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The Evolution of Dispersal in the Trinidadian Guppy (*Poecilia reticulata*)

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by

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ABSTRACT OF THE DISSERTATION

The Evolution of Dispersal in the Trinidadian Guppy (*Poecilia reticulata*)

by

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For decades there has been considerable interest in understanding how variation in dispersal arises in nature. However, studying the dispersal of natural populations in an evolutionary framework is logistically challenging, thus, much of what we know about dispersal evolution comes from studies performed in artificial environments or in species with simplified dispersal morphologies. The objective of this dissertation is to examine how divergent natural populations vary in their tendency to disperse. To do so, I examined dispersal in guppies (*Poecilia reticulata*) across the Northern Range Mountains of Trinidad. In Chapter 1, I used spatially-explicit, mark-release-recapture experiments to identify differences in dispersal patterns among natural populations adapted to high- and low-levels of predation. I found that across all comparisons, the high-predation (HP) individuals were more likely to disperse and dispersed further than their low-predation (LP) counterparts. In Chapter 2, I collected HP and LP guppy populations and tested for movement differences in multi-patch stream mesocosms. I found that HP guppies are more inclined to move and make more movements within the mesocosms. In Chapter 3, I

collected and reared wild HP and LP populations to a F2 generation and used multi-patch stream mesocosms to compare their movements with wild populations. The results revealed that the movement differences are retained even after being reared in a common environment, which suggests that dispersal has a strong genetic component. In Chapter 4, I experimentally displaced fish and examined whether there is intraspecific variation in homing success that is related to predation regime or dispersal status. I found no association between homing success and dispersal at the individual level, but I found a strong effect of phenotype. HP individuals exhibited greater homing success compared to LP fish. Across all 4 chapters I have documented consistent and predictable differences in dispersal traits between HP and LP populations. These studies include 6 evolutionarily independent replicates, two of which were experimental introductions. Overall, this work highlights the ecological and evolutionary relevance of intraspecific, genotypic variation in dispersal tendency and demonstrates that dispersal evolves under selective regimes that also drive the rapid evolution of life history traits.

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Prologue

Many of the world's ecosystems are entirely different than they were just a century ago. These differences include land cover change for human development or agriculture, overexploitation of natural resources, invasion of non-native species, and climate change, to name a few (Nelson et al. 2006). This extreme shift in environmental conditions is likely to leave many species with just two ways of persisting: adapt or disperse. Adaptation to living in a population's historical range may not always be possible because this environmental change is rapid and may include the addition of detrimental interspecific interactions, loss of beneficial interactions, and vast abiotic changes. Therefore, one of the most important traits that will determine a species ability to cope with rapidly changing environments is dispersal (Thompson and Fronhofer 2019, Román-Palacios and Wiens 2020). In this context, we will need to understand which species have the capacity to disperse as well as how that dispersal might evolve in response to rapid, global scale environmental change. However, we still are limited in what we know about how dispersal evolves in nature, and this gap in knowledge limits our ability to predict the outcomes of populations and species exposed to climate change and habitat degradation, among many other applied ecological problems.

Dispersal can be defined as any movement of an individual that has the potential for gene flow (Ronce 2007). Many definitions of dispersal exist, some more or less strict than this definition (Bowler and Benton 2005, Clobert et al. 2012, Duputié and Massol 2013), however, I use this definition here because it encompasses both the physical movement of an individual and the potential evolutionary consequence of dispersal,

which is gene flow, or the incorporation of the migrant into the local gene pool or successful establishment of a new population. This definition is commonly used and can be applied to a wide range of systems. Dispersal can also be viewed as a complex phenotype that is both multidimensional and genetically variable amongst individuals, populations, or species (Saastamoinen et al. 2018).

Dispersal occurs in three stages (departure/emmigration, transfer, settlement/immigration). Each of these stages can be influenced by a unique combination of environmental and evolutionary forces (Clobert et al. 2009, 2012). As such, dispersal is often described by numerous dispersal traits (e.g. dispersal propensity, dispersal distance, etc.) which describe different aspects of the dispersal process. The interaction between these traits forms the complex, multivariate phenotype that is broadly referred to as "dispersal". Furthermore, these dispersal traits may also be associated with other phenotypic traits (as a result of evolutionary trade-offs or correlated responses), resulting in what is commonly referred as a "dispersal syndrome" (Ronce and Clobert 2012, Stevens et al. 2013, 2014).

Dispersal can occur passively, where movement is largely controlled by external environmental forces, or actively, where the individual controls its own locomotion (Matthysen 2012). Plants, microbes, invertebrates, and other small species with low mobility often rely exclusively on passive dispersal. The environmental forces responsible for the movement of these species can include wind, water currents, gravity, or even other organisms (Nathan et al. 2008, Fontaneto 2019, Seale and Nakayama 2020). Conversely, active dispersal is common for most species that aren't limited by

their own mobility (Matthysen 2012). Many actively dispersing species may also move passively from time to time. For example, stream fish may be washed downstream passively during storms or periods of unusually high water flow (Chapman and Kramer 1991). Overall, the mechanisms for movement and the selection on these mechanisms can vary widely across the animal kingdom.

The evolution of dispersal has been a major interest to theoretical biologists for over five decades, and in that time a robust body of knowledge has accumulated. Modern theory predicts that dispersal is non-random, dependent on condition, environment, and/or phenotype, and driven by numerous selective pressures (See reviews: Bowler and Benton 2005, Clobert et al. 2012, Duputié and Massol 2013). Of these selective pressures, spatiotemporal heterogeneity and dispersal costs receive the most attention, however, kin competition, inbreeding avoidance, mating systems, and other mechanisms can also select for alternative dispersal strategies.

Theory predicts that spatial heterogeneity selects against dispersal because high-quality sites will support a greater number of individuals, and on average, individuals will move from sites with high fitness potential to low fitness potential. By contrast, temporal heterogeneity is expected to select for dispersal, because a site with high fitness potential will ultimately transition to a site with low fitness potential (Hastings 1983, Holt 1985, McPeek and Holt 1992, Bowler and Benton 2005, Duputié and Massol 2013). These predictions become more complicated when the predictability, magnitude, and frequency of the spatiotemporal heterogeneity are considered (Travis 2001, Blanquart and Gandon 2011, Massol and Cheptou 2011).

Dispersal evolution is also driven by a fine balance between the costs and benefits of dispersal, thus, any time the costs of dispersal increase dispersal is selected against, and vice-versa (Bonte et al. 2012, Duputié and Massol 2013). The costs of dispersal can come in four forms: time, energy, risk, and opportunity costs (Bonte et al. 2012). Dispersing from one habitat to another takes time, and this time could have been spent foraging, mating, or performing other beneficial functions. There are also energetic costs associated with moving from one patch to another. These can be high for species that disperse long distances, through dangerous terrain or need to develop specialized morphologies to disperse, and alternatively, these costs can be low for species that only need to expend small amounts of metabolic energy to move to neighboring habitats, and even lower or nearly zero for species that disperse passively (Roff 1984, Fish et al. 2001, Aarestrup et al. 2005, Bonte et al. 2012). Risk costs include the potential settlement in an unfavorable habitat, the increased chance of detection by a predator during transit, and greater injury related losses in fitness when movement distances are far and the resources throughout the journey are scarce (Bonnet et al 1999, Bonte et al 2012, Nafus et al 2017). Opportunity costs encompass the loss of advantages associated with habitat familiarity or local adaptation. When individuals disperse they forego their knowledge of the location and availability of resources, they may lose their social status, and they may suffer greater levels of intra-and inter-specific competition. A more noteworthy case of opportunity cost occurs when locally adapted individuals disperse beyond their original habitat type, ultimately suffering from greater mortality and/or decreased fecundity (Blondel et al. 1993, Burt 1995).

The benefits of dispersal can include the escape of poor conditions, increased access to mates or resources, reduced competition and inbreeding amongst relatives, and increased variance in fitness from the distribution of offspring over heterogenous conditions, also referred to as bet hedging (Matthysen 2012).

The costs and benefits associated with dispersal are often different among alternative dispersal strategies as well as among the different stages of dispersal (departure, transfer, and settlement). In fact, the same environmental force may produce opposing selective pressures depending upon the stage of dispersal. For example, at the departure stage, dispersal is generally predicted to increase with the risk of predation (Weisser 2001). Mathematical models also suggest that increased risk of population extinction, which can be driven by predators, should drive increases in emigration rate (Johnson and Gaines 1990). Furthermore, the oscillatory nature of predator-prey dynamics can also select for increased prey emigration (Savill and Hogeweg 1999). In contrast, dispersal may be selected against due to the costs associated with the transit stage (Weisser 2001, Bonte et al. 2012). These costs increase as the time and distance it takes to disperse increases, due to greater attrition and increased chances of encountering a predator. Thus, as the potential for predation during transit increases, dispersal rates are predicted to decrease (Dieckmann et al. 1999). Ultimately, the net effect of predation on dispersal may vary depending on the relative intensity during each stage.

The rate at which dispersal occurs was initially thought to evolve as a direct, linear relationship with the cost of moving. One of the first dispersal models, developed by Hamilton and May (1977), evaluated the evolutionarily stable strategy (ESS) dispersal

rate as a function of the probability of surviving a dispersal episode; $v = 1/(2 - p)$, where v is the ESS dispersal rate and p is the probability of surviving a dispersal event. This model built the foundation for a multitude of other early ESS-based dispersal models (Comins et al. 1980, Hastings 1983, Holt 1985), and as a result, most of these models included some critical parameter that involves the costs of dispersal (Johnson and Gaines 1990, Gandon 1999). Historic and modern models generally predict lower levels of dispersal as costs increase, but this relationship is not always linear, especially in the presence of other selective pressures or complex dispersal phenotypes (Johnson and Gaines 1990, Billiard & Lenormand 2005, Duputié and Massol 2013). Ultimately, alternative dispersal strategies are likely to arise when the costs and benefits to dispersal vary among populations.

In contrast to its theoretical treatment, our empirical knowledge of dispersal evolution is still lacking. This is often because the empirical study of dispersal evolution is difficult and often constrained by logistical challenges (Hilário et al. 2015, Johnson et al. 2019, Swearer et al. 2019). Small organisms may be impossible to identify individually, and large organisms may disperse distances far beyond what is feasible to survey. Issues with sample size also exist when attempting to track certain organisms, and this is compounded by the fact that dispersal can be a rare event (Nathan 2001). As such, a large majority of empirical work has occurred in a limited range of taxa, predominately in species with discrete dispersal polymorphisms (e.g., wing dimorphic insect species), in systems where dispersal may be easily observed, or where dispersal can be measured in an artificial environment. Despite their importance for evaluating the

causes and consequences of dispersal, many of these studies are performed in systems which lack the complexity and stochasticity needed to produce the dispersal patterns observed in nature. Some studies have managed to document the rapid evolution of dispersal traits in natural or semi-natural settings, but these are exceedingly rare and often require a complex and rigorous combination of multiple experimental approaches.

Furthermore, thorough investigation of the drivers of dispersal rarely occurs at the population level. This choice rests upon the assumption that dispersal, like other life history traits, will vary more between species than within species, such that populations within a species vary negligibly in dispersal (Stevens, Pavione, and Baguette 2010). Thus, many demographic models use a single species-specific dispersal function to model spatially structured population dynamics (Hanski 1999, Jongejans, Skarpaas, and Shea 2008). If dispersal does indeed vary among populations, such assumptions may diminish the ability to accurately model the complexity of natural systems and the contribution of dispersal to ecological and evolutionary processes. Moreover, if dispersal has a genetic basis and responds to selection, then divergent selection pressures amongst populations should produce different dispersal strategies. Variation in dispersal strategies might emerge rapidly, but that will ultimately depend upon the genetic architecture, the variance in dispersal, and associations with other traits under selection (Orr 2005, MacKay et al. 2012, Saastamoinen et al. 2018). Overall, these methodological constraints and simplified treatment of dispersal limit our ability to make and test predictions about how dispersal traits respond to novel selection pressures.

While limited, there are some recent examples that demonstrate that dispersal can evolve rapidly and on ecological timescales. Some of the best examples of this are range-expanding species, where genetic variation in dispersal arises due to the spatial sorting of alleles (Travis and Dytham 2002, Phillips et al. 2010, Perkins et al. 2013, Ochocki and Miller 2017). During range expansion there is an abundance of highly dispersive phenotypes at the range margin, which leads to assortative mating among dispersive phenotypes. If dispersal is heritable, then this is likely to produce an equal or greater propensity to disperse in the following generation (Shine et al. 2011). These increases in dispersal rate are often associated with morphological, behavioral, and life history adaptations. A prime example of this process is the colonization and expansion of cane toads (*Bufo marinus*) in Australia. This species was introduced approximately 85 years ago for pest control within agricultural fields; however, they have spread rapidly across Australia and are one of the best studied examples of range expansion and dispersal evolution. The populations at the invasion front disperse significantly further than their range-core counterparts and this increased dispersal is associated with morphological and behavioral adaptations that enhance dispersal (Phillips et al. 2006). The morphology of the head, pectoral and pelvic girdles, and limbs are significantly different between range-core and invasion-front populations and serve to enhance the movement capabilities of the invasion-front populations (Hudson et al. 2016). The behavioral changes also enhance dispersal; the invasion-front populations exhibit a greater path straightness in their dispersal trajectories relative to the range-core populations (Brown, Phillips, and Shine

2014). These adaptations, in combination with spatial sorting at the range margins, likely facilitates the rapid evolution of dispersal and the acceleration of range expansion.

Another excellent example of intraspecific variation in dispersal traits involves the Glanville Fritillary butterfly populations that occur on the Åland Islands in Finland, where they exist across a network of thousands of small meadows (Hanski 1999). Extinction and recolonizations of these butterfly populations occurs frequently, and individuals from newly established vs. older populations often have a distinctly different set of dispersal and life-history traits (Hanski et al. 2004, Saastamoinen 2007). These polymorphisms are associated with changes in allele frequencies responsible for the regulation of a metabolic enzyme, *pgi* (Hanski et al. 2004, Mattila and Hanski 2014). Additionally, alleles from a separate gene, *sdhd*, have been shown to influence respiratory efficiency and flight endurance, which also influences dispersal abilities. Moreover, certain alleles within the *sdhd* gene have epistatic interactions with *pgi* (Wheat et al. 2011). Overall, the landscape structure, frequent extinction and recolonization of patches, genetic architecture, and correlation with other life history traits interact in such a way that dispersal evolves rapidly and in a relatively consistent manner (Hanski 2011).

Despite these examples, our empirical evidence of rapid dispersal evolution in a natural setting is still quite scarce, especially in systems where rapid range expansion, spatial sorting, or habitat fragmentation are not the main drivers of dispersal evolution. Further study of dispersal evolution across novel suites of selective pressures is required to build a robust and thorough body of knowledge that facilitates the prediction of how species might respond to novel shifts in environmental and selective conditions.

Study system

A potentially valuable system for examining rapid dispersal evolution in a natural system is the guppy, *Poecilia reticulata*. Guppies are native to the freshwater streams of Trinidad where they can be found across alternative environments that vary in ways that produce differences in life histories, and these differences might also shape the evolution of dispersal (Reznick and Endler 1982, Endler 1995, Reznick et al. 1996, 2001, 2019, Travis et al. 2014). In high predation (HP) habitats, guppies co-occur with several piscivorous cichlids and characins, among other species (Haskins 1961, Seghers 1973). Guppies from these HP sites have repeatedly dispersed upstream across a series of barrier waterfalls that exclude predators. In these low predation (LP) sites, guppies co-occur with only one other fish species, the killifish *Anablepsoides hartii* (previously *Rivulus hartii*), which rarely preys on guppies, and when it does, it preys almost exclusively on immature size classes (Seghers 1973, 1974). Guppies from LP sites experience drastically lower predation risk, which results in twofold increases in guppy density and fourfold increases in biomass (Reznick, Butler, and Rodd 2001). This transition from HP to LP habitat is accompanied by a shift from top-down to bottom-up population regulation, which drives a rapid shift in life histories (Reznick and Endler 1982, Reznick et al. 1997, Bassar et al. 2013). Guppies adapted to LP sites have slower growth rates, lower investment in reproduction, and an older age at maturity than their HP counterparts. LP guppies are larger on average because of the absence of predation risk on large size classes (Reznick et al. 1997, Travis et al. 2014). This life history evolution is further associated with many behavioral adaptations. For example, HP guppies school more often while LP guppies are

more likely to experience intraspecific aggression (See Table 1 in Endler 1995). Furthermore, many of these life history adaptations have a genetic basis (Reznick and Endler 1982). These coupled changes in ecology and evolution make guppies an ideal organism for investigating the evolution of dispersal strategies.

High- and low-predation guppy populations also vary significantly in their levels of isolation and gene flow, and these might have profound consequences for the evolution of dispersal traits. The barriers which separate HP and LP populations often include large waterfalls or other features that make upstream dispersal extremely rare, if not impossible. The efficacy of these barriers is evidenced by that fact that some of these populations were only established because they were introduced by scientists. Thus, individuals may move freely from LP sites to HP sites, but not in the reverse direction. If dispersal has a genetic basis, then genes that increase dispersal tendency will gradually be lost as these individuals disperse across the barriers that separate HP and LP. Thus, it is possible that these LP populations have evolved a decreased tendency to disperse relative to their downstream counterparts due to this asymmetric gene flow.

While limited, there have been a few studies which have focused on the dispersal of guppy populations. These studies have shown that male-biased dispersal exists (Croft et al. 2003), that density-dependent dispersal varies across guppy life stages and throughout a population colonization (De Bona et al. 2019), and that there are reproductive benefits associated with dispersal (Borges et al. 2021). There has also been a suite of studies that analyze variation in behavioral traits that are strongly associated with dispersal across other systems (Endler 1995, Harris et al. 2010, Blondel et al. 2020).

However, there has been no direct examination of whether dispersal traits vary amongst high- and low-predation populations of guppies. Regardless, these previous studies confirm that the guppy is an appropriate and relevant system for studying the evolution of dispersal.

Research outline

Here, I take advantage of the repeated invasion of HP guppies (*Poecilia reticulata*) into LP habitat, which occurred naturally and through the artificial introductions of HP guppies into LP habitat (Reznick and Bryga 1987, Gordon et al. 2009). Thus, this system not only allows for a fully replicated analysis of whether dispersal evolves, but it can address whether this evolution can occur on a contemporary timescale or under spatial dynamics that differ from a natural colonization.

To fully address the evolution of dispersal in guppies, I utilize a combination of mark-release-recapture, artificial stream mesocosm, common-garden, and translocation experiments. I begin by evaluating the differences in dispersal traits across pairs of natural HP and LP populations via spatially-explicit, mark-release-recapture methods (Chapter 1). Then, I compare these results to the movement tendencies of natural HP and LP guppy populations in an artificial stream mesocosm, where I control for and manipulate factors which may influence dispersal (Chapter 2). This experiment, in combination with the mark-recapture experiment, provides an excellent examination of the variation in dispersal amongst HP and LP populations of guppies, however, it does not determine whether a genetic basis for dispersal exists. Thus, I utilize a common garden approach to address this shortcoming; I rear HP and LP guppy stocks to a F2

generation and compare their movement tendencies with wild-caught individuals from their ancestral populations (Chapter 3). Doing so allows for an assessment of whether a genetic component underlies the observed variation in dispersal traits. Finally, I use additional mark-recapture experiments in combination with translocations to assess how dispersal traits are related to homing ability and whether intraspecific variation in homing success exists amongst HP and LP populations (Chapter 4).

Overall, this work aims to develop a better mechanistic understanding of how dispersal responds to natural selection. Through a series of experiments and observations, I address how dispersal traits evolve among guppy populations adapted to fundamentally different sources of population regulation. I do so by considering each condition necessary for natural selection to operate, as well as considering other traits and environmental factors which may be related to dispersal or influence the way in which dispersal traits evolve. The experimental design also allows for the examination of populations that developed their phenotypic differences relatively recently and under spatial conditions that differ from a normal colonization event. Ultimately, this dissertation aims to investigate whether the same forces responsible for producing rapid evolutionary shifts in life history can also produce consistent, predictable, and genetic changes in dispersal amongst populations exposed to alternative suites of selections pressures. Such knowledge will enhance our understanding of how multiple selective pressures in nature interact to produce changes in dispersal patterns, and this will inherently improve our ability to forecast the fate of populations exposed to environmental change, habitat degradation, and other forms of detrimental disturbance.

Chapter 1: Quantifying dispersal variability across paired high- and low-predation populations of guppies (*Poecilia reticulata*)

Abstract

Recent work has shown that intra-specific variation in dispersal behavior can be strong and can arise under a suite of different selective regimes. These studies also demonstrate that dispersal can evolve rapidly and on the same time scale as changes in local ecology. Despite its importance, our empirical evidence of rapid evolution of dispersal in nature is still limited. Here, I address that limitation by evaluating intra-specific variation in dispersal across natural populations of the Trinidadian guppy (*Poecilia reticulata*). Guppy populations exist in alternative types of habitats that have produced rapid, consistent and predictable differences in morphology, behavior, and life-history traits. The pairs of populations analyzed here encompass a historic population and two experimental introductions of high-predation (HP) guppies into previously guppy-free low-predation (LP) habitats. I evaluate dispersal in these populations with spatially explicit, individual-based mark-release-recapture experiments. I found that HP populations have a greater propensity to disperse and disperse greater distances relative to their LP counterparts. These results were consistent across all three pairs of populations. I also found population-level differences in dispersal direction, which further depends on local density. Thus, I've shown that the same conditions which produce intraspecific variation in life history traits are associated with consistent and predictable differences in dispersal traits, and that these differences in dispersal can arise rapidly in both natural and experimental introductions.

Introduction

Dispersal influences the ecology and evolution of almost all natural populations. Populations are spatially structured such that active dispersal among patches allows individuals to escape poor local conditions, select advantageous habitats and improve fitness. Thus, the tendency and ability to disperse becomes a key component of an organism's life history (Bonte and Dahirel 2017). Dispersal shifts allele frequencies within and among populations, and because of this, it can have population genetic consequences, like facilitating or constraining local adaptation (Wright 1932, Bowler and Benton 2005). Moreover, dispersal is a central component of many applied ecological issues, such as predicting the movement of invasive species and forecasting the fate of natural populations and communities exposed to climate change and habitat degradation (Melbourne and Hastings 2009, Travis et al. 2013, Phillips 2015, Thompson and Fronhofer 2019).

Traditional ecological theory largely ignores within-species variation in dispersal. This choice rests upon the assumption that dispersal, like other life history traits, will vary more between species than within species, so that populations within a species vary negligibly in dispersal (Stevens, Pavione, and Baguette 2010). Thus, many demographic models use a single species-specific dispersal function to model spatially structured population dynamics (Hanski 1999, Jongejans, Skarpaas, and Shea 2008). If dispersal does indeed vary among populations and if dispersal is a readily evolvable trait, then treating dispersal as a constant may diminish the ability of these models to accurately capture the complexity of natural systems.

The available empirical evidence argues against this assumed lack of variation in intraspecific dispersal. Some examples of dispersal variation come from populations exposed to habitat fragmentation (Thomas, Hill, and Lewis 1998, Hanski, Saastamoinen, and Ovaskainen 2006, Cheptou et al. 2017) and those which are expanding their ranges (Phillips et al. 2006, 2010, Ochocki and Miller 2017). Fragmentation can drive the evolution of either a decrease or increase in a population's dispersal rate, depending heavily upon the costs of transfer and the potential for colonization (Cote et al. 2017, Saastamoinen et al. 2018). The amount of genetic variation in dispersal traits may also impose constraints upon this process. Range-expanding species also provide evidence for genetic variation in and the evolution of dispersal. For example, newly established populations on the range margins often have inherently higher dispersal rates than individuals found within the core of the species range (Travis and Dytham 2002, Phillips, Brown, and Shine 2010, Perkins et al. 2013). This gradient of dispersal occurs because of spatial sorting; the most dispersive individuals on the range margins mate assortatively with other dispersive individuals, thus creating an even greater propensity to disperse in the following generation (Shine et al. 2011). This generational change in dispersal tendency highlights the reality of intraspecific variation, but also serves as an example of how evolutionary changes in dispersal can interact with ecological dynamics.

While the evidence for intraspecific variation in dispersal is strong, it is severely limited in scope. The results are taxonomically biased towards a few systems where dispersal is easily tractable and genetic determinism can be established. Dispersal is incredibly intricate and responds to a wide variety of spatial and ecological pressures,

thus, a greater breadth of dispersal studies is needed before we can confidently generalize across systems and organismal groups that represent the complexity of dispersal strategies that we see in the natural world.

Here, I assess intraspecific variation in dispersal among divergent populations of guppies. The guppy, *Poecilia reticulata*, is a model organism for studying how predation risk influences rapid life history evolution in natural settings (Reznick, Bryga, and Endler 1990, Reznick et al. 2019). Guppies are native to the freshwater streams of Trinidad where they can be found in alternative habitats that might select for alternative dispersal strategies. Below, I describe the comparative life history of high- and low-predation guppies and explain why these differences might also be associated with variation in dispersal.

Comparative life-history of high- and low-predation guppies

In high-predation (HP) habitats, guppies co-occur with a diverse suite of piscivorous predators, such as the pike cichlid, *Crenicichla alta*, or the wolf fish, *Hoplias malabaricus* (Haskins 1961, Seghers 1973). Guppies from these HP sites have repeatedly dispersed upstream across a series of barrier waterfalls that exclude almost all predator species (Endler 1978). In these low-predation (LP) sites, guppies co-occur with only one other fish species, the killifish, *Anablepsoides hartii* (formerly *Rivulus hartii*), which rarely preys on guppies (Seghers 1973, 1974). When it does, it preys selectively on immature size classes. Once guppies colonize these low predation habitats they rapidly adapt to the dramatic shift in selection pressures (Reznick et al. 1997). This rapid shift from HP to LP is associated with a twofold increase in guppy density and a fourfold

increase in biomass (Reznick, Butler, and Rodd 2001, Potter et al. 2018). This causes a change from top-down to bottom-up population regulation, which drives a rapid shift in life histories (Reznick and Endler 1982, Bassar et al. 2013). In fact, much of this life history evolution is an indirect effect of high population density in the LP populations (Reznick et al. 2019).

Previous research has demonstrated that LP guppies have slower growth rates, lower investment in reproduction, and an older age at maturity, among dozens of other phenotypic differences (See table 1, Endler 1995, Reznick and Bryga 1996). LP guppies are larger on average because of the absence of predation risk on large size classes. This life history evolution is further associated with many behavioral adaptations. For example, HP guppies exhibit stronger schooling behavior while LP guppies are more likely to experience intraspecific aggression (Seghers 1973, Seghers 1974, Seghers and Magurran 1991). LP guppies also have a greater sustained swimming ability, whereas HP guppies have a faster burst speed (Nicoletto and Kodric-Brown 1999, O'Steen et al. 2002, Ghalambor et al. 2004, Gordon et al. 2015). Many of these life history adaptations have a genetic basis and have evolved independently across each of the drainages in the Northern Range Mountains (Reznick and Endler 1982). Overall, these coupled changes in population regulation, ecology and evolution make guppies an ideal organism for investigating the evolution of dispersal strategies.

Here, I outline competing hypothesis for why high- and low-predation guppies might have evolved differences in dispersal tendency. Greater dispersal in the low predation populations might be explained by the lasting effects of spatial sorting or the

costs of dispersal, whereas greater dispersal in the high predation populations might be explained by asymmetric gene flow and isolation, or associations with life history (Table 1.1).

Evolutionary history of the populations

The evolutionary history behind the colonizations of the high and low predation populations might explain any observed differences in dispersal. This is because the LP phenotype is derived from the ancestral HP phenotype across all of the Northern Range Mountains (Alexander et al. 2006). What this means is that LP populations are all younger than their HP counterparts, and these newly established LP populations were likely established by individuals that were more dispersive than the range-core. If dispersal is heritable, then this could lead to the persistence of greater dispersal rates in the LP populations. This effect is more commonly referred to as spatial sorting or spatial selection and has been demonstrated in nature (e.g. Australian cane toads: Phillips et al. 2006, Hudson et al. 2016). When range expansion occurs, there is an abundance of highly dispersive phenotypes at the leading edge of the range margin, which leads to assortative mating among dispersive phenotypes. If dispersal is heritable, then this can produce an equal or greater propensity to disperse in the following generation (Shine et al. 2011). These effects can be strong and produce divergent dispersal strategies that are also associated with morphological, behavioral, and life history changes.

Thus, if the evolutionary history produces differences in dispersal, then I might expect LP populations to have a greater tendency to dispersal. However, I would not expect the patterns of variation to be consistent among natural and artificial introductions.

This is because the individuals that colonized the LP sites in the experimental introductions were a random selection of fish from the range-core instead of individuals which naturally breached significant barriers and colonized LP sites.

Costs and benefits of dispersal

Theory predicts that alternative dispersal strategies are likely to arise when the costs and benefits to dispersal vary among populations (Clobert et al. 2012, Duputié and Massol 2013). It is the relative magnitude of the costs and benefits that determines the selection on dispersal, and this balance is likely different in high- and low-predation populations of guppies.

The costs of dispersal can come in four main forms: time, energy, risk, and opportunity costs (Bonte 2012). Time and energy costs are the direct costs associated with the time and energy invested into dispersal. Risk costs include the costs associated with increased mortality risk for dispersers. Opportunity costs encompass the costs of losing benefits associated with being adapted to or familiar with a specific habitat.

Dispersal in HP sites is almost certainly accompanied with higher risk and opportunity costs. This is because movement is likely to increase the probability of being detected by a predator. Also, dispersal for high-predation fish also means foregoing the social benefits associated with schooling and conspecific familiarity. Conversely, movement in LP sites has little costs as it is not associated with an increase in predation. Moreover, the social benefits for LP fish are less pronounced (Seghers and Magurran 1991), and foregoing these might not have much of a detriment to the individual. However, if the habitat is stable and spatially heterogenous, then movements may, on

average, be accompanied by a decrease in resource and/or mate availability (Bowler and Benton 2005, Duputié and Massol 2013). The time and energy costs associated with dispersal are unlikely to differ between HP and LP populations in any significant manner. Overall, the differences in dispersal costs suggest that dispersal should be greater in LP populations.

The benefits of dispersal can include the escape of poor conditions, increased access to mates or resources, reduced competition and inbreeding amongst relatives, and increased variance in fitness from the distribution of offspring over heterogenous conditions, also referred to as bet hedging (Matthysen 2012). For HP individuals, dispersal may allow escape from patches with high predation risk, and as a result might increase survival. For LP individuals, dispersal has some reproductive benefits (Borges et al. 2021) and may also allow escape from intense intraspecific competition, leading to acquisition of more resources and a higher growth rate, but these benefits might be marginal and diminish for the larger size classes. Overall, it is possible that these benefits are greater for HP individuals. This is because dispersal in HP might serve to improve survival, whereas dispersal in LP sites improves growth or reproduction. Comparisons of LP and HP individuals have demonstrated that the survival component of fitness outweighs that of growth or probability of reproduction (Bassar et al. 2013, Bassar et al. 2017). Thus, dispersal may be incredibly important for HP populations as it may increase survival, whereas in LP sites dispersal may allow for marginal increases in reproduction or growth, which has diminishing benefits as fish mature and reach larger size classes, however, it is unlikely that these outweigh the high costs of moving in HP habitats.

Isolation and asymmetric gene-flow

Guppy populations vary in their levels of isolation and gene flow, and this might produce differences in how dispersal evolves. The barriers which separate HP and LP populations include large waterfalls that make upstream dispersal extremely rare, if not impossible. The efficacy of these barriers is evidenced by that fact that some of these populations were only established because they were introduced by scientists. Thus, individuals may move freely from LP sites to HP sites, but not in the reverse direction. If dispersal has a genetic basis, then genes that increase dispersal tendency will gradually be lost in the LP populations as these individuals disperse across the barriers that separate HP and LP. The association between isolation and dispersal reduction has been documented across a wide range of taxa (Waters et al. 2020). For example, island birds may lose their ability to fly, alpine insects might undergo reductions in wing size, and marine invertebrates may lose their planktonic larval stage (Garcia and Trewick 2014, Hume and Martill 2019, Jossart et al. 2019, McCulloch et al. 2019). Thus, it is possible that the LP guppy populations have evolved a decreased tendency to disperse relative to their HP, downstream counterparts due to this isolation and asymmetric gene flow.

Associations with life-history strategies

A robust body of work has shown that dispersal syndromes are common and can encompass nearly all dimensions of the phenotype (See review: Ronce and Clobert 2012). Dispersal syndromes are associations between dispersal and other phenotypic traits such as morphology, behavior, physiology, or life-history. These syndromes can arise because of genetic correlations between dispersal and other traits, or through

correlated responses to the environment (Ronce and Clobert 2012, Saastamoinen et al. 2017). Dispersal syndromes are incredibly important in the context of dispersal evolution because they might shape or constrain the evolutionary trajectory of the traits and inform us about the proximate and ultimate drivers of dispersal (Baker and Stebbins 1965, Bonte et al. 2012).

If the evolution of dispersal in guppies is constrained by or associated with the corresponding shift in life history strategies, then I predict a greater dispersal tendency in HP populations. This is because dispersal is often assumed to be integrated within the fast-slow continuum of life histories, such that faster life histories are associated with increased rates of dispersal. Since HP populations exhibit a 'faster' life history strategy, this pace of life concept predicts greater dispersal in the HP populations (Réale et al. 2010, Wolf and Weissing 2012, Stevens et al. 2012, 2013).

