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The Role of Local Adaptation on Biting Performance in Trinidadian Guppies

Hannah E. Cohen

THE ROLE OF LOCAL ADAPTATION ON BITING PERFORMANCE IN TRINIDADIAN

GUPPIES

by

HANNAH E. COHEN

(Under the Direction of Emily A. Kane)

ABSTRACT

Divergent selection pressures in populations that occupy different environments can result in
phenotypic differentiation in traits that provide a local fitness advantage. Trinidadian guppy
(*Poecilia reticulata*) populations are separated by physical barriers such as waterfalls which
result in repeated shifts in selective pressures from predator avoidance in high predation
environments towards resource competition in low predation environments. Such shifts in
selection pressures have previously shown that a range of locally adapted morphological and
behavioral traits are changed. However, the role of local adaptation on biting behaviors remains
unclear. I analyzed morphological differences such as body length, jaw position, eye area and
body depth to validate known differences between populations. I then filmed adult females from
replicate high/low predation pairs while they used biting behaviors to feed on an agar substrate.
I did not find divergence in either morphological or kinematic traits, suggesting a general lack of
local adaptation, contrary to previous findings. A lack of divergence could be due to less
pronounced morphological divergence in females, perhaps as a constraint of bearing young, and
the absence of divergent selection on prey capture performance. In female guppies, morphology
and performance are not locally adapted, and divergence may exist primarily in behavioral traits
(consumption rates) as a result of competition in low predation environments.

INDEX WORDS: *Poecilia reticulata*, Kinematics, Local adaptation, Predator/Prey interactions

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HANNAH E. COHEN

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HANNAH E. COHEN

Major Professor: Emily A. Kane
Committee: Christine N. Bedore
                             James H. Roberts

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CHAPTER 1

INTRODUCTION

Adaptation is fundamental to our understanding on how the world evolves. As the world changes, so too do the organisms that live in it. Through gradual change these organisms become well-equipped to survive in their respective environments. Adaptation is the process of changing phenotypes through natural selection and improves fitness (Williams 1966). This genetic change helps an organism survive in its environment and is passed to its descendants. Examples of adaptations include structural traits such as the long caudal fin of the thresher shark (*Alopias pelagicus*) used for stunning fish (Oliver et al 2013), or behavioral traits such as migration in many animal species (Wilcove & Wikelski 2008). However, populations within species can also adapt to local environments. Local adaptation is when there are changing phenotypes within a local population of the same species that are connected by dispersal and gene flow (Kawecki & Ebert 2004). Without constraints, divergent selection between populations can cause each local population to evolve traits that provide an advantage under its local habitat despite the consequences for fitness in other habitats (Fitzpatrick et al 2015). This can be seen in brown anoles (*Anolis sagrei*), where limb lengthening allows for the ability to sprint on broad surfaces like the ground and tree trunks, allowing them to exploit resources there. However, those that have shorter limbs are able to be more careful with their movements and so when anoles with long hindlimbs must run on narrow substrates, like tree branches, they are more likely to fall (Losos et al 2000).

Evolution and speciation is a continual process yet how does this explain the difference of a connected population to two separate species? Species are groups of interbreeding natural populations, which are reproductively isolated from other such groups (Mayr 1942) due to lower

fitness in other habitats (though with exceptions such as sympatric speciation). Local adaptation

of a species can be hindered by gene flow and opposed by natural selection due to its temporal

environmental variability and constrained by a lack of genetic variation (Kawecki & Ebert 2004).

Gene flow can restrict those that have been able to breach into new habitats due to continual

immigration (De Meester et al 2002). For example, the threespine stickleback (*Gasterosteus*

aculeatus) in streams and lakes where there should be an adaptive divergence between these two

different environments, however, there is only divergence with increasing distance. The constant

gene flow from lake to stream and vice versa constrains adaptation (Moore & Hendry 2005).

The growth, survival, reproduction of organisms is dependent on their ability to perform

specific tasks, such as evading predators or capturing prey (Arnold 1983). The ability to perform

those tasks is dependent on interactions with morphology (Wainwright 1996), which can set the

maximum capacity of the individual to make use of specific resources. By establishing the limits

of an individual's ability to perform a certain task, the design of functional systems can

determine how behaviors are performed. Arnold's paradigm describing these links between

morphology, performance, and fitness provides a framework for how an organism is affected by

environmental stressors (Arnold 1983). Arnold's paradigm is a statistical method to test for

changes to morphology that will impact fitness through performance. By using regression

methods, morphological variation's on organismal performance can be quantified and in turn on

an individual's fitness (Addis et al 2017). However, behavior can be used as a filter between

performance and fitness and can determine a certain performance level in relation to

morphological constraints (Garland & Losos 1994). Therefore, we can add behavior to Arnold's

paradigm, where morphology, performance, and behavior all have an effect on the organism's

fitness (Blake & Domenici 2000). In the context of this thesis, morphology is the shape and size

of an organism, performance the organism's absolute ability to do a task (speed, force, etc), behavior modulates performance, and fitness the ability to survive and reproduce. An animal may modify their performance (behaviorally) to give what performance they may actually need (Blake & Domenici 2000). For example, in escape performances the prey may decrease speed in order to turn more effectively (Langerhans et al 2003).

