartig, 2021) to assess model fit. Covariates in all models included stream, sex, hybrid index, and longevity. Longevity was calculated as the total number of months a fish was captured in our study, which likely underestimates the true number of months that individuals live due to imperfect detection probability and because it does not account for the time when fish are too small to be captured (less than 14 mm).

To test whether *P. reticulata* move more in the downstream direction and in the wet season, we first investigated whether movement differed in distance and direction between seasons and streams. We used generalised linear mixed models to test for the effect of season on the movement of fish for each capture occasion, with individual and month as random effects. Seasonal analyses were done separately for each stream.

To test the hypothesis that smaller males disperse more often and farther, we tested for relationships between standard length and dispersal status and total dispersal distance. Female's size was not tested because females have indeterminate growth, making size and

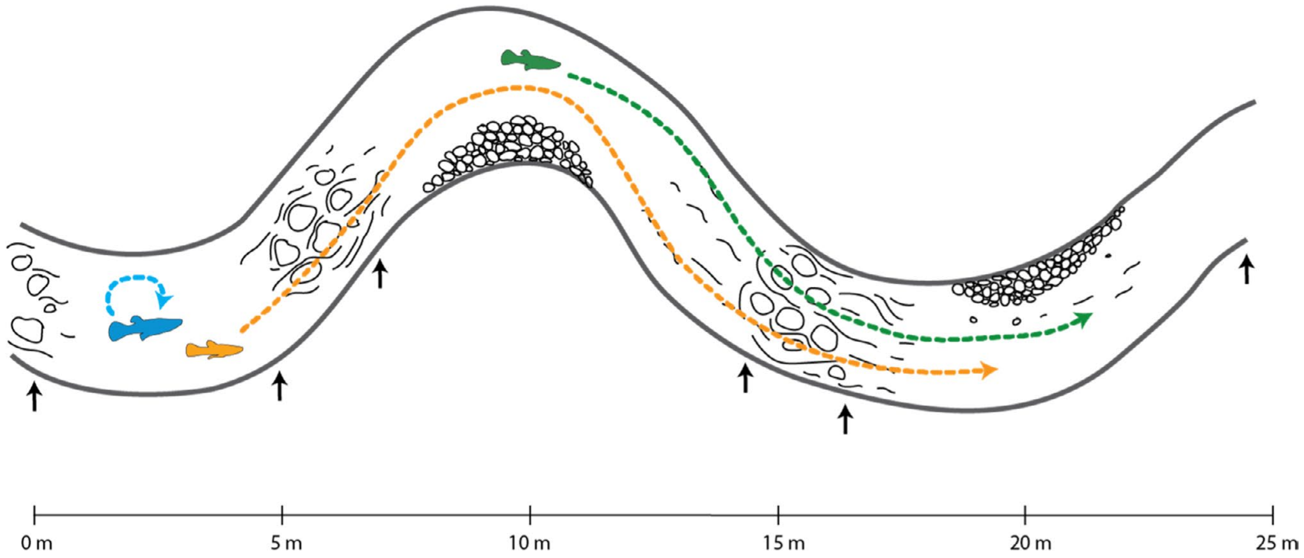

FIGURE 1 How dispersal distances were calculated. Arrows represent boundaries between pools and riffles along the stream. Dispersal distances for all fish were measured based on the distance between the pools where they were captured. Distances between pools were measured as the minimum distance an individual would have to move to change pools. For example, the yellow fish was initially found in a pool that extended from 0 to 5 m, then captured in a pool that extended from 17 to 25 m, and so was recorded to have moved 12 m (17 minus 5). The green fish, having moved from a pool extending from 7 to 14 m to the same 17–25 m pool, was considered to have moved only 3 m (17 minus 14). Our metric of total distance, then, reflects a conservative minimum distance that each fish moved during the study. Fish that were always captured in the same pool, like the blue fish represented in the figure, were not considered dispersers

longevity strongly colinear. All models included stream, hybrid index, longevity, and the interaction between hybrid index and stream as covariates.