Methods

I used standard mark-recapture methods to repeatedly survey three paired high- and low-predation guppy populations: the St. Joseph, Damier, and El Cedro. The former represents a natural invasion of HP guppies into a LP habitat, while the two latter sites are artificial introductions performed approximately 25 and 40 years ago, respectively (Reznick and Bryga 1987, Gordon et al. 2009). The LP guppies from these introductions have been shown to exhibit phenotypic differences that mirror those found in natural invasions. Thus, these populations are no longer transitioning from HP to LP phenotypes, and I consider these populations to be at stable evolutionary endpoints. While there is actually a continuum of change in the composition of predator communities (Endler

1978), I have chosen to contrast the extremes of this continuum to enhance my ability to perceive differences among populations in dispersal tendency.

In addition to the historical information, I chose these sites based on the presence of appropriate fish communities, pool-riffle stream morphology, and other physical similarities that make quantifying dispersal tractable. Appropriate LP sites consist of guppies and the killifish, *Anablepsoides hartii*, whereas HP sites also contain several predators. For the southern slope populations, I documented the presence of *Crenicichla alta, Hoplias malabaricus, Aequidens pulcher,* and *Astyanax bimaculatus* in both HP sites. For the Damier, which is a northern drainage, I documented the presence of *Eleotris pisonis* and *Agonostomus monicola. Agonostomus* might have minor impacts on guppy mortality rate, however, its presence suggests that other hard to detect species might be present, such as *Gobiomorus dormitor* or *Dormitator maculatus*. I also documented an abundance of *Macrobrachium sp*. in both LP and HP sites of the Damier.

Guppies generally occupy pools and are seldom found in riffles; therefore, each pool represents an independent sub-population. Movement between these sub-populations may result in gene flow throughout the population, thus, movement between pools qualifies as dispersal. Each site was approximately 60-100m in length and contained anywhere from 6 to 9 discrete pools. I performed these experiments during the dry season (March-May) to enhance recapture probabilities and avoid large rainfalls that could wash individuals downstream outside the study area.

During capture events, I set out to capture every individual within the study site. Guppies are generally curious and swim freely in the water column or along the stream

banks, so almost all the individuals within a site can be easily captured. I monitored each pool and captured individuals with dip nets until no fish remained. I returned after a short period of time and captured any individuals that were previously not visible. I repeated this procedure until no fish remained.

Upon capture, I placed the guppies into a bottle specific to the pool they were captured in, then transferred them to our field station in the Arima Valley. I used MS-222, in combination with appropriate amounts of sodium bicarbonate as a buffer, to sedate each fish. Upon sedation, I gave each fish a unique combination of two elastomer marks (Northwest Marine Technologies). I used 8 body locations and 8 colors (in addition to the sexual dimorphism), which allowed me to give over 3500 unique marks per site. Juvenile individuals between approximately 10 and 12 millimeters in standard length were only given a single mark to maximize survival, however, marks were still distributed in an individual-based manner. I recorded the sex, pool of origin, standard length to the nearest hundredth of a millimeter, and wet mass to the nearest thousandth of a gram for each individual.

After this procedure, I transferred the fish to holding tanks and monitored their health for approximately 24 hours. I then repacked the fish into bottles and returned them to the pool in which they were captured. I placed the bottles at the edge of the stream and gave the container ample time to adjust to the temperature of the stream. Then, while submersed, I gently opened the cap, and let the fish swim out at their discretion. The bottles were placed at low-flow sections of each pool such that emerging guppies would not be swept downstream involuntarily. I repeated this mark-release-recapture process

approximately every 8 days for a total of 3 capture events per site. I did not mark guppies on the final recapture event as they would not be captured again during the scope of the study. This recapture interval is much shorter than most mark-release-recapture experiments on guppies. I shortened the intervals here to maximize the recapture rate in the high-predation sites (Reznick et al. 1996 and 2002).

I took physical measurements of each site's morphology upon complete removal of guppies from the experimental pools. I measured the length of each pool and the width at four evenly spaced transects, or a transect every 2 meters for pools longer than 8 meters. The depth of the pool was measured at 3 points along each width transect, which results in 12 measurements of depth per pool, or >12 for pools longer than 8 meters. I also measured the length of each riffle which connected the focal pools. Furthermore, a spherical densiometer was used to measure the canopy cover and light availability at each pool. Overall, these measurements allow for pool-specific estimations of volume at each capture interval, conspecific density at each capture interval, distance to adjacent patches, and light availability (which serves as a proxy for resource availability).

I analyzed three distinct response variables: propensity to disperse, dispersal distance, and dispersal direction. Dispersal is any movement of an individual beyond the boundaries of the pool in which it was originally captured, and propensity is a binary measure of whether an individual was ever captured outside of its original pool of capture. I calculated dispersal distance as the distance between the mid-point of the original pool of capture to the mid-point of the new pool of capture, thus, this measure

was 0 for all sedentary individuals. Direction is specific to dispersing individuals and refers to whether the movement was in the upstream or downstream direction.

The independent variables for these analyses include phenotype (HP/LP), river (El Cedro, Damier, St. Joseph), sex (male or female), length (standard length, millimeters), and local population density (individuals/m^3). I centered and scaled the standard length measurements to transform the units to the number of standard deviations from the population mean. For density, I log transformed the measurements and then scaled and centered them based on the population mean, making the units the number of standard deviations of the log transformed measurements. Differences in recapture interval were accounted for with the use of an offset variable. I also use site (the combination of river and predation regime) as a random effect.

For all the models described below, I utilize the Akaike information criterion (AIC) to perform model selection and identify the best fitting model(s) for the available data (Burnham and Anderson 2002, Zuur et al. 2009). I deemed models with a ΔAIC of 2 or lower to be the best fitting models (Burnham and Anderson 2002, Grueber et al. 2011). This threshold is more conservative than most (Richards 2008, Bolker et al. 2009, but see Grueber et al. 2011), however, it limits inference to only the models and combinations of variables best supported by the data. If there are multiple models with ΔAIC < 2, I use a model averaging approach to obtain a single set of parameter estimates ('model.avg' function, MuMIn package, version 1.47.1, Bartoń 2022). This approach uses a weighted average of parameter estimates such that models that explain more variation in the response variable are weighted higher and contribute more to the model averaged

parameter estimates. Using the (potentially model-averaged) parameter estimates and their standard errors, I calculated the Wald Z-statistic and associated p-values. These Wald Z-tests may provide unreliable results for GLMMs, because they depend upon multiple assumptions, some of which may be easily violated. These assumptions include that the sampling distribution of the parameters are multivariate normal and that the sampling distribution of the log-likelihood is proportional to χ^2. Thus, reported p-values should be treated with a healthy degree of skepticism and considered in the context of the overall pattern of the data and model estimates. Not all meaningful patterns will rise to statistical significance and not all significant differences will be meaningful.

The data shows an extreme excess of zero values. I analyzed over 1700 recaptures and only 242 (14%) of those were dispersal events. Given this excess of zeros, I feel the best approach to modelling the dispersal propensity and distance of these populations is the usage of a hurdle model. These hurdle models treat dispersal distance as the outcome of a two-step process. First, the hurdle model captures the propensity to disperse and assesses the factors that lead some individuals to disperse (distance > 0), while others do not (distance = 0). Then, for those individuals that dispersed, the conditional model of dispersal distance examines how the different variables explain the variation in the distance traveled by the dispersing individuals. Such an approach accommodates an excess of zeros in the response variable and allows for the inclusion of fixed and random effects in both the hurdle and conditional model components. The hurdle model uses a logit-link. The conditional model uses a log-link and a truncated negative binomial

family argument. These models were built in R (R Core team 2022) and fitted with the glmmTMB function (glmmTMB package, version 1.1.4, Brooks et al. 2017).

A total of 84 individuals remained juveniles and could not be sexed throughout the duration of the study. Thus, these results were analyzed separately. However, given the restricted sample size, I use an ANOVA to ask whether there are any differences between HP and LP in the juvenile dispersal propensity.

I also used generalized linear mixed-models to assess the variation in dispersal direction amongst high- and low-predation populations. As before, centered and scaled standard length, sex, river, phenotype (HP vs. LP), and density (log-transformed then centered and scaled) serve as the independent variables. I use site (the combination of river and predation regime) as a random effect. Since direction is binary (either upstream or downstream), I fit the models with the binomial family and a logit link function.

I ran Cormack-Jolly-Seber models in the MARK 9.0 program to estimate the recapture and survival probabilities for each population. Since there were only two recapture periods and the duration of the experiment was relatively short, I only considered models with constant survival and recapture probabilities over time. I also ran full likelihood closed capture recapture models to estimate the abundance of each population. For both models, I follow the protocols and procedures established by Cooch (2008). These estimates produced by these models are useful because they are a direct test of the effectiveness of the sampling regime as well as an evaluation of the differences between HP and LP.

I used ANOVAs to determine whether there were significant differences between each pair of HP and LP populations in terms of the light availability, distance between pools, pool length, conspecific density, and standard length. The distance between pools and pool length directly influences dispersal distance, thus, it is essential to ensure these do not vary among populations in any way that could significantly bias the results. The other parameters (conspecific density, standard length, light availability) serve to characterize the populations and demonstrate that they vary in the ways that is expected of divergent HP and LP populations.

Finally, I utilized the ggplot2 package (version 3.3.3, Villanueva and Chen 2019) to visualize the comparisons between high- and low-predation sites, for both the observed dispersal traits (propensity/rate and dispersal kernels) and other population parameters or environmental variables (grouped visualizations of all effects analyzed via ANOVA). I also plotted the significant fixed effects from each of the generalized linear mixed models. I visualized each of these effects via marginal effect plots ('plot_model' function from the sjPlot package, version 2.8.11, Lüdecke 2022). These plots provide predicted values (marginal effects) for estimates based on the model of choice and can accommodate second- and third-order interactions. I utilized the best fitting model for each response, as determined by AIC, to produce these plots.

Results

I recaptured 1738 individuals across all sites and sampling events, which encompasses 1266 unique individuals and 242 dispersal events. Thus, only 472 individuals were recaptured more than once. The Cormack-Jolly-Seber models reveal that

recapture rates ranged from about 60% to 90% and survival rates ranged from 65% to 90% (Table 1.2). This variation is associated with the underlying difference in predation, as HP populations had lower recapture and survival probabilities across each river.

The ANOVAs revealed some differences amongst the HP and LP pairs of focal populations/sites. For the Damier, there were no significant differences in light availability, guppy standard length, pool length, pool density, pool volume, or the distance between pools (Table 1.3). For the El Cedro, there were significant differences in light availability ($F = 7.542$, $p = 0.016$, Table 1.3, Figure 1.1), guppy standard length ($F = 41.132$, $p < 0.0001$, Figure 1.2), and local guppy density ($F = 31.887$, $p < 0.0001$, Table 1.3, Figure 1.3). For the St. Joseph, there were significant differences in light availability ($F = 14.556$, $p = 0.002$, Table 1.3, Figure 1.1) and guppy standard length ($F = 126.97$, $p < 0.0001$, Table 1.3, Figure 1.2). These models are summarized and visualized below (Table 1.3, Figures 1.1 – 1.6).

The selection procedure on the hurdle models yielded a single model with a ΔAIC value lower than 2 (Table 1.4). The analysis of dispersal propensity, via the hurdle component of the model, reveals consistent differences in dispersal propensity and distance amongst all three pairs of populations (Tables 1.5 - 1.7, Figures 1.7 and 1.8). Dispersal propensity is roughly 20.5% amongst HP populations, while it is only 8.8% in LP populations. The propensity model is summarized by strong effects of the interaction between phenotype and river, the interaction between phenotype and length, and the main effect of sex. The model also contains marginal effect of the interaction between phenotype and density. The strong interaction between phenotype and river demonstrates

that propensity is greater for HP populations across all rivers, however, the magnitude of this difference varies by river (Marginal mean propensity estimates: Damier HP: 21.5%; Damier LP: 8.1%; El Cedro HP: 40.1%; El Cedro LP: 9.4%; St. Joseph HP: 17.1%; St. Joseph LP: 9.2%). These differences are strong in contrasts between Damier and El Cedro ($\beta = 1.22$, $z = -2.53$, $p = 0.011$, Table 1.5, Figure 1.9) and El Cedro and St. Joseph ($\beta = -1.35$, $z = -3.52$, $p < 0.001$, Table 1.5, Figure 1.9), whereas the contrast between Damier and St. Joseph is weak ($\beta = -0.137$, $z = -0.29$, $p = 0.765$, Table 1.5, Figure 1.9). The interaction between phenotype and length indicates that there is a strong positive relationship between body size and dispersal propensity ($\beta = -0.52$, $z = -3.46$, $p = 0.001$, Table 1.5, Figure 1.10), however, this relationship is much stronger for the LP populations than the HP populations (HP slope: 0.077, LP slope: 0.627). Furthermore, the HP individuals have greater propensities across most body sizes, but this difference diminishes for the largest individuals. The main effect of sex shows that males are much more dispersive than females (male propensity: 21.2%, female propensity: 12.5%, $\beta = -0.69$, $z = -3.95$, $p < 0.001$, Table 1.5, Figure 1.11). Finally, the interaction between local guppy density and phenotype reveals almost no effect of density in the LP populations, but in the HP there is a positive relationship between density and dispersal propensity (HP slope: 0.267, LP slope: -0.024, $\beta = 0.28$, $z = 1.93$, $p = 0.054$, Table 1.5, Figure 1.12).

In terms of dispersal distance, HP individuals moved an average of 2.73 meters between sampling periods, while LP individuals only moved an average of 0.79 meters. However, if we only consider nonzero distance values (like the conditional component of the hurdle model) the average movement distance is 13.62 meters for HP and 9.21 meters

for LP. These distances ranged from 2 to 94.5 meters for HP and from 2 to 39 meters for LP. The hurdle model revealed that distance was explained by strong effects of the interaction between phenotype and river and the main effect of sex (Table 1.5 and 1.7). There is also a marginal effect of the interaction between phenotype and length. The strong interaction between phenotype and river demonstrates that distance is greater for HP populations across all rivers, however, the magnitude of this difference varies by river (Marginal mean distance estimates (meters): Damier HP: 23.0; Damier LP: 20.4; El Cedro HP: 16.3; El Cedro LP: 9.1; St. Joseph HP: 11.1; St. Joseph LP: 3.3). This difference is strong in contrasts between Damier and St. Joseph ($\beta = -1.06$, $z = -3.14$, $p = 0.002$, Table 1.5, Figure 1.13) and El Cedro and St. Joseph ($\beta = -0.56$, $z = -2.02$, $p = 0.043$, Table 1.5, Figure 1.13), whereas the contrast between Damier and El Cedro is weak ($\beta = -0.492$, $z = -1.496$, $p = 0.135$, Table 1.5, Figure 1.13). The main effect of sex shows that males disperse further than females do (Marginal mean distance (meters): male: 15.1, female: 9.8, $\beta = 0.47$, $z = 3.91$, $p = < 0.0001$, Table 1.5, Figure 1.14). Finally, the marginal effect of the interaction between phenotype and length indicates that there is a positive relationship between body size and dispersal distance ($\beta = 0.192$, $z = 1.78$, $p = 0.075$, Table 1.5, Figure 1.15), however, this relationship is much stronger for the LP populations than the HP populations (HP slope: 0.008, LP slope: 0.201). Furthermore, the HP individuals have greater propensities across most body sizes, but this difference diminishes for the largest individuals.

The selection procedure on the dispersal direction GLMMs yielded 3 models with ΔAIC values lower than 2 (Table 1.8). All three contained an interaction between

phenotype and density, two included the effects of body size, and one included sex (Table 1.8) The fixed effects from these models were averaged, and the results are summarized below (Table 1.9). These models are explained by a strong interaction between guppy density and phenotype. The interaction between density and phenotype ($\beta = 0.30$, $= 2.29$, $p = 0.02$, Table 1.9-1.10, Figure 1.16) reveals a strong relationship between local density and dispersal direction, however, the direction of this relationship depends upon phenotype. For HP individuals, there is a positive relationship between local density and the probability of upstream dispersal, whereas this relationship is negative for LP individuals (HP slope: 0.226, LP slope: -0.385, Figure 1.16). The main effects of length and sex were insignificant, but their inclusion in the top model set suggests they still provide information which improves the predictive power of the models.

Finally, I recorded only 4 dispersal events for the 84 juveniles, all of which were relatively short movements (~7 to 12 meters). The ANOVA revealed a significant difference amongst phenotypes ($F = 8.95$, $p = 0.004$). This was because all 4 dispersal events occurred in HP sites, and LP individuals made up about 2/3 of the 84 individuals.

Discussion

Overall, I observed a consistent difference in dispersal amongst high- and low-predation populations of guppies. Across all observed pairs of populations, HP populations were more likely to disperse and, on average, dispersed further than their LP counterparts. However, the magnitude of the difference, for both propensity and distance, varies among rivers. This is expected, as dispersal might be driven by environmental pressures that vary in intensity among sites. For example, the greater dispersal distances

observed in the Damier populations are likely a direct result of the larger pool sizes and distance needed to travel to move amongst patches.

Dispersal also varies by sex and size. Larger individuals and males are more likely to disperse and disperse further than smaller individuals and females. These results were expected. Previous analyses of guppy dispersal have all reported male-biased dispersal (Croft et al. 2003, De Bona et al. 2019, Borges et al. 2022). My findings on length also align with previous studies in terms of body length. Croft et al. (2003) found positive correlations between body size and dispersal for both sexes. For males, these results also align with those of Borges et al. (2022), who found a positive associated between length and dispersal. However, Borges et al. (2022) reported a negative relationship between body length and dispersal for females. De Bona et al. (2019) did not explicitly address the effects of body length. Regardless, a positive association between body length and dispersal, for either sex, is not surprising. Dispersal can be challenging, and larger individuals might be better equipped to move amongst populations. However, these results are unique in the fact that they compare across guppy phenotypes. Here, we see that male-biased dispersal exists across all rivers and both phenotypes. Furthermore, the positive association between body length and dispersal exists across both phenotypes, however, this association is much stronger for LP individuals.

The propensity to move, but not movement distance, was also influenced by a marginal effect of an interaction between density and phenotype. There was no association for LP individuals, but in the HP there was a positive relationship between density and movement propensity. This result is unexpected and contrasts the previous

analysis of density-dependent dispersal. De Bona et al. (2019) found that after HP guppies were transplanted to a LP habitat, they slowly shifted from negative-density dependent dispersal to positive density-dependent dispersal. Furthermore, HP guppies are much more likely to school, and the benefits of these behaviors are likely to be higher as density increases. Thus, it is confusing to find a positive relationship between density and dispersal for HP individuals. It might be possible that positive-density dependence emerges in HP populations because of extremely high densities and low resource availability, but this would require that the paired LP populations were simultaneously experiencing unusually low population densities and high resource availability. Overall, this scenario is unlikely and different from the patterns that are consistently observed across HP and LP populations.

The GLMMs built to explain variation in dispersal direction revealed a significant interaction between phenotype and local density (Table 1.9, Figure 1.16). HP individuals are more likely to move upstream as local density increases, whereas LP individuals are more likely to move downstream as density increases. As mentioned above, it is expected that density will regulate dispersal in some capacity due to previous results that documents a shift in density-dependent dispersal in guppies evolving from a HP to LP phenotype (De Bona et al. 2019). This work serves to expand on these findings by demonstrating that density influences multiple components of the dispersal phenotype.

While limited in sample size (n = 84), the results of the analysis of juvenile dispersal also provide some evidence that natal dispersal is greater in HP populations than it is in LP populations. I only observed successful juvenile dispersal in the HP

populations. This pattern came despite juvenile recapture and survival rate being much higher in LP populations. Overall, this result makes sense given the life history differences between HP and LP populations. The HP phenotype is generally characterized as being the "faster" or more r-selected phenotype, and early life dispersal might be consistent with this life history strategy due to correlations to other traits under selection (Reznick and Bryga 1996, Réale et al. 2010).

These results provide evidence that spatial sorting did not have lasting effects upon the dispersal patterns of guppies. This is because spatial sorting serves to increase dispersal at the range front, and as such, it predicts greater dispersal in the LP populations, which are younger and derived from their downstream, HP counterparts (Table 1.1). Instead, I found greater dispersal in the HP populations. In the absence of all other effects, spatial sorting is generally predicted to be a transient effect. Range expansion cannot continue indefinitely and once it stops the effects of spatial sorting will diminish. Here, this appears to occur even in combination with strong barriers that separate range-front and range-core populations (e.g., waterfalls).

The direct costs and benefits associated with dispersal do not seem to explain the observed patterns amongst HP and LP populations. This is because HP populations disperse more often and further, despite having greater risk and opportunity costs. However, it is likely that the relative magnitude of the benefits of dispersal are so strong for HP individuals that it outweighs these costs.

The patterns of variation observed here provides evidence for the asymmetric gene flow concept. This is because the isolated LP populations have a decreased dispersal

tendency relative to the downstream counterparts. This pattern has been observed in other systems, most notably islands. On islands and in other isolated areas, dispersers have a decreased probability of finding suitable habitat compared to the sedentary individuals, thus, dispersal is generally selected against. For LP guppies, dispersal might lead to unknowingly crossing a barrier that cannot be crossed in the opposite direction. When such an event occurs, any of those alleles which increase dispersal are likely lost permanently. Thus, LP guppies may have evolved decreased dispersal tendencies as a result of such isolation and asymmetric gene flow. However, this mechanism alone does not explain the emergence and maintenance of sex, age/size, or density driven dispersal, thus, this mechanism is likely working in combination with other ecological forces (e.g. fitness benefits in HP or correlations with other traits under selection) to produce the observed differences in dispersal patterns.

The dispersal patterns observed here also provide evidence for the pace of life concept. HP populations, which exhibit "faster" life history strategies, are also more dispersive. It is unclear whether this association is a result of genetic correlations or through similar responses to the same environmental and ecological differences associated with HP and LP sites. Thus, these results could be explained by strong links between dispersal and other life history traits under strong selection.

An interesting pattern associated with the results obtained in this experiment is the direction in which HP and LP guppies vary in their dispersal tendency. Previous studies of rapid dispersal evolution in nature often document differences between populations with different evolutionary histories, however, they almost always report a higher

dispersal rate in the new populations relative to the older ones (e.g. Hanski et al. 2004, Phillips et al. 2006). Furthermore, experimental and artificial evolution studies of dispersal almost always select for an increase in dispersal, thus, it is relatively unknown whether dispersal reductions take place at the same rate as increases in dispersal rate. In the wild, rapid increases in dispersal rate are usually driven by the spatial effects of habitat fragmentation and range expansion. Here, we demonstrate that the "new" guppy populations differ in such a way that their dispersal tendency has decreased relative to the ancestral populations. Furthermore, this change occurred quickly, since two of these populations were introduced 25 and 40 years ago. Moreover, there were no consistent patterns or differences in terms of the differences between the introduced vs. natural populations. In fact, the magnitude of difference for dispersal traits were often higher for the introduced populations (Damier, El Cedro) versus the natural population (St. Joseph).

While this is an interesting pattern, there are caveats. Here I have chosen LP populations that are stable, thus I am only comparing evolutionary endpoints. It is possible that more complex changes in dispersal occur throughout the colonization process, for both natural and introduced populations. For example, there might be selection for increased dispersal early in the colonization process when population are small and empty patches are abundant, however, once all available patches are inhabited and the population reaches carrying capacity then dispersal may be selected against. Regardless, this result is novel in that it demonstrates that reductions in dispersal can occur quickly and repeatedly in response to the similar ecological conditions.

I observed a consistent difference amongst HP and LP sites in terms of recapture probability and survival across all rivers. These differences confirm that HP individuals have lower survival and are less likely to be recaptured relative to LP individuals. The sampling design and effort remained constant across sites and sampling events; therefore, the difference in recapture probability is likely to be driven, in part, by a higher dispersal rate outside of the focal site or greater ability to avoid capture. Since HP individuals have an observed increase in dispersal relative to LP individuals in combination with a decreased recapture probability, it is extremely unlikely that these patterns biased the results. In fact, it is likely that this difference makes these results an underestimate of the difference in dispersal between HP and LP.

The observed differences in survival are expected. All HP populations experience lower survival relative to their LP counterparts. However, the difference in survival between the Damier populations is much smaller than is expected based on the other populations and previous comparisons of survival in HP and LP habitats (Reznick et al. 1996 and 2002). This might be because the north slope fish communities consist of a different predator community than the southern slope streams (*Eleotris pisonis, Gobiomorus dormitor, Dormitator maculatus, Agonostomus monicola* versus *Crenicichla alta, Hoplias malabaricus, Aequidens pulcher, Astyanax bimaculatus,* among others). It is possible that the impact of these predators on guppy survival rates is much lower than that of the south slope populations. However, previous studies performed in the Damier reported that survival rates are lower for HP individuals and that HP and LP populations have diverged as expected for life history phenotypes (Karim et al. 2007). Here, I did

document the presence of both *Eleotris pisonis* and *Agonostomus monicola* in the HP site, but their abundance was much lower than the abundance of the predators in the southern slope sites. Regardless, the estimated recapture and survival probabilities follow the expected pattern and do not bias the analysis of dispersal in any meaningful way.

There were no observed differences in pool length or distance between pools for HP/LP pairs in any of the three rivers. This is largely because sites were selected based on morphological similarities. However, it is impossible to select sites that are perfectly equal in size and spatial structure, thus this analysis is still useful for eliminating potential extraneous mechanisms which could bias the observed results.

Unlike the physical differences, I did find differences amongst HP and LP populations in terms of guppy body length, light availability, and density. However, these differences were only significant in the El Cedro and St. Joseph rivers. The absence of a difference in light availability was expected for the Damier, as these sites are near to each other (but separated by a large waterfall) and have extremely similar canopy conditions. Density and guppy body length do vary in the expected direction (higher density in LP and smaller body size in HP); however, the difference is miniscule, and the effect is insignificant. As mentioned above, this might be associated with a relaxed predation pressure in the Damier relative to that of the southern slope sites. Both El Cedro and St. Joseph have significantly different patterns of light availability. In the St. Joseph, there is significantly higher light availability in the HP site, while the opposite is true for El Cedro, where the light availability in the LP site is greater. Normally we would expect to see greater light availability in the HP sites, however, this effect can be variable,

especially when comparing relatively small portions of streams. The difference in these results might be associated with the differences in density across the three pairs of sites. For El Cedro, the density of guppies is significantly higher in the low predation sites, as expected. In the St. Joseph, the HP site had greater population densities, despite co-occuring with a robust and diverse predator community. This may be due to greater light availability, which in turn sustains higher primary productivity and supports denser populations. Finally, both St. Joseph and El Cedro vary in terms of guppy body length in the ways that are predicted for HP and LP populations; LP individuals are significantly larger than their HP counterparts. Overall, these results demonstrate that these populations vary in the ways that are consistent with the hypothesis that selective pressures in HP and LP populations differ.

Here, I've shown that the same conditions which produce variation in life history traits also are associated with consistent differences in dispersal propensity, distance, and direction. However, these results are purely observational and do not permit the inference of causation. The patterns of these observations could be driven by a suite of immeasurable variables that also vary with respect to HP and LP populations. Thus, a further manipulative, experimental approach should be utilized to tease apart the potential genotypic variation from variation that is driven by environmental influences.

In general, our ability to make accurate predictions about the invasion process is still limited (Hastings et al 2005, Miller and Tenhumberg 2010, Ochocki and Miller 2017). The guppy system seems well suited for generalizing about the invasion process, because many successful invasive species follow the same pattern of migrating to and

becoming established in locations with fewer predators than where they came from. In fact, the "predator release" hypothesis remains one of the better supported hypotheses in invasive species biology (Jeschke et al. 2012).

Understanding how dispersal evolves is also important for the management of native species, especially since many will be forced to disperse and shift their range to mitigate the direct and indirect effects of climate change (Nelson et al. 2006, Thompson and Fronhofer 2019). Furthermore, studies such as this continue to deepen our understanding of the causes and consequences of dispersal, from both ecological and evolutionary perspectives.

Overall, this work highlights the importance and complexity of intraspecific variation in dispersal traits. I have demonstrated that alternative environmental pressures can produce rapid reductions in dispersal traits, and this process appears to be consistent across multiple independent evolutionary origins. These consistent and predictable differences might arise because of spatial differences in the degree of isolation, as well as ecological differences that produce selection on both dispersal and life history traits. Continued exploration of dispersal variation across environmental gradients is likely to enhance our understanding of how multiple selective forces interact to produce differences in dispersal patterns. This will enable more rigorous testing of theory and can improve our ability to make accurate predictions about how populations will respond to rapid environmental changes.

Tables

Table 1.1. Hypothesis summary table.

Hypothesis	Description	Prediction(s)	Relevant citation
Evolutionary history and spatial sorting	Assortative mating amongst dispersers at the range front generates greater propensity to disperse, and this could have lasting impacts upon colonization of isolated LP habitats.	Greater dispersal in LP; differences between experimental and natural colonizations	Shine et al. 2011
Costs/benefits of dispersal	High risk and opportunity costs associated with movements in HP sites is likely to select against dispersal.	Greater dispersal in LP	Bonte et al. 2012
Asymmetric gene flow and isolation	Isolation is a result of asymmetric gene flow down, but not up, barrier waterfalls, and this may result in a gradual loss of genes which increase dispersal tendency.	Greater dispersal in HP	Waters et al. 2020
Associations with life-history	Dispersal is correlated with life history traits through genetic correlations or other mechanisms, and as such, it might evolve in concert with other life history traits under selection.	Greater dispersal in HP	Réale et al. 2010

Table 1.2. MARK 9.0 parameter estimates. The total recaptures are the sum from both resampling periods. Recapture probability and survival probability were estimated with a standard Cormack-Jolly-Seber model. The population size was estimated via a full likelihood abundance model and produces an estimate of the number of individuals in the population that were large enough to mark.

River	Phenotype	Individuals marked	Total recaptures	Recapture probability ± SE	Survival probability ± SE	Estimated population size ± SE
Damier	HP	145	146	0.719 ± 0.058	0.876 ± 0.052	164.18 ± 3.82
	LP	175	211	0.753 ± 0.049	0.899 ± 0.045	179.19 ± 2.45
El Cedro	HP	118	76	0.697 ± 0.090	0.660 ± 0.069	138.62 ± 6.87
	LP	464	561	0.854 ± 0.023	0.858 ± 0.020	473.78 ± 3.56
St. Joseph	HP	1049	552	0.584 ± 0.036	0.641 ± 0.031	1339.82 ± 28.94
	LP	151	192	0.912 ± 0.030	0.863 ± 0.028	152.95 ± 1.72

Table 1.3. Summary of ANOVAs built to test whether each pair of HP and LP populations vary in terms of pool length (m), pool volume (m^3), distance between pools (m), pool density (individuals/m^3), light availability and guppy standard length (mm).

River	Response	F-value	p-value	HP mean ± SD	LP mean ± SD
Damier	Pool length (m)	0.143	0.713	9.29 ± 8.57	10.85 ± 3.88
	Pool volume (m^3)	0.005	0.944	7.02 ± 13.54	6.55 ± 6.31
	Distance between pools (m)	0.069	0.798	4.25 ± 7.33	3.29 ± 4.10
	Pool density (individuals/m^3)	0.160	0.697	4.11 ± 2.25	4.64 ± 2.49
	Light Availability	2.793	0.123	2.12 ± 0.45	3.31 ± 1.99
	Guppy standard length (mm)	0.0277	0.868	13.85 ± 2.47	13.89 ± 2.34
El Cedro	Pool length (m)	0.043	0.839	4.55 ± 1.26	4.34 ± 2.37
	Pool volume (m^3)	0.768	0.396	1.77 ± 1.06	1.29 ± 1.12
	Distance between pools (m)	2.578	0.131	1.49 ± 0.97	0.80 ± 0.73
	Pool density (individuals/m^3)	31.887	< 0.0001	5.95 ± 2.82	37.95 ± 14.67
	Light Availability	7.542	0.016	1.26 ± 0.52	2.44 ± 1.03
	Guppy standard length (mm)	41.132	< 0.0001	13.72 ± 3.52	16.16 ± 3.13
St. Joseph	Pool length (m)	2.832	0.116	6.35 ± 4.26	3.47 ± 1.60
	Pool volume (m^3)	2.276	0.155	6.95 ± 9.96	1.21 ± 1.11
	Distance between pools (m)	0.507	0.488	1.07 ± 0.98	0.78 ± 0.57
	Pool density (individuals/m^3)	1.466	0.248	36.98 ± 40.83	17.64 ± 10.86
	Light Availability	14.556	0.002	6.01 ± 1.56	2.75 ± 1.75
	Guppy standard length (mm)	126.970	< 0.0001	14.35 ± 2.46	17.27 ± 4.42

Table 1.4. Model selection table for the hurdle models of dispersal distance. The columns on the right side of the table describe the degrees of freedom used by the model, it's log-likelihood value, its AIC value, and the difference in AIC value between the current and best-fitting model. Some models with large ΔAIC values were excluded for brevity. An asterisk or colon between variables indicates an interaction.