Fish are another example of how the modified paradigm diverges body shape across different habitats (Webb 1982, Webb 1984), as well as in feeding morphology, performance, behavior and diet (Ehlinger & Wilson 1988, Gerry et al 2011). For example, bluegill sunfish (*Lepomis macrochirus*) that inhabit open (pelagic) zones have more fusiform bodies, larger dorsal fin area, and higher pectoral fin aspect ratio in comparison to bluegill in the vegetated (littoral) zones (Gerry et al 2011). Additionally, littoral fish have wider pharyngeal jaws that enables them to grab more though would come at the cost of suction velocity (Liem & Kaufman 1984, Robinson et al 1993, Wainwright et al 1994, Wainwright et al 2007). These differences enable pelagic bluegill to feed on zooplankton in an open environment, whereas littoral bluegill feed on benthic invertebrates in a more complex environment (Ehlinger & Wilson 1988, Gerry et al 2012). In this example, divergence may be the result of phenotypic plasticity in response to alternative food sources, but local adaptation of populations within species can also drive changes (Reznick & Travis 1996).

Feeding is essential for acquiring energy to survive and reproduce. If prey resources are temporally and/or spatially distinct then prey acquisition would be expected to experience strong local selection (Staples & Nomura 1976, Gerking 2014). Many animals, particularly aquatic vertebrates such as fish, use different prey capture strategies such as biting, suction, ram, and filter feeding that differ in the degree of movement and contact between predator and prey

(Montuelle & Kane 2019). Additionally, in biting there are many different ways fish can catch prey: Labridae (wrasses) rely on suction force in combination with biting (Ferry et al 2012), Scaridae (parrotfishes) have fused beak-like jaws that can be used to scrape algae and/or coral from substrates (Bellwood & Choat 1990), Pomacanthidae (marine angelfishes) can grip food items while they are protruded due to the intramandibular joint (IMJ) between their angular and dentary bones of the lower jaw (Konow & Bellwood 2005) which allows them to feed on benthic invertebrates. Girellidae (blackfishes), Acanthuridae (surgeonfishes), Poeciliidae (livebearers), and some Scaridae also have an intramandibular joint that allows for gape expansion to scrape the surface (Vial & Ojeda 1990, Purcell & Bellwood 1993, Streelman et al 2002, Konow et al 2008, Ferry et al 2012). However, even within a fish species there can be a difference in feeding, due to niche partitioning. Bluegill sunfish are able to partition into different niches with those living in the open water and those in the littoral zone. With the absence of a predator these bluegill can exploit new areas and populations have adapted their morphology to perform new tasks (Wainwright 1996, Gerry et al 2012). But bluegill feed using suction, and it is unclear how biting species might display similar patterns.

Trinidadian guppies (*Poecilia reticulata*) are specialized scrapers, possessing jaws adapted for removing encrusted food items (Gibb et al 2008, Dial et al 2017), and can have divergent populations that are kept separated by a physical barrier, often waterfalls, which result in a repeated spatial pattern of local adaptation due to the presence and absence of predators (Reznick & Endler 1982). Populations that live below these barriers are called high predation (HP) due to the prevalence of predators such as pike cichlids (*Crenicichla alta*) and killifish (*Rivulus hartii*). Populations that live above these barriers lack major predators, like the pike cichlid, and therefore are called low predation (LP) (Reznick 1982). They are and have been a

model for understanding local adaptation and the role of genes and the environment (or plastic and genetic responses). For example, guppies in transplant experiments maintain locally adapted phenotypes despite the increased gene flow from the introduced populations (Fitzpatrick et al 2015). This suggests that in natural populations, where gene flow is primarily upstream, local adaptation is likely maintained under strong selection. However, it is less clear how these differences affect feeding performance.

Predation can directly reduce fitness in prey populations through increased mortality and indirectly through stress responses that lead to changes in behavior, reduced foraging time, and reduction in growth rates (Reznick 1982, Reznick et al 2001, Torres-Dowdall et al 2012). Such reduction in growth can be shown in HP guppies, who mature earlier than LP guppies. LP guppies are less fusiform than HP guppies, whose bodies must be adapted in escaping predation (Zandona et al 2011). Due to much less predation, LP guppies instead face a different selection pressure. LP populations are larger than HP populations, raising intraspecific competition for food and mates. LP guppies are greater in size, resulting in bigger jaws that may be used to grab more food (Reznick 1982, Endler 1991, Reznick et al 2001). LP guppies have developed larger jaws that provide a competitive edge over others (Reznick 1982, Zandona et al 2011, Torres-Dowdall et al 2012). Like other poeciliids, guppies are specialized scrapers, possessing jaws adapted for removing encrusted food items (Gibb et al 2008, Dial et al 2017). One would suspect that if the LP guppies are larger than the HP guppies, there should be an increase in the rotation at the IMJ, increasing the gape and allowing them to grab food more efficiently. However, Kane et al (2019) did not find differences in gape size in the two different populations of guppies, so it is also possible that in biting there are no differences in kinematics between the populations. Thus although a shift in selective pressure from predator avoidance in HP toward resource

competition in LP environments has resulted in local adaptation of many traits, whether these changes result in local adaptation of feeding performance remains unclear (Endler 1991, Palkovacs & Hendry 2010, Zandona et al 2011).

