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Behavioral diversity and biomechanical determinants of the outcome of a fish predator–prey interaction

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ORIGINAL RESEARCH

Behavioral diversity and biomechanical determinants of the outcome of a fish predator–prey interactionQ. G. A. Milton III^{1,*} & P. J. Bergmann¹ ¹Department of Biology, Clark University, Worcester, MA, USA**Keywords**

boldness; C-start; kinematics; performance; subjugation; predator–prey interactions; biomechanics; high-speed video.

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Abstract

Predator–prey interactions are ubiquitous and under strong selection because of the consequences experienced by both predator and prey if they lose the interaction. Biomechanics and behavior play important roles in the outcome of these interactions, but many studies focus on the prey, restrict the range of behaviors considered, and the role of prey boldness in the outcome is not understood. We used high-speed video to test for effects of multiple measures of performance and kinematics of both the predator and prey, and boldness of prey on the outcome of interactions between Pike Cichlids (*Crenicichla* sp.) and Guppies (*Poecilia reticulata*). We found high variation in the behaviors employed during the predator–prey interactions, including in suction versus raptorial feeding, strike accuracy, and guppy responsiveness. We also found that predators moving relatively slower and prey moving relatively faster were more successful at consuming the prey and evading the predator, respectively. Prey that reacted farther from the predator was more likely to escape predation, but boldness of the prey did not affect the interaction. Our work suggests that a high level of variation in predator–prey interactions is widespread, even when strike and escape behaviors are stereotyped. We also showed that what both the predator and the prey do during an interaction are important in determining the outcome.

Introduction

Predator–prey interactions are ubiquitous in nature and result in strong selective pressures because the resulting outcomes are either prey death or the predator going hungry (Combes et al., 2012; Lima, 2002). These interactions affect the evolution of predators and prey by shaping predator stalking behavior, prey evasion behavior, locomotor performance of both, and traits such as hunting and defensive weaponry (Brodie III & Brodie Jr., 1999a, 1999b; Harris et al., 2010; Laundré et al., 2010; Wheatley et al., 2015; Wilson et al., 2020). An evolutionary arms race of reciprocal adaptations often drives the evolution of predators and prey (Brodie III & Brodie Jr., 1999a, 1999b; Shepherd et al., 2019). Predator–prey interactions affect prey populations through consumption of prey, and modification of prey behavior (Brown et al., 2005; Laundré et al., 2010; Mirza & Chivers, 2003; Peckarsky et al., 2008). Both predators and prey influence these interactions and the abundance of either can influence other trophic levels in an ecosystem (Ioannou et al., 2008; Lima, 2002;

Paine, 1966; Thrush et al., 1994). Predators can have a top-down effect by changing population sizes at lower trophic levels (Paine, 1966; Ripple et al., 2016). Although prey suffers the ultimate cost if they lose, predators are still under strong selection to secure resources for growth and reproduction (Brodie III & Brodie Jr., 1999b).

Predator–prey interactions are complex and consist of several stages. Prey may detect the predator before being detected themselves and avoid an interaction altogether (Gazdewich & Chivers, 2002; Main, 1987). The ability of the predator to conceal itself, and prey's tolerance of risk can affect detection (Gazdewich & Chivers, 2002; Hulthen et al., 2017; Ioannou et al., 2008; Main, 1987). Prey perceive risk from the intensity of predator cues, habitat structure, and number of conspecifics around them (Fraser & Cerri, 1982; Gazdewich & Chivers, 2002; Van Buskirk et al., 2011). Prey assess and respond to perceived risk while foraging for food, searching for mates, or defending territory (Brown et al., 2005; Harris et al., 2010; Hulthen et al., 2017). Populations that are under heavy predation pressure often have bolder individuals that are risk tolerant

to maximize opportunities to forage and find mates (Brown et al., 2005; Harris et al., 2010; Ioannou et al., 2008).

The evaluation stage begins once a predator detects the prey (Whitford, Freymiller, Clark, et al., 2019). During evaluation, prey must detect predators and determine when to flee based on predator proximity, known as reaction distance (Moller & Erritzoe, 2014). The prey's detect of a predator can be hindered by predator concealment, prey foraging distraction or orientation away from the predator (Krause & Godin, 1996; Lima & Dill, 1990; Moore & Biewener, 2015; Morley & Buckel, 2014). A long reaction distance may result in predators not attacking, but results in loss of foraging opportunities (Krause & Godin, 1996; Moller & Erritzoe, 2014; Morley & Buckel, 2014).