Conditional Models	**Hurdle model**	**df**	**logLik**	**AIC**	**ΔAIC**
Phenotype + Sex + River + Density + Length + Phenotype:Length + Phenotype:River + (1|Site) + offset(log(time))	Phenotype + Density + Length + Sex + River + Phenotype:River + Phenotype:Length + Phenotype:Density + (1|Site) + offset(log(time))	23	-1445.4	2936.8	0
Phenotype * River + Length + Sex + (1|Site) + offset(log(time))	Phenotype + Density + Length + Sex + River + Phenotype:River + Phenotype:Length + (1|Site) + offset(log(time))	21	-1448.8	2939.5	2.7
Phenotype * Length + Sex + River + (1|Site) + offset(log(time))	Phenotype + Density + Length + Sex + River + Phenotype:Density + Phenotype:Length + (1|Site) + offset(log(time))	19	-1456	2950.1	13.3
Phenotype * River + Density + Length + Sex + (1|Site) + offset(log(time))	Phenotype * River + Density + Length + Sex + (1|Site) + offset(log(time))	19	-1455.1	2952.1	15.3
Phenotype * Length + Sex + River + Density + (1|Site) + offset(log(time))	Phenotype * Length + Sex + River + Density + (1|Site) + offset(log(time))	19	-1457.6	2953.2	16.4
Phenotype * Length + Sex + River + (1|Site) + offset(log(time))	Phenotype * Density + Length + Sex + River + (1|Site) + offset(log(time))	18	-1462.1	2960.2	23.4

Phenotype * Density + Length + Sex + River + (1|Site) + offset(log(time))	Phenotype * Density + Length + Sex + River + (1|Site) + offset(log(time))	19	-1463.7	2965.4	28.6
Phenotype + Sex + River + Density + Length + (1|Site) + offset(log(time))	Phenotype + Sex + River + Density + Length + (1|Site) + offset(log(time))	17	-1466.1	2966.3	29.5
Phenotype * Sex + River + Density + Length + (1|Site) + offset(log(time))	Phenotype * Sex + River + Density + Length + (1|Site) + offset(log(time))	19	-1465.2	2968.4	31.6

Table 1.5. Fixed-effect parameter estimates from the best fitting hurdle model of dispersal distance. An asterisk between variables indicates an interaction.

Model	Fixed Effect	Estimate	SE	z-value	p-value
Conditional	Intercept	0.801	0.159	5.034	< 0.0001
	Phenotype	-0.233	0.274	-0.851	0.395
	Length	0.009	0.069	0.129	0.898
	Sex	0.467	0.119	3.912	< 0.0001
	River (Damier vs. El Cedro)	-0.302	0.216	-1.401	0.161
	River (Damier vs. St. Joseph)	-0.838	0.174	-4.810	< 0.0001
	River (El Cedro vs. St. Joseph)	-0.536	0.172	-3.124	0.002
	Phenotype:Length	0.192	0.108	1.783	0.075
	Phenotype:River (Damier vs. El Cedro)	-0.492	0.329	-1.496	0.135
	Phenotype:River (Damier vs. St. Joseph)	-1.056	0.336	-3.144	0.002
	Phenotype:River (El Cedro vs. St. Joseph)	-0.564	0.279	-2.021	0.043
Hurdle	Intercept	0.101	0.244	0.412	0.680
	Phenotype	0.705	0.386	1.828	0.068
	Density	-0.210	0.091	-2.300	0.021
	Sex	-0.691	0.175	-3.949	< 0.0001
	Length	-0.098	0.103	-0.952	0.341
	River (Damier vs. El Cedro)	-1.160	0.334	-3.469	0.001
	River (Damier vs. St. Joseph)	-0.697	0.252	-2.762	0.006
	River (El Cedro vs. St. Joseph)	0.463	0.268	1.727	0.084
	Phenotype:Density	0.282	0.146	1.925	0.054
	Phenotype:Length	-0.521	0.151	-3.462	0.001
	Phenotype:River (Damier vs. El Cedro)	1.216	0.480	2.533	0.011
	Phenotype:River (Damier vs. St. Joseph)	-0.137	0.458	-0.290	0.765
	Phenotype:River (El Cedro vs. St. Joseph)	-1.353	0.384	-3.524	0.0004

Table 1.6. Marginal mean estimates for the conditional component of the hurdle models, which analyzed dispersal distance of guppies across phenotype (HP/LP), length (measured as the number of standard deviations from the population mean, estimated here at -2, 0, and 2), sex (F/M), and river (Damier, El. Cedro, St. Joseph). Distance refers to the estimated marginal mean of dispersal distance. Standard errors are also given.

Phenotype	Length	Sex	River	Distance	SE
HP	-2	F	Damier	19.425	4.125
LP	-2	F	Damier	10.477	3.524
HP	0	F	Damier	19.773	3.145
LP	0	F	Damier	15.666	3.645
HP	2	F	Damier	20.126	4.192
LP	2	F	Damier	23.425	5.793
HP	-2	M	Damier	30.974	6.220
LP	-2	M	Damier	16.706	5.215
HP	0	M	Damier	31.528	5.542
LP	0	M	Damier	24.980	5.772
HP	2	M	Damier	32.092	7.818
LP	2	M	Damier	37.351	10.254
HP	-2	F	El Cedro	14.359	3.072
LP	-2	F	El Cedro	4.735	1.326
HP	0	F	El Cedro	14.616	2.216
LP	0	F	El Cedro	7.079	1.022
HP	2	F	El Cedro	14.877	2.903
LP	2	F	El Cedro	10.586	1.812
HP	-2	M	El Cedro	22.896	4.773
LP	-2	M	El Cedro	7.549	1.886
HP	0	M	El Cedro	23.306	4.105
LP	0	M	El Cedro	11.288	1.588
HP	2	M	El Cedro	23.722	5.638
LP	2	M	El Cedro	16.879	3.507
HP	-2	F	St. Joseph	8.403	1.537
LP	-2	F	St. Joseph	1.576	0.478
HP	0	F	St. Joseph	8.553	0.844
LP	0	F	St. Joseph	2.357	0.488
HP	2	F	St. Joseph	8.706	1.346

LP	2	F	St. Joseph	3.524	0.863
HP	-2	M	St. Joseph	13.399	1.991
LP	-2	M	St. Joseph	2.513	0.662
HP	0	M	St. Joseph	13.639	1.275
LP	0	M	St. Joseph	3.758	0.706
HP	2	M	St. Joseph	13.882	2.532
LP	2	M	St. Joseph	5.619	1.458

Table 1.7. Marginal mean estimates for the the hurdle model, which analyzed dispersal propensity of guppies across phenotype (HP/LP), density (measured as the number of standard deviations from the population mean, estimated here at -2, 0, and 2), sex (F/M), length (measured as the number of standard deviations from the population mean, estimated here at -2, 0, and 2) and river (Damier, El. Cedro, St. Joseph). Propensity refers to the estimated marginal mean of dispersal distance. Standard errors are also given.

Phenotype	Density	Sex	Length	River	Propensity	SE
HP	-2	F	-2	Damier	0.088	0.033
LP	-2	F	-2	Damier	0.019	0.009
HP	0	F	-2	Damier	0.142	0.042
LP	0	F	-2	Damier	0.018	0.008
HP	2	F	-2	Damier	0.220	0.065
LP	2	F	-2	Damier	0.017	0.009
HP	-2	M	-2	Damier	0.165	0.050
LP	-2	M	-2	Damier	0.037	0.017
HP	0	M	-2	Damier	0.253	0.057
LP	0	M	-2	Damier	0.036	0.015
HP	2	M	-2	Damier	0.366	0.079
LP	2	M	-2	Damier	0.034	0.016
HP	-2	F	0	Damier	0.102	0.029
LP	-2	F	0	Damier	0.062	0.023
HP	0	F	0	Damier	0.162	0.033
LP	0	F	0	Damier	0.060	0.018
HP	2	F	0	Damier	0.248	0.056
LP	2	F	0	Damier	0.057	0.022
HP	-2	M	0	Damier	0.188	0.047
LP	-2	M	0	Damier	0.120	0.041
HP	0	M	0	Damier	0.283	0.049
LP	0	M	0	Damier	0.115	0.033
HP	2	M	0	Damier	0.402	0.072
LP	2	M	0	Damier	0.110	0.040
HP	-2	F	2	Damier	0.117	0.035
LP	-2	F	2	Damier	0.189	0.061
HP	0	F	2	Damier	0.184	0.044
LP	0	F	2	Damier	0.182	0.052
HP	2	F	2	Damier	0.278	0.070
LP	2	F	2	Damier	0.175	0.063
HP	-2	M	2	Damier	0.212	0.063
LP	-2	M	2	Damier	0.323	0.097
HP	0	M	2	Damier	0.315	0.072

LP	0	M	2	Damier	0.312	0.086
HP	2	M	2	Damier	0.440	0.095
LP	2	M	2	Damier	0.302	0.101
HP	-2	F	-2	El Cedro	0.214	0.067
LP	-2	F	-2	El Cedro	0.022	0.009
HP	0	F	-2	El Cedro	0.318	0.073
LP	0	F	-2	El Cedro	0.021	0.008
HP	2	F	-2	El Cedro	0.443	0.092
LP	2	F	-2	El Cedro	0.020	0.008
HP	-2	M	-2	El Cedro	0.358	0.086
LP	-2	M	-2	El Cedro	0.043	0.016
HP	0	M	-2	El Cedro	0.487	0.078
LP	0	M	-2	El Cedro	0.041	0.013
HP	2	M	-2	El Cedro	0.619	0.083
LP	2	M	-2	El Cedro	0.040	0.015
HP	-2	F	0	El Cedro	0.241	0.058
LP	-2	F	0	El Cedro	0.072	0.020
HP	0	F	0	El Cedro	0.352	0.057
LP	0	F	0	El Cedro	0.069	0.012
HP	2	F	0	El Cedro	0.481	0.075
LP	2	F	0	El Cedro	0.066	0.019
HP	-2	M	0	El Cedro	0.394	0.079
LP	-2	M	0	El Cedro	0.137	0.034
HP	0	M	0	El Cedro	0.526	0.068
LP	0	M	0	El Cedro	0.131	0.021
HP	2	M	0	El Cedro	0.654	0.073
LP	2	M	0	El Cedro	0.126	0.033
HP	-2	F	2	El Cedro	0.271	0.070
LP	-2	F	2	El Cedro	0.214	0.055
HP	0	F	2	El Cedro	0.388	0.073
LP	0	F	2	El Cedro	0.206	0.040
HP	2	F	2	El Cedro	0.520	0.090
LP	2	F	2	El Cedro	0.198	0.056
HP	-2	M	2	El Cedro	0.431	0.100
LP	-2	M	2	El Cedro	0.357	0.087
HP	0	M	2	El Cedro	0.564	0.090
LP	0	M	2	El Cedro	0.346	0.070
HP	2	M	2	El Cedro	0.688	0.089
LP	2	M	2	El Cedro	0.336	0.088

HP	-2	F	-2	St. Joseph	0.073	0.023
LP	-2	F	-2	St. Joseph	0.020	0.009
HP	0	F	-2	St. Joseph	0.118	0.028
LP	0	F	-2	St. Joseph	0.019	0.008
HP	2	F	-2	St. Joseph	0.185	0.046
LP	2	F	-2	St. Joseph	0.019	0.009
HP	-2	M	-2	St. Joseph	0.138	0.036
LP	-2	M	-2	St. Joseph	0.041	0.017
HP	0	M	-2	St. Joseph	0.214	0.037
LP	0	M	-2	St. Joseph	0.039	0.013
HP	2	M	-2	St. Joseph	0.317	0.058
LP	2	M	-2	St. Joseph	0.037	0.015
HP	-2	F	0	St. Joseph	0.084	0.018
LP	-2	F	0	St. Joseph	0.068	0.021
HP	0	F	0	St. Joseph	0.135	0.016
LP	0	F	0	St. Joseph	0.065	0.015
HP	2	F	0	St. Joseph	0.210	0.035
LP	2	F	0	St. Joseph	0.062	0.020
HP	-2	M	0	St. Joseph	0.157	0.032
LP	-2	M	0	St. Joseph	0.129	0.037
HP	0	M	0	St. Joseph	0.241	0.027
LP	0	M	0	St. Joseph	0.124	0.026
HP	2	M	0	St. Joseph	0.352	0.052
LP	2	M	0	St. Joseph	0.119	0.035
HP	-2	F	2	St. Joseph	0.096	0.025
LP	-2	F	2	St. Joseph	0.203	0.059
HP	0	F	2	St. Joseph	0.154	0.029
LP	0	F	2	St. Joseph	0.195	0.046
HP	2	F	2	St. Joseph	0.237	0.052
LP	2	F	2	St. Joseph	0.188	0.059
HP	-2	M	2	St. Joseph	0.178	0.049
LP	-2	M	2	St. Joseph	0.342	0.092
HP	0	M	2	St. Joseph	0.271	0.056
LP	0	M	2	St. Joseph	0.332	0.077
HP	2	M	2	St. Joseph	0.388	0.081
LP	2	M	2	St. Joseph	0.321	0.093

Table 1.8. Model selection table for the generalized linear mixed models built to explain variation in dispersal direction. The columns on the right side of the table describe the degrees of freedom used by the model, its log-likelihood value, its AIC value, and the difference in AIC value between the current and best-fitting model. Some models with large ΔAIC values were excluded for brevity. An asterisk or colon between variables indicates an interaction.

Response	**Models**	**df**	**logLik**	**AIC**	**ΔAIC**
Direction	Phenotype * Density + (1|Site)	5	-160.4	330.8	0
Direction	Phenotype * Density + Sex + Length + (1|Site)	7	-158.7	331.4	0.6
Direction	Phenotype * Density + Length + (1|Site)	6	-159.7	331.4	0.6
Direction	Phenotype + (1|Site)	3	-163.4	332.9	2.1
Direction	Phenotype * Density + Sex + River + Length + (1|Site)	9	-157.7	333.3	2.5
Direction	Phenotype + Density + (1|Site)	4	-163.4	334.8	4
Direction	Density + (1|Site)	3	-164.8	335.5	4.7
Direction	Phenotype + Length + Density + Sex + River + (1|Site)	8	-160	335.9	5.1
Direction	Phenotype * Length + Density + Sex + River + (1|Site)	9	-159.6	337.2	6.4
Direction	Phenotype * Sex + River + Length + Density + (1|Site)	9	-159.7	337.4	6.6
Direction	Phenotype * River + Length + Density + Sex + (1|Site)	9	-158.7	337.5	6.7

Table 1.9. Model-averaged fixed effect parameter estimates from the best fitting GLMMs for dispersal direction. A colon between variables indicates an interaction.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	-0.099	0.145	0.675	0.500
Phenotype	0.219	0.146	1.491	0.136
Density	-0.092	0.132	0.691	0.489
Length	-0.128	0.163	0.781	0.435
Sex	0.056	0.119	0.470	0.639
Density:Phenotype	0.302	0.131	2.294	0.022

Table 1.10. Marginal mean estimates for the best-fitting model of dispersal direction of guppies across phenotype (HP/LP) and density (measured as the number of standard deviations from the population mean, estimated here at -2, -1, 0, 1, and 2). Direction refers to the estimated marginal mean of the probability of upstream movement. Standard errors are also given.

Phenotype	Density	Direction	SE
HP	-2	0.419	0.092
LP	-2	0.599	0.109
HP	-1	0.475	0.061
LP	-1	0.504	0.074
HP	0	0.531	0.041
LP	0	0.409	0.056
HP	1	0.587	0.050
LP	1	0.320	0.071
HP	2	0.641	0.076
LP	2	0.243	0.090

Figures

Figure 1.1. Box and whisker plots for the differences in light availability across the pairs of HP and LP populations. The boxes represent the upper and lower quartiles, the middle bar represents the median, and the lines which extend from the boxes represent the maximum and minimum values.

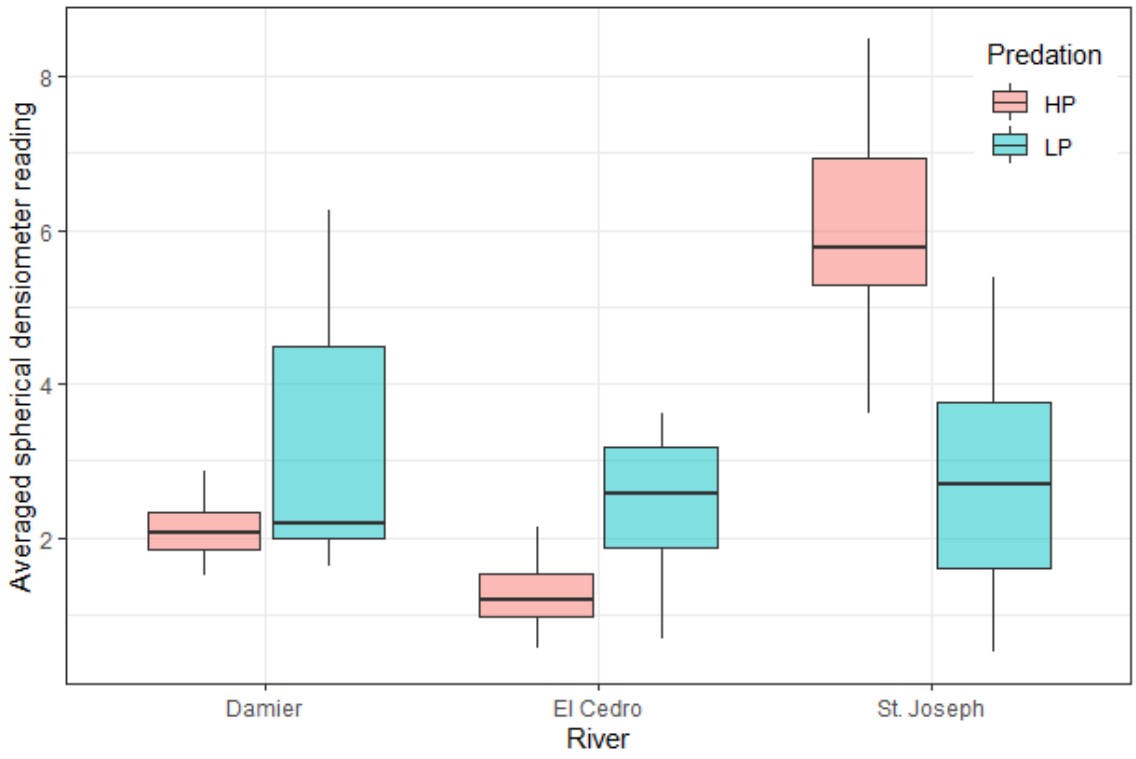


Figure 1.2. Box and whisker plots for the differences in guppy standard length (mm) across the pairs of HP and LP populations. The boxes represent the upper and lower quartiles, the middle bar represents the median, and the lines which extend from the boxes represent the maximum and minimum values, with dots representing the most extreme outliers.

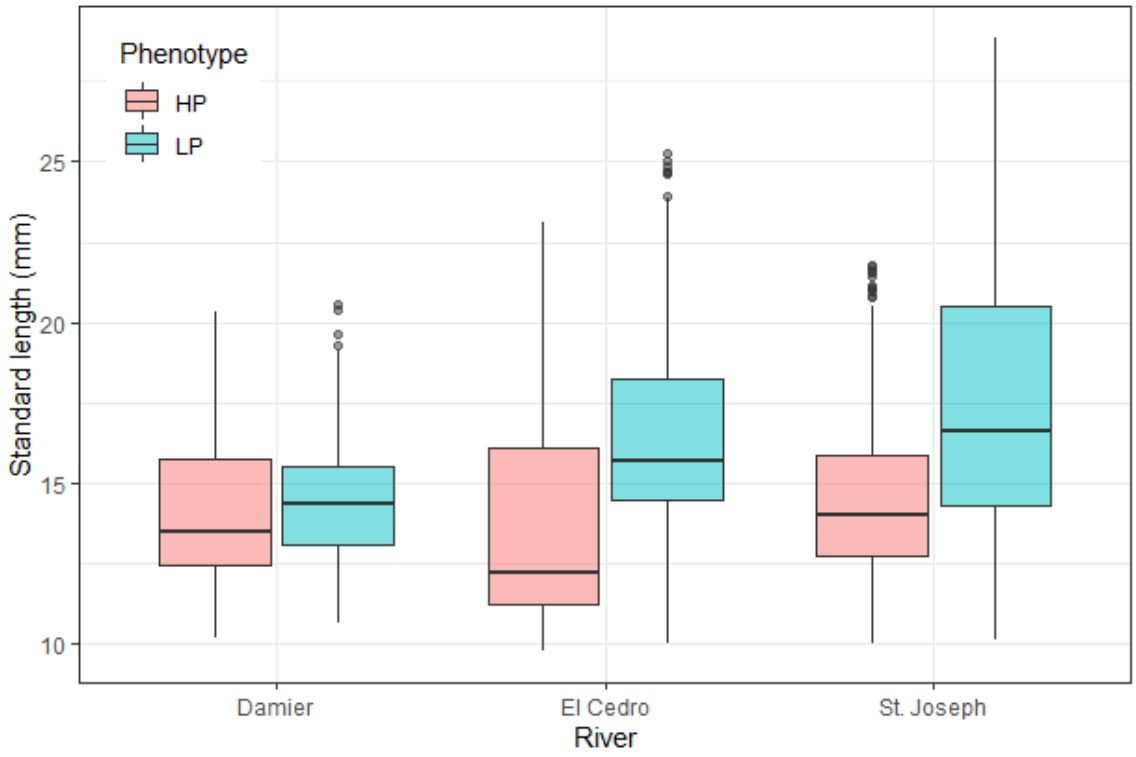


Figure 1.3. Box and whisker plots for the differences in conspecific density (individuals/m^3) across the pairs of HP and LP populations. The boxes represent the upper and lower quartiles, the middle bar represents the median, and the lines which extend from the boxes represent the maximum and minimum values, with dots representing the most extreme outliers.

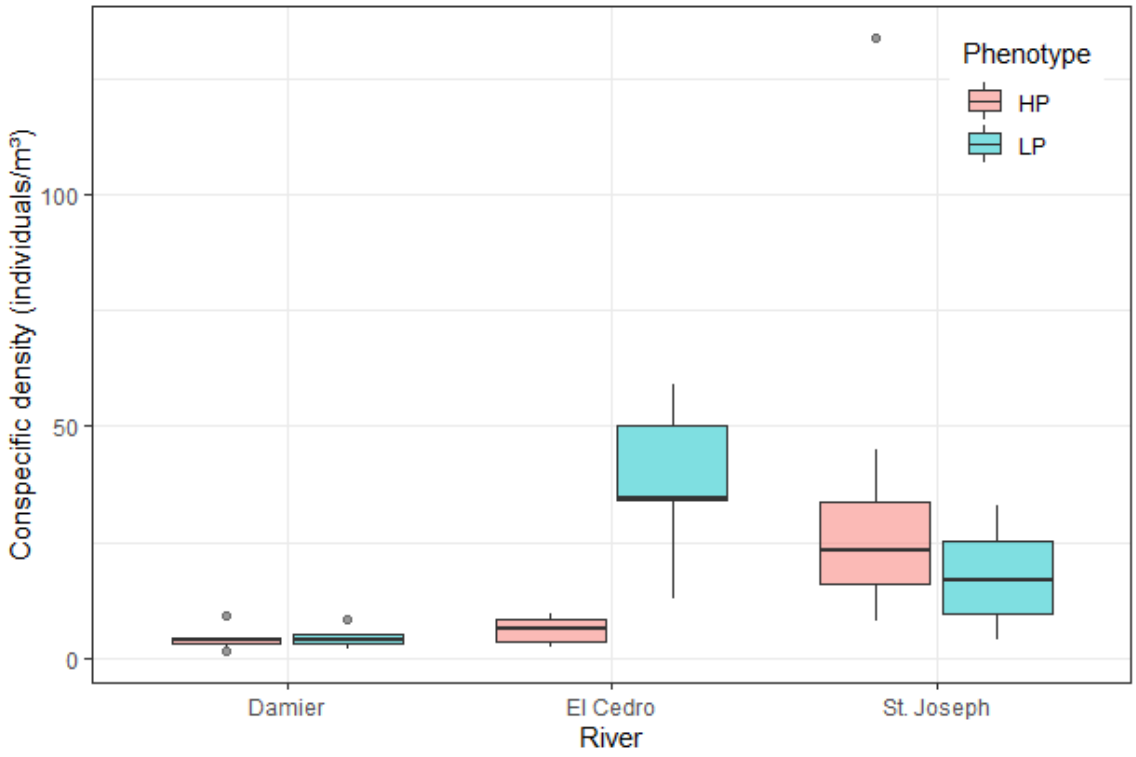


Figure 1.4. Box and whisker plots for the differences in pool length (meters) across the pairs of HP and LP populations. The boxes represent the upper and lower quartiles, the middle bar represents the median, and the lines which extend from the boxes represent the maximum and minimum values, with dots representing the most extreme outliers.

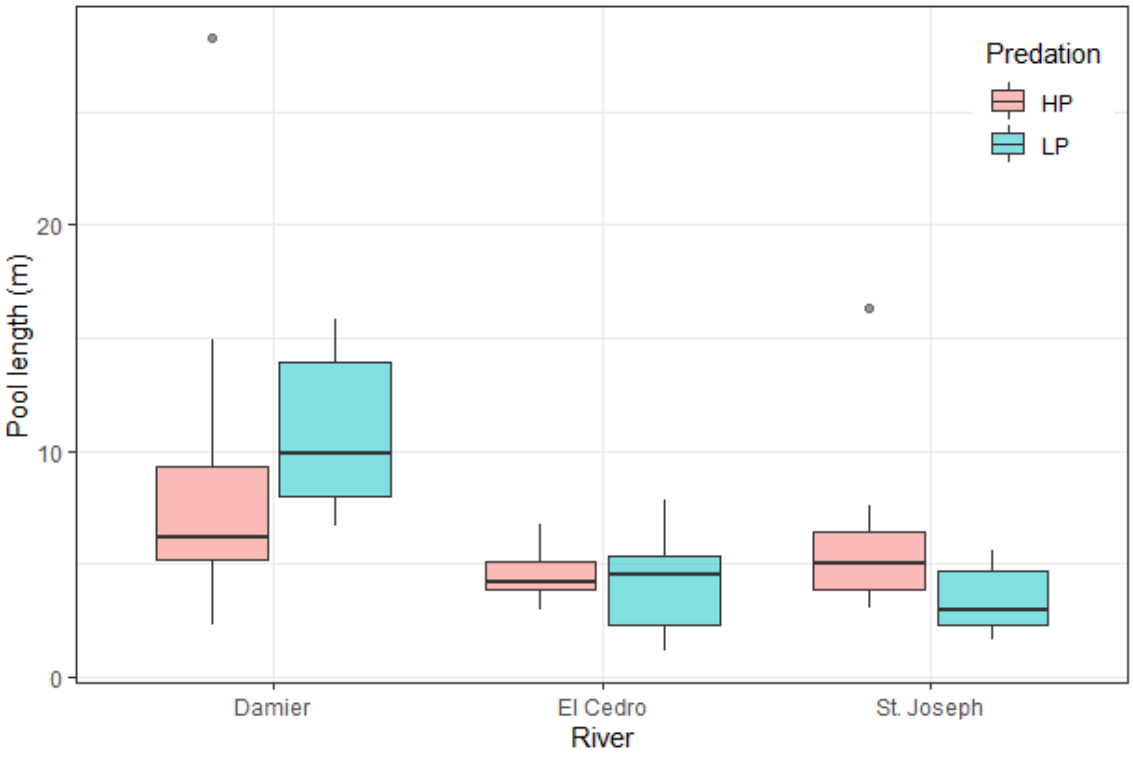


Figure 1.5. Box and whisker plots for the differences in pool volume (m^3) across the pairs of HP and LP populations. The boxes represent the upper and lower quartiles, the middle bar represents the median, and the lines which extend from the boxes represent the maximum and minimum values, with dots representing the most extreme outliers.

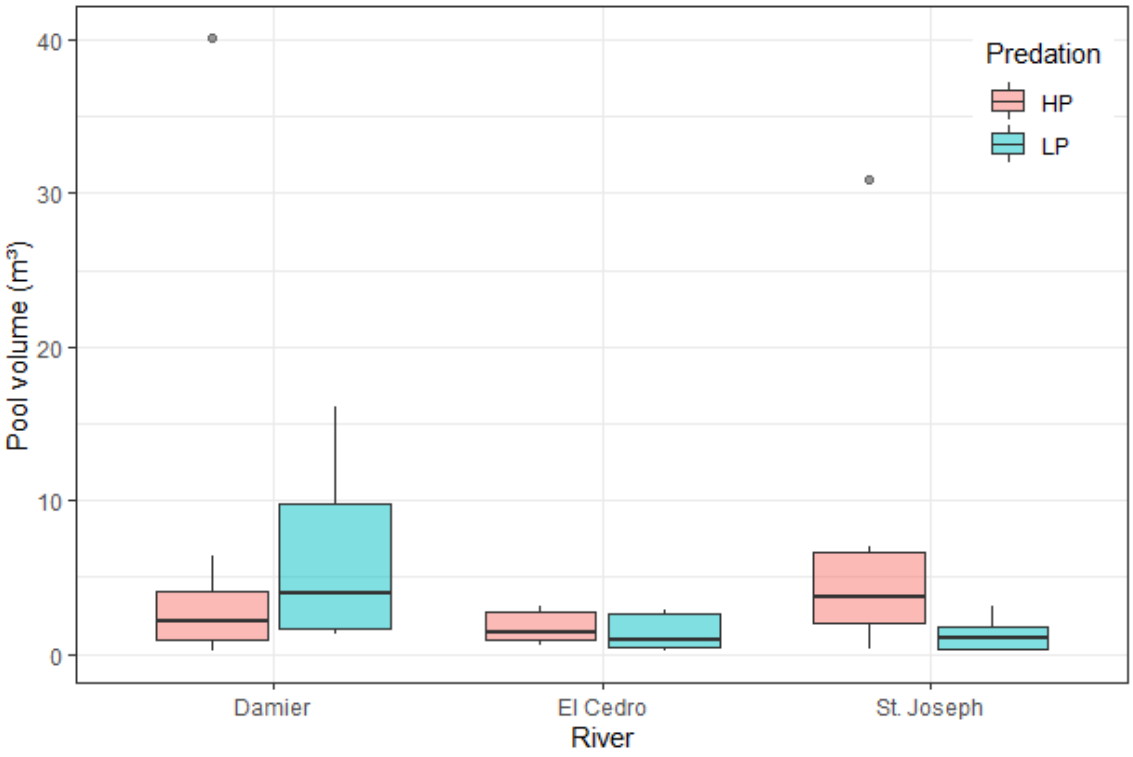


Figure 1.6. Box and whisker plots for the differences in the distance between pools (meters) across the pairs of HP and LP populations. The boxes represent the upper and lower quartiles, the middle bar represents the median, and the lines which extend from the boxes represent the maximum and minimum values, with dots representing the most extreme outliers.

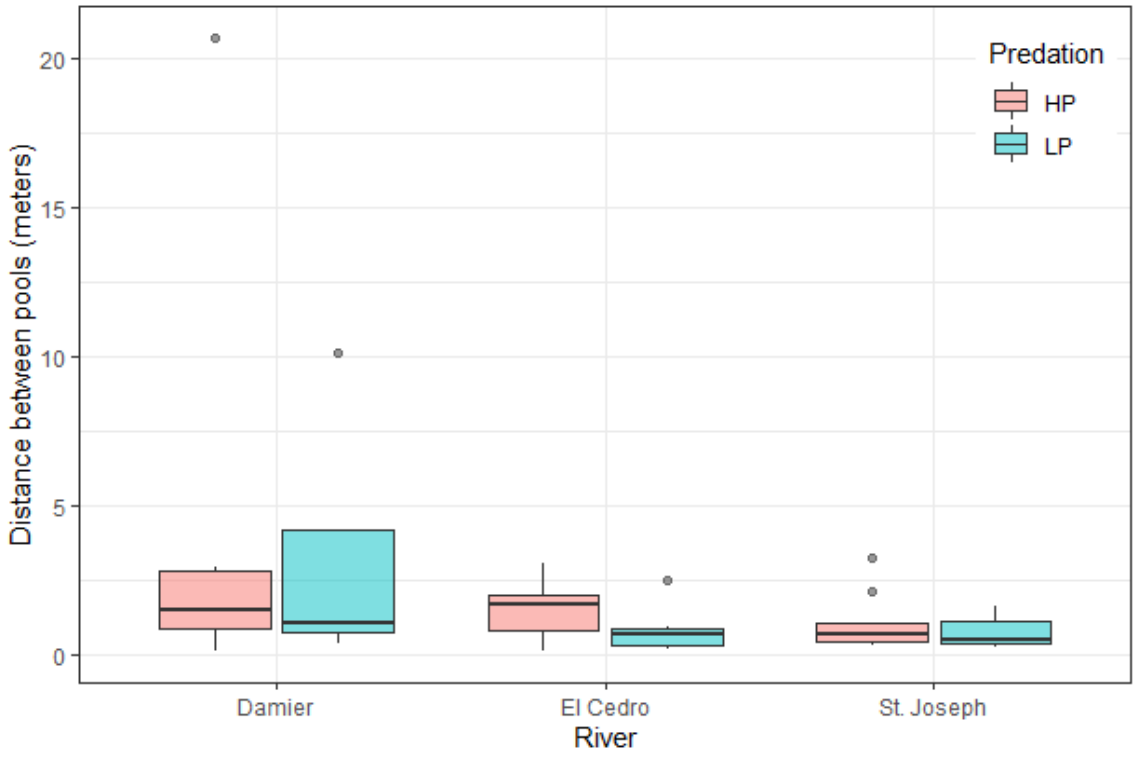


Figure 1.7. The observed dispersal rate (number of dispersal events/total recaptures) across the three pairs of HP and LP populations. The error bars represent the standard deviation.