To attempt to assess whether local adaptation is affecting the biting kinematics of Trinidadian guppies, I first asked whether morphological differences between populations are present, then quantified differences in biting kinematics across high and low predation populations. I used still images of individuals taken from high-speed video of prey capture to analyze known morphological differences from literature in LP and HP populations. LP population of guppies are known to be larger than those of HP, so I calculated the standard length (the length from snout to caudal peduncle) (Haskins et al 1961, Seghers 1973) and accounted for this difference statistically. Previous literature has suggested that LP guppies would have a larger maximal body depth than HP guppies, as HP guppies are more fusiform in order to escape predators (Haskins et al 1961). A larger caudal peduncle would be beneficial for escape performance in HP populations with more muscle area to propel the fish (Haskins et al 1961, Burns et al 2009, Palkovacs et al 2011). High predation populations have been noted to have a different jaw position than those of low predation where high predation guppies will have a more dorsal mouth than those of low predation (Handelsman et al 2014). Therefore, I selected body depth, caudal peduncle depth, and jaw position as relevant morphological traits. Next, I analyzed filmed high-speed videos of fish while they fed to analyze feeding kinematics. If differences in selection pressures cause changes in resource use that drive adaptation for feeding, then low predation guppies should have increased ability in biting kinematics compared to high predation guppies, meaning that they would have a larger gape and time of contact with the

substrate. Alternatively, differential selection may be weak or the ability to respond to selection

may be constrained, resulting in a lack of local adaptation.

CHAPTER 2

MATERIALS AND METHODS

Collection and housing

Female guppies (N=28) were collected from two replicate low and high predation

populations in the Aripo and Oropuche drainages in Trinidad, March 2017 (Figure 1). Exact

numbers of populations and standard lengths were recorded (Table 1). Sites were determined by

previous researchers (Reznick 1982, 1989, Reznick & Bryga 1996, Reznick & Endler 1982,

Reznick et al 1996). Adult females were chosen due to being more resource driven than males

(needing resources to give birth) (Dussault & Kramer 1981, Reznick 1983) and easier to

visualize on film due to larger size. The current sample of fish were transported to Georgia

Southern University and housed in individual 1.5 L tanks on a recirculating system. Temperature

was maintained at 24 °C and fish were fed commercially prepared flake food daily (API tropical

greens, Mars Inc.). All methods were approved by the Georgia Southern University IACUC

(protocol #17005).

Filming

Filming of fish for biting kinematics began in August 2017 and lasted until March 2018.

Prior to filming, fish were starved for up to two days to encourage feeding behavior. Fish

remained in their holding tank for filming and were allowed to remain still on a countertop for 24

hours to acclimate after being moved from the recirculating system. In the guppies' natural

environment their main source of food is encrusted algae that must be scraped off (Dussault &

Kramer 1981). To imitate this, a fish flake-agar substrate was attached to a baffle and placed into

the tank during filming. While the fish fed upon the substrate, it was filmed laterally with a high-

speed camera (Edgertronic SC1, Sanstreak Corp., San Jose, CA, USA) using near-IR

illumination (JCheng Security, Amazon.com) at 500 fps (Figure 2). This filming set-up is replicated from previous studies, though with a biting rather than suction-inducing prey type (Kane et al 2019). A total of 112 trials were filmed, with an average of 4 trials per individual.

Morphology and Analysis

Still frames of videos were used to analyze morphological differences between different populations of guppies using ImageJ v.1.52a (National Institutes of Health, Bethesda, MD, USA). The frame was determined by having the clearest lateral view of the fish, with minimal swimming movement so body was not curved and its mouth being closed. One video was used per an individual to measure: standard length, caudal peduncle height, eye area, maximal body depth, and jaw position (Figure 3, Panel A). To calculate the standard length, fish were measured from snout to the end of the caudal peduncle. Maximal body depth was measured where the body was the thickest and the mouth position was determined as the difference between the body angle and the upper jaw angle. Caudal peduncle height (minimal body depth) was determined by measuring the length of the caudal peduncle. Body angle was determined from the center of the fish with a straight line through the body and the upper jaw measured by the angle when the mouth was closed. Together these were used to determine the jaw position. Eye area was measured and used as a variable independent from swimming and feeding-related morphological traits.

In addition to samples collected from March 2017, still frames from videos obtained for additional population pairs collected in 2015 and 2016 (Kane et al 2019) were added to enhance inferences on morphological differences. These samples were collected from the Aripo drainage (duplicating my own samples from 2017) and Yarra drainage in 2015 and 2016 with corresponding HP and LP populations (Table 1). As the samples from the Aripo drainage were

sampled in the same sites as the ones collected in 2017, they were pooled across collection years for further analyses. Yarra is an independent drainage on the north slope of the island of Trinidad, and data were analyzed together.

All morphometric data were $\log_{10}$-transformed prior to analysis. Differences in body length were expected *a priori* between the different populations of guppies due to previous literature (Haskins et al 1961, Endler 1983, Reznick & Endler 1982, Reznick et al 1996). Therefore body length, population, and drainage were used as covariate factors in general linear models (GLM) identifying the effects of these factors and their interactions on each morphological trait. All statistics were performed in JMP (JMP 13, SAS Institute Inc., Cary, NC, USA).

