Patterns of Phenotypic and Life History Change in Populations Adapting to Changing Density

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Author Contributions

This thesis includes collaborative work in method development and data generation:

Collaborator Willem Bonnaffe assisted in the development of machine learning methods for extracting body length from photographic data and contributed text to the section titled ‘Guppy Body Length Measurement’ in the general Introduction. Marti Murara helped with image annotation but did not participate in any thesis writing. Collaborators Sunny Howard and Jordan Lee contributed to the development of machine learning methods used to extract handwritten guppy identification information from images and contributed text to the section titled ‘Handwritten Guppy ID Extraction’ in the general Introduction. The results from both of these methods were incorporated into the database used for analyses in Chapters 3, 4, and 5 of the thesis.

Collaborator Daniel Turek assisted in the development of code used for the mark-recapture model presented in Chapter 3 but did not contribute to the thesis writing.

Supervisor Tim Coulson and co-supervisor Robert Montgomery helped with revising the chapters.

Author contributions to each of the four data chapters contained in this thesis

	Introduction	**Chapter 2**	**Chapter 3**	**Chapter 4**	**Chapter 5**
Tianqi Wang	Writing	Writing and method development	Writing and method development	Writing and method development	Writing and method development
Willem Bonnaffe	Writing of ‘Guppy Body Length Measurement’		Method development	Method development	Method development
Marti Murara			Method development	Method development	Method development
Sunny Howard	Writing of ‘Handwritten Guppy ID Extraction’		Method development	Method development	Method development
Jordan Lee	Writing of ‘Handwritten Guppy ID Extraction’		Method development	Method development	Method development
Daniel Turek			Method development		
Tim Coulson	Revision	Revision	Revision	Revision	Revision
Robert Montgomery		Revision	Revision		

Declaration on the Use of Generative AI

ChatGPT (versions 4, 4.5, and 5) was used during the preparation of this thesis to improve the standard of my written English. This support was limited to language refinement in the chapters and was carried out in accordance with the University's regulations on the use of generative AI in research at the time of submission. No substantive use of generative AI tools was made in the production of this thesis.

General Abstract

Life history theory explores how organisms allocate resources across survival, growth, and reproduction under varying environmental constraints and trade-offs. A well-studied model of life history evolution is the Trinidadian guppy (*Poecilia reticulata*), where populations from high-predation and low-predation habitats have been shown to evolve distinct strategies. In common garden experiments, guppies translocated from high- to low-predation regimes exhibit slower life histories and extended lifespans, reflecting adaptation to reduced extrinsic mortality. However, it remains unclear whether similar evolutionary patterns can be detected in wild populations and how ecological factors might obscure these signatures - a phenomenon termed ‘cryptic evolution’.

In this thesis, I analyse 12 years of monthly mark-recapture data from four freshwater streams in Trinidad to investigate whether life history traits have changed in a manner consistent with experimental predictions. Using linear modelling approaches, I test population-level trends in survival while accounting for age, sex, seasonality, and stream-specific environmental variation. To assess individual-level patterns, I implement Bayesian survival models that incorporate temporal and demographic covariates. Results reveal a general decline in survival and life expectancy across all four populations over the 12-year study period. However, this downward trend may be partially driven by a concurrent decline in recapture probability. Despite this uncertainty, the observed pattern stands in stark contrast to findings from common garden experiments, where guppies translocated to predator-free environments typically evolve longer lifespans as a response to reduced extrinsic mortality. To investigate growth patterns, I compare several growth models and identify the best-fitting trajectory for each sex-specific population. Using these models, I assess temporal changes in growth rates and find a clear sex-specific pattern: female guppies show a consistent increase in growth rates over time, while male growth rates exhibit no significant temporal trend.

These results again deviate from the expectations derived from common garden studies, which suggest that guppies in low-predation environments should evolve slower growth. Taken together, the patterns of declining survival and accelerating female growth suggest that while evolutionary change may be occurring, its phenotypic expression is masked by environmental variation and ecological feedbacks. These findings offer compelling evidence for cryptic evolution where underlying genetic changes are not reflected in observed trait dynamics due to shifting ecological conditions in the wild.

I then examine how intra-stream dispersal and microhabitat variation influence survival and growth. I find that both habitat type and individual movement patterns significantly affect life history outcomes, with distinct sex-specific dispersal strategies. These results highlight how local environmental heterogeneity interacts with individual behaviour to shape demographic patterns in natural populations. Overall, this thesis provides empirical evidence for cryptic evolution in wild guppy populations and demonstrates how long-term ecological data can complement laboratory studies to reveal the complex interplay between evolutionary change and ecological dynamics in natural systems.

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Chapter 1

Introduction

Life history theory

Among sexually reproducing organisms, an individual's lifetime can be coarsely divided into two stages: pre and post sexual maturity. Different phenotypic traits, often called life history traits, impact an organism's reproductive and survival performance during these stages of their life cycle. The seven principal life history traits are: size at birth; growth pattern; age and size at maturity; number, size and sex ratio of offspring; age- and size-specific reproductive investments; age- and size-specific mortality schedules; and length of life (Stearns 1992). These traits can covary due to trade-offs and together determine individual fitness by affecting the probability of surviving to, and reproducing at, a certain age or certain stage of life. These probabilities describe a species' life history (Hutchings 2021). For instance, age-specific survivorship, or an individual's probability of surviving until a given age, is calculated from cumulative age-specific survival rates. The survivorship schedule often covaries with the reproductive schedule across species and populations, reflecting a trade-off between different life history traits. Age-specific survivorship tends to decrease when individuals allocate more energy toward increased reproductive output (Leisnham *et al.* 2008). In environments characterized by unpredictable conditions, animals tend to prioritize earlier reproduction, often at the cost of reduced survivorship in later stages of life (Guha *et al.* 2013).

When discussing life history traits associated with sexual reproduction, two traits are often used to describe male reproductive strategies. For males in a wild population, both energy invested per brood and size at sexual maturity are important factors shaping life history strategy (Evans *et al.* 2011). Male house mice (*Mus musculus domesticus*) that encounter the scent of other male mice - their potential competitors - exhibit an increase in daily sperm production (Ramm & Stockley 2009). In Greater Rhea (*Rhea americana*) populations, males provide parental care to their chicks and devote a significant amount of time and energy to their offspring. As a consequence, they lose more body weight by the start of the next breeding season compared to those males who failed to reproduce in the previous year (Simoy *et al.* 2014). A comparative study across different species in the genus *Drosophila* focused on male sexual maturity. The study found that larger size at sexual maturity, though it requires a longer time to achieve, allows for the development of larger testes, which is a prerequisite for producing longer sperm (Pitnick *et al.* 1995).

In most animal species, females contribute more to reproduction than males, and seven life history traits are widely used to describe female reproductive strategies: presence or absence of superfetation, inter-brood interval, degree of maternal provisioning (lecithotrophy vs matrotrophy), energy invested per brood, number of offspring per brood, size of offspring per brood measured by mass, and age and size at first reproduction (Evans *et al.* 2011). Like males, females must balance the energy devoted to producing robust offspring while maintaining their own fitness and chances of survival. In the case of superfetation, a second conception occurs during an ongoing pregnancy, resulting in females carrying multiple embryos at different developmental stages simultaneously (Roellig *et al.* 2011). Lecithotrophy and matrotrophy are two different ways of providing energy to offspring in viviparous (live-bearing) animals, often studied in the family *Poeciliidae* (Evans *et al.* 2011). In lecithotrophy, the embryo relies entirely on the nutrients provided by the yolk in the egg. In contrast, with matrotrophy, the mother supplies nutrients to the embryo via an elaborate placenta (Panahi Hassan Barough *et al.* 2024). A study on the life history strategies of a wild fish species (*Phalloceros harpagos*) living in Brazilian streams compared how female life history traits vary between environments with high and low predation pressures (Gorini-Pacheco *et al.* 2018). Under higher predation pressure, females exhibited a higher proportion of superfetation in all pregnancies and an increased degree of matrotrophy, allocating more energy to offspring rather than to their own fitness.

In evolutionary ecology, life history theory was developed to study how organisms evolve survivorship and reproductive schedules as they adapt to life in a particular environment (Roff 1992). This theoretical foundation articulates that organisms evolve to develop different life history strategies under variable natural conditions, with trades-off between growth, reproduction, and survivorship playing a central role (Bonsall & Mangel 2004, Sasaki *et al.* 2009, Coulson *et al.* 2010, Brommer *et al.* 2012, Thys *et al.* 2019, Hastings *et al.* 2021, Paoletti *et al.* 2021). Partridge and Harvey defined life history as ‘the probabilities of survival and the rates of reproduction at each age in a lifespan’ (Partridge & Harvey 1988). Herein, there are three basic assumptions in life history theory: measure of fitness is maximized; there exists both constraints and trade-offs between traits that limit the set of possible combinations; and there exists sufficient genetic variation to permit the attainment of maximized fitness (Roff 1992). Organisms attempt to pursue maximum lifetime reproductive success in the face of both genetic and environmental constraints (Hill & Kaplan 1999, Coulson *et al.* 2011, Flatt & Heyland 2011, Capdevila *et al.* 2020). The life history strategy they take on allows them to do this, balancing making a reproductive allotment against staying alive.

Life history strategies, and traits used to summarise those strategies such as generation length and life expectancy, are known to evolve in response to changes in environmental conditions. A wide range of biotic and abiotic environmental factors have been found to affect survivorship by altering the probability of survival for individuals at certain stages of life, or under certain conditions. Such biotic factors include population density (Hixon & Jones 2005, Breed *et al.* 2013, Gosselin & Anderson 2013, López-Roig & Serra-Cobo 2014) of other organisms in the community such as predators (Kishida *et al.* 2014, Wethington *et al.* 2018, Cairns *et al.* 2020), producers (Hammill & Beckerman 2010), competitors (Sandlund *et al.* 2013, Britton & Elizabeth 2018), and parasites (Nidelet *et al.* 2009, Sears *et al.* 2015). Abiotic factors include light (Zhang *et al.* 2014, Demory *et al.* 2020), temperature (Ardia *et al.* 2009, Lu *et al.* 2010, Tobin & Wright 2011, Singh *et al.* 2020), toxins (Bricelj *et al.* 2010, Van Ommen Kloeke *et al.* 2014), and properties of water for aquatic organisms (Reznick *et al.* 1990, Charlesworth 1994, Nislow & Armstrong 2012, Hoving *et al.* 2013, Marsh *et al.* 2015).

Trade-offs between life history traits

Previous studies across different species have examined how selection affects the evolution of life history traits in a population (Saether 1997, Wilkin *et al.* 2006, Barausse *et al.* 2011). With limited resources, organisms must make trade-offs between life history traits to achieve optimal reproductive success. Individuals constantly balance the allocation of energy between survival, growth, and reproduction across different stages of life, as shown in Figure 1 (Roff 1992). Over 40 different trade-offs between different life history traits have been identified in various species (Stearns 1989).

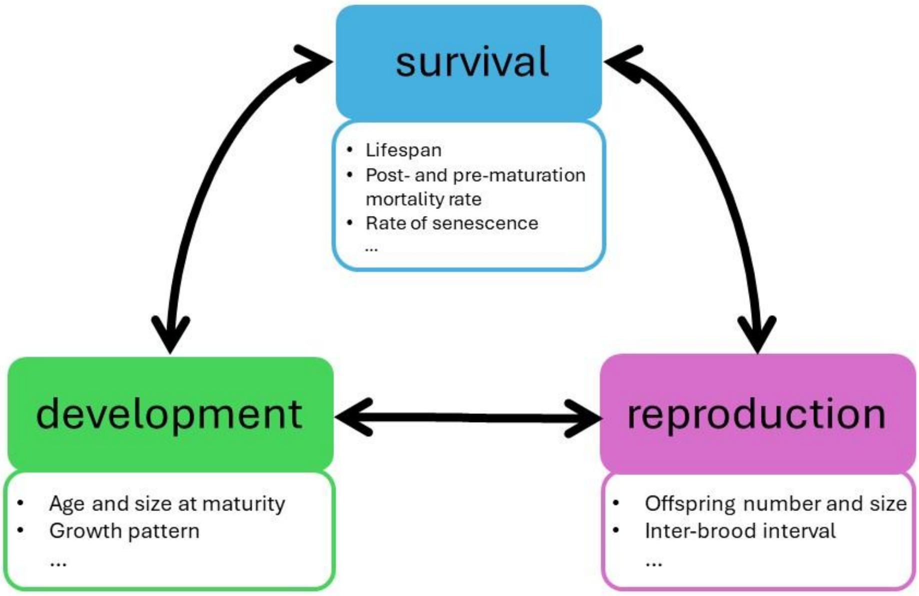


Figure 1. Trade-offs between 3 fundamental life history facets: survival, development, and reproduction in life history theory. Some common life history traits for studying animal life history strategies are listed.

Survival-reproduction trade-offs have been a focal point in life history studies in recent decades, aiming to understand how individuals balance energy expenditure between survival and reproduction. When animals allocate more resources to reproduction during early life stages, the trade-offs are thought to limit survival in later life (Lemaître *et al.* 2015). These trade-offs can differ between the sexes. For instance, research on western gulls (*Larus occidentalis*) has shown that earlier initiation of breeding imposes costs on females but not on males (Pyle *et al.* 1997). Females with more annual breeding attempts had lower survival rates. Similarly, observations of a population of Weddell seals (*Leptonychotes weddellii*) also confirmed predictions from life-history theory that the age at first reproduction in females is associated with survival (Hadley *et al.* 2006). Another example is the population of Galapagos marine iguanas (*Amblyrhynchus cristatus*), where competition for mating opportunities among male individuals is intense, with females preferring larger males (Wikelski 2005). However, during periods of famine caused by El Niño, larger individuals are more likely to starve. There are also examples where outcomes contradict predictions based on trade-offs between life history traits. For example, selective pressure in a 10-year laboratory study on fruit flies (*Drosophila melanogaster*) led to unique evolutionary outcomes. The trade-off between early fecundity and longevity, which is commonly observed in natural populations, disappeared under specific experimental conditions, demonstrating how artificial selection can alter typical life history patterns (Leroi *et al.* 1994).

In terms of survival-development trade-offs, various studies have investigated how organisms allocate resources between individual development and survival. In three-spined sticklebacks (*Gasterosteus aculeatus*), individuals that grow rapidly early tend to have shorter lifespans (Lee & Neil, 2013). Their strategy is to allocate more energy to rapid body development at the expense of increased rates of senescence later on. In another study on two Mediterranean fish species, European hake (*Merluccius merluccius*) and red mullet (*Mullus barbatu*s), body condition of juvenile individuals is positively associated with survival but negatively linked to growth at the same time (Karametsidis *et al.* 2023).

Development-reproduction trade-offs have also been widely studied across various wild species. A comparative study on fast-growing and slow-growing garter snakes (*Thamnophis elegans*) found that slow-growing individuals benefit from lower reproductive effort compared to their fast-growing counterparts (Sparkman *et al.* 2007). In another study, researchers used two populations of grey kangaroos (*Macropus giganteus*) to investigate the negative effects of reproduction on annual increases in body mass and leg growth (Gélin *et al.* 2016). Differences in energy allocated to raising female and male offspring have also been observed.

Besides the aforementioned studies of trade-offs between survival, development, and reproduction, there are also investigations of trade-offs between life history traits within each of the three genera. For instance, there are trade-offs between offspring number and offspring size, and many mathematical models have been developed to determine optimal strategies under varying conditions (Sakai & Harada 2004). A trade-off between egg size and egg number has been observed in the marine copepod (*Euterpina acutifrons*) (Guisande *et al.* 1996). As food abundance increases, the mean number of eggs per brood rises while the mean egg size decreases. Conversely, in nutrient-poor conditions, females prioritize allocating more energy per offspring rather than producing larger broods to enhance survival rates and achieve optimal reproductive success.

Factors shaping life history trade-offs

Trade-offs between different life history traits are constantly influenced by both inter- and intra-specific factors. Population density has been one of the most extensively studied examples of these factors. Another factor that has often been the focus of research is resource availability, which has in some studies been indirectly measured by rainfall or environmental chlorophyll levels (Pecuchet *et al*. 2017). An 11-year study on the life history evolution of sagebrush lizards analysed the relationships between body size, sexual maturity, and population density (Tinkle *et al.* 1993). Both the survival rate and growth rate of juvenile lizards were found to be negatively correlated with total population density. Environmental factors such as temperature and rainfall were also found to impact lizards' age-specific survivorship and reproductive schedules. Similarly, a 40-year observational study of African wildebeest (*Connochaetes gnou*) examined the effects of population density, rainfall, and predation on animals in different life history stages, highlighting the complex interplay between these factors and reproductive strategies (Simon *et al.* 1999). Under higher population density, individuals reach sexual maturity at a later age, and calves experience a higher death rate during the dry season. The study also suggested that the impact of predation on the survival rates of Serengeti wildebeest was not as significant as the availability of resources.

Different contexts can lead to contrasting trade-offs for different populations within the same species. For instance, populations living in predator-limited regions often exhibit trade-offs that favour faster growth during early life stages and greater energy allocation to reproduction. In environments with high predation rates, individuals face the risk of dying before reaching sexual maturity and failing to produce any offspring. As a result, life history trade-offs that prioritize earlier maturation and higher reproductive output are favoured in such populations. Evidence for this can be found in a comparative study of two calanoid copepods: *Calanus* and *Pseudocalanus*. *Calanus* faces predation pressure during early life stages, whereas its *Pseudocalanus* neighbour is free from such threats, leading to differences in life history trade-offs (Ohman *et al.* 2002). Compared to *Pseudocalanus* collected from the same sites, *Calanus* shows significantly higher birth rates but lower offspring survivorship. The increased energy investment in fecundity within *Calanus* populations compensates for their disadvantage in surviving in predator-limited environments.

In contrast to predator-limited contexts, populations living in food-limited environments tend to exhibit trade-offs towards achieving larger body sizes and producing fewer yet more robust offspring, both of which enhance performance in competition for food resources. In a damselfly (*Ischnura verticalis*) population facing food limitation before reaching sexual maturity, larvae show faster growth rates once food availability increases, allowing them to catch up in body size compared to their counterparts with sufficient food supplied early in life (Dmitriew & Rowe 2005). Similarly, in the species *Daphnia carinata*, populations in the most food-limited ponds invest more energy in offspring, producing only 1 or 2 eggs per clutch (Chapman & Burns 1994). In contrast, in ponds with better food availability, *Daphnia carinata* produce smaller eggs and larger clutch sizes.

Studying different aspects of life history evolution provides invaluable insights into how organisms strategically navigate the challenges of their environments to enhance their reproductive success and survival. And the concept of trade-offs serves as a cornerstone in understanding the evolution of life history traits. By examining trade-offs between survival, individual development, and reproduction, the intricate decisions organisms must make to optimize their fitness under varying ecological pressures are uncovered. Through empirical studies and theoretical models, scientists have demonstrated that trade-offs are pervasive and consequential in evolutionary biology. The dynamic interplay between conflicting demands as environmental condition changes for a species helps determine the adaptive strategies that ultimately define species' survival and persistence in the wild. These investigations not only illuminate the diverse strategies employed by species but also underscore the fundamental importance of trade-offs in shaping evolutionary outcomes.

Species of study

One example where vertebrate life history has been studied, and the focus of this thesis, is the Trinidadian guppy (*Poecilia reticulata*). The Latin name *Lebistes reticulatus* has also been used in some earlier publications for this species (Comfort 1963). Like all species in the family *Poeciliidae*, with the exception of *Tomeurus gracilis*, guppies exhibit viviparity (Evans *et al.* 2011). Guppies are small freshwater fish originally found in tropical streams. They can adapt quickly to rising water temperature (Sage 1971). Due to their excellent adaptability, they are now widely distributed globally as aquarium fish. However, parasites can impact performance in guppy populations when they coexist with parasitic species in the aquatic environment (Sato *et al.*1995, Cable & van Oosterhout 2007).

Wild guppies typically feed on a variety of sources including algae, aquatic insect larvae, zooplankton, and other aquatic invertebrates (Dussault 1980). Cannibalism among guppies is common - females often consume their own offspring immediately after birth, while newborns seek shelter in areas inaccessible to adult fish (Reznick & Endler 1982). Female guppies give birth for the first time when they are 10-20 weeks old, and then give birth every 3-4 weeks, continuing for 24-30 months. Males can reach sexual maturity at 7 weeks old (Reznick *et al.* 2001). Due to their short life cycle, fast reproduction, and rapid adaptation to new environment, guppies serve as a model organism in ecology, evolution, and behavioural studies (Reznick *et al.* 2019).

Guppies are also known as rainbow fish, or ‘peacock fish’ in Chinese due to their striking resemblance to peacocks. Like the birds known for their beautiful plumage, guppies also exhibit sexual dimorphism (Farr 1976). Females are larger as they reach sexual maturity, while males are smaller but display more bright coloured appearances. Females and males differ in many other traits as well. Females forage at the bottom more often than males and are less likely to be affected by predation (Hendry *et al.* 2006). Males have a different response to stress compared to females under the same predation environment. Males release more cortisol per weight and maintain this higher level of cortisol release over time (Chouinard-Thuly *et al.* 2018). Such significant sexual dimorphism is believed to be driven by sexual selection by females (Farr 1976).

Male guppies use their ornamental caudal and dorsal fins for courtship display (Farr 1975). As male density increases and sex ratio changes in the population, male guppies also switch to different tactics with more attempted sneak copulations and less time spent in postcopulatory guarding (Jirotkul 1999a, Jirotkul 1999b). Research indicates that females tend to prefer mating with males displaying novel colours, with the hypothesis being that these paternal novel colours align with the females' preference to produce more attractive offspring (Farr 1977, Farr 1983, Hughes *et al.* 1999). In addition to their vibrant appearance, courtship display and persistent harassment are key strategies employed by male guppies in mating rituals. Studies suggest that female guppies exhibit more pronounced schooling behaviour compared to males, which is believed to reduce unwanted mating harassment (Evans *et al.* 2011). Schooling behaviour also serves both as a defence against predators and a means of social interaction (Seghers 1974). Consequently, new foraging information spreads significantly faster through females than males in the same population (Reader & Laland, 2000).

There are two different types of habitats where guppies are found in Trinidad: low predation and high predation streams (Reznick & Bryga 1987, Reznick *et al.* 1996a). In low predation streams, only occasional guppy predation occurs from killifish (*Rivulus hartii*). High guppy density in these regimes leads to food-limited populations. In high predation regimes, where guppies co-exist with predators including the pike cichlid (*Crenicichla alta*) and the wolf fish (*Hoplias malabaricus*), all age classes of guppies experience high predation pressure, resulting in an elevated mortality rate compared to low predation ecotypes (Reznick *et al.* 1996b). High-predation guppies swim faster than their low-predation counterparts when facing predation risk, either as juveniles or after reaching sexual maturity (Dial *et al.* 2016). But this difference diminishes when female guppies are pregnant (Ghalambor *et al.* 2004). This exemplifies a life history trade-off between reproduction and swimming performance, which is crucial for survival.

Previous comparisons across low and high predation streams have shown that the guppy populations adapted to these different regimes have different life history traits (Coulson 2021). For instance, guppies from high predation regimes reach maturity at an earlier age and smaller size and reproduce more frequently and devote more energy into producing their offspring. In contrast, guppies in low predation streams tend to produce larger offspring and feed on low-quality food, while maintaining a lower metabolic rate compared to their high predation counterparts (Reznick 1982, Auer *et al.* 2018, Reznick 2019). Guppies are capable of making adaptive changes in new environments, and they evolve towards slower life histories in the absence of predators. Common garden experiments have shown that when guppies were moved from their natural high predation regimes to low predation streams, their offspring exhibited greater longevity in common gardens with fixed food level (Potter *et al.* 2020). Many other aspects of their phenotype also evolve as guppies adapt to low predation environments, including their metabolic rate, jaw morphology, coloration, diet, and social behaviour (Reznick *et al.* 2019). This evolution occurs relatively rapidly, with observable shifts happening within a few generations, thus making Trinidadian guppies an ideal animal model for studying life history evolution.

Cooccurring species in Trinidadian streams

As with all other wild animal populations, guppies coexist with other species in their local community. There are two main predators of guppies living in Trinidadian streams: the pike cichlid (*Crenicichla alta*) and the wolf fish (*Hoplias malabaricus*). It is possible for Trinidadian guppies to encounter occasional avian or terrestrial predators, but no regular predation by these has been recorded.

The pike cichlid has an elongated body and large head, similar to that of a pike, and preys upon small fish in South American tropical streams (Piálek *et al.* 2019). Pike cichlids are excellent at adapting to different environments, demonstrating phenotypic plasticity and rapid adaptation over a few generations (Burress *et al.* 2023). Despite this plasticity, under experimental conditions, pike cichlids actively select the largest guppies as their prey (Johansson *et al.* 2004). In natural settings, such predation has contributed to driving the life history evolution of wild guppies in high predation environments.

The wolf fish, also known as tiger fish or trahira (Faria *et al.* 2019), prefers to inhabit lotic freshwater environments and exhibits good tolerance for hypoxic water conditions. Experiments have shown that wolf fish preferentially attack shoals of guppies over individual stragglers, suggesting that the likelihood of detection likely outweighs the risk of confusion during hunting (Botham & Krause 2005). Wolf fish prey on guppies both day and night. In the presence of both pike cichlid and wolf fish, guppies evolve a fast life history strategy and invest large amounts of energy into reproduction (Reznick *et al.* 1996b).

The main competitor for Trinidadian guppies is the killifish (*Rivulus hartii*) (Rodd & Reznick 1997). Guppies and killifish function as intraguild predators, with both species capable of preying on future competitors before they grow too large to be consumed. Previous studies in different Trinidadian streams have found that at high elevations, only killifish are present. At intermediate elevations, guppies and killifish coexist, while at low elevations, guppies and killifish are found alongside the larger predatory fish (Walsh *et al.* 2011). When killifish and guppies occupy the same streams in low elevation reaches, they face the same predators and compete for food. However, adult killifish can feed on both juvenile and adult guppies. In contrast, the much smaller guppy can only prey on killifish eggs and juveniles. After reaching adulthood, killifish grow larger than their guppy counterparts living in the same stream. In Trinidadian streams, wild killifish can reach up to 100 mm in length, while the maximum body length for guppies is about 32 mm. Unlike guppies, killifish are oviparous and produce eggs rather than live young. When co-occurring with guppies, killifish exhibit a higher growth rate, faster maturation, and higher fecundity (Walsh & Reznick 2010). Tadpoles can also be found in the habitats of guppies in Trinidad, but no interaction between the two animals has been observed so far.

Wild guppies are omnivorous, feeding on a algae, aquatic insect larvae, zooplankton, and other aquatic invertebrate species (Dussault 1980). Guppies can also become infected with various parasites. Two main guppy parasites are *Gyrodactylus turnbulli* and *Gyrodactylus bullatarudis*. A previous study suggests that more than 75% of guppies in natural Trinidadian streams are infected by *Gyrodactylus*. They attach themselves to guppies and feed on their gills, causing a negative impact on the host's swimming ability, fecundity, and overall survival (Stephenson *et al.* 2015). *Gyrodactylus bullatarudis* occurs more frequently in upstream regions, while *Gyrodactylus turnbulli* is more prevalent in downstream areas (van Oosterhout *et al.* 2006b). In a lab study, larger guppies were found to carry more parasites and have higher mortality rates than smaller individuals. These results indicate the possibility of parasites playing a part in selecting guppies with smaller body size and shaping their life history evolution together with other environmental factors (Cable & van Oosterhout 2007).

Cryptic evolution

When species evolve to adapt to a new environment, they can also impact the ecosystem and often alter that environment. As guppies evolved to live at higher densities in a predator-free environment, they drove their food to lower densities (Reznick *et al.* 2019). This environmental feedback of reduced food availability per capita can lead to challenges in quantifying life history evolution in the field (Burns *et al.* 2009, Cameron *et al.* 2013, Govaert *et al.* 2019). Cryptic evolution might occur where genetic changes that should alter phenotypic trait means are masked by opposing changes in the environmental component of phenotypes.

Cryptic evolution has been observed in several vertebrate species, with one notable example being the Soay sheep (*Ovis aries*) of St Kilda (Wilson *et al.* 2007). The small population of sheep, residing on Scottish islands, is subject to natural selection based on body size. Both theoretical predictions and genetic analyses suggest positive selection for larger body size, which should enhance individual survival and fecundity. However, data collected over a twenty-year study show that the sheep are not increasing in size; in fact, they are shrinking at various life stages.

Similarly, cryptic evolution has been documented in long-term studies of great tits (*Parus major*) (Garant *et al.* 2004). Over 36 years of research in Wytham Woods, Oxford, for example, scientists investigated life history evolution in this bird population characterized by distinct body coloration and their two-syllable song. Despite consistent selection for larger body mass at fledging, which should make young birds more competitive than their siblings and improve their survival chances, the population has exhibited a trend of decreasing mean body mass as they mature and prepare to leave the nest.

Another example of cryptic evolution is seen in the collared flycatchers (*Ficedula albicollis*) (Merilä *et al.* 2001). Scientists tracked a population of this species on the island of Gotland, Sweden, for over twenty years and observed a declining trend in the mean phenotypic breeding value despite selection in the opposite direction for this trait. It is hypothesized that warmer temperatures, which affect the hatching time of caterpillars, have led to a shortage of food. This food scarcity for young collared flycatchers has, in turn, led to a decline in mean fitness of the bird population.

In contrast to the previous examples, guppies offer a particularly tractable system for studying cryptic evolution. They are easily reared in common garden settings, allowing researchers to disentangle environmental effects from genetic changes in life history traits. In the guppies, environmental changes such as a decrease in food availability can lead to negative impacts on survival, potentially masking genetic changes in phenotypic traits that act to slow the life history. Previous common garden experiments have documented life history evolution of high predation guppies to low predation environments (Burns *et al.* 2009, Bassar *et al.* 2010), but it is unknown whether we can document these changes with demographic data collected from the natural habitat. If we are unable to do so, a plausible hypothesis would be that life history evolution has resulted in the guppies modifying their environment, feeding back to influence their survivorship and reproductive schedules in such a way that it masks ongoing evolution – cryptic evolution.

First developed in plant studies (Hubbs 1941) and later adopted in animal research, common garden experiments are designed to isolate the genetic contribution to phenotypic traits by standardizing the environment across populations. When combined with findings from field studies in wild animal populations, results from common garden experiments can reveal how phenotypic traits are influenced by the complex environmental factors of natural habitats (Gonda *et al.* 2011). By removing the constantly changing environmental conditions present in the wild, the common garden approach controls for the effects of phenotypic plasticity, making it both easily replicable and highly compatible with increasingly common high-throughput genotyping and genome-wide analyses (de Villemereuil *et al.* 2016).

One of the main limitations of conducting common garden experiment is the difficulty of applying it to animal species that are hard to breed and rear under laboratory conditions, restricting its applicability to a relatively small range of taxa. Another limitation is when common garden experiments are conducted under a single, standardized environment, genotype-by-environment interactions that may also shape phenotypic variation are neglected, and thus more complex experimental designs are needed to address this limitation (Mori *et al.* 2022).

Previous genetic studies on guppy

For the past few decades, scientists have conducted genetic studies on Trinidadian guppies, to gain insight into their evolution. Back in 1989, a study of mitochondrial DNA (mtDNA) sequencing was conducted on guppy populations occupying different river drainages in northern Trinidad (Fajen & Breden, 1992). Using maximum parsimony analysis, researchers estimated the divergence time between different wild guppy populations to be between 0.6 and 1.2 million years. They concluded that the genetic isolation of Trinidadian guppies occurred before the physical separation of the island of Trinidad from the South American mainland. The results from a later study suggested that natural barriers such as waterfalls and physical distances, rather than differing predation pressures or habitat types, are responsible for the observed genetic divergence and reduced gene flow in Trinidadian guppy populations with time (Crispo *et al.* 2006). In another research paper published in the same year, mtDNA analysis indicated that the region encompassing eastern Venezuela and western Trinidad might be the places of origin of the species. Another study concluded that divergence of morphological traits in guppies was not strongly correlated with mtDNA genetic divergence, but was instead a response to selection pressures within the drainages (Alexander *et al.* 2006). A later study using genomic DNA also concluded that genetic convergence could not be detected in different guppy populations experiencing contrasting selection pressures across different streams (Fraser *et al.* 2015).

In 2007, cDNA libraries were constructed for Trinidadian guppy populations (Dreyer *et al.* 2007). Subsequently, in 2014, the first complete mitochondrial genome for guppies was reported (Kong *et al.* 2014). Genetic relatedness among different guppy populations was found to influence the formation of their social networks (Croft *et al.* 2012). In Trinidadian streams, females tend to maintain more stable pair-wise associations within groups compared to males, which may be attributed to the frequent sexual harassment they encounter from males. Additionally, other studies have focused on additional aspects of guppy genetics, such including the evolution of sex chromosomes in guppy populations (Nanda *et al.* 1992), the major histocompatibility complex (Sato *et al.* 1995; van Oosterhout *et al.* 2006a), and genetic diversity in invasive guppy populations in different parts of the world (Lindholm *et al.* 2005).

In 2016, the genome sequence for guppies occupying the Guanapo drainage was assembled and published (Künstner *et al.* 2016). A later study in 2022 provided evidence of convergent evolution in guppies from high- and low-predation environments (Whiting *et al.* 2022), and a specific region on chromosome 15 was identified as a candidate for selection as guppies from high-predation streams rapidly adapted to new low-predation environments (Zee *et al.* 2022).

Methodology Overview

In this thesis, I analyse the evolution of guppy life history traits based on data collected from four wild streams in Trinidad: Caigual (abbreviated as CA in thesis data chapters; two-letter abbreviation applied to the other three streams as well), Lower LaLaja (LL), Taylor (TY), and Upper LaLaja (UL). Locations of the streams are shown below in Figure 2.

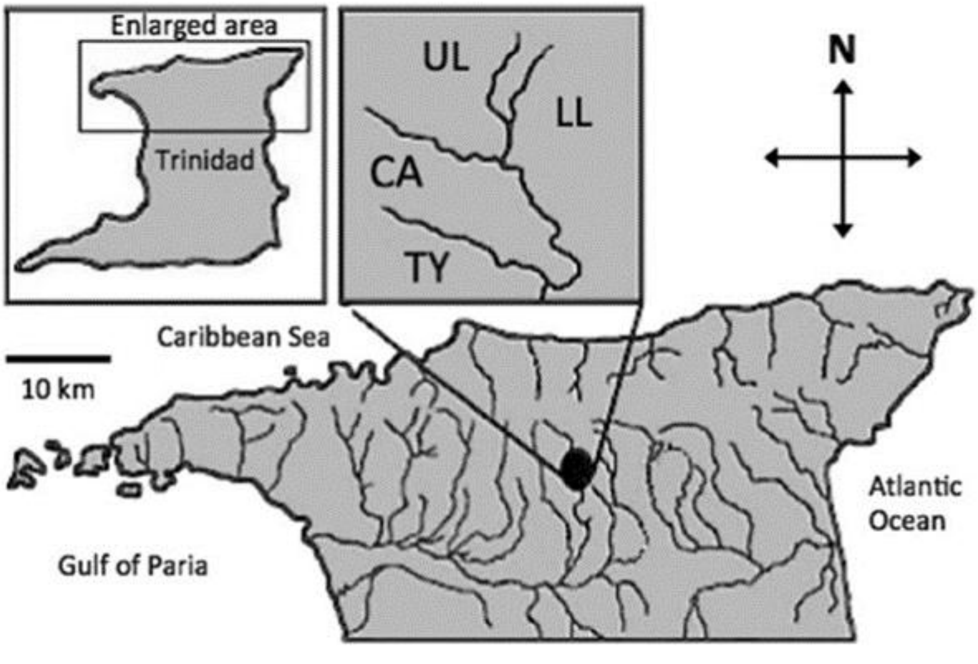


Figure 2. Map of the study streams located in the Northern Range of Trinidad (Bassar 2021). UL, LL, CA and TY, correspond to Upper LaLaja stream (10°43'03.8"N, 61°16'03.0"W), Lower LaLaja stream (10°43'00.8"N, 61°15'58.2"W), Caigual stream (10°42'53.0"N, 61°16'29.2"W) and Taylor stream (10°42'31.7"N, 61°16'22.9"W), respectively.

Data Collection

The four populations studied were seeded with fish from high-predation streams that were moved into low-predation reaches of streams in the Northern Range of Trinidad. Guppies were sourced from high predation areas in the Guanapo drainage, and a breeding design was used to ensure uniform genetic diversity among introduced guppies across all streams (Zee *et al.* 2022). In March 2008, these high-predation guppies bred in the lab to maximize genetic variety were introduced into the wild. A total of 38 pairs were placed into Lower LaLaja and 38 pairs into Upper LaLaja, both with no natural predators for guppies. One year later, in March 2009, 64 pairs were introduced into Caigual and 52 pairs into Taylor, both in similar low predation environments. In all four streams, killifish are the only co-occurring species that can potentially prey on young guppies and compete with adult guppies due to their similar body size. The canopy cover was left intact in Caigual and Lower LaLaja, but was manually thinned in Taylor and Upper LaLaja to create an experimental treatment for assessing the potential impact of stream primary production on guppy populations. Natural waterfalls served as upstream and downstream barriers, and there were no native guppies in the stream before the introduction. Thus, population immigration is unlikely. Guppies may move downstream and leave the study region, but due to the waterfall's nature, they cannot return and are thus considered deceased.

Trinidad, being a tropical island, experiences warm weather throughout the year. During the wet seasons, which typically last from June to December, periodic flooding events occur, leading to changes in stream environments and a decline in food resource availability. Apart from these seasonal events, the stream environment remains relatively unchanged throughout the year. Over time, the introduced guppies adapted to the low-predation environments, and the current populations closely resemble the phenotypes of naturally occurring low-predation guppies in other parts of the watershed. In March 2020, the COVID-

19 pandemic necessitated a temporary halt in the study. Monthly data collection resumed in November 2021 and is still ongoing to date. For my thesis, I used data only up to March 2020, as the gap in data would have created challenges for the planned statistical analysis in each chapter.

Our dataset includes 145 continuous monthly capture sessions, comprising 100,073 uniquely marked individuals and 463,080 recaptures in total. The Caigual population is the smallest observed over the 12-year period, with a total of 6,760 females and 5,959 males recorded. It is followed by Lower LaLaja with 10,843 females and 9,726 males, and Taylor with 11,691 females and 10,438 males. Upper LaLaja had the largest population, with 22,303 females and 20,493 males recorded through monthly mark-recapture protocols.

Guppies were studied using mark-recapture methods, where individuals were captured, marked, and tracked monthly. Effort has been made to capture as many guppies as possible from each population every month using butterfly nets. Subsequent to capture, all individuals were marked and measured before being released back into the same location within the stream where they were initially caught. Guppies exceeding a standard length of 14mm were marked using coloured elastomer injections. Typically, guppies are approximately 7mm in length at birth, with most reaching 14mm within their first month of life. By utilizing 12 distinct colours and 8 marking locations on each fish, we could uniquely identify all individuals within a population. Guppies smaller than 14mm were exempt from marking to minimize mortality risks. Guppies unmarked for six consecutive months (details will be provided in data chapters) were presumed deceased, and their status was updated in the database to reflect mortality.

Data collected over the twelve-year period were compiled into a .csv file, comprising 463,080 rows, each representing a capture event, and seventeen columns providing information about the captured individual. These columns were labelled ‘stream’, ‘sampling occasion’, ‘fish ID’, ‘individual ID’, ‘sampling year’, ‘sampling month’, ‘location’, ‘habitat’, ‘distance’, ‘upstream’, ‘downstream’, ‘weight’, ‘standard length’, ‘sex’, ‘population density’, ‘female density’, and ‘male density’. ‘Stream’ indicates the stream where the capture took place and comprises four levels (UL, LL, CA, and TY, corresponding to Upper LaLaja, Lower LaLaja, Caigual, and Taylor, respectively). ‘Sampling occasion’ denotes the sequential count of months from the inception of the experiment, ranging from 1 (March 2008) to 145 (March 2020). ‘Fish ID’ is the information recorded on the label assigned to each individual upon each capture (explained in detail below). ‘Individual ID’ is the unique numerical identifier assigned to each individual throughout the study period, with 98213 distinct IDs in total. ‘Sampling year’ (1-13, corresponding to 2008-2020) and ‘sampling month’ (1-12, corresponding to January-December) describe the year and month in which the capture took place. ‘Location’ specifies the particular section of the stream where the fish was captured, as divided by small waterfalls within each stream. It records the location of both upstream and downstream waterfalls, which serve as the start and end points for each section. ‘Habitat’ categorizes the type of water environment within each section and is split into five categories: P (pool, the most common type in each stream, with both inflow and outflow and comparatively still and large water area), R (riffle, similar to a pool but with faster water flows, creating a turbulent, fast-moving environment), B (backwater, similar to a pool but connected to the stream by a single combined inflow/outflow), S (side-water, areas not connected to the main stream, such as puddles that form as water levels decrease during dry seasons), or N (none, mixed features, making classification difficult). ‘Distance’ (measured in metres) refers to the distance between the centre of that water section and the upstream starting point for measurement. ‘Upstream’ (measured in metres) is the distance between the beginning of a section and the upstream starting point of the stream. ‘Downstream’(measured in metres) is the distance between the end of a section and the upstream starting point of the stream. ‘Weight’ is recorded in grams, and ‘standard length’ is the body length measured from the tip of the nose to the beginning of the tail in millimetres for each individual upon each capture event. ‘Sex’ comprises two levels: F (for female) and M (for male), which can be easily distinguished by body shape and the presence of a gonopodium. This dataset is utilized to investigate whether the same evolutionary trends observed in previous common garden studies can also be detected in wild populations, as detailed in chapters below. ‘Population density’ is calculated as the total number of individuals recorded during each sampling month divided by the total stream space, which is measured monthly using morphological methods. The sex-specific population densities, referred to as ‘female density’ and ‘male density’, are calculated separately and sum to the total ‘population density’ for each month.