A predator attack consists of pursuit and subjugation stages, which occur in close quarters and are often determined by the locomotor performance and kinematics of both predator and prey (Combes et al., 2012; Whitford, Freymiller, Higham, et al., 2019). Absolute maximal velocity is a common, ecologically relevant measure of performance (Grigaltchik et al., 2012; Husak, 2006; Irschick & Meyers, 2007; Le Galliard et al., 2004; Miles, 2004). Predators typically are larger than prey, so have higher velocity but lower maneuverability (Combes et al., 2012; Walker et al., 2005; Wilson et al., 2018). The higher maneuverability of prey often allows them to control the escape path to which the predator must react (Moore et al., 2017; Moore & Biewener, 2015; Wilson et al., 2020). Predators have evolved predation strategies such as ambush or ballistic interception to nullify prey maneuverability (Lima & Dill, 1990; Marras et al., 2015).

Work *in silico* shows the importance of size, with relative velocity (body lengths/s) being a stronger predictor of prey escape than absolute velocity (m/s; Van Damme & Van Dooren, 1999). Such work also shows that the relative sizes of predators and prey dictate the ability of prey to escape a predator (Wilson et al., 2020). The outcome of a predator–prey interaction is also dependent on habitat complexity, substrate, obstacles, and refuge availability (Husak, 2006; Irschick, 2003; Moore & Biewener, 2015; Wilson et al., 2020). This *in silico* work has identified variables that may be important in predator–prey interactions, but that still need testing using live animals.

Kinematics such as strike and escape reaction times, distances, angles, and durations can also affect the outcome of the interaction (Combes et al., 2012; Corcoran & Conner, 2016; Lima & Dill, 1990; Morley & Buckel, 2014; Walker et al., 2005; Whitford, Freymiller, Higham, et al., 2019). Some prey, including kangaroo rats (*Dipodomys deserti*), employ unpredictable escape tactics including kicks, turns, and jumps that deter predators (Whitford, Freymiller, Higham, et al., 2019). Other organisms also use unpredictable movements to evade predation (Combes et al., 2012; Lima & Dill, 1990; Wilson et al., 2020). Predators tend to strike at short distances to maximize success (Corcoran & Conner, 2016; Wilson et al., 2015). However, strike timing of predators and reaction timing of prey also depend on predation strategy. Sit-and-wait predators strike suddenly at close proximity, selecting for reduced prey reaction time (Moore & Biewener, 2015). In

contrast, when escaping active pursuit predators, prey must react at a sufficient distance to not be overtaken and must evade the predator until it tires (Corcoran & Conner, 2016; Wilson et al., 2015). How all of these factors collectively affect the outcome of predator–prey interactions remains poorly understood.

During fish predator–prey interactions, both predator and prey are anatomically similar, swim in the same medium, and use stereotyped fast starts for escape and attack (Domenici & Blake, 1997; Domenici & Hale, 2019; Walker et al., 2005). Prey fish escape predators by bending their body into a “C” and rapidly propelling themselves in a new direction (Domenici & Blake, 1997). Predators capture prey by bending into an “S” to propel themselves toward the prey (Domenici & Blake, 1997; Harper & Blake, 1991). The prey's ability to rapidly change direction during a C-start reduces the predictability of its movements (Walker et al., 2005), but a slow reaction time or insufficient reaction distance can nullify this advantage (Katzir & Camhi, 1993). Although we know much from past fish predator–prey research, it has frequently prioritized sampling of prey and used stringent exclusion criteria to maximize comparability of trials. In contrast, work on kangaroo rats and jerboas suggests considerable variation in how prey behave to escape predators (Moore et al., 2017; Whitford, Freymiller, Higham, et al., 2019).

Here, we study interactions between Pike Cichlids (*Crenicichla* sp.) and guppies (*Poecilia reticulata*) to test which aspects of performance and kinematics determine the outcome of the interaction during the evaluation, pursuit, and subjugation stages. The life history and biomechanics of this system are well studied, making it ideal for further study (Ghalambor et al., 2004; Johansson et al., 2004; Reznick & Endler, 1981; Walker et al., 2005). We consider trials with a wide range of behavioral characteristics to understand what factors of both predators and prey influence the outcome. First, we test the hypothesis that bolder prey will be at higher risk of predation. We predict that bolder guppies will have longer reaction times and shorter reaction distances, resulting in lower survival (Katzir & Camhi, 1993; Morley & Buckel, 2014). Second, we test whether relative and absolute performance differ in explanatory power of the outcome, predicting that relative performance will be the better predictor of outcome (Van Damme & Van Dooren, 1999). Third, we test the hypothesis that C- and S-start performance and kinematics are important predictors of outcome. We predict that faster relative velocities of the predator and prey will increase their respective success. We also predict that predators with shorter strike distances and prey with quicker reaction times and longer reaction distances will be more successful. Finally, we categorize all observed interactions qualitatively to understand the range of behaviors used by both predator and prey (Whitford, Freymiller, Higham, et al., 2019).