Video analysis and Statistics

Before analyzing videos, permutations were run on two individuals (ARHP061 and ARLP067) with five trials each to understand how many trials should be used per individual. An analysis of variance (ANOVA) testing the variation of one kinematic variable showed that three trials approximated kinematic means sufficiently. For instance, when looking at ARHP061 and analyzing peak gape, the ANOVA showed that three (mean 0.012±0.0014), four (mean 0.012±0.0019), and five (mean 0.012±0.0043) trials have no difference between the means. Another argument for using three trials per an individual is seen in ARLP067. When doing an ANOVA of the variable velocity at peak gape, above three trials there is only a 0.01 cm difference in means, allowing for argument's sake that three trials will be enough to run tests. Therefore, we chose to rely on up to 3 trials per fish, where available, to describe intraspecific variation in kinematics. The three best videos were chosen for analysis based on

being in focus and well lit, the fish being perpendicular to the axis of the camera lens, and all movements being visible within the frame.

Once the trials were chosen six points were digitized to determine kinematics using a custom Matlab program DLTdv5 (Hendrick 2008). These six points were: the upper jaw, the lower jaw, the intramandibular joint (IMJ), the eye, a pectoral fin, and the last vertebrae of the spine (Figure 3, Panel B). From these, I was able to calculate the forward and backward body velocity and acceleration (maximum and at the time of peak gape), body angle, peak body angle rate of change, peak gape, time to peak gape, the peak gape (lower jaw) angle, time to peak gape angle, and jaw angle at peak gape. Velocity was determined by using the pectoral fin as a point to calculate the distance traveled throughout the video. Jaw angle was determined from the eye, IMJ, and the lower jaw. Jaw angle at peak gape, not to be confused with peak gape angle, is determined from when the angle of the gape is largest during the video. Peak gape angle was then calculated from the time of the peak gape with the gape angle. The body angle was made from a point on the last vertebrae of the fish as well as a virtual point plotted 5 cm from the vertebrae point that together helped determine the overall body position in the video. Peak body angle rate is the rate of change of the body angle throughout the entire video. Peak gape was determined by calculating the distance between the upper and lower jaws opened at the maximum point.

Visualization of differences in biting kinematics between populations were tested using a principal component analysis (PCA) in the statistical program JMP Pro 13. If individuals cluster in groups, this would indicate a separation by population. However if there was no clustering then this would show that there is no population effects. Next, a mixed model was used with individual nested within population used as a random effect due to utilizing replicate trials per

individual. Fixed effects were population and drainage, used to understand what components were actually driving differences in the PCA.

Table 1. Populations (LP = low predation, HP = high predation) and number of individuals used, as well as mean body length. Sites: Aripo = AR, QD = Quare, VAL = Valencia, CR = Caroni, and YA = Yarra.

Population	Number of Individuals	Mean Body Length with Standard Deviation (cm)
ARLP	8	2.97±0.29
ARHP	8	2.65±0.24
QDLP	7	2.83±0.11
VALHP	5	2.64±0.19
ARLP2	17	2.51±0.2
CRHP	21	2.44±0.35
YAHP	20	1.97±0.32
YALP	23	2.33±0.03
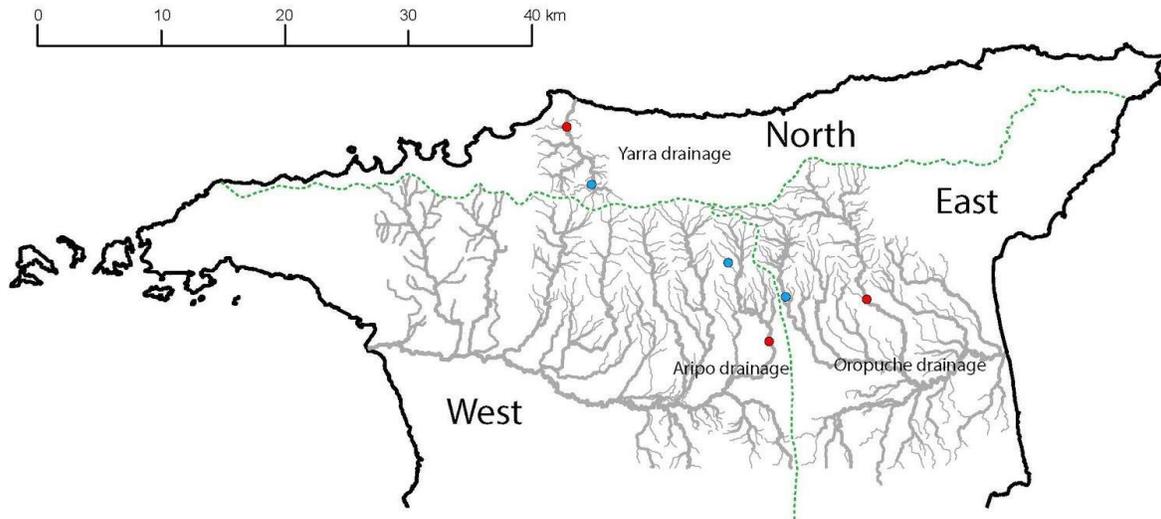
Figure 1. Map of Trinidad sites, showing the six locations that guppies were collected from the three drainages. Red means high predation and blue means low predation.