Effects of dispersal on fitness

Lifetime reproductive success was determined for each individual by reconstructing pedigrees for Caigual and Taylor populations using individual genotypes from 12 polymorphic microsatellite markers (see Fitzpatrick et al., 2016 for genetic data collection methods and Fitzpatrick et al., 2020 for details on pedigree reconstruction). Final pedigrees consisted of 1,106 individuals in Caigual (458 maternal links, 655 paternal links) and 1725 individuals in Taylor (975 maternal links, 994 paternal links) spanning 4–6 overlapping generations. We used the pedigrees to estimate the number of offspring that reached a minimum size of 14 mm for each individual, as well as the total number of mates for each individual that produced at least one offspring that survived to 14 mm.

We tested for a relationship between dispersal and lifetime reproductive success using zero-inflated negative binomial regression because 55% of fish were assigned zero offspring in the pedigree analysis. As with distance, we were interested in how our variables affected the probability of zero versus non-zero values of offspring as well as total counts. Number of mates was also modelled with a zero-inflated negative binomial regression for similar biological reasons. Dispersal status and total distance were used as predictor variables in separate models, with stream, hybrid index, and longevity as covariates. We included the interaction between hybrid index and stream in these models, given higher immigration into the Taylor during the study period, and overall higher fitness of hybrid individuals (Fitzpatrick et al., 2020). We analysed males and females separately when modelling reproductive success, because the offspring from each fish were not independent of the other parent. In models with males, standard length was also included as a covariate, while female size is accounted for by incorporating longevity in models of reproduction.

Finally, we explored whether guppies with a larger range have an increased number of mates, where a ‘mate’ is defined as an individual that shared at least one surviving offspring with the focal individual. Range was used in this analysis because it directly reflects the extent to which fish explored the stream beyond their natal pools––total distance, on the other hand, includes backtracking and reflects overall movement (Figure 1). We again used a negative binomial zero-inflated model with stream, hybrid index and longevity as covariates. All analyses were conducted in R 3.5.3 (R Development Core Team, 2019).

RESULTS

Patterns of dispersal

A total of 1357 fish were caught and recaptured at least once in our 13 sampling occasions from June 2009 to July 2010. On average, fish in our study were recaptured 3.6 times during that time period. A total of 525 (38.7%,

Table S1) individuals in our data set were classified as dispersers (i.e. moved ≥10 m during the study). Our data consisted overwhelmingly of resident genotypes, with 954 out of 1357 fish having a hybrid index lower than 0.5, and 726 of those falling between zero and 0.1 (Figure S1). The distribution of dispersal distances was highly skewed, with 50% of all dispersing fish moving between 10 and 26 m, a mean dispersal distance of 41.5 m, and a maximum of 248 m (Figure 2, Table 1). The proportion of fish that dispersed was higher in Caigual (48.6%) than in Taylor (28.9%, Table S1).

Individual and environmental correlates of dispersal

We found that the likelihood of fish being dispersers increased with longevity ($N = 1357$, $z = 7.825$, $p < 0.001$) and was higher for guppies of resident descent ($N = 1357$, $z = -2.848$, $p = 0.004$). Longer-lived fish also moved greater total distances ($N = 1357$, $z = 9.667$, $p < 0.001$; Figure S2a), as did fish from Taylor ($N = 1357$, $z = 11.709$, $p < 0.001$). We did not find evidence that fish in older age classes are more likely to move. That is, we found that most dispersal happens between a fish's first and fifth captures, and there does not seem to be an age threshold after which fish begin to disperse (Figure S3, Table S2). We also uncovered an interaction between stream and hybrid index, where fish moved higher total distances if they were from Taylor and had low hybrid indexes ($N = 1357$, $z = -4.247$, $p < 0.001$). Thus, we kept longevity, stream, hybrid index, and the interaction between stream and hybrid index as covariates in all subsequent models.

