

SHORT COMMUNICATION

Integration between swim speed and mouth size evolves repeatedly in Trinidadian guppies and aligns with suction-feeding fishes

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ABSTRACT

Well-supported correlations between swim speed and mouth size during prey capture suggest the broad existence of an integrated relationship between locomotion and feeding in suction-feeding fishes. However, the influence of specialization on this relationship is unclear. We used divergent populations of Trinidadian guppies (*Poecilia reticulata*) to test whether integration during suction is generalizable to a non-suction specialist and whether intraspecific specialization of component systems affects their integration. Guppies from replicate high- and low-predation streams were recorded capturing wild-type zooplankton using suction. Alternative general linear models supported a positive correlation between swim speed and mouth size in derived low-predation populations, suggesting that the relationship can be extended in some cases. High-predation populations lack this integration, which may be the result of direct selection or constraints imposed by selection on locomotion. As guppies invade new habitats they may be evolving a new, integrated performance phenotype from a non-integrated ancestor.

KEY WORDS: Locomotion, Feeding, Performance, *Poecilia reticulata*, Local adaptation

INTRODUCTION

Many animals, including fishes, rely on integrated locomotor and feeding performance during prey capture to ensure the correct positioning relative to prey (Higham, 2007b; Kane and Higham, 2015). The need for integrated parts to work together successfully (Olson and Miller, 1958) can have consequences for the ability of traits to evolve (Goswami et al., 2014). Fishes are a useful taxa for understanding performance integration during prey capture because many exploit suction to capture prey (Wainwright et al., 2015), a behavior that relies on the locomotor system to maximize its effectiveness (Kane and Higham, 2014; Longo et al., 2015; Wainwright et al., 2001). Suction is generated as rapid mouth expansion pulls water and prey into the mouth (Day et al., 2015; Muller et al., 1982). However, this mechanism is temporally and spatially limited (Day et al., 2005, 2007; Ferry-Graham et al., 2001; Jacobs and Holzman, 2018) such that prey must be located close to the mouth at the time suction is generated and integration with swimming movements is critical.

Swim speed and mouth size have been established as primary drivers of the relationship between locomotor and feeding

performance. As suction is generated prior to opercular opening, the faster a fish swims with this valve closed the more likely it will be to push the water away from its mouth rather than pull it in (Muller and Osse, 1984; Van Leeuwen, 1984) and swim speed is likely sub-maximal. Additionally, because water has to move faster for the same volume to travel through a smaller opening, fishes with smaller mouth size relative to body size create a steeper pressure gradient and increased pulling force (suction) on the prey (Wainwright et al., 2007; Wainwright and Day, 2007). Therefore, fish with smaller mouth apertures should rely on slower swim speeds and vice versa. This prediction of integration has been supported using correlations between swim speed at peak gape and peak gape in several fishes (Table 1).

Despite this broad pattern of integration, considerable residual variation in correlations remains. This variation suggests that integration may be flexible and may not represent an ultimate constraint for fishes. For example, suction velocity was not compromised with increased swim speed in bluegill sunfish (Higham et al., 2005). But mouth size was not reported and these fish used comparatively slow approach speeds where integration may be less necessary. Whether this relationship is a constraint for fishes that primarily use other feeding modes is also unknown. For example, in eels and labrid fishes which are specialized for biting, correlations break down or potentially change when fish rely on biting to capture prey (Collar et al., 2014; Rice, 2008). Therefore, the relationship between swim speed and mouth size may not generally apply to fishes specialized for alternative feeding modes, where suction forces may be less important.

Understanding the effects of specialization on the integration of locomotion and feeding has been confounded by additional differences among experimental taxa in previous research. Our current understanding is based on interspecific comparisons of divergent but primarily suction-feeding species (Table 1) or by comparing these fishes with different species that use biting (Rice, 2008; Rice and Westneat, 2005). However, comparisons of phylogenetically distinct fish exhibiting large differences in physiology or morphology can confound interpretations of adaptation and specialization (Harvey and Pagel, 1991). To control for this, we utilized divergent populations of Trinidadian guppies (*Poecilia reticulata*) to ask: (1) is the correlation between swim speed and mouth size generalizable to a morphological biting specialist utilizing suction to capture prey?; and (2) is this integration maintained between populations that are locally adapted to their environments?