Figure 2. Filming experimental setup.
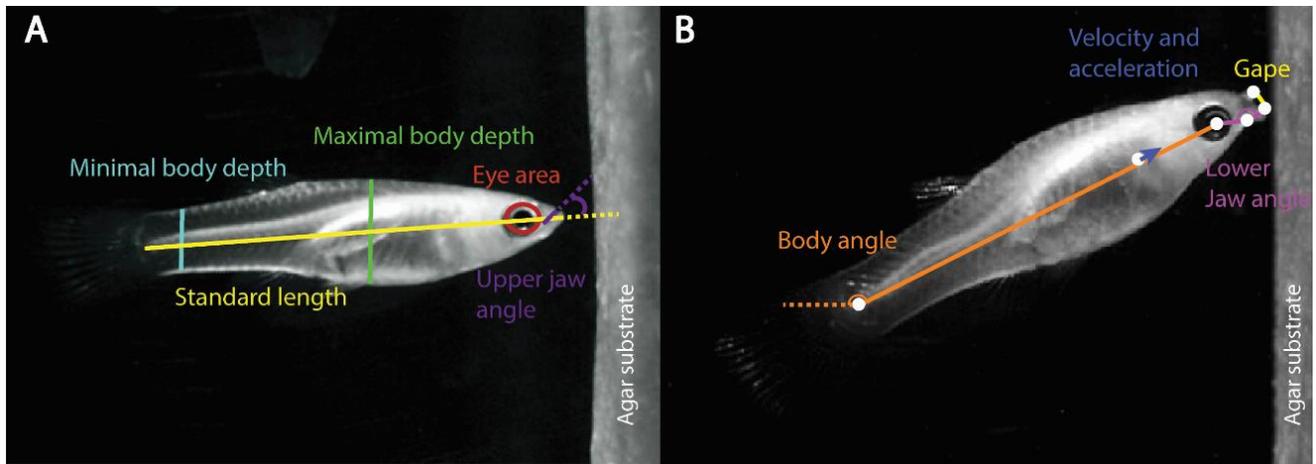
Figure 3. Panel A: Still image from a high-speed near-IR video of a female guppy. Morphology was measured using ImageJ to calculate body angle, jaw angle, standard length, eye area, and maximal and minimal body depths. Panel B: Six points were digitized and used to calculate the kinematic variables shown.

CHAPTER 3

RESULTS

Morphology

In contrast to differences demonstrated in the literature, morphological characteristics did not differ between populations when size differences were accounted for, rather body length and drainage differences have the greatest effect on traits. If the drainages are taken into account, such as an analysis of covariance (ANCOVA) with body length, population, and drainage, body length and drainage have effects on all the variables (Table 2). Maximal body depth (body length $F_{1,11}$= 12.07, p<0.0008; Drainage $F_{1,11}$= 3.4, p<0.038) and minimal body depth (body length $F_{1,11}$= 20.3, p<0.0001; Drainage $F_{2,11}$= 3.4, p<0.037) were affected by body length and drainage while eye area is only affected by body length ($F_{1,11}$= 6.47, p<0.013). Interestingly the jaw position is affected by the drainage ($F_{2,11}$=3.4, p<0.037), though the reason for this is unknown. However, all variables are consistent with having no population effect. Together this shows that drainage effects and body length differences are causing the differences in morphology, and populations are not likely locally adapted in morphology.

Kinematics

As with morphology, kinematics also show a lack of differentiation between the populations. I performed a principal components analysis (PCA) to examine the variation in kinematics. For both drainages, the first axis explains only 19% of the variation (Figure 4; Table 3) with peak gape angle (PC1 loading= 0.48) and jaw angle at peak gape (PC1loading= 0.49) driving the variation. The second axis explained 16.7% of the variation with peak forward velocity (PC2 loading= 0.44) and peak gape (PC2 loading= 0.41) driving the variation. Overlap

of the populations shows that there is no clustering indicating that the populations are not likely different.

To understand if the separate populations of guppies have different kinematics, a mixed model was ran using individual as a random effect. Each variable is individually examined rather than all together, though only if the test of the whole is significant. From this test, three kinematic variables had significant differences due to body length (Table 4). Jaw angle at peak gape ($F_{1,55.4}$=12.7, p<0.0008), which is the angle of the lower jaw when gape is open at its widest, was affected by body length. Peak gape angle was affected as well, with smaller fish having a larger angle in comparison to the larger fish ($F_{1,55.2}$=12.4, p<0.0012). Thirdly, the peak forward velocity which is the speed of the approach to the substrate, had the same result ($F_{1,43.4}$=4.6, p<0.037). In conclusion, the mixed model reveals that again, body length may be the biggest determinant of kinematics.

Table 2. ANCOVA with drainage x body length x population for morphology. Significant results are highlighted in red.