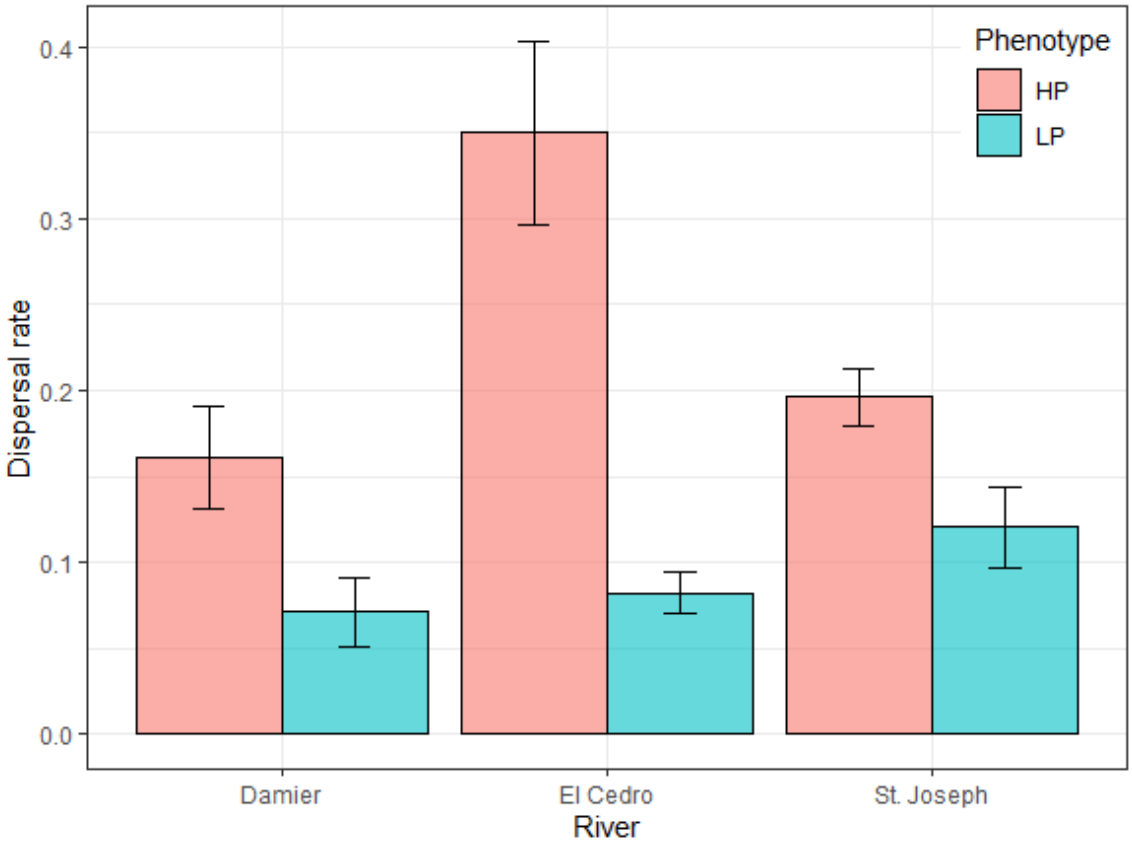


Figure 1.8. The empirical dispersal kernel (probability density function) for each of pair of HP and LP populations, generated with the geom_density function in ggplot2, and the histogram of the underlying data.

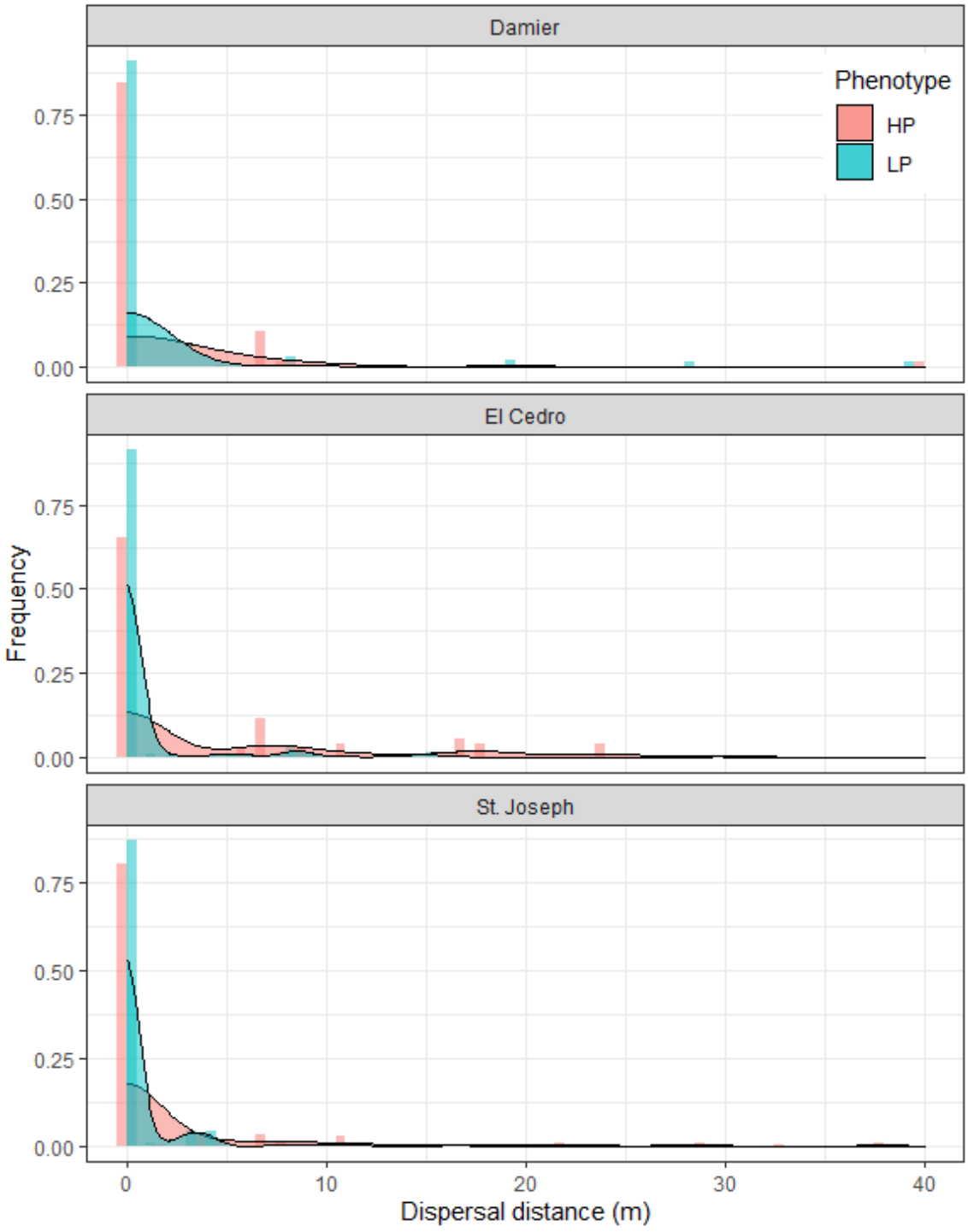


Figure 1.9. Marginal effects plot for the effect of river on the predicted value of dispersal propensity for HP and LP populations. The error bars represent the 95% confidence interval.

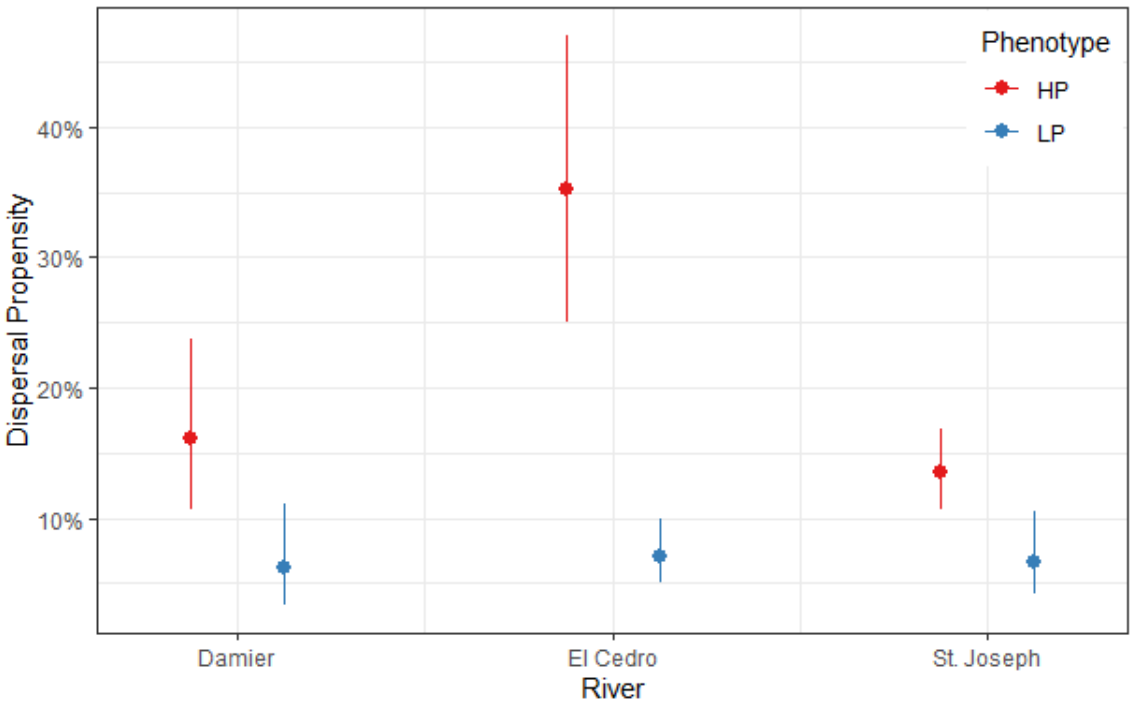


Figure 1.10. Marginal effects plot for the effect of guppy length (measured in standard deviations from the population mean) on the predicted value of dispersal propensity for HP and LP populations. The error bars represent the 95% confidence interval.

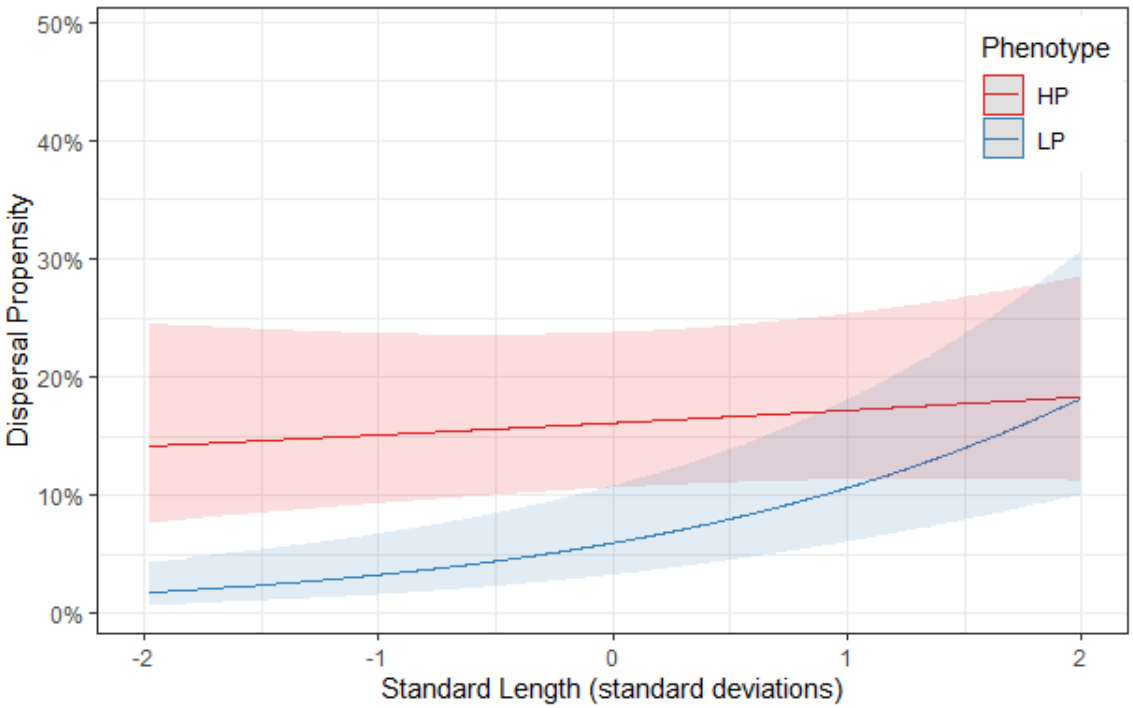


Figure 1.11. Marginal effects plot for the effect of sex on the predicted value of dispersal propensity for HP and LP populations, across all three rivers. The error bars represent the 95% confidence interval.

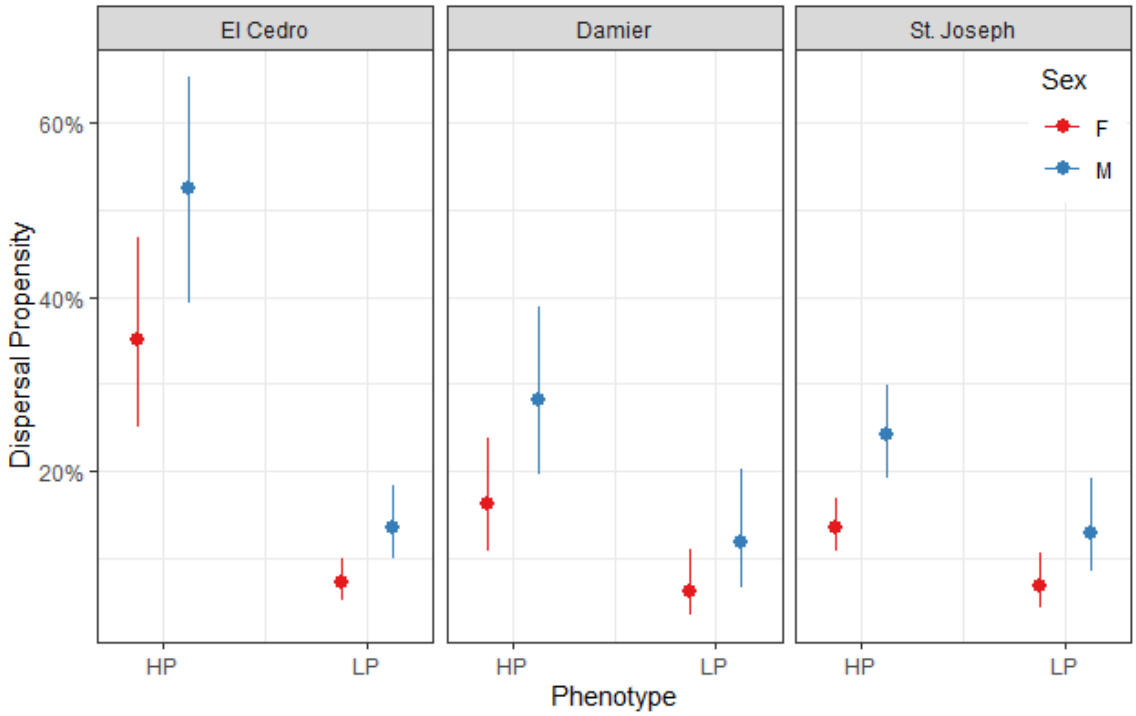


Figure 1.12. Marginal effects plot for the effect of density (measured in standard deviations from the population mean) on the predicted value of dispersal propensity for HP and LP populations. The error bars represent the 95% confidence interval.

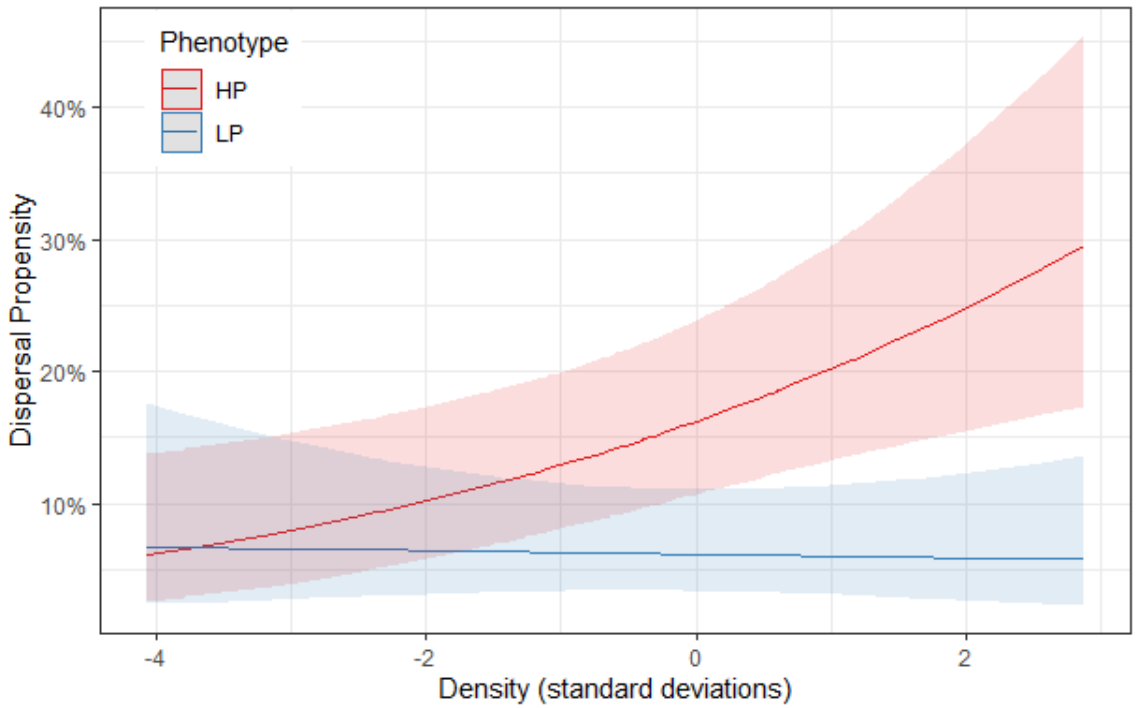


Figure 1.13. Marginal effects plot for the effect of river on the predicted value of dispersal distance (meters) for HP and LP populations. The error bars represent the 95% confidence interval.

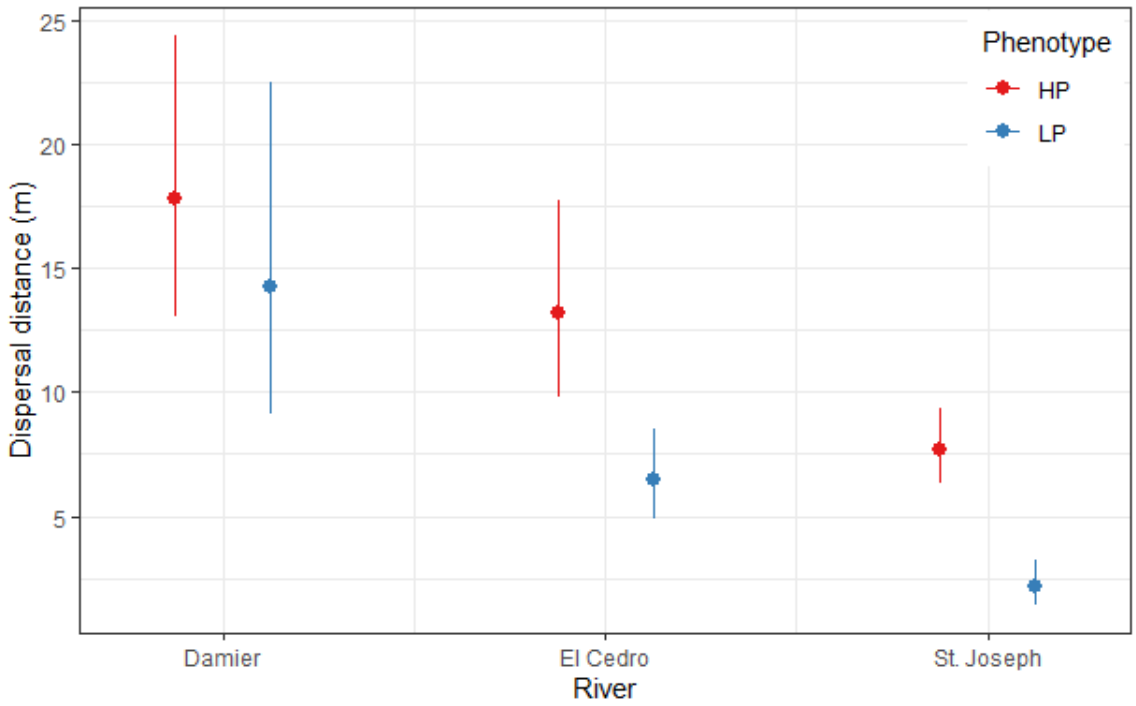


Figure 1.14. Marginal effects plot of the effect of sex on the predicted value of dispersal distance for HP and LP phenotypes. The error bars represent the 95% confidence interval.

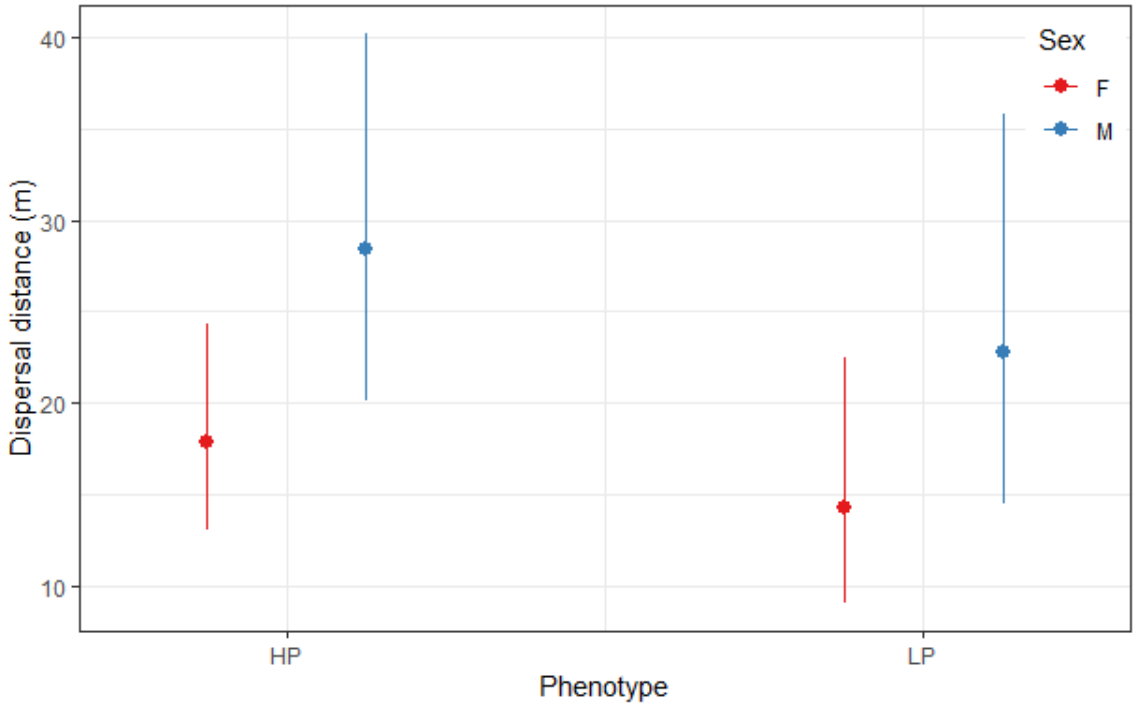


Figure 1.15. Marginal effects plot effect of guppy standard length (measured in standard deviations from the population mean) on the predicted value of dispersal distance for HP and LP phenotypes. The shaded region represents the 95% confidence interval.

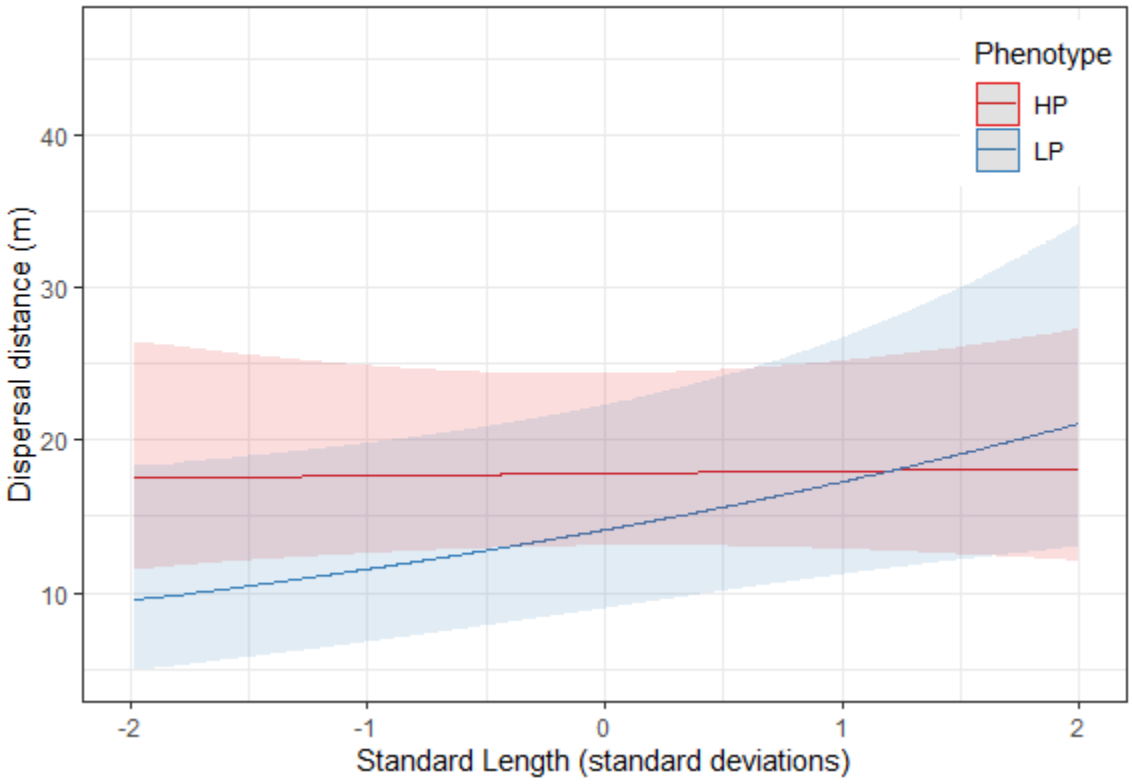
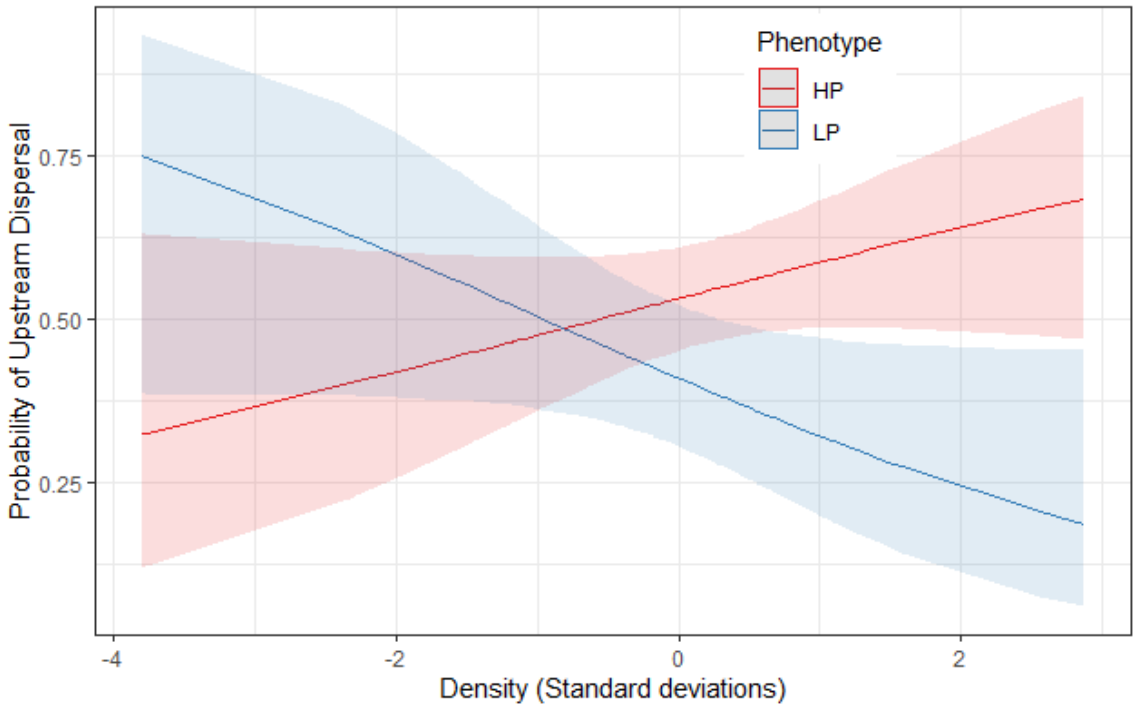


Figure 1.16. Marginal effects plot for the significant effect of the interaction between density and phenotype on the predicted probabilities of dispersal direction. The Y-axis is a measure of the percentage of movements that are in the upstream direction. The shaded regions represent the 95% confidence interval.



Chapter 2: The effects of population, flow, and conspecific density on movement traits in stream mesocosms

Abstract

The study of dispersal evolution is of tremendous importance due to its direct influence on many ecological and evolutionary processes. Despite this, study of the evolution of dispersal amongst natural populations is often constrained by a vast array of challenges. This is because dispersal is complex, multidimensional, and driven by numerous selective pressures, yet measuring all possible drivers in a natural setting might not be possible. To address this difficulty, I expand upon my previous work which utilized mark-release-recapture experiments to demonstrate a consistent and predictable pattern of variation in dispersal traits amongst high-predation (HP) and low-predation (LP) populations of guppies (*Poecilia reticulata*). Here, I collected natural populations of HP and LP guppies and measured their tendency to move amongst patches in an artificial stream mesocosm. I controlled and manipulated for factors that might influence dispersal, such as flow rate and conspecific density. I recorded the overall propensity to move, frequency of movements, and timing of the movements. The analyses revealed that the HP populations are more likely to move from the starting patch, move across the barriers more times, and make their first movements earlier than their LP counterparts. The pattern of variation observed here largely parallels the trends observed in the previous mark-recapture experiment from Chapter 1. Individuals from HP populations have a significantly greater tendency to disperse and disperse farther than individuals from LP populations. Overall, these results provide strong evidence of the rapid emergence of

intraspecific variation in dispersal traits amongst populations exposed to alternative selective regimes. These results demonstrate that the same forces responsible for driving the rapid evolution of life history traits can also drive predictable and consistent differences in dispersal traits.

Introduction

Dispersal influences the ecological and evolutionary processes of most natural populations. Populations and habitats are heterogenous, such that active dispersal among patches allows individuals to escape poor local conditions, select advantageous habitats and improve fitness. Thus, the tendency and ability to disperse becomes a key component of an organism's life history (Bonte and Dahirel 2017). Like many other life history traits, dispersal can be driven by a wide variety of selective pressures (Duputié and Massol 2013). Dispersal shifts allele frequencies within and among populations, and because of this, it can have immense population genetic consequences, like facilitating or constraining local adaptation (Wright 1932, Bowler and Benton 2005). Moreover, dispersal is a central component of many applied ecological issues, such as predicting the movement of invasive species and forecasting the fate of natural populations and communities exposed to climate change and habitat degradation (Melbourne and Hastings 2009, Travis et al. 2013, Phillips 2015, Thompson and Fronhofer 2019).

Despite its multidisciplinary importance, the empirical study of dispersal evolution is still lacking relative to its theoretical treatment, especially in natural systems (Ronce 2007, Duputié and Massol 2013). This is likely driven by a suite of reasons. One of the most prominent is the many logistical challenges associated with studying the

evolution of dispersal. Empirical studies of dispersal evolution take vastly different approaches to overcome these challenges.

One approach involves the direct observation of dispersal in natural systems (e.g. Fraser et al. 2001, Lindström 2013, Hendrix et al. 2017). These types of studies often compare dispersal traits amongst populations exposed or adapted to different selective regimes. Differentiation in dispersal traits amongst these populations can be driven by spatial selection, habitat fragmentation, or other selective processes (Clobert et al. 2012, Duputié and Massol 2013). Dispersal can be detected through various methods, such as mark-release-recapture, radio tracking, or even by genetic approaches (Turchin 1999, Saastamoinen et al. 2018). The species of interest will usually dictate what approaches are feasible. These studies of dispersal are powerful because they occur in nature and with populations that exist in the complex and stochastic environments that produce alternative dispersal strategies; however, it is often not possible to measure or control for all potential drivers of dispersal. Furthermore, these results are usually observational, which limits inference of causation.

An alternative approach to studying dispersal evolution involves assessing dispersal variation in artificial laboratory arenas, microcosms, or mesocosms (Ronce and Olivieri 2003, Friedenberg 2003, Fjerdingstad et al. 2007, Hauzy et al. 2007, Wiersma 2022). These studies utilize spatially structured systems in combination with experimental designs that allow individuals to express variation in dispersal traits. For some species (e.g. protists, nematodes, coleopterans), it may be possible to stimulate and measure dispersal evolution *in situ* (Fjerdingstad et al. 2007, Gray and Cutter 2014,

Ochocki and Miller 2017). The physical design of these systems is highly specific to the size, movement distances, and habitat requirements of the focal species, as well as the hypotheses under consideration. Common designs include a two-patch system in which a corridor connects two suitable patches of habitat (Lemel et al. 1997, Friedenberg 2003, Trochet et al. 2013, Jacob et al. 2019, Wiersma 2022), a linear array of patches (Fronhofer et al. 2017, Ochocki and Miller 2017, Moerman et. al. 2020, Mortier et al. 2021), or a complex network of patches (Fronhofer et al 2014, De Roissart et al. 2015, Masier and Bonte 2020). These studies of dispersal are useful because they are manipulative and allow for careful estimation of the causes and consequences of dispersal variation. Despite this, they may be overly simplistic and fail to account for the complexity and stochasticity that might drive dispersal in natural systems. Other alternatives do exist for evaluating dispersal evolution (Clobert et al. 2012, Saastaimoinen et al. 2018), but ultimately, a combination of multiple observational and experimental approaches is likely necessary to overcome these challenges and to gain a thorough mechanistic understanding of how novel selection pressures drive the rapid evolution of dispersal traits in natural populations.