Trinidadian guppies belong to a clade of fishes that is specialized for scraping and picking prey (Ferry-Graham et al., 2008; Gibb et al., 2008; Hernandez et al., 2008, 2009). However, guppies retain the ability to feed on suspended prey using suction, facilitating direct comparisons of behaviors with other suction-feeding fishes. Guppies can be found in contrasting habitats that vary in their exposure to

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Table 1. A review of regression (r^2) and correlation (r) statistics between swim speed and mouth size across fishes

Taxon	Design	r^2	r	References
Tarpon	Univariate, within species	0.25		Tran et al., 2010
<i>Megalops cyprinoides</i>	Multivariate, within species	0.46		
Bluegill sunfish	Univariate, across prey types	0.294	0.542	E.A.K. and T. E. Higham, unpublished
<i>Lepomis macrochirus</i>	Multivariate, across prey types	0.717	0.847	E.A.K. and T. E. Higham, unpublished
Largemouth bass	Univariate	0.58	0.762	Higham, 2007a
<i>Micropterus salmoides</i>				
Silver-spotted sculpins	Univariate	0.29	0.539	Kane and Higham, 2011
<i>Blepsias cirrhosus</i>	Multivariate	0.585	0.765	Kane and Higham, 2015
Tidepool sculpins	Univariate	0.18 ^{NS}	0.424	Kane and Higham, 2011
<i>Oligocottus maculosus</i>	Multivariate	0.524	0.724	Kane and Higham, 2015
Cichlids	Without phylogenetic correction	0.49	0.7	Higham, 2007b
Family Cichlidae	With phylogenetic correction	0.64	0.8	Higham, 2007b
Serranids	Across species	0.327	0.572	Oufiero et al., 2012
Family Serranidae				
Fishes	Meta-analysis	0.436	0.66	Kane and Higham, 2015

NS, not significant. Studies usually only reported one value and these were converted by either squaring or taking the square root of the value provided. A value closer to 1 indicates stronger integration in both cases.

predation pressure, prey resources and competition, leading to local adaptation in the ability to escape from predators using a locomotor fast-start response (Dial et al., 2015; Ghilambor et al., 2004; O'Steen et al., 2002; Walker et al., 2005), feeding morphology and prey capture behavior (Bassar et al., 2010; Dussault and Kramer, 1981; Palkovacs et al., 2009, 2011). Therefore, divergent populations may differ in their ability to employ suction and/or integrate this behavior with swimming. Wild guppies from both high-predation and low-predation environments consume similar prey types ranging from periphyton to invertebrates (although in different proportions and with different selectivity depending on the season) (Zandonà et al., 2011, 2017), suggesting that divergent populations may alternatively retain a generalized prey capture strategy and show similar levels of integration. Because low-predation populations have repeatedly evolved from adjacent high-predation populations (Willing et al., 2010), such comparisons also allow testing of how patterns of integration have changed between ancestral and derived populations.

MATERIALS AND METHODS

Guppies (*Poecilia reticulata* W. Peters 1859) were collected in the Northern Range Mountains of Trinidad, West Indies, from replicate high-predation (ancestral) and low-predation (derived) populations found in independent river drainages on the north and south slopes (Table S1). These sites were chosen by considering accessibility and our confidence in their undisturbed or natural state. Only adult females were collected as they gestate young internally, suggesting that prey acquisition behaviors could have fitness consequences. Up to 15 fish from each population were used to facilitate detection of linear relationships (Garland and Adolph, 1994) but unforeseen circumstances limited sample size in one population (see discussion below). No individuals were intentionally excluded from analysis. Fish were shipped to the lab in Fort Collins, CO, USA and housed individually in 1.5 l tanks (Pentair Aquatic Eco-systems, Atlanta, GA, USA) on a recirculating system, similar to other studies (Broder and Angeloni, 2014; Handelsman et al., 2013). Fish were maintained on 40 µl of flake paste (1:1 ratio of ground flake and water; API tropical greens, Mars Inc.) fed once daily. All methods were approved by the Colorado State University IACUC (protocol 14-4998A).

Several factors affected the length of stay in the lab prior to filming trials (described below), resulting in fish being filmed at time points that varied between 43 and 385 days since arrival. As

stage of pregnancy affects locomotor performance (Ghilambor et al., 2004, 2003) and wild-caught adults could not be considered virgin, fish were allowed to acclimate to the lab environment and give birth to previously fertilized developing offspring. The birth schedules of individual females were tracked daily and guppies were not used unless they had just given birth or birth rates slowed to fewer than 3 babies per month. In all cases, females were visibly lacking a distended abdomen, suggesting female performance was unlikely to be impacted by pregnancy. In addition to this, several unavoidable circumstances arose during this project that resulted in the need to re-sample populations or postpone filming trials (e.g. failure of equipment, unexpected death of fish and/or an inability to acquire local plankton prey in winter). However, we argue that this variation in lab acclimation time (Table S1) had little consequence for our results and conclusions. The most significant result of this variation was an increase in body size over time, as female guppies experience indeterminate growth. However, as differences in body size were anticipated *a priori* between high- and low-predation populations and this factor was included in statistical analyses, an acclimation effect was not modeled separately. The strength of divergence between populations (see below) despite these unfortunate circumstances further supports our conclusion that an acclimation effect was minimal and suggests either that differences in prey capture behaviors may be genetically fixed or that plastic responses may be relatively fixed in adult fish such that responses to the lab environment appear negligible.