Materials and methods

Animal husbandry

All work was approved by the Clark University Institutional Animal Care and Use Committee, with particular emphasis on minimizing distress to the subjects. We acquired fish from

commercial dealers and kept them in aquaria with water temperatures of 26–29°C. Wild-type guppies (*Poecilia reticulata*) were housed in a 38 L aquarium equipped with ceramic beads for biological filtration and substrate, and plastic plants for refuge. Fish were fed commercial flake food daily and allowed at least 1 day to acclimate before use in trials.

We obtained nine *Crenicichla sveni* and three *Crenicichla* sp. “Venezuela” pike cichlids and housed them singly or in pairs, separated by dividers, in 114 L or 189 L aquaria with a sand substrate, and large rocks for hiding (Montaña & Wine-miller, 2009). We fed cichlids bloodworms daily except the day prior to trials. Water changes were conducted bi-weekly and all aquaria had activated charcoal filtration.

We collected standard length data by imaging fish with a ruler for scale (4000 × 6000 pixels) using a Canon EOS Rebel T7 camera with a Canon Macro 100 mm lens (Canon U.S.A. Inc. Melville, NY, USA). Guppies were imaged in a petri dish with water, and cichlids were imaged postmortem. We measured the standard length from the tip of the snout to the posterior end of the caudal peduncle using ImageJ (Rasband, 2011).

Boldness trials

We quantified boldness of guppies using a standard approach and arena (Brown et al., 2005; Harris et al., 2010). We used a 10 cm cube refuge box glued to the bottom of a 51 x 26 x 31 cm (38 L) aquarium against the center of a 26 cm wall. The box contained a 5 cm x 5 cm opening in the front covered by a removable trap door. We blacked out the arena on all sides except the top to allow illumination and video recording.

For boldness trials, we carefully poured each guppy into the refuge box. After a 5-min acclimation period, we removed the trap door, allowing the guppy to exit. Guppies were video recorded using a Casio EX-ZR700 camera (30 Hz, 1920 x 1080 pixels) until they emerged or 10 min had elapsed. We conducted two trials per guppy, with a 1–2 h rest between trials. Guppies were then returned to their containers and used in predator–prey trials the following day. The water was changed in the boldness arena before each trial to avoid chemical cues from previous subjects. Boldness was the average number of seconds it took each guppy to leave the refuge box over the two trials (Brown et al., 2005).

Predator–prey trials

A 25 x 15 x 20 cm (L x W x H) acrylic arena was used for predator–prey trials, filled with water from the cichlids’ aquaria. Guppies were poured into the arena and allowed a 5-min acclimation period. Then cichlids were placed into the arena. To minimize stress on guppies, each was used in a single predator–prey trial, and cichlids were allowed only one strike attempt per trial, defined as a rapid acceleration toward the guppy accompanied by a buccal expansion (Walker et al., 2005). Guppies were either eaten or escaped and none were visibly injured. Cichlids were allowed a maximum of

three trials up to 10 min each per day, but only one trial in which they consumed the guppy.

We recorded each trial using two synchronized AOS Promon U750 cameras, controlled with AIS v4.6.0.5 software (AOS Technologies ag, Baden, Switzerland) at 480 Hz and 800 x 600 pixel resolution. Cameras were positioned in dorsal and lateral position, aligned to record the same volume. A calibration object made of LEGO was recorded prior to each session to allow the calculation of 3D coordinates.

Digitizing and performance

Videos were calibrated and digitized in MATLAB 2020a (MathWorks, Natick, MA, USA) using DLTdv8a (Hedrick, 2008). Cichlids were digitized at two points: the tip of their snout, and the center of the head at eye level. Given their small size, guppies were only digitized at the tip of their snout. Digitizing videos from two views followed by direct linear transformation using DLTdv8a provided us with xyz coordinates of each point in each frame. We used the spline tool in MATLAB to fit a quintic spline to cumulative displacement and time data for the guppy and the eye-level point of the cichlid. Splines were smoothed until secondary oscillations disappeared and the maximal value of the second derivative stabilized (Bergmann et al., 2017). The first and second derivatives of the spline represented frame-by-frame velocity and acceleration, respectively. We calculated the maximum velocity and acceleration for both predator and prey, and the average velocity during the cichlid’s strike. Dividing absolute velocities and accelerations by standard length gave relative measures. We also recorded if the guppy was within one body length of an arena wall.