Here, I aim to address these limitations by expanding upon my previous investigation of dispersal evolution in natural guppy populations (*Poecilia reticulata)*. The guppy is a model organism for studying how predation risk influences rapid life history evolution in natural settings (Reznick and Endler 1982, Reznick et al. 1996, 2019). Guppies from high-predation (HP) localities have repeatedly dispersed upstream, colonizing higher elevation streams that lack predators (LP, Haskins 1961, Endler 1978).

This release from predation, and the ultimate decrease in mortality rate, precipitates the evolutionary shift from a fast to slow life history (Reznick et al. 1996, Travis et al. 2014). It also drives a shift from top-down population regulation to bottom-up regulation (Bassar et al. 2013). Low-predation populations experience twofold increases in population density and fourfold increases in biomass (Potter et al. 2018), which intensifies intraspecific competition. Ultimately, the indirect effects of the increase in density are largely responsible for producing the differences in life history amongst HP and LP populations (Reznick et al. 2019).

In my previous examination of guppy dispersal (Chapter 1), I used mark-release-recapture techniques to evaluate intraspecific variation in dispersal traits amongst paired high- and low-predation populations of guppies. I demonstrated that HP guppy populations have a greater propensity to disperse and disperse further than their LP counterparts. The pattern of this result is consistent across all three pairs of high- and low-predation populations and suggests that the different selective forces in these environments have also shaped dispersal. However, the differences in fish communities may be confounded with differences in other features of the environment, and these differences might play a role in the observed dispersal patterns. Because Chapter 1 was observational, it is limited in its ability to tease apart the role of genetics versus confounding features of the environment as causes of the differences among populations in dispersal behavior.

The goal of this chapter is to test of whether the patterns observed in Chapter 1 persist in an environment where the potential drivers of dispersal are controlled. I achieve

this control by utilizing artificial stream mesocosms. These systems replicate the natural world yet allow for manipulation of the many potential drivers of dispersal, such as conspecific density or environmental conditions. If the divergent selection pressures associated with HP and LP populations drives the evolution of divergent dispersal strategies, then I predict that the patterns of movement in artificial stream mesocosms will parallel those found in natural habitats.

Methods

I used eight artificial stream channels (mesocosms) to test for movement differences among natural HP and LP populations. These mesocosms mimic a natural habitat in which two small pools are separated by a riffle. I constructed the mesocosms by joining three 1m x 0.5m plastic troughs (Rotoplastics Trinidad Limited, Trinidad) in a linear fashion. The outer compartments had no substrate or structure, and when filled with water, were approximately 30cm deep. The center compartment was filled with clay bricks and gravel such that it formed a riffle with a depth of 2-3cm of flowing water. The system utilized a 500-gallon head tank in which gravity produced the flow to the mesocosms. Valves at the inflow of each channel enabled control of water flow. The water flowed out of each channel through a mesh covered drain and down to a 55-gallon sump tank, where it was then pumped back up to the top head tank. The water is sourced directly from a nearby tributary to the Arima River and has similar water properties as the source populations. Furthermore, the distance between the mid-point of the upper and lower compartment is similar (within 1 SD for most sites) to the distances between pools

observed in Chapter 1 (Figure 1.6). Overall, this system effectively mimics a natural pair of pools connected via a riffle.

Wild guppies were captured using dip nets and transferred to our field station in 2-liter Nalgene® bottles. The populations were collected from the high- and low-predation communities in the Quare and Aripo rivers. These rivers represent well-studied, independent evolutionary origins of the HP and LP phenotypes (Reznick and Endler 1982, Reznick et al. 2001, Reznick et al. 2012). I used MS-222 to sedate each fish and, upon sedation, I recorded the sex, standard length to the nearest hundredth of a millimeter, and wet mass to the nearest thousandth of a gram. In addition, each fish received a unique combination of two bright dorsal elastomer marks (Northwest Marine Technologies). The use of 4 dorsal body locations and 7 of the most easily detectable colors (in addition to the sexual dimorphism) allows me to give 588 unique marks per replicate, but since I only needed a maximum of 30 unique marks, I choose a to utilize a more distinguishable pattern of marks amongst the individuals. This made identifying all individuals in a channel an easy procedure and removed the need to capture the fish at each observation. After the marking procedure the individuals were placed into 3-gallon aquaria with their treatment groups and their health was monitored for approximately 24 hours prior to the start of the experiment.

I utilized a 2x2x2 factorial design in which I crossed flow rates (high: 6 liters per minute, low: 3 L/min), conspecific density (high: 30 guppies, low: 15 guppies), and community type (HP or LP) across the eight available mesocosms. I replicated the experiment 4 times within each drainage for a total of eight replicates with 1440 unique

fish. Sex ratio was held constant at a 1M:2F ratio, which is typical of natural guppy populations (Arendt et al. 2014). Individuals were only utilized if their sex could be determined, thus, most juveniles (aside from those near sexual maturity) were excluded from this experiment. Flow rate and conspecific density usually differ amongst LP and HP populations and this difference might influence dispersal rate. The crossing of these factors with phenotype allows me to test for whether dispersal has adapted to these alternative local contexts and distinguish between potential genotypic differences in dispersal amongst HP and LP populations versus differences in the local proximate drivers of dispersal, which were confounded in the first mark-recapture study.

The experiment started with an acclimation phase, where fish were gently placed into the bottom ("downstream") patch of each channel for one hour. The top patch was left empty, and a mesh barrier was installed to prevent movement into the riffle or top patch. After the acclimation phase was over, I removed the barriers and surveyed the location of each fish every three hours during daylight, plus one nighttime survey, for a total of nine observations. Thus, the maximum number of observable movement events is also nine. The timing of the experiment, in terms of the time of day for the start and each observation period, was held constant across all replicates. Guppies are diurnal, so this sampling schedule adequately captures their movements. This design allows for the collection of data on whether an individual ever moved, the timing of the first movement, and the overall number of movements. Each experimental replicate lasted for 36 hours, which proved to be enough time to allow for movement throughout the mesocosms.

I analyzed three distinct response variables: propensity to move from the starting patch, frequency of movements, and the time at first movement event. Propensity to move is a response representing whether the individual ever moved from the initial patch. Frequency is the total number of crossings that occurred during the experiment. Time represents the observation period in which the first movement event was observed, and individuals that did not move were excluded for this model. These responses were analyzed in R (Version 4.2.1, R Core Team 2022) via GLMMs (Generalized Linear Mixed Models). The independent variables include intrinsic individual traits (sex, length), phenotype (HP/LP), stream (Aripo/Quare), and treatment effects (flow, density). I centered and scaled the standard length measurements to transform the units to the number of standard deviations from the population (phenotype x river) mean. I also employed a random effect which combined replicate and channel number to account for spatial and temporal differences among the channels.

For all the models described below, I utilize the Akaike information criterion (AIC) to perform model selection and identify the best fitting model(s) for the available data (Burnham and Anderson 2002, Zuur et al. 2009). I deemed models with a ΔAIC of 2 or lower to be the best fitting models (Burnham and Anderson 2002, Grueber et al. 2011). This threshold is more conservative than most (Richards 2008, Bolker et al. 2009, but see Grueber et al. 2011), however, it limits inference to only the models and combinations of variables best supported by the data. If there are multiple models with ΔAIC < 2, I use a model averaging approach to obtain a single set of parameter estimates ('model.avg' function, MuMIn package, version 1.47.1, Bartoń 2022). This approach uses a weighted

average of parameter estimates such that models that explain more variation in the response variable are weighted higher and contribute more to the model averaged parameter estimates. Using the (potentially model-averaged) parameter estimates and their standard errors, I calculated the Wald Z-statistic and associated p-values. These Wald Z-tests may provide unreliable results for GLMMs, because they depend upon multiple assumptions, some of which may be easily violated. These assumptions include that the sampling distribution of the parameters are multivariate normal and that the sampling distribution of the log-likelihood is proportional to χ^2. Thus, reported p-values should be treated with a healthy degree of skepticism and considered in the context of the overall pattern of the data and model estimates. Not all meaningful patterns will rise to statistical significance and not all significant differences will be meaningful.

I fitted the propensity candidate models with the glmer function (lme4 package, version 1.1.27.1, Bates et al. 2015) and I utilized a binomial family argument and a logit link function. I fitted the frequency candidate models with the glmer function and utilized a poisson family argument and log link function. I fitted the timing of first movement candidate models with the glmmTMB function (glmmTMB package, version 1.1.4, Brooks et al. 2017) and utilized a negative binomial family argument and a log link function. I switch packages here because lme4 does not support this type of negative binomial model.

Results

I observed the 1,440 guppies 12,960 times across all experimental replicates. In total, 936 of the 1,440 (65%) fish made at least one movement during the experimental

trials and 3,134 total movements were observed for an average of 2.18 movements per individual (range: 0 – 8). For individuals that moved, the first movement occurred after 2.90 observation periods, which is just shy of 9 hours after the experimental period began, or approximately 32.2% of the way through the duration of the experiment.

The selection procedure on the propensity models yielded 3 models with ΔAIC values lower than 2 (Table 2.1). All three models contain an interaction between phenotype and length, two contain the main effect of density, and one contains the main effect of river. The model-averaged fixed effect parameter estimates are summarized by a strong interaction between phenotype and length ($\beta = -0.33$, $z = 2.38$, $p = 0.017$, Table 2.2 and 2.3, Figure 2.1), and negligible effects of density or river ($p > 0.05$, Table 2.2). The interaction reveals that HP movement propensities are greater than LP across all size classes (Marginal mean propensity: HP: 89.1%; LP: 43.8%, Table 2.3). Furthermore, there is a negative association between length and propensity, however, this relationship is much stronger for LP individuals (HP slope: -0.101 , LP slope: -0.439).

The selection procedure on the frequency models yielded 2 models with ΔAIC values lower than 2 (Table 2.4). Both of these models contain an interaction between phenotype and length, and one contains the main effect of density. The model-averaged fixed effect parameter estimates are summarized by a strong interaction between phenotype and length ($\beta = -0.25$, $z = 5.68$, $p < 0.0001$, Table 2.5 and 2.6, Figure 2.2), and negligible effects of density (Table 2.5). The interaction reveals that HP movement propensities are greater than LP across all size classes (Marginal mean frequency (number of movements): HP: 2.85; LP: 1.09, Table 2.6). Furthermore, there is a weak

association between length and propensity for HP individuals, however, this relationship is negative for LP individuals (HP slope: 0.010 , LP slope: -0.239).

The selection procedure on the time models yielded 6 models with ΔAIC values lower than 2 (Table 2.7). The model-averaged fixed effect parameter estimates are summarized by a weak effect of phenotype ($\beta = 0.16$, $z = 1.64$, $p = 0.102$, Table 2.8, Figure 2.3), and negligible effects of density, length, sex, and a phenotype by sex interaction ($p > 0.3$, Table 2.8). The weak effect of phenotype shows that HP individuals move sooner than their LP counterparts (Marginal mean timing of first movement (observation periods): HP: 2.7; LP: 3.2).

Discussion

These results highlight the nature of intraspecific variation in dispersal in the Trinidadian guppy. Here, I found consistent population level differences in movement tendency in artificial streams (mesocosms) that parallel those found in the wild. HP populations, on average, have a greater propensity to leave the starting patch (Tables 2.2 and 2.3, Figure 2.1), move more times (Tables 2.5 and 2.6, Figure 2.2), and move slightly sooner relative to their LP counterparts (Table 2.8, Figure 2.3).

The models for propensity and frequency also both revealed a significant interaction between length and phenotype, and both can largely be summarized by a weak association between length and propensity for HP individuals and a negative effect for LP individuals, such that large LP individuals moved less and less frequently than their HP counterparts. Interestingly, for the HP individuals this pattern is largely the same as observed in the wild, but the direction of association is reversed for LP individuals.

I did not find any evidence for an effect of the density or flow treatments on any of the guppy movement traits. It is possible that the magnitude of difference between these treatments was not sufficient enough to produce an effect over such a short period of time. It is also likely that these differences in movement tendency are strong and driven by genetic contributions, and thus exist over a wide range of environmental conditions (Saastamoinen et al. 2018). I also did not reveal any sex-biases in movement. This may be because sex-ratio was held constant over all replicates (2F:1M, Arendt et al. 2014), however, it suggests that if there is a genetic contribution to dispersal, that it might not vary between the sexes. Finally, there were no major differences between the Quare and Aripo rivers.

Dispersal is complex, comprised of multiple stages, and driven by multiple selective pressures. The experimental design employed accounts for this complexity. First, it incorporates several movement traits (propensity, frequency, timing), and as such, it allows for a more thorough examination of how different aspects of dispersal might vary amongst HP and LP populations. It also controls for and manipulates many drivers of dispersal that may have been confounded in experiment 1. However, it does not account for maternal effects or the effects of living in or developing in a HP/LP habitat. For example, in a similar mesocosm experiment, Baines and McCauley (2018) assessed how habitat quality might influence the dispersal and movement behaviors of a backswimmer species. They found that their experimental manipulations of habitat quality had little to no effect on movement, instead, it was the habitat quality of their original source habitat that explained variation in movement tendencies (Baines and

McCauley 2018). Thus, it is possible that these results here are driven by the residual effects of the source habitat. However, this seems unlikely given the statistical control for differences among river and the consistent pattern of differentiation among HP and LP habitats across multiple dispersal traits and in both natural and artificial environments. Overall, these results do suggest some level of genetic differentiation in dispersal, however, a common-garden experiment will be necessary to confirm this (Saastamoinen et al. 2018). Nevertheless, these patterns highlight the reality and complexity of intraspecific variation in dispersal.

This experiment, in combination with Chapter 1, serves to demonstrate consistent and predictable differences among dispersal traits in HP and LP populations of guppies. The HP populations are characterized by a greater propensity to disperse and dispersal distance/number of dispersal events across all pairs of high- and low-predation populations evaluated (Aripo, Damier, El Cedro, Quare, St. Joseph). Thus, the same forces responsible for producing the rapid evolution of life history traits are also likely to be driving the divergence of dispersal traits amongst HP and LP populations of guppies.

Overall, this work demonstrates that populations exposed to different spatial and selective pressures may undergo rapid reductions in dispersal traits. This is likely to occur under the joint effects of spatial constraints, and ecological causes that also promote the rapid evolution of life history traits. Further exploration of rapid dispersal evolution across novel selective regimes is likely to increase our understanding of how dispersal evolves as well as improve our ability to predict the evolutionary response of species and populations under rapid environmental change.

Tables

Table 2.1. Model selection table for the propensity response variable. All models were fit with logit link functions. Models with a ΔAIC of two or less were deemed to be the best fitting models. The columns on the right side of the table describe the degrees of freedom used by the model, its log-likelihood value, its AIC value, and the difference in AIC value between the current and best-fitting model. An asterisk or colon between variables indicates an interaction.

Models	**df**	**logLik**	**AIC**	**ΔAIC**
Phenotype * Length + (1|Channel)	5	-720.2	1450.4	0
Phenotype * Length + Density + (1|Channel)	6	-719.5	1450.9	0.5
Phenotype * Length + Density + River + (1|Channel)	7	-718.9	1451.7	1.3
Phenotype * Length + Density + Flow + River + (1|Channel)	8	-718.8	1453.6	3.2
Phenotype * Length + Sex + Density + Flow + River + (1|Channel)	9	-718.8	1455.5	5.1
Phenotype + Length + Sex + Density + Flow + River + (1|Channel)	8	-721.6	1459.2	8.8
Phenotype * Sex + Length + Density + Flow + River + (1|Channel)	9	-721.3	1460.6	10.2
Phenotype * Density + Sex + Length + Flow + River + (1|Channel)	9	-721.4	1460.8	10.4
Phenotype * Flow + Sex + Length + Density + River + (1|Channel)	9	-751.5	1460.9	10.5

Table 2.2. Model-averaged fixed effect parameter estimates for the analysis of propensity. The models averaged here were the best fitting models identified in the model selection procedure (Table 2.1). An asterisk or colon between variables indicates an interaction.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	2.0562	0.2511	8.1830	< 0.0001
Phenotype	-2.35659	0.2836	8.3020	< 0.0001
Length	-0.1004	0.1078	0.9300	0.3525
Density	0.1891	0.2676	0.7060	0.4801
River	-0.0687	0.1830	0.3750	0.7073
Phenotype:Length	-0.3379	0.1420	2.3770	0.0174

Table 2.3. Marginal mean estimates for the best-fitting model of movement propensity of guppies across phenotype (HP/LP) and length (measured as the number of standard deviations from the population mean, estimated here at -2, -1, 0, 1, 2, and 3).

Phenotype	**Length**	**Movement Propensity**	**SE**
HP	-2	0.909	0.025
LP	-2	0.652	0.059
HP	-1	0.901	0.022
LP	-1	0.548	0.051
HP	0	0.891	0.021
LP	0	0.438	0.047
HP	1	0.881	0.025
LP	1	0.335	0.047
HP	2	0.870	0.034
LP	2	0.245	0.050
HP	3	0.858	0.046
LP	3	0.173	0.049

Table 2.4. Model selection table for the frequency response variable. All models were fit with log link functions. Models with a ΔAIC of two or less were deemed to be the best fitting models. The columns on the right side of the table describe the degrees of freedom used by the model, its log-likelihood value, its AIC value, and the difference in AIC value between the current and best-fitting model. An asterisk or colon between variables indicates an interaction.

Models	**df**	**logLik**	**AIC**	**ΔAIC**
Phenotype * Length + (1|Channel)	5	-2580.2	5170.5	0
Phenotype * Length + Density + (1|Channel)	6	-2579.5	5171.1	0.6
Phenotype * Length + Density + Flow + (1|Channel)	7	-2579.3	5172.6	2.1
Phenotype * Length + Sex + Density + Flow + (1|Channel)	8	-2579.3	5174.6	4.1
Phenotype * Length + Sex + Density + Flow + River + (1|Channel)	9	-2579.3	5176.6	6.1
Phenotype * Sex + Length + Density + Flow + River + (1|Channel)	9	-2592.8	5203.6	33.1
Phenotype + Length + Sex + Density + Flow + River + (1|Channel)	8	-2595.6	5207.2	36.7
Phenotype * Density + Sex + Length + Flow + River + (1|Channel)	9	-2594.6	5207.3	36.8
Phenotype * Flow + Sex + Length + Density + River + (1|Channel)	9	-2595.5	5209.1	38.6

Table 2.5. Model-averaged fixed effect parameter estimates for the analysis of frequency. The models averaged here were the best fitting models identified in the model selection procedure (Table 2.4). A colon between variables indicates an interaction.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	1.013	0.116	8.710	< 0.0001
Phenotype	-0.962	0.144	6.672	< 0.0001
Length	0.010	0.022	0.428	0.669
Density	0.071	0.124	0.568	0.570
Phenotype:Length	-0.248	0.044	5.681	< 0.0001

Table 2.6. Marginal mean estimates for the best-fitting model of movement frequency of guppies across phenotype (HP/LP) and length (measured as the number of standard deviations from the population mean, estimated here at -2, -1, 0, 1, 2, and 3).

Phenotype	**Length**	**Movement Frequency**	**SE**
HP	-2	2.797	0.305
LP	-2	1.757	0.219
HP	-1	2.824	0.288
LP	-1	1.383	0.151
HP	0	2.851	0.284
LP	0	1.089	0.115
HP	1	2.879	0.294
LP	1	0.858	0.098
HP	2	2.907	0.318
LP	2	0.676	0.090
HP	3	2.934	0.353
LP	3	0.532	0.085

Table 2.7. Model selection table for the time response variable. All models were fit with log link functions. Models with a ΔAIC of two or less were deemed to be the best fitting models. The columns on the right side of the table describe the degrees of freedom used by the model, its log-likelihood value, its AIC value, and the difference in AIC value between the current and best-fitting model. An asterisk or colon between variables indicates an interaction.

Models	**df**	**logLik**	**AIC**	**ΔAIC**
Phenotype + (1|Channel)	4	-1796.3	3600.6	0.0
Phenotype * Sex + Length + (1|Channel)	7	-1793.9	3601.7	1.1
Phenotype + Sex + Length + (1|Channel)	6	-1794.9	3601.8	1.2
Phenotype + Sex + (1|Channel)	5	-1795.9	3601.8	1.2
Phenotype * Sex + (1|Channel)	6	-1794.9	3601.9	1.3
Phenotype * Sex + Length + Density + (1|Channel)	8	-1793.2	3602.5	1.9
Sex + (1|Channel)	4	-1797.8	3603.6	3.0
Phenotype * Sex + Length + Density + River + (1|Channel)	9	-1792.9	3603.9	3.3
Phenotype * Sex + Length + Density + Flow + River + (1|Channel)	10	-1792.9	3605.8	5.2
Phenotype + Length + Sex + Density + Flow + River + (1|Channel)	9	-1793.9	3605.8	5.2
Phenotype * Length + Sex + Density + Flow + River + (1|Channel)	10	-1793.5	3606.9	6.3
Phenotype * Flow + Sex + Length + Density + River + (1|Channel)	10	-1793.5	3607	6.4
Phenotype * River + Sex + Length + Density + Flow + (1|Channel)	10	-1793.7	3607.3	6.7
Phenotype * Density + Sex + Length + Flow + River + (1|Channel)	10	-1793.8	3607.6	7

Table 2.8. Model-averaged fixed effect parameter estimates for the analysis of time at first movement. The models averaged here were the best fitting models identified in the model selection procedure (Table 2.7). An asterisk or colon between variables indicates an interaction.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	0.99381	0.06982	14.216	< 0.0001
Phenotype	0.16501	0.1007	1.637	0.102
Sex	-0.05944	0.06308	0.942	0.346
Length	-0.01469	0.02357	0.623	0.533
Phenotype:Sex	0.05154	0.08348	0.617	0.537
Density	0.01149	0.04527	0.254	0.8

Figures

Figure 2.1. Marginal effects plot for the effect of the interaction between length and phenotype on movement propensity. The shaded regions represent the 95% confidence interval.

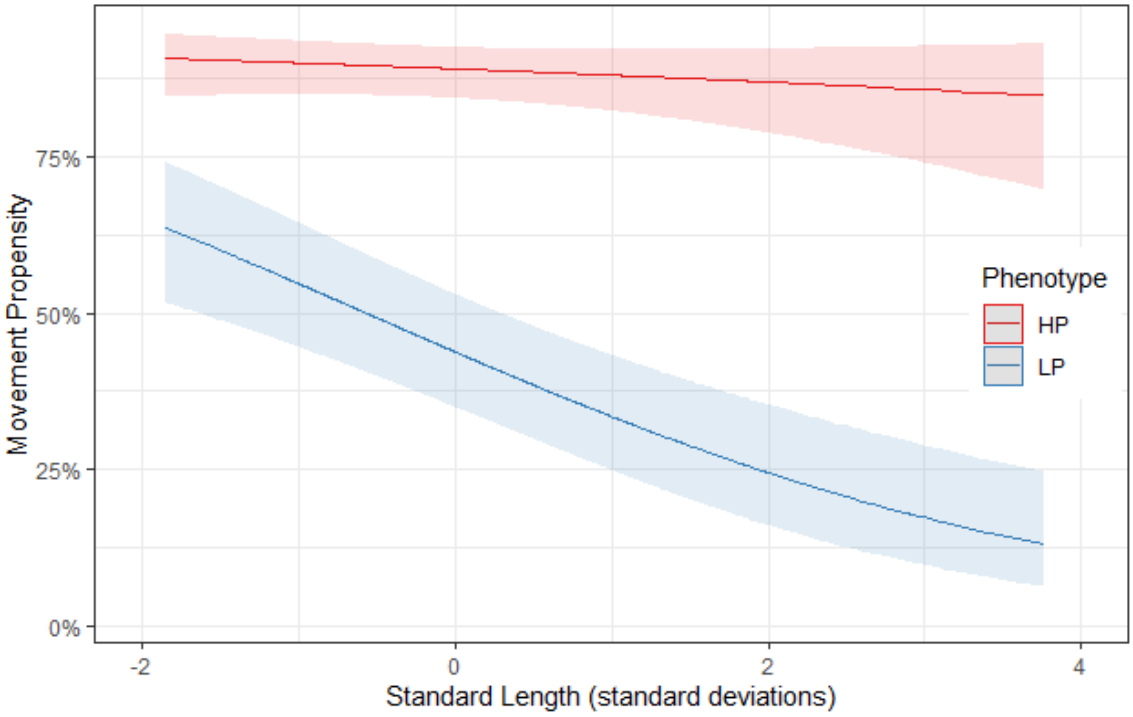


Figure 2.2. Marginal effects plot for the effect of the interaction between length and phenotype on movement frequency. The shaded regions represent the 95% confidence interval.

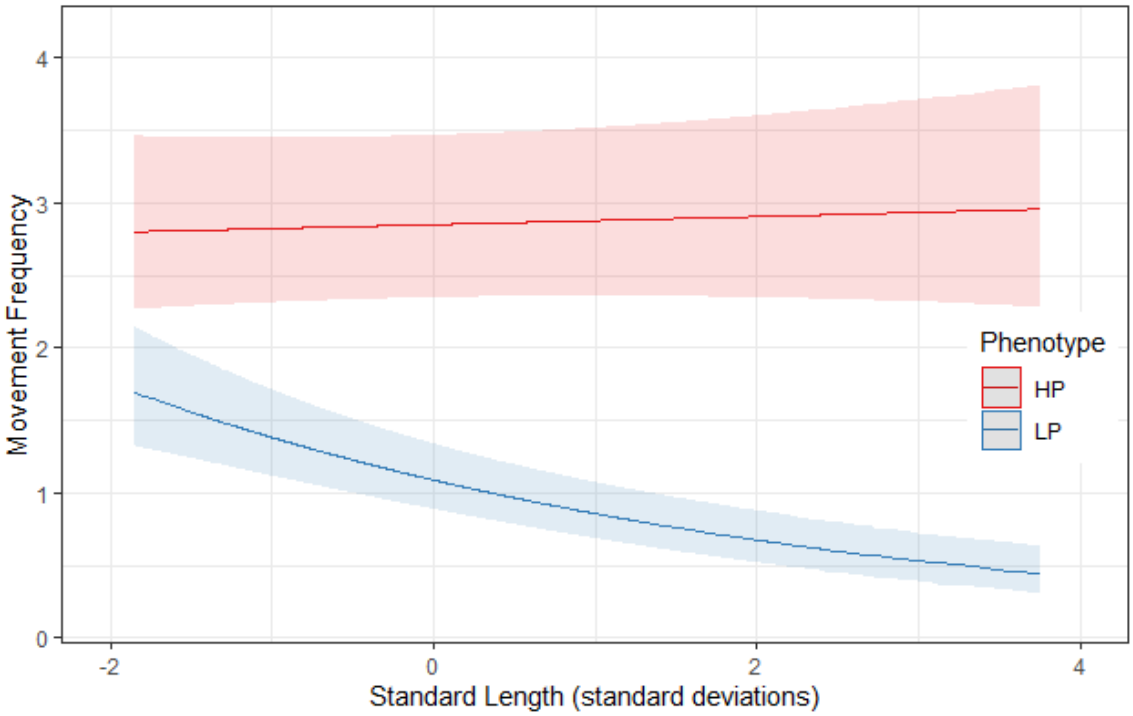
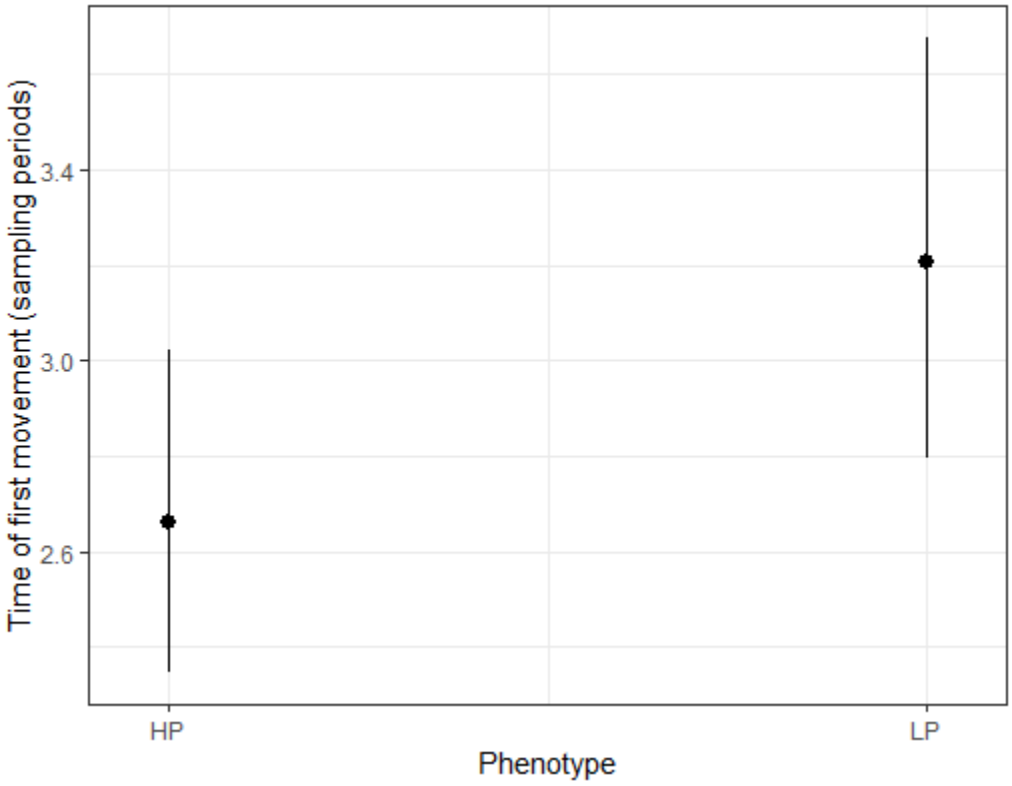


Figure 2.3. Marginal effects plot for the effect of phenotype on the timing of the first movement event. The error bars represent the 95% confidence interval.



Chapter 3: Genotypic variation in dispersal traits: A common garden experiment

Abstract

For decades, dispersal was considered to be a species-specific trait, however, recent studies have revealed high degrees of intraspecific variation in dispersal amongst populations exposed to different selective regimes. However, many of these studies are constrained by the fact that they do not disentangle the effects of plastic responses to novel environments and genetic shifts in traits values. Thus, further investigation into the genetic determination of dispersal is warranted. Here, I utilized wild, divergent populations of guppies (*Poecilia reticulata*) and a common garden approach to determine whether the previously observed differences in dispersal traits amongst high- and low-predation populations are attributable to environmental or genetic differences. I bred two independent sources of the high- and low-predation phenotype for multiple generations under identical conditions. I then analyzed and compared the dispersal traits of these lab-bred lineages to wild populations from the same localities from which the lab-bred lineages were collected. To assess variation in dispersal, I used artificial stream mesocosms which mimicked two natural pools separated by a riffle. This system allowed for the collection of data on the propensity to move, the total number of movements, and the timing of movements. Overall, the factors that explained variation in the dispersal traits are highly variable. Propensity to disperse is largely controlled by genetic components, the total number/frequency of movements is explained by an interaction between the genetic component and environmental effects, and the timing of the dispersal events is not explained by any of the variables in this study. Furthermore, the effect of

phenotype remains strong even upon removal of the wild-caught populations. These results highlight the ecological and evolutionary relevance of intraspecific, genotypic variation in dispersal tendency and demonstrates that dispersal evolves under the same selective regimes that drives the rapid evolution of life history traits.

Introduction

Dispersal, the movement of individuals which results in gene flow, is a complex, multivariate life history trait that has extensive influence on ecological and evolutionary processes. Ecologists are interested in dispersal because it affects the distribution and abundance of species, community structure and diversity, as well as the demography, dynamics, and persistence of populations (Dieckmann et al. 1999, Bowler and Benton 2005, Clobert et al. 2012, Leibold and Chase 2017). Evolutionary biologists are interested in dispersal because it produces gene flow, which directly influences processes such as local adaptation and speciation (Wright 1932, Clobert et al. 2012). Dispersal traits can also influence or evolve in tandem with other life history traits (Duputié and Massol 2013). Moreover, dispersal may respond to a wide variety of selective forces and can evolve on ecological timescales (Bowler and Benton 2005, Ochocki and Miller 2017). Its far-reaching influence on many biological processes make dispersal a central component of many applied ecological and conservation issues. For example, understanding how dispersal patterns evolve in response to shifting selective pressures is crucial for predicting the spread of invasive species and forecasting the fate of populations exposed to climate change and habitat degradation. Thus, a large body of work has been devoted to understanding the causes and consequences of variation in dispersal traits (Bowler and

Benton 2005, Clobert et al. 2012, Duputié and Massol 2013). Despite this, our ability to predict how dispersal will evolve in response to novel selection pressures remains limited.