Supporting our hypothesis about male-biased dispersal, we found that males were 12% more likely to disperse than females ($N = 1357$, $z = 4.425$, $p < 0.001$; Table S1). Males also moved farther total distances (Figure 2; $N = 1357$, $z = 2.451$, $p = 0.014$). Contrary to our hypothesis, we found positive correlations between male body size and likelihood of dispersing ($N = 604$, $z = 4.142$, $p < 0.001$) as well as total distance moved ($N = 604$, $z = 5.429$, $p < 0.001$; Figure S4).

The probability of movement was higher in the wet season for the Taylor population ($N = 469$, $z = 6.499$, $p < 0.001$; Figure S5a), but was consistent across seasons in Caigual ($N = 651$, $z = -0.41$, $p = 0.685$; Figure S5b). The Caigual population also showed no seasonality in the extent of upstream ($N = 651$, $z = -0.698$, $p = 0.485$) versus downstream ($N = 651$, $z = -0.278$, $p = 0.781$) dispersal, indicating fish did not have a directional bias throughout the year of the study. However, as expected, fish in the Taylor population moved more in both directions during the wet season, with a stronger effect of the wet season on increasing downstream dispersal distances ($N = 469$, $z = 11.36$, $p < 0.001$), compared to upstream movement ($N = 469$, $z = 5.036$, $p < 0.001$).

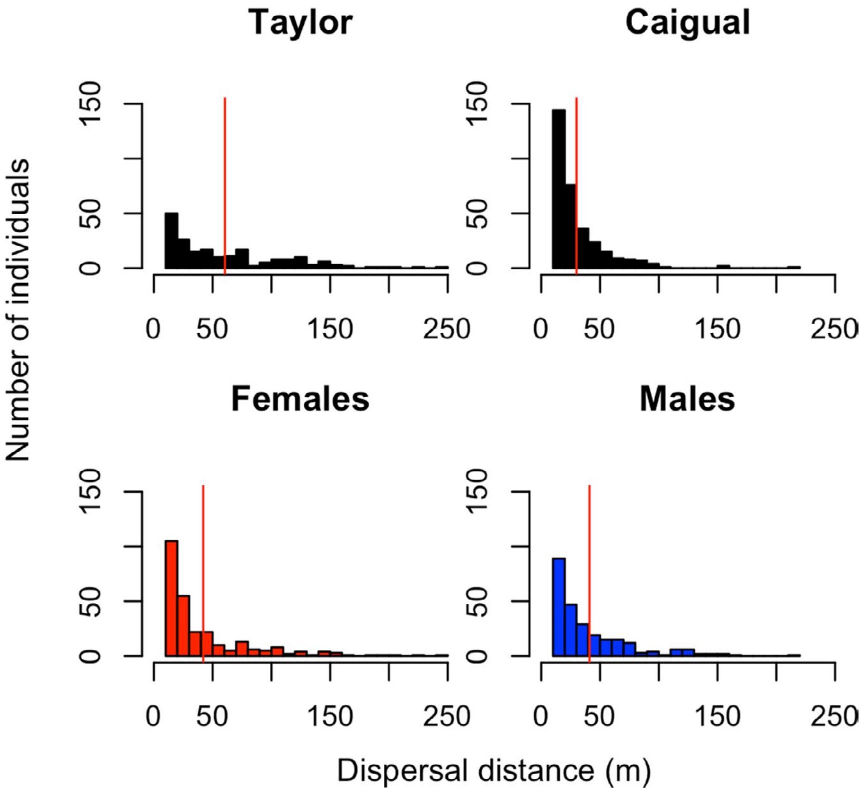

FIGURE 2 Total movement of fish considered dispersers (total distance moved ≥10 m) grouped by sex and stream. Red lines indicate means for each group

TABLE 1 Average and maximum values for dispersal distance of all fish of both sexes in both streams, and for number of offspring of dispersing (moved ≥10 m) and non-dispersing individuals