Predator–Prey interactions and kinematics

We calculated the durations of particular events during trials by dividing number of frames by frame rate. We calculated cichlid strike duration from when the caudal fin began displacing to one side at the beginning of the S-start to when the cichlid began closing its mouth after buccal expansion (Rand & Lauder, 1981). Strike distance was the Euclidean distance between the xyz coordinates of the cichlid and guppy snouts at the beginning of the strike. Strike angle was measured at the beginning of the strike as the angle between a line connecting the guppy’s snout and dorsal fin (the vertex) and the middle of the cichlid’s snout with ImageJ. Strike accuracy was defined as whether a cichlid would have touched the guppy had the guppy not moved (similar to Whitford, Freymiller, Higham, et al., 2019). To do this, we drew a line in ImageJ along the length of the lateral line and dorsal midline of the guppy in the frame before it moved in both videos, and determined if the cichlid intersected both lines during the trial, which was an accurate strike. We also recorded whether cichlids employed suction (Wainwright et al., 2015) or raptorial (Hocking et al., 2014) feeding. Suction occurred when the guppy moved toward the cichlid not by swimming, prior to the cichlid touching it (Wainwright et al., 2001). Raptorial feeding involved the

cichlid biting the guppy (Ferry et al., 2015). Ram swimming was used in both suction and raptorial feeding because the cichlid moved closer to the guppy during its strike (Ferry et al., 2015; Longo et al., 2016; Wainwright et al., 2001).

Guppies typically reacted to cichlids by initiating a C-start. We calculated guppy C-start duration for the first two C-start stages (Walker et al., 2005). Stage one began when the guppy started bending into a “C” shape and ended when it was maximally bent. Stage two immediately followed stage one until the tail was maximally bent in the opposite direction. Guppy reaction distance was the 3D Euclidean distance between the cichlid and guppy snouts at the first frame of the C-start. Reaction time was the time from the beginning of the cichlid’s strike to the beginning of the guppy’s C-start.

We only analyzed trials when both cameras captured the event. In six trials the cichlid’s tail was out of frame, so strike angle, strike distance, and reaction time were not ascertained. We also could not digitize trials where either fish was facing away from cameras. Ninety of 246 trials were digitizable. Three of the 90 were discarded because the cichlid did not have any successful subjugations. One was discarded because the cichlid missed and the guppy did not react, but this trial was included in our qualitative analysis. We converted reaction and strike distance to meters, strike angle to radians, and divided relative accelerations by 100 so that variables had similar magnitudes. We added one to each boldness score to avoid zeros, allowing log-transformation.

To capture the complexity of the interactions, we tallied the number of trials with different qualitative outcomes and calculated their percentages (Fig. 1; Whitford, Freymiller, Higham, et al., 2019). We tallied whether the guppy was eaten or not, whether the guppy reacted or not, the subjugation strategy (suction or raptorial) of the cichlid, accuracy of the strike, and whether or not the guppy jumped out of the water.

Statistical analysis

Statistical analyses were conducted in R v4.0.2 (R Core Team, 2020). We compared guppy standard length, boldness, performance, and kinematic variables between sexes using ANOVA. None of these variables differed between females, males, or juveniles of unknown sex (Table S1.), so we pooled all guppies in subsequent analyses. To test the effect of boldness on reaction, we used bivariate regressions with the log of boldness as the explanatory variable, and reaction distance or reaction time as response. To test whether boldness affected the binomial response of whether or not the guppy reacted, we used logistic regression.

To test the effect of C- and S-start performance, kinematics, and guppy boldness on subjugation success, we fit generalized mixed effects logistic regressions using the *glmer* function in the “lme4” package (Bates et al., 2014). Subjugation success was the binary response: whether the guppy escaped (0) or was eaten (1). We included cichlid species, and individual nested in species as random effects. We calculated standardized odds ratios as effect sizes, which represent the fold change in the likelihood of subjugation success if an explanatory variable increased by one standard deviation (Walker