To quantify prey capture behavior, fish were recorded as they captured live, locally collected, plankton prey that included cladocerans and copepods. Although these specific prey species have not been represented in natural diets (Zandonà et al., 2011), they are an ideal choice for these experiments because they (1) elicit a mid-water suction response in guppies comparable to that of other fishes and (2) perform evasive escape responses that challenge guppies and can help determine differences between populations in prey capture ability. Fish were starved for up to 3 days before filming and were removed from the recirculating system in their housing tanks and placed on a table so the long axis of the tank was perpendicular to the camera. Additional baffles were added to the tank to restrict the fish to an approximately 5 cm width×12 cm length×12 cm water height filming arena. Fish were allowed at least 15 min to re-acclimate before filming. All fish

were provided the opportunity to practice with novel plankton prey prior to recording video. During trials, a 600 W tungsten light (Smith-Victor Corporation, Bartlett, IL, USA) was used to illuminate the filming arena. Fish were recorded capturing prey in the lateral perspective at 500 frames s^{-1} using a single high-speed camera (Edgetronic SC1, Sanstreak Corp., San Jose, CA, USA) with a fixed lens (50 mm, Nikon, Nikon Corporation, Tokyo, Japan). At least 3 trials were saved per fish, and the best trial was used for analysis. These were trials where the fish was in focus and perpendicular to the camera, the fish's mouth was at least 1 cm away from a surface, and prey were verified as plankton. Video data were managed in accordance with best practices for video data management in organismal biology at level 2 or above (Brainerd et al., 2017).

Trials were digitized and analyzed using Matlab (version 7.14, MATLAB, MathWorks Inc., Natick, MA, USA) to determine swimming and feeding kinematics (Hedrick, 2008). All videos were digitized (Fig. 1A) starting several frames before mouth opening and ending several frames after mouth closing. Kinematic traces were smoothed using a quintic spline (Korff and McHenry, 2011) and visually inspected for accuracy of the smoothed trace. Gape was calculated as the distance between the upper and lower jaws and peak gape (hereafter PG) was the maximum value of this measurement. Swim speed was determined by calculating the

speed of the approximate center of mass as the distance traveled between frames divided by the elapsed time between frames, or 2 ms. Swim speed was taken at the time of peak gape (hereafter SPG) as this measure of locomotor performance has shown the strongest correlation with mouth size in previous studies (Kane and Higham, 2011; 2015). Standard length (SL) was determined by calculating the distance between the lower jaw and the tail using a single frame prior to mouth opening when the fish was in a resting position.

Three general linear models (GLMs) were used to assess the relationship between mouth size and swim speed in guppies. These models differed in how they accounted for fish body size and the degrees of freedom available to detect significant differences. Qualitative comparisons among models were used to assess the effect of different data transformations on the results. In each case, predictors were sequentially removed from the model using the criteria that (1) effects with the lowest sum of squares at each iteration were removed and (2) effects could not be removed if they were contained in interactions with a larger sum of squares value. In this case, the predictor with the next lowest sum of squares was then evaluated. Predictors were removed until the predicted residual error sum of squares (PRESS, a leave-one-out cross-validation statistic of model fit) no longer decreased. This point indicates that additional predictors could result in the model