Variable	R^2 adjusted	$F_{11,97}$ ratio	P value	Source	Standard Error	F ratio	P value	Partial effect size
		ANOVA		Effect Tests				
Maximal Body Depth	0.703	20.86	0.0001	**Log[SL]**	**0.213**	**12.07**	**0.0008**	**0.11**
				Drainage	**0.0328, 0.0607**	**3.40**	**0.0375**	**0.655**
				Population	0.0314	0.158	0.692	0.0016
				Log[SL]*Drainage	0.222, 0.404	2.89	0.06	0.056
				Drainage* Population	0.0328, 0.0607	0.981	0.379	0.020
				Log[SL]* Population	0.213	1.16	0.285	0.012
				Log[SL]* Population*Drainage	0.22, 0.404	1.12	0.331	0.023
Minimal Body Depth	0.813	43.67	0.0001	**Log[SL]**	**0.175**	**20.26**	**0.0001**	**0.17**
				Drainage	**0.0269, 0.0499**	**3.40**	**0.0374**	**0.066**
				Population	0.0258	0.798	0.374	0.0081
				Log[SL]*Drainage	0.183, 0.332	2.14	0.123	0.042
				Drainage* Population	0.0269, 0.0499	1.567	0.214	0.031
				Log[SL]* Population	0.175	0.0874	0.768	0.0009
				Log[SL]* Population*Drainage	0.183, 0.332	1.03	0.363	0.021
Eye Area	0.681	21.97	0.0001	**Log[SL]**	**0.372**	**6.47**	**0.0126**	**0.062**
				Drainage	0.0574, 0.106	2.39	0.0973	0.047
				Population	0.055	0.472	0.494	0.0048
				Log[SL]*Drainage	0.389, 0.707	0.697	0.501	0.014
				Drainage* Population	0.0574, 0.106	0.219	0.804	0.0045
				Log[SL]* Population	0.372	0.013	0.910	0.00013
				Log[SL]* Population*Drainage	0.389, 0.707	1.35	0.265	0.027
Jaw Position	0.073	1.779	0.068	Log[SL]	0.811	0.266	0.607	0.0017
				Drainage	**0.125, 0.232**	**3.422**	**0.0366**	**0.066**
				Population	0.12	2.663	0.607	0.0027
				Log[SL]*Drainage	0.848, 1.54	1.55	0.218	0.031
				Drainage* Population	0.125, 0.232	0.381	0.683	0.0078
				Log[SL]* Population	0.811	0.0957	0.758	0.001
				Log[SL]* Population*Drainage	0.848, 1.54	3.05	0.052	0.059

Table 3. Loadings of each morphological variable onto the first and second principal component, for Aripo and Oropuche drainages combined. Variables in red are driving the most variation.

	Components	
Variables	**PC1**	**PC2**
Peak Gape	0.055	**0.41**
Time to Peak Gape	-0.0005	-0.33
Peak Gape Angle	**0.48**	0.002
Time to Peak Gape Angle	-0.27	-0.12
Jaw Angle at Peak Gape	**0.49**	-0.01
Body Angle at Peak Gape	-0.25	-0.06
Peak Body Angle Rate	0.01	0.30
Time to Peak Body Angle Rate	0.21	0.23
Velocity at Peak Gape	-0.07	0.28
Acceleration at Peak Gape	0.23	-0.13
Peak Forward Velocity	-0.21	**0.44**
Time to Peak Forward Velocity	-0.11	0.13
Peak Backward Velocity	-0.15	-0.33
Time to Peak Backward Velocity	0.34	0.02
Peak Backward Acceleration	-0.02	-0.38
Time to Peak Backward Acceleration	0.30	-0.10

Table 4. Mixed model for kinematic variables to find if population, body length, and/or the interaction of population and body length are significant effects.