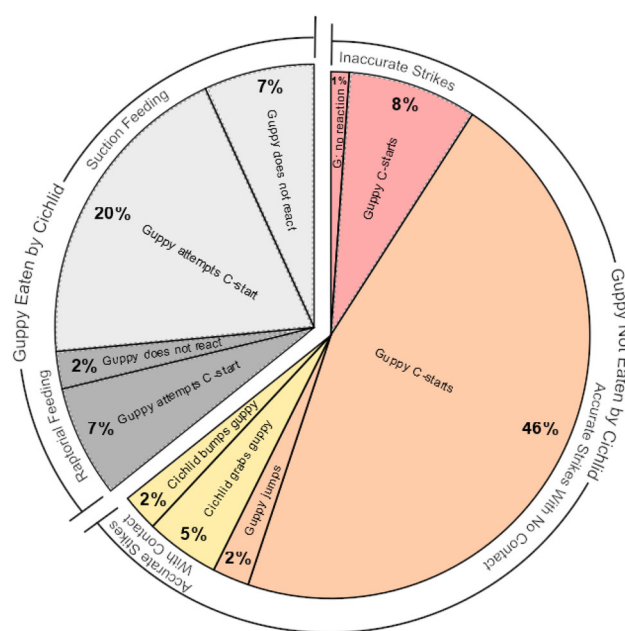


Figure 1 Frequencies of all observed outcomes ($n = 87$ total). Red shades indicate inaccurate unsuccessful strikes. Orange shades indicate accurate unsuccessful strikes in which no contact was made with the guppy. Yellow shades indicate accurate unsuccessful strikes in which contact was made with the guppy. Dark gray shades indicate subjugation by raptorial feeding. Light gray shades indicate subjugation by suction feeding.

et al., 2005). To test if bolder prey were more at risk of being eaten, we fit a model with the log of boldness as the explanatory variable.

We tested whether relative and absolute performance differed in their predictive ability by fitting two mixed effects logistic regressions. The first included absolute cichlid and guppy maximum velocity and maximum acceleration, and the average absolute velocity of the cichlid strike as explanatory variables. The second model included relative measures of the same variables. We compared these models with ANOVA (Crawley, 2012), and calculated their conditional (variance explained by the entire model) and marginal R^2 (variance explained by fixed effects) using the *r.squaredGLMM* function in the “MuMIn” package (Barton, 2010; Nakagawa & Schielzeth, 2013). We used the best model to test which aspects of performance affected the outcome. We also ran two-sample t -tests of whether cichlid maximum and average strike velocity differed between successful suction and raptorial feeding strikes, and between accurate and inaccurate strikes.

We tested whether the kinematics of fast starts predicted subjugation success by fitting a mixed effects logistic regression using strike angle, strike distance, reaction distance, and reaction time as explanatory variables. We fit a separate model with C-start stage durations because of sample size differences. The walls of the arena could interfere with the interaction, so we fit a model with subjugation success as the response and whether the guppy was within a body length of the wall as a binary explanatory variable.

Models with binary responses used a z -statistic while models with continuous responses used a t -statistic. We calculated tolerances for analyses with multiple explanatory variables to evaluate collinearity, with tolerances >0.1 being acceptable.

Results

Behavioral variation in predator–prey interactions

We observed a wide range of qualitative outcomes from the predator–prey trials (Fig. 1). In 64% (56 of 87 trials) the guppy escaped, while in 36% (31) the cichlid subjugated the guppy. Eighty-five percent (48) of the unsuccessful cichlid strikes were accurate and 15% (8) were inaccurate. Most commonly, the guppy employed a C-start in a rapid escape attempt, but on two occasions the guppy also jumped out of the water to evade the cichlid. The cichlid grasped or made contact with the guppy in six of the unsuccessful strikes but the guppy managed to escape. The guppy did not react in nine trials and was subjugated in eight of those. In the remaining trial, the cichlid missed the guppy. Of the 31 successful subjugation trials, 74% (23) were by suction feeding and 26% (8) were raptorial.

Guppy boldness

Guppy boldness did not influence the guppies' reaction distance or time, or whether the guppy reacted (Table 1). A guppy's boldness also did not influence the subjugation success of the cichlid (Table 1). Although there was a wide range of boldness scores among the guppies, there was also a heavy right skew, with 34 of 85 individuals exiting the box within the first 10 s (Fig. S1.). However, 27 guppies took taking ≥ 30 s to emerge (Fig. S1.).

Predator and prey performance

Size-relative performance measures explained the subjugation success of the cichlid significantly better than absolute measures (ANOVA: $\chi^2 = 0.482$, $P = <0.001$). However, they only explained 2.6% more of the variance in subjugation success than the absolute performance model (relative: $R^2_m = R^2_c = 0.398$, Table 2; absolute: $R^2_m = R^2_c = 0.372$, Table S2). A one standard deviation (SD) decrease in cichlid relative maximum velocity resulted in 9.09 higher odds of capturing the guppy, while a one SD unit increase in guppy

relative maximum velocity resulted in 4.35 higher odds of escaping subjugation (Table 2, Fig. 2a). Although cichlid maximum velocity had a low tolerance (Table 2), its exclusion did not change the results (Table S3).

Cichlids did raptorial strikes at an average velocity of ~ 2.8 body lengths per second faster than suction strikes (d.f. = 19.8, $t = 2.44$, $P = 0.025$). Although cichlid maximum velocity was 1.8 body lengths per second higher in raptorial than suction strikes, this result was not significant (d.f. = 16.2, $t = 1.14$, $P = 0.272$). Cichlid average and maximum strike velocity were 1.6 and 0.8 body lengths per second faster for accurate than inaccurate strikes, respectively, but these differences were not significant (Average: d.f. = 4.9, $t = -0.72$, $P = 0.502$; Maximum: d.f. = 8.7, $t = -1.51$, $P = 0.167$).