				Average number of offspring per individual		Maximum number of offspring	
Stream	Sex	Average dispersal distance (m)	Maximum dispersal distance (m)	Non-dispersers	Dispersers	Non-dispersers	Dispersers
Taylor	F	17.57	248	1.74	4.03	24	51
	M	19.12	170	1.42	4.66	26	22
Caigual	F	13.88	157	0.75	1.02	11	20
	M	16.94	216	1.31	3.38	43	55

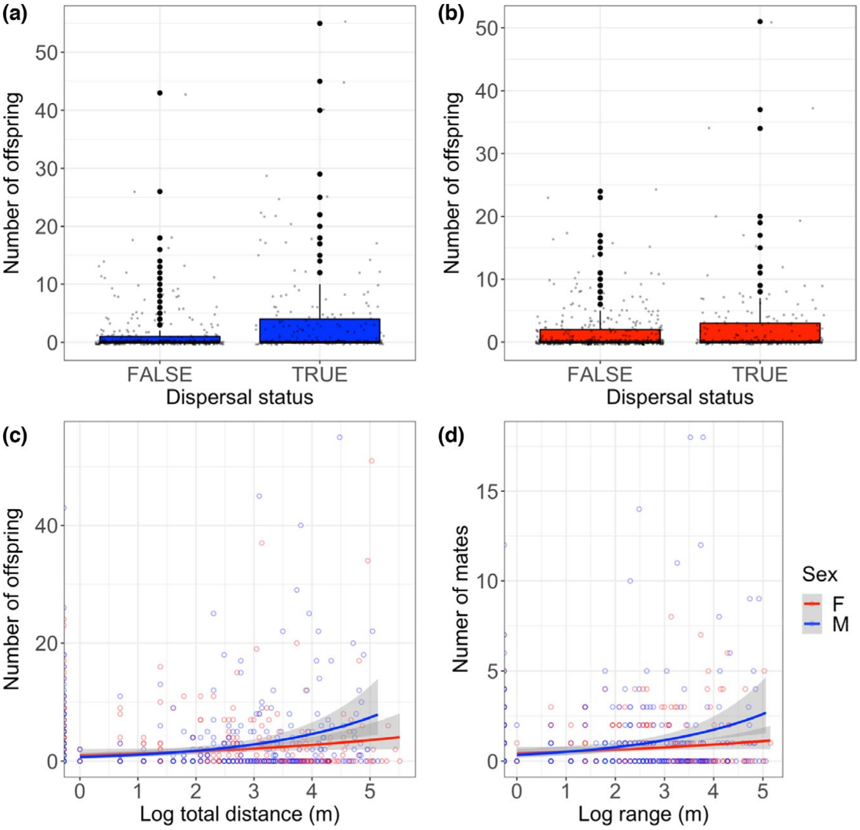

FIGURE 3 Response of fitness metrics to dispersal status, distance, and range. (a) Males that disperse are more likely to have at least one surviving offspring, and show a trend towards having more offspring; (b) Female dispersers do not show trends towards increased reproductive success compared to females that do not disperse. (c) Males have a higher chance of having offspring with longer distance moved, and females show a trend towards more offspring with higher distance moved; (d) Males with larger ranges have an increased number of mates, and that effect was not statistically significant for females. Lines show negative binomial regression and shading as 95% confidence intervals

Fitness consequences of dispersal

We observed different effects of dispersal status and distance on reproductive success between the sexes. In all models, longevity (Figure S2b), male standard length, higher immigrant ancestry, and being from Taylor had positive effects on reproductive success, so these covariates were always included. Male dispersers had a higher chance of having at least one surviving offspring than philopatric males ($N = 604$, $z = -2.877$, $p = 0.004$; Table 1), as well as a non-significant trend towards more total offspring ($N = 604$, $z = 1.693$, $p = 0.090$; Table 1). The chance of males having a non-zero number of offspring also increased with total distance moved ($N = 604$, $z = -2.243$, $p = 0.025$, Figure 3a), though there was no effect of total distance on the number of offspring for males ($N = 604$, $z = 1.002$, $p = 0.316$). Unlike males, a female's chance of having at least one surviving offspring was not influenced by dispersal status ($N = 753$, $z = -1.527$, $p = 0.127$), or dispersal distance ($N = 753$, $z = -1.204$, $p = 0.229$). Being classified as a disperser did have a marginally significant positive effect on the number of offspring in females ($N = 753$, $z = 1.864$, $p = 0.062$), as did total dispersal distance ($N = 753$, $z = 1.845$, $p = 0.065$, Figure 3a). Given the tight biological links between longevity and reproductive success, we re-ran our analyses on subsets of individuals of the same age, and found qualitatively similar results across longevities (Figures S6 and S7). We also conducted fitness analyses using absolute distance (distance between first and last capture locations) as a predictor, which gave us qualitatively similar results to our metric of total distance, and these analyses are described in Supplemental Materials Appendix 1.