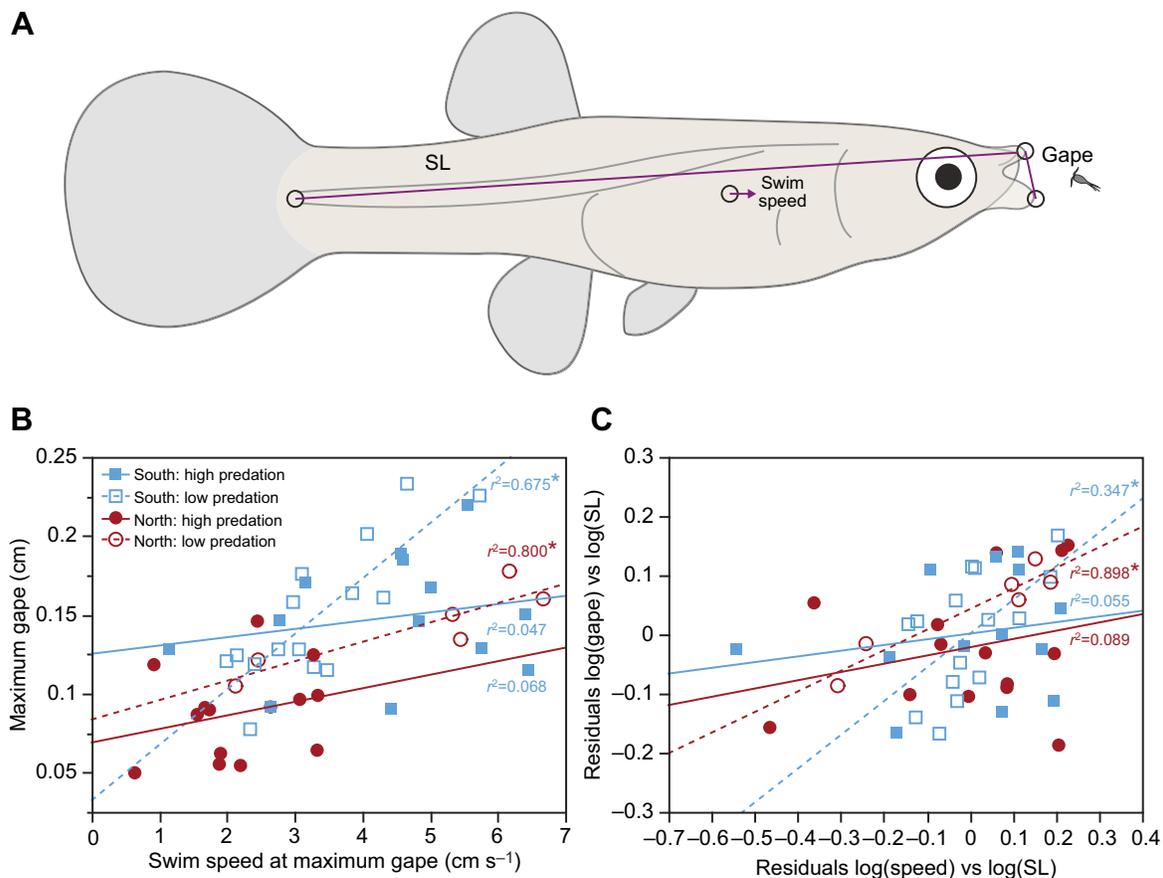


Fig. 1. Integration in guppies. (A) Four points were digitized and were used to calculate gape (the distance between the jaws), swim speed (the change in distance over each frame of the approximate center of mass) and standard length (SL; the distance between the tail and lower jaw in a single frame before mouth opening) across two replicate high- and low-predation populations (Table S1). (B) A visual representation of the raw data (Model 1) and (C) the size-corrected residuals of log-transformed regressions with SL (Model 3). Points represent one video per fish. Regression lines do not represent significant model effects (for these, see Table 2) and are shown only for visual comparison. Fit of each line is shown using the r^2 statistic ($*P < 0.05$). A repeatable pattern of the relationship only occurring in low-predation populations is supported by all three general linear models (Table 2).

overfitting the data. Once the model was selected, a partial eta-squared (η^2) statistic was then calculated for each predictor to determine effect size relative to other predictors (Maher et al., 2013).

For the first model, raw data were used to determine the effect of swim speed on mouth size without accounting for differences in body size. This model provided a baseline to determine the effects of further transformations on the results. In this case, PG was the response and drainage (north versus south slope), predation (high versus low), SPG and all interactions in a full factorial design were included as predictors (Model 1). Second, all kinematics were \log_{10} -transformed and the role of body size was added as a covariate to retain degrees of freedom and account for variation in body size among populations. In this model (Model 2), $\log(\text{PG})$ was the response and drainage, predation, $\log(\text{SPG})$, $\log(\text{SL})$ and all interactions were included as predictors. Finally, residuals from regressions of \log_{10} -transformed kinematics were used to account for the effect of body size while minimizing the degrees of freedom in the model. These residuals represent variation in mouth size and swim speed that is not attributable to the scaling effect of body size. Allometric relationships were determined for log-transformed data by first using a GLM to determine whether mouth size and swim speed scale similarly with size across populations, and second by using ordinary least squares regression to determine the scaling relationships. For the third model, PG residuals were the response and drainage, predation, SPG residuals and all interactions were included as predictors (Model 3). Models were compared qualitatively as well as using Akaike's information criterion (corrected) (AICc) scores (Burnham and Anderson, 2002). All statistical analyses were performed in JMP 12.1.0 (SAS Institute Inc., Cary, NC, USA).

RESULTS AND DISCUSSION

All three statistical approaches supported the same result, showing a correlation between swim speed and mouth size, as in previous studies (Table 1), but that this relationship only occurs in low-predation guppy populations (Table 2). This pattern was more prominent when body size effects were accounted for (Fig. 1C). All models indicated that swim speed and the predation level \times swim speed interaction are strong predictors of mouth size (Table 2). Despite a lack of significance for the interaction in Model 3, an effect size of 0.071 indicated that this factor is likely relevant. Therefore, we conclude that the relationship between swim speed and mouth size is present, but differs between the high- and low-predation populations in a repeatable way. Specifically, a lack of response is observed in high-predation populations (regression, north slope: $F_{1,12}=0.8788$, $P=0.3670$; south slope: $F_{1,11}=0.5406$, $P=0.4776$) compared with a strong response in low-predation populations (north slope: $F_{1,4}=16.0461$, $P=0.0161$; south slope: $F_{1,13}=27.0239$, $P=0.0002$) (Fig. 1B). The strong fit in the north slope low-predation population is an artifact of the small sample size and the true correlation of these traits is likely more similar to the south slope low-predation population. Despite this, all three models lead to the same general conclusion across drainages and suggest the presence of an effect in this population is likely accurate. The consistency of swim speed and population interaction effects across populations and statistical techniques suggests that the population-level differences in the correlation are potentially ecologically significant as guppies invade and adapt to low-predation environments.