| Variable	Factor	Degrees of Freedom	Fratio	P value
		Fixed Effect Tests		
Body angle at Peak Gape	Population	1, 27.4	0.37	0.55
	Body Length	1, 46.2	3.35	0.074
	Population*Body Length	1, 46.2	0.97	0.33
Jaw angle at Peak Gape	Population	1, 24	0.079	0.79
	Body Length	**1, 55.4**	**12.7**	**0.0008**
	Population*Body Length	1, 55.4	0.081	0.78
Velocity at Peak Gape	Population	1, 26.5	0.091	0.77
	Body Length	1, 51.1	0.37	0.55
	Population*Body Length	1, 51.1	0.81	0.37
Peak gape angle	Population	1, 22.95	0.025	0.88
	Body Length	**1, 55.2**	**11.6**	**0.0012**
	Population*Body Length	1, 55.2	0.048	0.83
Time to Peak Gape	Population	1, 23.26	0.0043	0.95
	Body Length	1, 43.8	1.87	0.18
	Population*Body Length	1, 43.8	0.3	0.58
Forward velocity peak	Population	1, 25.3	0.87	0.36
	Body Length	**1, 43.4**	**4.6**	**0.037**
	Population*Body Length	1, 43.4	0.28	0.60
Acceleration at Peak Gape	Population	1, 20.6	0.029	0.87
	Body Length	1, 48.2	0.077	0.78
	Population*Body Length	1, 48.2	0.38	0.54
Peak Body Angle Rate	Population	1, 26.8	0.97	0.33
	Body Length	1, 50.5	0.0025	0.96
	Population*Body Length	1, 50.5	1.54	0.22
Peak Gape	Population	1, 23.12	0.33	0.57
	Body Length	1, 45.8	2.15	0.15
	Population*Body Length	1, 45.8	0.0004	0.98
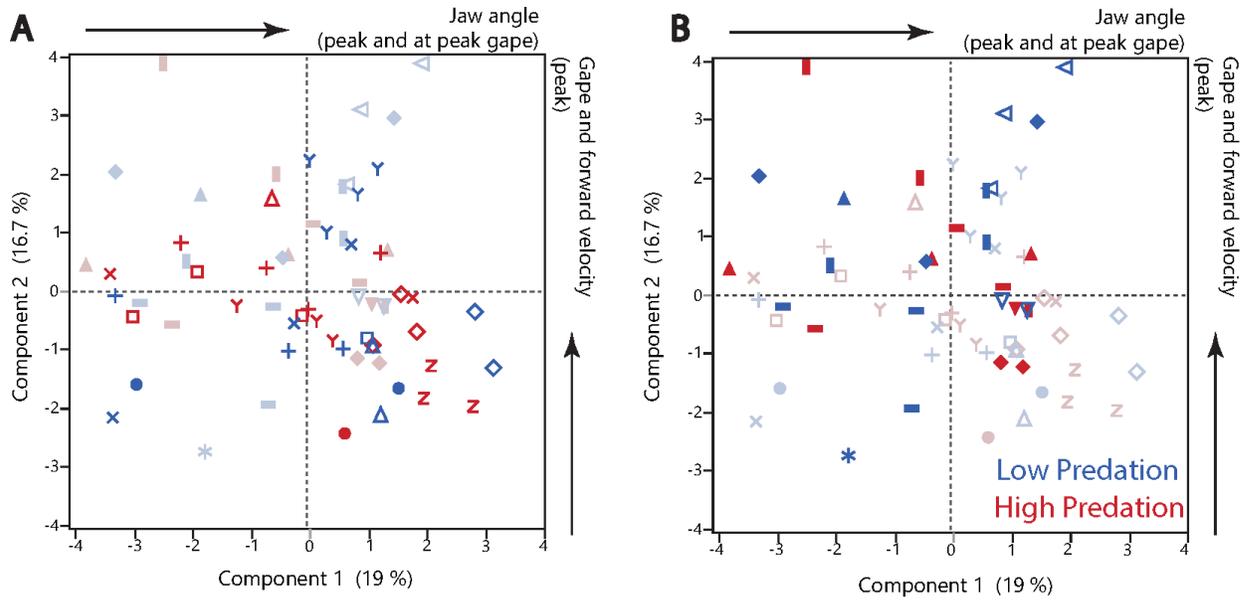
Figure 4. PCA graph that is replicated twice to show each drainage. Aripo (A) and Oropuche (B). Symbols in blue mark low predation population and symbols in red are of high predation. Individuals have different shaped symbols.

CHAPTER 4

DISCUSSION

I found no morphological and kinematic differences between high predation (HP) and low predation (LP) guppy populations despite previous evidence (Haskins et al 1961, Endler 1983, Reznick & Endler 1989, Reznick et al 1996c). Rather, body length and drainages (Aripo, Yarra, and Oropuche) had a stronger effect on differences between populations than an actual population effect. Differences in morphology were due to body length rather than populations, and the populations were not likely locally adapted with respect to morphology. For kinematics, three variables had significant differences due to body length. Peak gape angle, the maximum gape angle, was a larger angle for smaller fish than expected. Jaw angle at peak gape, the measurement of the jaw angle at the time of peak gape, was also affected by body length. This may indicate that fish are using different forms of biting: the bigger fish are picking while the smaller fish are scraping. Thirdly, the peak forward velocity, the speed of the approach to the substrate, was greater in larger fish.

A lack of differences between populations in morphometric or kinematic traits may be due to a lack of divergence in selection pressures or differences in response to selection in females compared to males used in previous work. Previous studies are in conflict with each other whether body shape (morphology) responds to predation in guppies. Burns et al (2009) found no relationship between predation regime and body shape for Trinidadian guppies. Langerhans and DeWitt (2004), found differences in both body depth and caudal peduncle height but only examined males. Handelsman et al (2014) also declined to use females when studying phenotypic plasticity and its effect on body shapes, finding that high predation males have more dorsal mouths than those of low predation. Both studies excluded using females, as they cite that

female body shapes change over gestation. The females I used were filmed at the earliest point of gestation to avoid effects of pregnancy. Therefore, my results suggest that body shape in females may not follow expected patterns that are based on patterns observed in male guppies.

We are still not fully sure how changes in predator composition affects body shape in fish. For instance, the density of predators could differ between rivers, but how that might affect guppy body shape is unknown (Burns et al 2009). We know even less about possible differences between the rivers in what are considered to be minor predators such as kingfishers and other species of fish. Many studies only focus on *Rivulus hartii* and *Crenicichla alta* as predators of guppies (Haskins et al 1961, Reznick & Bryga 1996, Magurran & Phillip 2001). But differences in predation from site to site, in both density and composition, rather than presence and absence of specific predators, may be a reason why functional traits do not appear to be locally adapted.