Kinematic variables

Guppy reaction distance was the only kinematic variable to significantly affect subjugation success. A one SD increase in reaction distance resulted in a 6.67 times higher chance of escape (Table 3, Fig. 3). Although we took account of cichlid species and individuals as random effects, they explained a negligible amount of variation, so had little effect on subjugation success (Table 3). The duration of the guppy C-start stages explained almost no variation (Table 3). Finally, the walls of the arena had no effect on subjugation success (Table 3).

Discussion

Predator–prey interactions are complex

Despite the stereotyped nature of fast starts in fishes, we found an incredible amount of behavioral variation in the predator–prey interactions between *Crenicichla* and guppies. Some studies of predator–prey interactions have stringent exclusion criteria for trials, excluding some of the variation that we observed (Domenici & Blake, 1997; Wakeling, 2001; Walker et al., 2005). We found that on several occasions, guppies used a C-start to garner enough speed to leap out of the water. This likely acted to decrease their exposure to danger and land safely in an unpredictable location. Guppies were also able to maneuver out of the cichlid's mouth by undulating rapidly or taking advantage of the cichlid reopening its mouth to swallow. However, the guppy sometimes did not react, providing the cichlid with a stationary target. In two trials, the guppy was oriented away from the cichlid. Krause and Godin (1996)

Table 1 Summary of models testing the effect of guppy boldness on their reactions to cichlids and the outcome of the interaction

Response variable	Slope	SE	Test Stat	P	R^2_m	R^2_c
Reaction distance	<0.001	0.002	$t = -0.015$	0.988	<0.001	<0.001
Reaction time	-0.004	0.005	$t = -0.915$	0.363	0.010	0.001
Guppy reaction (Y/N)	-1.338	0.763	$z = -1.817$	0.062	0.043	0.043
Subjugation success	0.092	0.417	$z = 0.222$	0.825	<0.001	<0.001

Partial slope, standard error, test statistic (z -statistic for binomial and t -statistic for continuous response variables), P -value, and R^2 are included for each analysis (reaction distance: $n = 66$ and reaction time: $n = 81$, guppy reaction: $n = 85$, subjugation success: $n = 85$).

Table 2 Summary of mixed effects logistic regression model using relative measures of performance

Fixed effect	Slope	SE	Tol	z	P	Odds
Cichlid max velocity	−0.586	0.295	0.095	−1.987	0.047	0.110
Cichlid max acceleration	0.177	0.099	0.666	1.787	0.074	2.490
Cichlid avg velocity	0.679	0.384	0.105	1.770	0.077	6.090
Guppy max velocity	−0.070	0.025	0.557	−2.825	0.005	0.230
Guppy max acceleration	0.021	0.012	0.550	1.727	0.084	2.207

Presented are the partial slopes and their standard errors, tolerances, z-statistics, P-values, and standardized odds ratios. $R^2_m = R^2_c = 0.398$, $n = 51$.

found that guppies were at a higher risk of predation when oriented away from a predator, and that cichlids preferred to strike at individuals that appeared distracted by foraging. One cichlid in our study failed to accurately strike a guppy that did not react, suggesting that the cichlid was anticipating the guppy's movements. Whitford, Freymiller, Higham, et al. (2019) also found considerable behavioral variation during interactions between kangaroo rats (*Dipodomys deserti*) and sidewinder rattlesnakes (*Crotalus cerastes*) in the field. The variation we observed in a lab arena suggests that behavioral variation during predator–prey interactions is widespread, both terrestrially and aquatically, and that less stringent exclusion criteria are needed to capture that variation.

Effects of performance, kinematics, and boldness on subjugation success

We found that relative measures of start performance were modestly better predictors of subjugation success than absolute measures, similar to the results of Van Damme and Van

Dooren (1999), but using an *in vivo* predator–prey system. Only relative maximum velocity of both the predator and prey influenced the outcome. Relatively faster guppies were more likely to escape, while relatively slower cichlids were more likely to capture guppies. The majority of successful cichlid strikes involved suction, where the timing and accuracy of the strike, and timing of buccal expansion likely play a more important role than swimming speed (Kane & Higham, 2014; Wainwright et al., 2007). This is likely indicative of a speed–accuracy tradeoff common in many dynamic behaviors (Stone, 2014; Wheatley et al., 2015). Billfishes similarly use swim velocities below their maximum to subdue prey because the accuracy of their strikes and stability of their swimming decreases at higher speeds (Marras et al., 2015). Theoretical modeling and work with quolls (*Dasyurus hallucatus*) also show that the probability of mistakes increases as speed and task difficulty increases (Amir Abdul Nasir et al., 2017; Stone, 2014; Wheatley et al., 2015).