The effect of body size was stronger for mouth size than for swim speed, suggesting that functional systems are not performing at similar levels. Body size was the only significant effect on

Table 2. General linear model statistics

	AICc	r^2	Adjusted r^2	PRESS	d.f.	F	P	Partial η^2
Model 1: PG~drainage+predation+SPG+interactions								
Whole model	-185.94	0.62	0.55	0.049	7, 40	9.242	<0.0001	
Drainage					1	8.797	0.0051*	0.180
Predation					1	2.429	0.127	0.057
Drainage \times predation					1	0.469	0.4973	0.012
SPG					1	16.216	0.0002*	0.288
Drainage \times SPG					1	1.641	0.2076	0.039
Predation \times SPG					1	4.878	0.033*	0.109
Drainage \times predation \times SPG					1	2.960	0.0931	0.069
Model 2: $\log(\text{PG})$ ~drainage+predation+ $\log(\text{SPG})$ + $\log(\text{SL})$ +interactions								
Whole model	-52.27	0.76	0.64	0.874	15,32	6.581	<0.0001	
Reduced model	-73.77	0.74	0.67	0.460	9, 38	11.787	<0.0001	
Drainage					1	1.185	0.2833	0.030
Predation					1	0.002	0.9675	0.000
$\log(\text{SL})$					1	6.509	0.0149*	0.146
Drainage \times $\log(\text{SL})$					1	1.609	0.2124	0.041
$\log(\text{SPG})$					1	4.185	0.0477*	0.099
Drainage \times $\log(\text{SPG})$					1	0.186	0.6685	0.005
Predation \times $\log(\text{SPG})$					1	5.470	0.0247*	0.126
$\log(\text{SL}) \times \log(\text{SPG})$					1	0.024	0.8774	0.001
Drainage \times $\log(\text{SL}) \times \log(\text{SPG})$					1	2.936	0.0948	0.072
Model 3: PG residuals~drainage+predation+SPG residuals+all interactions								
Whole model	-75.72	0.24	0.10	0.495	7, 40	1.769	0.1207	
Reduced model	-84.94	0.20	0.15	0.442	3, 44	3.720	0.0181	
Predation					1	0.769	0.3854	0.017
SPG residuals					1	10.274	0.0025*	0.189
Predation \times SPG residuals					1	3.348	0.0741	0.071

*Significant at $\alpha=0.05$. Partial η^2 is a measure of effect size, as a fraction of the variation in the response that is explained by each predictor while accounting for the other predictors. PG, peak gape; SPG, speed at the time of peak gape; SL, standard length; AICc, Akaike's information criterion (corrected); PRESS, predicted residual error sum of squares.

mouth size [retained effects: predation, $\log(\text{SL})$, and predation $\times\log(\text{SL})$ interaction; adjusted $r^2=0.62$, ANOVA $F_{3,44}=026.559$, $P<0.0001$, effect test $F_1=45.9098$, $P<0.0001$, other effects $P>0.13$] and a single regression of log-transformed traits was performed prior to Model 3. However, the only significant effect on swim speed was the drainage \times predation interaction [retained effects: drainage, predation, drainage \times predation interaction, and $\log(\text{SL})$; adjusted $r^2=0.325$, ANOVA $F_{4,43}=6.6475$, $P=0.0003$, effect test $F_1=7.8788$, $P=0.0075$, other effects $P>0.09$] and log-transformed regressions for swim speed were performed for each population separately. Individuals can utilize a range of performance values depending on the stimulus, and kinematic traits will more likely relate to body size if they represent a maximum ability that is dependent on size. Therefore, guppies likely relied on near-maximum mouth opening to capture suspended prey, but sub-maximal swim speeds. In fact, guppies from all populations often slowed to a near-stop prior to mouth opening and forward velocity in many trials was due to suction generation (E.A.K., unpublished observation).