Prior to the beginning of this study, data in the columns ‘stream’, ‘sampling occasion’, ‘fish ID’, ‘individual ID’, ‘sampling year’, ‘sampling month’, ‘location’, ‘habitat’, ‘distance’, ‘upstream’, ‘downstream’, ‘weight’, ‘sex’, ‘population density’, ‘female density’, and ‘male density’ were recorded for all 145 months of the study period. The data in the ‘standard length’ column of the .csv file were recorded monthly before June 2012 (‘sampling occasion’ 52), with the average proportion of missing fish body length data each month remaining below 10% before June 2012. These measurements were recorded through manual observation of photos, which included a fish and a ruler as shown below in Figure 3. However, starting in June 2012, due to inaccuracy in human processing the photos and recording the data, the average proportion of recorded body length data dropped below 50% each month, with some months having no recorded data at all. As a result, the ‘standard length’ data after June 2012 is not entered into the dataset. The subset with missing body length data contains a total of 323,586 entries. While manual effort could be applied to supplement the data, it would take too long for my project. Therefore, machine learning methods were developed with the help of colleagues and used to generate the missing data.

Figure 3. A sample photo for reading body length data with recorded fish ID.

To fill in the missing data, two separate AI codes were developed to extract first the fish ID and then the standard body length. The fish ID, a partially handwritten label located at the top of the fish photo, follows the format 'sex and stream abbreviation-marking spots and colours-date of capture'. For example, the fish ID in the sample photo is recorded as 'FUL-6W7K-09/05/13'. This ID is recorded and then converted into a unique number for each individual guppy, which is saved as 'individual ID' in the dataset. Standard length is extracted by locating both ends of the guppy trunk and measuring the distance between them, using the ruler in the photo as a scale. Details will be provided in 'Guppy Body Length Measurement' below. After extracting the body length and converting the fish ID to individual ID, the new data is added to the dataset by registering the individual ID associated with body length, along with the individual ID already in the dataset, which includes weight and other data columns. As a result, the period of data available for statistical analysis is expanded from 61 months to 145 months. Both methods are described in detail in the following sections.

Handwritten Guppy ID Extraction

When manually recording the fish ID on the label, the three lines of information for each individual are saved as one line, with hyphens separating the components. Each photo follows the same format as the sample fish, which is identified as ‘FUL-6W7K-09/05/13’ (Figure 3). The fish ID includes two printed lines and one handwritten line in between. In the first line, ‘F’ stands for female, ‘UL’ refers to the Upper LaLaja stream, and there are 8 possible combinations in total, corresponding to the 8 sex- and stream-specific subsets: CAF, CAM, LLF, LLM, TYF, TYM, ULF, and ULM. The bottom line, ‘09/05/13’, represents the date of capture (day/month/year). The middle line, written by hand, consists of an even number of characters in the format of number-letter-number-letter. For example, ‘6W7K’ refers to marking spot number 6 injected with white colour and marking spot number 7 injected with black colour. Most individuals are marked with a combination of two different marking spots and two different colours, though occasionally a third or even fourth marking spot and colour are used. A total of 8 marking spots and 12 marking colours are used in the study. All possible marking spots and colours are listed below (Table 1).

Table 1. All the spots and colours used for marking guppies.

Spot number	Position on the fish	Letter for colour	Colour injected
1	before dorsal fin, left side	B	Blue
2	under dorsal fin, left side	F	Forest (dark green)
3	before dorsal fin, right side	G	Green (bright green)
4	under dorsal fin, right side	K	Black
5	before caudal fin, left side	N	Brown
6	before caudal fin, right side	O	Orange
7	above anal fin, left side	P	Pink
8	above anal fin, right side	R	Red
		S	Sky (light blue)
		V	Violet
		W	White
		Y	Yellow

The task of Optical Character Recognition (OCR), the extraction of handwritten characters from images, is widespread in the increasingly digital world (Memon *et al.* 2020).

The problem is notorious in the field of machine learning, largely due to the popularity of the MNIST dataset, which consists of examples of handwritten numbers and is a widely used elementary benchmark for computer vision models (Lejeune 2020). Models designed for this purpose generally fall into the category of Convolutional Neural Networks (CNNs). This architecture consists of first sequentially convolving the input image with trainable convolutional kernels, which allows the network to extract increasingly complex features independently of where they are in the image. The output is then flattened before being passed into a fully connected network where the predictions are made. Many big companies have incorporated models to solve this task into their APIs, such as Google Cloud Vision (Hegghammer 2022). The AI-based label text extraction methods described below were developed in collaboration with two Oxford researchers and have been applied to the photo set spanning from June 2012 to March 2020.

Manual pre-training of the model

To generate a testing dataset that models could be evaluated on, 1000 samples were manually classified by two researchers, by simply reading and recording the label. This process took a total of 4 hours, indicating the infeasibility of this approach for the entire dataset of 323,586 data samples. An initial attempt to extract the label was then made using Google's OCR model. This model takes images and outputs predicted characters along with bounding boxes. While it achieved high accuracy on recovering the machine-printed date (>98%), it performed poorly on the handwritten ID (30%). Additional challenges arose from the misinterpretation of starred labels and label boundaries, resulting in the erroneous identification of undesirable characters such as '*', 'A', '^' and '|', 'l', 'I'. Moreover, the model encountered difficulty in distinguishing between alphanumeric characters and similar symbols, such as 'V' and '√', as well as '1' and '/'. These complexities, along with others, further contributed to a reduction in the accuracy of the final predictions.

Initially, the researchers believed systematically correcting these errors would raise the accuracy to above the required value. These corrections are split into 4 main stages:

1. Replacing Special Characters. First, ‘special’ characters (‘(’, ‘\’, ‘√’) are replaced with matched alternatives (‘1’, ‘1’, ‘V’). In addition, it was noted that the date format was inconsistent between labels, using either ‘-’ or ‘/’ to split days months and years. It was chosen to replace ‘-’ with ‘/’ in the interest of consistency.
2. Bounding Label Characters. The characters in the label must be identified and any characters preceding or trailing these characters are removed. Firstly, all labels begin with either ‘F’ or ‘M’ (specifying the sex of the guppy) and the start of the label can be determined by identifying the index of this character. If no ‘F’ or ‘M’ is present in the list of characters, the label is returned as invalid, and no prediction is made. Secondly, all labels end with the date, written as **/**/** (this is not strictly true, but will suffice for this section). Therefore, the end of the label can be found by identifying the index of the final ‘/’ in the of characters and adding two. If there are no ‘/’ characters (noting that ‘-’ characters have already been replaced with ‘/’ characters), the label is returned as invalid, and no prediction is made.
3. Removing stars. Once the label has been bounded, the 4th character index is investigated. If the label has been starred in the top right, since there are three characters in the title, the 4th character index is often misinterpreted. If the 4th character is one of ['X', 'A', '*', '•', 'x', '☆'], it is removed. This is possible as ‘X’ and ‘A’ are not used in the labelling system.
4. Correcting ID. The characters used in the ID are a subset of alphanumeric characters, alternate between numbers and letters, and have an even number of total characters. Therefore, each character in the ID can be investigated and, if any of these imposed

rules are invalidated, replaced with an alternative. The alternatives are generated by comparing predicted characters with true characters and identifying common errors.

In addition to these corrections, checks are made to ensure each section of the label is the correct length and contains valid characters. If these checks are failed in the title or date, the label is returned as invalid, and no prediction is made since the YOLO method (discussed later) only re-predicts the ID.

The final postprocessed Google predictions attained a final retention rate of 85% and an accuracy on this sample set of 85%, which was below the predetermined threshold of 92%. It was noted that the handwritten section was the leading cause of low accuracy, and this must be the focus of improvement. Google's model is designed to be robust to many applications, but it was assumed that a handcrafted approach for this specific task would attain a higher accuracy. Firstly, this involved significantly more preprocessing. Rather than discarding Google's predictions, the bounding boxes were used to extract the patch of the image containing the handwritten ID (Figure 4a). This patch was then fed through a 'cleaning routine' consisting of 9 steps:

1. The hand-written ID is identified. The Google response is split into pages, paragraphs, sentences, words and finally characters. The 'end' and 'beginning' of the label has already been identified and the content that falls outside of this range removed. Of the remaining words, the second-to-last one is expected to be the ID and retained (with the last word being the date).
2. The centre character is most likely to correctly be a character in the ID, but also, if the label is slanted, this character is likely to lie at the vertical midpoint. Therefore, the heights of the other characters in the ID are checked against this central character. If the difference between their height and the central character is deemed too large, this

character is removed from the ID. This stops date characters incorrectly being added to the ID bounding box.

3. The bounding boxes of all remaining characters are then combined with a small amount of ‘flat’ (not able to change via flags) padding (±20 along both axes).
4. Next, the whole image is reduced to just this bounding box, with some variable padding (padx, pady variable) (Figure 4b).
5. Each pixel has three values corresponding to the three primary colours. We average over these values. This results in white having high values (255) and black having very low values (0) (Figure 4c).
6. To remove the white background from the image, a histogram is taken of each pixel (Figure 5). The vast bulk of the image is white background, and the wide spike at large values (160-180 in Figure 5) corresponds to these white background pixels. We therefore find an upper threshold. Empirically, we find the point at which the value first exceeds max(value)/4 and multiply this value by 0.95.
7. Next, the darkest parts of the image are the black printed characters, which we want to remove since we are only interested in hand-written characters in the ID at this stage. Therefore, we take horizontal lineouts across the image (lines at 1/3 and 2/3) and combine them to make the lineout as shown in Figure 6. The lines at 1/3 and 2/3 are chosen as the date and title characters are unlikely to be found this far into the ID. We can then find the smallest of these peeks and use this as the lower bound, noting that in the image, the values have been inverted (multiplied by -1). All handwritten characters are then expected the lie between the upper and lower bounds, with the upper bound removing pixels whiter than the handwritten text and the lower bound removing pixels darker than the handwritten text. All pixels outside these bounds are set to 0 (Figure 4d).

8. While the majority of the image now contains only handwritten content, it is still quite messy with undesirable parts from other areas of the label. To deal with this, we single out each pixel and look at its surrounding. When the pixel is non-zero, we look at the surrounding pixels and if less than 1/5th of the surrounding pixels is non-zero, the pixel is set to zero. This ensures that the only remaining non-zero pixels are bulk features (Figure 7a).
9. We then use a clear boarder function from SKImage to remove contiguous strands stemming from the board (Figure 7b). However, it was found that this process is often a bit too harsh and removes some of the wanted characters. Therefore, after clearing the board we re-add the initial image without padding onto the centre of the image. Finally, we 'remove deltas' once again to eliminate any remaining unwanted changes from previous operations (Figure 7c).

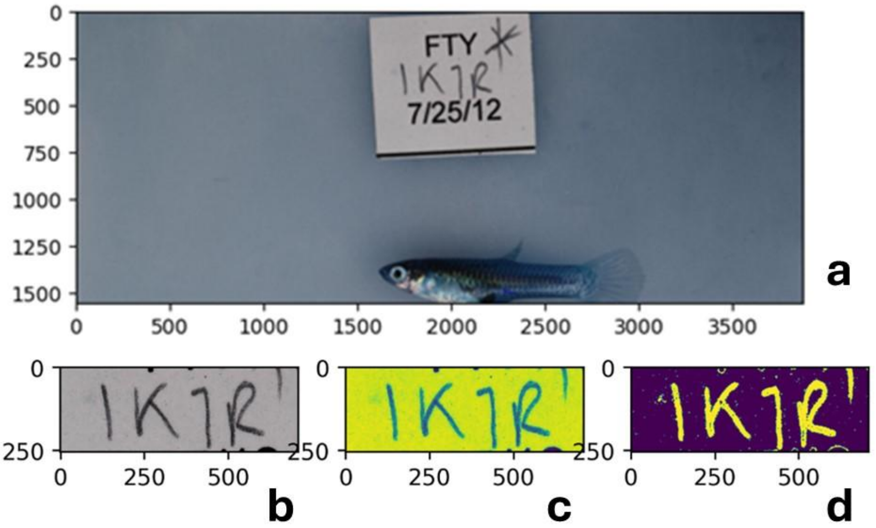


Figure 4. Cropping the handwritten text area and distinguishing characters from the white background. 4a. Original image after cropping, with bounding box defined by the Google Cloud Vision API. 4b. Image after applying bounding boxes and padding. 4c. Averaging RGB pixel values in the image. 4d. Masking of lighter and darker pixels based on thresholding.

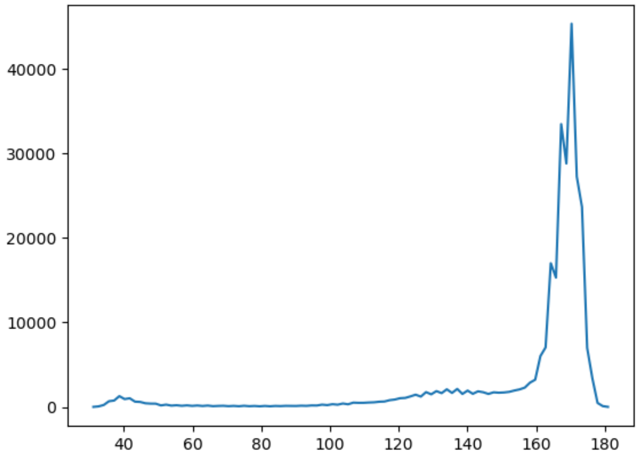


Figure 5. Histogram of averaged pixels. Whiter pixels in wide bulk around 160-180.

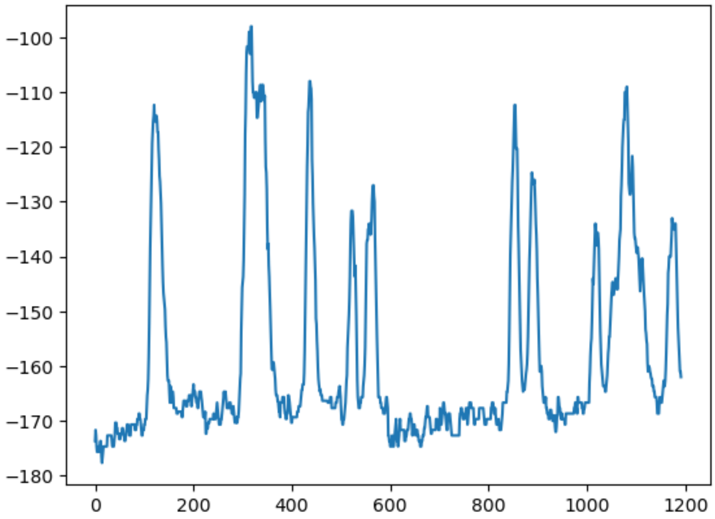


Figure 6. Horizontal lineout from averaged image. Highest peak is used as a lower bound.

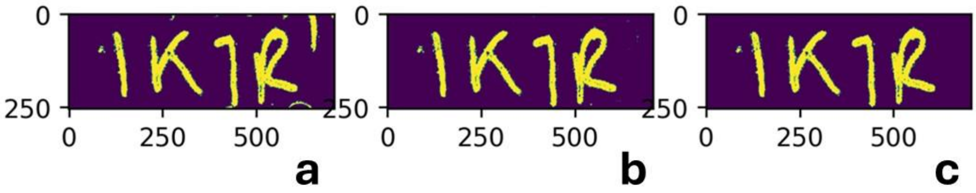


Figure 7. Removing deltas and clearing boarder process. 7a. Initial delta removal based on surrounding pixels. 7b. Applying SKImage clear boarder function. 7c. Re-adding image and final delta removal.

Applying YOLO

Google’s model has been trained to perform a broad range of tasks, using an architecture that is not publicly disclosed. For our specific task, a new model was trained to predict the characters from the cleaned patches using the you-only-look-once (YOLO) method. The YOLO model was chosen for this problem because of its leading accuracy, generalisation, and speed within the task of object detection. Since YOLO has been created, there have been a number of incremental improvements. For this study, an implementation of YOLO v8. is used (Reis *et al.* 2023).

Conceptually, YOLO is simple. The input image is split into an SxS grid. Each of these grid elements is responsible for identifying objects whose centre falls within them. Each grid element makes B predictions. A prediction contains the centre position of the object, its width and height relative to the image size, and a confidence in the prediction. This prediction confidence is composed by the multiplication of the probability that the box is in the right place, and the probability that an object has been identified there. In the case that the box is empty, the confidence values for all B predictions should be 0. Also predicted is a vector containing the probability that the object belongs to each class (in our case, each character). The neural network structure is a standard convolutional architecture, containing subsequent convolutional and max-pooling layers before being fed into a fully connected sub-network. The model is then trained to predict both the bounding boxes and the class probabilities. Naturally, for the training set, the class probabilities are all 0 or 1, depending on the class of each sample.

Dataset Creation

An obstacle to training YOLO was the lack of a labelled dataset. For this reason, one needed to be created synthetically. For each data sample, 4 characters from the EMNIST dataset (like MNIST but including alphabetical characters) were upsampled (i.e. interpolated to a larger format) and randomly placed within two dimensional arrays, whilst the label was formed by an array of the class of the characters and their bounding boxes. Some random noise was also added to the image to make the model more robust. An example of this process is shown below in Figure 8.

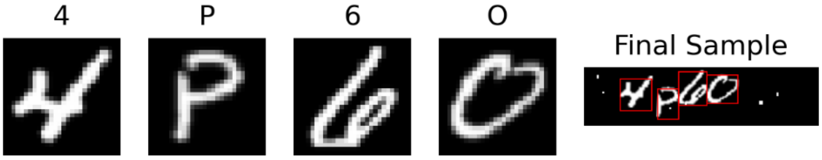


Figure 8. Example of synthetic dataset creation for YOLO training.

The network was trained on a dataset of 20,000 such synthetic data samples. Then, in order to make sure the model was correctly calibrated to the true experimental images, it was finetuned on 1000 examples of the true images. This has been shown to significantly improve performance in the true environment, despite the lack of a large quantity of data samples. A further test dataset of 2000 manually labelled true images was created to assess the model's performance. We note that this dataset was even more cumbersome to extract, due to the need for bounding boxes. To do this, we manually analysed the Google model's predictions, to remove incorrect predictions.

Having trained the custom YOLO model, one could compare its performance to the Google model on the test set. For both methods, the previously described post processing techniques were applied to the predictions.

There were two key observations; firstly, the YOLO model was more stringent in its estimation of the probability of its predictions. When choosing a probability threshold, this meant that in some images fewer than 4 characters were predicted, even though every image contains at least 4 characters. After post-processing, YOLO made a valid prediction on 85% of samples, compared to 86% for the Google model. However, on the set of valid predictions, where at least 4 characters were predicted, YOLO significantly outperformed Google, with 95% correctly predicted compared to 82% from Google.

Critically, the set of invalid predictions for Google and YOLO were not entirely overlapping (i.e. there were some samples that YOLO made a valid prediction, where Google did not, and vice versa). This meant that it was possible to make a prediction with both models, and to combine their predictions to find a new final prediction. If both models made a prediction, the YOLO one was favoured. However, if YOLO failed to make a valid prediction, the Google one was taken instead. In the case that both models failed, the sample was flagged as having no prediction. Using this algorithmic approach, our final accuracy was 93.8% for our data.

Guppy Body Length Measurement

'Standard length' is the body length measured from the tip of the nose to the end of the body trunk for each guppy upon each capture event (Figure 9). In practice, the end of the body trunk is defined by the point where the curved blood vessels are clearly visible. This is because the semi-transparent junction between the body and tail can be confusing for both human and AI readings.

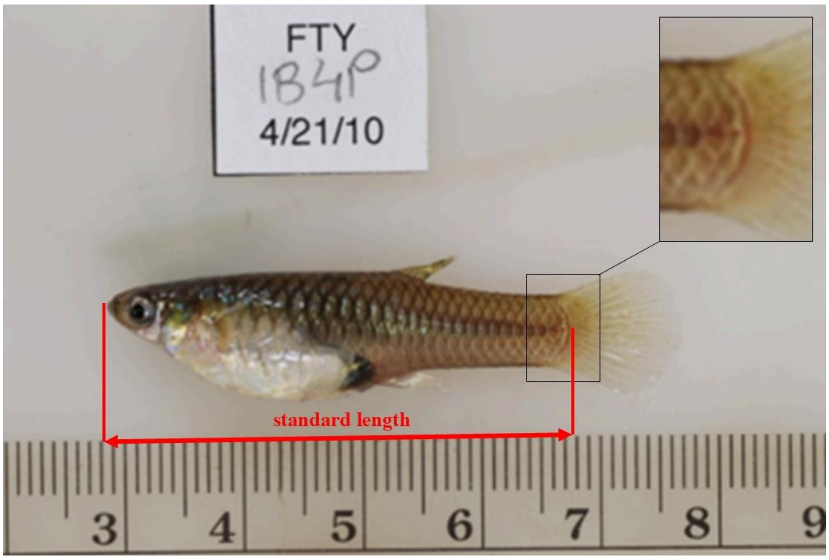


Figure 9. Example of a guppy standard length measurement, with the tail region enlarged for clarity. The end of the fish body trunk is defined by the curved blood vessels to aid visualization.

The pipeline used to measure guppy standard length is outlined below (Figure 10). The phenotyping of guppies from standardised images is performed by segmenting body parts and computing morphological properties of these compartments. This requires the following steps: (1) generation of suitable pixel-level annotations of the different body parts of guppies and the scale by trained annotators; (2) defining a dual semantic segmentation deep learning models (UNet and UNet-Transformer, Figure 10A) specialising in segmenting each body part or measurement scale; (3) training these models to reproduce annotations of the observers (Figure 10B); (4) apply the model to new data and compute morphological properties of the guppies (Figure 10C).

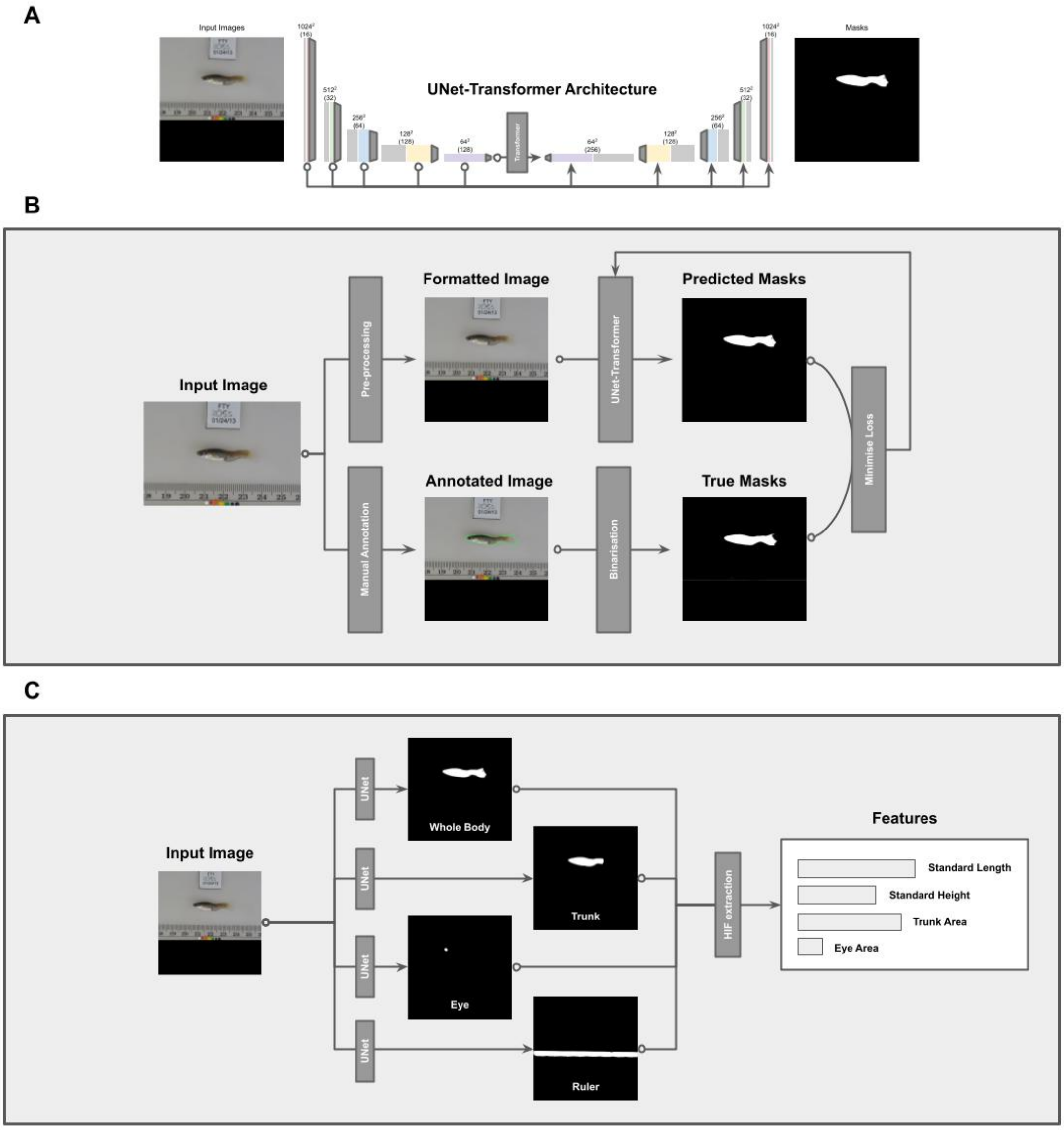


Figure 10. Pipeline overview for semantic segmentation and phenotyping of guppy fish from standardised images. 10A. UNet-Transformer architecture used to perform the segmentation of the different body parts of guppies. 10B. The training procedure by which the UNet models are trained to reproduce the ground truth annotations produced by the observers. 10C. The application of the different UNets, trained to segment either the whole body, main body (trunk), eye, and caudal fin (not shown), and computation of features from the resulting masks, including standard length, height, and area of the different body parts.

Generation of annotations for training segmentation model

Images selected for manual annotation were sampled from a large dataset (N > 500,000 images). The selection followed a stratified sampling strategy to ensure temporal and spatial diversity across years, months, and locations. Specifically, the procedure involved selecting a fixed number of images from each unique combination of year, sampling month, and collection stream. Images were sampled for every sixth month (i.e., January and July), ensuring seasonal representation. For each selected month, 3 images were drawn at random. Random sampling was performed with a fixed seed (random_state=42) to ensure reproducibility. Excluding missing years due to the coronavirus pandemic resulted in the identification of 333 images for annotation by observers. The sampled images were saved into a designated folder and renamed to encode metadata such as year, month, and a sample index. A corresponding metadata CSV file was also generated to track image provenance and facilitate downstream use in annotation tasks.

Manual annotations were performed to generate ground truth segmentation masks of guppy anatomical structures for training and evaluating the segmentation models (Figure 11). Four regions were annotated: the main body, caudal fin (not used in this study), eye socket (not used in this study), and the millimetre tick marks of the scale ruler embedded in the image. Each region was annotated separately, following a standardized protocol to ensure consistency across images and annotators. The end of the main body was defined by the point of insertion of the caudal fin rays, corresponding approximately to the location of the caudal artery. This artery is generally visible as a darker internal line near the junction between the peduncle and the fin and was used as the anatomical landmark for separation. In cases where the boundary was unclear, annotators were instructed to follow a conservative approach based on the best visible approximation of the caudal artery's position. Annotations were created using high-resolution versions of the guppy images, using a tablet and a digital pencil. Each annotation was performed on a clean, unaltered copy of the original image to avoid interference from overlapping markings. Line thickness was not constrained but was required to follow the outer contour of the structure accurately.

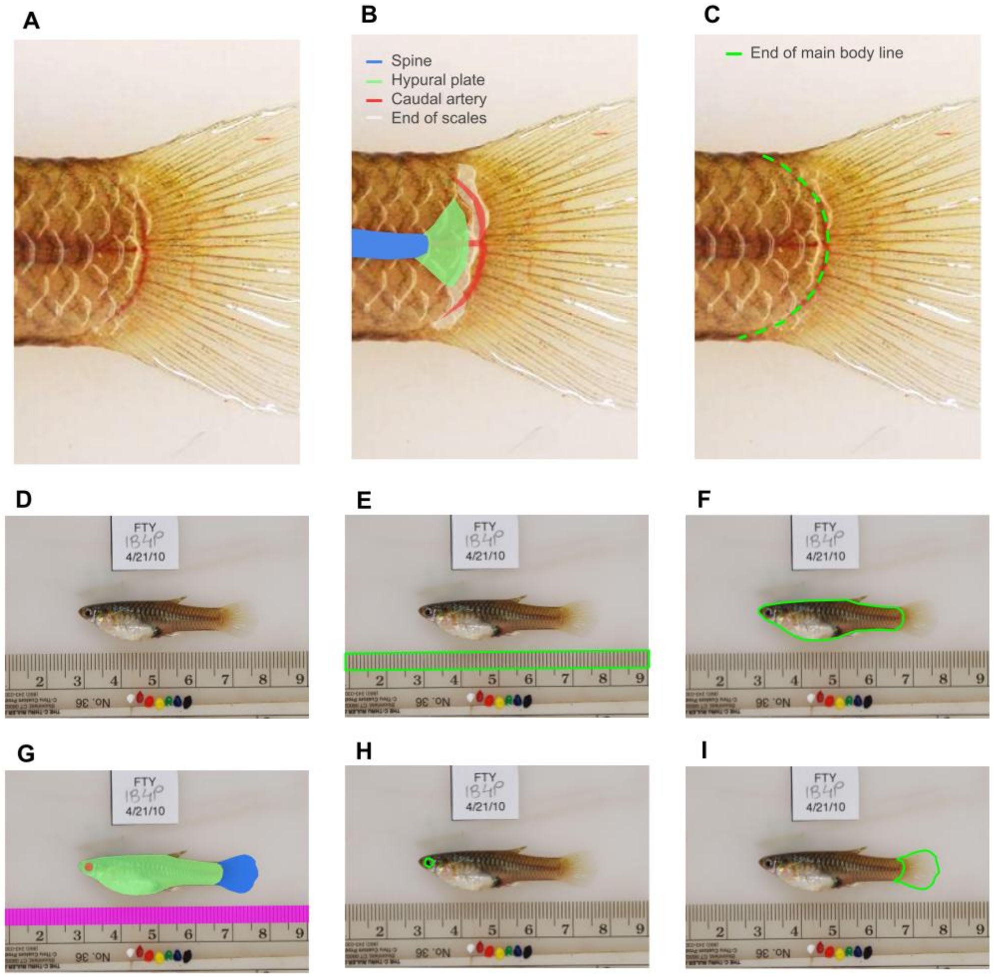


Figure 11. Simplified anatomy guide for finding the point of insertion of caudal fin rays (A-C) and example of annotation of the three fish compartments and ruler (D-I). The first image A shows the detail of the junction between the caudal peduncle and the fin rays of the caudal fin. The image B shows simplified anatomical components noticeable by eye and usable as landmarks for annotation. The image C shows the line of separation between the caudal peduncle and caudal fin, indicated by the location of the caudal artery. The eye socket is marked in red (G), the main body is marked in green (G), the caudal fin is marked in blue

(G), and the ruler is marked in pink (G). Corresponding hand-drawn annotations are displayed in panels (E-F and H-I).

In total, this resulted in 333 images annotated by three observers. This structured annotation procedure enabled the creation of high-quality ground truth masks necessary for robust supervised training of the segmentation models. In addition, 30 images were randomly sampled from the entire database which were annotated by all three observers for cross-comparison and reserved for an independent check of the performance of the AI.

Segmenting model design, training, and application

Two separate deep learning architectures were implemented to perform semantic segmentation of guppy anatomical regions. The first model was a standard UNet, while the second incorporated a Transformer module into the UNet backbone. Both models were implemented in PyTorch and trained independently per anatomical target.

The UNet model followed a conventional encoder–decoder structure with skip connections. It consisted of four downsampling blocks, each composed of a max pooling operation followed by two sequential 3×3 convolutional layers with batch normalization and ReLU activation. The number of feature channels increased from 16 to 128 across the encoder. In the decoder, learned upsampling was performed using bilinear interpolation followed by convolution, with symmetric skip connections from corresponding encoder layers. The final output was produced by a 1×1 convolution to generate a single-channel probability map.

The Transformer-augmented model, referred to as the UNet-Transformer, preserved the same UNet backbone but incorporated a Transformer encoder at the bottleneck. After the fourth downsampling stage, the 128-channel feature map was flattened into patch embeddings with a spatial resolution of 64×64 and passed through a sequence of Transformer encoder layers. Each encoder layer included multi-head self-attention (8 heads), layer normalization, and a feed-forward multilayer perceptron with GELU activation and dropout (rate 0.1). Positional encodings were learnable and added to the input tokens. The Transformer output was reshaped and passed into the decoder pathway, which mirrored the UNet upsampling structure. This hybrid design aimed to enrich the contextual representation of the encoded features, particularly useful for capturing spatial dependencies in fine anatomical structures such as fins and eyes.

Both models were designed for input images with three channels (RGB) and produced binary masks per target. While the input image size can vary, we used a standard image size of 1024 by 1024 pixels. The final segmentation masks were derived by averaging the outputs of both models to improve prediction robustness.

Model training was conducted independently for each of the four segmentation targets: main body, caudal fin, eye, and ruler. Both the UNet and Transformer-augmented UNet (UNet-Transformer) architectures were trained using identical procedures for consistency. The training was performed on a Mac platform using PyTorch (v1.13) with the Metal Performance Shaders (MPS) backend for GPU acceleration. The data was split into a train (N = 297) and validation (N = 36) set, by sampling 1 image every 10 images from the 333 images annotated by observers to ensure similar spatial and temporal coverage in the train and validation sets. An additional test set (N = 30) sampled at random from the entire database was also prepared as a final post-training test. The test set corresponded to images that were annotated by all observers to allow for cross-comparisons between observers and AI-predictions.

The UNet models were trained for 30 epochs with a batch size of 3, while the UNet-Transformers required 90 epochs to reach the same segmentation performance. The loss function used was the Dice loss computed on the raw logits (dice_with_logits_loss), designed to optimize overlap between predicted and ground truth masks. The optimizer used was

Adam with a learning rate of 1×10^{-4}, and model weights were saved at each epoch for checkpointing. Input data were organized into separate training and validation sets (set_train and set_validation), with original images and binary masks stored in parallel folder structures.

Training datasets were constructed using a custom SegmentationDataset class that accepts original images and thresholded annotation masks. During training, basic data augmentations, such as rotations and flips, were optionally applied, although this was disabled (transform=None) in the final runs as we noticed that this decreased overall performance. The model input was RGB (3 channels), and the output was a single-channel on the real space (Figure 10B).

For evaluation, the trained models were tested on the validation dataset. Predictions were generated by applying a sigmoid activation to the output logits and scaling to the 0–255 intensity range. Model performance was quantified using the Dice coefficient, calculated on binarized predictions using a threshold of 0.5. The compute_dice_scores function was used to compute Dice scores across multiple images and anatomical targets, and predictions were visualized side-by-side with input images and ground truth masks for qualitative assessment. Testing was performed with a batch size of 1 to allow detailed image-wise analysis. The same model architecture was loaded per target using the appropriate .pth weight file, and testing followed a deterministic inference pipeline without augmentation or shuffling.

Application of model and phenotyping

We implemented a fully automated pipeline in Python (v3.9) to extract morphological measurements from standardised images of guppies. The pipeline consists of five stages: image preprocessing and orientation correction, dual deep-learning-based segmentation, mask refinement and alignment, ruler-based scale calibration, and handcrafted morphological feature extraction.

All guppy images were acquired in a standardised setup and stored in RGB format. File paths were supplied via a CSV file with an include column used to filter valid samples. Images were read using OpenCV and initially assessed for orientation. Typically, images would be horizontal with the guppy in the centre and the ruler at the bottom. However, some images were rotated by 90-180 degrees. To account for this, we checked if the image height exceeded its width, it was then rotated 90 degrees clockwise. To further determine uprightness, we computed the vertical sum of pixel intensities across colour channels and applied Gaussian smoothing ($\sigma \approx 5$ pixels). The position of minimum intensity, consistently corresponding to the location of the ruler, was compared to the centre of mass of the exponential-transformed signal. If the minimum occurred above the centre, the image was assumed to be upside down and rotated an additional 180 degrees. This approach ensured that the fish were consistently presented in a horizontal, head-left orientation.

Segmentation was performed using two independently trained deep learning models for each target structure. The models included a UNet and a Transformer-based UNet (UNet-Transformer), both implemented in PyTorch and trained with a Dice loss function.
Four regions were targeted: the main body, caudal fin, eyes, and ruler. Each model was trained separately on 1024×1024 pixel crops and saved as .pth checkpoint files. For inference, models were executed on Apple Silicon GPUs using Metal Performance Shaders (device = "mps"). Each image was passed through both models per target, and the sigmoid-transformed probability outputs were averaged to create the final prediction mask. This is because both models tend to hallucinate differently, namely they generate false positives in different regions. This allows the models to cross-check each other. Eight models in total (two per target) were loaded during runtime.

The averaged prediction masks were postprocessed to reduce false positives. For each mask, only the largest connected component was retained using a custom brightness-based

filtering function. Pixels with intensities below 100 (on a 0–255 scale) were zeroed out. This step removes small residual hallucinations that might be present in both models.
Masks were re-aligned with their corresponding images. If the resulting mask height exceeded its width, the image and all masks were rotated 90 degrees clockwise to maintain horizontal alignment. All masks were stored as three-channel (RGB) arrays for visualization and subsequent overlay.

To convert measurements from pixels to millimetres, we extracted the embedded scale ruler in each image. The ruler mask was applied to the original image, which was then normalized and enhanced using contrast-limited adaptive histogram equalization (CLAHE, tile size 8×8, clip limit 2.0). The orientation of the ruler mask was determined by principal component analysis, which allowed for alignment of the cropped-out ruler image with the horizontal plane.

A one-dimensional horizontal projection of the ruler intensity was calculated across a window centred at the mean ruler position. The projection window spanned 50% of the image width (±25%). Transitions from dark to light regions in this binarized strip were counted as tick marks. The number of tick marks (typically 20–40) was divided by the physical window width in pixels to calculate the mm/px scaling factor. This metric was image-specific and used in all subsequent measurements performed on that image.

Similar to the ruler, the main body mask was used to compute the principal orientation of the fish via principal component analysis. The fish and all segmentation masks were rotated such that the primary body axis aligned with the horizontal plane. The mask centroid was used to define cross-sectional slices for computing standard length and width. Standard length (centroid-based) was measured as the horizontal span of the body mask at the vertical midpoint of the aligned image, and was recorded with floating-point precision and saved per image.

Images were grouped into user-defined ‘superbatches’ for parallel processing, with each superbatch containing 4 to 20 images (default = 20). Within each superbatch, images were processed sequentially, and the resulting features were stored in a CSV file named according to the superbatch index. If an output file already existed, the corresponding batch was skipped to allow checkpointed execution. Command-line execution of the pipeline was enabled using three arguments: the input CSV path, superbatch size, and output folder.

We compared standard length measurements derived from model-predicted segmentation masks with those obtained from manual observer annotations. The goal was to benchmark the automated segmentation model's output against the variability observed among human annotators. Standard length was extracted independently by three human observers (denoted WB, MM, and TW) and two automated pipelines based on independently trained UNet models (denoted AI1 and AI2). Each observer or model annotated the same subset of test images (N = 30), and the resulting phenotypic values were saved in structured CSV files. These were loaded into a 3D array with dimensions (5 sources, 30 samples, 2 features), enabling direct comparison across all annotation sources. Pairwise scatter plots were generated between all combinations of annotators and models to visually assess agreement (Figure 12). Each plot included a 1:1 reference line. The plots show how closely automated phenotyping approximates human-level performance, while also revealing systematic deviations and showing the extent to which automated estimates fall within the range of inter-observer variability.

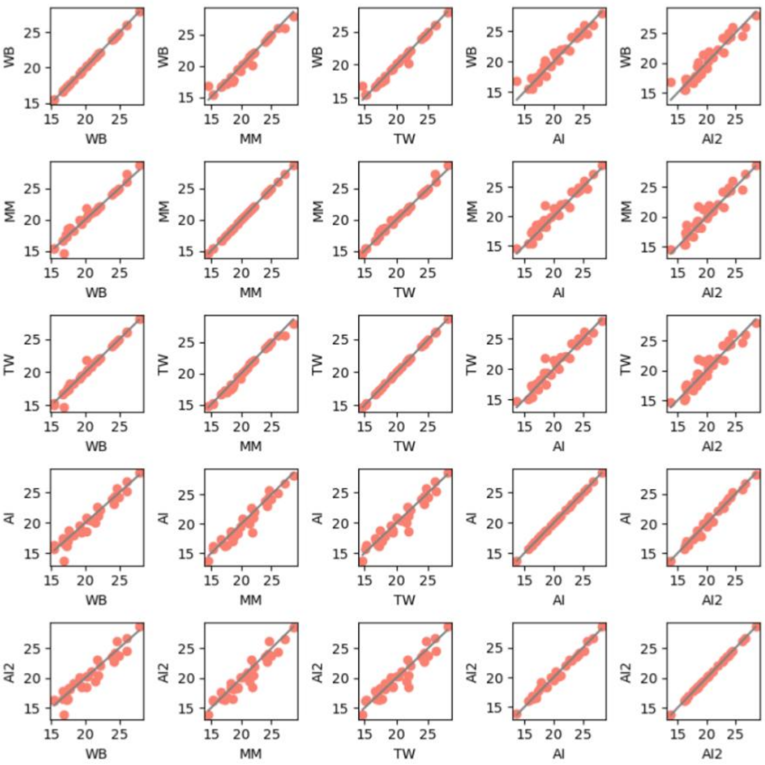


Figure 12. Benchmark of AI phenotype predictions against observers. This figure displays all pairwise comparisons of standard lengths predicted by the two types of AI models (UNet: AI1 and UNet-Transformer: AI2) to those derived from ground truth annotations obtained from observers (WB, MM, and TW). Each orange dot corresponds to the standard length of one of the 30 guppies of the test set. The one-one line is showing the prediction expected when a perfect agreement is found between observers and machines.