Until recently, dispersal was largely considered to be a species-species specific trait (Travis and French 2000, Goodwin 2003, Bonelli et al. 2013). This is exemplified by the fact that most early models on the evolution of dispersal traits as well as the majority of metapopulation models consider dispersal to be fixed at the species level (Johnson and Gaines 1990, Hanski 1999, Jongejans, Skarpaas, and Shea 2008). This is, in part, because on average, variation in life history is traits is assumed to be greater among than within species (Stevens, Pavione, and Baguette 2010). Despite this assumption, a growing body of work has documented significant intraspecific variation in dispersal (Travis and Dytham 2002, Hanski et al. 2004, Fjerdingstad et al. 2007, Phillips, Brown, and Shine 2010, Stevens, Pavione, and Baguette 2010, Perkins et al. 2013, Hendrix et al. 2016, Ochocki and Miller 2017). Furthermore, this variation has the potential to arise rapidly and on ecological timescales (Ochocki and Miller 2017). However, differences amongst populations in dispersal traits, no matter how consistent or predictable, is not evidence for genotypic variation in dispersal traits (Saastamoinen et al. 2018). Immeasurable environmental effects, maternal effects, and the effects of developing under or existing in different conditions may all produce variation in dispersal traits (Fowler 2005, Mestre and Bonte 2012, Baines and McCauley 2018). Thus, interpreting variation in dispersal as an evolved response demands evidence that is indeed a heritable trait. One way of doing so is to couple observations of intraspecific variation in dispersal traits with common-

garden breeding experiments. Common-garden experiments have been successfully employed across a wide variety of systems and study designs, and they normally entail breeding distinct populations for multiple generations under identical conditions and then comparing the trait of interest (de Villemereuil et al. 2016). Differences among populations that persist for multiple generations in the absence of appropriate environmental stimuli are likely to have a genetic basis. These procedures thus make it possible to disentangle plastic responses to the environment from heritable shifts in the trait of interest; however, they are limited to systems where it is possible to breed and maintain populations in controlled conditions. If used for dispersal, the breeding design will need to be combined with a spatially structured device, such that the dispersal/movement of the lab-bred populations can be measured and compared under controlled environmental conditions.

Our current evidence for intraspecific genetic variation in dispersal traits is fairly strong, but it is limited to a small range of taxa and systems. This is largely due to methodological constraints; it is difficult to assess genetic determination in larger species where dispersal is easily tractable, and conversely, it is difficult to perform-individual based studies of dispersal in species where assessing the genetic determination of traits is more feasible. Thus, combining divergent, lab-raised populations with a spatially structured device appears to be a powerful approach for assessing whether intraspecific genotypic variation in dispersal traits exist.

The goal of this experiment is to assess whether intraspecific genetic variation in dispersal traits exists across divergent population of guppies (*Poecilia reticulata*). The

guppy is a species frequently used for studying rapid life history evolution in natural settings. Guppies are endemic on the island of Trinidad, where they exist across environments that differ in their exposure to predators. In high-predation (HP) localities, guppies co-occur with several piscivorous predators (Haskins 1961, Seghers 1973). Guppies from HP localities have repeatedly dispersed upstream over barrier waterfalls, colonizing higher elevation streams that lack predators. In these low-predation sites (LP), guppies only co-occur with one other fish species, the killifish *Anablepsoides hartii*, which rarely preys on guppies, and when it does, it selectively targets the smallest size classes (Seghers 1973, 1974). The release from predation and decrease in mortality rate is accompanied by a two-fold increase in density and fourfold increase in biomass (Potter et al. 2018). This shifts the competitive environment and produces a change from top-down to bottom-up population regulation (Bassar et al. 2013). Overall, it is largely the indirect effects of the increase in density that drive the shift from fast to slow life history strategy (Reznick et al. 2019). Until recently, it was unknown whether this change in selective regime also produced divergent dispersal strategies.

In Chapter 1, I observed the dispersal rates of natural populations to assess whether HP and LP populations vary in their tendency to disperse. I used mark-release-recapture experiments and demonstrated that HP guppy populations have a greater propensity to disperse and disperse further than their LP counterparts. The pattern of this result is consistent across all three pairs of HP/LP populations and suggests that the different selective forces in these environments have also shaped dispersal. In Chapter 2, I showed that these results are consistent in artificial mesocosms, where potentially

confounded environmental variables were controlled for. HP populations were more likely to move from the starting patch, made more movements, and moved sooner than their LP counterparts. This result was consistent across both source populations used. I manipulated potential drivers of dispersal such that I could tease apart potential genotypic differences from extraneous environmental variables amongst populations.

Between Chapter 1 and 2, I have shown a consistent and predictable differences in dispersal traits across 5 distinct pairs of HP and LP populations (Aripo, Damier, El Cedro, St. Joseph, Quare). These populations are all independent evolutionary origins of the HP and LP phenotype and they span all three major drainages where guppies are commonly studied (Caroni, Oropuche, North Slope). Furthermore, 2 of the 5 populations studied are artificial introductions which occurred approximately 25 and 40 years ago. (Damier and El Cedro), which suggests that these patterns can arise rapidly and without the spatial selection that might occur during range expansion. Despite the consistency of this pattern of differentiation, these results alone do not confirm that genotypic differences exist.

Here, I aim to use a common garden experiment to assess whether the observed variation in dispersal traits amongst high- and low-predation guppies is due to plastic responses or genetic differences in dispersal traits. If dispersal traits are of a plastic origin, I do not predict an effect of phenotype (HP vs. LP) on the movement tendencies of the lab-raised populations, however, if dispersal traits have a genetic component, I predict that the lab-raised HP populations will have a greater tendency to disperse than their lab-raised LP counterparts.

Methods

In August of 2018, I collected stock populations of HP and LP guppies from the Yarra and Aripo rivers, at both HP and LP localities. The fish were collected from the stream with butterfly nets and were added to 2L Nalgene® bottles. The fish were transferred to and monitored at our field station laboratory in the Arima Valley for at least three days, and afterwards, were transported from Trinidad to our vivarium facilities at the University of California, Riverside. I received all permits and documentation necessary for the collection, exportation, and importation of these fish. Furthermore, I constructed a crate which held 12 large bags of fish, yet still fit within the necessary carry-on dimensions for travel. I used Kordon® breather bags, which allow for the transfer of CO_2 out of the bag and oxygen into the bag, which diffuses into the water and supplies a constant source of fresh oxygen to the fish. These procedures allowed me to monitor the condition and maximize the survival of fish during the journey from Trinidad to our vivarium facilities in Riverside.

Upon arrival the fish were established in a series of 5-gallon tanks and were kept under nearly identical conditions for the duration of the experiment. Breeding occurred naturally between the small group of individuals selected to occupy each of the tanks. Each of the representative populations was raised under identical conditions to a F2 generation to begin the experiment in March of 2020. Unfortunately, the COVID pandemic postponed the timeline for this experiment due to the closure of Trinidadian borders. During this time, I continued to maintain the stock lineages under the same conditions, however, to achieve ample sample size, I used many F3 or F4 individuals in

the experiment. Going forward, I will refer to this experimental group as “F2+”. This mixed generation design makes the results a robust test of the potential genetic influence of phenotype on dispersal and movement tendency.

In November 2021, shortly after Trinidad reopened its borders, I transported approximately 160 of the F2+ guppies back to our field facilities in Trinidad. I housed the populations in 3-gallon aquaria, where they were kept at identical conditions and appropriate densities until the experimental trials began. I also returned to the exact location where each of the F2+ populations were captured and collected approximately the same number of individuals as I had in the F2+ generations. These fish were transported back to the field station laboratory and maintained under the same conditions as the F2+ fish.

I used artificial stream channels (mesocosms) to test for movement differences among F2+ and wild caught (WC) populations of HP and LP guppies. I built 8 identical mesocosms and designed them to mimic a natural habitat in which two small pools are separated by a riffle. Each mesocosm was constructed by joining three 1m x 0.5m plastic troughs (Rotoplastics Trinidad Limited, Trinidad) in a linear fashion. The outer compartments were left empty, and when filled, were approximately 30cm deep. The center compartment was filled with clay bricks and gravel such that it formed a riffle with 2-3cm of flowing water. The system utilized a 500-gallon head tank in which gravity produced the flow to the mesocosms. Valves at the inflow of each channel enabled control of water flow. The water flowed out of each channel through a mesh covered drain and down to a 55-gallon sump tank, where it was then pumped back up to the top

head tank. The water is sourced directly from a nearby tributary to the Arima river and has similar water properties as the source populations. Furthermore, the distance between the mid-point of the upper and lower compartment is similar (within 1 SD for most sites) to the distances between patches observed in the wild (Chapter 1, Figure 1.6). Overall, this system effectively mimics a natural pair of pools connected via a riffle, and it allows for replication and control of extraneous parameters which might influence dispersal or movement rate.

Before the start of the experiment, I used MS-222 to sedate each fish, and upon sedation I recorded the sex, standard length to the nearest hundredth of a millimeter, and wet mass to the nearest thousandth of a gram. In addition, each fish received a unique combination of two bright dorsal elastomer marks (Northwest Marine Technologies). The use of 4 dorsal body locations and 7 of the most easily detectable colors (in addition to the sexual dimorphism) allows me to give 588 unique marks per replicate, but since I only needed a maximum of 12 unique marks, I choose to utilize a more distinguishable pattern of marks amongst the individuals. This made identifying all individuals in a channel an easy procedure and removed the need to capture the fish at each observation point. After the marking procedure the individuals were placed into 3-gallon aquaria with their treatment groups and their health was monitored for approximately 24 hours prior to the start of the experiment.

I utilized a 2x2 factorial design in which I crossed phenotype (HP vs. LP) and generation (F2+ and WC) across the eight available mesocosms. The crossing of phenotype by generation allows for a direct comparison of lab-reared and wild

populations that is not confounded by the timing or execution of the experiment. Furthermore, it may allow for the detection of an interaction between the environmental and genetic components of dispersal traits. It is assumed that G x E interactions are common amongst dispersal strategies, however, they are rarely documented in natural populations (Saastamoinen 2018). This is because dispersal is expected to have a genetic component across a wide variety of systems, yet dispersal is also usually dependent upon some feature of the environment (e.g. density). However, documenting G x E interactions in nature is met with a suite of logistical difficulties and only currently feasible in a narrow range of systems/organismal groups.

I kept density and flow constant due to constraints with sample size and insignificance of these effects in the previous experiment. Flow was kept constant at 4L/min and density was kept at 12 individuals per channel. Sex ratio was held constant at a 1M:2F ratio (Arendt et al. 2014). Individuals were only utilized if their sex could be determined, thus, most juveniles (aside from those near sexual maturity) were excluded from this experiment. To maximize sample size, I utilized a small number of individuals in multiple trials, purely to maintain consistency in density and sex-ratio of the experimental channels. The data for individuals on their successive trials was not used in any of the analyses.

The experiment started with an acclimation phase, where fish were gently placed into the bottom ("downstream") patch of each channel for one hour. The top patch was left empty, and a mesh barrier was installed to prevent movement into the riffle or top patch. After the acclimation phase was over, I removed the barriers and surveyed the

location of each fish every three hours during daylight, plus one nighttime survey, for a total of 9 observations. Thus, the maximum number of observable movement events is also 9. Guppies are diurnal, so this sampling schedule adequately captures their movements. This design allows for the collection of data on whether an individual ever moved, the timing of the first movement, and the overall number of movements. Each experimental replicate lasted for 36 hours, which proved to be enough time to allow for movement throughout the mesocosms.

I analyzed three separate response variables: the propensity to move from the starting patch, the frequency of movements, and the time at the first movement event. Propensity to move is a response representing whether the individual ever moved from the initial patch. Frequency is the total number of crossings that occurred during the experiment. Time represents the observation period in which the first movement event was observed. Individuals that did not move were excluded from the time models. These responses were analyzed in R (Version 4.2.1, R Core Team 2022) with generalized linear mixed models. The independent variables include sex, standard length, phenotype (HP/LP), river (Aripo/Yarra), and generation (F2+/WC). I centered and scaled the standard length measurements to transform the units to the number of standard deviations from the population mean (population meaning each combination of phenotype, river, and generation). I also employed a random effect which combined replicate and channel number to account for spatial and temporal differences among the channels.

For all the models described below, I utilize the Akaike information criterion (AIC) to perform model selection and identify the best fitting model(s) for the available

data (Burnham and Anderson 2002, Zuur et al. 2009). I deemed models with a ΔAIC of 2 or lower to be the best fitting models (Burnham and Anderson 2002, Grueber et al. 2011). This threshold is more conservative than most (Richards 2008, Bolker et al. 2009, but see Grueber et al. 2011), however, it limits inference to only the models and combinations of variables best supported by the data. If there are multiple models with ΔAIC < 2, I use a model averaging approach to obtain a single set of parameter estimates ('model.avg' function, MuMIn package, version 1.47.1, Bartoń 2022). This approach uses a weighted average of parameter estimates such that models that explain more variation in the response variable are weighted higher and contribute more to the model averaged parameter estimates. Using the (potentially model-averaged) parameter estimates and their standard errors, I calculated the Wald Z-statistic and associated p-values. These Wald Z-tests may provide unreliable results for GLMMs, because they depend upon multiple assumptions, some of which may be easily violated. These assumptions include that the sampling distribution of the parameters are multivariate normal and that the sampling distribution of the log-likelihood is proportional to χ^2. Thus, reported p-values should be treated with a healthy degree of skepticism and considered in the context of the overall pattern of the data and model estimates. Not all meaningful patterns will rise to statistical significance and not all significant differences will be meaningful.

The propensity candidate models were fitted with the glmer function (lme4 package, version 1.1.27.1, Bates et al. 2015) and utilized a binomial family argument and a logit link function. The frequency candidate models were built with the glmer function and utilized a Poisson family argument and log link function. The time candidate models

were fitted with the glmmTMB function (glmmTMB package, version 1.1.4, Brooks et al. 2017) and utilized a negative binomial family argument and a log link function.

Results

I observed the 306 guppies 2,754 times across all experimental replicates. Two hundred and nineteen of the 306 (71.6%) fish made at least one movement during the experimental trials. A total of 781 movements were observed for an average of 2.55 movements per individual (range: 0 – 8). For individuals that moved, the average time of the first movement was at 2.28 observation periods, which is shortly after the observation event that occurs 6 hours into the experiment, or approximately 25.3% through the duration of the experiment.

The selection procedure on the propensity models yielded 4 models with ΔAIC values lower than 2 (Table 3.1). Of these, 4 included phenotype and generation, 3 included river, and one included sex. The model averaged fixed effects are summarized by a strong effect of phenotype ($\beta = -1.44$, $z = 3.96$, $p < 0.0001$, Tables 3.2 and 3.3, Figure 3.1), and insignificant effects of generation, sex, and the interaction between river and phenotype (Table 3.2). However, generation appears in all of the top models which suggests it adds some predictive value, even if the effect on its own is insignificant. Overall, HP individuals have a greater movement propensity than LP, regardless of generation or river (Marginal mean propensity: HP: 86.0%; LP: 56.4%, Tables 3.2 and 3.3, Figure 3.1).

The selection procedure on the frequency models yielded 3 models with ΔAIC values lower than 2 (Table 3.4). All three contained an interaction between phenotype

and generation, two contained the river variable, and one contained the length variable. The model averaged parameter estimates yielded a modest interaction between phenotype and generation (β = -0.36, z = 2.40, p = 0.016, Tables 3.5 and 3.6, Figure 3.2). The remaining main effects were insignificant (Table 3.5). The interaction reveals that the HP populations had greater movement frequencies across both generations, however, this difference was stronger for the wild-caught populations (Marginal mean movement frequencies: HP F2+: 2.78; LP F2+: 2.08, HP WC: 3.55; LP WC: 1.86, Tables 3.5 and 3.6, Figure 3.2).

The selection procedure on the time candidate models yielded two models with an ΔAIC value lower than 2 (Table 3.7). Both contained the phenotype, generation, and river variables, and only one contained the length variable. Taken together, these models improve predictive performance as measured by AIC, but individually, the parameter estimates cannot be statistically distinguished from zero (Table 3.8, Figure 3.3).

Following these results, I reperformed the analyses for propensity and frequency excluding all wild caught populations. The selection procedure on the propensity models yielded 2 models with ΔAIC values lower than 2 (Table 3.9). Of these, 2 included phenotype and one included river. The model averaged fixed effects are summarized by a strong effect of phenotype (β = -1.42, z = 3.585, p = 0.0003, Table 3.10, Figure 3.4), and insignificant effects of river (Table 3.10). Here, HP individuals have a greater movement propensity across both rivers (Tables 3.10, Figure 3.4). The selection procedure on the frequency models yielded 2 models with ΔAIC values lower than 2 (Table 3.11). Of these, 2 included phenotype and one included river. The model averaged fixed effects are

summarized by a strong effect of phenotype (β = -0.29, z = 2.722, p = 0.006, Table 3.12, Figure 3.5), and insignificant effects of river (Table 3.12). Here, HP individuals have greater movement frequencies across both rivers (Tables 3.12, Figure 3.5).

Discussion

The results obtained from this experiment demonstrate that there is a strong genetic component to dispersal in guppies, however, phenotype alone does not determine dispersal tendency. Some traits, such as propensity, may be strongly influenced by phenotype, while others may be dependent upon the environment or other factors. These traits may also be explained by an interaction between genetic and environmental effects, as was the case for movement frequency.

The decision to leave the starting patch is explained by a strong effect of phenotype. This result suggests that this trait has a strong genetic component and has evolved amongst HP and LP phenotypes. The frequency of movements is largely explained by a significant interaction between phenotype and generation. This suggests that the frequency of movements (and perhaps distance) is controlled by an interaction between genetic and environmental influences. The differences between HP and LP in terms of propensity and frequency also exist once the wild-caught individuals were removed from the analyses, further suggesting that these are evolved differences.

The variation in the timing of the first movement was not explained by any variables in the models. This result suggests that the timing of dispersal events is not under genetic control, but instead, depends upon other intrinsic or environmental traits

that were not measured here. This seems reasonable given that dispersal is usually triggered by a suite of environmental variables in the source patch.

Overall, these results, in combination with the results obtained in Chapter 1 and 2, provide extremely strong evidence for the rapid evolution of dispersal traits in guppy populations. High-predation populations that exhibit fast life histories and are under top-down population regulation have consistently higher dispersal rates (or propensities) and disperse further or more often than low-predation populations that have slower life histories and are regulated by bottom-up population regulation. This result was demonstrated via mark-release-recapture experiments, mesocosm experiments with natural populations, and common garden experiments that compared lab-bred and natural populations. In total, 6 independent evolutionary origins of the HP and LP genotype were investigated, and the results were consistent across each pair. Of these 6 populations, 2 represent recent artificial introductions that occurred approximately 25 and 40 years ago. Therefore, these results demonstrate that these divergent genotypes likely arise rapidly, as do other divergences in life history traits in this system (Reznick et al. 2019).

The results from this experiment also serve to highlight the complexity of dispersal. It has been previously demonstrated that dispersal is comprised of multiple stages (departure, transfer, settlement), and the interaction between all the traits/stages produces the dispersal phenotype. Here, depending upon the dispersal trait of interest, dispersal is determined by genotype, the environment, or by an interaction between the two. Thus, not only is dispersal a combination of multiple traits, but these traits may be under entirely different patterns of genetic and environmental control.

This experimental approach is powerful because it allowed for a thorough and robust test of whether variation in dispersal traits is due to phenotypic plasticity or genotypic differences. However, this methodology only begins to scratch the surface of the potential genetic complexity that underlies dispersal. Other factors, such as the heritability, architecture, and genetic correlations with other traits may all play a major role in the trajectory and speed in which dispersal evolves (Saastamoinen 2018). Further exploration into the genetic and environmental determinants of the dispersal of naturally divergent populations is likely to further our understanding of how different selective pressures interact to produce rapid genotypic changes in dispersal. This knowledge will enhance our ability to predict whether species exposed to climate change and habitat degradation can adequately respond and persist through such challenges.

Tables

Table 3.1. Model selection tables for the analysis of the propensity response variable. All models were fit with logit link functions. The columns on the right side of the table describe the degrees of freedom used by the model, its log-likelihood value, its AIC value, and the difference in AIC value between the current and best-fitting model. An asterisk or colon between variables indicates an interaction.

Models	**df**	**logLik**	**AIC**	**ΔAIC**
Phenotype * River + Generation + (1|Channel)	6	-163.5	338.9	0
Phenotype + River + Generation + (1|Channel)	5	-164.5	338.9	0
Phenotype + Generation + (1|Channel)	4	-165.7	339.3	0.4
Phenotype * River + Generation + Sex + (1|Channel)	7	-163.4	340.8	1.9
Phenotype + Generation + Sex + Length + River + (1|Channel)	7	-164.4	342.7	3.8
Phenotype * River + Generation + Sex + Length + (1|Channel)	8	-163.4	342.7	3.8
Phenotype * Length + Generation + Sex + River + (1|Channel)	8	-163.9	343.8	4.9
Phenotype * Generation + Sex + Length + River + (1|Channel)	8	-164.2	344.4	5.5
Sex + River + Generation + (1|Channel)	5	-179.2	368.4	29.5
River * Generation + (1|Channel)	5	-179.3	368.6	29.7

Table 3.2. Model-averaged fixed effect parameter estimates for the analysis of propensity to move from the starting patch. The models averaged here were the best fitting models identified in the model selection procedure. A colon between variables indicates an interaction.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	1.619	0.328	4.917	< 0.0001
Phenotype	-1.438	0.362	3.960	< 0.0001
River	0.550	0.549	1.000	0.317
Generation	-0.061	0.272	0.222	0.824
Sex	0.012	0.102	0.121	0.904
Phenotype:River	-0.354	0.573	0.617	0.537

Table 3.3. Marginal mean estimates for the best-fitting model of movement propensity of guppies across phenotype (HP/LP), river (Aripo/Yarra), and Generation (F2+/WC).

Phenotype	**River**	**Generation**	**Movement propensity**	**SE**
HP	Aripo	F2+	0.811	0.046
LP	Aripo	F2+	0.552	0.070
HP	Yarra	F2+	0.921	0.032
LP	Yarra	F2+	0.589	0.067
HP	Aripo	WC	0.802	0.050
LP	Aripo	WC	0.537	0.068
HP	Yarra	WC	0.916	0.035
LP	Yarra	WC	0.574	0.061

Table 3.4. Model selection tables for the analysis of the frequency response variable. All models were fit with log link functions. Models with a ΔAIC of lower than 2.0 were averaged to produce a single set of fixed-effect parameter estimates. Those estimates are summarized below (Table 3.4). The columns on the right side of the table describe the degrees of freedom used by the model, its log-likelihood value, its AIC value, and the difference in AIC value between the current and best-fitting model. An asterisk or colon between variables indicates an interaction.

Models	**df**	**logLik**	**AIC**	**ΔAIC**
Phenotype * Generation + (1|Channel)	5	-640.3	1290.7	0
Phenotype * Generation + River + (1|Channel)	6	-639.4	1290.8	0.1
Phenotype * Generation + Length + River + (1|Channel)	7	-638.9	1291.8	1.1
Phenotype * Generation + Sex + Length + River + (1|Channel)	8	-638.9	1293.8	3.1
Phenotype * River + Generation + Sex + Length + (1|Channel)	8	-640.4	1296.8	6.1
Phenotype + Length + Sex + River + (1|Channel)	6	-642.9	1297.7	7
Phenotype * Length + Generation + Sex + River + (1|Channel)	8	-641.8	1299.5	8.8
Length + Sex + River + (1|Channel)	5	-654.7	1319.3	28.6
Generation + Length + Sex + River + (1|Channel)	6	-654.6	1321.2	30.5

Table 3.5. Model-averaged fixed effect parameter estimates for the analysis of the frequency response variable. The models averaged here were the best fitting models identified in the model selection procedure above (Table 3.4). A colon between variables indicates an interaction.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	0.996	0.073	13.575	< 0.0001
Phenotype	-0.295	0.107	2.745	0.006
Generation	0.242	0.090	2.673	0.008
River	0.057	0.073	0.783	0.434
Length	-0.008	0.023	0.343	0.731
Phenotype:Generation	-0.358	0.148	2.403	0.016

Table 3.6. Marginal mean estimates for the best-fitting model of movement frequency of guppies across phenotype (HP/LP) and Generation (F2+/WC).

Phenotype	**Generation**	**Movement Frequency**	**SE**
HP	F2+	2.784	0.179
LP	F2+	2.077	0.179
HP	WC	3.551	0.227
LP	WC	1.857	0.149

Table 3.7. Model selection tables for the analysis of the time response variable. All models were fit with log link functions. The columns on the right side of the table describe the degrees of freedom used by the model, its log-likelihood value, its AIC value, and the difference in AIC value between the current and best-fitting model.

Models	**df**	**logLik**	**AIC**	**ΔAIC**
Phenotype + Generation * River + Length + (1|Channel)	8	-403.1	822.3	0
Phenotype + Generation * River + (1|Channel)	7	-404.1	823.1	0.8
Phenotype + Generation * River + Sex + Length + (1|Channel)	9	-402.9	823.8	1.5
Phenotype + Generation + Sex + Length + River + (1|Channel)	8	-404.1	824.2	1.9
Phenotype * River + Generation + Sex + Length + (1|Channel)	9	-403.2	824.4	2.1
Phenotype * Length + Generation + Sex + River + (1|Channel)	9	-403.7	825.4	3.1
Phenotype * Generation + Sex + Length + River + (1|Channel)	9	-403.9	825.8	3.5

Table 3.8. The fixed effect estimates from the best fitting model of the time at first movement event.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	0.928	0.149	6.209	< 0.0001
Phenotype	0.081	0.140	0.571	0.568
River	-0.308	0.198	1.544	0.123
Generation	-0.240	0.205	1.164	0.245
Length	-0.088	0.062	1.424	0.155
Sex	0.081	0.123	0.660	0.509
Generation:River	0.427	0.276	1.539	0.124

Table 3.9. Model selection tables for the analysis of the propensity response variable, excluding the wild-caught populations. All models were fit with logit link functions. The columns on the right side of the table describe the degrees of freedom used by the model, its log-likelihood value, its AIC value, and the difference in AIC value between the current and best-fitting model. An asterisk between variables indicates an interaction.

Models	**df**	**logLik**	**AIC**	**ΔAIC**
Phenotype + (1|Channel)	3	-81	167.9	0
Phenotype + River + (1|Channel)	4	-80.4	168.8	0.9
Phenotype + River + Length + (1|Channel)	5	-80.4	170.7	2.8
Phenotype + River + Sex + Length + (1|Channel)	6	-80.3	172.7	4.8
Phenotype * River + Sex + Length + (1|Channel)	7	-80.1	174.1	6.2

Table 3.10. Model-averaged fixed effect parameter estimates for the analysis of propensity to move from the starting patch, excluding the wild-caught populations. The models averaged here were the best fitting models identified in the model selection procedure.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	1.684	0.327	5.109	< 0.0001
Phenotype	-1.422	0.393	3.585	0.0003
River	0.417	0.391	1.056	0.291

Table 3.11. Model selection tables for the analysis of the frequency response variable, excluding the wild-caught populations. All models were fit with log link functions. The columns on the right side of the table describe the degrees of freedom used by the model, its log-likelihood value, its AIC value, and the difference in AIC value between the current and best-fitting model. An asterisk between variables indicates an interaction.

Models	**df**	**logLik**	**AIC**	**ΔAIC**
Phenotype + (1|Channel)	3	-318.8	643.5	0
Phenotype + River + (1|Channel)	4	-318.4	644.8	1.3
Phenotype + River + Length + (1|Channel)	5	-318.1	646.1	2.6
Phenotype + River + Sex + Length + (1|Channel)	6	-318	648.1	4.6
Phenotype * River + Sex + Length + (1|Channel)	7	-318	650	6.5

Table 3.12. Model-averaged fixed effect parameter estimates for the analysis of the frequency response variable, excluding the wild-caught populations. The models averaged here were the best fitting models identified in the model selection procedure.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	1.010	0.073	13.758	< 0.0001
Phenotype	-0.294	0.107	2.722	0.006
River	0.088	0.103	0.847	0.397

Figures

Figure 3.1. Marginal effects plot for the predicted effect of phenotype on the propensity to move from the starting patch. Error bars represents the 95% confidence interval. F2+ are the populations reared in the common garden, while WC refers to individuals that were wild-caught.

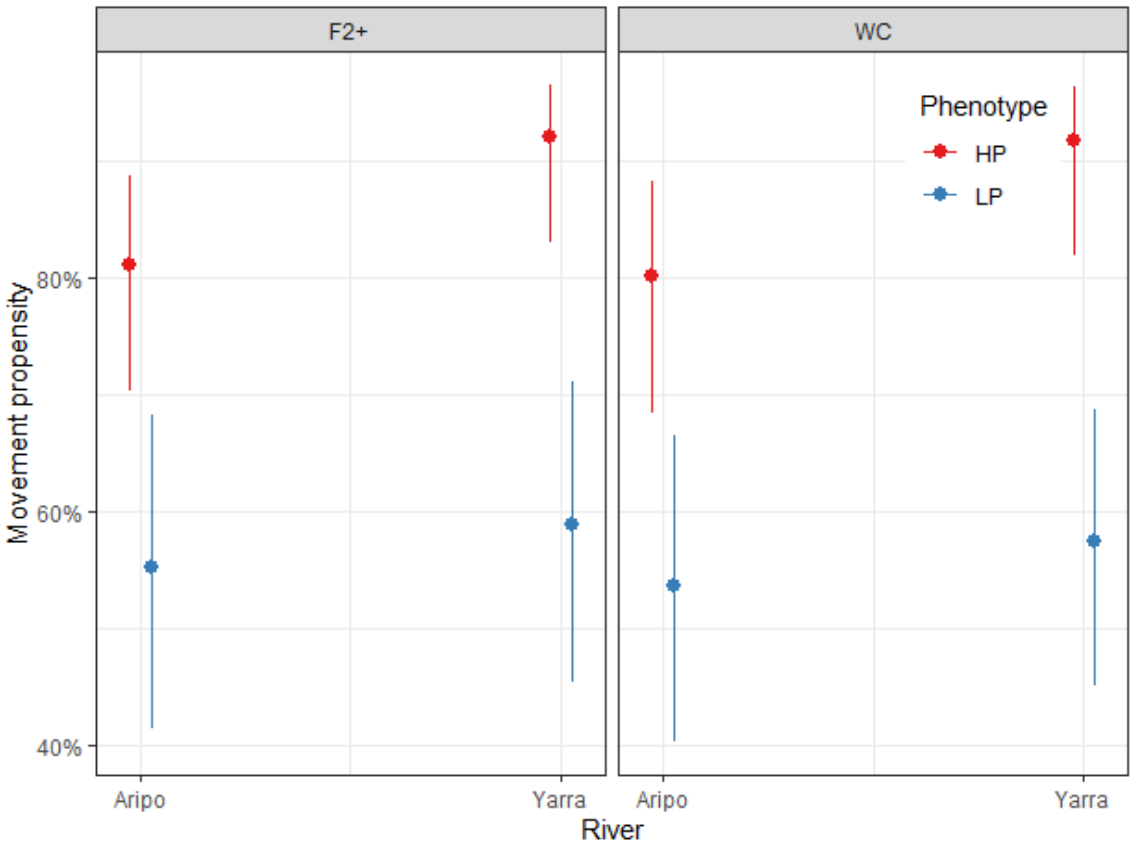


Figure 3.2. Marginal effects plot for the predicted effect of the interaction between phenotype and generation on the frequency of movements. Error bars represents the 95% confidence interval. F2+ are the populations reared in the common garden, while WC refers to individuals that were wild-caught.

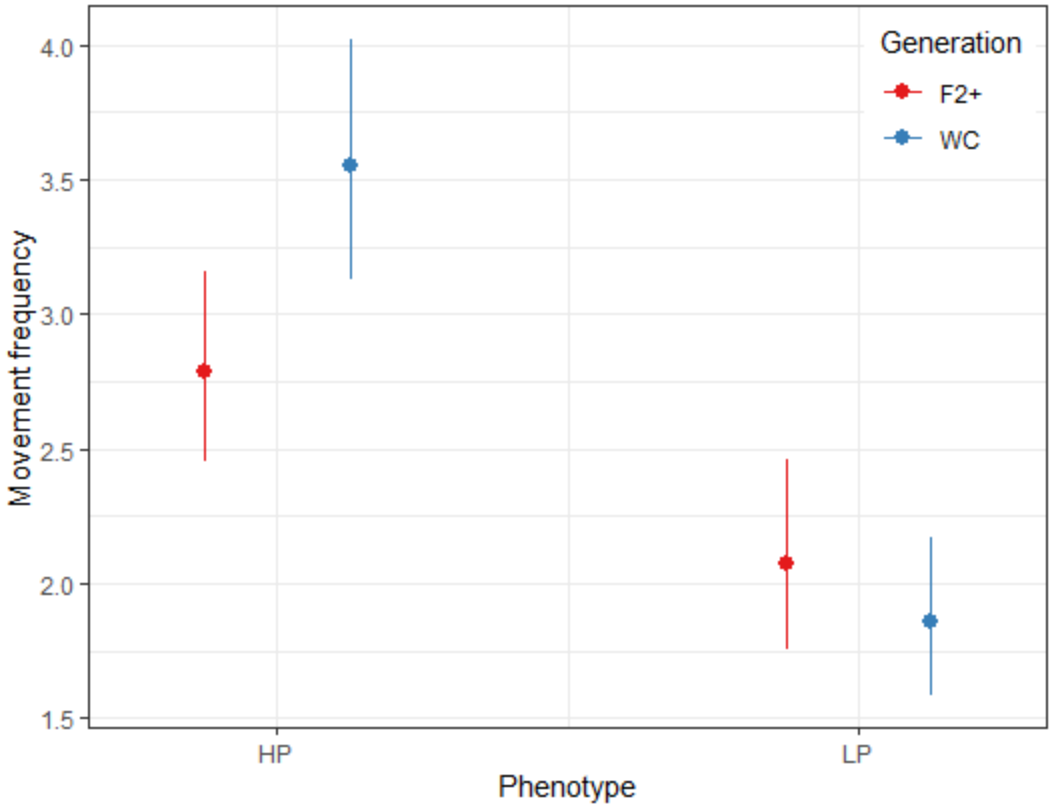


Figure 3.3. Marginal effects plot for the predicted effect of the interaction between river and environment (generation) on the timing of the first movement event. Error bars represents the 95% confidence interval. F2+ are the populations reared in the common garden, while WC refers to individuals that were wild-caught.