We also analysed the effects of range on number of mates (Figure 3B). In these models, longevity, hybrid index and the interaction between lower hybrid index and being from Taylor all significantly increased number of mates. Range had a positive effect on number of mates for males ($N = 604$, $z = 2.754$, $p = 0.006$, Table 2), and a marginally significant effect on number of mates for females ($N = 753$, $z = 1.809$, $p = 0.070$, Table 2). For both sexes, we found no effect of range on the chance of having at least one mate ($N = 753$, $z = 1.224$, $p = 0.221$ for females, $N = 604$, $z = -0.970$, $p = 0.332$ for males). Tables 1 and 2 describe summary statistics for dispersal distance, range, reproductive success and number of mates. Detailed model outputs are provided in Tables S3-S6.

DISCUSSION

This study provides novel insights into the ecological drivers and evolutionary consequences of dispersal in two populations of Trinidadian guppies. Our results reveal variation in dispersal propensity and distances within and between our study populations, with size, genetic ancestry, and seasonality influencing dispersal. We found strong evidence for sex-specific reproductive benefits of dispersal consistent with observed patterns of male-biased dispersal behaviour, thus exemplifying how dispersal evolution can occur in natural populations.

Characterisation of dispersal behaviour

Our study directly measured fine-scale dispersal distances for all adult individuals in two populations of *P. reticulata* for over 1 year, adding to what is known about dispersal behaviour in natural settings and the specific characteristics of movement in this system. Overall, we observed some variation in dispersal between seasons and streams, but mostly consistent patterns: large male guppies were most likely to disperse, and the majority of fish moved short distances or not at all. Not surprisingly, the overall proportion of dispersers we observed over the course of a year (39% across both sexes and streams, Figure 2) was significantly higher than what was observed for a single recapture event (Croft et al., 2003; Reznick et al., 1996), but similar to estimates from a 5-year period (De Bona et al., 2019), suggesting that variation in dispersal can be adequately captured over the course of a year.

We also detected seasonal variation in dispersal distance in Taylor, where guppies were more likely to disperse downstream in the wet season, but not in Caigual (Figure S3). This was expected given that Taylor has a higher probability of flooding in the wet season, as it is a steeper and more channelised stream (Fitzpatrick et al., 2014). Floods, which primarily occur in the wet season, may therefore increase the prevalence of long-distance dispersal in the wet season in Taylor. We cannot determine whether increased wet season dispersal by *P. reticulata* is primarily active, due to floods and high water levels reducing dispersal barriers, or passive, due to fish being carried by stronger stream flows. We also note that while upstream dispersal can be interpreted as active, downstream movement could be either active or passive. There were no other strong biases in up- versus downstream dispersal, consistent with previous studies of *P. reticulata* dispersal (Crispo et al., 2006; Croft et al., 2003) and findings of positive rheotaxis in this system (Blondel et al., 2020). As a whole, these data suggest that guppy dispersal is often active, raising questions about the environmental and individual triggers of this behaviour.