Data Integration and Merging

Both the ID-reading and standard length-reading AI algorithms were independently applied to the same extensive photo dataset, spanning June 2012 to March 2020. The results from these two algorithms were combined by matching file paths and photo names to ensure a 100% accurate correspondence between IDs and standard lengths. As a result, standard length records, paired with their respective IDs, are now available for the full period from

June 2012 to March 2020. These data were subsequently supplemented into the existing .csv dataset to enhance its completeness.

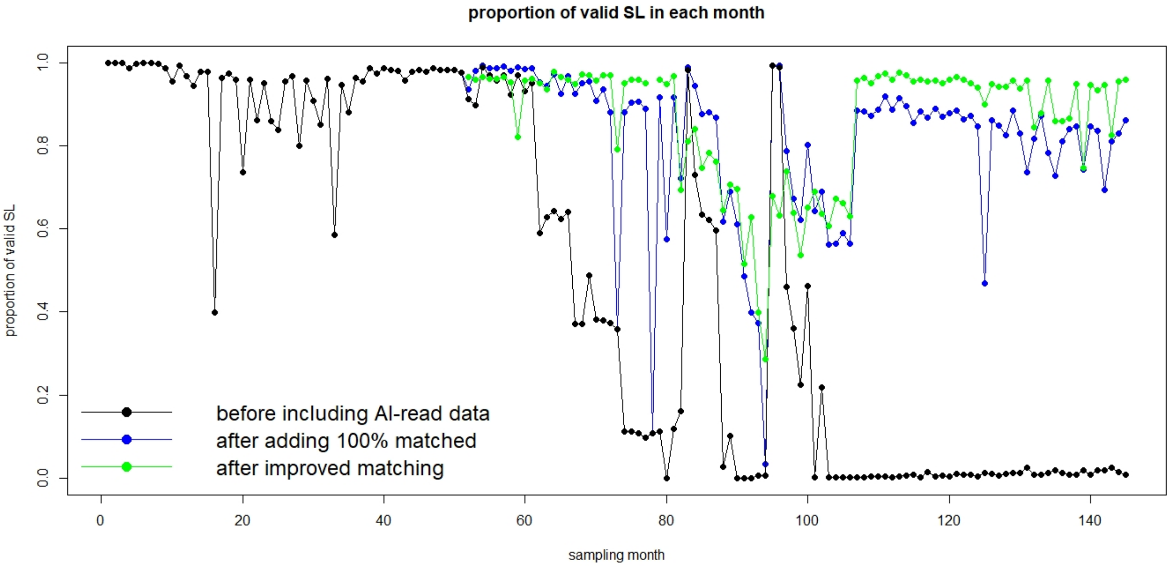


Figure 13. Proportions of valid standard length data by month during the study, before and after incorporating AI-read data into the dataset. The black line represents the proportion of valid standard length data prior to the integration of AI-read data. The blue line indicates the proportion of valid standard length data after incorporating AI-read data matched by 100% accurate Fish ID. The green line represents the proportion of valid standard length data after further improving the matching process by applying a supplemental approach that utilized additional variables (e.g., sex, stream, capture date, and marking codes) to identify individuals.

Initially, attempts to match the AI-generated ID data with existing human-generated ID records by directly comparing the AI-read IDs to the 'fish ID' column in the existing dataset resulted in a low matching rate of approximately 20% across most months (Figure 13). This low success rate stemmed from multiple factors, including inconsistency in the formatting of capture dates across datasets, AI errors in reading and identifying printed or handwritten text, and human errors during manual entry of records into the dataset. To address the first two sources of inaccuracy and improve the matching rate, an alternative approach is used, which involves utilizing additional data columns in both datasets to cross-verify individual records. The columns included:

1. Sex: In the supplementary dataset, the first AI-read character from the label is extracted and saved in a separate column labelled ‘sex’. The AI was trained to output either "F" (female) or "M" (male) as the first letter read from the label.
2. Stream: While the existing dataset’s ‘stream’ column includes only four stream names (CA, LL, TY, UL), the AI-read stream name was not restricted to these predefined options and sometimes made mistakes in identifying and outputting the correct letters. Therefore, stream names from the photo file path are used in the supplementary dataset to accurately reflect the correct stream information, as the stream names are included in the photoset folder names for each sampling month.
3. Month and year of capture: Though the capture date is printed on each label and is more accurate in AI predictions compared to handwritten parts, there are still occasional mistakes in the AI's output. The same approach used for stream names is applied to the time of capture in the supplementary dataset, where the more accurate information is extracted from the photo file path.
4. Marking spot and colour codes: In both the supplementary and existing datasets, the second line of the label, which indicates the combination of body marking spots and colours, is saved in a separate column.

We then re-align the two datasets. A record is considered a successful match if all five columns (sex, stream, sampling year, sampling month, and marking spots and colours) align perfectly, indicating that the same individual has been identified. We then check for potential mismatches caused by AI errors, where two different marking combinations might be incorrectly interpreted as the same, leading to the body length of one individual being mistakenly recorded as another’s. A total of 10,679 repeated records with all five columns identical were identified, corresponding to 5,283 individuals (5.28% of the 100,073 individuals in the dataset).

To minimize the impact of these repeated records, a filtering step was applied. Specifically, for all the repeated records, the standard length was filtered out if the value for the current month was smaller than in any previous month(s), as guppies do not shrink, and such data likely represents two different individuals erroneously recorded as one. If no valid standard length records remained after filtering, the first recorded standard length in the dataset was retained (consistent with the approach that would have been used without this additional filtering step).

Following these refinements, the matching rate increases significantly to approximately 80% across most months (Figure 13). This improvement ensures that a significant proportion of standard length data, now matched with individual IDs, has become available for future statistical analysis. Consequently, more than 80% of individuals in most sampling months during the study period now have valid standard length records, representing a substantial enhancement compared to the initial dataset.

Thesis Structure

The key question of this thesis is: Can we observe the same evolutionary changes detected in common garden experiments in guppy populations living in natural streams, where eco-evolutionary feedback has the potential to obscure direct evidence of adaptation? The null hypothesis is that the same trend observed in previous common garden experiments, where guppies collected from different regimes were kept under the same lab conditions, will also be observed in natural stream populations. If the null hypothesis is rejected, we then try to investigate why. All four data chapters expand on this key question, addressing it through different approaches and analyses.

The key question for Chapter 2 is: Can we observe changes in population-level survival rates consistent with the results from common garden experiments? In this chapter, I analyse extensive data on high-predation guppies introduced into low-predation streams, focusing on how population survival rate changes over the study period. I examine the number of individuals at different life stages and sex classes across four streams. Based on differences in survival probabilities, I categorize individuals into age groups and divide months into seasons. Generalized linear models are applied to examine how age, sex, and seasonal factors impact survival rates. Results show that females and males have different life history trajectories, with males exhibiting higher age-specific mortality and shorter life spans. Both sexes show a similar pattern, with survival increasing early on and decreasing in later life stages. Seasonal factors, particularly floods during wet seasons, significantly impact survival. The survival patterns in three of the four streams contradict common garden expectations. Guppies in Caigual and Lower LaLaja, and female guppies in Upper LaLaja show a decline in survivorship, rather than the expected increase. These findings may reflect eco-evolutionary feedbacks due to resource limitations. The absence of expected patterns suggests they are either weak or not present, motivating further individual-level analysis in subsequent chapters.

The key question for Chapter 3 is: How does individual variation in survival and capture rates contribute to the patterns observed in Chapter 2? Chapter 3 conducts a mark-recapture analysis as a continuation of the work in Chapter 2 and uses individual-level data to investigate age-specific survival patterns and recapture rates, exploring whether there is evolutionary change in age structure, whether recapture rate is decreasing over the years and causing potentially skewed results, and whether the incorporation of individual-based data helps reveal patterns characterised in the common garden experiments. Given the dataset's unprecedented size and complexity, highly efficient likelihood functions are developed with the Markov Chain Monte Carlo (MCMC) methods to generate Bayesian survival and recapture rate models. The models show sexually dimorphic survival baselines and environmental influences. No significant temporal trends in survival are detected in any population across the 12-year study period. In contrast, recapture probabilities exhibit a consistent decline over time in all four streams. This downward trend in detectability may explain the apparent reductions in survival observed at the population level in Chapter 2, highlighting the importance of accounting for recapture variation when interpreting survival data.

The key question for Chapter 4 is: Can we detect changes in population-level growth rates that align with the findings from common garden experiments? In this chapter, I examine whether the growth patterns observed in common garden experiments, where guppies evolve slower growth rates in predator-free environments, can also be observed in natural settings. Several growth models, including the von Bertalanffy, Gompertz, logistic, Weibull, and two-phase growth models, are compared to predict body length growth patterns. Models are developed to explore temporal changes in growth rates across the streams during the study period. The results reveal sexual dimorphism in body length growth patterns: males exhibit determinate growth, while females demonstrate indeterminate growth, as is typical in the family *Poeciliidae*. Seasonal effects have a strong influence on growth rates, with female trajectories showing greater sensitivity to environmental variation. In all four female populations, gradually increasing growth rates are detected, while males show no clear temporal trend – both contradicting expectations from common garden experiments, where slower growth in low-predation environments was previously observed. These patterns, like the survival trends observed in earlier chapters, provide evidence of cryptic evolution in the Trinidadian guppy populations.

The key question for Chapter 5 is: How does individual dispersal within streams relate to life-history traits, and do different stream habitats impact survival and growth? Given that the results from the previous chapter contradict our initial null hypothesis, this chapter explores potential environmental factors that may explain the discrepancies between the common garden findings and our field observations. I investigate intra-stream habitat variation, individual dispersal preferences, and their potential effects on life-history traits such as survivorship schedules and growth rates. Intra-stream dispersal follows a roughly normal distribution around natal sites, with both sex and personality shaping individual dispersal preferences. Survival and growth models indicate that females and males benefit from distinct dispersal strategies: females gain more from fewer but longer dispersal events, while males benefit from frequent, shorter movements. Additionally, fine-scale microhabitat variation within streams is found to significantly influence guppy survival, reinforcing the importance of spatial heterogeneity in shaping life-history outcomes.

Collectively, these findings deepen our understanding of the mechanisms driving wild guppy life history evolution. The differences between the research results in these chapters and previous common garden experiments on Trinidadian guppies highlight the need for caution when studying life history traits and other biological indicators of wild animals. Field observations are inevitably influenced by the natural environment, and it is crucial to critically reflect on experimental data, especially when dealing with species that cannot be observed or maintained in laboratory conditions, or when genetic-level analysis is lacking.

Chapter 2

Cryptic Evolution Beneath the Stream's Mask: a 12-Year Observation of Trinidadian Guppies (*Poecilia reticulata*)

Abstract

Life history evolution in guppies (*Poecilia reticulata*) has been characterised in common garden experiments. But whether these evolutionary patterns can be observed in natural habitats, where the environment fluctuates and may be impacted by evolution, remains uncertain. By conducting a long-term census and collecting monthly data from four guppy populations in Trinidadian streams, we were able to examine evidence for the evolution of age-specific survival and survivorship in free-living guppies. We built generalized linear models of population level rates corrected for sex, individual age, season, and time. A statistically significant signature of time on age-specific survival or survivorship would be consistent with these schedules evolving. We were unable to detect any evidence of a temporal trend of survivorship or survival schedules in our four streams, suggesting that the evolution of these life history traits that can be detected with common garden experiments may be masked by changes in the environment under natural settings. Our results demonstrate the challenges of detecting life history evolution in nature without recourse to common garden experiments. Our findings highlight the complexity of studying life history traits and detecting evolutionary changes in natural settings. Understanding how environmental fluctuations can obscure evolutionary patterns is crucial for understanding the dynamics of natural populations.

Introduction

Life history theory was developed, in part, to explore how survivorship and reproductive schedules change as organisms adapt to new environments (Roff 1992). The theory aims to explain how organisms evolve life history strategies in different environments, balancing trade-offs between growth, reproduction, and survivorship (Stearns 1992). Constraints resulting from these trade-offs can also evolve as life history strategies develop (Bonsall & Mangel 2004, Sasaki *et al.* 2009, Coulson *et al.* 2010, Brommer *et al.* 2012, Thys *et al.* 2019, Hastings *et al.* 2021, Paoletti *et al.* 2021). Iteroparous organisms maximise lifetime reproductive success in the face of genetic and environmental constraints by balancing reproductive allotment and survival across multiple breeding events (Hill & Kaplan 1999, Coulson *et al.* 2011, Flatt & Heyland 2011, Capdevila *et al.* 2020). Understanding such life history strategies can offer valuable insights into how organisms adapt to different ecological contexts.

Life history strategies, and traits used to describe these strategies such as generation length, age at sexual maturity, and age-specific mortality, can evolve in response to environmental change (Flatt & Heyland 2011). As populations adapt to their environment, they can modify it via changing interactions with other species within the ecosystem (Bassar *et al.* 2012). For instance, if a prey species has evolved a better form of camouflage such that the risk of predation declines for the average individual in the population, the ratio of predators to prey may change, as the prey is expected to become more abundant. This increase in prey population size will result in greater pressure on the resources they consume, which could lead to cascading consequences throughout the ecosystem (Palkovacs *et al.* 2009). When these changes play out and the ecosystem moves from one state to another, the life history traits of the prey and predator species may also adapt to the changing environment. As the factors that limit the population of prey shifts away from predation towards food availability, age-specific survivorship and reproductive schedules can change as well (Sparkman *et al.* 2013, Reznick *et al.* 2019). Characterising such changes requires long-term data on individual survival and reproductive schedules, which can be hard to obtain in wild populations.

Environmental change can also mask concurrent evolutionary trends in life history traits, a phenomenon referred to as cryptic evolution, which is usually studied with recourse to quantitative genetic approaches. A primary assumption in quantitative genetics is

$$\mathbf{P = G + E}$$

The equation states that an individual's phenotypic trait value, P, can be decomposed into a genetic contribution, G, and an environmental contribution, E. Different individuals can have the same phenotypic trait value but different genetic and environmental values. Evolution occurs when the genetic composition of a population changes over generations, which is reflected in a change in the mean value of G across the population. However, such evolution can be masked if the change in mean G is countered by an opposite change in mean E. In such cases, cryptic evolution occurs. When researchers study wild populations undergoing cryptic evolution by solely focusing on changes in their phenotypic traits over time, they may not detect evolution. In addition, the quantitative genetic approaches used have been shown to fail for my study system (Potter *et al.* 2020).

Setting aside the potential failure of quantitative genetics to adequately capture cryptic evolution when eco-evolutionary feedbacks occur, the phenomenon has been reported several times. For instance, in the case of wild Soay sheep (*Ovis aries*) on Scottish islands, quantitative genetic analysis suggests strong selection for genetically larger individuals via survival and fecundity. However, phenotypic data indicate that sheep are not increasing in size; in fact, they are shrinking (Wilson *et al*., 2007). Similar cryptic evolution has been observed in long-term studies of great tits (*Parus major*). Despite consistent selection for larger body mass, the bird population exhibited a trend of decreasing mean phenotypic value of body mass over 36 years of study (Garant *et al.*, 2004). Both cases are consistent with evolution resulting in a deteriorating environment and plastic responses of the phenotype masking evolution from observation, which suggests eco-evolution is operating and this has the potential hinder the utility of quantitative genetic approaches to detect cryptic evolution. Other empirical studies have also proposed cryptic evolution as a mechanism for explaining the difference in evolution detected in the lab and observed in the wild (Merilä *et al.* 2001a, Merilä *et al.* 2001b, Hadfield *et al.* 2010, Hadfield *et al.* 2011).

Guppies (*Poecilia reticulata*) are a species that are known to evolve rapidly following changes to their predation regime through the application of common garden experiments – an experimental approach that has greater power to detect evolution than observational quantitative genetics in natural environments. In Trinidad, there are two distinct types of habitats where guppies are found: low predation and high predation regimes (Reznick & Bryga 1987, Reznick *et al.* 1996a). In low predation regimes, only occasional guppy predation occurs from killifish (*Rivulus hartii*). High guppy density in these regimes leads to a food-limited population. In high predation regimes where guppies co-exist with predators including the pike cichlid (*Crenicichla alta*) and the wolf fish (*Hoplias malabaricus*), all age classes of guppies are under predation pressure, resulting in an elevated death rate compared to low predation ecotypes (Reznick *et al.* 1996b, Botham *et al.* 2006, Walsh & Reznick 2010). Previous work has revealed that when guppies adapted to high-predation environments are introduced to low-predation reaches of the same stream, over the course of less than thirty generations they evolve to a low-predation ecotype (Gordon *et al.* 2009).

Comparative studies between guppy populations from high-predation and low-predation regimes have reported differences in many aspects of their phenotype, including several life history traits (Reznick 1982, Reznick 2019). Using a common garden setting, life history evolution of high predation guppies to low predation environments has been measured by rearing ancestral high and young low guppy populations under the same conditions (Burns *et al.* 2009, Bassar *et al.* 2010). The mesocosm results has shown that survival rates across all ages evolve to be higher as populations from high predation regimes adapt to low predation environments. However, if cryptic evolution is occurring, we may be unable to document these changes from demographic data collected from populations adapting to a low predation habitat. If we are unable to detect such change, a plausible hypothesis would be that life history evolution has resulted in the guppies modifying their environment, feeding back to influence their survivorship in such a way that it masks ongoing evolution (Potter *et al.* 2020).

Since March 2008 a monthly mark-recapture study of Trinidadian guppies has been conducted in four natural streams in Trinidad. Each stream was guppy-free prior to the implementation of the study, and at its inception was seeded with guppies from high-predation regimes. Since the introduction, the guppies have adapted to the low-predation environments, and the current cohorts inhabiting the streams now phenotypically closely resemble naturally occurring populations of low-predation guppies found elsewhere in our study sites' watershed. The dataset we have collected consists of 145 monthly capture sessions, 100,073 uniquely marked individuals, and 463,080 recaptures. Frequent common garden experiments have been conducted that reveal life history evolution (Burns *et al.* 2009, Reznick *et al.* 2019).

Here, we used these extensive data on high predation guppies introduced into low predation streams to examine how their survivorship has changed. We built population level models to explore pattern of population age-specific survivorship during our twelve-year observation, taking age, sex, and seasonal factors with an impact on population survival rate into consideration. Because the common garden experiments report population level sex and age-specific rates that is what we analyse. We do not conduct individual-level mark-recapture analyses in this chapter as our initial question is can we see evolution as characterised under laboratory conditions.

By incorporating time into these models, we aimed to identify evidence of changing survival schedules while accounting for other influential factors in these wild populations. We predicted that the probability of survival for guppies at a specific age should evolve as they adapt to the new low predation environment. Given the results from previous common garden experiments, we expected survivorship schedules of guppies to have evolved to lead to an increase in life expectancy. Otherwise, a pattern of decreased or unchanged age-specific survivorship is consistent with cryptic evolution. This paper serves as a comprehensive overview of population-level data without considering individual-level phenotypic traits, reserving these more complex analyses for a future paper. This work consequently provides a solid population-level foundation for subsequent individual-level analyses.

Methods

Study Species

Guppies (*Poecilia reticulata*) are a model animal system for studying vertebrate life history evolution (Evans *et al.* 2011). They are small-bodied tropical fish living in freshwater with a short generation time, native to South American streams. Female guppies start to breed at about 10 weeks after birth and continue to give birth to litters every three to four weeks afterwards. Guppies are sexually dimorphic, with males exhibiting a brighter colour pattern than females (Endler 1980). Females mature at a larger size and have a longer life expectancy than males (Reznick & Endler 1982).

Study Area

In 2008 and 2009, we introduced four experimental high-predation guppy ecotypes into previously guppy-free low predation reaches of streams in the Northern Range of Trinidad (Figure 1). The four streams are named Caigual (CA), Lower LaLaja (LL), Taylor (TY), and Upper LaLaja (UL). The canopy cover was left intact in two streams—Caigual and Lower La Laja—and, for comparison, was manually thinned in Taylor and Upper La Laja. This treatment aimed to assess the potential impact of stream primary production and food availability on guppy populations.

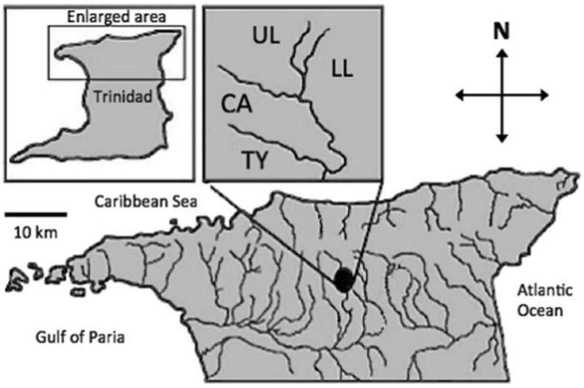


Figure 1. Map of the study streams located in the Northern Range of Trinidad (Bassar 2021). UL, LL, CA, and TY correspond to Upper LaLaja, Lower LaLaja, Caigual, and Taylor streams respectively.

Guppies used for the introduction were collected from high predation regimes in the Guanapo drainage and a breeding design chosen to ensure introduced guppies had the same degree of genetic diversity across streams. In March 2008, we conducted paired introductions in LL and UL by introducing 38 pregnant females and 38 males into each stream. One year later, in March 2009, we introduced 64 pregnant females and 64 males into a new stream CA, and 52 pregnant females and 52 males into another stream TY. UL and TY have experimentally thinned canopies to increase primary productivity, and all four streams have natural barriers preventing immigration and emigration. During the wet seasons in Trinidad, occasional flooding events cause changes in the stream environments and decreases in resource availability.

Data Collection

We used capture-mark-recapture methods to track the life history evolution of male and female guppies across our four populations (Croft *et al.* 2003). In doing so, we captured as many guppies as possible in each population each month via collection with butterfly nets. After collection, we marked and measured all individuals before release into the same point in the stream where each individual had been caught. We marked all individuals with a standard length of above 14mm by injecting coloured elastomer. Guppies are about 7mm in length at birth, and most guppies reach 14mm in their first month or two of life. The combination of 12 different colours and eight marking places on the fish made it possible to identify all individuals in a population. Guppies smaller than 14mm were not marked to minimise their risk of mortality. Guppies were captured and identified every month from the beginning of the introductions until the COVID-19 pandemic led to a temporary cessation of the study in March 2020. The guppy recapture rate was high, and thus, unmarked guppies were considered to be in their first or second month of life. When we no longer caught guppies in the monthly collections, we updated the database to record death. We did not use mark-recapture analysis because of the high recapture rate and the challenges of conducting such analyses of such a large dataset. In the subsequent paper (Chapter 3) we find a way to solve this problem and conduct an analysis of recapture rates motivated by findings from this paper.

Data Preparation

Data collected over the twelve-year period were saved into a .csv file. There are 463,080 rows of data, each representing a capture, and seventeen columns with information about the captured individual. Six out of the seventeen columns are relevant for our monthly survival analysis. These columns were named ‘stream’, ‘sampling occasion’, ‘individual ID’, ‘sampling year’, ‘sampling month’, and ‘sex’. ‘Stream’ shows the stream where each capture event took place and has four levels (UL, LL, CA, and TY, corresponding to the four streams studied). ‘Sampling occasion’ is the sequential count of months from the beginning of the study, ranging from 1 (March 2008) to 145 (March 2020). ‘Individual ID’ is the unique numerical identifier assigned to each individual throughout the study period, ranging from 1 to 169080. ‘Sampling year’ and ‘sampling month’ describe the year and month in which the capture took place. ‘Sampling year’ ranges from 1 to 13, corresponding to 2008 to 2020. ‘Sampling month’ ranges from 1 to 12, corresponding to January to December. And 'sex' comprises two levels: F (for female) and M (for male).

Based on our monthly collected data, we determined the first and last time each guppy was captured. A new variable ‘surv’ was defined to show whether the individual survived till the next capture. For each fish, all months between the first (inclusive) and last (exclusive) capture were assigned ‘surv’ = 1, indicating survival. The final month of capture was assigned ‘surv’ = 0, representing that the individual was considered deceased in the database. In this way, missing capture events were accounted for by assuming individuals were alive between captures, providing a corrected and continuous record of survival status. We removed 536 individuals that were not captured for five consecutive months or more on the assumption that a subsequent recapture was an error in identification. In other words, such events were probably the consequence of two different individuals mistakenly being identified as the same fish given our high recapture rate.

Then we calculated each individual’s age at each sampling occasion measured in months, with age 1 being assigned to first month of capture. And finally, we deleted 254 duplicated records in the database where the same individual was marked twice in the same month, and also removed 71 individuals where sex was not measured.

Model fitting

We predicted that the probability of survival for guppies at a specific age should evolve as they adapt to the new low predation environment based on the findings from common garden analyses. We also expected there should be a difference between male and female guppies because of their sexually dimorphic traits.

Using capture records of all individuals in the cleaned data file, we first checked the total number of individuals known to be alive and plotted the distribution of ages at last capture for both sexes in all streams. Next, we calculated the age-specific, sex-specific, and stream-specific probability of survival for each sampling session. We split the database into eight separate sub-databases and used these to build eight sex- and stream-specific models. We did this because examination of the data revealed different patterns of survival between streams and sex that could not be obviously corrected for by fitting stream as a fixed effect in a single analysis. The sexes had very different age-specific survival rates, which is why we conducted separate analyses for each sex. A unified analysis would have resulted in significant higher order interactions which may not be well-supported by the distributions of data. The names for new sub databases reflect the stream and sex trait of the individuals. For instance, CAF stands for Caigual females, and CAM stands for Caigual males.

We created a response variable consisting of the number of surviving individuals and the number of individuals that died, for each sex in each sampling month in each stream. Values of 604 and 203 would represent 604 successes (survival) and 203 failures (deaths). To these response variables, we fitted generalized linear models in R (version 4.1.1) using the glm function to predict the proportion of individuals that survived in each month in each sex, age, and stream class. The ratio of residual variance to residual degrees of freedom suggested the data were not over-dispersed in any of the models assuming a binomial error structure, and that there was no need to use a quasi-binomial or other distribution. We consequently used a binomial error structure to analyse the number of survivors and deaths each month. To identify the most parsimonious generalized linear model to explain the data, we selected three variables to explore. These variables include: *i*) Crude age defined as the number of months since an individual was first captured and marked. It can be further modified into a categorical variable with three different age classes, *ii*) month of study defined as a continuous variable describing the time since the experiment began, measured in months, up to 145. It is termed as 'sampling' in the database, *iii*) season defined as a categorical variable based on the calendar month of each capture, reflecting how seasonal changes in the stream environment affect guppy population survival.

To find the best model for predicting the effects of age, season, and time since the study started on class-level survival, we fitted the three variables as either numerical or categorical variable into the models, and then simplified the categorical variables into factors with as levels as possible that did not significantly impact model fit.

Fitting age into the model

To explore how age affects the probability of survival, we tried including age and age^2 into a model because there appeared that a quadratic might describe patterns across age (Supplementary Material, Table S2.1). A model of this form includes age^2 in its name – for example CAF.age^2. There was considerable heteroskedasticity, and the lines failed to adequately describe the data for most streams when we examined plots of age against survival rates, so we instead chose to fit age as a factor called age class.

We then attempted to fit each age as a factor level. We built a model where age was treated as a categorical variable, with each age represented as a separate level. Based on the statistical estimates for each age, we then grouped the data into three distinct age groups, which are typically used in constructing age-related models. Age was divided into three categories ('newborn', 'prime.adult' and 'old'). 'Newborn' was set as the first month after birth, because death rates in the first month were higher than the following month(s) for both sexes in all four populations. We then compared all possible division points for ‘prime.adult’ and ‘old’, and selected the optimal models for each sex-stream combination based on AIC values. For females from Taylor, we selected the model with second smallest AIC value which provided a similar division point to other female populations. After the optimal model was determined, we have the second model named as CAF.age_group.

Adding season into the model

After optimizing the age classes for each model, season was fitted into models because seasonal events such as floods are known to have an impact on survival. We first fitted sampling month into the model as a factor and examined whether the estimates of 12 months varied predictably across the year. This model was named CAF.age_group.12months (Supplementary Material, Table S2.2). We also calculated and plotted the population survival rates across 12 calendar months to intuitively reflect the seasonal differences. We categorised 12 months in one calendar year into two or three seasons, by testing all possible divisions within 12 months. Models with minimum AIC were selected to check how guppy population survival changes as the stream environment changes annually. After the optimal model was determined, we have two models for each stream and sex: CAF.2seasons, and CAF.3seasons (Supplementary Material, Table S2.3).

Fitting time of study in the model

To examine whether age and sex-specific survival rates are changing with time over the course of the study, we built three models and included time as a variable in three different ways. In the models, we set time as: *i*) a linear predictor (‘sampling’ used as numeric data), or *ii*) a quadratic predictor (sampling + sampling^2 as numeric data), or *iii*) a categorical variable (with 145 levels in Lower LaLaja models, or 133 levels for Caigual and Taylor models because data collection started one year later in these streams, or 144 levels for Upper LaLaja models because data collection ended one month earlier in this stream) in the model with 3 age groups defined as above, and checked the estimates for these 3 models: CAF.age_group, CAF.sampling.quadratic, and CAF.by.month.

To examine the impact of seasonal factors on the model, we replaced the numeric variable 'sampling' with two categorical variables: sampling year and season. Definition of 'season' in the new models (CAF.by.year.3seasons) was based on the three season models tested above because they provided better predictions than two season models. Then we checked how estimates of each sampling year varied within the 12-year duration of the study.

Model selection

We used Akaike Information Criterion (AIC) to rank our testable models. AIC is commonly used in ecology research for model selection. It estimates the predictive accuracy of a model by both evaluating underfitting and penalizing overfitting. For predicting the same data, a model with the minimum AIC is considered as the best model (Auger-Méthé *et al.* 2021).

To visualize the predictions, we plotted the age-specific probability of survival predicted by the model CAF.age_group (and 7 models for other stream- and sex-specific databases, same for all the plots below) and compared it to the actual age-specific population survival rate. We chose the 72nd month of study (February in the seventh year, the midpoint of the study, with no flooding events occurring in any of the four streams during that month) to plot the predicted probability of survival to avoid extreme impact of environmental factors on the prediction. We also plotted time-specific probability of survival predicted by CAF.age_group and compared it to the actual population monthly survival rates during our study to check if the model can reflect any changing trend of population survival over time. We chose an age of 5 months for plotting predictions of model CAF.age_group because both male and female individuals in all streams at this age have a moderate average survival rate.

Using the age-specific probability of survival predicted by CAF.3seasons, we calculated and plotted the predicted pattern of survivorship as age increases at the beginning (month 1 for LL and UL, or month 13 for CA and TY) and by the end (month 145 for CA, LL, and TY, or month 144 for UL) of the study. The two months chosen fall into the same season for both sexes in all streams. The predicted survivorship curve was then compared to the actual survivorship curve calculated from the age-specific and stream-specific population survival rate to check whether survivorship schedules are changing throughout the study.

Results

Population statistics

During our twelve years of study, we recorded 463,080 captures, marking 100,073 different individuals in total. After cleaning the data, we retained 453,386 valid capture records of 98,213 unique individuals. The total number of male and female guppies that have valid capture records for model construction varies in each stream (Table 1). Between LL and UL with the same initial population size and time of introduction, more individuals have been recorded during the study in UL with thinned canopy and increased primary productivity. The same trend was observed in CA and TY.

Table 1. Initial condition and total number of guppies studied during the study in each stream. Capture records that cannot be used for building models have been excluded.

Stream	**Caigual**	**Lower LaLaja**	**Taylor**	**Upper LaLaja**
Time of introduction	Mar 2009	Mar 2008	Mar 2009	Mar 2008
Initial population size	64 pairs	38 pairs	52 pairs	38 pairs
Canopy	intact	intact	thinned	thinned
Number of females studied	6,760	10,843	11,691	22,303
Number of males studied	5,959	9,726	10,438	20,493

The longest-lived female was from the Lower LaLaja and reached 54 months of age, while the longest-living male was from Taylor reached 30 months. All four streams have a similar distribution of ages at last capture. Most guppies were captured only once after birth for both males and females. Males were dying at an earlier age compared to females (Figure 2).

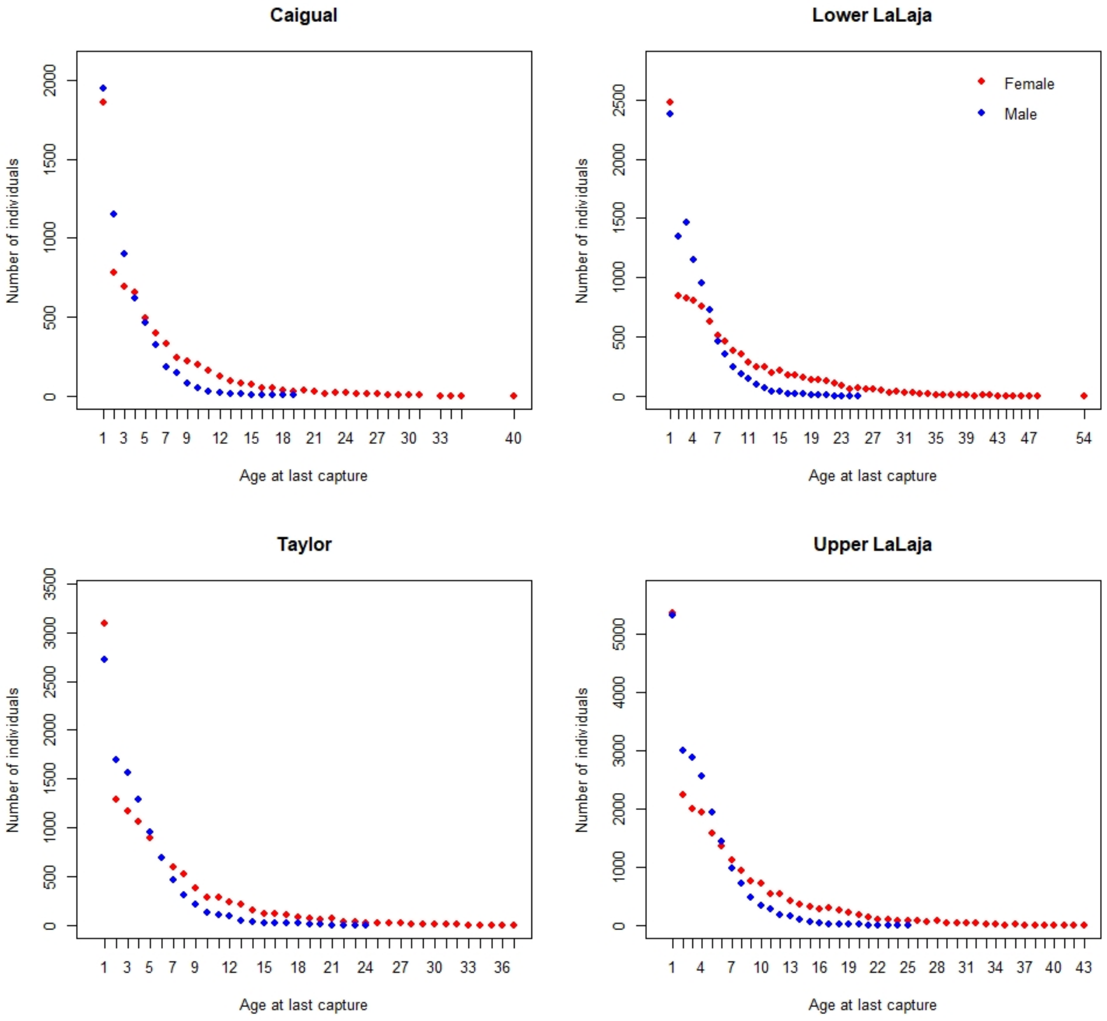


Figure 2. Age-specific distribution of ages at last capture for males and females in four experimental streams. Longest-living female in Caigual, Lower LaLaja, Taylor and Upper LaLaja lived up to 40, 54, 37, and 43 months respectively. And longest-living male in Caigual, Lower LaLaja, Taylor and Upper LaLaja lived up to 19, 27, 30, and 26 months respectively.

Age-specific probability of survival

When we checked the age-specific survival rates for both males and females in all four streams, survival over the first month of life were always lower than the second month. In all streams, survival rates tend to be lower in month 1, higher in month 2, then became constant for between 3 and around 25 months in females, and between 3 and around 15 months in males, before gradually declining to 0. There was considerable heteroskedasticity in plots of age against survival rates, which led us to fit age class as a factor to avoid the distortions and unreliability in statistical analyses caused by the non-homogeneity of the variance. Age group 'newborn' was defined as the first month of capture, and division point between age classes 'prime.adult' and 'old' were selected based on minimum AIC. The only exception was TY female model, where we chose the model with second smallest AIC value 55473 instead of the minimum AIC 55471. Because the division point for all other female populations were above 15 months, while all four male populations had a division point within the first 5 months (Table 2).

Table 2. Optimal age classes for building all final models with variable 'age.group' (age measured in months). *The optimal model we chose for TY females has the second smallest AIC value 55473. Defining 'prime.adult' as 2-3 and 'old' as 4-37 for TY females produced the minimum AIC 55471.

Age class	Newborn	Prime.adult	Old
Caigual females	1	2-26	27+
Caigual males	1	2-4	5+
Lower LaLaja females	1	2-19	20+
Lower LaLaja males	1	2	3+
Taylor females*	1	2-25	26+
Taylor males	1	2-3	4+
Upper LaLaja females	1	2-16	17+
Upper LaLaja males	1	2-3	4+

When we fitted age class as a three-level factor and treated month of study as a continuous variable in the models, the predicted curve was a close resemblance to the average population survival rate throughout the study. For female guppies, individuals in age class ‘prime.adult’ always have the highest survival. In LL and UL, the age class ‘old’ has higher survival rate than ‘newborn’, while in CA and TY ‘old’ is the most vulnerable age class. For male guppies, LL and UL share the similar pattern of ‘prime.adult’ being the most robust group. For CA and TY males, a continuous decline in probability of survival against age was predicted. Across all 8 databases, the decline in the actual survival rate in the last few months is attributed to the significant decrease in the number of individuals surviving to this age (Figure 3).

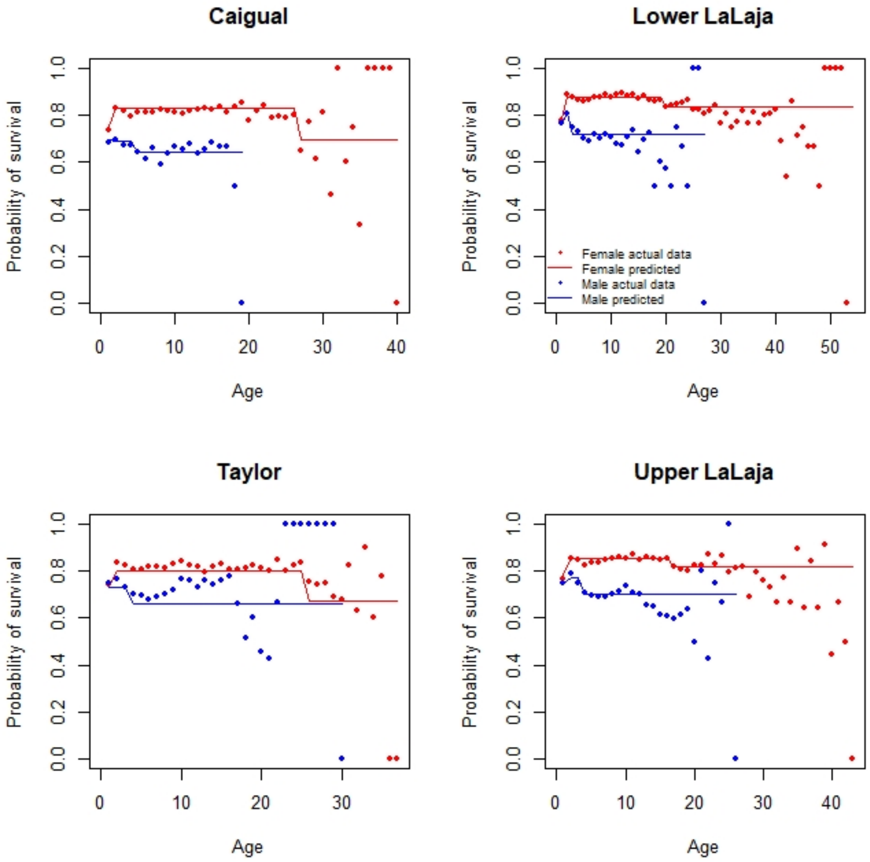


Figure 3. Age-specific probabilities of survival predicted by CAF.age_group and models with the same parameters from other databases (lines) and actual average age-specific survival rate of guppy population during the entire study (dots) for males and females in four experimental streams Caigual, Lower LaLaja, Taylor and Upper LaLaja.