A covariate model including body size (Model 2) was the best model for understanding the relationship between swim speed and mouth size (Table 2). When body size was not accounted for, a drainage effect was recovered but this was due to the larger size of south slope fish (Table S1). Drainage effects were small in the additional models, suggesting that patterns recovered are repeated across drainages when size is accounted for (Table 2, Fig. 1C). Model 2 explained 67% of the variation in mouth size, which was a 12% increase compared with when size was excluded (Model 1), and body size was the largest effect on mouth size. This model also had the largest AICc value, corroborating this increase in explanatory power. Although Model 3 had fewer predictors, potentially more power to detect effects and a similarly high AICc value, it was constrained to explaining only residual variation. This is likely the reason the explanatory power of Model 2 was 4.5 times greater than that of Model 3 and its AICc values were also greater (Table 2). The poor fit of Model 3, the large effect of SL and the highest AICc values indicate that Model 2 should be given the most weight in drawing conclusions.

The presence of a relationship between swim speed and mouth size in low-predation guppies supports the hypothesis that a correlated relationship is common among fishes relying on suction to capture prey (Higham, 2007b; Kane and Higham, 2015), despite morphological specialization for other behaviors. When present and with the effect of body size removed (Fig. 1C, pooled size-residual $r^2=0.40$), this relationship is stronger than a similar univariate measure in bluegill sunfish (*Lepomis macrochirus*), a species that is a model for suction-feeding mechanics. It was also stronger than in young silver-spotted sculpins (*Blepias cirrhosus*), which were more similar in body size to guppies (Table 1). However, the magnitude of the observed relationship is consistent with that of other interspecific comparisons (Table 1), suggesting that the level of integration in low-predation guppies is reasonable.

The most surprising result is the lack of any observed integration in guppies from high-predation environments (pooled size-residual $r^2=0.05$). This may be the first example of a lack of performance integration during a suction-feeding behavior. It is possible that univariate analyses may not be sufficient to capture integration. For example, tidepool sculpins (*Oligocottus maculosus*) were the only previously documented species lacking integration ($r^2=0.18$), but this changed when a re-analysis included additional locomotor and feeding variables (Table 1). A similar scenario is unlikely in guppies

as the correlation in high-predation guppies is an order of magnitude lower than that of tidepool sculpins. Alternatively, decreased performance may be associated with decreased integration such that at low swim speeds integration may not be necessary (Higham et al., 2005). In guppies, swim speeds are similarly low across populations (Fig. 1C) suggesting that integration should be possible in high-predation guppies as it is present in contrasting populations. Therefore, the kinematics of each functional system and their integration are likely decoupled, such that integration is difficult to predict based on underlying components. In this way, performance integration is an emergent organismal property of system-level kinematic performance (Korn, 2005) that may be responding to differences in selection pressures that manifest at the level of the whole organism.

We suggest that direct selection on integration or indirect selection on component functional systems could result in the absence of integration in some populations. Intraspecific competition for rare high-value prey items is strong in low-predation populations (Zandonà et al., 2017) and may drive selection for specialized solutions for prey capture in these habitats. Low-predation guppies may be prioritizing stability and accuracy during prey encounters that require precision (Kane and Higham, 2015), leading to an integrated phenotype that helps individuals compete for limited resources. When competition is reduced and prey availability changes seasonally (Zandonà et al., 2017), such as in high-predation environments, a generalist strategy including biting may be more prominent. A lack of integration may allow for flexibility across prey types or feeding modes (Kane and Higham, 2015) and provide a selective advantage. An alternative hypothesis is that selection may act on component systems, affecting the ability to integrate across systems. It is well documented that the superior ability to escape from predators in high-predation guppies is due to differences in both morphology and performance of the locomotor system (Dial et al., 2015; Ghalambor et al., 2004; O'Steen et al., 2002; Walker et al., 2005). If the whole-organism response is tuned for high speed or acceleration during interactions with predators (Walker et al., 2005), guppies may find it difficult to coordinate functional systems, even at slow speed. This may be similar to the difficulty we have in coordinating walking while manipulating a cell phone, where the ability to avoid collisions (integration) is compromised despite decreased walking speed, especially for those of us who do this integrated behavior less frequently. We suggest that specialization of one functional system may come at a cost to integrated behaviors at the level of the whole organism. Additional comparative studies of integration could provide a better understanding of when such trade-offs might occur.

Guppies have repeatedly and independently invaded and evolved in low-predation habitats from ancestors in high-predation habitats (Willing et al., 2010). Therefore, similarities in integration among replicate drainages suggest the repeated evolution of an integrated phenotype from a non-integrated ancestor. The strong presence of integration across fishes using suction coupled with the divergence in integration between guppy populations suggests that integration may provide an advantage in certain contexts and could readily evolve. However, these selection pressures might only be imposed above a critical threshold of specialization for prey capture behaviors. Below this threshold, regardless of kinematic similarity, integration may be absent because of the need for flexibility or in response to demands imposed on component systems. Nevertheless, this work provides key insights into the potential for integration to evolve, as well as how these patterns may govern diversification patterns in fishes.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: E.A.K., M.M.R., M.L.D., C.K.G.; Methodology: E.A.K., M.M.R., M.L.D.; Validation: E.A.K.; Formal analysis: E.A.K.; Investigation: E.A.K., M.M.R., M.L.D.; Resources: E.A.K., C.K.G.; Data curation: E.A.K.; Writing - original draft: M.M.R., M.L.D.; Writing - review & editing: E.A.K., M.M.R., M.L.D., C.K.G.; Visualization: E.A.K.; Supervision: E.A.K.; Project administration: E.A.K.; Funding acquisition: E.A.K., C.K.G.