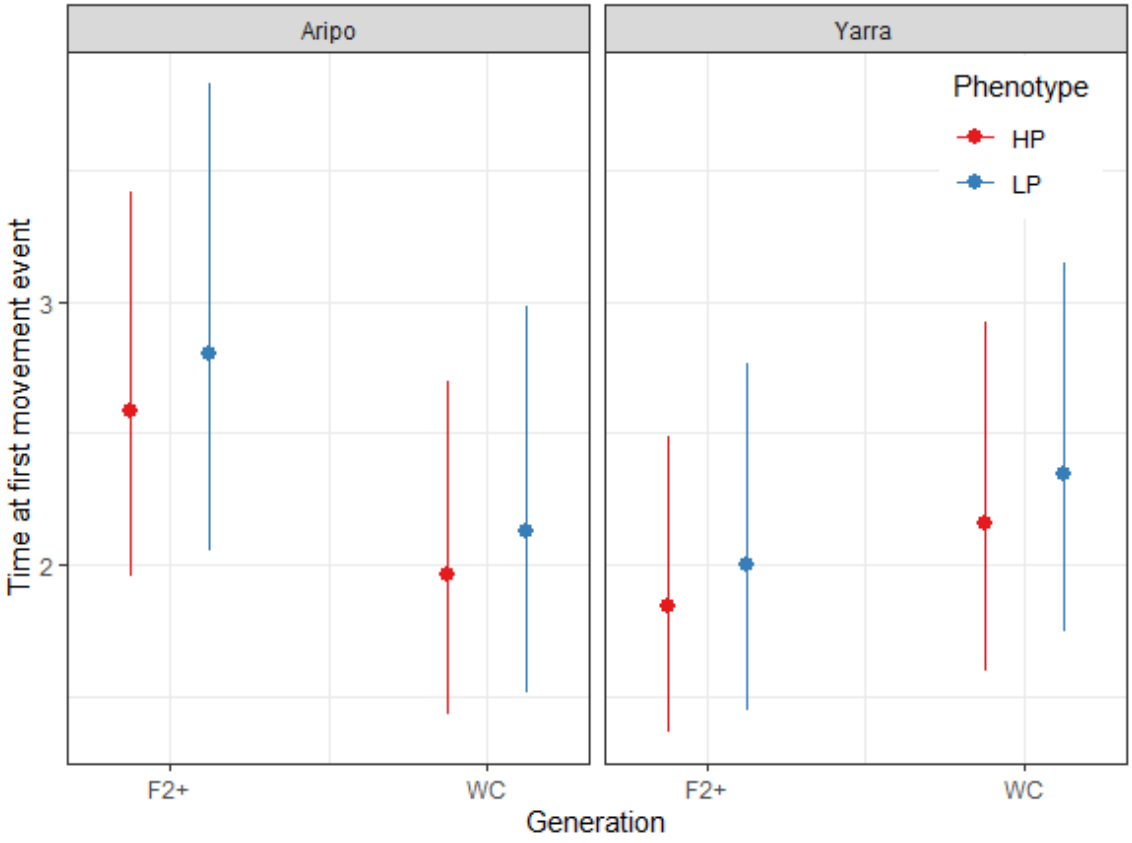


Figure 3.4. Marginal effects plot for the predicted effect of phenotype and river on the propensity to move from the starting patch. This only contains the F2+ individuals that were reared in a common garden. Error bars represents the 95% confidence interval.

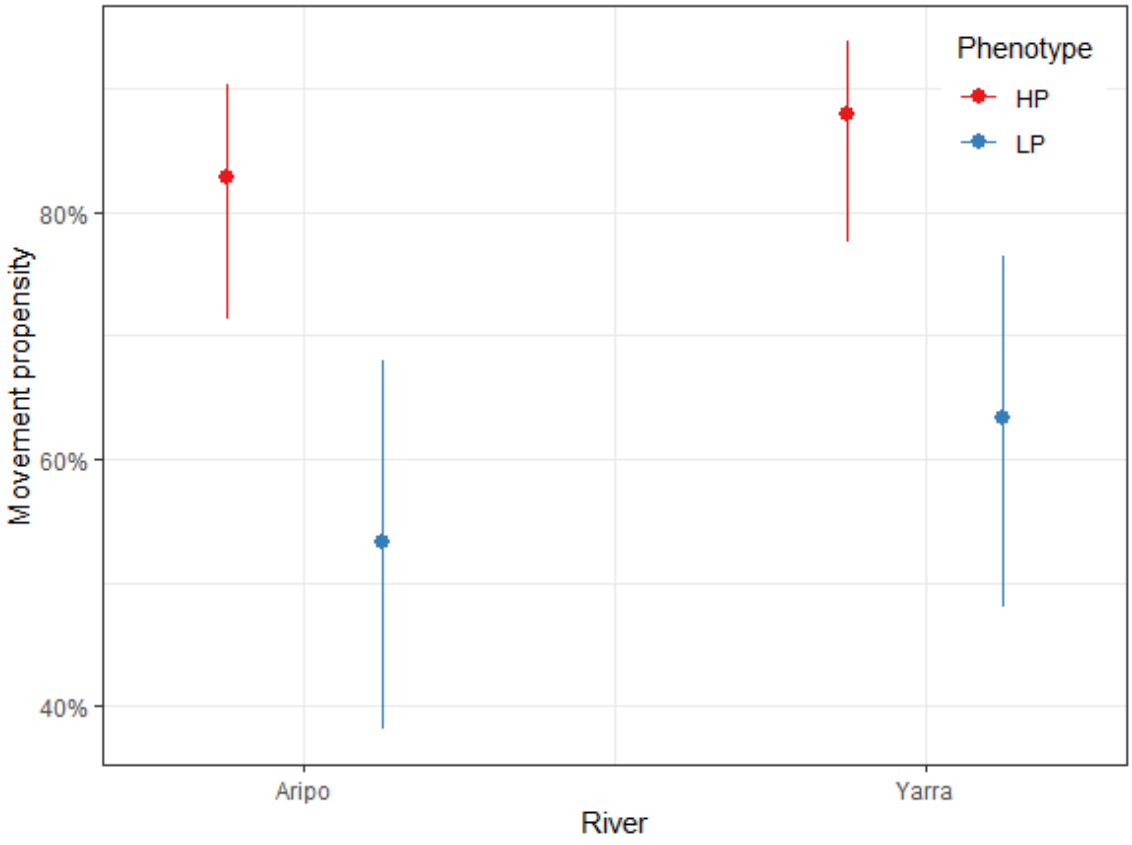
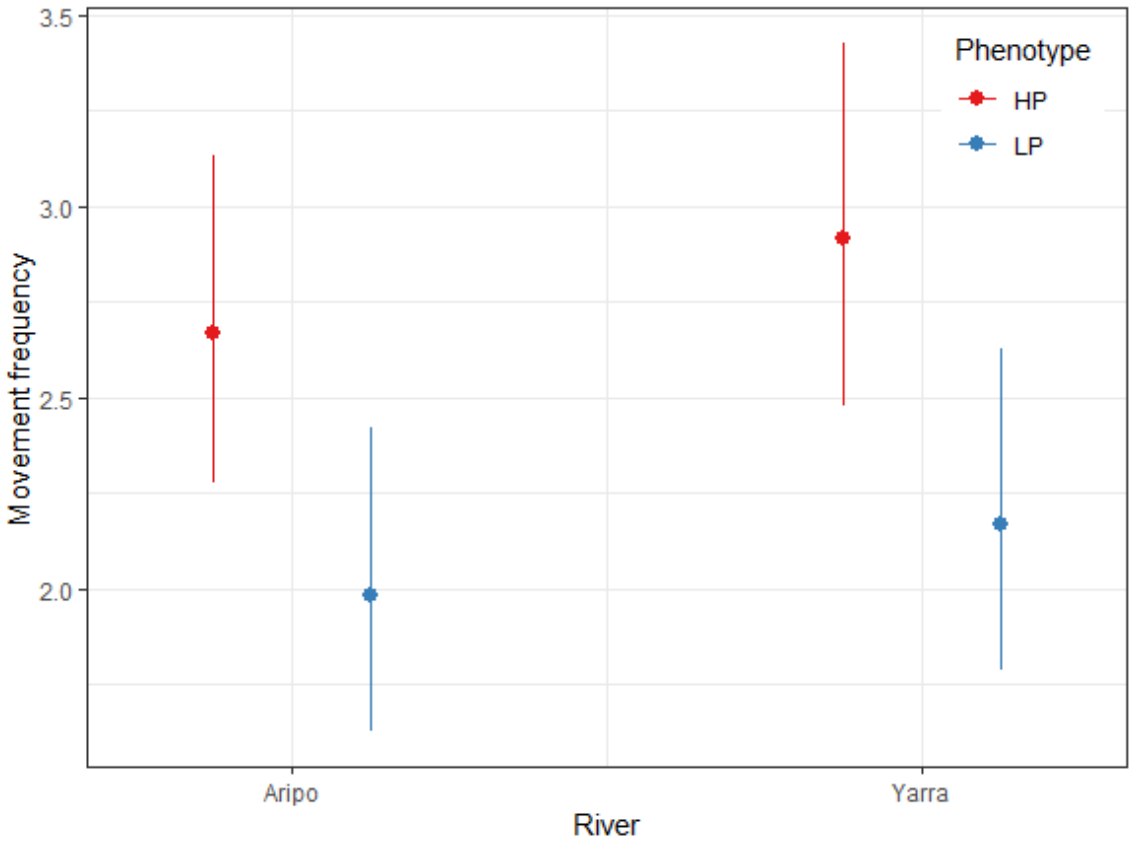


Figure 3.5. Marginal effects plot for the predicted effect of phenotype and river on movement frequency. This only contains the F2+ individuals that were reared in a common garden. Error bars represents the 95% confidence interval.



Chapter 4: Homing in the Trinidadian Guppy: Its relation to dispersal and variation amongst populations

Abstract

Homing ability, or the ability for animals to use environmental cues to navigate and return to a known location following a displacement event, is a trait that can have substantial implications for survival, and ultimately fitness. This is because homing ability, like dispersal, serves to better enable individuals to escape poor conditions and reside in habitats with high fitness potential. However, little is known about the environmental factors that produce variation in homing ability, especially at the intraspecific level. Moreover, little is known about how homing ability might be related to other traits associated with habitat selection, such as dispersal. Here, I investigate variation in homing ability across wild populations of guppies (*Poecilia reticulata*) that are adapted to high or low levels of predation. I also assess whether homing ability is correlated with dispersal propensity, or other aspects of the individual's phenotype (sex, size/length/age). To do so, I use a series of spatially-explicit, mark-recapture experiments paired with translocation treatments. Overall, I found that guppies in all populations exhibit some degree of homing ability. However, I found strong and consistent differences between high and low predation populations in terms of homing ability. HP individuals were more successful at homing across nearly all populations and treatments. Furthermore, I often found that females, as well as larger individuals, were more likely to exhibit successful homing behavior. I did not find any relationship between homing ability and dispersal propensity at the individual level. Overall, these experiments suggest

that the alternative selection pressures associated with high- and low-predation habitats produce consistent differences in homing ability.

Introduction

Homing behavior is the tendency for an individual to navigate and return to a familiar location following displacement (Papi 1992). This behavior is widespread across the animal kingdom due to its ability to convey significant fitness advantages (Crump 1986, Papi 1992, Yoshiyama et al. 1992, Gibson 1999, Campbell et al. 2019). Displacement from a familiar location can be extremely costly to an individual, as they may lose the benefits from known social dynamics, local resources and predators and these losses might result in reduced survival or mating opportunities (Reinert and Rupert 1999, Lfjty et al. 2003, Bonte et al. 2011, Piper et al. 2011, Spencer 2012). Displacement may occur naturally from a variety of ecological phenomena, such as extreme weather or via widespread foraging. For example, birds may be blown away in strong winds and aquatic species may be washed downstream during floods (Lack 1958, Chapman and Kramer 1991, Nesterova et al. 2009). Additionally, individuals may rapidly flee their habitats as a direct response to predation attempts or other threats (Ydenberg and Dill 1986, McIntosh et al. 2002). Furthermore, human disturbances can also lead to the widespread displacement of animals (Trayford and Farmer 2012). Thus, homing ability can better enable individuals to escape poor local conditions and return to habitats with greater fitness potential.

However, to successfully home, an individual must have the cognitive ability to be able to recognize and use cues to direct their navigation (Papi 1992, Walcott 2005,

Luschi et al. 2007, Steck 2012). Homing is thought to be more important in habitats that are extreme, fluctuate greatly over space and time, or have a high probability of displacement (Yoshiyama et al. 1992, White and Brown 2013, Jergenson et al. 2014). It is likely that the increased pressures associated with these habitats selects for increased cognitive ability and greater homing success. This idea is more formally known as the "ecological cognition hypothesis", and states that complex behaviors that require cognitive ability are largely shaped by the environmental pressures and associated challenges that individuals must experience and persist through (Healy and Braithwaite 2000). For example, White and Brown (2013) found that species that live exclusively within the intertidal zone have greater homing success when compared to species that are only secondary residents. This is likely because the permanent residents of rocky intertidal zones need to remember the locations of high-quality pools and must also be able to return to them before being stranded by low tides (Williams 1957, Yoshiyama et al. 1992). This necessity might select for greater cognitive ability. Moreover, comparative studies across a wide range of taxa have shown that variation in telencephalon size (the area of the brain responsible for spatial learning) is related to differences in the spatial demands of one's life history (Gaulin and FitzGerald 1986, Basil et al. 1996, Burns and Rodd 2008, Costa et. al 2011). For example, various Blenniid fish exhibit a polygynandric mating system in which the male defends their breeding territory while the females move among breeding sites in search of the highest-quality mating opportunities. This difference in life history is associated with larger dorsolateral telencephalon sizes in females and is likely to be directly associated with the difference in spatial abilities

(Costa et al. 2011). Thus, if homing ability is limited by cognitive ability, and cognitive ability arises because of environmental challenges and the associated spatial learning that occurs because of such challenges, then populations exposed to more extreme and challenging environments should exhibit greater homing ability. Despite the abundance of work examining homing behavior, this hypothesis has seldom been explored at the intraspecific level.

Furthermore, it is possible that homing ability is associated with other behavioral and life-history strategies, and this might impact what we know about the factors driving and producing variation in homing ability. A possible candidate is dispersal because it involves habitat selection and navigation between habitats. Dispersal has vast evolutionary and ecological consequences, and as such, a great deal of work has been devoted to understanding the causes of dispersal and the mechanisms behind how it evolves (Bowler and Benton 2005, Clobert et al. 2012). One important element of dispersal evolution is the potential for syndromes to emerge. Dispersal syndromes are associations between dispersal and other phenotypic traits such as morphology, behavior, physiology, or life-history (Ronce and Clobert 2012). These syndromes can arise because of genetic correlations between dispersal and other traits, or through correlated responses to the environment (Ronce and Clobert 2012, Saastamoinen et al. 2017). Dispersal syndromes are incredibly important in the context of dispersal evolution because they might shape or constrain the evolutionary trajectory of the traits and inform us about the proximate and ultimate drivers of dispersal (Baker and Stebbins 1965, Bonte et al. 2012).

Furthermore, these syndromes can have intense genetic and demographic consequences (Bernard and McCauley 2008, Clobert et al. 2009).

A robust body of work has shown that dispersal syndromes are common and can encompass nearly all dimensions of the phenotype (Ronce and Clobert 2012). However, systematic patterns in terms of the direction of correlation between dispersal and a phenotypic trait are rare. For well-studied syndromes, these inconsistencies among systems may be explained by the proximate and ultimate forces that drive the emergence of those syndromes. But for many syndromes, we lack the empirical evidence to make general conclusions. Some syndromes, such as those related to habitat selection and preferences, are likely to exist but have seldom been explored (Ronce and Clobert 2012). Homing ability, like dispersal, may better enable individuals to escape poor local conditions and return to habitats with greater fitness potential (Papi 1992, Bowler and Benton 2005). Moreover, both dispersal and homing ability have similar physical and cognitive requirements. Thus, it seems plausible that dispersal syndromes could include homing ability, but this has rarely, if ever, been tested experimentally.

Here, I use the Trinidadian guppy (*Poecilia reticulata*) as a system to explore intraspecific variation in homing success and its relation to dispersal propensity. Natural populations of guppies in streams draining the slopes of the Northern Range Mountains of Trinidad are confronted by alternative environments that differ in ways that have been shown to produce differences in brain anatomy and cognition (Burns and Rodd 2008, Kotrschal et al. 2017). Downstream populations live with predators and experience high mortality rates in combination with low population densities and high resource

abundance (Reznick et al. 1996, Reznick et al. 2019). Those found upstream instead have a low risk of predation but, as an indirect consequence, live at high population densities and have low resource availability. Guppies are well suited for studying homing behavior because they are abundant, can be individually marked, live in spatially discrete habitats, have relatively short dispersal distances, have a high probability of recapture, and are accompanied by a robust body of life-history literature (Endler 1995, Reznick et al. 2001, De Bona et al. 2019, Borges et al. 2021).

I explore homing in the guppy system through a series of three spatially explicit individual-based mark recapture experiments. In the first I use a single population to ask whether guppies respond to experimental displacement and to what degree guppies exhibit homing behavior following this displacement. In the second, I use two paired HP and LP populations to examine whether these environmental differences produce differences in homing success. I also investigate whether there is an association between homing success and natural dispersal propensity. In the third and final experiment, I further examine intraspecific variation in homing success across greater displacement distances. Across all three experiments I examine whether intrinsic traits such as sex or body size play a role in homing success.

If spatial cognition can be shaped by environmental differences and contributes to homing ability, then the ecological cognition hypothesis predicts that HP populations would have a greater homing ability relative to LP populations. This is because HP guppies are more mobile (Chapters 1, 2, and 3) and spatial cognition is likely to be an important part of surviving and co-occuring with a diverse predator community.

Furthermore, since homing is a behavior which better enables individuals to remain sedentary, I expect that if it is associated with dispersal behaviors that any of these associations would be negative. By the same logic, since males are more dispersive, I expect females to exhibit greater homing tendency and success. Moreover, since older (and larger) individuals have had more time to develop their cognitive skills, I expect that larger individuals are more likely to exhibit homing behavior.

Methods

I used mark-recapture methods in combination with experimental translocations to investigate homing success across all three experiments. In the first experiment, I used a small population in the Ramdeen river, a small tributary to the Arima river. The fish community in the Ramdeen consists of guppies, *Anablepsoides hartii*, *Aequidens pulcher*, *Synbranchus marmoratus* and *Hoplias malabaricus*. In the second and third experiments, I used paired HP and LP populations from the St. Joseph and El Cedro rivers. The former represents a natural invasion of HP guppies into a LP habitat, while the latter was experimentally introduced approximately 40 years ago (Reznick and Bryga 1987). In addition to the type of fish community, I chose these streams based on the presence of a pool-riffle morphology and other physical similarities that make quantifying movement tractable. Guppies prefer pools and are seldom found in riffles; therefore, each pool represents an independent sub-population. I deemed homing to be successful only when a displaced individual was recaptured in its original pool of capture.

During capture events, I set out to capture every individual within the study site. Guppies are curious and swim freely in the water column or along the stream banks, so

almost all the individuals within a site can be captured. I surveyed each pool and captured all visible individuals. I returned after a short period of time and captured any individuals that were previously not seen. I repeated this procedure until no fish remained.

Upon capture, I placed the guppies into a bottle specific to their capture location, then transferred them to our field station in the Arima Valley. I used MS-222, in combination with appropriate amounts of sodium bicarbonate as a buffer, to sedate each fish. Upon sedation, each fish received a unique combination of two elastomer marks (Northwest Marine Technologies). I used 8 body locations and 8 colors (in addition to the sexual dimorphism), which allowed me to uniquely mark thousands of fish per site. I only used individuals if their sex could be determined, thus, most juveniles (aside from those near sexual maturity) were excluded from this experiment. I recorded the sex, pool of origin, standard length to the nearest hundredth of a millimeter and wet mass to the nearest thousandth of a gram for each fish, then randomly assigned a treatment.

In the first experiment, I randomly assigned each fish to one of three treatments: upstream translocation, downstream translocation, or a control treatment of no translocation. I did not move individuals outside of the boundaries of the focal site, so individuals in the upper and bottom pools could only be assigned to the control and one translocation treatment. For example, in the uppermost pool, individuals would be randomly assigned the downstream translocation or control treatments.

In the second experiment, all fish were returned to the pool in which they were caught for the first two recapture intervals (See Chapter 1). The natural dispersal propensity of individuals was monitored during these recaptures. Following two

recaptures with return to the pool of capture, I performed the same random assignment of treatments as the first experiment, as described above by assigning each fish to the control, upstream, or downstream treatment groups.

In the third experiment, I randomly assigned two separate translocation treatments: direction (upstream or downstream) and distance (20 meters and 100 meters). These distance treatments are designed to represent an average and a long-distance movement/displacement event.

After processing, I transferred the fish to holding tanks where their health was monitored for approximately 24 hours. The fish were then repacked into bottles and returned to the stream in accordance with their treatments. I placed the bottles at the edge of the stream and gave the container ample time to adjust to the temperature of the stream. Then, while submersed, I gently opened the cap, and let the fish swim out at their discretion. The bottles were placed at low-flow sections of each pool such that emerging guppies would not be swept downstream involuntarily. The recapture intervals for the three experiments were 14, 8, and 5 days, respectively. After the recapture interval had ended, I returned to each of these sites and sampled and collected data on the individuals in the same way as during the initial capture.

In the first experiment, I used a chi-square analysis to examine the relationship between the translocation treatments and the control treatment in terms of their propensity to move from the pool they were returned to. I then used a planned comparison approach, via GLMs (Generalized linear models), to test whether the movement distances for each treatment group were significantly different from the

control. If guppies are homing, then I expected that the movements of the translocation treatments would be different from the control. I built an independent model for each population and included movement distance as the response variable and treatment as the independent variable. I use the control treatment as the reference group, and as such, the fixed effect parameter estimates for the downstream and upstream treatments are direct comparisons with the control.

I used another GLM to examine the difference in homing success (the binary measure of whether an individual returned to its home pool) between upstream and downstream treatment groups, as well as between sexes and across body sizes (standard length, mm). I utilized a binomial family argument and a logit link function.

In the second experiment I also utilized the planned comparison approach to evaluate whether the upstream and downstream treatments differed from the control treatment. I performed an independent planned comparison analysis, via GLMs, for each population. I also utilized a GLM to examine whether the variation in homing success across populations was related to phenotype, sex, length, or prior dispersal status. I centered and scaled the standard length measurements such that they became a measure of number of standard deviations from the mean of that population. Prior dispersal is a binary measure that represents whether the individual had dispersed before the translocation treatment occurred. I utilized a binomial family argument and a logit link function in these models.

In the third experiment I utilized a GLM to examine whether variation in homing success is related to phenotype (HP vs. LP), sex, length, or treatment (20 vs 100 meter

displacement). I centered and scaled length such that it became a measure of number of standard deviations from the mean of that population. I utilized a binomial family argument and a logit link function in these models.

For all the GLM analyses of homing success described above, but not the planned comparisons, I utilize the Akaike information criterion (AIC) to perform model selection and identify the best fitting model(s) for the available data (Burnham and Anderson 2002, Zuur et al. 2009). I deemed models with a ΔAIC of 2 or lower to be the best fitting models (Burnham and Anderson 2002, Grueber et al. 2011). This threshold is more conservative than most (Richards 2008, Bolker et al. 2009, but see Grueber et al. 2011), however, it limits inference to only the models and combinations of variables best supported by the data. If there are multiple models with ΔAIC < 2, I use a model averaging approach to obtain a single set of parameter estimates ('model.avg' function, MuMIn package, version 1.47.1, Bartoń 2022). This approach uses a weighted average of parameter estimates such that models that explain more variation in the response variable are weighted higher and contribute more to the model averaged parameter estimates. I performed all analyses in R (Version 4.2.1, R Core Team 2022).

Results

Experiment 1: I caught, marked, and released a total of 114 fish. Of these, 79% (n = 90) were recaptured; a total of 61 were from the translocation treatments and 29 from the control. I found that translocated fish had a strong tendency to move from that pool. Approximately 77% of displaced fish that were recaptured had moved to a different pool from where they were released, while only 24% of the control group that was recaptured

dispersed from their original pool (χ^2=21.848, p-value < .0001, assuming an equal probability of staying or departing).

Of the fish that were translocated, 51% (n = 31) returned to their original pool (Table 4.1). A further 10% (n = 6) of fish had moved in the direction of their home pool. The planned comparisons revealed that fish in both translocation treatments were more likely to move than those in the control treatment (Downstream: t = -3.87, p = 0.0001; Upstream: t = 2.32, p = 0.02, Table 4.2).

The model selection procedure for the GLM models of homing success produced three models with ΔAIC < 2 (Table 4.3). All of these models contained the effect of sex, one included the effect of body length, and one included the upstream vs. downstream treatment effect. These models revealed a significant female bias in homing success (female homing success: 64.7%, male homing success 29.1%, β = -1.57, z = 2.53, p = 0.01, Table 4.4). Female fish made up roughly 60% of the displaced fish, which reflects the natural female biased sex ratio of most natural guppy populations (Arendt et al. 2014), yet 77% of the fish that had successfully homed were female. These models also revealed that there were negligible differences in homing success between the upstream and downstream treatments (β = -0.05, z = 0.16, p = 0.88, Table 4.4), with the success rate for each being 53% and 50%, respectively. There was also a negligible effect of body size on homing success (β = -0.02, z = 0.27, p = 0.79, Table 4.4).

Experiment 2: I initially marked and released 743 fish. I recaptured 465 of these fish, 291 of which were experimentally displaced while the remainder were returned to their site of capture as controls. Of these 291 fish, 30.6% (n = 89) homed successfully

(Table 4.1). This lower rate of homing was expected given the difference in sampling interval (14 vs. 8 days). Approximately 57.8% of the displaced HP individuals homed successfully, while only 14.3% of displaced LP fish homed successfully.

The planned comparisons, via GLM, for movement distance revealed that the difference between the control group and the treatment groups was much stronger in HP populations than it was in LP populations. 3 of the 4 of the HP treatment groups were significantly different than the control group (Table 4.5). The only group which was not significant for the HP populations was the comparison between the control and the upstream treatment in the El Cedro. Conversely, only 1 of the 4 treatment groups (the downstream St. Joseph treatment) were significantly different for the LP treatment groups (Table 4.5).

The model selection procedure for the GLM models of homing success produced two models with $\Delta AIC < 2$ (Table 4.6). A threshold of 4 AIC points would have also resulted in just these two models. These models both contained a three way interaction between phenotype, body length, and sex. These also both contain the river variable, and only one of the models contains the variable that corresponds to prior dispersal tendency. The two best fitting models, and their averaged parameter estimates, reveal that homing success was explained predominantly by a three-way interaction between phenotype, sex, and length ($\beta = -2.91$, $z = 2.48$, $p = 0.01$, Table 4.7), in addition to the main effect of river ($\beta = 1.42$, $z = 3.82$, $p < 0.001$, Table 4.7). The interaction shows that the HP individuals have greater homing success than LP across all sizes of females and for all but the smallest of males. The relationship between homing success and length is positive for

both sexes in the HP and females in the LP, but negative for males in the LP populations (HP female slope: 0.535, HP male slope: 1.409, LP female slope: 0.919, LP male slope: -1.064). The effect of river demonstrated that the homing success of the St. Joseph populations is greater than those from the El Cedro. I did not find any relationship between prior dispersal and homing success ($\beta = -0.09$, $z = -0.879$, $p = 0.379$, Table 4.7).

Experiment 3: All experimental fish were displaced (n = 333, Table 4.1), and of these, 47 (14.2%) had successfully homed. This lower rate of homing was success was expected given the further displacement distances and the shorter recapture interval (5 days). The model selection procedure for the GLM models of homing success produced a single model with $\Delta AIC < 2$ (Table 4.8). The independent variables in this model include the interaction between phenotype and displacement direction (upstream vs. downstream treatment), the main effect of distance (20m vs. 100m displacement treatment), and the main effect of body length. Each of these effects explain a meaningful amount of variation of homing success. The interaction between phenotype and direction demonstrates that HP individuals are more successful at homing than LP across both direction treatments, however, this difference is much smaller for the downstream treatment group ($\beta = -1.92$, $z = -2.08$, $p = 0.04$, Table 4.6). HP individuals have approximately the same success when displaced downstream or upstream, whereas LP individuals have a much lower success rate when displaced upstream (Marginal mean homing success: HP down: 19.4%, HP up: 18.6%, LP down: 11.8%, LP up: 1.8%). The distance effect shows that regardless of phenotype or distance treatment, individuals experienced lower homing success at 100 m as compared to 20 m (Marginal homing

success: HP 20 m: 32.7%, HP 100 m: 7.5%, LP 20 m: 10.2%, LP 100 m: 1.9%, $\beta = -1.78$, $z = -4.34$, $p < 0.001$, Table 4.6). Finally, there is a strong positive correlation between body length and homing success for both phenotypes ($\beta = 0.71$, $z = 4.21$, $p < 0.001$, Table 4.6).

Discussion

The first experiment demonstrates that displaced guppies are likely to return to the pool they were originally captured in. This result suggests that guppies can recognize that they have been displaced and that this drives a greater probability of movement. Moreover, since >50% of these displaced individuals returned to their original pool, these results provide strong evidence of homing ability. The differences in the movement distributions between the control, upstream, and downstream treatment groups provide further evidence that guppies are actively homing, particularly because they are as likely to return home regardless of whether they were displaced up- or downstream. Overall, this suggests that guppies can use some form of environmental cue to navigate back towards known, familiar habitats. Since guppies were moved randomly, often with just a few other members of its original population, it is unlikely that these fish use social cues alone to navigate. It is possible that olfactory and visual cues are used to navigate.

These results provide evidence for a female-bias in homing behavior. Since males are more dispersive and female guppies exhibit stronger site fidelity (Croft et al. 2003, De Bona et al. 2019, Borges et al. 2022), I expected females to exhibit greater homing success. Moreover, female guppies grow larger and live longer than males (Arendt et al. 2014), which may enable them to develop superior spatial and navigational abilities.

Since movement can have negative impacts on an individual's fitness, I assumed that individuals would home only if the benefits of homing outweighed the potential costs of moving. These results suggest that the fitness advantages associated with occupying a familiar home range do indeed outweigh the costs of movements, even when predators may be present. Additionally, the frequency of guppies that had successfully homed were equal between groups that were displaced upstream or downstream, even though the energetic costs of moving upstream far outweigh the costs of moving downstream. These differential costs of movement, yet equal responses in terms of homing behavior provide further evidence that guppies reap benefits from occupying a familiar habitat.

The second experiment provides significant evidence that a guppy's tendency and ability to home is a function of differential environmental pressures. Guppies from HP populations are significantly more likely to home when compared to their LP counterparts. In the HP populations, 75% of the planned comparisons between treatment groups and control groups were significant, whereas only 25% were significant for the LP populations. Furthermore, the GLM revealed a significant interaction between phenotype, sex, and length that demonstrates that HP are more likely than LP guppies to home for all but the smallest males. Moreover, all groups have a positive relationship between length and homing success, except for LP males where the relationship is negative. There also is no relationship between an individual's tendency to disperse and homing behavior.

The third experiment provided further evidence that HP and LP populations vary in their homing success. As before, HP individuals were much more likely to home, and this experiment shows that this relationship exists at both regular movement distances (20

meters) and distances far beyond what is common for individual guppy movements (100 meters). However, displacement distance did have a strong negative effect on homing success for both populations, or at least success as assessed in a single recapture event five days after they were displaced. Individual body size was important, as larger guppies had greater homing success compared to smaller individuals. This is likely because larger, and older, individuals may have developed superior spatial abilities and may be better equipped for long distance movements. Furthermore, the direction treatment was important for LP, but not HP populations. LP individuals exhibited greater homing success when displaced downstream. This is despite that the homing for this treatment group requires moving back upstream, which is energetically more costly than moving downstream. This might be an adaptive response to dislocation in LP guppies that drives them to avoid downstream movement, which might better enable them to persist above barrier waterfalls. Similarly, LP guppies might just respond to displacement by swimming upstream, whereas HP guppies might utilize cues to travel towards their home pool.

In combination, the second and third experiments provide some evidence that the differentiation in homing ability between high- and low-predation populations can occur quickly and on contemporary timescales. The El Cedro LP population was experimentally transplanted from a high predation site below a barrier waterfall to a low predation site above the barrier approximately 40 years ago, whereas the St. Joseph LP population is assumed to have breached the barriers naturally. We do not know when guppies invaded the St. Joseph LP site, but as with other natural LP populations, it is

likely this occurred long before the experimental introduction occurred in El Cedro (Fraser et al. 2015). It is thus plausible that this differentiation in homing success evolves rapidly; however, because this experiment was performed on wild-caught fish, it remains possible that the differences among predation communities in homing also reflects behavioral plasticity.

Overall, these experiments demonstrate that guppies have a strong tendency to home. Generally, females and larger individuals have the highest homing success. Despite the functional similarity between dispersal and homing, there was no relationship between dispersal and homing success in the form of individual variation within populations. However, guppies from high predation populations consistently have greater homing success compared to low predation populations and also have higher probabilities of dispersing. It is possible that natural selection has selected for differences in spatial cognition amongst HP and LP populations, and that this differences in spatial cognition produced the observed differences in homing success.