Season-specific probability of survival

The wet season in Trinidad is between June and December, while the dry season is between January and May. Past studies have shown that during wet seasons guppies usually have fewer offspring (Reznick 1989). Floods during the wet season can also affect survival rates either by causing physical stress to individuals or via apparent mortality (Fitzpatrick *et al.* 2014).

We plotted crude monthly survival rates for males and females in all four streams during the twelve-year study. The mark-recapture experiment of CA and TY started at month 13, one year later than LL and UL, and ended one month earlier in UL at month 144. In all four streams, female guppies had a consistently higher survival rate compared to male guppies throughout the twelve years of study, with only a few exceptional months in each stream. Population survival rates of most months ranged between 0.6 and 1.0. Occasional floods caused dramatic decreases in the survival rates for both sexes. LL seemed to be less affected by flood events compared to CA, TY and UL where populations were severely impacted by the same flood events, which might be due to differences in stream morphology (Figure 4).

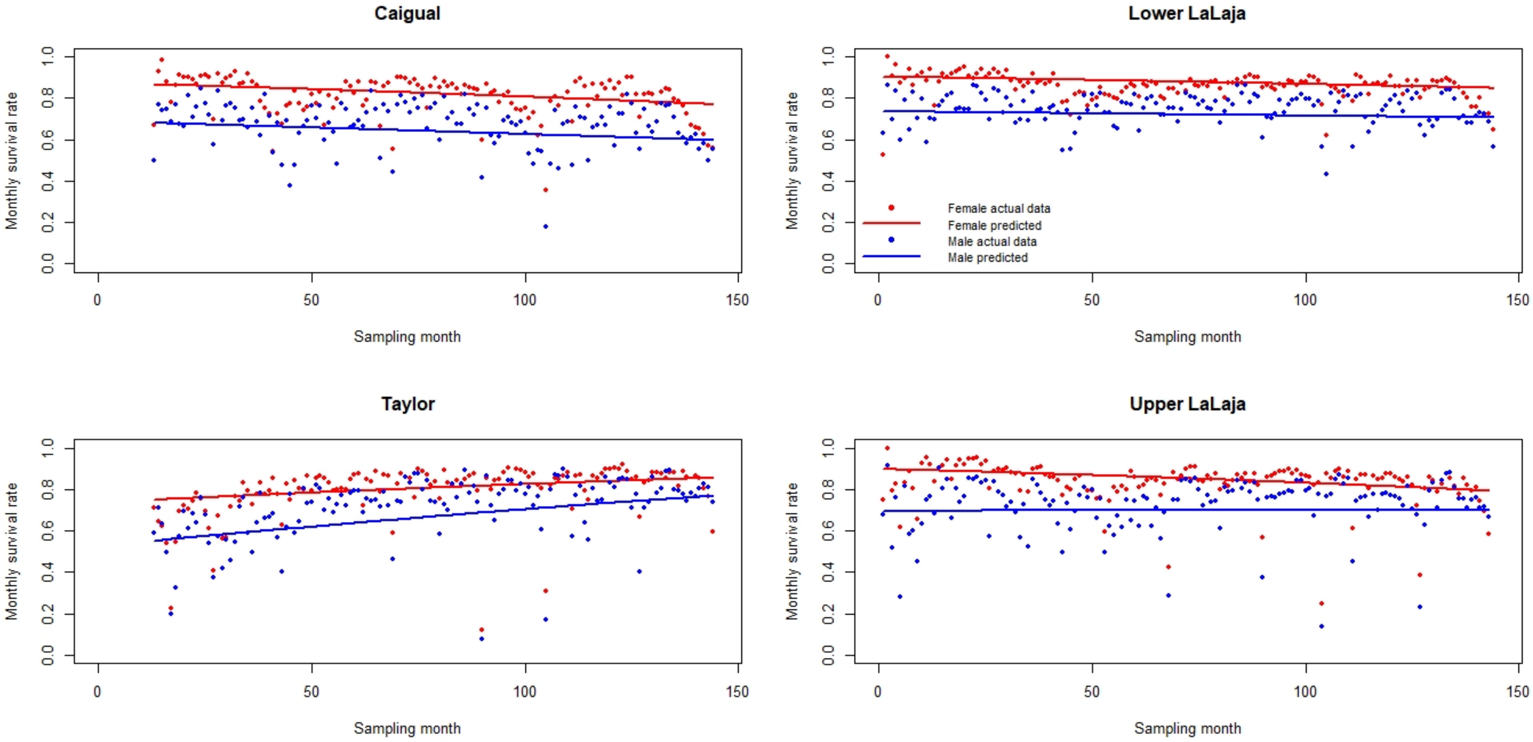


Figure 4. Actual monthly survival rate of guppy populations in eight Trinidadian streams (dots) and monthly probabilities of survival predicted by CAF.age_group and other seven models with the same parameters (lines). Sampling month 1 is March of 2008.

To focus on the seasonal impact on stream environment, we also plotted the population survival rates by 12 calendar months (Figure 5). Across all 8 databases, the monthly average survival rate in the first half of the year is generally higher than the months in the second half of the year, which is consistent with the local climatic distinction between dry season (from January till May) and wet season (from June till December).

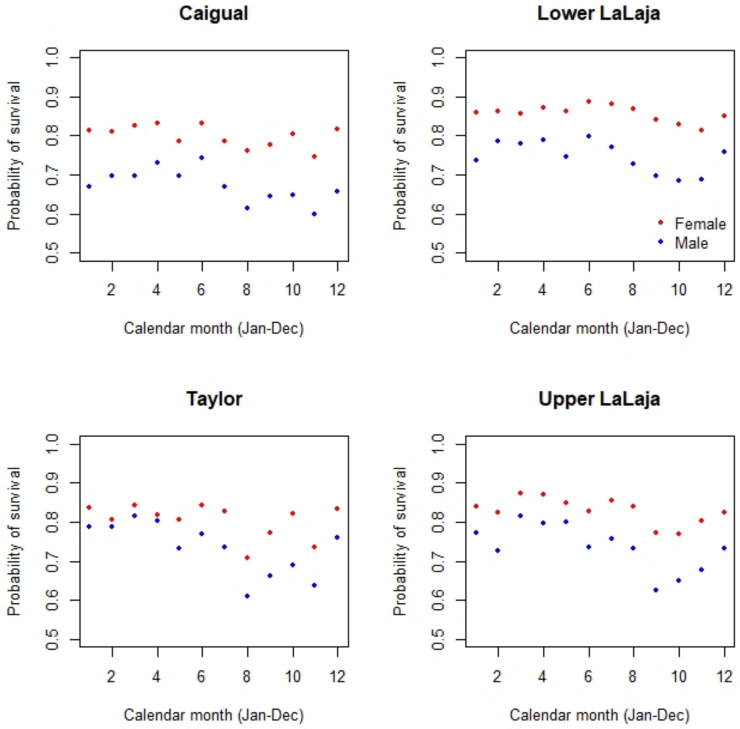


Figure 5. Month-specific population survival rate in each database. Blue dots for males and red dots for females in four experimental streams Caigual, Lower LaLaja, Taylor and Upper LaLaja.

Based on the differences of estimates between adjacent months, we categorised 12 months in one calendar year into two or three seasons. After the optimal model was determined, all the streams shared a similar division between different seasons. For all the 8 sub-databases, three-season division models made better predictions than two-season models (Supplementary Material, Table S2.3). In our three-season models, season three with lowest estimate always falls into local wet season and season two with greatest estimate coincides with the dry season, which is consistent with findings in previous studies. The intermediate season one falls between the other two seasons and has a more varied distribution of time (Table 3).

Table 3. Optimal seasons for building all final models. Month 1-12 (Jan-Dec) in one calendar year are divided into three seasons for building models. Season two is defined as the season

with greatest estimate value in model output, season three with lowest, and season one with second lowest estimate value.

Season	one	two	three
Caigual females	7-10	12-6	11
Caigual males	12-1	2-6	7-11
Lower LaLaja females	12-3	4-8	9-11
Lower LaLaja males	8	12-7	9-11
Taylor females	9-11	12-7	8
Taylor males	5-7	12-4	8-11
Upper LaLaja females	11	12-8	9-10
Upper LaLaja males	7-8	12-6	9-11

Evolution of probability of survival

After we've determined the optimal way to define age classes and seasons, we checked whether changes in the survival rate of guppy populations were linear over the course of the study. AICs of all models are presented in Table S2.4 in Supplementary Material, and delta-AICs between each model and the optimal model are calculated.

We plotted the predicted monthly survival rate of guppy populations where evolution happens in a linear pattern and compared them to the actual monthly population survival rates. Both sexes in CA and LL, as well as females in UL, exhibited a pattern with population's average survival rate decreasing over time, while both sexes in TY and males in UL evolved in an opposite pattern, with increased population survival by the end of the study (Figure 4).

Survivorship

Although the longest-living female reached 54 months of age and the longest-living male reached 30 months, more than half of the guppies in each stream died by the age of 4 months. In all four populations, more than 90% of the females died within 18 months since birth and males within 8 months.

Predicted survivorship curves of males and females in each population were plotted for both the beginning and end of the study, and they were compared to the actual survivorship curves (Figure 6). Survivorship schedules in all populations changed throughout the study, aligning with the patterns of age-specific probabilities of survival described above. As guppies adapted to a low predation environment, the predicted age-specific survivorships of CA population, LL population and UL females went down, while age-specific survivorships of TY population increased. UL males also had a slightly increasing predicted age-specific survivorship during the study.

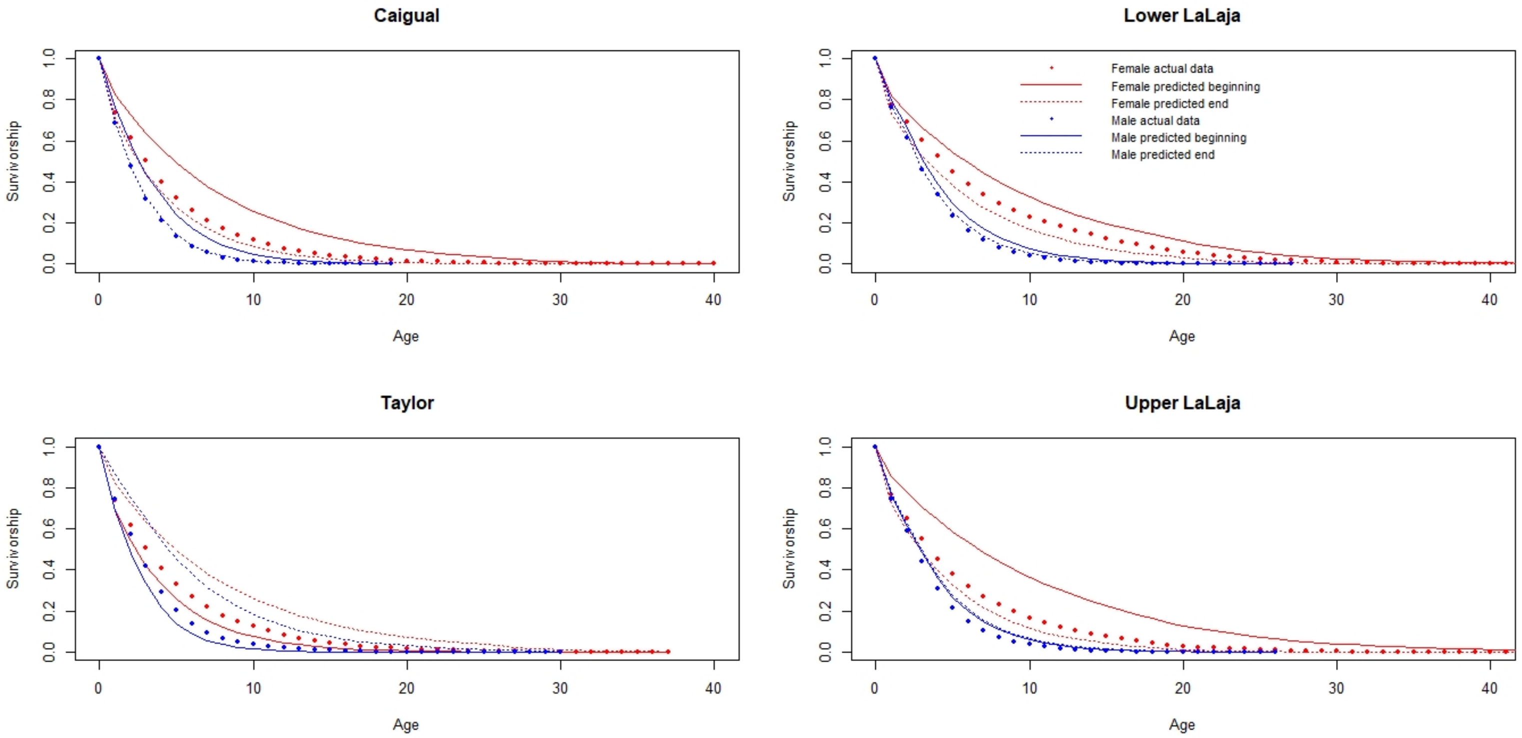


Figure 6. Survivorship of guppy populations across four streams (Caigual, Lower LaLaja, Taylor and Upper LaLaja) predicted by CAF.3seasons (and models with same parameters used for seven other streams) at the beginning of the study (solid lines) and by the end of the study (dotted lines), and the actual average survivorship of guppy populations during the study (dots).

Discussion

In this study we tracked introduced wild guppy populations in four predator-free Trinidadian streams and recorded changes in their age-specific survival and survivorship over the course of 12 years. Our results reveal that probabilities of survival in all four streams have exhibited slight directional change over the course of the study, but the patterns in different streams go in opposite directions. As guppies from high predation regimes were moved into predator-free streams, they started adapting to this new environment and this process is reflected in shifting survival rates. The entire TY population and UL males showed an increasing monthly survival rate as the study has progressed, which is in accordance with findings from common garden experiments where guppies from high predation regimes exhibited greater longevity (Potter *et al.* 2020). The opposite pattern was observed for individuals in CA and LL as well as females in UL. These populations had a decreasing pattern of survival with time, which seemingly contradicts findings from common garden experiments (Burns *et al.* 2009, Bassar *et al.* 2010). Given that no predator and other obvious threats exist in these streams, food limitation could act to mask the evolutionary changes in life history seen in common garden experiments. Supporting evidence has been found in previous studies of Trinidadian guppy populations. Their results suggested that guppy evolution influences food availability in the wild (Reznick *et al.* 2019). Research conducted in streams with similar environmental settings revealed that the co-evolution of guppies and a competitor species, killifish, significantly affected total invertebrate biomass in their habitat. The study also found that guppy evolution alone had a significant impact on algal biomass and accrual rates (Palkovacs *et al.* 2009).

Researchers have tracked life history evolution in wild Trinidadian guppy populations over the past few decades. This research has previously demonstrated life history evolution in wild freshwater fish populations experiencing changing natural conditions. It provides compelling evidence that evolution can shape ecological processes within relatively short timescales, thereby influencing subsequent evolutionary trajectories. This phenomenon, known as eco-evolutionary feedback, has been hypothesized in many studies but direct evidence remains scarce. In a previous study, the small herbivorous rotifer (*Brachionus calyciflorus*) exhibited rapid adaptation to phosphorus-limited environments (Declerck *et al.* 2015). The authors suggested the possibility of rapid evolution impacting standing stocks of primary producers and subsequently primary production for the population's survival. Similarly, research on three-spine stickleback (*Gasterosteus aculeatus*) showed that these top predators influence both ecological dynamics and evolutionary processes within the aquatic community, thereby affecting primary productivity and community structure (Ware *et al.* 2019).

When comparing our results to previous studies of cryptic evolution, such as those involving wild Soay sheep on Scottish islands and great tits in Wytham Woods (Garant *et al.* 2004, Wilson *et al.* 2007), we have observed similar patterns in wild guppy populations: phenotypic traits may evolve in a direction opposite to known ongoing genetic changes. Those studies on ungulates and birds both focused on body size and body weight as indicators of fitness. A 29-year study on collared flycatchers (*Ficedula albicollis*) on the island of Gotland, Sweden, examined the survival rate of young birds and also found evidence of cryptic evolution (Merilä *et al.* 2001a, Merilä *et al.* 2001b). The study suggested that poor food availability led to a decline in survival rates, even though selection pressures were measured to act in the opposite direction.

In the context of our study, we suggest that life history evolution in wild guppy populations could also be cryptic, but other interpretations remain plausible. The observed divergence between field and common-garden patterns could also reflect environmental deterioration or sampling biases rather than masked genetic change (Martin et al. 1995, Hadfield *et al.* 2011). Demonstrating true cryptic evolution would require independent genetic evidence such as a directional change in breeding values or allelic frequencies for life history traits that contrasts with the phenotypic trend observed in the wild. In TY and UL where the canopy has been thinned and primary productivity increased, the evidence of cryptic evolution is weaker than in CA and LL, where canopy blocks sunlight and therefore competition over food resource should be fiercer. Our interpretation therefore emphasizes that the phenotypic trends we observed are consistent with the possibility of cryptic evolution, highlighting how environmental and ecological factors such as food availability and population density may obscure or even reverse the expression of underlying genetic changes.

To draw a more sound conclusion from the observation, we must consider all plausible explanations. More work will be needed to investigate what has caused the unexpected decline in survival rates in some of the streams. It is worth noticing that by only looking at the survivorship curves, it is impossible to distinguish causes of mortality from external biotic or abiotic factors or a poor genetic fit to the environment. One limitation of this study is that we did not record sufficient information about the environmental conditions within each stream. The only indicator related to food availability included in our study is canopy cover (intact or reduced). However, we did not measure primary productivity, algae biomass, or other relevant parameters that are often used in water environment studies (Carpenter *et al.* 1987, Croome & Tyler 1975). Additionally, floodings appear to significantly affect food availability and individual fitness, and eventually cause the dramatic decreases in population survival rates. Another issue is that floods may wash guppies out of the study site while still alive; however, they are considered dead due to the statistical methods used, which may introduce inaccuracies into our results.

Another factor that may influence our results is individual heterogeneity in survival, where variation occurs among individuals within the same population in their intrinsic susceptibility to mortality, rather than assuming that frailty is solely age dependent. Such heterogeneity has been documented in previous studies of wild animal populations (Vaupel & Yashin 1985, Nussey *et al.* 2008) and can strongly influence apparent survival patterns at the population level. For example, an analysis on multiple invertebrate species found that unobserved individual heterogeneity is widespread and can account for up to 35% of the variance in longevity (Hartemink & Caswell 2018). In our case, covariation between individual frailty and lifespan could also partly explain the divergent temporal trends in survival observed among streams. Incorporating this heterogeneity into future analyses through more complex statistical approaches such as mixed-effects models could potentially improve the accuracy and biological realism of our survival estimates (Muff *et al.* 2020, Blozis & Craft 2024).

While most studies examining cryptic evolution use quantitative genetic approaches to assess trends in breeding values, our study focuses directly on analysing phenotypic trends to determine whether they are consistent with common garden results. Multiple common garden experiments have been conducted before to compare Trinidadian guppies occupying different ecological regimes (O'Steen *et al.* 2002, Potter *et al.* 2020, Potter & Anja 2022). A study published in 2020 was based on data collected from guppy populations in Lower Lalaja stream during the first three years following the introduction in 2008, overlapping with our study period (Potter *et al.* 2020). In that study, researchers collected DNA samples from individuals each month and constructed a microsatellite-based pedigree for the Taylor population. They then employed quantitative genetic approaches to predict the evolution of size at maturity, which suggested positive selection for larger size at sexual maturity and an evolutionary response. But this prediction contradicted the patterns observed in common garden experiments, where guppies actually became smaller over the course of the study. The researchers concluded that the lack of environmental factors, specifically population density in the stream, incorporated into the model led to the failure in detecting cryptic evolution.

It is worth noting that when only looking at our survivorship curves, we cannot rule out the possibility that such evolution is caused by trends in the changing recapture probability in our study system. If our recapture rate declines over the 12-year period, we could mistakenly interpret the drop in recapture probability as a decrease in survival rate and lifespan. Previous studies have identified capture-shy individuals who are better at avoiding human capture (Coulson 2010, McLean 2014), and fish can develop a fear of fishing gear after repeated exposure (Arlinghaus *et al.* 2017). In practice, we have also noticed that guppies in some streams, such as TY, appear to have become more alert when field investigators come close to the small pools they are living in. Therefore, the capture rate must be examined, which will be analysed with in our future work.

This study provides a population-level statistical analysis of the changing patterns in life history traits across four wild guppy populations, all experiencing similar shifts in environmental factors. Although our findings are consistent with the potential for cryptic evolution, they do not by themselves constitute definitive evidence. Instead, they underscore the complexity of disentangling genetic adaptation from ecological and methodological influences in natural populations. Future work integrating quantitative genetic data or genomic markers with long-term demographic records would be required to confirm whether evolutionary change underlies the observed phenotypic patterns. Our observation provides valuable preliminary insight and lays the groundwork for future individual-based studies to explore the mechanisms underlying these population-level dynamics. If further genetic evidence supports this interpretation, it would imply that wild populations can undergo cryptic evolution more commonly than currently recognized. Consequently, new methodologies may be necessary to study species that cannot be easily maintained under experimental conditions. This demonstration of life history evolution underscores the significant ecological impacts that evolution can generate - a feedback loop widely theorized but infrequently quantified in empirical studies. Expanding our understanding of these eco-evolutionary dynamics could provide compelling evidence for the intricate interplay between evolutionary change and ecological processes across diverse natural systems.

Chapter 3

Hide and Seek - Using Bayesian Models to Examine Trends in Recapture Rates in a Long-term Mark-recapture Study of Wild Trinidadian Guppies

Abstract

Life history evolution in guppies (*Poecilia reticulata*) has been extensively studied in controlled common garden experiments. However, in their natural habitats, evolution may be obscured by fluctuating environmental factors, making it unclear whether the same evolutionary patterns emerge in the wild. This study examines the population survival rates of Trinidadian guppies over a 12-year period using capture-mark-recapture (CMR) methods. Two Bayesian models were developed and implemented. The first model incorporates a dynamic age structure to investigate the effect of senescence on survival, while also accounting for time as a random effect in recapture rates. The second model focuses on body size as an indicator of growth's impact on survival, using time as a linear factor. Both models incorporate external factors such as sex, population density, and seasonal variations, providing insights into survival and recapture rates across four streams. Sex-based differences in survival were observed, with females generally exhibiting higher survival rates than males. The effect of size on survival was sex-specific, and population density influenced survival differently across streams. While high variability in recapture rates was detected across months, a consistent negative trend in recapture probability over time suggests that guppies could potentially be evolving behavioural adaptations to avoid capture. These findings challenge previous conclusions about declining survival rates over time in some streams, emphasizing the importance of considering temporal variations in recapture rates when interpreting population dynamics.

Introduction

When studying population dynamics in the wild, conducting a comprehensive census that covers as many individuals as possible enables researchers to accurately characterize the population dynamics and life history of animals. However, an inherent limitation of census efforts is the inability to record every individual alive within the population, leading to potential biases in estimates of individual survival and other life history traits. In our previous analysis outlined in earlier work, we utilized data collected over 12 years on Trinidadian guppies. While the recapture rate was notably high, it was not 100%, and we did not adjust for detection inaccuracies, which could introduce bias into our findings, particularly if they have trended with time.

To better understand these potential biases, it is important to assess whether changes in detection rates occurred throughout the study period in such a way as to bias survival rates, as the absence of a consistent temporal trend in survival rates across all streams could potentially be attributed to changes in recapture rates. For example, it is possible that the fish have developed strategies to evade capture, considering that the monthly captures recurred throughout their lifespan, and that such events could potentially impact survival and reproductive success.

Various methods can be employed to track individuals and record their life history traits in wild animal populations (Ross & Reeve 2011). Direct observation is commonly employed where individuals are easily spotted and distinguished within the population (Brockett 2002). However, the accuracy of direct observation is influenced by factors such as the number and expertise of observers, and the extent of the area covered. Indirect observation using feces or nests is often used for more cryptic or rare animal species, but it can also yield inaccurate results (Guschanski *et al.* 2009). When these methods cannot be applied to wild populations, such as fish inhabiting streams, Capture-mark-recapture (CMR) methods are a common individual-based method that is used.

The fundamental principle of CMR involves tagging individual animals with identifiable markers that are theoretically harmless to their survival, and subsequently recapturing these marked animals after releasing them back into the population (Thorstensen *et al.* 2022). Initially used to estimate population density, CMR has evolved to enable long-term tracking of individuals across various life history stages when a reasonable sample size is achieved, and has become a cornerstone in ecological and evolutionary studies (Pradel 1996, Reznick *et al.* 2007, Leirs *et al.* 2023). By conducting a CMR study within a wild population, researchers can gain a comprehensive understanding of population dynamics and demography that may otherwise be unattainable.

In CMR studies, inaccuracies can arise, just like with any other method. The reliability of results depends on three crucial steps: capturing, marking, and recapturing. Capture processes can introduce biases. For instance, in a close-kin mark–recapture study of Atlantic salmon, different sampling location of adult individuals led to significantly different population abundance estimates (Wacker *et al.* 2021). Immature individuals, being smaller in size, may also be harder to catch and mark (Reznick *et al.* 2007). To improve the tagging process, various methods have been explored for marking fish in CMR studies, such as anchor tags, passive integrated transponder tags, and visible implant elastomer tags (Thorstensen *et al.* 2022). These methods vary in mark persistence, intrusiveness, and ease of observation. Losing tags during the study or tags affecting individual survival can bias results (McDonald & Bryan 2003). Double tagging, as done in the study of American white bass, reduced tag loss rate from 24.8% per year to 6.2% per year, improving estimation of demographic parameters (Muoneke 1992).

However, tagged fish may exhibit altered behaviours, potentially affecting their survival and leading to variable recapture rates, which can influence the observations of CMR studies (Dekker 1989). Over time, animals may develop net- or hook-avoidance skills, leading to reduced recapture rates. For instance, in a CMR study of pike, fish became difficult to catch again when a significant proportion of the population had been captured by spinner fishing, and a different bait fishing method must be used to maintain a high recapture rate (Mosley *et al.* 2024).

Here, we conducted a CMR study on guppies inhabiting four streams in Trinidad, spanning a 12-year period with monthly capture intervals. To better assess the factors influencing survival rates, we incorporated advanced modelling techniques. Specifically, we used an extensive long-term dataset to analyse the evolution of life history traits across the populations. We constructed Bayesian models, incorporating parameters such as age, sex, body weight, and seasonal influences, to observe shifts in population survival rates and recapture rates across the four populations. The model also integrated the time of study to investigate whether there is any evidence of a temporal trend in recapture rates masking the evolution of survival rates. We expected that the evolving survivorship patterns will align with findings from previous analyses employing linear models, and that recapture rates will remain consistently high without any significant decline over time.

Methods

Species and Area of Study

We chose guppies (*Poecilia reticulata*) as the study species, building on previous long-term research (Reznick & Endler 1982). These small freshwater fish have a short generation time and are native to South American tropical streams, though they have been introduced to various aquatic environments worldwide (Lindholm *et al.* 2005). Female guppies begin breeding approximately 10 weeks after birth and continue to produce litters every three to four weeks. Guppies exhibit sexual dimorphism, with males being small and displaying brighter colour patterns and engaging in courtship behaviour (Endler 1980). As viviparous fish, female guppies give birth to live young but may prey on their offspring immediately after birth.

In 2008 and 2009, we introduced four high-predation guppy populations into previously guppy-free, low-predation sections of streams in Trinidad's Northern Range (Figure 1). These four streams are named Caigual (CA), Lower La Laja (LL), Taylor (TY), and Upper La Laja (UL). In two of these streams, Caigual and Lower La Laja, the canopy cover was left intact, while in Taylor and Upper La Laja, the canopy was manually thinned to compare the effects of varying levels of stream primary production and food availability for guppies. The four streams are bounded by waterfalls at both the upstream and downstream ends, acting as natural barriers that largely prevent immigration and emigration, thereby maintaining the populations in a relatively closed environment. In March 2008, we conducted paired introduction in LL and UL by introducing 38 pregnant female and 38 males into each stream. In March 2009, we introduced 64 pregnant female and 64 males into CA, and 52 pairs into TY.

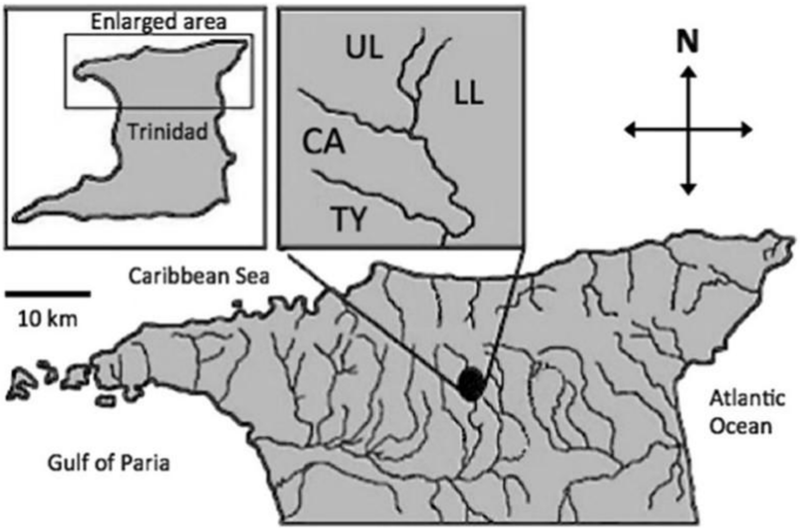


Figure 1. Map of the study streams located in the Northern Range of Trinidad (Bassar 2021). UL, LL, CA and TY, stands for Upper LaLaja, Lower LaLaja, Caigual and Taylor streams.

Data collection

Since the beginning of the introductions, we have been using a monthly capture-mark-recapture method to track the population structure of these four populations. Every month, we used butterfly nets to capture as many guppies as possible in each stream. After collection, all individuals were taken to the lab where they were anaesthetized with MS222 and marked by injecting coloured elastomer on their first capture. The combination of 12 different colours and eight marking places on the fish made it possible to identify all the individuals in a population. Guppies smaller than 14mm were not marked to minimise their risk of mortality. Sex can be easily identified by physical differences, with the most notable trait being the presence of a long gonopodium in males, a specialized fin used for reproduction, which is absent in females. We measured the body length by taking a photo of the fish next to a ruler and weighed each animal with a scale. The entire process of marking and measuring should take no longer than two minutes per fish, and the rate of individual deaths during the capture and identification process was 4.22% (2,232 died in 52,831 individuals marked). In March 2020, the COVID-19 pandemic resulted in a temporary halt in data collection for our study and marked the conclusion of the data used in our models.

Data Preparation

The data collected over the twelve-year period were saved in a single .csv file. This file contained a total of 463,080 rows, each representing a capture event, and included seventeen columns with information about the captured individuals. In each row, eight columns relevant to our mark-recapture analysis were labelled as follows: ‘stream’, ‘sampling occasion’, ‘individual ID’, ‘sampling year’, ‘sampling month’, ‘standard length’, ‘sex’, ‘population density’. The ‘stream’ column indicates the stream where each capture took place, with four levels corresponding to the streams in our study (UL, LL, CA, and TY). ‘Sampling occasion’ represents the sequential count of months from the study's start, ranging from 1 (March 2008) to 145 (March 2020). ‘Individual ID’ is a unique numerical identifier assigned to every guppy marked throughout the study, with 98213 distinct IDs recorded for individuals captured over the 12-year period. ‘Sampling year’ and ‘sampling month’ indicate the year and month of each capture, with ‘sampling year’ spanning from 1 to 13 (corresponding to year 2008 to 2020) and ‘sampling month’ ranging from 1 to 12 (corresponding to January to December). ‘Standard length’ (SL) measures the body length from the tip of the nose to the base of the tail in millimetres for each capture event. Column ‘sex’ is categorized as either F (female) or M (male). The last column ‘population density’ represents the total population density for each stream in each month, calculated as the number of individuals divided by the estimated water volume of the stream measured during that month.

We cleaned data prior to building the models. A total of 254 duplicate records were identified and deleted where the same individual was recorded twice in the same month. We also removed 71 individuals for which sex was not recorded. And finally, we excluded 536 individuals that were not recaptured for five consecutive months or more, assuming that any subsequent recapture was likely an identification error.

Mark-recapture analysis

The Markov Chain Monte Carlo (MCMC) algorithm has been widely employed in statistical analysis involving complex probability distributions (Wang 2022). The MCMC algorithm was originally developed in the 1940s by Stanislaw Ulam, John von Neumann, and other physicists (Metropolis & Ulam 1949, Metropolis 1985). The Monte Carlo method employs random sampling to obtain results. A Markov Chain is a sequence of random elements X_1, X_2, ... X_n with a key feature that the value of each element only depends on the previous element, meaning the conditional distribution of X_n given X_1, X_2, ... X_{n-1} depends solely on X_{n-1} (Geyer 2011).

To estimate the recapture rate and probability of survival by month during the study, we employed the Bayesian approach with Markov Chain Monte Carlo simulations on our capture data of guppies across all four streams. By treating survival of an individual (0 for dead and 1 for alive) as the hidden state and the capture record (1 for captured and 0 for uncaptured) as the observable state in each month of the study, we could build a hidden Markov model (HMM) that uses multiple simulation chains to estimate the posterior parameter estimates that are too difficult, if possible at all, to calculate otherwise.

In an MCMC model for survival, a transition matrix is utilized. Within this matrix, an individual's status for the current observation (in our case, survival this month) depends solely on its status during the previous observation (in our case, survival last month). If φ represents the survival rate in the population, then $1- \varphi$ represents the death rate. The matrix comprises four statuses and their corresponding probabilities, as follows:

$$\begin{matrix} \text{alive} \rightarrow \text{alive} & \text{alive} \rightarrow \text{dead} \\ \text{dead} \rightarrow \text{alive} & \text{dead} \rightarrow \text{dead} \end{matrix} = \begin{matrix} \varphi & 1-\varphi \\ 0 & 1 \end{matrix}$$

During mark-recapture analysis of wild populations, however, the transition between life and death cannot usually be directly observed due to imperfect detection. As the Markov process for survival was only partially observed each month in our study, we used a hidden Markov model for prediction. An observation matrix, similar to the transition matrix but with p representing the monthly capture rate instead of φ for survival rate, was employed:

$$\begin{matrix} \text{alive} \rightarrow \text{detected} & \text{alive} \rightarrow \text{undetected} \\ \text{dead} \rightarrow \text{detected} & \text{dead} \rightarrow \text{undetected} \end{matrix} = \begin{matrix} \mathrm{p} & 1-\mathrm{p} \\ 0 & 1 \end{matrix}$$

Modelling in R

We developed two sets of HMMs with different parameters to estimate survival and recapture rates, both tailored to the stream- and sex-specific subsets within our capture record database (Table 1). One HMM (Model 1) incorporated two shifting age boundaries to assess potential changes in the categorization of age groups defined in our study. The other HMM (Model 2) replaced age classification with continuous standard length measurements to examine how variation in body size influenced survival and recapture probabilities. All models were fitted using R (version 4.1.1).

Before running the MCMC mark-recapture model, we used the packages ‘dplyr’ and ‘zoo’ to build the matrix of parameters and capture occasions. For each individual, we compiled an observation record covering the entire study period. This record consists of a binary sequence indicating capture events, where 1 represents an observed capture and 0 indicates a missed capture. The record spans from the first capture to the last, accounting for the possibility of missed captures in between. Alongside the observation record, we included several variables for each capture occasion: the standardized SL, standardized population density, season, and age. The SL was recorded during each capture, and if missing, it was estimated using a linear interpolation between the most recent previous and the next earliest SL records. Population density was recorded in each month. Season was defined based on the month of each capture to account for seasonal variations using the approach in Chapter 2. Age was set to 1 during the first capture event for each individual and updated accordingly throughout the capture duration. These variables were recorded consistently for each capture occasion, providing a comprehensive dataset to support the model. Subsequently, we employed the 'NIMBLE' package to construct and execute the models.

Table 1. Summary of parameters used in two Mark-Recapture models for analysing monthly survival (φ) and recapture rate (p) in wild guppies.

		Model 1	**Model 2**
Parameters in estimating φ	population density	x	x
	standard length (SL)	x	x
	time since study began		x
	season	x	x
	baseline (intercept) values for two age boundaries	x	
	effect of time on two age boundaries	x	

	senescence effect in the last age group	x	
Parameters in estimating p	population density		x
	standard length (SL)	x	x
	season	x	x
	time since study began		x
	random effect for sampling occasion	x	

The functions used to predict monthly population survival φ resembled the one employed in Chapter 2, but differed in that they were based on individual-level data rather than population averages and also incorporated models of recapture. Model 1 and Model 2 included parameters such as population density in the current month, individual standard length at the time of capture, season of the capture event, and time elapsed since the study began.

In Model 1, which includes two changing age boundaries, we initialized these boundaries as two random values between 1 and the maximum observed age within each sex- and stream-specific subset. We then examined how these two boundaries shifted over time using a linear model. We also used a constraint to make sure that the first age boundary is always smaller than the second, maintaining a logical ordering of our three age categories.

$$\text{age\_boundary}[i,t] = \text{age\_boundary\_intercept}[i] + \text{slope}[i] \times \text{time} \quad (i=1,2)$$

Additionally, we tested for potential senescence effects in the oldest age group by incorporating a senescence factor into the survival calculation specifically for the third age category. This decision was based on our previous population-level analysis, which indicated a decline in survival rates among aging individuals. In Model 2, we did not define discrete age groups but instead used standard length as a continuous variable to assess how growth influences survival.

The monthly recapture rate p was predicted using similar functions. The parameters for calculating the recapture rate included: *i*) Individual standard length for the month, enabling the examination of whether individual guppies have gradually developed techniques to avoid capture throughout their life; *ii*) Season of the capture event, considering that the water environment of wild streams in the dry season and the wet season can vary significantly and may have different impacts on capture probability *iii*) Population density, as a more dense population could either lead to an increased capture rate due to crowding, or decrease if fish are more dispersed and harder to locate; and *iv*) Time of capture since the start of the study, providing insights into whether the guppy population has gradually acquired the ability to avoid capture over generations (Model 2), and whether the random effects of the sampling month are influencing the observed capture rate patterns rather than temporal factors (Model 1).

Season was incorporated into our models because events such as floods can significantly reduce survival rate (Fitzpatrick *et al.* 2014). In Trinidad, the wet season runs from June to December, while the dry season extends from January to May. We defined two distinct seasons: season one with lower survival rates, roughly corresponding to the local wet season, and season two with higher survival rates, aligning with the dry season. The definition of these two seasons varies slightly across the eight subsets, as shown in Table 2 below.

Table 2. Optimal seasons for building Mark-Recapture models. Months 1–12 (January–December) in one calendar year are divided into two seasons for each sex- and stream-specific dataset. Season one is defined as the season with lower average survival rates and season two with higher survival rates.

population	**season one**	**season two**
Caigual females	7-11	12-6
Caigual males	7-1	2-6
Lower LaLaja females	9-12	1-8
Lower LaLaja males	8-11	12-7
Taylor females	8-11	12-7
Taylor males	8-11	12-7
Upper LaLaja females	9-11	12-8
Upper LaLaja males	9-11	12-8

Model 1 provides three separate sets of estimates for φ across different age groups. As an example, the functions for predicting φ and p in the oldest age group of Model 1 are defined as follows:

$$\varphi[3] = \frac{1}{1 + e^{-(\varphi 0[3] + \varphi D[3] + \varphi L[3] + \varphi S[3] + \varphi A)}}$$

$$p = \frac{1}{1 + e^{-(p0 + pL + pS + pR)}}$$

where $\varphi_0[i]$ represents the baseline survival for age group i, which has two boundaries that change linearly over time, with i = 1, 2, 3 representing the youngest, prime adult, and oldest age groups, respectively. $\Phi_D[3]$ is the effect of population density on the oldest age group, $\varphi_L[3]$ is the effect of standard length within the third (oldest) age group, $\varphi_S[3]$ is the effect of season on this age group, and φ_A accounts for the influence of senescence on the oldest individuals. Similarly, for recapture probability p, p_0 is the intercept, p_L is the effect of standard length, p_S is the seasonal effect, and p_R represents the random effect of time, where each of the 145 months in the study period is treated as a separate factor in the model.

Compared to Model 1 with three dynamic age groups, Model 2 had a simpler age structure and fewer parameters, and took less time to run. The functions for predicting φ and p in Model 2 can be summarized as follows:

$$\varphi = \frac{1}{1 + e^{-(\varphi 0 + \varphi D + \varphi L + \varphi S + \varphi T)}}$$

$$p = \frac{1}{1 + e^{-(p0 + pD + pL + pS + pT)}}$$

where, like described above, φ_0 is the intercept for estimating φ, Φ_D is the effect of population density on survival, φ_L is the effect of standard length, φ_S is the effect of season on individuals, and φ_T represents the effect of time since the study began. And for recapture probability p, p_0 is the intercept, p_D is the effect of population density, p_L is the effect of standard length, p_S is the seasonal effect, and p_T represents the effect of time as a continuous numeric variable, capturing the linear temporal trend over the study period.