In this study, we cannot draw conclusions about the causes of dispersal, but are instead interested in characterising dispersal patterns within these streams and understanding their fitness consequences. Similar to previous studies of *P. reticulata* (Croft et al., 2003; De Bona et al., 2019), we found that dispersal was male-biased: 42% of males and 36% of females in our study were classified as dispersers. This corroborates studies on a wide range of other species, supporting the hypothesis that polygynous mating systems tend to have male-biased dispersal (Trochet et al., 2016). The 'resource competition hypothesis' for the evolution of sex-biased dispersal (Greenwood, 1980) proposes that competition for local resources and mates leads to increased dispersal of the sex that most strongly competes

TABLE 2 Average and maximum values for range of all fish of both sexes in both streams, and for number of mates of dispersing (moved ≥10 m) and non-dispersing fish

Stream	Sex	Average range (m)	Maximum range (m)	Average number of mates per individual		Maximum number of mates	
				Non-dispersers	Dispersers	Non-dispersers	Dispersers
Taylor	F	14.38	173	0.64	1.17	7	8
	M	17.19	158	0.52	1.54	7	9
Caigual	F	9.65	56	0.42	0.48	4	7
	M	11.69	61	0.45	1.32	12	18

for mates, while extensions of this hypothesis suggest that systems in which female choice is prevalent should evolve male-biased dispersal (Dobson, 1982). Though abundant evidence supports these hypotheses in mammals and birds, data on other taxa remain scarce (Trochet et al., 2016), making *P. reticulata* an important example of how these ideas may apply to other species. Finally, contrary to our expectations, but in line with previous results (Croft et al., 2003), we found that larger males dispersed more often and farther—suggesting that larger fish are more likely to leave local pools or survive dispersal. This may be because larger fish are less susceptible to predation by gape-limited predators (Gosline & Rodd, 2008), better at acquiring resources (Potter et al., 2019), or stronger swimmers (more able to resist passive downstream movement and/or complete active upstream movement; Kieffer, 2000; Radinger & Wolter, 2014).

Fitness correlates of dispersal

Quantifying the fitness of dispersing individuals is a fundamental step towards understanding how dispersal shapes the ecology and evolution of natural populations. Successful gene flow between populations, colonisation of new environments, and maintenance of range boundaries all crucially depend on the ability of dispersing individuals to reproduce. We found strong effects of dispersal on reproductive success in our study: 60.25% of non-dispersers had zero offspring, compared to only 37.79% of dispersers. We also saw a trend towards increased number of offspring for dispersers, where dispersing males had 35% more offspring than non-dispersing males when holding all other variables constant. Given that most fish do not leave behind any successful offspring, this metric reflects the most important reproductive achievement in these populations, namely, having at least one offspring survive to the minimum markable size of 14 mm (Figure S1a). Thus, our results demonstrate that dispersal is a major factor in male reproductive success.

Several aspects of guppy natural history and mating biology may contribute to the increased reproductive output of dispersing males. Theoretical models for the evolution of sex-biased dispersal suggest that the strength of selection for male dispersal in polygynous systems depends on female choice, kin recognition and the strength of inbreeding depression in the system (Lehmann & Perrin, 2003). In *P. reticulata*, female choice plays a major role in determining male reproduction, such that increasing encounters with females is in itself not sufficient to increase number of successful matings (Daniel & Rodd, 2016; Pitcher et al., 2008; Zajitschek & Brooks, 2008). Rather, females prefer unrelated males and those with novel phenotypes, and are able to differentiate between kin and non-kin individuals (Daniel & Rodd, 2016, 2020; Hampton et al., 2009; Hughes et al., 1999, 2013). Female preference may be important for inbreeding avoidance in this system, given ample evidence that guppy populations in small headwater streams such as Caigual and Taylor can suffer from significant inbreeding depression (Crispo et al., 2006; Fitzpatrick et al., 2014, 2016; Van Oosterhout et al., 2003). Male colour, a key phenotypic marker used in female choice, is highly heritable (Endler, 1980; Endler & Houde, 1995; Kemp et al., 2009), such that dispersal between pools may offer males a chance to exploit unrelated females' preference for novelty. Overall, the correlation between fitness and dispersal we observed for males reflects a selective pressure for increased dispersal resulting from the combination of female choice and inbreeding avoidance in this system, providing an empirical example for how these factors interact to shape dispersal evolution.