Tables

Table 4.1. Homing success summary across all experimental treatments. The success ratio is the number of individuals that were recaptured in their home pool over the total number of individuals that were displaced.

Experiment no.	River(s)	Treatments	HP success ratio (%)	LP success ratio (%)
1	Ramdeen	Control	N/A	N/A
1		Down	22/44 (50%)	N/A
1		Up	9/17 (53%)	N/A
2	El Cedro, St. Joseph	Control	N/A	N/A
2		Down	38/58 (65.5%)	25/130 (19.2%)
2		Up	25/51 (49.0%)	1/52 (1.9%)
3	El Cedro, St. Joseph	Down 20m	11/41 (26.8%)	9/40 (22.5%)
3		Down 100m	6/43 (13.9%)	1/41 (2.4%)
3		Up 20m	14/41 (34.1%)	2/42 (4.8%)
3		Up 100m	3/44 (6.8%)	0/41 (0%)

Table 4.2. Experiment 1: Planned comparisons of the control vs. upstream and downstream treatments. Parameters include the effects estimate, the standard error, the z-value and the p-value.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Treatment (Control vs. Downstream)	-4.01	1.04	-3.87	0.0001
Treatment (Control vs. Upstream)	3.08	1.33	2.32	0.02

Table 4.3. Experiment 1: GLM model selection table for the analysis of homing success. All models were fit with logit link functions. The columns on the right side of the table describe the degrees of freedom used by the model, its AIC value, and the difference in AIC value between the current and best-fitting model. An asterisk between variables indicates an interaction.

Models	**df**	**AIC**	**ΔAIC**
Sex	2	80.95	0.00
Sex + Length	3	82.52	1.57
Sex + Treatment	3	82.81	1.86
Sex * Length	4	83.04	2.09
Sex * Length + Treatment	5	83.80	2.85
Sex + Length + Treatment	4	84.32	3.38
Length	2	87.51	6.56
Sex * Length * Treatment	8	87.76	6.82
Treatment	2	88.51	7.56

Table 4.4. Experiment 1: Model-averaged fixed effect parameter outputs for the GLM of homing success. Parameters include the effects estimate, the standard error, the z-value and the p-value.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	1.00	1.39	0.71	0.48
Sex	-1.57	0.61	2.53	0.01
Length	-0.02	0.07	0.27	0.79
Treatment (Upstream vs. Downstream)	-0.05	0.29	0.16	0.88

Table 4.5. Experiment 2: Planned comparisons of the control vs. upstream and downstream treatments for each combination of phenotype (HP vs LP) and river (St. Joseph and El Cedro). Parameters include the effects estimate, the standard error, the z-value and the p-value.

Phenotype	**River**	**Fixed Effect**	**Estimate**	**SE**	**z-value**	**p-value**
HP	St. Joseph	Treatment (Control vs. Down)	-12.300	1.910	-6.440	< 0.0001
HP	St. Joseph	Treatment (Control vs. Up)	6.520	2.040	3.200	0.001
LP	St. Joseph	Treatment (Control vs. Down)	-3.090	1.160	-2.670	0.008
LP	St. Joseph	Treatment (Control vs. Up)	-0.972	1.790	-0.544	0.586
HP	El Cedro	Treatment (Control vs. Down)	-17.600	8.950	-1.970	0.049
HP	El Cedro	Treatment (Control vs. Up)	5.730	8.080	0.709	0.479
LP	El Cedro	Treatment (Control vs. Down)	-0.802	0.956	-0.839	0.401
LP	El Cedro	Treatment (Control vs. Up)	-0.486	1.180	-0.414	0.679

Table 4.6. Experiment 2: GLM model selection table for the analysis of homing success. All models were fit with logit link functions. The columns on the right side of the table describe the degrees of freedom used by the model, its AIC value, and the difference in AIC value between the current and best-fitting model. An asterisk between variables indicates an interaction. Some models with large ΔAIC were excluded for brevity.

Models	**df**	**AIC**	**ΔAIC**
Phenotype * Length * Sex + River	9	274.53	0
Phenotype * Length * Sex + River + Dispersal	10	275.98	1.45
Phenotype * Length * Sex * Dispersal + River	17	278.78	4.25
Phenotype * Length + Sex + River	6	279.16	4.63
Phenotype * River + Sex + Length	6	279.7	5.17
Phenotype * River * Sex * Length	16	280.85	6.32
Phenotype + Length + Sex + River	5	281.22	6.69
Phenotype + Length + Sex + River + Dispersal	6	282.88	8.35
Phenotype * Length * Sex	8	287.91	13.38
Phenotype + River	3	288.7	14.17
Phenotype + River + Dispersal	4	290.4	15.87
Phenotype + Length	3	293.36	18.83
Phenotype + Sex	3	302.01	27.48
Sex + Length + River	4	302.21	27.68

Table 4.7. Experiment 2: Model averaged fixed effect parameter outputs for the GLM of homing success. Parameters include the effects estimate, the standard error, the z-value and the p-value. A colon between variables indicates an interaction.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	-0.60	0.43	1.38	0.17
River	1.42	0.37	3.82	< 0.001
Phenotype	-2.60	0.57	4.53	< 0.001
Sex	0.09	0.72	0.13	0.90
Length	0.52	0.32	1.63	0.10
Dispersal	-0.09	0.26	0.35	0.73
Phenotype:Length	0.10	1.14	0.09	0.93
Phenotype:Sex	0.41	0.49	0.84	0.40
Length:Sex	0.92	0.81	1.13	0.26
Phenotype:Length:Sex	-2.91	1.17	2.48	0.01

Table 4.8. Experiment 3: GLM model selection table for the analysis of homing success. All models were fit with logit link functions. The columns on the right side of the table describe the degrees of freedom used by the model, its AIC value, and the difference in AIC value between the current and best-fitting model. An asterisk between variables indicates an interaction.

Models	**df**	**AIC**	**ΔAIC**
Phenotype * Direction + Distance + BodyLength	6	223.32	0
Phenotype * Direction + Distance + BodyLength + Sex	7	226.04	2.72
Phenotype + BodyLength + Distance + Direction	5	226.44	3.12
Phenotype * BodyLength + Distance + Direction	6	226.56	3.24
Phenotype + BodyLength + Distance	4	226.85	3.53
Phenotype * Distance + BodyLength + Direction	6	227.93	4.61
Phenotype + BodyLength + Distance + Direction + Sex	6	228.01	4.69
Phenotype * Sex + Direction + Distance + BodyLength	7	228.64	5.32
Phenotype * BodyLength * Distance + Direction	9	231.22	7.9
BodyLength + Distance + Direction	4	240.69	17.37
BodyLength * Distance * Direction	8	242.99	19.67
Phenotype * Distance	4	243.74	20.42
Phenotype * Sex * Distance * Direction	16	248.68	25.36
Phenotype * Direction	4	259.74	36.42

Table 4.9. Experiment 3: Fixed effect parameter outputs for the GLM of homing success. Parameters include the effects estimate, the standard error, the z-value and the p-value.

Fixed Effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	-0.70	0.32	-2.23	0.03
Phenotype	-0.80	0.48	-1.67	0.09
Treatment(Direction)	-0.06	0.42	-0.14	0.89
Treatment(Distance)	-1.78	0.41	-4.34	< 0.001
BodyLength	0.71	0.17	4.21	< 0.001
Phenotype:Treatment(Direction)	-1.92	0.92	-2.08	0.04

Figures

Figure 4.1. Experiment 1: Probability density functions (aka dispersal kernels) for the movement distance of each treatment group, produced with the geom_density function in ggplot2. The dashed lines represent the mean of each treatment group. Histograms show the underlying data. Negative movement distances refer to downstream movements, whereas positive movement distances refer to upstream movements.

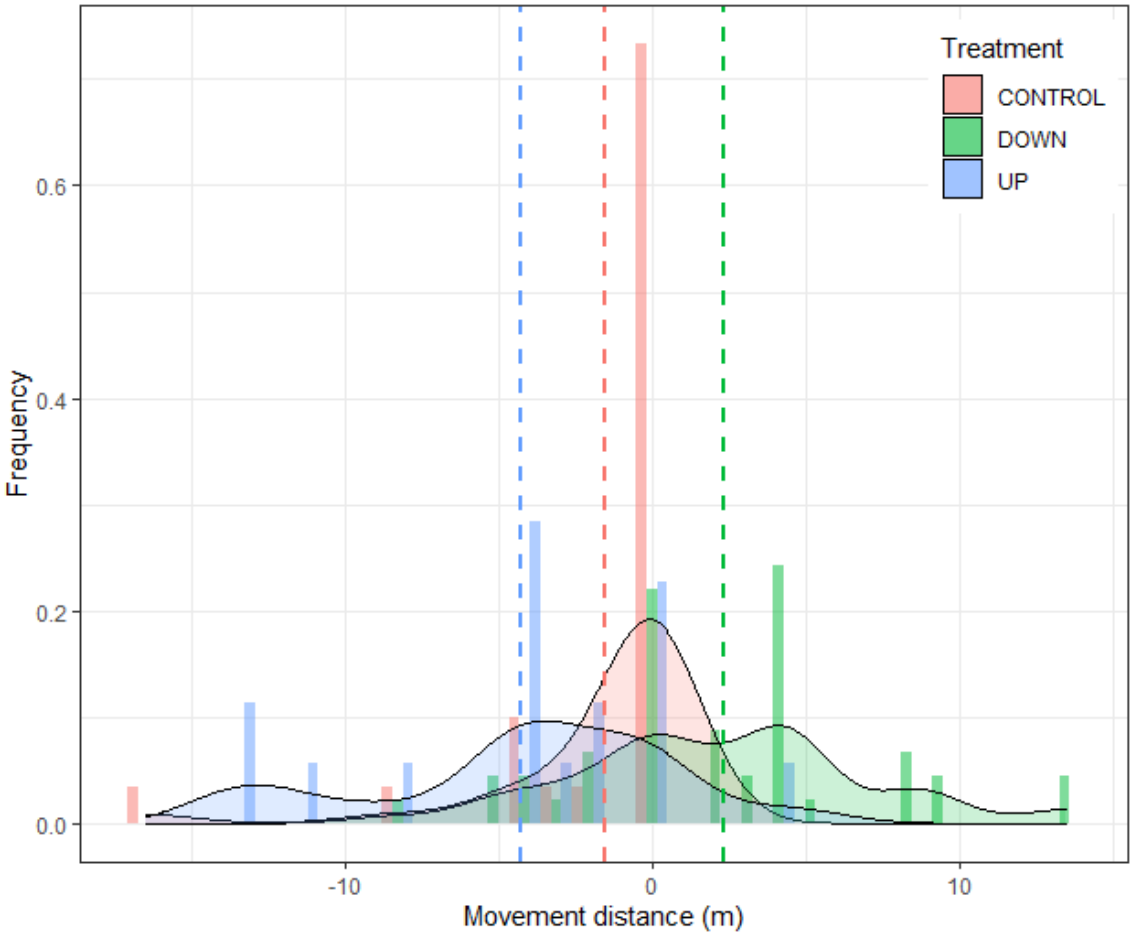


Figure 4.2. Experiment 2: Probability density functions (aka dispersal kernels) for the movement distance of each treatment group at each combination of phenotype (HP vs. LP) and river (El Cedro vs. St. Joseph), produced with the geom_density function in ggplot2. The dashed lines represent the mean of each treatment group. Histograms show the underlying data. Negative movement distances refer to downstream movements and positive movement distances refer to upstream movements.

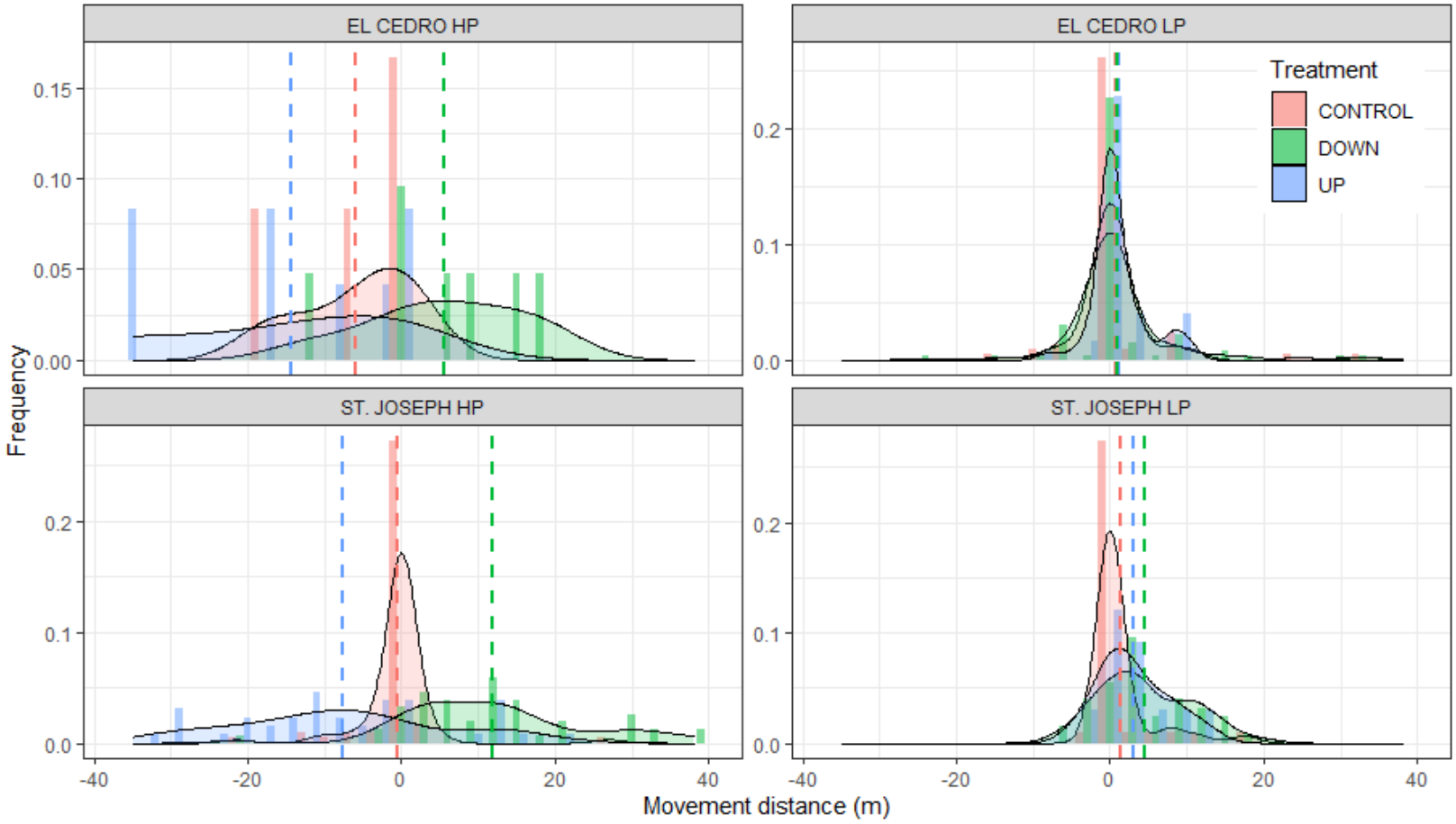


Figure 4.3. Experiment 2: Interaction plot for the three-way interaction between length (measured in standard deviations from the population mean), phenotype (HP vs. LP), and sex. The shaded regions represent the 95% confidence interval.

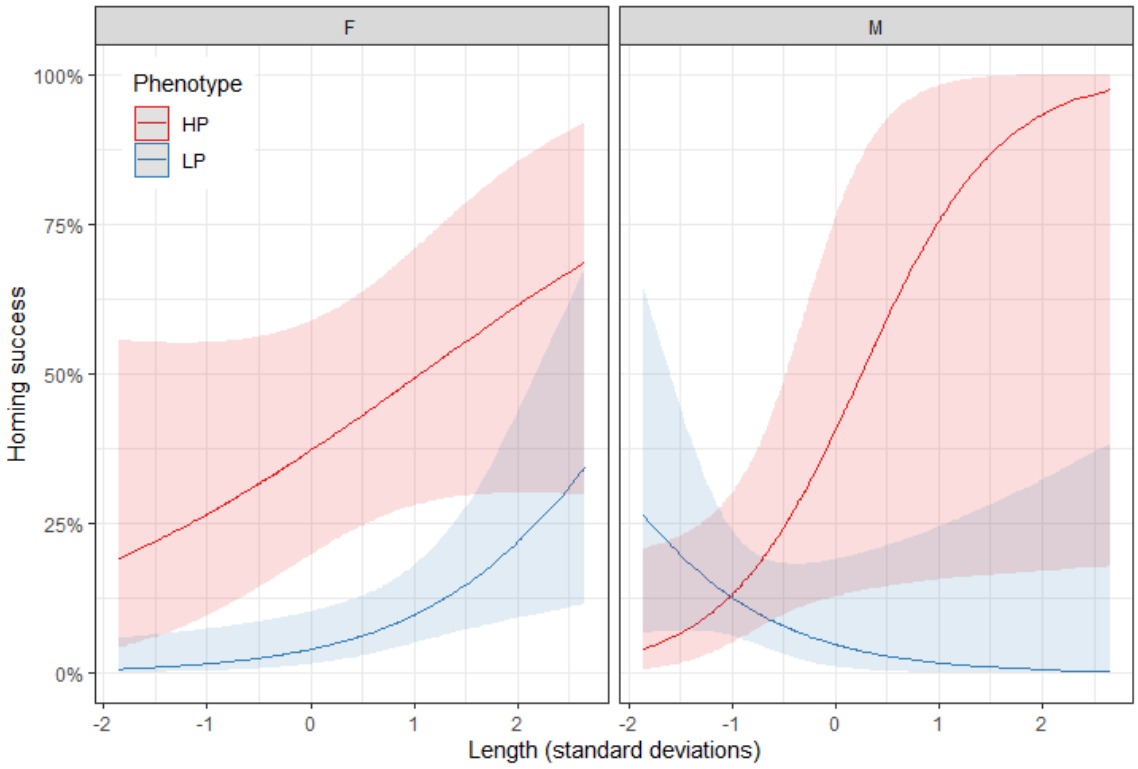


Figure 4.4. Experiment 3: The effect of phenotype (HP vs. LP) and displacement (20m vs. 100m) on homing success. The error bars represent the 95% confidence interval.

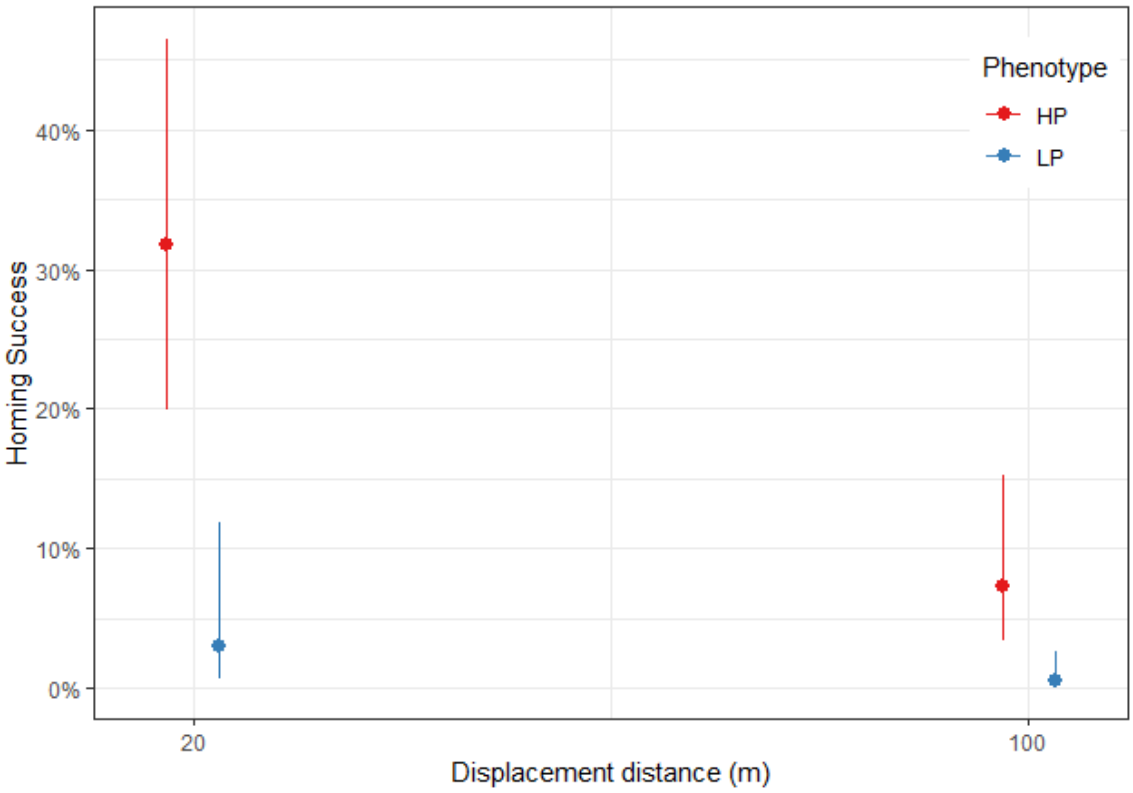


Figure 4.5. Experiment 3: The effect of phenotype (HP vs. LP) and length (measured in standard deviations from the population mean) on homing success. The shaded region represents the 95% confidence interval.

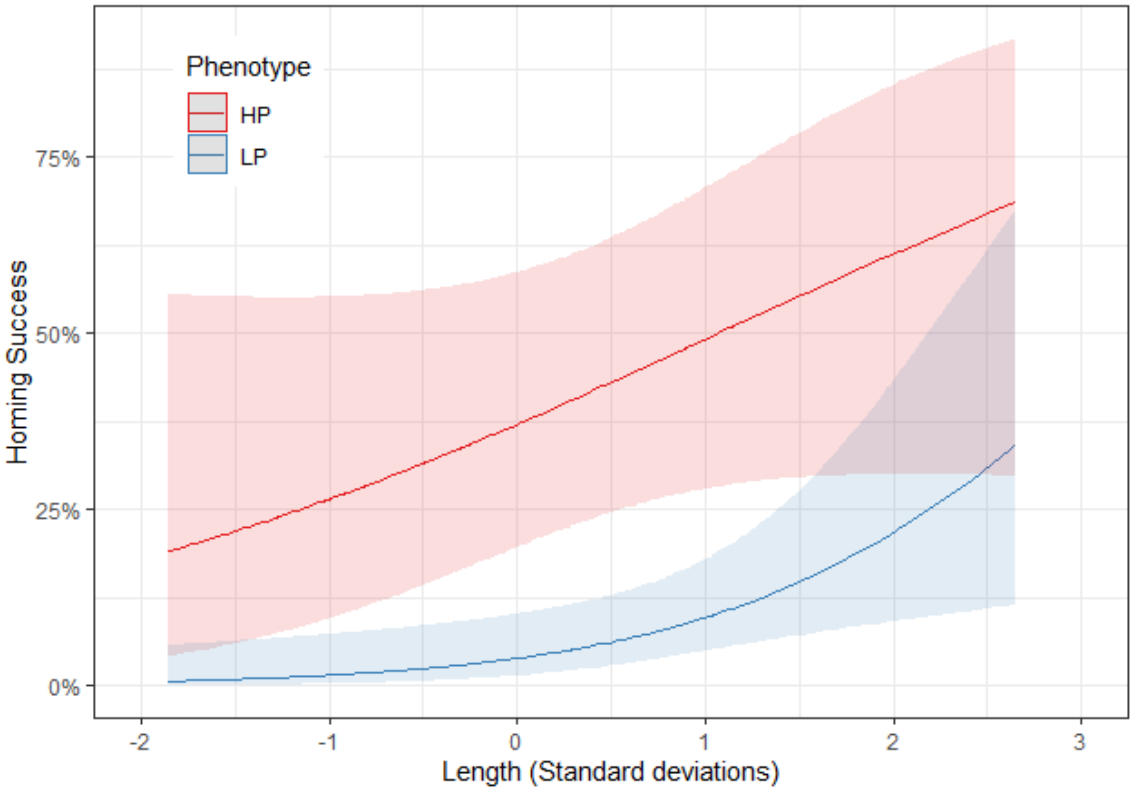
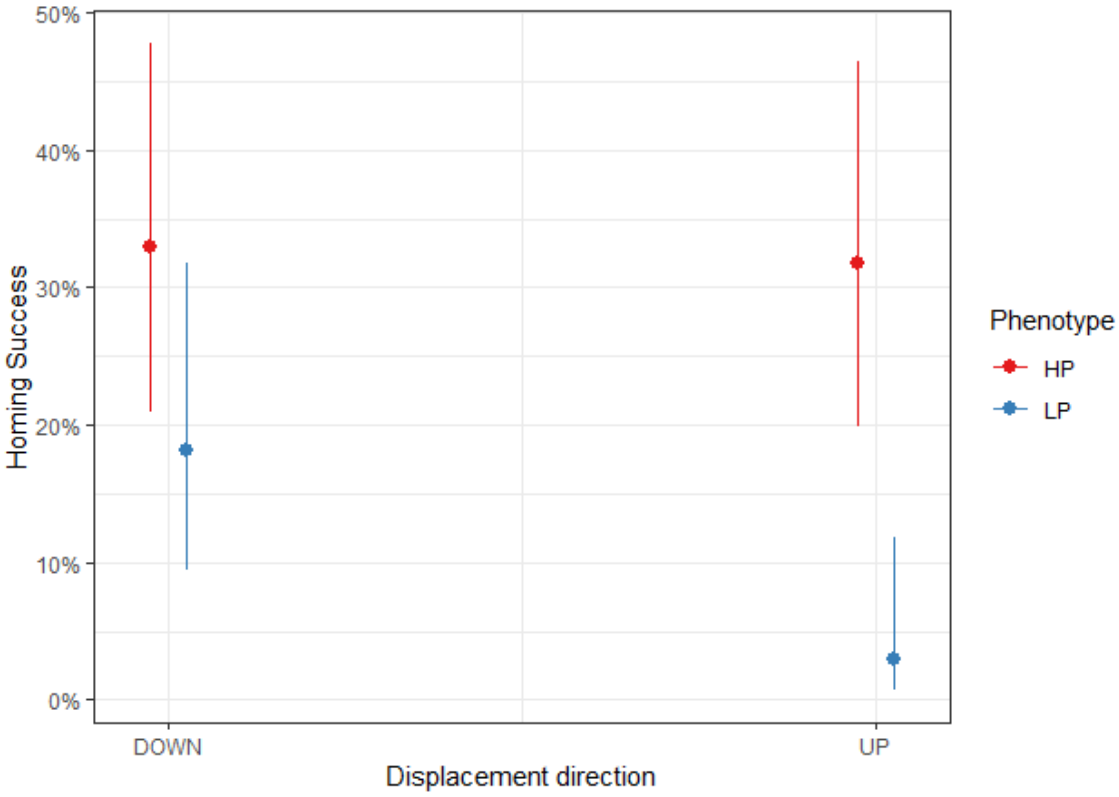


Figure 4.6. Experiment 3: The effect of the interaction between phenotype (HP vs. LP) and displacement direction. The error bars represent the 95% confidence interval.



Epilogue

Dispersal has vast ecological and evolutionary consequences. Given its importance, there has been considerable interest in understanding how variation in dispersal arises and is maintained in nature. In this dissertation, I have examined how dispersal evolves amongst populations of guppies (*Poecilia reticulata*) that are locally adapted to alternative environments that have produced dramatic differences in life history traits.

Chapter one demonstrated that wild populations of guppies adapted to alternative habitats differed in their dispersal patterns. Across all paired comparisons, high predation individuals were more likely to disperse and dispersed further distances than their low predation counterparts. These differences were consistent across all sites and were not an artifact of differential survival or recapture probability. There was also a strong sex-bias in dispersal such that males were more like to disperse and dispersed greater distances than the females did. Juvenile dispersal was also observed to be greater in HP populations. These differences in dispersal patterns might arise through a number of means. First, this might be driven by the spatial effects of isolation and asymmetric gene flow. Dispersal might be selected against in LP sites because individuals can readily disperse out of LP habitats, whereas dispersal into LP habitats is extremely rare. Thus, if dispersal has a genetic component, then alleles responsible for dispersal will gradually be lost in LP populations. However, this concept requires that dispersal has a genetic basis and does not explain a sex, age, or density driven bias in dispersal, so it is likely that dispersal is also responding to local selective pressures, and these might include the

ecological differences that drive rapid life history evolution. Dispersal and life history traits might be linked through genetic correlation or through similar responses to the same ecological conditions. Overall, it is likely that the different ecologies of HP and LP environments and the spatial isolation experienced by LP populations interact to produce the consistent and predictable patterns observed here.

The second chapter used artificial stream mesocosms to demonstrate that HP and LP guppies continue to vary in their tendency to disperse when tested in multi-patch stream mesocosms, where likely drivers of dispersal are controlled for and manipulated. Overall, HP fish were more likely to move, moved more frequently, and made their first movements sooner than the LP fish, across all combinations of density and flow treatments. This result strengthens the results from the first chapter and eliminates immeasurable environmental differences as a possible direct influence of the observed pattern of variation amongst HP and LP.

The third chapter used a common garden design in combination with multi-patch stream mesocosms to demonstrate that movement propensity and movement distance both have strong genetic components. Fish that were reared in a common environment for multiple generations continued to exhibit movement differences in the mesocosms that mirrored their wild-caught counterparts. The analyses revealed that propensity was explained solely by a strong genetic effect, whereas frequency was explained by a G x E interaction. For the frequency variable, the F2+ group varied in the same way that the wild-caught populations did, however, the magnitude of this difference was smaller. The timing of dispersal did not appear to have a genetic component, and instead was

explained mostly by river. Generally, these results confirm that high- and low- predation guppies have dispersal patterns that are locally adapted to their respective environmental pressures. This result also strengthens the isolation and asymmetric gene flow hypothesis from Chapter 1, which hinged on dispersal having a genetic component. Moreover, this highlights the complexity of the genetic underpinnings of dispersal. Depending on the dispersal trait in question, there might be a strong genetic influence, a gene by environment interaction, or only environmental influences.

The fourth chapter demonstrated that guppies from all populations exhibit some degree of homing success when displaced experimentally, however, HP individuals are much more likely to successful home than their LP counterparts. It is possible that the pressures associated with coexisting with predators, in addition to their increased dispersal tendency, have produced differences in cognition and spatial learning that result in greater homing success in high predation populations. These results were replicated across multiple rivers, years, and displacement distances. In fact, these patterns continue to exist when guppies were moved far beyond their typical dispersal distances. However, despite this, I did not find an association between homing success and dispersal propensity. Nevertheless, it is likely that the same forces which produce rapid shifts in life history traits have also selected for differences in spatial cognition amongst HP and LP populations, and these differences in spatial cognition are associated with the observed differences in homing success.

Overall, this work highlights the ecological and evolutionary relevance of intraspecific, genotypic variation in dispersal tendency and demonstrates that dispersal

evolves under the same selective regimes that drives the rapid evolution of life history traits. Throughout this dissertation I have investigated dispersal differences across 6 independent evolutionary origins of the HP and LP phenotype, 2 of which were experimental introductions. The fact that these differences are similar across all 6 evolutionary replicates suggest that these differences are not produced via the effects of spatial sorting during range expansion or other lasting effects of the pattern of colonization events. Furthermore, the costs and benefits of dispersal do not clearly explain the observed patterns, as dispersal is thought to be much more costly for HP individuals because of the higher risk and opportunity costs. It is possible that extremely large benefits in the form of increased survival outweigh these costs. However, it is also possible that these dispersal patterns emerge as a joint result of isolation and ecological pressures which produce shifts in life history. For LP guppies, dispersal might lead to unknowingly crossing a barrier that cannot be crossed in the reverse direction. When such an event occurs, those alleles which increase dispersal are lost permanently. Thus, LP guppies may have evolved decreased dispersal tendencies as a result of such isolation and asymmetric gene flow. However, this effect alone is unlikely to be solely responsible for producing the observed patterns. This is because this effect alone does not predict for the emergence and maintenance of sex-differences or other finer patterns of variation described here. Thus, it is possible that this effect interacts with the same forces which drive life history evolution. The dispersal patterns observed here also provide some evidence for the pace of life concept. HP populations, which exhibit “faster” life history strategies, are also more inclined to disperse, disperse further distances, and home more

successfully. It is unclear whether these associations are a result of genetic correlations or are similar responses to the same environmental differences associated with HP and LP sites, however, it provides some degree of support to the pace of life theory.

In a broader context, these results show that although dispersal is often highly plastic and driven by numerous environmental pressures, consistent and predictable dispersal evolution may still occur in evolutionarily independent populations experiencing similar environmental differences. These differences in dispersal may emerge rapidly amongst populations experiencing rapid shifts in environmental conditions. However, the way in which dispersal evolves will depend upon spatial effects such as habitat fragmentation or isolation and will also depend upon the ecological drivers of dispersal, life history evolution, and other phenotypic components of the dispersal syndrome. The speed at which this occurs will depend upon the amount of genetic variation in the traits of interest as well as the strength of the selection pressures. Moreover, there can be a great amount of complexity of the genetic underpinnings of dispersal, depending upon the dispersal trait which is measured. Thus, in order to get a more thorough understanding of dispersal, one must take a more detailed and integrative approach to the study of the dispersal phenotype. Finally, further exploration of dispersal evolution through integrated approaches, which involves studying natural populations in combination with carefully designed laboratory experiments, can overcome logistical challenges and further our understanding of how dispersal traits evolve in nature and enhance our ability to forecast the fate of populations exposed to the detrimental effects of environmental change, habitat destruction, and anthropogenic disturbance.

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