The HMM model was run through all individuals in the dataset, which in our case includes all individuals of the same sex in the stream over a period of 12 years. Two chains, each with a length of 11,000, were run for each of the HMM models. The first 1,000 iterations were discarded as burn-in, and the remaining 10,000 iterations were collected without thinning. The MCMC algorithm iteratively updates the parameters by sampling from the posterior distribution, with convergence assessed by comparing the two chains. During the iterations, it samples from regions where the model fits the data better more frequently. And best fit parameters are those with the highest posterior probability, occurring most frequently among the collected samples after convergence. The command set.seed() was used for repeatability.

The model output includes the following summary statistics for each parameter: the mean, standard deviation (sd), 2.5% quantile, median (50%), 97.5% quantile, Rhat, and the effective sample size (n.eff). 'Rhat' is the Gelman-Rubin diagnostic, indicating the convergence of the MCMC chains, with values close to 1.0 suggesting good convergence, and values significantly greater than 1.1 suggesting poor convergence and unreliability of the estimate; 'n.eff' is the effective sample size, which measures how much independent information the sample provides, with larger values indicating better reliability in the estimate. An n.eff greater than 500 would be ideal for our complex models, with n.eff smaller than 100 showing poor convergence (Gelman & Hill 2007, Kéry & Kellner 2024). To assess model convergence, we also checked the trace plots and posterior density estimates for the all the parameters of both Model 1 and Model 2 using commands from the NIMBLE package.

Using a similar structure to Model 2, but treating each month as a categorical variable instead of modelling time as a linear effect and excluding the seasonal effect on recapture rate, we built an alternative model to estimate empirical monthly recapture rates. This model was applied to the Lower LaLaja dataset (with the longest observed period of 145 months among the four streams studied) as an example to evaluate how well the estimated recapture rates in Model 1 and Model 2 align with observed data.

Results

Overview of Models

Figure 2 presents the output distribution from both models, using the Caigual females as an example. Outputs for other model subsets are available in Supplementary Material, Table S3.1.

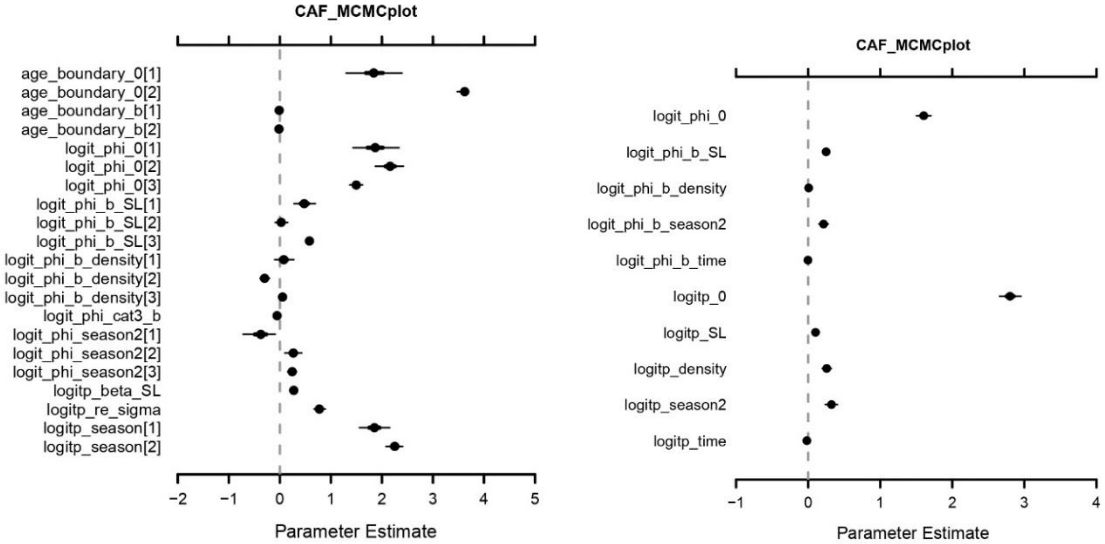


Figure 2. Output distribution of Caigual females from Model 1 (left) and Model 2 (right). The dots show the estimated mean values for each parameter, with horizontal lines representing the 95% credible intervals, and thicker segments indicating the 50% credible intervals. In Model 1, age_boundary_0[i] represents the intercept for age boundary i, age_boundary_b[i] is the slope for the same age boundary, logit_phi_0[i] is the intercept for survival within age group i, logit_phi_b_SL[i] is the effect of standard length on the survival of age group i, logit_phi_b_density[i] is the effect of population density on the survival of age group i, logit_phi_season2[i] is the effect of season two (dry season) on the survival of age

group i, logit_phi_cat3_b is the senescence effect on the survival of age group 3; logitp_beta_SL is the effect of standard length on the recapture rate, logitp_re_sigma is the random effect of time on the recapture rate, and logitp_season[i] is the effect of season i on the recapture rate. In Model 2, logit_phi_0 is the intercept for survival, logit_phi_b_SL is the effect of standard length on survival, logit_phi_b_density is the effect of population density on survival, logit_phi_season2 is the effect of season two (dry season) on survival, logit_phi_b_time is the effect of time on survival; logitp_0 is the intercept for recapture rate, logitp_SL is the effect of standard length on recapture rate, logitp_density is the effect of density on recapture rate, logitp_season2 is the effect of season two on the recapture rate, and logitp_time is the effect of time on recapture rate.

The figures for the first three parameters in both models' trace plots and posterior density estimate plots are shown in Figure 3 below. The left panel of Figure 3 shows an example of convergence issues in Model 1, where the two chains show very poor mixing, aligning with the high Rhat values reported in Table 3 for parameters related to dynamic age boundaries: age_boundary_0[1] (Rhat = 2.15) and age_boundary_b[1] (Rhat = 2.12). Additionally, age_boundary_0[2] exhibits a concerning Rhat = 1.1, indicating that while the two chains mix reasonably well, further diagnostics are needed for credibility. Similar convergence issues were also observed across seven other subsets besides Caigual females, where poor mixing in chains for age boundary-related parameters suggests that further reparameterization adjustments are necessary to ensure reliable model outputs (Supplementary Material, Table S3.2). In contrast, the right side of Figure 3 demonstrates much better mixing and stationarity across chains for logit_phi_0, logit_phi_b_SL, and logit_phi_b_density in Model 2, indicating better convergence and more reliable parameter estimates. Other parameters related to φ and p in Model 2 also exhibit acceptable convergence (Supplementary Material, Table S3.3).

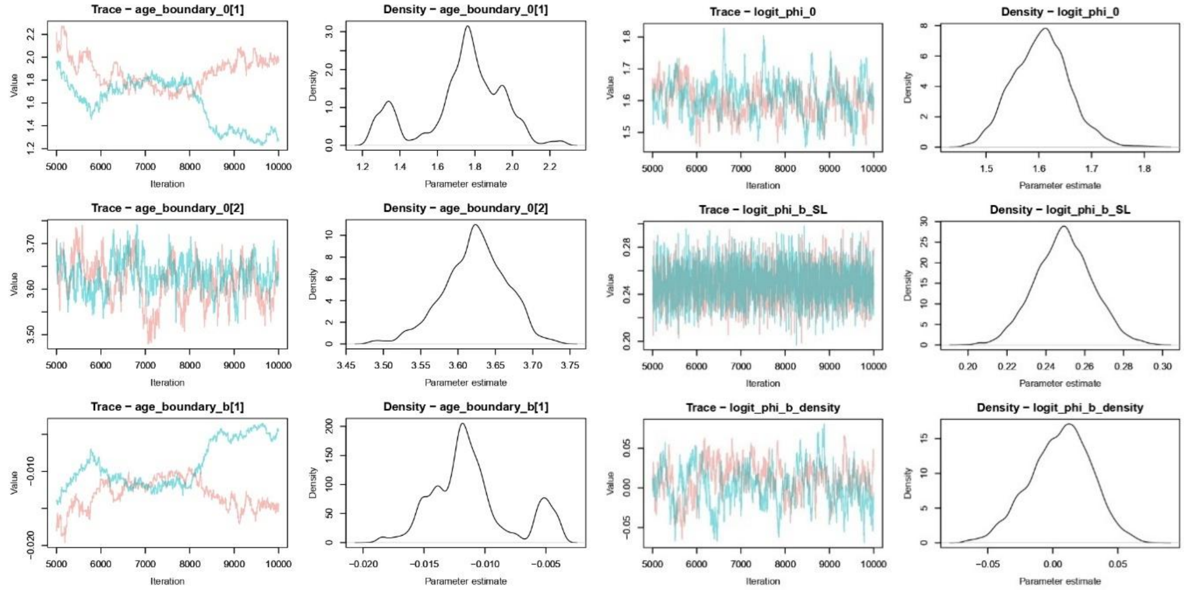


Figure 3. Convergence diagnostics for the first three parameters in two tested MCMC models. Model 1 (left), showing poor convergence between the two chains for parameters age_boundary_0[1], age_boundary_0[2], and age_boundary_b[1]. Model 2 (right), demonstrating good convergence between the two chains for parameters logit_phi_0, logit_phi_b_SL, and logit_phi_b_density. Both subfigures present both trace plots (left) and posterior density estimates (right) for the respective parameters.

Beyond the convergence issues, the estimates for the three dynamic age groups in Model 1 remained uninformative (Table 3). The two baseline (intercept) values for the age boundaries were either too close (e.g., 1.85 and 3.61 months for the Caigual female subset, 4.78 and 4.83 months for the Taylor males) or impractically high (e.g., 72.11 months for Caigual males' second age boundary, 13.71 and 19.00 months for Lower LaLaja females).

The two slopes also did not provide any informative output. After calculating the age boundaries at the end of the study, which spans 145 months, the predicted age boundaries either became too low (e.g., 0.4 and 0.71 for Caigual females) or too high (e.g., 73.56 for the second age boundary for Caigual males).

Table 3. Estimates of parameters in the Mark-Recapture model for defining age structure. age_boundary_0[1] and age_boundary_0[2] represent the baseline estimates for the first and second age boundaries, which together divide the age range from 1 to the maximum age into three categories. age_boundary_b[1] and age_boundary_b[2] are the slopes that estimate how the age boundaries change linearly over time. * indicates that the estimate is not credible with suboptimal n.eff or Rhat values in the original model output (omitted here).

parameter estimate	Caigual		Lower LaLaja		Taylor		Upper LaLaja	
	female	**male**	**female**	**male**	**female**	**male**	**female**	**male**
age_boundary_0[1]	1.85*	2*	13.71*	1.59*	8.37*	4.78*	15.75*	8.45*
age_boundary_0[2]	3.61*	72.11	19*	4.55*	11.41*	4.83*	30.52*	9.82*
age_boundary_b[1]	-0.01*	0*	-0.02*	-0.09*	-0.2*	-0.1*	0.02*	-0.3*
age_boundary_b[2]	-0.02*	0.01	-0.14*	-0.02*	-0.09*	-0.01*	-0.26*	0.02*

Since the baseline estimate of survival φ, as well as the impact of standard length, population density, and season on φ, are all estimated separately for the three age categories in Model 1, and the definition of these age categories has not been successful due to the problematic age boundaries described above, we now refer to Model 2, which does not include age boundaries, for analysing the changing patterns of φ and p during the study period (Supplementary Material, Table S3.3).

Recapture probability patterns

Baseline recapture probability was generally high, ranging from 0.858 (Lower LaLaja males) to 0.953 (Caigual males). These are impressive recapture rates, especially considering the large population size in each stream. The effect of standard length on recapture probability was sex-specific. For females in all four streams, the effect was either zero or near zero. In contrast, for males in all streams, a positive effect was observed, meaning that larger individuals are more likely to be recaptured. Density effects on recapture probability were positive across all streams, aligning with the intuitive assumption that individuals in higher-density areas are more likely to be recaptured. Seasonal effects on recapture probability differed from those on survival. While most populations exhibited higher recapture rates during the dry season, Taylor females showed lower recapture rates, while Upper LaLaja females showed no difference between seasons.

Time effects on recapture probability were modelled differently across the two models: as a random effect in Model 1 and as a linear effect in Model 2 (Table 4). Both models included season as a separate factor in predicting recapture probability, allowing us to focus on how recapture rates might change over the entire 12-year study period, without accounting for annual seasonal fluctuations. In Model 1, where time was treated as a random effect, we see high variability in recapture rates across sampling months. This suggests that recapture probabilities fluctuated unpredictably, possibly due to external factors such as sampling conditions, researcher variation, or temporary environmental changes in the streams.

Table 4. Estimates of time as either a random or linear factor in the Mark-Recapture models for analysing recapture rate (p) across eight sex- and stream-specific datasets, all demonstrating good convergence (Rhat ≤ 1.01, n.eff > 1700).

parameter estimate	**Caigual**		**Lower LaLaja**		**Taylor**		**Upper LaLaja**	
	female	**male**	**female**	**male**	**female**	**male**	**female**	**male**
time (random) in Model 1	0.78	0.99	0.64	0.71	0.85	1.05	0.79	0.97
time (linear) in Model 2	-0.02	-0.02	-0.01	-0.01	-0.02	-0.02	-0.02	-0.02

In Model 2, where time was treated as a linear numeric variable to examine the overall temporal trend, the effects of time were consistently negative (-0.01 to -0.02) across all datasets, indicating a downward trend in recapture probability over time. If we consider the hypothetical average-sized male from Lower LaLaja and Caigual, both with average population density, the male from Lower LaLaja—who has the lowest baseline recapture probability—would have a probability of 0.890 at the beginning of the study and a probability of 0.657 at the end of the study. The male from Caigual, with the highest baseline recapture probability, would have a probability of 0.965 at the first month and a probability of 0.606 at the last month. The estimated monthly recapture rates from Model 2 are shown in Figure 4, alongside the observed monthly recapture rates of the Lower LaLaja population for comparison. Season had the strongest influence on male recapture rates in Caigual, particularly as recapture rates declined over time. In seven of the subsets, recapture rates were higher during the dry season, likely due to reduced flooding and improved sampling conditions. An exception was observed in Taylor females, which showed the opposite pattern. No seasonal effect was detected in the Upper LaLaja female population.

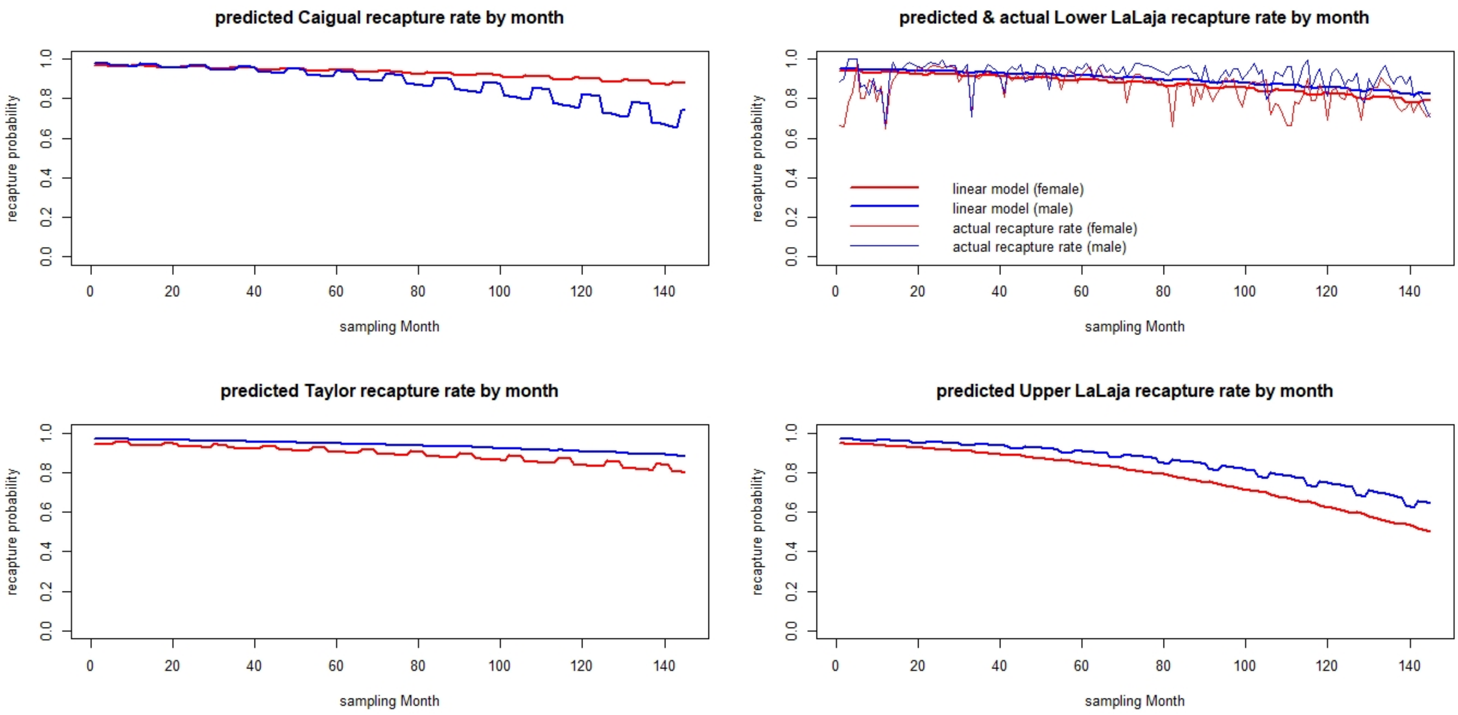


Figure 4. Estimated monthly recapture rates from Model 2 across the four streams, along with observed monthly recapture rates in the Lower LaLaja population. Blue lines represent males, and red lines represent females. Thick lines correspond to Model 2, where time is modelled as a continuous linear effect, while thin lines show the empirical monthly recapture rates in Lower LaLaja, estimated using a model where each sampling month is treated as an

independent categorical variable. Both models use a hypothetical average-sized individual from an average population density, ignoring the impact of seasons and focusing solely on the effect of time on recapture rates.

Survival patterns

The baseline survival rate varied across datasets but consistently showed higher estimates for females than for males in all four streams. This sex-based difference in mortality aligns with previous studies on guppies, where females generally live longer than their male counterparts.

The effect of standard length on survival also exhibited a sexually dimorphic pattern. For females in all streams, the effect was positive, suggesting that larger individuals may have higher survival. However, for males, the effect was slightly negative or near zero across all models, indicating that size does not influence male survival in the same way.

Density dependence in survival varied across models, with no consistent pattern. In Caigual and Upper LaLaja streams, population density positively affected survival. In contrast, in Taylor, increased density was associated with lower survival, likely due to competition or resource limitation. While in Lower LaLaja, the effect of density was sex-specific, being positive for females but negative for males.

The effects of the dry season on survival were consistently positive across all datasets. This finding aligns with expectations, as the definition of seasons were based on prior analyses of monthly population survival rates. Stronger seasonal effects were observed in Taylor and Upper LaLaja streams, while weaker effects are detected in Caigual and Lower LaLaja populations.

After accounting for all the factors above, there was no apparent effect of time on survival in any dataset. This suggests that survival probabilities have remained stable over the study period, with no significant temporal trends.

Discussion

We used two Mark-Recapture models with different parameters to estimate monthly survival and recapture rates, as well as to examine the impact of various factors on these estimates. We aimed to assess temporal trends in age structure, for which we introduced two linearly changing age boundaries for survival function in Model 1, applied to each of our eight sex- and stream-specific datasets. This approach provided a more nuanced view of age structure than the simple population-level analysis performed in Chapter 2. However, issues were identified during the convergence diagnostics of Model 1, specifically with the dynamic age boundaries. Poor mixing between the two MCMC chains was evident across all eight subsets, indicating that the chains were not adequately exploring the parameter space.

Our Model 2, which does not incorporate age structure but instead uses standard length to examine how growth and aging may influence survival, demonstrated more stable convergence diagnostics and produced more reliable estimates of survival and recapture rates. The survival estimates from Model 2 revealed interesting sex-based and stream-specific differences. The baseline survival rate consistently showed higher values for females than for males, which aligns with the well-established sexually dimorphic pattern in the *Poeciliidae* family (Dawes 1991, Evans *et al.* 2011).

The effect of standard length on survival was also sexually dimorphic. For females, larger individuals had higher survival probabilities, while for males, this effect was weaker or even negative, suggesting that size may not play as important a role in male survival. This finding may be related to sex-specific life-history strategies, where larger males might face trade-offs between growth and survival, such as increased predation risk or energy expenditure in reproductive efforts (Abrahams 1993, Mahmud-Al-Hasan *et al.* 2004).

Population density effects on survival varied across streams, potentially reflecting differences in resource abundance and inter-species competition in the streams. Seasonal effects on survival were consistent across all streams, aligning with previous studies on Trinidadian guppies that found the local wet season negatively impacts guppy survival (Zandonà *et al.* 2017).

One interesting finding, particularly when compared to the results in Chapter 2, is that no significant temporal trend in survival was observed in any population, suggesting that survival rates remained relatively stable throughout the study period. In contrast, Chapter 2's linear models at the population level revealed that most populations (except for the entire TY population and UL males) exhibited a decreasing survival pattern over time, which contradicts the findings of previous common garden experiments (Burns *et al.* 2009, Bassar *et al.* 2010). The mark–recapture analysis therefore does not provide direct evidence for life-history evolution within these streams but instead highlights the potential influence of environmental or sampling effects on apparent survival trends. The lack of detectable life history evolution in the streams, despite its occurrence in experimental settings, is noteworthy and warrants further investigation.

The baseline recapture rates were generally high across all streams, especially for males in Caigual, which had a recapture probability of 0.953. The effect of standard length on recapture probability was sex-specific. For females, the effect was negligible, while for males, larger individuals had a higher likelihood of being recaptured. This could be due to differences in behaviour, with larger males possibly engaging more in territorial defence and courting behaviours (Brown *et al.* 2009, Katwaroo-Andersen *et al.* 2016). Density dependence in recapture probability was positive across all streams, supporting the intuitive expectation that higher density leads to easier detection and higher probability of capture. Seasonal effects on recapture probability were mixed, with most streams exhibiting a pattern similar to that observed for survival, but Taylor females showed a negative effect, and Upper LaLaja females showed a negligible effect.

We incorporated time differently into our two models to assess whether variations in recapture probabilities across months were random or exhibited a temporal trend. In Model 1, where time was treated as a random effect, high variability in recapture rates across sampling months was detected. This variability could reflect short-term fluctuations in recapture rates due to external factors such as sampling conditions, researcher variation, or temporary environmental changes in the stream. Model 2 treated time as a linear numeric variable and revealed a consistent negative trend in recapture probability over the 12-year study period across all four streams. This decline in recapture rate was not apparent when examining raw capture counts, as the overall population sizes remain large and all streams exhibit increasing population trends with annual fluctuations. However, the decreasing recapture rates over time could lead to an underestimation of survival if undetected guppies are mistakenly considered dead, potentially explaining the declining survival trend observed in Chapter 2.

The observed decline in recapture probability was unexpected, and therefore it is important to consider possible explanations for this pattern. The declining trend in recapture rate over the 12-year study period could reflect within-individual behavioural change, where guppies that have previously been captured become more cautious or learn to avoid traps, as observed in other fish species. Willow warblers with previous capture experience took longer to respond to lures (Linhart *et al.* 2012). Similarly, cliff swallows learned to avoid trapping nets during a 20-year mark-recapture study (Roche *et al.* 2013). In fish, the recapture rate of rainbow trout dropped sharply within a week when exposed to repeated angling (Askey *et al.* 2006). Such behavioural avoidance would reduce the likelihood of recapturing the same individuals, leading to an apparent decrease in lifespan and survival rate, as individuals are missing from the observed dataset, without implying any true demographic change.

Alternatively, the decline could represent between-individual or cohort-level differences, where successive generations have become generally less catchable, possibly due to selection favouring individuals that are more wary of human activity. This explanation would suggest an evolutionary or long-term behavioural shift in response to repeated sampling pressure. However, distinguishing such adaptation from environmental or methodological effects requires genetic or pedigree data demonstrating heritable variation in capture probability (Hadfield *et al.* 2011). The impact of such a shift on survival remains unknown, as it is unclear how the development of human-avoidance behaviours might influence those life-history traits of our interest. Similar declines in recapture probability have been observed in previous studies on other species and have been a common problem for conducting long-term mark-recapture studies. For example, cliff swallows became progressively less likely to be captured over the course of a 20-year mark–recapture study (Roche *et al.* 2013).

Distinguishing between these two mechanisms would require analyses that partition variation in recapture probability within and between individuals, potentially through random-effects models (Zheng *et al.* 2007). Such analyses would clarify whether the observed decline reflects behavioural plasticity, environmental change, or genetic adaptation. Separating within- and between-individual variation in recapture probability would also help determine whether changes in catchability are behavioural responses or reflect broader population-level shifts, further improving the interpretability of our survival estimates. Furthermore, understanding the underlying mechanism has more direct implications: if the decline arises primarily from behavioural avoidance, methodological adjustments could quickly restore recapture efficiency, whereas if it reflects longer-term evolutionary change, mitigation would require more sustained adaptation of field protocols. Either outcome highlights the need for measures to be taken to restore and maintain high recapture efficiency in our ongoing mark–recapture systems.

One common recommendation to improve recapture rates is switching to observation methods with less human contact. However, wild horses, for example, still tend to avoid detection when helicopter photography is used repeatedly each year (Vernes *et al.* 2009). Because guppies are small and live in aquatic environments, alternative tracking methods such as camera traps or non-invasive tagging are not practical. Potential ways to increase recapture rates include increasing the number of researchers, improving the equipment used, and utilizing lures.

Fitting a Bayesian model to the large dataset we have presents significant challenges, primarily due to the computational complexity and the volume of data involved. Given that this has never been done before for a dataset of this size, we had to develop our own code to run the models. The models are extremely time-consuming to run, and various other combinations of factors were also tested to assess their impact on survival and recapture probability. These additional combinations either led to similar conclusions or failed to provide further insights, and as such, are not reported in this chapter. The attempt to incorporate a dynamic age structure remains an important aspect of this research, though it did not yield successful results. It reflects the innovative approach of the study, exploring the evolution of life history strategies, while also acknowledging the limitations inherent in large-scale, data-intensive analyses.

In conclusion, our Model 2, which does not rely on dynamic age boundaries, provides more reliable estimates of survival and recapture rates, revealing important patterns related to sex, stream, and environmental factors. These patterns highlight the complexity of ecological interactions and suggest that both intrinsic (e.g., sex-specific survival strategies) and extrinsic (e.g., population density, seasonal variation) factors influence population dynamics. The observed temporal decline in recapture probability is best viewed as a signal that detection processes themselves may change through time, potentially biasing population-level inferences. While this could indicate behavioural adaptation, the current data cannot distinguish that possibility from environmental or methodological explanations. Future research should incorporate additional covariates to enhance model fit and account for variations in recapture probability. Integrating individual-based capture histories or genetic data would allow stronger inference about whether observed behavioural shifts have an evolutionary basis. We also need to consider improving the capture methods for the guppy system to ensure more reliable data sources and more credible model analyses.

Chapter 4

Determinate or Indeterminate? Describing the Growth of Trinidadian Guppies with Models Incorporating Intrinsic and Extrinsic Factors

Abstract

This study investigates the life history traits of Trinidadian guppies (*Poecilia reticulata*) in wild streams, focusing on monthly growth rates and lifetime growth trajectories of individuals, to complement the extensively studied common garden data collected from this species. We examine whether evolutionary changes observed in common garden experiments, including greater adult body size and slower growth rates in predator-free environments under controlled lab conditions, can be detected in the wild, or whether these evolutionary trends are masked by environmental variation, resulting in cryptic evolution in natural settings. Using long-term body length data from four Trinidadian streams, we apply several growth models - von Bertalanffy, Weibull, Gompertz, logistic, and two-phase models - to describe the growth trajectories of male and female guppies. The results show that Trinidadian guppies exhibit sexual dimorphism in growth trajectories, with males displaying determinate growth and ceasing to increase in body length at later life stages, while females continue to grow, reach larger body sizes, and follow an indeterminate growth pattern. We conclude that evolutionary trends observed in common garden settings are less evident in natural populations likely due to the confounding effects of environmental factors, suggesting cryptic evolution is occurring in the streams. Our findings provide valuable insights into the challenges of studying evolution in wild populations and emphasize the role of environmental variation in shaping life history traits.

Introduction

All species on Earth face complex trade-offs that can induce stress responses. Factors that can create these trade-offs include climate change over geological and contemporary time periods (Wing & Dimichele 1995, Millien *et al.* 2006, Barnosky & Kraatz 2007, Sievers *et al.* 2007, Wang *et al.* 2019, Wilson *et al.* 2020), habitat loss and fragmentation (Herrera *et al.* 2011, Ito *et al.* 2013), introduction of invasive species, outbreaks of novel infectious diseases (Sakai *et al.* 2001, Rahel *et al.* 2008, Afelt *et al.* 2018), production and accumulation of toxic chemicals (Berny 2007, Reid *et al.* 2016), and other unforeseen events (Wingfield & Romero 2015). Some of these environmental changes can occur dynamically and can result in rapid microevolution. Body size and growth rate are often studied as key life-history traits that respond to these environmental pressures (Teplitsky & Millien 2014), as they can directly influence individual survival, reproduction, and overall fitness. Many studies have found that body size and growth rate can evolve rapidly as adaptive responses to changing environmental conditions (Handelsman *et al.* 2013, Kvalnes *et al.* 2017), as well as gradually over time as populations experience sustained environmental shifts (Hussey *et al.* 2009, Mundinger *et al.* 2021).

Over time (i.e., across generations), species adapt to environmental changes through evolution, which occurs via shifts in allele frequencies and, in some cases, is also observable at the phenotypic level (Fox *et al.* 2019). To quantify these selection pressures that drive evolution, researchers conduct genetic sequencing and phenotypic studies in the lab where the environment can be controlled. However, when wild populations evolve, as they adapt, they often modify their environment, via, among other mechanisms, changes in population size and density. Such changes triggered by adaptation can mask signatures of phenotypic evolution via phenotypic plasticity, leading to the occurrence of cryptic evolution defined as genetic change in the absence of phenotypic change.

According to his fundamental theorem, Fisher proposed that evolution can result in environmental deterioration for a species (Fisher 1958). Such deterioration can impact development of traits, masking evolution at the level of the population – so called cryptic evolution. Evidence of cryptic evolution has been documented in wild bird populations, including the collared flycatchers (*Ficedula albicollis*) on the island of Gotland (Merilä *et al.* 2001) and the great tits (*Parus major*) in Oxford's Wytham Woods (Garant *et al.* 2004). Consistent positive selection for increased body mass at fledging has been detected on a genetic level for both species, but a contrasting evolutionary trend toward decreasing body mass was observed in wild nestlings. However, this approach was subsequently criticised by casting doubt on whether the trends were real rather than a statistical artefact (Hadfield *et al.* 2011).

A potential solution to obtaining more robust evidence of genetic evolution lies in common garden experiments seeded with individuals from evolving wild populations. The common garden experiment presents a controlled environment where individuals from distinct populations are raised under identical conditions, effectively disentangling any interplay between genetics and environment (de Villemereuil *et al.* 2016, Patterson *et al.* 2019). It offers the advantage of isolating genetic factors as the primary drivers of observed changes. Researchers can confidently attribute observed differences in traits solely to genetic differences, as the controlled environment eliminates the potential influence of varying ecological conditions on phenotypic expression (Bassar *et al.* 2010).

One driver of phenotypic change that can be factored out using a common garden experiment is population density. In wild populations, population density can be altered by evolution, as observed in a wide variety of species including bacteria (Hiltunen & Becks 2014), green peach aphid (Turcotte *et al*. 2013), hare (Sinclair *et al.* 2003), Soay sheep

(Wilson *et al.* 2007), and Trinidadian killifish (Reznick & Endler 1982, Walsh & Reznick 2008).

Apart from the killifish, another small fish species - the guppy (*Poecilia reticulata*) - also inhabits the streams of Trinidad. The guppy belongs to the family *Poeciliidae*, which exhibits sexual dimorphism in body length growth patterns. Males in the *Poeciliidae* family typically show determinate growth, ceasing to grow after reaching sexual maturity, whereas females exhibit indeterminate growth, allowing them to continue growing, ultimately attaining a larger body size (Evans *et al.* 2011). Trinidadian guppies are naturally found in two distinct ecotypes characterised by high and low-predation (Reznick & Endler 1982). Population density of guppies living in low-predation streams with no large predatory fish is higher than for guppies living in high-predation environments (Bassar *et al.* 2010). Comparative studies of wild Trinidadian guppy populations inhabiting low-predation and high-predation streams have revealed distinct variation in life history and phenotypic traits (Reznick & Endler 1982). One of the remarkable advantages of the guppy system is the possibility of conducting common garden experiments. Through common garden experiments, researchers have been able to draw insightful comparisons between guppies introduced into low-predation streams and their counterparts residing in high-predation habitats (Bassar *et al.* 2010). Under laboratory conditions with ample food and a stable environment, guppies from high-predation localities exhibit significantly faster growth rates and reach sexual maturity earlier and at a smaller body size compared to guppies from low-predation areas (Reznick 1982). Analysis has shown that male guppies repeatedly evolve towards a later age and larger size at sexual maturity when introduced into low-predation streams, with a consistent 2-3-year lag between the guppy introduction and the end of their evolutionary journey (Arendt & Reznick 2005, Reznick *et al.* 2019).

Unlike common gardens with constant food supply and little disturbance, freshwater streams in Trinidad experience environmental variation and a harsher environment than the lab (van der Zee *et al.* 2022). A key question that arises is whether the same growth patterns observed under lab conditions can be detected in natural populations, where population density may gradually be changing as evolution proceeds. With long-term monthly census data collected from the same streams that were used for common garden experiments, it is possible to determine if evolution toward larger body size and slower growth rate is obscured by counteracting effects of changing population density and other environmental factors. If evidence of genetic evolution is detected in common garden experiments, but cannot be detected in the wild, it could provide compelling evidence for cryptic evolution.

Various growth models have been employed to describe individual growth patterns in bony fish, including von Bertalanffy models, logistic models, Gompertz models, and two-phase models (Lobón-Cerviá & Mortensen 2006, Koya & Goshu 2013). For our study, we built growth models to explore how body length changes with age in wild guppy populations. We compare different growth models including von Bertalanffy, Gompertz, logistic, Weibull, and two-phase growth models. We select the best-fitting models—the Weibull growth model for males and the two-phase growth model for females—to describe the determinate growth pattern in male guppies and the indeterminate growth pattern in females, respectively, while also assessing environmental influences and temporal trends over the 12-year study period (Arendt & Reznick 2005).

We hypothesize that, after correcting for the masking effects of environmental factors, our growth models will reveal a significant temporal trend on guppies' growth consistent with patterns reported from common garden experiments. We construct sex- and stream-specific models and assess the influence of population density and season on the observed guppy growth patterns. We anticipate that the increasing population density and the wet season (characterized by increased flooding) will obscure the detection of shifts in individual growth patterns. We also hypothesize that, after accounting for the counteracting effects of external factors, an evolutionary trend similar to that observed in common garden experiments can be detected, where growth rates slow down and both sexes gradually evolve toward a larger body size over the 12-year course.

Methods

We parameterised age-specific growth models including temporal environmental changes and shifts in population density. We put population density and seasonal factors into our models to access how they mask the detection of evolutionary trends regarding growth patterns. It was anticipated that a notable impact of the elapsed time since introduction should be observed after correcting for the impact of extrinsic masking variables. Through this approach, we aimed to discern the effect of evolution of the population's growth trajectories.

Study species and study area

We selected guppies (*Poecilia reticulata*) from four natural streams in northern Trinidad for our study. These small freshwater fish exhibit distinct sexually dimorphic traits, with males being smaller with brighter colour patterns than females (Endler 1980). There is also significant difference in the growth trajectories of male and female guppies (Reznick and Endler 1982).

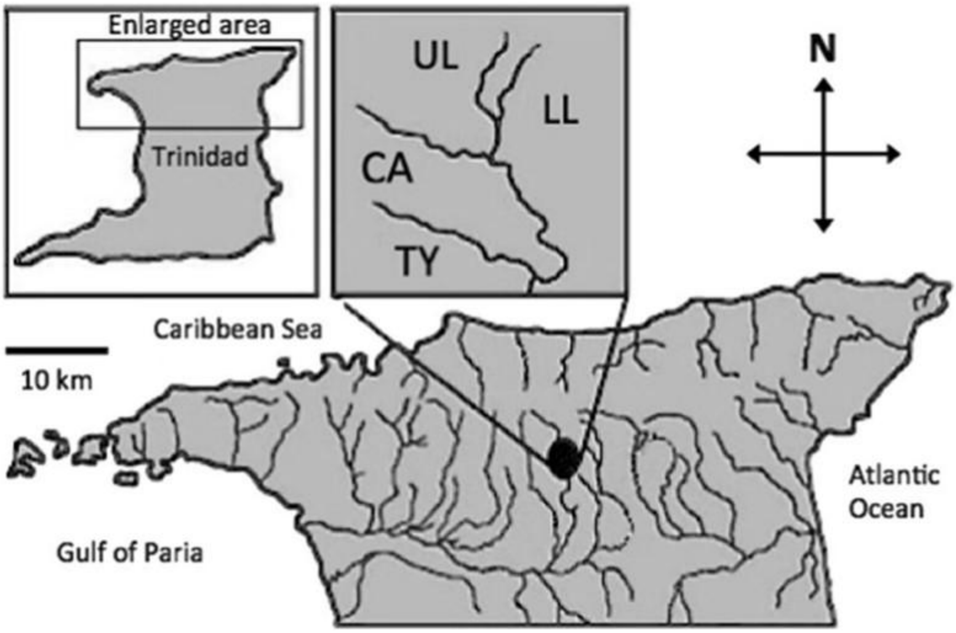


Figure 1. Map of the study streams in the Northern Range of Trinidad, with names marked (Bassar 2021). CA represents Caigual, LL represents Lower La Laja, TY represents Taylor, and UL represents Upper La Laja.

The four freshwater streams we focused on are: Caigual (CA), Lower LaLaja (LL), Taylor (TY), and Upper LaLaja (UL) located in the Northern Range of Trinidad as shown in Figure 1. Prior to the introductions, neither guppies nor their two main predators—the pike cichlid and the wolf fish—were present in these streams. Taylor and Upper LaLaja have artificially thinned tree canopies to increase primary productivity, while Caigual and Lower LaLaja have intact canopies for comparison. In the absence of predators, food availability is the main limiting factor for population size. Additionally, all four streams experience flooding events due to seasonal variations in rainfall, which can significantly affect population size, and short food availability, of guppy populations.

We bred guppies with high-predation genotypes and phenotypes using a design to maximize genetic diversity before introducing them into each stream (Zee *et al.* 2022). In March 2008, we conducted paired introductions in LL and UL by introducing 38 pregnant females and 38 males into each stream. Then in March 2009, we introduced 64 pregnant females and 64 males into CA, and 52 pregnant females and 52 males into TY. All four streams have waterfalls at both ends, serving as natural barriers to reduce the number of emigrants.

Data collection and preparation

We conducted monthly capture-mark-recapture using butterfly nets in all four streams to generate individual growth records for large numbers of fish (Croft *et al.* 2003). Effort was made to make sure that most individuals in the population were captured when we conduct each census. The monthly recapture ceased in March 2020 due to COVID-19 pandemic, and that is when our data records end.

Every individual with a standard length measurement of 14mm or greater was marked with coloured elastomer on first capture. To avoid the potential of serious injury or death, we did not mark guppies below 14mm, a size usually attained in the first month of life. We used 12 different colours and eight marking locations on each guppy to identify all the thousands of individuals in the population. For every marked individual, we identified the sex by checking for the presence or absence of a long gonopodium, a specialized fin used by males for reproduction. We also weighed each individual using a digital scale, recording the weight in grams to three decimal places. All data were then saved in a .csv text file. After processing, the fish was released back to the same location in the stream of its capture.

To minimize anaesthesia time, each captured guppy was photographed alongside a ruler, and body length was later extracted from the image, rather than measured directly during anaesthesia. There are several different methods for measuring fish body length (Önsoy *et al.* 2011). Due to the potential for tail damage and the difficulty of distinguishing the semi-transparent tail against the pale background used in this study, we chose standard length, which is measured from the furthest point of the jaw to the furthest point of the hypural bone, as our primary measurement (Howe 2002). We measured the distance between the front of the mouth to the end of the caudal peduncle. The distance (measured in mm, rounded to two decimal places) was recorded as the individual's standard length and was stored in a database with additional information about each capture. It is worth noting that standard length was manually recorded each month during the first half of the study. To improve consistency and accuracy in measurements, an AI algorithm was developed and implemented to obtain standard length data for all captures starting from June 2012 to the end of the study period. A dual semantic segmentation deep learning approach (UNet and UNet-Transformer) was developed to identify guppy body parts and extract standard length measurements. The models were trained using three sets of human annotations on 333 randomly selected sample images from across the study period. Model outputs were compared against human measurements, showing high agreement and smaller deviations than the observed inter-observer variability. This suggests that the AI-based measurements provide more consistent and accurate standard length data for growth modelling. The development and implementation of this AI approach are detailed in the Introduction and are not repeated here.

The guppy database we used contained 463,080 records of capture data across twelve years, and seventeen columns with information about each capture. Eleven columns were used for building our growth models: 'stream', 'sampling occasion', 'individual ID', 'sampling year', 'sampling month', 'standard length', 'weight', 'sex', 'population density', 'female density', and 'male density'. The 'stream' column contains abbreviated names of the streams where each capture occurred (UL, LL, CA, and TY, corresponding to the four streams studied). 'Sampling occasion' represents the sequential count of months since the study began in March 2008, ranging from 1 to 145 (March 2020). 'Individual ID' is a unique numerical identifier for each individual throughout the 12-year study, with 98213 different IDs recorded in total. 'Sampling year' (ranging from 1 to 13) and 'sampling month' (ranging from 1 to 12, corresponding to January to December) show the year and month of each capture. ‘Standard length’ and ‘weight’ refer to the body length and body weight of an individual at each capture, measured and recorded as described above. The ‘sex’ column contains either F (female) or M (male). ‘Population density’, ‘female density’, and ‘male density’ contain the total and sex-specific population densities for each month, calculated as the number of individuals divided by the estimated volume of each stream.