Between the sexes there are also behavioral differences that can shape morphology. Males tend to stick closer to shore while females may inhabit deeper water where water is faster (Croft et al 2004, 2006). This can cause these females to look like what Hendry et al (2006) have seen while males are more gibbose. There is possibly even sexual dimorphism in feeding kinematics, showcased for the first time in fishes in the threespine stickleback (*Gasterosteus aculeatus*), where males had faster jaw protrusion than females but females had greater jaw protrusion (McGee & Wainwright 2013). This morphological and kinematic divergence in the species could have resulted from ecological use differences between the sexes. No known studies have compared feeding kinematic differences between the sexes in guppies so it may be possible that males, who have greater morphological differences among populations (Haskins et al 1961), will also have greater kinematic differences. Such kinematic and morphological differences in the sexes may allow for colonization of new environments, something that guppies are

particularly known for (Carvalho et al 1996, Reznick et al 1996). Unlike males however, females may be restricted due to a constraint on the evolution of phenotypic plasticity (Magurran 1998). Guppies are livebearers and morphological diversification may be muted due to that constraint (Robinson & Wilson 1995).

Seasons may also have a part to play in affecting the morphology and performance of populations of Trinidadian guppies. During the year the prey composition changes with the locations where the populations are, so perhaps although guppies are feeding on different things seasonally overall they eat the same foods just in different times of the year (Reznick 1989, Zandona et al 2017). In this case, there may not be a need to change morphology and performance in these populations. The wet season in Trinidad is from May to December and the fecundity in guppies is reduced during this time. Life history traits between the populations are muted (gestational periods, number of offspring, etc.) during the wet season as there is high river discharge with faster water velocity that can displace guppies as well as a build-up of silt that may make feeding more difficult (Reznick 1989, Reznick et al 1990). Zandona et al (2017) found that LP sites had higher trophic position and proportion of invertebrates and assimilate less epilithon than HP sites. LP could be more efficient invertebrate consumers than HP, perhaps due to an evolutionary response to greater intraspecific competition for higher quality food. This could be intensified by seasonality, where HP guppies are more selective and specialized on higher quality food items. Or simply LP guppies may have adapted to high intraspecific competition for limited resources (Zandona et al 2017). However, again I did not find differences in my study, suggesting that the earlier hypothesis of the guppies having no need to specialize because they eat the same things but at different times of the year may be why there were no differences in morphology nor kinematics.

Biting in fishes allow for them to acquire resources in new ways. Poeciliidae are specialized scrapers who eat algae and invertebrates from the benthos (Dussault & Kramer 1981, Reznick 1989, Hernandez et al 2008). Because of previous evidence of guppy morphology differing between populations, I had expected this to affect kinematics as well (Haskins et al 1961, Endler 1983, Reznick & Endler 1982, Reznick et al 1996). A previous study of feeding kinematics in guppies has shown no differences in kinematics between the populations (Kane et al 2019). However, their analysis on whether integration during suction feeding in a non-suction feeding fish is generalized showed that high predation populations lack the integration of swim speed and mouth size, unlike low predation populations. This lack of integration was hypothesized that it may allow for flexibility across feeding modes (Kane & Higham 2015) and allow the guppy populations to colonize new areas. However, my study, like theirs, showed no differences between the populations, and these differences in integration may not be the result of feeding specialization. Alternatively, specialization may occur more on a behavioral level, than with morphology and performance. For example, guppies from low predation environments may be biting at a higher rate than those from high predation, which may be advantageous in a more competitive environment with less resources (Palkovacs et al 2011). Therefore, competition may drive divergence in how feeding performance in utilized in each environment, rather than feeding performance itself, and this selective force needs to be studied further.

Behavior can be used as a filter between performance and fitness and can impose boundaries on performance in combination with morphological constraints (Garland & Losos 1994). The modified Arnold's paradigm (morphology-performance-behavior-fitness) allows an animal to modify their maximum performance using behavior to give the performance they may actually need (Blake & Domenici 2000). For prey capture in female guppies competition may be

the primary selective force (Reznick et al 2019, Reznick & Travis 2019), rather than differences in prey, resulting in local adaptation at the level of behavior, but not at morphology and performance. In other words, the selective force is acting on behavior and down (behavior-performance-morphology) rather than bottom up (morphology-performance-behavior).

By studying local adaptation in guppies we can better understand it as a whole in all manner of organisms, as well as adaptation and evolution. Guppies are a model organism, meaning that they already have a wealth of research behind them, are plentiful in many different environments, and are easy to take care of in the laboratory (Reznick et al 2008). We use this species to understand such concepts of evolution in place of others that would not be so easily accessible. Other organisms have been used to study evolution, such as *Drosophila* and mice whose quick generation times allow us to see evolution in short timescales (Hedges 2002). In my study species, Trinidadian guppies, I found no local adaptation in their feeding morphology and kinematics. This is in stark contrast to many other studies where many morphological differences have been documented in the fish. However, even though I found a lack of local adaptation in their feeding, this allowed me to make speculations on why that was the case. Other studies have also found a lack of local adaptation in different organisms, for example in *Buddleja davidii*, an invasive ornamental plant in Europe. Ebeling et al (2011) found that all of the populations responded in a similar way to the different environments they were placed in, suggesting a lack of local adaptation to climate. Understanding how an organism may or may not adapt to a habitat is complex, and using a model organism such as the Trinidadian guppy to study local adaptation is useful because it represents a further case where local adaptation between populations for feeding may not be present. In this case, it may either be due to weak or absent selection, or

guppies may provide an example where behavior is influenced by selective forces such as competition, masking selection in functional traits.

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