Cichlids that were unsuccessful but made contact with the guppy, often attempted a raptorial strike. In these situations, the cichlids had to reopen their mouth to swallow their prey, allowing a chance to escape. The raptorial strikes we observed had greater swimming speeds than suction strikes, possibly to facilitate biting the prey. It is possible that suction strikes were slower to optimally position the cichlid's mouth relative to the guppy. We did not find a difference in speed between accurate and inaccurate strikes.

The guppies ranged from 2.8 to 7.0 times smaller than their cichlid predators (Fig. S2), which likely meant that they were performing closer to their maximum speed (Wilson et al., 2015, 2018, 2020). However, escaping along a complicated path can require that prey perform at a sub-maximal speed to maximize maneuverability and minimize mistakes (Amir Abdul Nasir et al., 2017; Wheatley et al., 2015; Wilson et al., 2020). *Crenicichla* are ambush predators, so prey need to react with sufficient reaction distance and acceleration to escape (Moore & Biewener, 2015). Ambush predators often conceal themselves and strike once to surprise the prey. Our cichlids could not hide, but still made only a single strike at

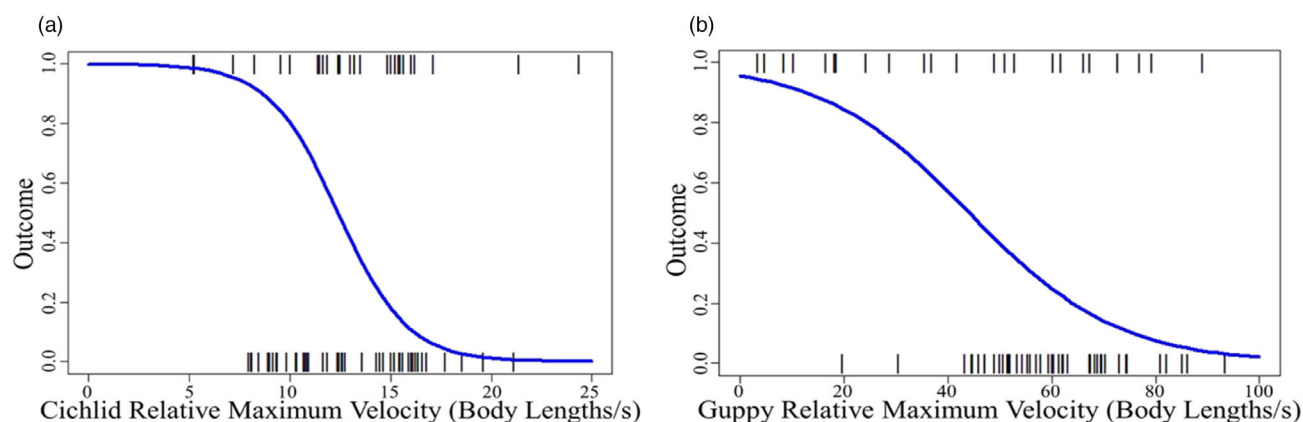


Figure 2 Cichlid (a) and guppy (b) relative maximum velocity against outcome (1 indicates the guppy was eaten, 0 that it escaped). The logistic regression curve displays the predicted probabilities of an event occurring based on each animal's relative maximum velocity.

Table 3 Summary of mixed effects logistic regression models using kinematics, C-start stage one and two, and wall interference

Fixed effect	Slope	SE	Tol	z	P	Odds ratio
Strike distance	38.437	76.470	0.398	0.503	0.615	1.370
Strike angle	0.305	0.482	0.614	0.632	0.527	1.310
Reaction distance	−273.110	118.555	0.300	−2.304	0.021	0.150
Reaction time	−24.290	25.860	0.532	−0.939	0.348	0.662
C-start stage 1	−115.546	294.105	0.998	−0.393	0.694	0.777
C-start stage 2	10.661	41.117	0.998	0.259	0.795	1.440
Wall interference	0.260	0.470	NA	0.549	0.583	1.130

Presented are partial slope, standard error, tolerance, z-statistic, P-value, and standardized odds ratio. Strike and reaction model: $R^2_m = 0.335$, $R^2_c = 0.383$, $n = 61$, C-start model: $R^2_m = R^2_c = 0.039$, $n = 53$, Wall Interference Model $R^2_m = R^2_c = 0.004$, $n = 86$.