Prior to building the growth models, we checked and processed the raw data. There were 254 duplicate records where the same individual was marked twice in the same month that were deleted from the database. Furthermore, 71 individuals with no recorded sex were removed to avoid ambiguity. Finally, we removed 536 rows that were found again after not being captured for five or more consecutive months. Such reappearances are probably due to two different individuals with similar marks mistakenly being identified as one. We also removed outliers with extreme body length records (>100.00mm and <10.00mm) as these are likely data entry errors.

Next, the value of monthly body size growth (measured in mm) for each month was calculated in an individual’s lifetime. These monthly records were calculated as below, and were recorded as NA when there is no standard length data in the previous month, such as for the month of an individual’s first capture. We also calculated the monthly body length growth rate (measured in decimals) for each month in an individual’s lifetime. Formulas for calculating body length monthly growth and growth rate are shown below. Body size at time t is denoted as z_t, growth in body size at time t is denoted as Δz_t, and body size growth rate at time t is denoted as r_t.

$$\Delta z_t = z_t - z_{t-1}$$

$$r_t = \Delta z_t / z_{t-1}$$

Stream-specific population density of each month was calculated by dividing the number of individuals within the stream by the stream volume, which was obtained from morphology measurements (Gregory 1977, Wohl 2010). We also calculated sex-specific population density for females and males separately to determine whether this approach better reflects the stress that guppies are experiencing.

In addition to population density, we also considered ‘season’ as a two-level categorical variable in our model. In Trinidad, there are distinct dry season and wet seasons, marked by significant differences in flooding occurrences. This variation directly influences the accessibility of food resources and thus the growth rates among wild guppy populations (Fitzpatrick *et al.* 2014) with it being lower in the wet season. To explore seasonal variation, we tested all possible ways to divide these 12 months into two seasons by checking how monthly effects differ on population growth rates. We incorporated sampling month as a factor into a generalized linear model for each sex- and stream-specific subset to assess how monthly growth estimates systematically vary across months. We then tested all possible seasonal divisions of the 12 months and applied the Akaike Information Criterion (AIC) to identify the best-fitting seasonal split. Models with the lowest AIC were selected as the optimal categorization for ‘season’ (Auger-Méthé *et al.* 2021). In this way, we identified two distinct seasons: one with higher monthly growth rates, corresponding roughly to the local dry season, and another with slower monthly growths, corresponding to the local wet season (Table 1).

Table 1. Optimal seasons for building Mark-Recapture models. Months 1-12 (January - December) in one calendar year are divided into two seasons for each sex- and stream-specific dataset. Season one is defined as the months with higher monthly growth rates and generally corresponds to the dry season in Trinidad. Season two includes the months with lower monthly growth rates and aligns roughly with the local wet season.

population	season one	season two
Caigual females	2-9	10-1
Caigual males	2-9	10-1
Lower LaLaja females	1-9	10-12
Lower LaLaja males	12-6	7-11
Taylor females	3-4	5-2
Taylor males	1-6	7-12
Upper LaLaja females	3-6	7-2
Upper LaLaja males	1-7	8-12

Model selection and fitting

Before fitting statistical models, we checked the distribution of standard length data and also monthly growth data in all four streams for extreme values. Previous analysis in our study has shown that guppy populations in the four streams differ in their rates of adaptation to the predator-free environment, and our data showed that females and males have significantly different body length trajectories, so we split out data into eight sex- and stream-specific subsets here to perform different modelling analysis on different populations.

We checked the age records for both sexes in each stream separately, and a group of roughly 30 longest-lived individuals for each subset was selected. Then line graphs of standard length against individual age for these top survivors were plotted to check the growth patterns of males and females in different populations. To take short-lived individuals into consideration, rather than only focusing on a small proportion of our data, we also plotted the age-specific distribution of standard length for all the individuals in each stream.

After determining the determinate growth pattern in male guppies and indeterminate growth pattern in female guppies, we built von Bertalanffy, Gompertz (Oliveira *et al.* 2019), logistic (Hernandez-Llamas & Ratkowsky 2004), and Weibull (Schnute & Richards 1990, Mondal 2007, Swintek *et al.* 2019) growth models for each subset and selected the best-fitting model. Besides these four asymptotic functions, we also fit two-phase model in our analysis, which is capable of expressing non-asymptotic growth curves. The functions of all models used are listed below in Table 2. The von Bertalanffy model, Gompertz model, logistic model, and Weibull model all describe asymptotic growth and share a similar functional structure, with a theoretical maximum length that cannot be reached. In the von Bertalanffy model, the growth rate decreases with age, while in the Gompertz and logistic models, the growth rate initially increases and then slows down after reaching an inflection point where the maximum growth rate occurs. The shape of the Weibull growth curve is determined by a shape parameter (denoted as 'α' in Table 2).

Traditionally, the von Bertalanffy method is the most commonly used body length growth model for fish (von Bertalanffy 1957, Flinn & Midway 2021). It is based on a simple assumption that energy intake is proportionate to an individual's body surface, while energy consumption is proportionate to its volume. There are several different ways of defining a von Bertalanffy growth model. One way is to include three growth parameters in the model: L_{inf}, K, and t_0 (Table 2). L is body length at certain age. L_{inf} is the asymptotic length, which is the theoretical maximum length the animal can never reach but will get infinitely close to. K is the growth coefficient and describes how quickly the maximum length can be 'reached'. A third growth parameter (t_0) is used to determine the shape of the growth curve. It is the theoretical age at which the animal would be at zero length at the very beginning of its hypothetical growth.

Table 2. Functions of all models (von Bertalanffy growth model, Gompertz model, logistic model, Weibull model, and two-phase growth model) and the parameters included in each model.

Model	Function	Parameters
von Bertalanffy model	$L = Linf \times (1 - e^{-K(age-t0)})$	L_{inf}: asymptotic length K: growth coefficient t_0: theoretical age at zero length
Gompertz model	$L = Linf \times e^{-e^{-K(age-t1)}}$	L_{inf}: asymptotic length K: growth coefficient t_1: inflection point with maximum growth rate
logistic model	$L = \frac{Linf}{1 + e^{-K(age-t1)}}$	L_{inf}: asymptotic length K: growth coefficient t_1: inflection point with maximum growth rate
Weibull model	$L = Linf \times (1 - e^{-(K \times age)^{\alpha}})$	L_{inf}: asymptotic length K: growth coefficient

		α: function curve shape parameter
two-phase model	Phase one (von Bertalanffy): $L = Linf \times (1 - e^{-K(age-t0)})$ Phase two (linear): $L = L_1 + b(age\text{-}t_2)$	L_{inf}: asymptotic length in phase one K: growth coefficient in phase one t_0: theoretical age at zero length in phase one L_1: length at the threshold point t_2: age at the threshold point b: slope of the linear growth in phase two

Two-phase models can be used to describe the growth trajectories for organisms that continue growing after reaching sexual maturation (Lobón-Cerviá & Mortensen 2006). The model divides a growth trajectory into two distinct phases, each characterized by its own growth rate (Araya & Cubillos 2006). The distinctiveness of this growth model lies in its incorporation of a threshold age. Individual growth rate changes after the threshold age, indicating a potential shift in intrinsic metabolic factors. We selected the von Bertalanffy growth model for the first phase and a linear growth model for the second phase in our two-phase models, based on the observed age-specific growth patterns of the populations.

All modelling was conducted in R (version 4.1.1). Package ‘FSA’ was used for building von Bertalanffy models (Ogle *et al.* 2023). Package ‘segmented’ was used for building two-phase linear regression growth model (Muggeo 2023). Package ‘minpack.lm’ was used for nonlinear least squares fitting when building the two-phase growth models and for incorporating environmental factors into von Bertalanffy model predictions (Elzhov *et al.* 2016). The two-phase growth models and von Bertalanffy models incorporating environmental covariates were run with 1000 iterations due to the model complexity. We wrote the functions for the Gompertz, logistic, and Weibull models, and package ‘nls.multstart’ was used to find the best-fitting parameter values for these models (Szabelska *et al.* 2010, Rao *et al.* 2010, Ritz *et al.* 2016). Gompertz, logistic, and Weibull models were run with 500 iterations to obtain stable parameter estimates. Eight sex- and stream-specific models were built and compared to study effects of sexual dimorphism and environmental factors on guppy growth. For all models, initial values were first estimated from preliminary runs and then refined in subsequent runs to improve convergence and enhance parameter accuracy.

A goodness of fit analysis was performed on all models using Akaike Information Criterion (AIC), which is a reliable method for comparing models based on their relative fit to the data when using the same dataset across several models. We also assessed how well the predicted growth curves aligned with the actual growth trajectories. For each subset, all body length records collected, as well as an average standard length-by-age, were plotted in scatterplots and compared to the predicted standard length growth curves. After comparing the outputs of the different models, we selected the Weibull model for further analysis of female growth and extrinsic factors, and the von Bertalanffy model for males. Although the Weibull growth model yielded the best fit for both sexes, we used the von Bertalanffy model to males for two key reasons. First, the improvement in fit provided by the Weibull model for males was marginal relative to other models. Second, unlike the von Bertalanffy model, which includes three biologically interpretable parameters, the Weibull model introduces the shape parameter α, which influences the entire curvature of the growth trajectory in a nonlinear manner.

To bring environmental factors into the models, we used Weibull and von Bertalanffy functions defined above and added: *i*) either population density or sex-specific density, and *ii*) ‘season’ defined as above into the best-fitting models, and then *iii*) time since the beginning of the study introduced as a continuous variable. These covariates were added to examine how body length growth rates have evolved over time across the four streams.

Building on the basic Weibull model and von Bertalanffy model, we incorporated the effects of population density (D), seasonal impact (S), and elapsed time of study (E) by allowing both the asymptotic length (L_{inf}) and the growth coefficient (K) to vary as linear functions of these factors. This adjustment enables the model to account for density-dependent growth constraints and seasonal variations in growth rates. The modified Weibull growth model for female was defined as follow:

$$L = Linf\ (D,S,E) \times (1 - e^{-(K(D,S,E)\times age)^{\alpha}})$$

And the modified von Bertalanffy growth model for male was defined as follow:

$$L = Linf(D,S,E) \times (1 - e^{-K(D,S,E)\times(age-t0)})$$

where both K and L_{inf} are linear functions of K_0 or L_{inf0}, population density, seasonal impact, and time since the beginning of the study:

$$K(D,S,E) = K0 + d1 \times D + \mathrm{s}1 \times S + \mathrm{e}1 \times E$$
$$Linf(D,S,E) = Linf0 + \mathrm{d}2 \times D + \mathrm{s}2 \times S + \mathrm{e}2 \times E$$

Results

Distribution of body length data and growth patterns across four streams

To check how standard length changes with age, a dot plot was created for all individuals captured during the study period (Figure 2). Most standard length records for male guppies were distributed between 14-22mm, and most standard length records for females were distributed between 14-32mm. Females generally reached a longer length, consistent with findings from previous studies. Age-specific standard length varied among individuals, with the difference between the longest and shortest individuals reaching over 10 mm.

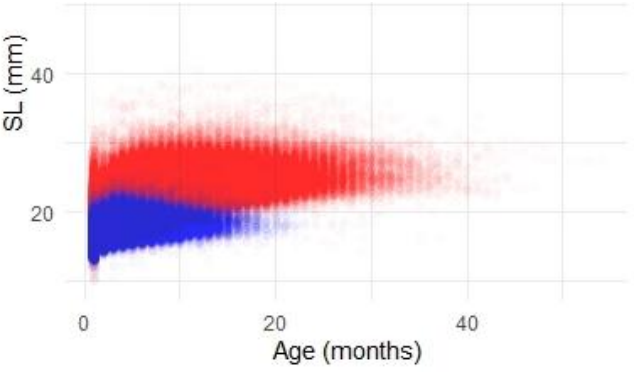


Figure 2. Age-SL dot plot for all individuals captured during the study period, with red representing females and blue representing males. Darker-coloured dots represent higher numbers of individuals.

Figure 3a shows the distribution of all the body length growth data collected across four streams. Extreme negative growth values are likely the result of measurement errors in standard length, while extreme positive values may indicate a significant time gap between two captures, potentially due to missed captures or a typo. Notably, approximately 25% of the growth values were negative, leading to a further examination of the monthly frequency of standard length growth. Figure 3b helps investigate whether the high proportion of negative growth is linked to human or machine learning errors, particularly since the study involved a transition from manual to AI-based measuring methods in the middle of the study. Another possible cause of the high proportion of negative growth is natural shrinkage due to seasonal environmental factors. The pattern in Figure 3b reveals an annual trend, with a higher frequency of negative growth observed during the local wet season (June-December), and no obvious differences were observed in the negative growth distribution patterns between periods read by humans and those read by AI during the study. This suggests that temporary shrinkage in body length may occur as a result of harsh seasonal conditions in the streams.

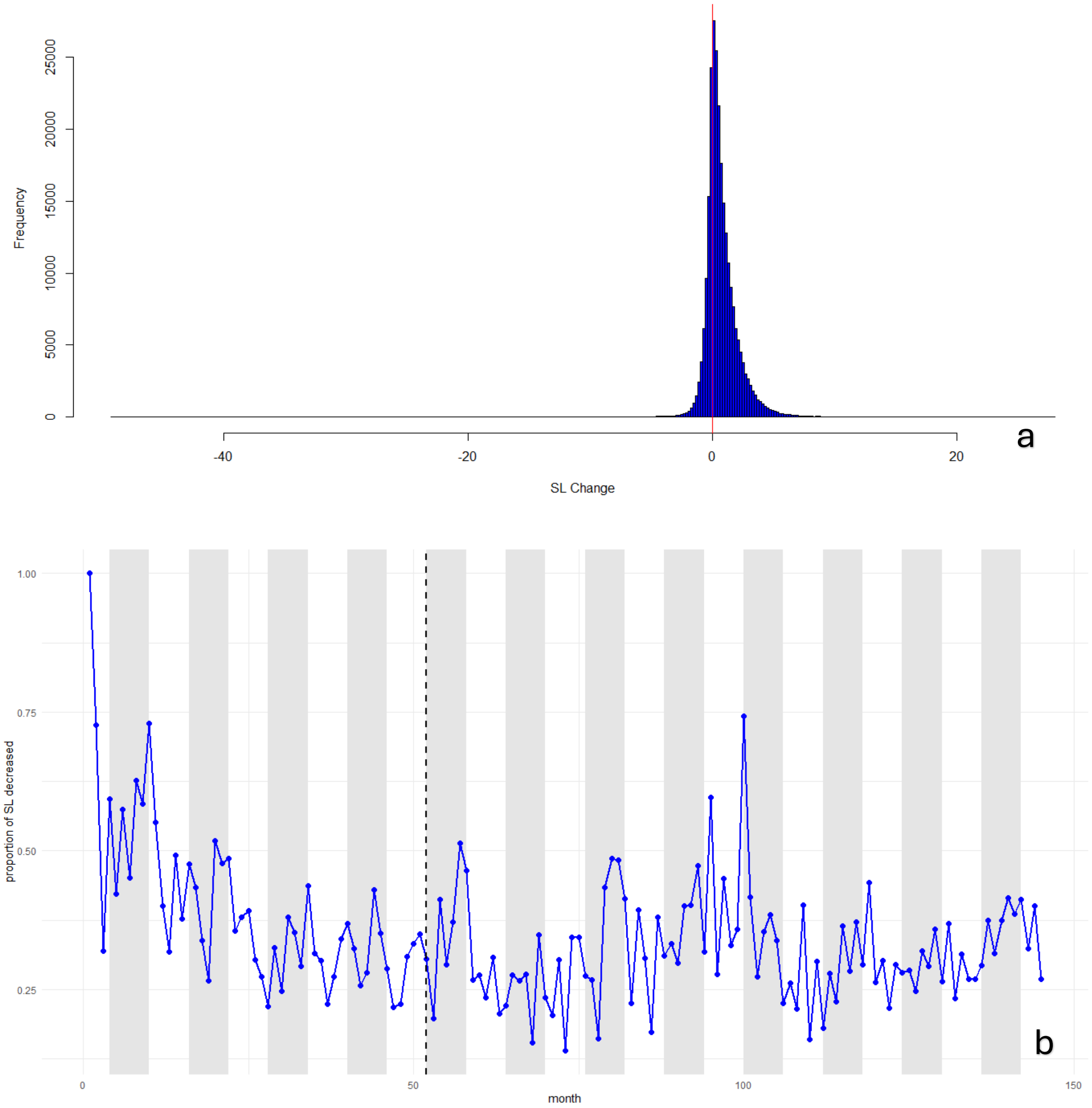


Figure 3. (a) Distribution of body length growth data across all four streams during the entire study period. (b) Temporal pattern of the monthly frequency of negative growth values across all four streams throughout the study period. Grey background indicates the local wet season (June - December), while the white background represents the local dry season (January - May). The black dashed line marks the transition from human to AI-based standard length (SL) measurements, occurring at the 52nd month (June 2012).

For selecting the sex- and stream-specific longest-lived individuals, we manually set a threshold for each subset (Table 3) based on the lifespan distribution of individuals in each subset. About 30 individuals above the sex- and stream-specific thresholds in Table 2 were used for plotting standard length growth patterns. Table 2 also shows that females always have a significantly longer life expectancy than males in the same stream.

Table 3. Sex- and stream-specific threshold for defining ‘longest-lived individuals’ with valid body length records. When an individual from a certain subset lives longer than the age threshold for its subset, it is defined as a ‘longest-lived individual’ and will be used for future plotting.

Subset	Age threshold (months)
Caigual female	27
Caigual male	13
Lower LaLaja female	37
Lower LaLaja male	18
Taylor female	29
Taylor male	18
Upper LaLaja female	35
Upper LaLaja male	17

After the groups of longest-lived individuals were selected using thresholds defined above, body length growth curves were plotted (Figure 4). As predicted, male guppies stopped growing at a smaller size around 20mm in all four streams, while females continued to grow and some female guppies can eventually reach 35mm. It is worth noting that the data are not perfect. There are missing months representing unsuccessful recaptures for the individual. For some individuals, there are unreasonable steep declines which are most likely to be the result of measurement errors.

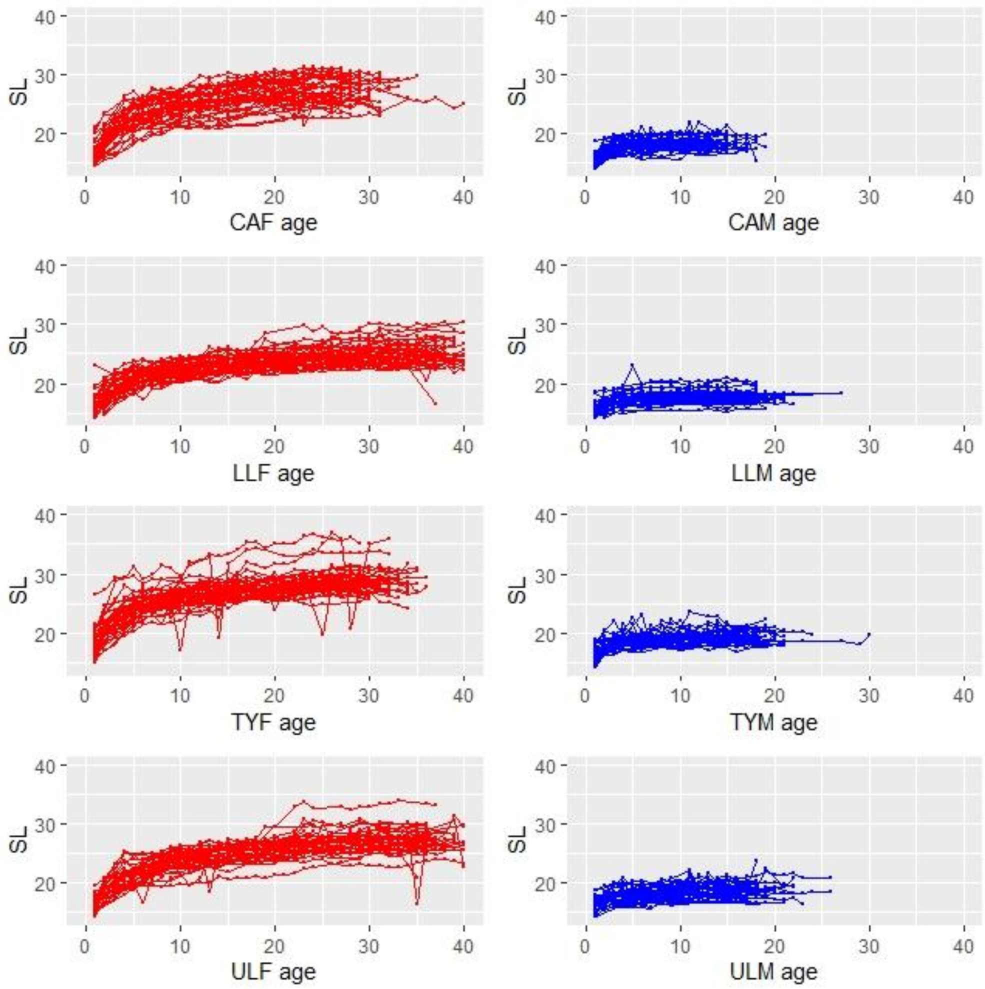


Figure 4. Standard length growth patterns for sex- and stream-specific longest-lived individuals. Each curve shows a long-lived individual's body length records at each capture. Red curves are for females and blue curves for males.

The long-lived individual can help us understand guppies' growth patterns, but they are by no means good representation of the entire database. In fact, for both sexes, guppies that lived for only a few months make up the vast majority of the database. Figure 5 describes the distribution of all the standard length records in each stream. The boxplots show that average standard length was increasing as age increases, while monthly growth rate was gradually going down. Very similar patterns to Figure 4 above can be found, in that males stopped growing around 20mm as females kept getting larger after the first few months of their life.

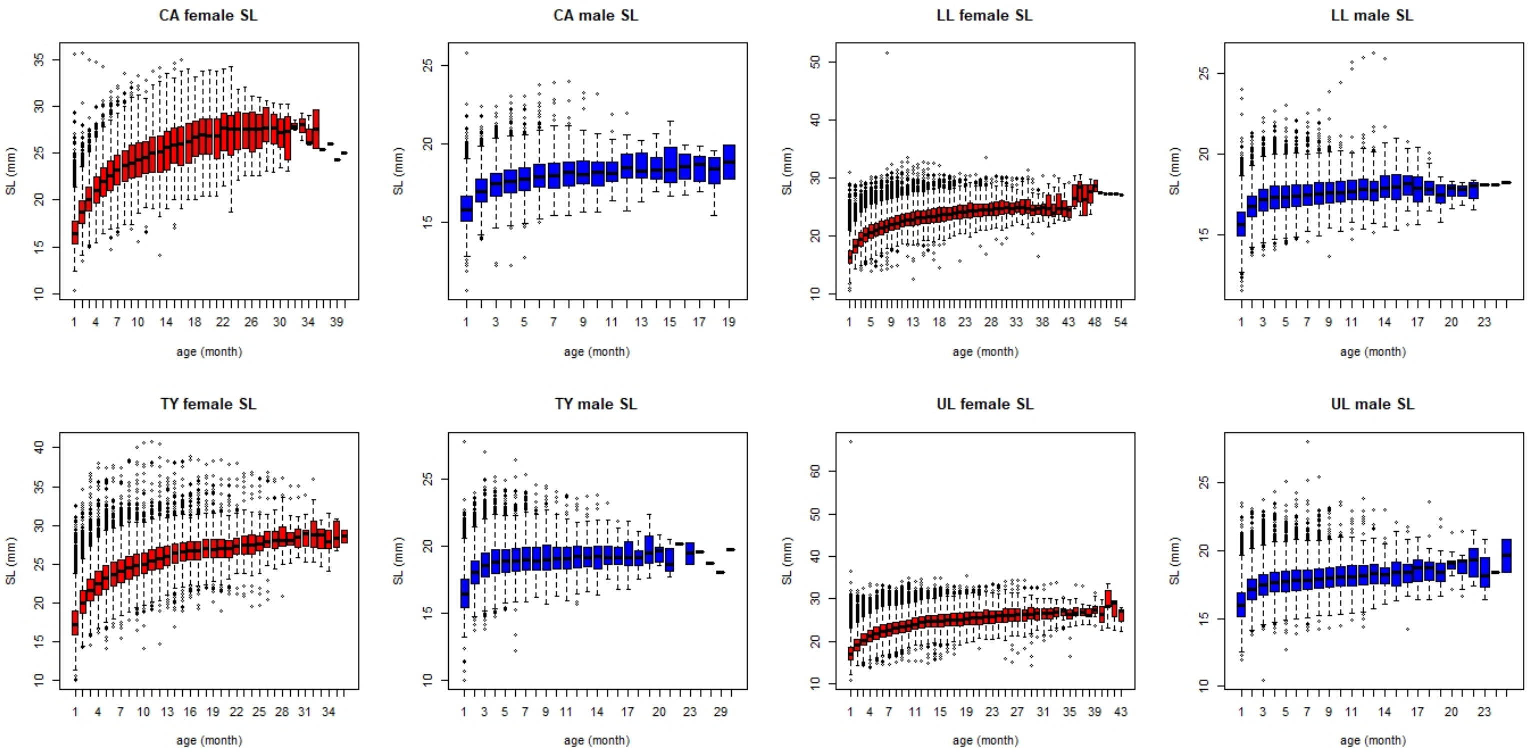


Figure 5. Sex- and stream-specific distribution of standard length (SL) data collected. Red boxplot is for females and blue boxplot for males in each of the four streams (CA, LL, TY, and UL stand for Caigual, Lower LaLaja, Taylor, and Upper LaLaja).

Asymptotic models for standard length growth

We used the AIC to rank the four models and select the best-fitting one. In all eight sex- and stream-specific models, the Weibull model had the lowest AIC, followed by the von Bertalanffy model with the second-lowest AIC, the Gompertz model with the second-highest AIC, and the logistic model with the highest AIC (Table 4).

Table 4. AIC values for the Weibull, von Bertalanffy, Gompertz, and logistic models along with the delta AIC between each model and the best-fitting model (lowest AIC). The models are separated by sex (F for female, M for male) and stream (CA for Caigual, LL for Lower LaLaja, TY for Taylor, and UL for Upper LaLaja).

Stream	Sex	Model	AIC	Delta-AIC
CA	F	Weibull	126445.3	0
		von Bertalanffy	126742.4	297.1
		Gompertz	126882.3	437
		logistic	127031.2	585.9
	M	Weibull	48180.79	0
		von Bertalanffy	48237.27	56.48
		Gompertz	48242.5	61.71
		logistic	48247.8	67.01
LL	F	Weibull	256698.2	0
		von Bertalanffy	258144.2	1446
		Gompertz	258465.3	1767.1
		logistic	258789.4	2091.2
	M	Weibull	91156.73	0
		von Bertalanffy	91246.48	89.8
		Gompertz	91253.18	96.5
		logistic	91259.94	103.2
TY	F	Weibull	224395.4	0
		von Bertalanffy	225534.5	1139.1
		Gompertz	225817.7	1422.3
		logistic	226102.2	1706.8
	M	Weibull	107171.8	0
		von Bertalanffy	107196.6	24.8
		Gompertz	107200.6	28.8
		logistic	107204.8	33
UL	F	Weibull	452837.7	0
		von Bertalanffy	454057.8	1220.1
		Gompertz	454427.8	1590.1
		logistic	454812.3	1974.6
	M	Weibull	188461.7	0
		von Bertalanffy	188612.8	151.1
		Gompertz	188623.8	162.1
		logistic	188635	173.3

Besides AIC, we also examined the parameter estimates for all four models (Table 5). For all populations, the Weibull model consistently predicted the highest asymptotic length (L_{inf}) values among the four asymptotic growth models tested. Notably, asymptotic length estimates for females were significantly higher under the Weibull model compared to the other three models across all streams (e.g., ~36 mm vs. ~26 mm for Caigual females). In contrast, for males, the difference between the Weibull and other model predictions was much smaller (always under 0.5 mm).

Across all four streams, the growth coefficient (K) was consistently higher for males than females across all models, indicating faster growth rates in males. Additionally, the inflection point (t_I) for the Gompertz and logistic models was consistently negative across all datasets, and the curve shape parameter in the Weibull model (α) was smaller than 1, both suggesting that growth rate continuously declines over time in all observed populations, despite the models' inherent structure allowing for an initial increase followed by a decrease with age. For both sexes in the same stream, the curve shape parameter α in the Weibull model was constantly higher for males than females, meaning that the males' growth curve takes on a pattern of rapid early growth phase before slowing down later, while females have a more gradual and steady growth rate, indicating a different strategy in energy investment in growth and reproduction.

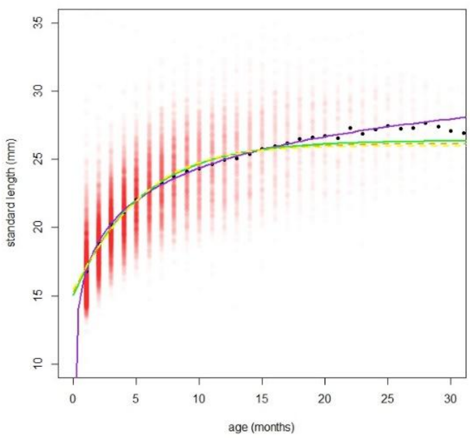
Compared to Caigual and Lower LaLaja, which have intact canopies and presumably lower primary productivity, Taylor and Upper LaLaja were expected to offer higher food availability due to greater light exposure and increased primary production especially during the dry season. As predicted, Upper LaLaja exhibited the highest growth rates among the four streams, while Caigual consistently showed the lowest. Lower LaLaja and Taylor displayed similar growth rate estimates to one another.

Table 5. Estimates of parameters from sex- and stream-specific von Bertalanffy, Gompertz, logistic, and Weibull models (all statistically significant). L_{inf} represents the asymptotic length (measured in mm), K is the growth coefficient, t_0 is the theoretical age at zero length in von Bertalanffy model (measured in months), t_I denotes the inflection point where the maximum growth rate occurs in Gompertz and logistic models (measured in months), and α

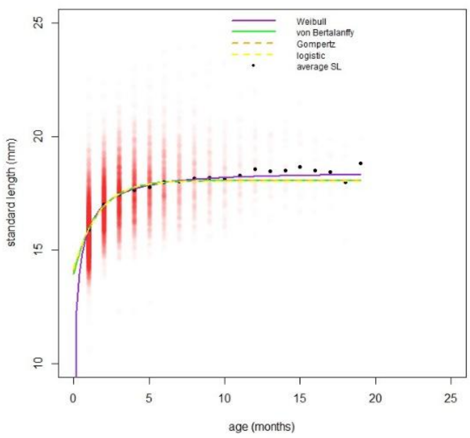
is the curve shape parameter for the Weibull model. CA refers to the Caigual stream, LL to the Lower LaLaja stream, TY to the Taylor stream, and UL to the Upper LaLaja stream.

dataset	**model**	**parameter estimates**				
		L_{inf}	**K**	**t_0**	**t_1**	**α**
CA female	von Bertalanffy	26.37564	0.190872	-4.41028		
	Gompertz	26.16086	0.226371		-2.73867	
	logistic	25.98811	0.263281		-1.47452	
	Weibull	36.27299	0.152228			0.255077
CA male	von Bertalanffy	18.05525	0.64711	-2.28761		
	Gompertz	18.0444	0.67962		-2.04566	
	logistic	18.03411	0.71279		-1.82197	
	Weibull	18.37229	6.94486			0.35882
LL female	von Bertalanffy	24.05066	0.185816	-5.55721		
	Gompertz	23.95741	0.21011		-4.08022	
	logistic	23.87893	0.235059		-2.87555	
	Weibull	28.81732	0.54198			0.2435
LL male	von Bertalanffy	17.57345	0.77393	-1.89535		
	Gompertz	17.56825	0.80526		-1.71722	
	logistic	17.56324	0.83722		-1.54954	
	Weibull	17.71495	6.520476			0.414265
TY female	von Bertalanffy	26.63243	0.247211	-3.52862		
	Gompertz	26.48592	0.285853		-2.32181	
	logistic	26.36324	0.32604		-1.36956	
	Weibull	30.26162	0.672266			0.318558
TY male	von Bertalanffy	19.10076	0.90618	-1.23153		
	Gompertz	19.09436	0.94904		-1.05964	
	logistic	19.08819	0.9931		-0.89893	
	Weibull	19.18983	3.649771			0.531759
UL female	von Bertalanffy	25.52239	0.193786	-5.05535		
	Gompertz	25.40292	0.221466		-3.57891	
	logistic	25.3037	0.249936		-2.39492	
	Weibull	31.39685	0.41729			0.24815
UL male	von Bertalanffy	17.9952	0.7694	-1.9462		
	Gompertz	17.9898	0.80002		-1.76942	
	logistic	17.9846	0.83125		-1.60296	
	Weibull	18.15014	6.96247			0.404933

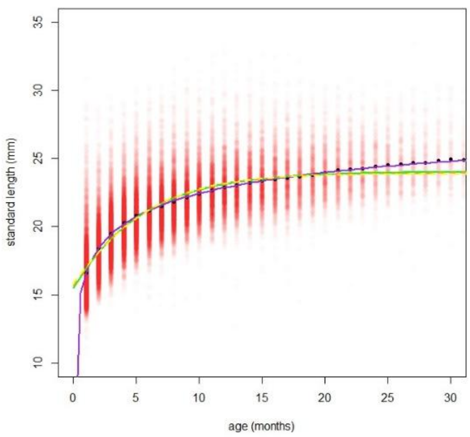
We compared the predicted growth curves of Weibull, von Bertalanffy, Gompertz, and logistic models against the actual growth trajectories in all four populations. In Figure 6, all collected body length records were plotted as pale red dots, the population's average age-specific standard length for each month was plotted as solid black dots, and the predicted growth curves of the four models were shown in different colours. All four different models can accurately describe the growth pattern in the initial months of life, with a continuously decreasing monthly growth in standard length. In female populations, the predicted growth curves from the Weibull model aligned more closely with the observed average body length data during later life stages compared to the other three asymptotic models, all of which tend to underestimate growth in larger females. In the Caigual population, it overestimated body length in most months after 20 months of age, whereas in the Taylor population, it underestimated growth beyond the same age threshold. In male populations, the differences among models were less pronounced, with all four models generally underestimating body length after 10 months of age.



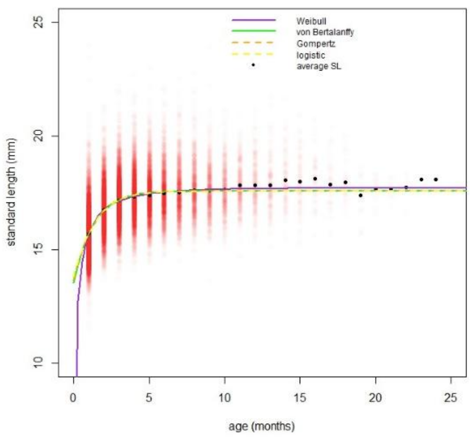
Caigual female



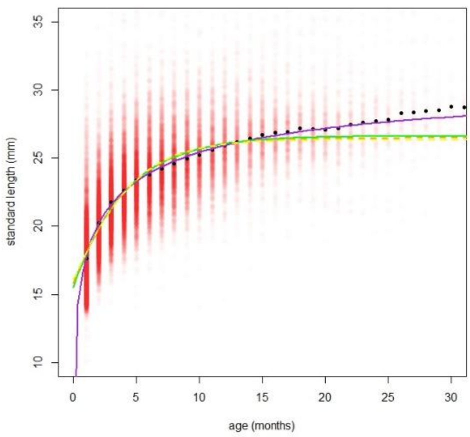
Caigual male



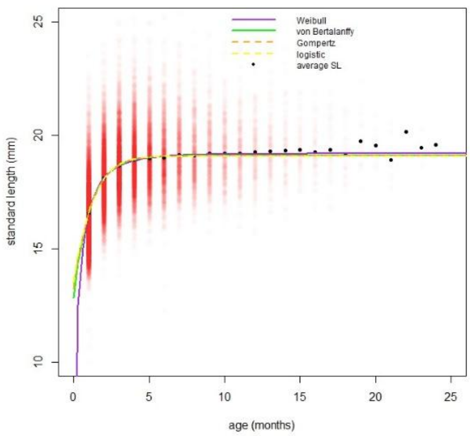
Lower LaLaja female



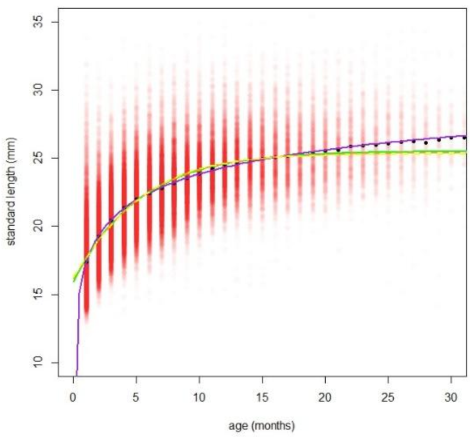
Lower LaLaja male



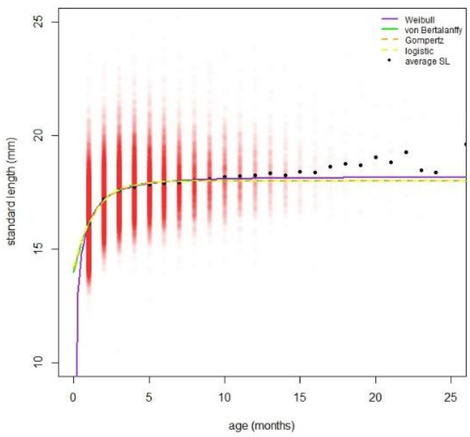
Taylor female



Taylor male



Upper LaLaja female



Upper LaLaja male

Figure 6. Predicted growth curves of Weibull, von Bertalanffy, Gompertz, and logistic models against the actual growth trajectories in all four populations. Transparent red dots (alpha=0.01) represent the actual age-specific standard lengths recorded for all individuals in the dataset. Solid black dots represent the population's average age-specific standard length for each month during the study period. The growth curves for the Weibull (purple solid line), von Bertalanffy (green solid line), Gompertz (orange dashed line), and logistic (yellow dashed line) models are shown in different colours. Females with ages beyond 30 months and standard length records above 35mm or below 10mm, and males with ages beyond 25 months and standard length records above 25mm or below 10mm are omitted in the plots.

Non-asymptotic body length growth models

Since the asymptotic functions applied above did not perform well, particularly for females at older ages, we also tested non-asymptotic two-phase models across all populations. We used a non-linear function to model growth during the earlier stages of life and a linear growth pattern for the later stages based on the population data obtained. Also, all four models performed well in describing growth patterns during the early life stages. Therefore, the von Bertalanffy model was selected as the basis for the first phase of our two-phase models. After a certain threshold age in our two-phase growth models, phase two transitions into a linear growth pattern.

The parameter estimates for all the two-phase growth models are provided in Supplementary Material, Table S4.1. All two-phase models provided similar estimates for the three von Bertalanffy parameters in the first phase, with a slight decrease in the asymptotic length and an increase in the growth coefficient. In the second phase, females exhibited a faster linear growth rate (0.132–0.228 mm per month), while males showed slower growth. Males from the Caigual and Upper LaLaja streams had about half the growth rate compared to females during the linear phase, while the other two streams showed near-zero growth for body length in the second phase, consistent with earlier model predictions (Table 5) and expectations that females continue to grow after reaching sexual maturity, while male growth slows down. Figure 7 shows the predictions from the two-phase model compared to the actual growth patterns. For females, most data points after the threshold age were above the model curve in younger individuals and below it in older ones, suggesting a gradual decrease in growth rate during the second phase. It is important to note, however, that only a few individuals survive beyond the threshold age, which may influence both the observed growth pattern and the model's predictions. A similar pattern—initial underestimation followed by overestimation—was observed in the second phase for males, although the model fit was slightly better in comparison.