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Data availability

All videos and data representing analyzed points have been deposited in ZMAportal.org in the study 'Guppy feeding integration' with permanent ID ZMA15. Calculated swim speed and mouth size data used in the statistical analysis are available from the Dryad digital repository (Kane et al., 2018): dryad.kr5rr2c.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.190165.supplemental>

References

- Bassar, R. D., Marshall, M. C., López-Sepulcre, A., Zandonata, E., Auer, S. K., Travis, J., Pringle, C. M., Flecker, A. S., Thomas, S. A., Fraser, D. F. et al.** (2010). Local adaptation in Trinidadian guppies alters ecosystem processes. *Proc. Natl. Acad. Sci. USA* **107**, 3616-3621.
- Brainerd, E. L., Blob, R. W., Hedrick, T. L., Creamer, A. T. and Müller, U. K.** (2017). Data management rubric for video data in organismal biology. *Integr. Comp. Biol.* **57**, 33-47.
- Broder, E. D. and Angeloni, L. M.** (2014). Predator-induced phenotypic plasticity of laterality. *Anim. Behav.* **98**, 125-130.
- Burnham, K. P. and Anderson, D. R.** (2002). *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach*. New York: Springer.
- Collar, D. C., Wainwright, P. C., Alfaro, M. E., Revell, L. J. and Mehta, R. S.** (2014). Biting disrupts integration to spur skull evolution in eels. *Nat. Commun.* **5**, 5505.
- Day, S. W., Higham, T. E., Cheer, A. Y. and Wainwright, P. C.** (2005). Spatial and temporal patterns of water flow generated by suction-feeding bluegill sunfish *Lepomis macrochirus* resolved by Particle Image Velocimetry. *J. Exp. Biol.* **208**, 2661-2671.
- Day, S. W., Higham, T. E. and Wainwright, P. C.** (2007). Time resolved measurements of the flow generated by suction feeding fish. *Exp. Fluids* **43**, 713-724.
- Day, S. W., Higham, T. E., Holzman, R. and Van Wassenbergh, S.** (2015). Morphology, kinematics, and dynamics: the mechanics of suction feeding in fishes. *Integr. Comp. Biol.* **55**, 21-35.
- Dial, T. R., Reznick, D. N. and Brainerd, E. L.** (2015). Effects of neonatal size on maturity and escape performance in the Trinidadian guppy. *Funct. Ecol.*
- Dussault, G. V. and Kramer, D. L.** (1981). Food and feeding behavior of the guppy, *Poecilia reticulata* (Pisces: Poeciliidae). *Can. J. Zool.* **59**, 684-701.
- Ferry-Graham, L. A., Wainwright, P. C. and Lauder, G. V.** (2001). Sources of fluid flow during feeding in bluegill sunfish as identified using DPIV. *Am. Zool.* **41**, 1442-1442.
- Ferry-Graham, L. A., Gibb, A. C. and Hernandez, L. P.** (2008). Premaxillary movements in cyprinodontiform fishes: an unusual protrusion mechanism facilitates "picking" prey capture. *Zoology* **111**, 455-466.
- Garland, T. and Adolph, S. C.** (1994). Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiol. Zool.* **67**, 797-828.
- Ghalambor, C. K., Walker, J. A. and Reznick, D. N.** (2003). Multi-trait selection, adaptation, and constraints on the evolution of burst swimming performance. *Integr. Comp. Biol.* **43**, 431-438.
- Ghalambor, C. K., Reznick, D. N. and Walker, J. A.** (2004). Constraints on adaptive evolution: the functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). *Am. Nat.* **164**, 38-50.
- Gibb, A., Ferry-Graham, L. A., Hernandez, L. P., Romansco, R. and Blanton, J.** (2008). Functional significance of intramandibular bending in Poeciliid fishes. *Environ. Biol. Fishes* **83**, 507-519.
- Goswami, A., Smaers, J. B., Soligo, C. and Polly, P. D.** (2014). The macroevolutionary consequences of phenotypic integration: from development to deep time. *Philos. Trans. R. Soc. B* **369**.
- Handelsman, C. A., Broder, E. D., Dalton, C. M., Ruell, E. W., Myrick, C. A., Reznick, D. N. and Ghalambor, C. K.** (2013). Predator-induced phenotypic plasticity in metabolism and rate of growth: rapid adaptation to a novel environment. *Integr. Comp. Biol.* **53**, 975-988.
- Harvey, P. H. and Pagel, M. D.** (1991). *The Comparative Method in Evolutionary Biology*. New York, NY: Oxford University Press.