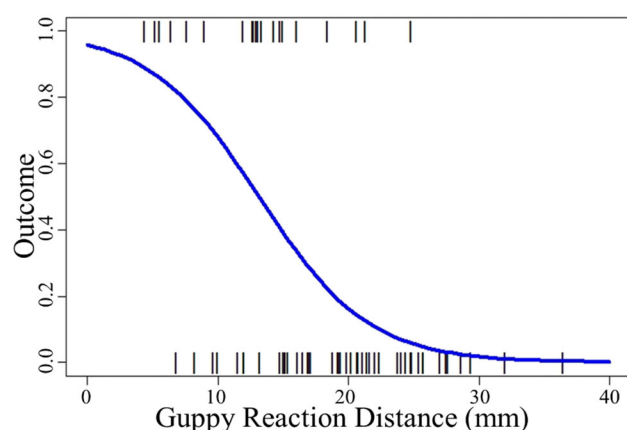


Figure 3 Guppy reaction distance against subjugation success. The logistic regression curve displays the predicted probabilities of an event occurring based on the reaction distance of the guppy to a cichlid strike.

the guppies, necessitating that the guppies initiated their C-start at a sufficient reaction distance. Indeed, the only kinematic variable that affected subjugation success was guppy reaction distance (Fig. 3). This is a general finding in predator–prey literature, as longer reaction distances may result in prey fleeing before a predator begins pursuit, and can be influenced by predator approach speed (Domenici & Hale, 2019; Kramer & Bonenfant, 1997; Moller & Erritzoe, 2014). In one trial, a cichlid approached a guppy but did not strike, causing it to C-start. The cichlid adjusted its attack angle and successfully ate the guppy, who C-started again but too close to the cichlid. Reaction distance increases with distance from a refuge in animals as different as reef fishes and woodchucks (*Marmota monax*; Bonenfant & Kramer, 1996; Nunes et al., 2015). However, our arena lacked refuges, likely putting a higher premium on longer reaction distances.

We expected that C-start duration would affect subjugation success because faster starts enhance escape success (Walker et al., 2005), but we did not find this. We observed a range in duration of stages one and two (0.006–0.017 s) despite finding that higher guppy maximum velocity increased their survival success. This suggests stage duration did not affect velocity and acceleration. Indeed, Walker et al. (2005) found that guppy

fast start ability was more related to their tangential acceleration and rotation. Therefore, relative velocity, acceleration, and distance traveled by fish may be more important than fast start duration (Walker et al., 2005; Webb, 1976).

Although we expected bolder prey to be at higher risk of predation, this was not the case, likely because boldness did not influence the guppies' reaction distance. There is evidence that various wild populations of poeciliid fishes have bolder individuals in higher predation environments (Brown et al., 2005; Harris et al., 2010). Our guppies were raised in a captive environment and likely never encountered a predator, and this may affect their boldness and predator response. The boldness of the captive fishes that we used (mean = 38 s, range: 0 s to ~6 min) was comparable to that of wild populations of guppies (Harris et al., 2010) and other poeciliids (Brown et al., 2005). We observed guppies swimming toward the cichlids in multiple trials, and although fish often inspect a predator to assess danger, it is possible that our guppies did not initially recognize the cichlids as predators (Dugatkin & Alfieri, 2003). Dugatkin and Alfieri (2003) found that bolder captive-reared guppies had stronger associative learning in the presence of a predator than less bold individuals. Therefore, boldness can be an important facet of behavior even in captive fish. If our guppies were naïve to predators and did not perceive the risk until the cichlid was striking, then this could explain why boldness did not influence subjugation success. It is possible that an assay of boldness that included a predator cue would have given different results. However, boldness is phenotypically plastic, is influenced by exposure to different predators, and differs by population and size (Bell & Sih, 2007; Bell & Stamps, 2004; Brown et al., 2005; Harris et al., 2010). Therefore, a boldness assay that exposed guppies to predator cues may have altered their future behavior during the predator–prey trial.

Conclusions

Our work treated predator and prey as equal contributors to determining the outcome of their interaction (Lima, 2002). The high behavioral variation we observed suggests that there are complex selection pressures acting on both predators and prey, and that even stereotyped strike and escape behaviors result in complex interactions. Given the variation we documented, fish

predator–prey systems are ideal for systematically manipulating a range of ecological factors that might affect the outcome of the interaction, including refuges and obstacles, foraging strategies of predators and prey, and the number of prey a predator encounters (Combes et al., 2012; Fraser & Cerri, 1982; Johansson et al., 2004; Wheatley et al., 2015; Whitford, Freymiller, Higham, et al., 2019).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

QGAM and PJB both conceived the ideas of the study, designed methodology, and contributed to data analysis; QGAM collected the data and led the writing of the manuscript; QGAM and PJB both revised drafts of the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1.