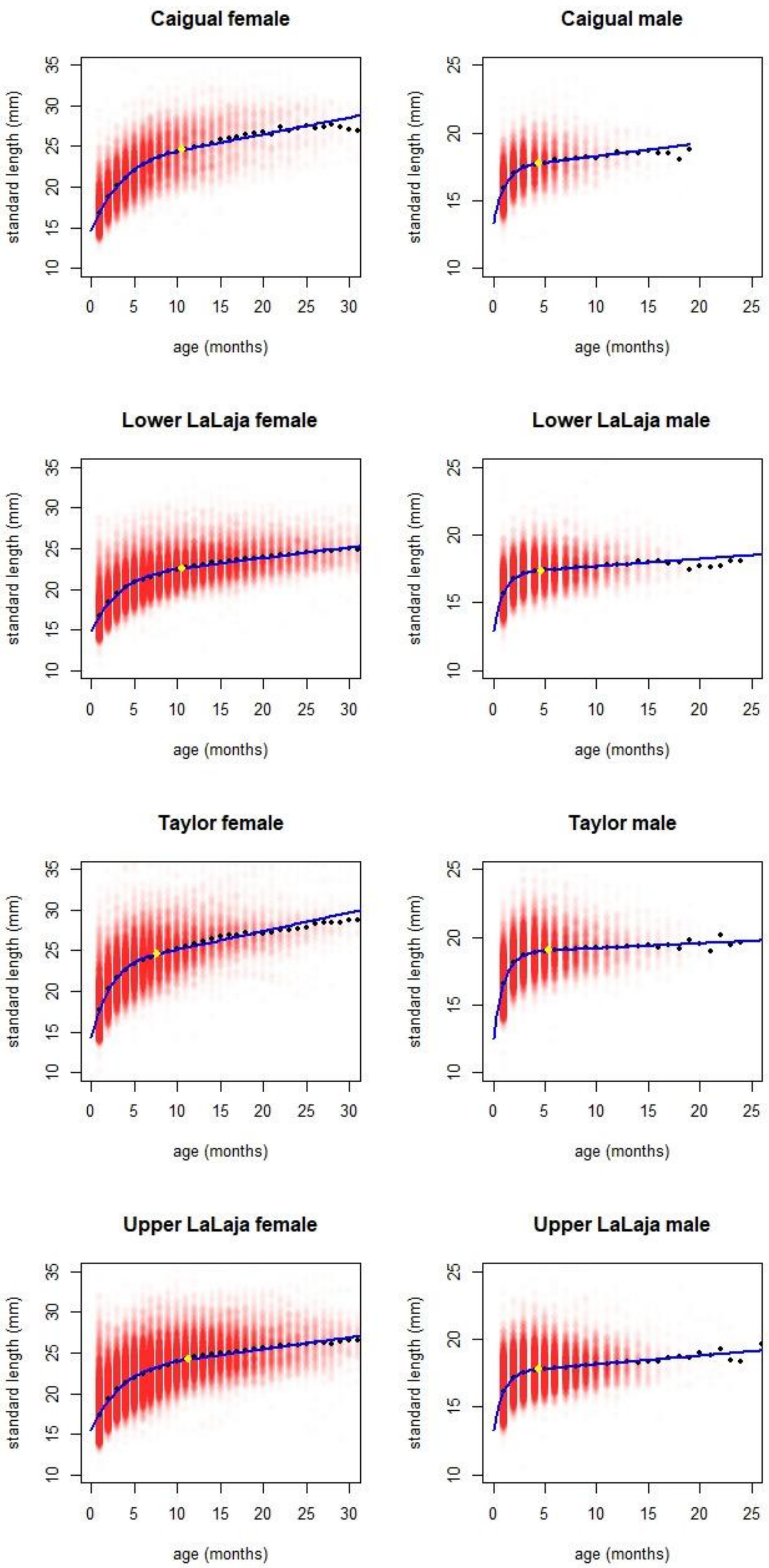

Caigual female
Caigual male
Lower LaLaja female
Lower LaLaja male
Taylor female
Taylor male
Upper LaLaja female
Upper LaLaja male
standard length (mm)
age (months)
10
15
20
25
30
35
0
5
10
15
20
25
30

Figure 7. Predicted growth curves from the two-phase model compared to actual growth trajectories in all four populations. Transparent red dots (with alpha = 0.01) represent the actual age-specific standard lengths recorded for all individuals in the dataset. Solid black dots indicate the population's average age-specific standard length for each month during the study period. Blue lines show the growth curves predicted by the two-phase model. Yellow dots mark the threshold point where the model transitions from phase one's Von Bertalanffy function to phase two's linear function.

The AIC values for the two-phase models were consistently lower than those for the von Bertalanffy models across all eight datasets (Supplementary Material, Table S4.1). However, the estimate for the threshold point was not significant for all eight datasets, with very large standard errors relative to the mean estimates. This suggests a failure to identify a clear breakpoint where the growth rate transitions from the von Bertalanffy model to the linear pattern. This indicates that a smoother transition function within the model, rather than a fixed threshold point, might better describe the change in body length growth rate. Such a model would involve more complex modelling than a typical biological two-phase model. Since the von Bertalanffy model in the first phase performs relatively well for both sexes, particularly for the first few months of guppy life when most individuals survive, we did not explore other plausible two-phase models with non-asymptotic body length growth patterns prior to incorporating environmental factors into the model.

Models with environmental covariates

To model the impact of environmental factors: density, season, and time, we constructed a modified Weibull model for females and a modified von Bertalanffy model for males, incorporating either total population density or sex-specific density to compare potential differences. In Table 6 below, parameters d_1, s_1 and e_1 represent the linear effects of density, season, and elapsed time on the growth coefficient (K_0), while d_2, s_2, and e_2 describe their respective effects on the baseline asymptotic length (L_{inf0}).

Table 6. Parameter estimates from the Weibull (for females) and von Bertalanffy (for males) growth models with environmental covariates for eight sex- and stream-specific datasets, incorporating either total population density or sex-specific density in the model predictions. The effects of population density (d_1 and d_2), seasonal impact (s_1 and s_2), and elapsed time of study (e_1 and e_2) are modelled as linear predictors of the growth coefficient (K_0) and the asymptotic length (L_{inf0}), respectively. α is the curve shape parameter for the Weibull model and t_0 represents the theoretical age at which body length is zero in the von Bertalanffy model. * indicates non-significant estimates.

Model	K_0	d_1	s_1	e_1	L_{inf0}	d_2	s_2	e_2	α	t_0
CA female (total density)	0.132	0.00595	-0.0636	0.000000529*	38.6	-0.433	3.79	-0.0142	0.249	
CA female (sex-specific)	0.145	0.00725*	-0.0608	0.0000370*	38.0	-0.646	3.00	-0.0147	0.253	
LL female (total density)	0.795	-0.192	-0.120	0.00351	29.4	0.292	0.216	-0.0235	0.256	
LL female (sex-specific)	0.814	-0.300	-0.089	0.00344	29.5	0.326	0.0928*	-0.023	0.259	
TY female (total density)	0.722	0.00531*	-0.248	0.000745	32.4	-0.129	0.784	-0.0163	0.322	
TY female (sex-specific)	0.726	-0.00168*	-0.249	0.00116	32.5	-0.291	0.874	-0.0148	0.322	
UL female (total density)	0.649	-0.0641	0.00997*	0.00222	28.9	0.432	-0.825	-0.00316	0.280	
UL female (sex-specific)	0.761	-0.134	0.0151*	0.00220	28.6	0.572	-0.837	-0.00117*	0.288	
CA male (total density)	0.667	0.00255*	-0.0272	-0.0000259*	17.7	0.0329*	0.186	0.00229		-2.22
CA male (sex-specific)	0.661	0.0197*	-0.0266	-0.0000994*	17.7	0.0884*	0.193	0.00226		-2.22
LL male (total density)	0.835	-0.0270	-0.0150	0.000134*	17.7	-0.195	0.183	0.00262		-1.87
LL male (sex-specific)	0.831	-0.0587	-0.0169	0.0000805*	17.5	-0.203	0.155	0.00231		-1.85
TY male (total density)	0.966	-0.00968	-0.0326	0.000207*	18.9	0.0157	-0.175	0.00165		-1.21
TY male (sex-specific)	0.965	-0.0241	-0.0387	0.000204*	18.9	0.0636	-0.161	-0.00121		-1.23
UL male (total density)	0.773	-0.00656	-0.0211	0.000538	17.6	-0.0263	-0.0941	-0.00598		-1.87
UL male (sex-specific)	0.766	-0.00792*	-0.0231	0.000498	17.5	0.0358	-0.0941	0.00527		-1.87

In both sets of models (with either total or sex-specific density), results largely aligned with those from the von Bertalanffy model without environmental factors: K_0 remained consistently higher in males, and L_{inf0} was larger in females with the difference between males and females even more pronounced than in earlier models. The effects of both total and sex-specific density on growth rate (d_1) were generally non-significant or slightly negative. For example, in Lower LaLaja males, the impact of total density, from the highest-density month to the lowest during the study period (3.47 vs 0.09), would result in a 0.091 difference in K_0, relative to a baseline value of 0.835. Interestingly, the effect of density on L_{inf0} (d_2) across the four streams always acted in opposite directions for both sexes. In all subsets tested, the impact of sex-specific density on both maximum body size and growth rate was consistently stronger than the effect of total population density, suggesting fiercer competition within each sex.

The impact of season two (previously defined as the season with lower average growth rates, generally aligning with the local wet season) was, as expected, consistently negative on growth rate (s_1) across all populations. In contrast, its effect on the asymptotic size (s_2) varied by stream. In Caigual, Lower LaLaja, and Taylor female models, season two showed a positive effect on the asymptotic size, especially pronounced in Caigual females, where L_{inf} predictions during the wet season can get above 3mm higher than in the dry season. Conversely, season two had a negative effect on L_{inf0} in Taylor males and Upper LaLaja population, with the strongest impact seen in Taylor females, where L_{inf} during the wet season was approximately 0.87mm lower than in the dry season.

The effect of elapsed time also revealed sexually dimorphic patterns. In all four female populations, the impact of time on K_0 (e_1) was slightly positive, although it was non-significant for the Caigual females. Among males, no significant time effect on K_0 was detected in three populations, except for a slightly positive effect in Upper LaLaja males. This suggests that growth rates in females may have gradually increased over the study period—contradicting findings from earlier common garden experiments—while such trends are largely absent in males. Regarding asymptotic length (e_2), when focusing on the models that include total population density, elapsed time showed a negative effect in all four female populations, again contrasting with expectations from previous common garden studies. The opposite trend was observed in males: positive effects of time were found in three streams except for Upper LaLaja. For instance, by the end of the study, L_{inf} in Lower LaLaja females would be approximately 3.41 mm smaller due to time of study alone, while Lower LaLaja males would exhibit a 0.038 mm increase in L_{inf}.

The influence of primary productivity remained largely consistent with earlier model predictions that excluded environmental covariates. Taylor and Upper LaLaja, both with thinned canopies and presumably higher primary productivity, generally exhibited faster growth rates. Caigual continued to show the slowest growth among all four streams, while Taylor males were the fastest-growing group. The Upper LaLaja population and Lower LaLaja males displayed moderate growth rates, whereas Lower LaLaja females exhibited relatively faster growth.

Discussion

By analysing the stream- and sex-specific growth trajectories across four Trinidadian streams, we evaluated how different growth models perform in describing the life history traits of both male and female guppies. We found that females grow larger than their male counterparts, exhibiting faster growth at all life stages and a longer period of continuous growth throughout their lifetime. However, age-specific body length varied greatly among individuals of the same sex, with the difference between the longest and shortest individuals reaching over 10 mm.

One particularly interesting finding is that approximately 25% of monthly body length growth measurements across the four streams were negative, with a higher frequency of shrinkage observed during the local wet seasons each year. This suggests that external factors, such as flooding and food shortage, may lead to temporary reductions in body length. Fish body length growth, like that of other vertebrate species, is generally unidirectional.

Only very few previous studies have observed similar temporary body length shrinkage in vertebrates. Examples of individual body size shrinkage have been documented in very few vertebrate species, including marine iguanas (Wikelski & Thom, 2000), salamanders (Bendik & Gluesenkamp, 2013), and stream-dwelling salmonid fish (Huusko *et al.*, 2011). In all cases, shrinkage was attributed to harsh environmental conditions and food shortages. However, some other studies have attributed similar observations of negative growth to measurement error rather than true biological shrinkage (Madsen & Shine 2001, Luiselli 2005). The observations from this study provide an example supporting the idea that environmentally induced reversals in growth and body size plasticity may be an overlooked phenomenon among vertebrates. However, more careful methodological consideration is needed before drawing firm conclusions. With the rapid advancement of AI-based image analysis in biological research (Norouzzadeh *et al.* 2018, Santangeli *et al.* 2022, Zhang *et al.* 2023), it appears promising that more precise and reliable data will be attainable in the near future.

We constructed and compared the sex-specific growth patterns estimated by several growth models, including Weibull, von Bertalanffy, Gompertz, logistic, and two-phase models. Among the asymptotic models for males, the Weibull model performed better than the von Bertalanffy, logistic, and Gompertz models. The two-phase growth model, which consists of an initial non-linear growth phase followed by a linear phase in which individuals continue to grow, could better capture the growth trajectories of female guppies during the later stages of life. Further improvements can be made to our two-phase models, which currently lack a reliable threshold age and rely on an overly simplistic linear model in the second phase. Enhancing model performance could involve adopting more flexible growth functions for the later phase and replacing the fixed age boundary with a gradual transition between the two phases, as demonstrated in another study on the two-phase growth of

Thylogale billardierii (McMahon *et al.* 2011). In male populations, the asymptotic models effectively described the determinate growth pattern. Such sexual dimorphism is commonly observed in the *Poeciliidae* family, and also aligns with our previous findings on the sex-specific differences in life expectancy and monthly survival rates. The use of the two-phase growth model in our study, which is rarely applied in fish studies, presents a promising approach for examining indeterminate growth in fish species. This model may provide a more accurate representation of growth dynamics, particularly in the later stages of life.

The growth model incorporating environmental factors suggests that during the wet season, which is characterized by increased flooding events that disrupt the stream environment and reduce food availability, both sexes experienced lower average growth rates. Female growth trajectories exhibited greater sensitivity to seasonal environmental variation, a pattern documented across various species, including red deer (Post *et al.* 1999) and temperate-zone birds (Ball & Ketterson 2008). Females tend to be more affected by environmental fluctuations, likely due to the energetic demands of reproduction, whereas males, lacking equivalent reproductive investment, are not impacted to the same extent.

A minor negative impact of population density was observed on individual growth rate, with sex-specific density exerting a stronger influence than total population density. Sexual competition is commonly observed among wild males, and Trinidadian guppies are no exception (Farr 1975, Jirotkul 1999). According to our model outputs, there is also evidence of intra-sexual competition for food. In females, this competition may be intensified by their tendency to school—i.e., to stay close to one another—which likely increases local resource competition (Reader & Laland 2000, Evans *et al.* 2011). As a result, intra-sex competition among guppies becomes inevitable.

Primary productivity plays a substantial role in shaping growth dynamics in these guppy populations. Streams with higher expected productivity (Taylor and Upper LaLaja) generally showed faster growth in our models. However, the influence was moderate rather than absolute, indicating that additional ecological or genetic factors may also contribute to the observed variation in growth rates.

In all four female populations, growth rates gradually increased over time, whereas males exhibited no temporal trend in growth rates. These findings contradict earlier common garden experiments, where a slower growth rate was observed. In a previous comparison of high- and low-predation Trinidadian guppy populations, researchers reported that guppies from high-predation environments exhibited approximately 45% slower growth than those from low-predation sites (Reznick *et al.* 2001). Another study found a similar pattern across four Trinidadian streams: guppies from two of the high-predation populations grew significantly faster than their paired low-predation counterparts-by roughly 20% when provided with sufficient food, whereas the other two pairs showed no significant difference (Arendt & Reznick 2005).

In contrast, the theoretical asymptotic length for males increased over time in three populations, aligning with expectations from previous common garden studies. A study focusing on predation's impact on male body size has revealed consistent life-history divergence across multiple sites of study (Reznick *et al.* 2019), with males from high-predation populations maturing at about 3 mm smaller than those from low-predation populations (~15 mm vs ~18 mm). These patterns observed in our study suggest that the growth trajectories of females and males are influenced by environmental factors in different ways. Since the effects of population density and seasonality were either inconsistent across streams, relatively weak, or even acted in opposing directions, further investigation into other external factors is required to determine the underlying causes of this cryptic evolution in guppy growth trajectories.

This study fills the gap in previous research on the growth rates and growth curves of guppies in wild environments, as well as the environmental factors that influence them. The results of this study offer valuable insights for future research on the evolution of life history traits in wild populations. Our findings in this chapter, along with observations on survival patterns from previous chapters, highlight the need for caution when interpreting evolutionary trends in wild populations. While evolutionary patterns from controlled environments are observable under lab conditions, they are less apparent in natural populations (Burns *et al.* 2009, Cameron *et al.* 2013, Govaert *et al.* 2019), possibly due to the masking effects of environmental factors such as seasonal impact, food availability, and other ecological variables. These insights underscore the complexity of studying evolution in wild populations and highlight the role of environmental covariates in shaping life history traits in natural settings. To gain a clearer understanding of ongoing evolution in natural settings, future research must take the complex interactions between genetics and environmental variables into consideration.

Chapter 5

Intra-Stream Dispersal and Microhabitat Effects on Growth and Survival in Trinidadian Guppies

Abstract

Understanding how dispersal behaviour interacts with local environmental conditions to shape life history traits is essential for interpreting ecological and evolutionary dynamics in the wild. In this study, we investigate how life expectancy and growth rate in Trinidadian guppies (*Poecilia reticulata*) are influenced by intra-stream dispersal and microhabitat variation across freshwater streams. Using long-term monthly census data from four guppy populations in northern Trinidad, we examine intra-stream dispersal patterns—testing whether movement is directional, sex-biased, or habitat-dependent—and use generalized linear models to evaluate how dispersal behaviour and habitat use affect individual growth and lifespan. We also assess whether potential emigration from the study sites might bias our estimates of survival. Our results reveal that guppy movement is largely diffusive rather than downstream-biased, with sex-specific differences in dispersal strategies: males tend to move more frequently, while females benefit more from fewer but longer movements. Individuals born in certain microhabitats, such as pools, exhibit higher life expectancy and lower propensity to disperse. These findings underscore the importance of local environmental heterogeneity and individual dispersal behaviour in shaping life history outcomes.

Introduction

Animal dispersal is crucial for activities such as foraging, predator evasion, courtship and reproduction, all of which contribute to the dynamics of populations. Individual dispersal pattern is influenced by a multitude of factors, encompassing both the intrinsic traits of the species and the constraints imposed by environmental conditions. The frequency and distance of dispersal varies not only between species but also within a population. Sex-specific reproductive allocation, migration, and human activities all contribute significantly to such variation (Morales *et al.* 2010, Soanes *et al.* 2024). In our study, we track the dispersal patterns of guppies in streams over a 12-year period on the tropical island of Trinidad and Tobago. Our objective is to examine variations in dispersal patterns within populations and determine the driving factors behind such variations.

Most studies on animal dispersal have prioritized a population-level approach for building models (Sanderson 1966, Worton 1987). However, more recent research has recognized the importance of individual variation. Evidence from studies on natal habitat, early life conditions, age, motivation (e.g., hunger, resting requirements), and behavioural traits (boldness and aggressiveness) highlight their role in generating variation in dispersal among individuals within populations (Sih & Johnson 2004, Martin *et al.* 2013, Shaw 2020). In the case of great tits (*Parus major*), individual variation has been documented in their exploratory behaviour when encountering a new environment (Dingemanse *et al.* 2002). For juvenile eagle owls (*Bubo bubo*), those in poorer physical conditions tend to cover shorter distances while searching for nesting positions, and there is sex-biased pattern with females settling at greater distances (Delgado *et al.* 2010). Conversely, in brown bears (*Ursus arctos*), females exhibit a lower dispersal probability compared to males (Zedrosser *et al.* 2007). In the freshwater fish burbot (*Lota lota*), mean dispersal rates vary among individuals with different dietary specializations (Harrison *et al.* 2017). In an invasive fish species the round goby (*Neogobius melanostomus*), sex-biased dispersal patterns were observed in both laboratory and field environments in Lake Ontario, North America (Marentette *et al.* 2011). Males consistently displayed higher activity levels when exploring new environments.

Numerous factors contribute to the dispersal trajectories of animals. Intrinsic factors, such as the age of a cheetah, can influence an individual's hunting strategy (Hilborn *et al.* 2012). External environmental elements such as small barriers in freshwater streams can impede the dispersal of Iberian barbel (*Luciobarbus bocagei*) (Branco *et al.* 2017). Long-term factors encompass phenomena like the seasonal migration of large herbivores in African savannas, influenced by the distribution of water resources, while transient influences include herbivores adjusting their dispersal patterns to evade predators near water sources (Owen-Smith *et al.* 2020).

Various techniques, such as radio transmitters, global positioning systems, cellular and satellite networks, acoustic transmitters, and light-level geolocators, are employed to track wild animal dispersal (Nathan *et al.* 2008). Advances in non-invasive tracking methods, such as camera traps, footprint tracking, faeces collection and analysis, and individual identification by natural markings (Mills *et al.* 2016, Francisco *et al.* 2020, Zemanova 2020), have enabled real-time tracking with minimal impact on animal dispersal. However, these methods present challenges in fish studies, making the mark–recapture technique a popular choice for studying fish dispersal across different time scales. Although telemetric methods have been successfully implemented in certain freshwater fish studies over the past two decades (Thorstad *et al.* 2013), mark-recapture remains a better option for tracking small fish due to its lower risk of tag loss or lethal harm to the individuals (Thorstensen *et al.* 2022). The frequency of recaptures in a mark-recapture study must strike a balance to capture meaningful details without unduly disrupting the normal life of wild fish.

In recent years, mark-recapture studies have been conducted on dispersal patterns and the factors influencing individual dispersal in a wide range of fish species. Research on the dispersal dynamics of the blackspotted topminnow (*Fundulus olivaceus*) identified population density as a factor influencing dispersal (Clark *et al.* 2019). Laboratory investigations into wild-caught creek chub (*Semotilus atromaculatus*) indicated that body condition and body length interact to influence fish dispersal (Kanno *et al.* 2022). A study focusing on pike (*Esoxlucius Linnaeus*) observed significant seasonal variation in dispersal patterns. Pike exhibited increased dispersal during summer, displaying a preference for submerged macrophyte beds over pelagic areas, while the reverse trend was noted in winter (Kobler *et al.* 2008). Other studies on pike have highlighted the impact of habitat spacing (Lonzarich *et al.* 2000) and water temperature, with sexually dimorphic effects, on their dispersal (Pauwels *et al.* 2014).

Guppies (*Poecilia reticulata*) are a small-bodied freshwater fish commonly found in tropical regions. They rely on dispersal as much as other fish species to accomplish various activities throughout different life stages. Guppies belong to the family *Poeciliidae*, which includes several successful invasive species (Deacon & Magurran 2016). Like other members of this family, guppies exhibit strong behavioural plasticity and physiological tolerance to a range of environmental conditions, including water temperature (Merino & Droste 1983), salinity (Chervinski 1984), light condition (Chapman *et al.* 2009), and predation pressure (Swaney *et al.* 2015). These traits enable them to move into and establish populations in new environments with relative ease. In their natural habitat on the tropical island of Trinidad, freshwater streams segmented by small waterfalls somewhat limit their dispersal. These waterfalls also serve as natural barriers, deterring larger predators and sparing guppies from the need to actively evade threats. Evidence from earlier studies on guppies inhabiting streams in different regions of Trinidad suggests that both geographic distance and physical barriers such as waterfalls limit gene flow by restricting guppy dispersal (Crispo *et al.* 2006). Additionally, research in the Arima River has shown that males tend to travel more than females, potentially due to sexually dimorphic schooling behaviour or differing reproductive strategies (Croft *et al.* 2003, Russell *et al.* 2004).

Here, we assess monthly mark-recapture exercises in four independent streams to investigate the dispersal patterns of wild guppies in Trinidad. We aim to analyse intra-stream dispersal patterns in four studied populations, assess how guppy dispersal behaviours influence their life history traits, and investigate potential emigration events from the study site.

Methods

Species and Area of Study

We tracked the trajectory of wild guppies in four freshwater streams in Trinidad. Guppies are sexually dimorphic and have a short generation time. Male guppies exhibit brighter colour patterns and perform courtship dances to attract females (Endler 1980). They also adopt the strategy of persistently harassing females for mating, leading to more schooling behaviour in female guppies compared to males (Evans *et al.* 2011). Female guppies begin breeding at about 10 weeks old and continue to give birth every three to four weeks after reaching sexual maturity. Young fish face predation from adult fish, including their parents, immediately after birth and must find shelters to survive and grow beyond a size that makes them vulnerable to predation by guppies or killifish, a common coexisting species in Trinidadian streams. Even after reaching adulthood, guppies still face predation pressure in some streams from larger predators such as the pike cichlid (*Crenicichla alta*) and the wolf fish (*Hoplias malabaricus*) (Reznick *et al.* 1996).

In March 2008 and March 2009, we introduced four high-predation guppy populations into previously guppy-free streams with no large predators in Trinidad's Northern Range. These four streams are named Caigual (10°42’53.0”N, 61°16’29.2”W, abbreviated as CA below), Lower La Laja (10°43’00.8”N, 61°15’58.2”W, abbreviated as LL below), Taylor (10°42’31.7”N, 61°16’22.9”W, abbreviated as TY below), and Upper La Laja (10°43’03.8”N, 61°16’03.0”W, abbreviated as UL below), as shown in Figure 1. Guppies were collected from streams with large predatory fish and bred in the lab to reach maximum genetic diversity before being introduced into new streams with no predators. In March 2008, we introduced 38 pregnant females and 38 males into LL and 38 pairs of guppies into UL. One year later, in March 2009, we introduced 64 pregnant females and 64 males into CA, and 52 pairs into TY. In TY and UL, we manually thinned the canopy to assess the effects of different levels of stream primary production and food availability on guppies. In contrast, we left the canopy cover intact in CA and LL for comparison. All four streams have waterfalls at both the upstream and downstream ends, which prevent most immigration and emigration events, and thus keep the populations in a relatively closed environment. In March 2020, the COVID-19 pandemic interrupted data collection, and the data used for our study ends in that month.

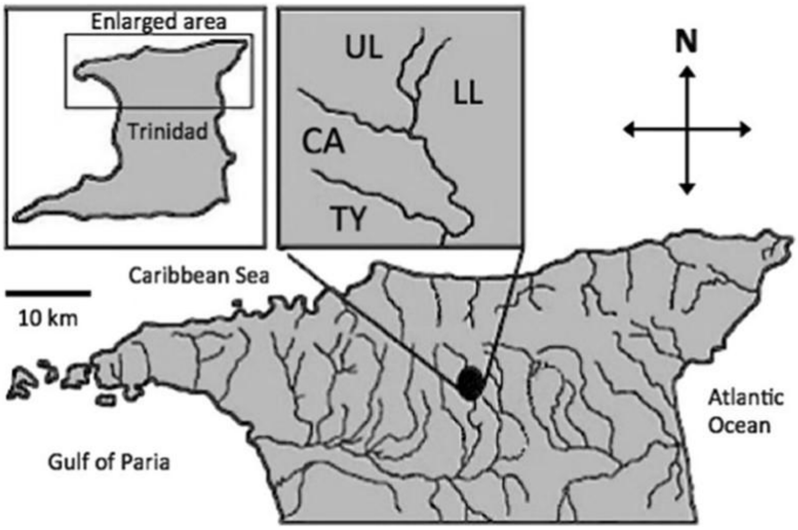


Figure 1. Location of the four streams of study in the Northern Range of Trinidad (Bassar 2021). UL, LL, CA and TY, stands for Upper LaLaja, Lower LaLaja, Caigual and Taylor streams respectively.

Data collection and preparation

We conducted monthly capture-mark-recapture for the entire population occupying the four streams CA, LL, TY, and UL to track the structure of the populations. Butterfly nets were used to capture as many individuals above 14 mm as possible in each stream to avoid casualties. All collected individuals were then taken to the lab and anesthetized with MS222. After anesthetization, we identified the sex, the presence or absence of a long gonopodium, weighed them, measured their body length, and marked each individual by injecting a unique combination of coloured elastomers. We used 12 different colours and eight marking locations on the fish to identify all the individuals in each population. The entire handling process was completed in under two minutes to minimize possible harm and injuries.

The data collected over the 145 months were saved into a .csv file, containing 463,080 rows in total. Each capture was recorded as a single row with seventeen columns detailing various aspects of the event; thirteen of these columns were used in this analysis. Column ‘stream’ shows the stream where the fish came from and comprises four levels: UL, LL, CA, and TY. Column ‘sampling occasion’ records the month when the capture took place, ranging from 1 (March 2008, the beginning of the study) to 145 (March 2020, the end of the study). ‘Individual ID’ is the unique number assigned to each individual during the 12-year course, with 98213 different IDs allocated to individuals across all four streams. ‘Sampling year’ ranges from 1-13, corresponding to 2008-2020, and ‘sampling month’ ranges from 1-12, corresponding to January-December. Both describe the exact time of each capture. ‘Location’ records the location within each stream where the fish was captured, with information on both upstream and downstream waterfalls at both ends of the small pools within each stream. ‘Habitat’ contains the categorical factor describing the type of stream environment within each small pool and is split into five categories: P (pool, the most common type in each stream, with both inflow and outflow and comparatively still and large water area), R (riffle, similar to a pool but with faster water flows, creating a turbulent, fast-moving environment), B (backwater, similar to a pool but connected to the stream by a single combined inflow/outflow), S (side-water, areas not connected to the main stream, such as puddles that form as water levels decrease during dry seasons), or N (none, mixed features, making classification difficult). ‘Distance’ is measured in metres and refers to the distance between the centre of that water section and the upstream starting point for measurement. ‘Upstream’ and ‘downstream’ record the starting and ending points of each water section respectively, both measured in metres. The next two columns, ‘weight’ (recorded in grams) and ‘standard length’ (recorded in millimetres), describe the condition of an individual upon each capture. The last column ‘sex’ comprises two levels: F (female) and M (male), which can be easily distinguished by body shape and the presence of a gonopodium.

Data cleaning before the statistical analysis included identifying and deleting 254 duplicate records where the same individual was recorded twice in the same month, removing 71 individuals for whom sex was not recorded, and excluding 536 individuals that were not recaptured for five consecutive months or more. We assumed that any subsequent recapture was likely an identification error, given our consistently high recapture rates in all four streams, as described in previous chapters. We removed individuals with extreme body length records (>100.00mm and <10.00mm) which are probably data entry errors. No extreme body weight records were found. We then removed 1,721 records lacking intra-stream location data, 839 records with either ‘upstream’ or ‘downstream’ values exceeding 200m (indicating entry errors) or with missing values, and 405 records where ‘downstream’ is smaller than ‘upstream’. Finally, we excluded 69 records where the water section length is either greater than 40m or less than 0.2m.

For each capture event, seven new columns were created: ‘age’, ‘lifespan’, ‘local density’, ‘primary habitat’, ‘migration’, ‘dispersal frequency’, and ‘dispersal distance’. ‘Age’ was defined as the crude monthly age of each individual, with the first capture defined as the age of one month. ‘Lifespan’ was calculated as the time between the first and last capture of the same individual. ‘Local density’ was computed as the number of individuals residing in the same water section as the focal individual in a given month, divided by the length of that section. ‘Primary habitat’ was defined as the most frequently occupied habitat type over the individual's lifetime; in cases where two or more habitat types were used equally, the natal habitat was assigned. ‘Migration’ was defined as 1 if the individual was found in a different water section compared to the previous month (i.e., the absolute difference between the current and previous ‘distance’ values exceeded half the length of the section), 0 if it remained in the same section, and NA for newborns. ‘Dispersal frequency’ was calculated as the proportion of months in which the individual underwent an immigration event over its entire lifespan. And ‘dispersal distance’ was calculated for individuals that immigrated, representing the difference in ‘distance’ between the two months. Positive values indicate downstream movement, while negative values indicate upstream dispersal against the flow.

Intra-stream dispersal analysis

We examined whether intra-stream dispersal is associated with individual behavioural tendencies and whether this relationship differs between sexes. To do so, we plotted dispersal trajectories of the longest-lived males and females in each stream separately. Lifespan thresholds were manually defined for each stream–sex combination based on the distribution of observed lifespans (Table 1), selecting the top 10-15 individuals per group. These individuals were then used to plot intra-stream dispersal over time, with age on the x-axis and recorded location within the stream on the y-axis to illustrate spatial displacement over their lifetimes.

Table 1. Sex- and stream-specific thresholds for defining ‘longest-lived individuals’. Individuals exceeding these thresholds are included in future trajectory plots.

Subset	Age threshold (months)
Caigual female	31
Caigual male	16
Lower LaLaja female	42
Lower LaLaja male	20
Taylor female	34
Taylor male	20
Upper LaLaja female	39
Upper LaLaja male	21

To incorporate shorter-lived individuals and broaden the analysis, we next focused on individuals with at least two consecutive months of location data. R (version 4.1.1) was used for all modelling. We first modelled the probability of inter-pool movement (i.e., ‘migration’ defined earlier) as a function of local environmental conditions using logistic regression via the glm function in R. We tested whether the likelihood of movement at time t was influenced by the habitat type and local population density at time t−1. We hypothesized that fish are more likely to migrate when local density is high or when habitat conditions suggest limited resource availability, such as in fast-flowing water sections. The model takes the form:

$$\mathrm{logit}(\Pr(\mathrm{migration}_t=1)) = \beta_0 + \beta_H \times \mathrm{Habitat}_{t-1} + \beta_D \times \mathrm{local.density}_{t-1}$$

To assess how life history traits are influenced by intra-stream environmental variation and dispersal behaviour, we used a generalised linear model with a Gamma distribution and log link after plotting the distribution of lifespan data across all individuals in our database. We first modelled lifespan as a function of dispersal frequency, average monthly dispersal distance, primary habitat type, and time of study. For each individual i, the model is expressed as:

$$\text{lifespan}_i = \beta_0 + \beta_F \times \text{dispersal.frequency}_i + \beta_D \times \text{average.distance}_i + \beta_P \times \text{primary.habitat}_i + \beta_T \times t + \varepsilon$$

where ε captures normally distributed random error. We then plotted the relationship between dispersal frequency and expected lifespan using model estimates to visualize how dispersal preferences affect both sexes. The intercept value for each model was based on the most common and representative water type: 'pool'.

We also modelled monthly growth rate for each individual i at time t as a function of age, dispersal distance in the previous month, and time of study, using a general linear model based on the monthly growth rate analysed in the earlier chapter:

$$\text{growth.rate}_{(i,t)} = \beta_0 + \beta_A \times \text{age}_{(i,t)} + \beta_D \times \text{dispersal.distance}_{(i,t-1)} + \beta_T \times t + \varepsilon$$

All models were fitted separately for each stream and sex, based on prior findings that these groups differ markedly in survival, growth, and behavioural patterns.

Assessing potential emigration from the system

All four streams are bounded by waterfalls at both ends. Nevertheless, we examined the potential for guppy emigration from the monitored stream sections. The four study streams were originally selected because they were guppy-free, making immigration events unlikely. To assess whether guppies were potentially leaving the study area by moving downstream over the waterfall, we first examined the distribution of monthly dispersal distances, which incorporated both directionality and magnitude of dispersal. We then tested whether lifespan varied with individuals' natal location to identify any location-specific survival differences that could suggest downstream emigration. We fitted a simple linear model with lifespan as a function of the distance between an individual's first capture location and the downstream end of the stream. We built two sex-specific models because previous analysis has shown that females and males have a significant difference in life expectancy. If emigration was occurring, we would expect the majority of dispersal events to be in a downstream direction, and guppies born downstream to exhibit shorter lifespans.

Additionally, we used boxplots to compare lifespan between individuals born at the upstream and downstream ends of each stream. These ends were defined manually for each stream by identifying water sections that accounted for approximately the first and last 10% of total population occupancy.

Results

Intra-stream dispersal patterns

Figure 2 displays the lifetime dispersal trajectories of the longest-lived individuals within each stream. Individual variation appears to influence dispersal behaviour: while most individuals remained largely localized within their natal or nearby water sections, a small number took several long-distance movements throughout their lives. Sex-specific differences in dispersal were evident in Lower LaLaja and Taylor, where males displayed more frequent and wide-ranging movement compared to females. However, such differences were less significant in Caigual and Upper LaLaja, suggesting that sex-based dispersal tendencies may also be influenced by stream-specific ecological features.

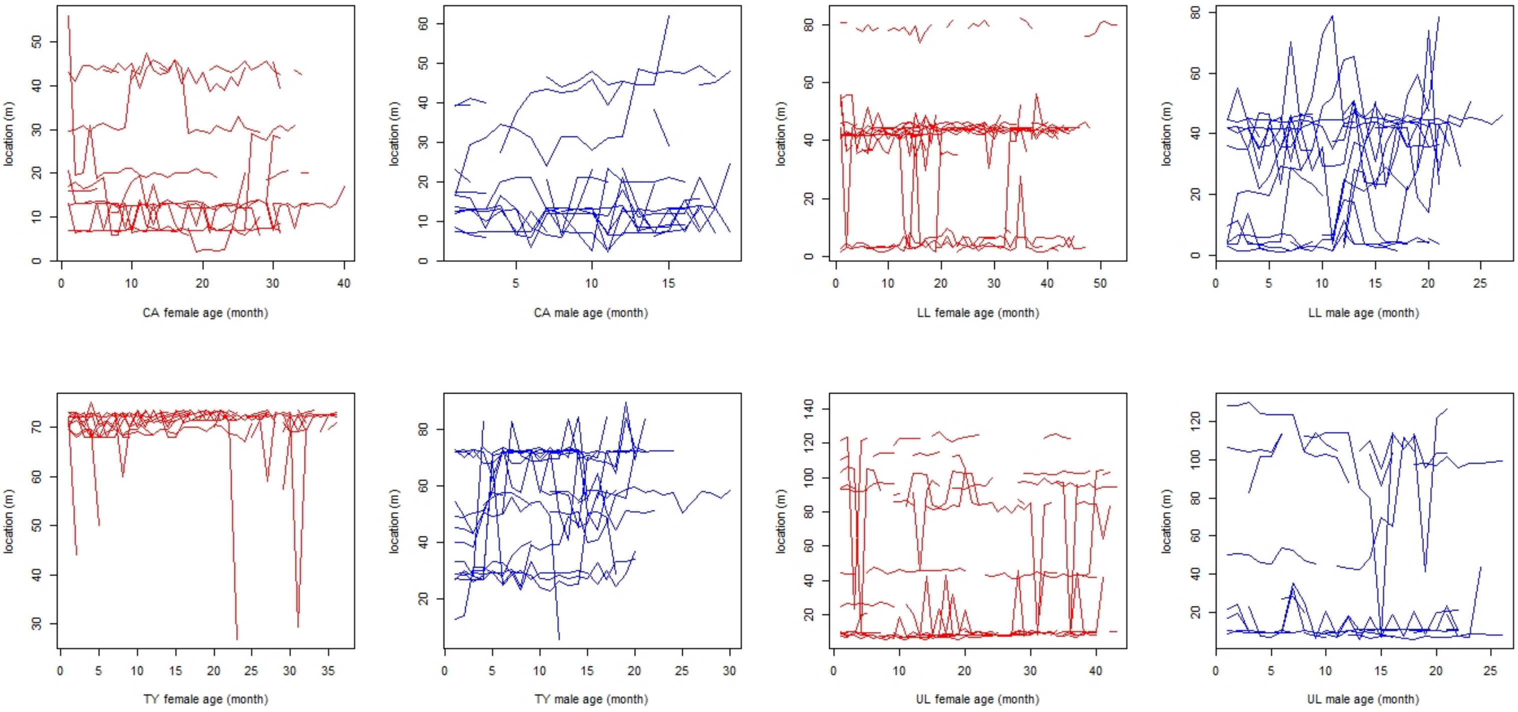


Figure 2. Dispersal trajectories of the longest-lived females (red) and males (blue) within each of the four study streams. Lifespan thresholds were set manually to define the subset. Lines indicate movement between inhabited water sections over the individual's lifetime. Abbreviations: CA (Caigual), LL (Lower LaLaja), TY (Taylor), UL (Upper LaLaja).

Table 2 presents the estimates from migration tendency models. Across most subsets examined, pools consistently showed the lowest migration estimates among the five different water types, indicating that individuals are less likely to move away when inhabiting relatively still water. In all eight subsets, individuals in riffles—characterized by more turbulent and faster water flow—were consistently more likely to migrate compared to those in pools. This pattern could either reflect an active choice, as faster water flow may reduce food availability, or it might result from fish being washed away, particularly during flooding events where water flow significantly impacts guppy fitness and survival. Contrary to our expectations, the tendency to migrate decreased as local population density increases. This suggests that different water sections vary in food availability and that guppies tend to aggregate in resource-rich areas, highlighting the important role of microhabitat in guppy ecology.

Table 2. Parameter estimates from the sex- and stream-specific migration logit models. Intercept values for five habitat types and the effect of local population density are shown separately. Abbreviations: CA (Caigual), LL (Lower LaLaja), TY (Taylor), UL (Upper LaLaja). * indicates non-significant estimates.

	pool	**riffle**	**sidewater**	**backwater**	**none**	**local density**
CA female	-1.094	-0.201	0.219	1.114	-0.783	-0.0073
CA male	-0.092	0.692*	0.264	1.026	-0.043	-0.0092
LL female	-0.722*	-0.150	-0.429	-0.897	-0.627	-0.0184
LL male	0.368	1.064	0.415	-0.344	0.702	-0.0149
TY female	-0.901*	0.100	1.189	-0.284*	-0.295*	-0.0201
TY male	-0.162*	0.845*	1.264*	0.380*	0.457*	-0.0190
UL female	-0.556	0.526*	1.608	0.936	-0.108	-0.0232
UL male	0.349	1.464*	1.865*	1.562	0.928*	-0.0293

Dispersal’s impact on life history traits

The distribution of sex- and stream-specific lifespans for all individuals in our dataset was plotted as histograms (Figure 3). The positively skewed distributions observed across all eight subsets support the use of a Gamma GLM for subsequent modelling.