Unlike males, females' chances of having at least one surviving offspring were not affected by any dispersal metric. If female choice is adaptive (e.g. inbreeding avoidance or 'good genes'; Anderson, 1982; Kodric-Brown & Brown, 1984; Perrin & Mazalov, 1999; Pusey & Wolf, 1996; Zahavi, 1977), we would expect females that dispersed farther to benefit from a larger pool of available mates, potentially leading to the observed trend in higher number of offspring for dispersing females. However, female reproduction in polygynous systems is more directly limited by resources than mates (Greenwood, 1980; Magurran, 2005; Perrin & Mazalov, 2000). For example, a study on density-dependent dispersal in *P. reticulata* found that females were likely to disperse out of high density pools (De Bona et al., 2019). Again, these findings are in line with hypotheses for the evolution of sex-biased dispersal in polygynous species: increased philopatry in resource-limited females and increased dispersal in mate-limited males (Greenwood, 1980; Lehmann & Perrin, 2003; Perrin & Mazalov, 2000).

Given the observed reproductive correlates of dispersal, males in the studied populations are under strong selection to disperse. Yet, dispersal was generally limited and occurred over short distances, even for males (Figure 2). One potential explanation for these contrasting results is the relationship between local adaptation, habitat heterogeneity, and dispersal in this system. *P. reticulata* populations adapted to low predation levels are likely to incur severe survival costs if they disperse into stream sections with higher predation, as will any of their offspring that retain low-predation phenotypes such as brighter coloration and weaker antipredator behaviours (Endler, 1980, 1987; Haskins et al., 1961; Magurran & Seghers, 1991; Reznick et al., 1996, 2001). As a consequence, this local adaptation to a gradient in predation regime should limit dispersal propensities through selective deaths of maladapted dispersers and/or adaptive dispersal decisions by individuals (Berdahl et al., 2015; Bolnick & Otto, 2013; McPeek & Holt, 1992). In other words, if dispersal is beneficial at the within-reach, between-pool scale––where we observed reproductive benefits—but costly between steep environmental gradients, most individuals should disperse only small distances.

In natural systems, it is notoriously difficult to directly determine causality between a behaviour, such as dispersal and reproductive success. In an observational study such as this, it is always possible that unaccounted for variables may lead to the observed correlation between reproductive success and dispersal. We dealt with this issue by including two important drivers of fitness and dispersal, longevity and size, as covariates in all our models of reproductive success. Though longevity and size are significant predictors of both dispersal distance and lifetime reproductive success in our system (Figure S2), accounting for them in our models allows us to statistically separate their effects on fitness from those of dispersal status and distance. Within the constraints of an observational study of natural populations, our approach strongly suggests a causative link between dispersal and reproduction, yet experiments that directly manipulate dispersal and longevity would be needed to fully disentangle these factors.

CONCLUSIONS

We provide empirical evidence that fine-scale dispersal correlates to reproductive benefits in *P. reticulata*. Our study highlights the value of multi-generational capture–mark–recapture data for understanding individual consequences of dispersal, especially when paired with fitness estimates from molecular data. Our characterisation of dispersal and reproductive success sheds light on how the benefits of dispersal behaviour vary between individuals and environments. Given drastic reductions in population connectivity caused by anthropogenic changes to the environment across the globe (Haddad et al., 2015), understanding patterns of dispersal and its consequences for fitness in natural populations will be vital to understanding population persistence in the future (Crispo et al., 2011; Kokko & López-Sepulcre, 2006).

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AUTHOR CONTRIBUTIONS

SWF, WCF and LMA conceived of the study; SWF collected the data; ILB and JCD analysed the data and wrote the first draft of the manuscript, and all authors contributed to subsequent writing of the manuscript.

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DATA AVAILABILITY STATEMENT

If the manuscript is accepted, all data supporting the results will be archived in Dryad, and the data DOI will be included in the article (https://doi.org/10.5061/dryad.2280gb5t6).

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