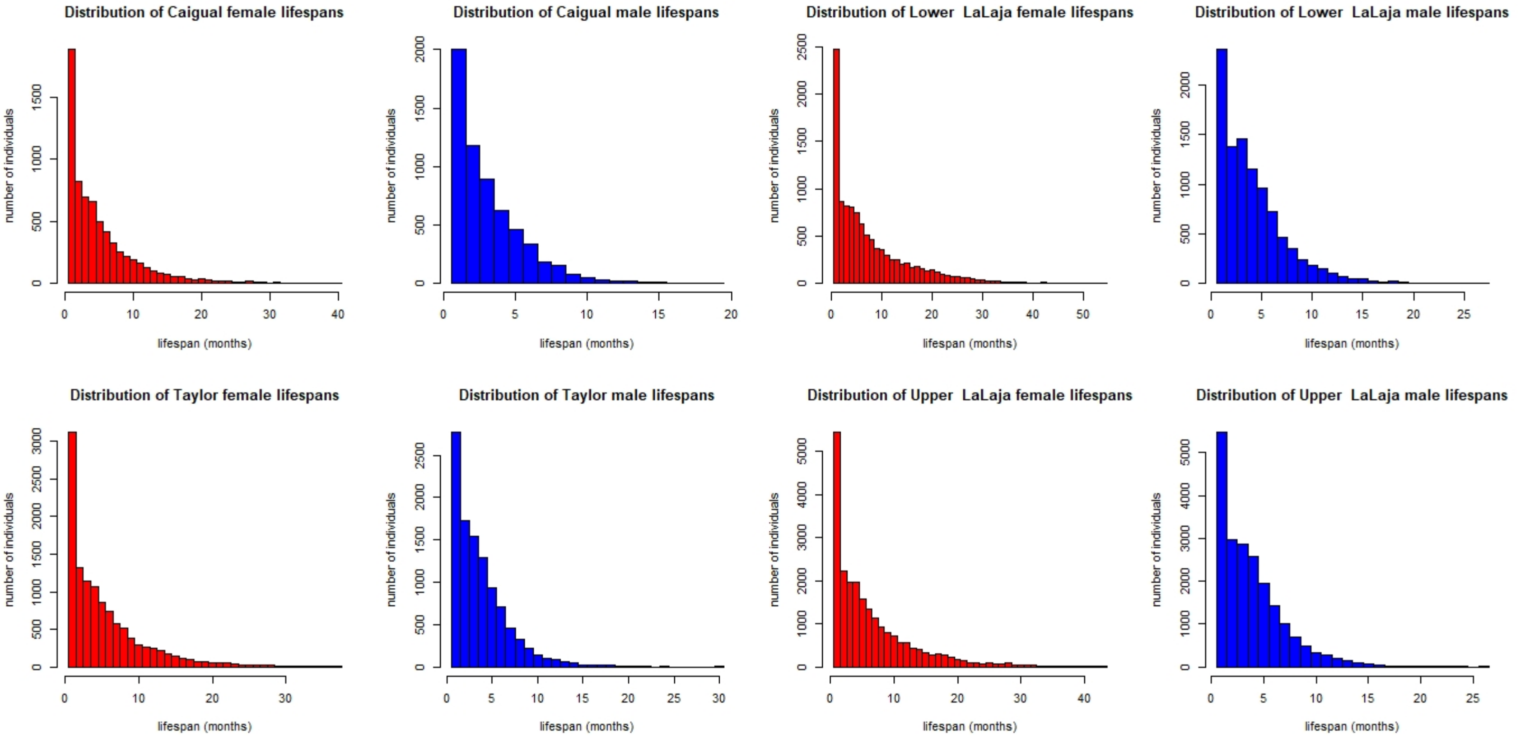


Figure 3. Distribution of sex- and stream-specific lifespans for all individuals recorded during the study period. Female data are shown in red and male data in blue.

When analysing the influence of dispersal preferences on life expectancy, we found that the primary habitat occupied during an individual's lifetime had a notable effect (Supplementary Material, Table S5.1). Guppies born in pools exhibited the longest life expectancy among all five water types, consistent with earlier migration model results that pools offer the most optimal living conditions. Dispersal frequency influenced life expectancy in a sexually dimorphic manner: in three of the four streams (excluding Caigual), female lifespan declined with increasing dispersal frequency, while in three streams (excluding Taylor), males who moved more frequently between water sections tended to live longer. In Caigual, females showed minimal benefit from increased dispersal, and in Taylor, frequent dispersal had a particularly detrimental effect on female lifespan (Figure 4). Across streams, females consistently derive less benefit or experience greater negative impacts from increased dispersal frequency compared to males.

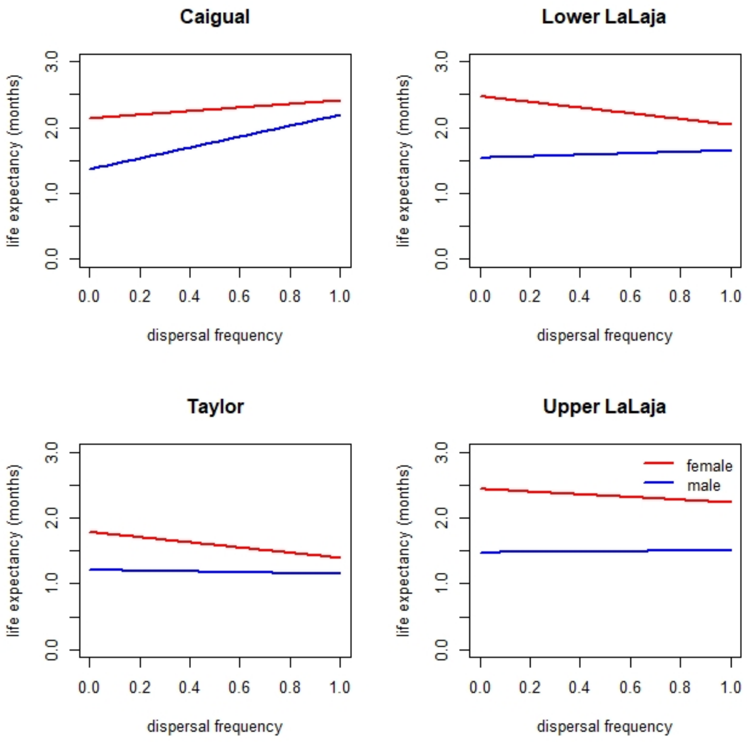


Figure 4. Effect of dispersal frequency on expected lifespan across four study streams. Dispersal frequency ranges from 0 (no movement between water sections at all) to 1 (dispersal in every month of life). Intercepts are based on model estimates using 'pool' as the reference water type. Red lines represent females, and blue lines represent males.

The effect of average monthly dispersal distance also differed between sexes. While dispersal distance positively influenced lifespan in both females and males, females were always more strongly affected. Regarding temporal effects, both sexes in Caigual and Lower LaLaja, as well as females in Upper LaLaja, showed a decline in lifespan over time. Conversely, both sexes in Taylor and males in Upper LaLaja exhibited an increase in lifespan throughout the study period.

In the growth rate models, growth rate decreased with longer travel distances in the corresponding month, with this effect being stronger for males than females across all four streams (Supplementary Material, Table S5.2). This aligns with the optimal dispersal strategy suggested by previous lifespan model results, where males benefit from making more frequent, shorter movements. As expected, growth rate declined with increasing age in all populations. Additionally, female growth rates decreased over time in all streams, whereas most males showed no significant temporal changes. In Caigual females with the steepest decline, growth rate dropped from 2.0396 mm/month at the start of the study to 1.4451 mm/month by the end when ignoring the effect of immigration habits and age. In Upper LaLaja males, the corresponding decrease was from 0.8151 mm/month to 0.6991 mm/month.

Assessing Downstream Emigration

The distribution of monthly dispersal distances was plotted as a histogram (Figure 5). Guppies were equally likely to travel in either direction, with similar frequencies observed for upstream and downstream dispersal. Overall, the frequency of dispersal decreased as the absolute distance increased, regardless of direction—suggesting most dispersal events were short-range.

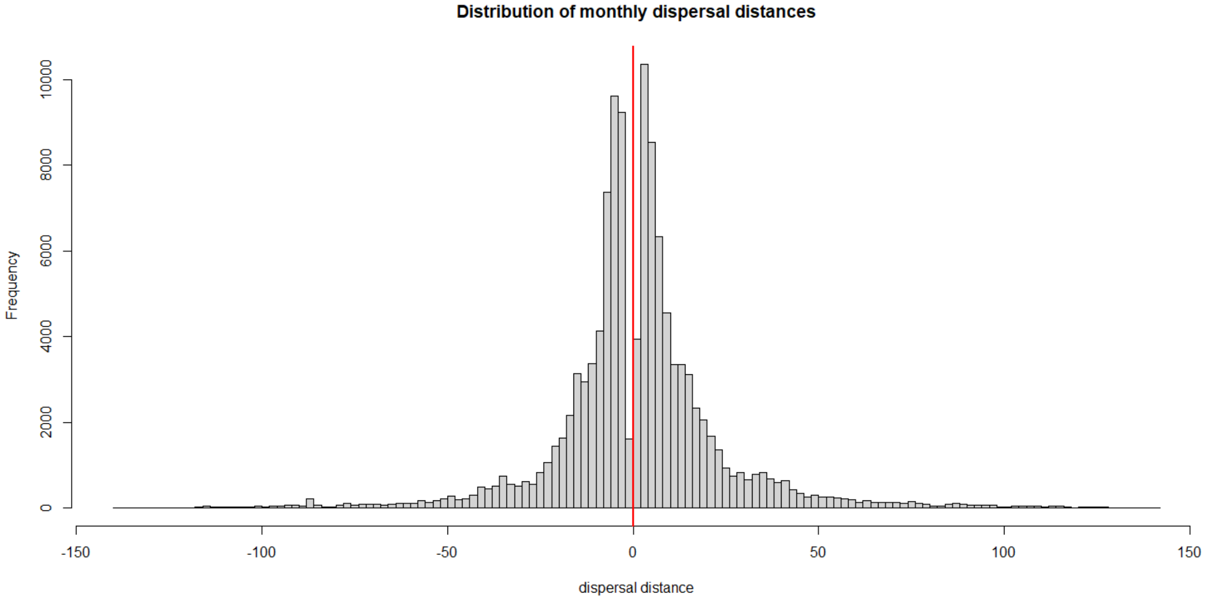


Figure 5. Distribution of monthly dispersal distances. The histogram includes all monthly dispersal events of individuals across the four study streams over the full study period. Positive values indicate downstream dispersal (with the flow), and negative values indicate upstream dispersal (against the flow). The red line at 0 marks instances of no dispersal.

Our sex-specific linear models examining lifespan as a function of natal location indicate that life expectancy declined with increasing distance from the upstream origin of each stream. For females, the slope estimate is -0.00624, while for males it is -0.00368. These correspond to a difference in average lifespan of 6.24 months for females and 3.68 months for males when comparing guppies born at the stream's headwaters versus those born 100 metres downstream. These effects are highly significant when contrasted with the average lifespan across all streams: 6.28 months for females and 3.80 months for males. This pattern suggests that individuals born closer to the downstream end either tended to have shorter lifespans or were more likely to emigrate from the monitored section, resulting in an underestimation of their actual lifespan due to leaving the observation area.

Because each of the four streams studied exhibited unique geomorphological characteristics, we defined the 'upstream ends' and 'downstream ends' individually for each stream (Table 3). Across all four streams, the upstream regions were more densely populated. Approximately 10% of the population was born within 10–20 metres of the stream's beginning point, and another 10% of the population was born in the final 50-metre segment near the stream's ending point.

Table 3. Defined upstream and downstream zones for each stream, based on the regions encompassing the ~10% of individuals born nearest to the waterfall at either end of the stream.

stream	**Caigual**	**Lower LaLaja**	**Taylor**	**Upper LaLaja**
'upstream end' beginning point (m)	0	0	0	0
'upstream end' ending point (m)	14.4	8.2	23.4	19.4
'downstream end' beginning point (m)	30.6	49.4	45.4	69.4
Total length of stream / 'downstream end' ending point (m)	81	102	100	175

Figure 6 illustrates differences in average lifespan between guppies born at the upstream versus downstream ends of each stream. Caigual males and females exhibited more pronounced differences in lifespan based on natal location compared to the other three streams. This may be attributed to differences in stream structure and water flow. The results suggest that in most streams, emigration is unlikely to have a strong effect on lifespan.

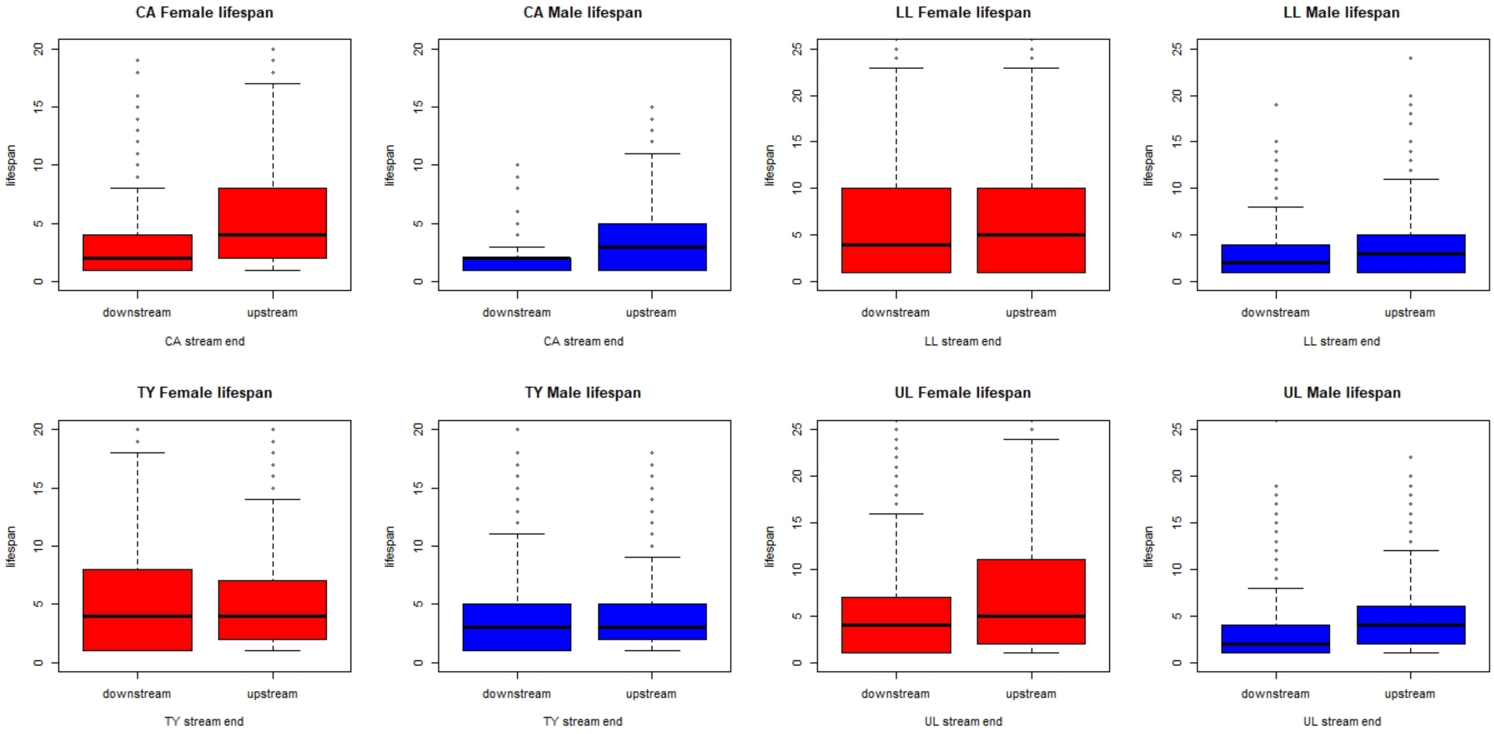


Figure 6. Boxplots comparing the lifespan of female (red) and male (blue) guppies born in the upstream and downstream zones across four streams. Extreme outliers are excluded for clarity. Abbreviations: CA (Caigual), LL (Lower LaLaja), TY (Taylor), UL (Upper LaLaja).

Discussion

Most previous studies on freshwater fish dispersal have focused on large river systems (Iitsuka *et al.* 2023), while our work emphasizes smaller streams, providing insight into underexplored habitats. We offer a long-term observation of intra-stream dispersal patterns in wild guppy populations in Trinidad, capturing fine-scale dispersal and life-history variation in a natural setting.

To investigate the drivers and consequences of dispersal, we examined dispersal behaviour in relation to individual traits. Personality differences appeared to influence travel preferences in the longest-lived individuals whose lifetime dispersal trajectories we reconstructed. While many guppies remained within the same water section throughout life, some exhibited a strong propensity to explore. Males, in general, were more mobile than females, in accordance with previous studies on Trinidadian guppies (Burns *et al.* 2016). Habitat type also played a role: guppies in fast-flowing riffles were more likely to relocate than those in pools, where dispersal was minimal. Interestingly, guppies tended to aggregate in areas with higher local densities, possibly drawn by greater food availability or social cues.

These distinct dispersal strategies had sex-specific consequences for life-history traits. If an individual is to travel the same total distance with the same total energetic investment, females would benefit more from making fewer, longer dispersal events, whereas males gain more from frequent, shorter dispersals. This suggests that sex-specific selection pressures may shape dispersal strategies differently within the same population. A similar pattern where females tending toward longer, exploratory dispersal and males exhibiting more frequent short-range dispersals was also observed in another small freshwater fish, the blackspotted topminnow (Clark *et al.* 2019).

To improve our understanding of the causes of intra-stream dispersal, future research should integrate a broader range of environmental variables. For example, it was found that male guppies were more likely to disperse when water temperature differed from their ancestral environment (Le Roy & Seebacher 2018). In addition, incorporating genetic lineage analyses could clarify how kin structure influences dispersal decisions. While dispersal can be favoured to avoid inbreeding (Lehmann & Perrin 2003), high relatedness may also promote philopatry through cooperative behaviours' benefits (Lambin *et al.* 2001, Hatchwell 2009).

We also examined potential emigration events from the study system by analysing the direction of guppy dispersal and comparing the lifespans of downstream individuals to those of their upstream counterparts. Contrary to our expectation that water flow would drive guppies to disperse predominantly downstream, we found that dispersal frequencies in both upstream and downstream directions were approximately equal. This indicates that intra-stream dispersal is best characterized as a diffusive process. Similar patterns where dispersal follows a roughly normal distribution around natal sites have also been documented in other freshwater fish species (Mayhew 2020, Steffensmeier *et al.* 2024).

When comparing individuals at the upper and lower ends of streams, most streams showed no significant difference in life expectancy. This suggests that emigration is unlikely to cause a systematic underestimation of lifespan in our earlier analysis. However, when linear models were used to test whether natal location influenced life expectancy, both males and females exhibited shorter lives when born closer to the stream ends. This, combined with the observation that approximately 10% of individuals are born within 10-20 metres of a stream's origin and another 10% near the final 50 metres, suggests that micro-environmental variation exists within streams and it can significantly impact guppy survival. These findings highlight the importance of considering fine-scale spatial heterogeneity in both ecological and evolutionary studies of animal dispersal.

Our study demonstrates that guppy's intra-stream dispersal in Trinidadian river systems is shaped by a complex interplay of environmental context, individual traits, and sex-specific life-history trade-offs. These findings have broad implications for understanding how microhabitat variation and dispersal strategies drive local adaptation and demographic dynamics in freshwater systems.

General Discussion

Understanding how life history traits evolve in natural populations requires disentangling genetic changes from the ecological contexts in which they occur. While controlled experiments, such as common garden studies, have provided strong evidence for adaptive shifts in life history traits under different selective regimes, applying these expectations to natural systems remains challenging. In this thesis, I used a comprehensive dataset from four wild Trinidadian guppy populations to assess whether long-term life history changes in survival and growth align with evolutionary predictions derived from common garden experiments. I complemented population-level analyses as well as individual-based models, while also evaluating how microhabitat variation and intra-stream dispersal shape demographic outcomes. Collectively, these chapters provide empirical evidence of cryptic evolution, wherein the effects of adaptive genetic change are masked by concurrent environmental variation in the wild.

Our findings in this thesis challenge the assumption that evolutionary trends observed under controlled conditions can be readily detectable in natural settings. The evidence for cryptic evolution across survival and growth traits underscores the importance of integrating long-term field data with robust statistical models that account for environmental variation, detection biases, and individual heterogeneity. This work adds to a growing body of literature suggesting that eco-evolutionary dynamics in the wild are more complex than previously assumed and may require novel tools and interdisciplinary approaches to fully understand.

A previous common garden experiment comparing guppies from high- and low-predation populations found no evidence of earlier senescence in mortality or reproduction among high-predation individuals, contrary to theoretical predictions that elevated extrinsic mortality should select for faster ageing (Reznick *et al.* 2004). The result indicates that physiological traits can evolve independently of reproductive or survival senescence, and highlights how different components of life history may respond differently to selective pressures. When considered alongside the field results presented in this thesis, these findings highlight the importance of distinguishing among multiple dimensions of survival, growth, and reproduction when interpreting evolutionary responses in the wild.

The results from the population-level survival analyses revealed varying patterns across streams. While some populations - such as both sexes in Taylor and males in Upper LaLaja - exhibited increasing survival rates over time, others, including both sexes in Caigual and Lower LaLaja, as well as females in Upper LaLaja, showed declining trends. This heterogeneity is inconsistent with the uniform expectation of increased survival following a shift to predator-free environments and suggests that eco-evolutionary feedbacks, such as food limitation and density dependence, may have played a role in masking underlying adaptive changes. These findings mirror patterns reported in other long-term studies of wild vertebrates, including Trinidadian guppies (Reznick *et al.* 2019, Palkovacs *et al.* 2009), where genetic trends and phenotypic outcomes diverged due to environmental constraints.

Individual-based Bayesian models provided additional insight into sex- and stream-specific variation in survival and recapture rates. After accounting for age structure and other individual-level factors influencing survival and recapture rates, no significant temporal trends in survival were detected in any of the four populations over the 12-year study period. Moreover, a consistent decline in recapture probability across all streams points to possible behavioural adaptation or methodological artifacts that may bias long-term survival estimates. These patterns emphasize the importance of accounting for detectability in mark-recapture studies and the challenges of interpreting apparent trends in mortality without considering potential sampling biases.

Growth rate analyses further supported the evidence for cryptic evolution. While female guppies exhibited increasing growth rates over time, which is opposite to predictions from common garden studies, males showed no consistent temporal trend. Seasonal and density-dependent effects were present but did not fully account for the observed changes, reinforcing the likelihood that phenotypic trends are being shaped by environmental variability rather than purely genetic adaptation. Similar to the survival analyses, these results confirmed strong sexual dimorphism in growth patterns, consistent with the reproductive strategies characteristic of the *Poeciliidae* family. The application of two-phase and Weibull growth models revealed meaningful differences in male and female growth strategies, underscoring the importance of selecting biologically appropriate models when evaluating life history traits in the wild.

Intra-stream dispersal analyses provided new insight into how microhabitat and dispersal preferences influence life history traits. Guppies in riffle habitats exhibited higher mobility than those in pools, and dispersal strategies differed between sexes: males benefited from frequent, shorter movements, while females gained more from fewer, longer dispersal events. These sex-specific patterns likely reflect differing energetic trade-offs and reproductive strategies. Dispersal showed no strong directional bias, suggesting that intra-stream movement is best described as a diffusive process. Individuals born near the stream edges exhibited shorter lifespans, highlighting the role of micro-environmental variation in shaping life history outcomes. These findings reinforce the importance of spatial context in ecological and evolutionary studies, particularly in heterogeneous environments like segmented freshwater streams.

Integrating artificial intelligence into Guppy Research

A promising avenue for future research lies in the application of artificial intelligence (AI) and computer vision techniques for rapid and accurate guppy measurement and information extraction. Manual measurement and transcription of guppy body length and hand-written label data are time-consuming and error-prone, particularly when dealing with large-scale photographic datasets collected over long time periods. Developing AI-assisted tools for automated guppy shape recognition, standard length measurement, and extraction of both printed and hand-written individual-based information from images could transform field-based life history research.

Advancements in wildlife monitoring in recent years have demonstrated the potential of AI for individual identification, behavioural tracking, environmental data extraction, and the interpretation of biological observations. In the context of the long-term guppy research programme, integrating AI for image-based standard length extraction and label reading could greatly increase the scale, consistency, and accuracy of future datasets, while also reducing observer bias. Further development of such tools may eventually allow for more frequent and less invasive monitoring methods.

This thesis lays a foundation for innovation in automated trait tracking for a model vertebrate species, providing a valuable training benchmark for broader machine learning applications in ecological and evolutionary research.

Conclusion

This thesis contributes a comprehensive, field-based perspective on life history evolution in wild guppy populations. By combining statistical modelling, trait analysis, and fine-scale dispersal ecology, it highlights the role of environmental variation in obscuring evolutionary trends and reveals the complex interplay between individual behaviour, habitat heterogeneity, and life history strategy. The findings caution against simplistic interpretations of evolutionary outcomes in nature and call for an integrative approach that incorporates genetic, ecological, and technological tools to better understand adaptation in the wild.

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Supplementary Material

S2

Table S2.1. Formulae of all models tested in Chapter 2. Models built for CA females are used as an example.

Model name	formula
CAF.model.age.sampling	glm(surv ~ age + age.square + sampling, family=binomial, data=CAF)
CAF.model.age_group.sampling	glm(surv ~ as.factor(age.group) + sampling, family=binomial, data=CAF)
CAF.model.age_group.12months	glm(surv ~ as.factor(age.group) + sampling + as.factor(sampling.month), family=binomial, data=CAF)
CAF.model.age_group.2seasons	glm(surv ~ as.factor(age.group) + sampling + as.factor(two.seasons), family=binomial, data=CAF)
CAF.model.age_group.3seasons	glm(surv ~ as.factor(age.group) + sampling + as.factor(three.seasons), family=binomial, data=CAF)
CAF.model.age_group.year.3seasons	glm(surv ~ as.factor(age.group) + as.factor(sampling.year) + as.factor(three.seasons), family=binomial, data=CAF)
CAF.model.age_group.months	glm(surv ~ as.factor(age.group) + as.factor(sampling), family=binomial, data=CAF)

Table S2.2. Estimates of each month in model.age_group.12months as shown in the model output. January was set as the reference level in the model by default. Models of Caigual (CA), Lower LaLaja (LL), Taylor (TY), and Upper LaLaja (UL) females (F) and males (M) are included.

Estimate	**CAF**	**CAM**	**LLF**	**LLM**	**TYF**	**TYM**	**ULF**	**ULM**
Jan	-	-	-	-	-	-	-	-
Feb	0.007501	0.1249603	0.0408756	0.2717976	-0.1812886	-0.0113722	-0.166793	-0.2367856
Mar	0.084919	0.0869520	-0.0195697	0.2160242	0.1525037	0.2218020	0.3058305	0.2463733
Apr	0.131334	0.2629755	0.1377251	0.2576082	0.0183420	0.1464571	0.2164076	0.1198217
May	-0.179763	0.0876164	0.0931140	0.0005493	-0.0640390	-0.2587901	0.1641689	0.1173744
Jun	0.104704	0.3211942	0.2771107	0.2925816	0.1176242	-0.0617423	-0.0649645	-0.2386625
Jul	-0.189626	-0.0335803	0.1937493	0.1558672	-0.0344309	-0.2457544	0.101782	-0.1189781
Aug	-0.303173	-0.2697172	0.0985085	-0.0520422	-0.7392366	-0.8347921	-0.0254919	-0.2219863
Sep	-0.225629	-0.1204840	-0.1656550	-0.2031046	-0.4246188	-0.6112580	-0.46048	-0.7117242
Oct	-0.063492	-0.1046858	-0.2645943	-0.2579422	-0.1196084	-0.4991974	-0.4669571	-0.5926948
Nov	-0.419617	-0.3181093	-0.3725637	-0.2374472	-0.6264884	-0.7328356	-0.3144836	-0.4708379
Dec	0.021196	-0.0605699	-0.0924631	0.1104581	-0.0650820	-0.1362821	-0.1195395	-0.2097207

Table S2.3. Optimal seasons for building all final models with variable 'three.seasons' and 'two.seasons'. Month 1-12 (Jan-Dec) in one calendar year are divided into two or three seasons for building models. In two-season models, season one is defined as the season with greater estimate value in model output, and season two with lower estimate value. In three-season models, season two is defined as the season with greatest estimate value in model output, season three with lowest, and season one with second lowest estimate value.

Population	Two-season models		Three-season models		
	season one	season two	season one	season two	season three
Caigual females	7-11	12-6	7-10	12-6	11
Caigual males	7-1	2-6	12-1	2-6	7-11
Lower LaLaja females	9-12	1-8	12-3	4-8	9-11
Lower LaLaja males	8-11	12-7	8	12-7	9-11
Taylor females	8-11	12-7	9-11	12-7	8
Taylor males	8-11	12-7	5-7	12-4	8-11
Upper LaLaja females	9-11	12-8	11	12-8	9-10
Upper LaLaja males	9-11	12-8	7-8	12-6	9-11

Table S2.4. AICs of all seven models and parameters included in each model for predicting probability of survival for male and female guppies in four experimental streams (CA for Caigual, LL for Lower LaLaja, TY for Taylor, and UL for Upper LaLaja, F stands for female and M stands for male). The seven Caigual female models ranked from smallest AIC to largest AIC are: CAF.by.month, CAF.by.year.3seasons, CAF.12months, CAF.3seasons, CAF.2seasons, CAF.age_group, and CAF.age^2 (same order for all seven other databases as well). Minimum AIC indicated in bold.

Stream	Sex	Model parameters									AIC	Delta-AIC
		age+ age^2	age.group	sampling (factor)	sampling (linear)	sampling (quadratic)	sampling. year	sampling. month	2 seasons	3 seasons		
CA	F		x	x							**31025**	0
CA	F		x				x			x	31690	665
CA	F		x		x			x			32171	1146
CA	F		x		x					x	32195	1170
CA	F		x		x				x		32211	1186
CA	F		x			x					32293	1268
CA	F		x		x						32297	1272
CA	F	x			x						32406	1381

CA	M		x	x							**21883**	0
CA	M		x				x			x	22217	334
CA	M		x		x			x			22343	460
CA	M		x		x					x	22360	477
CA	M		x		x				x		22366	483
CA	M		x		x						22455	572
CA	M		x			x					22456	573
CA	M	x			x						22459	576
LL	F		x	x							**58564**	0
LL	F		x				x			x	59127	563
LL	F		x		x			x			59456	892
LL	F		x		x					x	59480	916
LL	F		x		x				x		59519	955
LL	F			x		x					59743	1179
LL	F		x		x						59747	1183
LL	F	x			x						60144	1580
LL	M		x	x							**41666**	0
LL	M		x				x			x	42110	444
LL	M		x		x			x			42178	512
LL	M		x		x					x	42213	547
LL	M		x		x				x		42229	563
LL	M			x		x					42417	751
LL	M		x		x						42420	754
LL	M	x			x						42484	818
TY	F		x	x							**50753**	0
TY	F		x				x			x	53725	2972
TY	F		x		x			x			54751	3998
TY	F		x		x					x	54874	4121
TY	F		x		x				x		54961	4208
TY	F			x		x					55338	4585
TY	F		x		x						55473	4720
TY	F	x			x						55658	4905
TY	M		x	x							**39582**	0
TY	M		x				x			x	41656	2074
TY	M		x		x			x			42104	2522
TY	M		x		x					x	42179	2597
TY	M		x		x				x		42248	2666
TY	M			x		x					42768	3186
TY	M		x		x						42844	3262
TY	M	x			x						42881	3299
UL	F		x	x							**104491**	0
UL	F		x				x			x	109270	4779
UL	F		x		x			x			110256	5765
UL	F		x		x					x	110467	5976
UL	F		x		x				x		110485	5994
UL	F			x		x					111281	6790

UL	F		x		x						111311	6820
UL	F	x			x						111642	7151
UL	M		x	x							**80519**	0
UL	M		x				x			x	83985	3466
UL	M		x		x			x			84410	3891
UL	M		x		x					x	84659	4140
UL	M		x		x				x		84694	4175
UL	M			x		x					85461	4942
UL	M		x		x						85509	4990
UL	M	x			x						85630	5111

S3

Table S3.1. Estimates of parameters in the Mark-Recapture model for eight sex- and stream-specific datasets analysing monthly survival (φ) and recapture rate (p). * indicates that the estimate is not credible, either due to suboptimal n.eff or Rhat values in the original model output (omitted here), or because the 2.5%-97.5% credible interval spans across zero.

parameter estimate	**Caigual**		**Lower LaLaja**		**Taylor**		**Upper LaLaja**	
	female	**male**	**female**	**male**	**female**	**male**	**female**	**male**
logit_phi_0	1.6	0.61	1.52	1.05	0.72	0	1.54	0.49
logit_phi_b_SL	0.25	0	0.2	-0.04	0.17	-0.08	0.19	0.02
logit_phi_b_density	0.01	0.12	0.19	-0.07	-0.07	-0.04	0.08	0.07
logit_phi_b_season2	0.21	0.23	0.34	0.37	0.38	0.56	0.45	0.49
logit_phi_b_time	0	0	0	0	0.01	0.01	0	0
logitp_0	2.8	3	2.22	1.8	2.65	2.69	2.75	2.83
logitp_SL	0.1	0.68	-0.1	0.34	0.01*	0.56	0.01*	0.34
logitp_density	0.26	0.43	0.24	0.53	0.11	0.21	0.05	0.13
logitp_season2	0.32	0.33	0.07	0.3	-0.13	0.23	0	0.34
logitp_time	-0.02	-0.02	-0.01	-0.01	-0.02	-0.02	-0.02	-0.02

Table S3.2. Estimates of parameters in the Mark-Recapture model for Caigual females with 2 changing age boundaries for analysing monthly survival (φ) and recapture rate (p). * indicates that the estimate is not credible, either because the n.eff or Rhat value is not ideal, or because the 2.5%-97.5% credible interval spans across 0. age_boundary_0[i] represents the intercept for age boundary i, age_boundary_b[i] is the slope for the same age boundary, logit_phi_0[i] is the intercept for survival within age group i, logit_phi_b_SL[i] is the effect of standard length on the survival of age group i, logit_phi_b_density[i] is the effect of population density on the survival of age group i, logit_phi_season2[i] is the effect of season two (dry season) on the survival of age group i, logit_phi_cat3_b is the senescence effect on the survival of age group 3; logitp_beta_SL is the effect of standard length on the recapture rate, logitp_re_sigma is the random effect of time on the recapture rate, and logitp_season[i] is the effect of season i on the recapture rate.

parameter	Mean	Sd	2.50%	50%	97.50%	Rhat	n.eff
age_boundary_0[1]	1.85*	0.26	1.3	1.84	2.39	2.15	9
age_boundary_0[2]	3.61*	0.07	3.48	3.62	3.7	1.1	121
age_boundary_b[1]	-0.01*	0	-0.02	-0.01	0	2.12	10
age_boundary_b[2]	-0.02	0	-0.02	-0.02	-0.02	1.08	126
logit_phi_0[1]	1.87	0.23	1.43	1.87	2.34	1.02	188
logit_phi_0[2]	2.16	0.14	1.87	2.16	2.42	1.01	194
logit_phi_0[3]	1.5	0.07	1.37	1.5	1.62	1.09	219
logit_phi_b_SL[1]	0.48	0.11	0.28	0.48	0.7	1.01	340
logit_phi_b_SL[2]	0.03	0.07	-0.09	0.03	0.15	1.01	809
logit_phi_b_SL[3]	0.58	0.03	0.53	0.58	0.63	1.01	1159
logit_phi_b_density[1]	0.08*	0.09	-0.1	0.08	0.27	1.02	349
logit_phi_b_density[2]	-0.3	0.05	-0.39	-0.3	-0.2	1.01	225
logit_phi_b_density[3]	0.05	0.02	0.01	0.05	0.1	1.03	262
logit_phi_cat3_b	-0.05	0	-0.06	-0.05	-0.05	1.02	599
logit_phi_season2[1]	-0.38*	0.16	-0.72	-0.37	-0.09	1.1	445
logit_phi_season2[2]	0.26	0.08	0.1	0.26	0.43	1	758
logit_phi_season2[3]	0.24	0.04	0.15	0.24	0.33	1.02	766
logitp_beta_SL	0.27	0.03	0.21	0.27	0.33	1	2586
logitp_re_sigma	0.78	0.06	0.67	0.77	0.89	1	2419
logitp_season[1]	1.85	0.15	1.56	1.85	2.15	1.02	157
logitp_season[2]	2.25	0.08	2.08	2.25	2.41	1.02	224

Table S3.3. Estimates of parameters in the Mark-Recapture model for Caigual females with no age boundaries for analysing monthly survival (φ) and recapture rate (p). logit_phi_0 is the intercept for survival, logit_phi_b_SL is the effect of standard length on survival, logit_phi_b_density is the effect of population density on survival, logit_phi_season2 is the effect of season two (dry season) on survival, logit_phi_b_time is the effect of time on survival; logitp_0 is the intercept for recapture rate, logitp_SL is the effect of standard length on recapture rate, logitp_density is the effect of density on recapture rate, logitp_season2 is the effect of season two on the recapture rate, and logitp_time is the effect of time on recapture rate.

Parameter	Mean	Sd	0.025	0.5	0.975	Rhat	n.eff
logit_phi_0	1.6	0.05	1.5	1.6	1.7	1.04	232
logit_phi_b_SL	0.25	0.01	0.22	0.25	0.28	1	4418
logit_phi_b_density	0.01	0.02	-0.04	0.01	0.05	1.08	185

logit_phi_b_season2	0.21	0.03	0.15	0.21	0.28	1	884
logit_phi_b_time	0	0	0	0	0	1.04	291
logitp_0	2.8	0.08	2.65	2.8	2.95	1.01	244
logitp_SL	0.1	0.03	0.05	0.1	0.16	1	3701
logitp_density	0.26	0.03	0.2	0.26	0.32	1	235
logitp_season2	0.32	0.04	0.24	0.32	0.41	1	1138
logitp_time	-0.02	0	-0.02	-0.02	-0.02	1	198

S4

Table S4.1. Estimates for parameters in two-phase growth models and AIC values for the two-phase growth model compared to the von Bertalanffy model for the same sex- and stream-specific dataset. L_{inf} represents the asymptotic length (measured in mm), K is the growth coefficient, t_0 is the theoretical age at zero length in the von Bertalanffy model (measured in months). t_2 is the threshold point (measured in months) where phase one's von Bertalanffy model transitions into phase two's linear growth model, and b is the slope for the linear model. Delta-AIC is the difference between the two-phase model and the previous von Bertalanffy model (shown in Table 5). CA refers to the Caigual stream, LL to the Lower LaLaja stream, TY to the Taylor stream, and UL to the Upper LaLaja stream.

dataset	L_{inf}	K	t_0	t_2	b	AIC	Delta-AIC
CA Female	25.41	0.238	-3.578	10.62	0.206	126532	-210.4
CA Male	17.84	0.835	-1.652	4.397	0.095	48182.86	-54.41
LL Female	23.08	0.264	-3.892	10.62	0.132	257147.4	-996.8
LL Male	17.44	0.94	-1.448	4.621	0.055	91106.66	-139.82
TY Female	25.2	0.374	-2.249	7.671	0.228	224610.9	-923.6
TY Male	19.04	0.967	-1.112	5.338	0.036	107170	-26.6
UL Female	24.77	0.243	-4.05	11.29	0.145	453429.3	-628.5
UL Male	17.84	0.97	-1.411	4.353	0.065	188362	-250.8

S5

Table S5.1. Parameter estimates from sex- and stream-specific lifespan models. Intercept values for five primary habitat types, effects of dispersal frequency and average monthly dispersal distance throughout lifetime, and effect of elapsed time are shown separately. Abbreviations: CA (Caigual), LL (Lower LaLaja), TY (Taylor), UL (Upper LaLaja). * indicates non-significant estimates.

	pool	**riffle**	**sidewater**	**backwater**	**none**	**dispersal frequency**	**average distance**	**time**
CA female	2.138	1.6883*	1.73*	1.62	1.866*	0.272	0.033	-0.00313
CA male	1.362	1.046*	0.9603*	0.93	1.113*	0.829	0.0159	-0.000475
LL female	2.473	2.125	1.985*	1.73	2.462	-0.433	0.0215	-0.00267
LL male	1.538	1.1574*	1.1654*	1.1	1.493	0.11	0.0116	-0.00106
TY female	1.785	1.641	1.975	0.735*	1.519*	-0.394	0.0183	0.00204
TY male	1.21	0.986*	1.213	0.5*	0.967*	-0.0619	0.0176	0.00275
UL female	2.44	2.134	1.861*	1.16	2.29	-0.206	0.00982	-0.00442
UL male	1.475*	1.206*	1.046*	0.823	1.345*	0.0318	0.00739	0.000436

Table S5.2. Parameter estimates from sex- and stream-specific growth rate models. Effects of age, dispersal distance in the current month, and time of study are shown separately. Abbreviations: CA (Caigual), LL (Lower LaLaja), TY (Taylor), UL (Upper LaLaja). * indicates non-significant estimates.

	intercept	**dispersal distance**	**age**	**time**
CA female	2.0396	-0.0018*	-0.1116	-0.0041
CA male	0.9857	-0.0080	-0.1087	-0.0003*
LL female	1.2149	-0.0016	-0.0591	-0.0011
LL male	0.6969	-0.0052	-0.0666	-0.00002*
TY female	2.0000	-0.0019*	-0.1231	-0.0028
TY male	1.0410	-0.0046	-0.1085	-0.0003*
UL female	1.3250	-0.0024	-0.0796	0.0012
UL male	0.8151	-0.0027	-0.0813	-0.0008