- Hedrick, T. L.** (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 034001.
- Hernandez, L. P., Ferry-Graham, L. A. and Gibb, A. C.** (2008). Morphology of a picky eater: a novel mechanism underlies premaxillary protrusion and retraction within cyprinodontiforms. *Zoology* **111**, 442-454.
- Hernandez, L. P., Gibb, A. C. and Ferry-Graham, L.** (2009). Trophic apparatus in cyprinodontiform fishes: functional specializations for picking and scraping behaviors. *J. Morphol.* **270**, 645-661.
- Higham, T. E.** (2007a). Feeding, fins and braking maneuvers: locomotion during prey capture in centrarchid fishes. *J. Exp. Biol.* **210**, 107-117.
- Higham, T. E.** (2007b). The integration of locomotion and prey capture in vertebrates: morphology, behavior, and performance. *Integr. Comp. Biol.* **47**, 82-95.
- Higham, T. E., Day, S. W. and Wainwright, P. C.** (2005). Sucking while swimming: evaluating the effects of ram speed on suction generation in bluegill sunfish *Lepomis macrochirus* using digital particle image velocimetry. *J. Exp. Biol.* **208**, 2653-2660.
- Jacobs, C. N. and Holzman, R.** (2018). Conserved spatio-temporal patterns of suction-feeding flows across aquatic vertebrates: a comparative flow visualization study. *J. Exp. Biol.* **221**, jeb174912.
- Kane, E. A. and Higham, T. E.** (2011). The integration of locomotion and prey capture in divergent cottid fishes: functional disparity despite morphological similarity. *J. Exp. Biol.* **214**, 1092-1099.
- Kane, E. A. and Higham, T. E.** (2014). Modelled three-dimensional suction accuracy predicts prey capture success in three species of centrarchid fishes. *J. R. Soc. Interface* **11**, 20140223.
- Kane, E. A. and Higham, T. E.** (2015). Complex systems are more than the sum of their parts: using integration to understand performance, biomechanics, and diversity. *Integr. Comp. Biol.* **55**, 146-165.
- Kane, E. A., Roeder, M. M., DeRue, M. L. and Ghalambor, C. K.** (2018). Data from: Integration between swimming and feeding evolves repeatedly in Trinidadian guppies and aligns with suction-feeding fishes. *Dryad Digital Repository*.
- Korff, W. L. and McHenry, M. J.** (2011). Environmental differences in substrate mechanics do not affect sprinting performance in sand lizards (*Uma scoparia* and *Callisaurus draconoides*). *J. Exp. Biol.* **214**, 122-130.
- Korn, R. W.** (2005). The emergence principle in biological hierarchies. *Biol. Philos.* **20**, 137-151.
- Longo, S. J., McGee, M. D., Oufiero, C. E., Waltzek, T. B. and Wainwright, P. C.** (2015). Body ram, not suction, is the primary axis of suction feeding diversity in spiny-rayed fishes. *J. Exp. Biol.* **219**, 119-128.
- Maher, J. M., Markey, J. C. and Ebert-May, D.** (2013). The other half of the story: effect size analysis in quantitative research. *CBE—Life Sci. Educ.* **12**, 345-351.
- Muller, M. and Osse, J. W. M.** (1984). Hydrodynamics of suction feeding in fish. *Trans. Zool. Soc. Lond.* **37**, 51-135.
- Muller, M., Osse, J. W. M. and Verhagen, J. H. G.** (1982). A quantitative hydrodynamical model of suction feeding in fish. *J. Theor. Biol.* **95**, 49-79.
- Olson, E. C. and Miller, R. L.** (1958). *Morphological Integration*. Chicago, IL: The University of Chicago Press.
- O'Steen, S., Cullum, A. J. and Bennett, A. F.** (2002). Rapid evolution of escape ability in Trinidadian guppies (*Poecilia reticulata*). *Evolution* **56**, 776-784.
- Oufiero, C. E., Holzman, R. A., Young, F. A. and Wainwright, P. C.** (2012). New insights from serranid fishes on the role of trade-offs in suction-feeding diversification. *J. Exp. Biol.* **215**, 3845-3855.
- Palkovacs, E. P., Marshall, M. C., Lamphere, B. A., Lynch, B. R., Weese, D. J., Fraser, D. F., Reznick, D. N., Pringle, C. M. and Kinnison, M. T.** (2009). Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 1617-1628.
- Palkovacs, E. P., Wasserman, B. A. and Kinnison, M. T.** (2011). Eco-evolutionary trophic dynamics: loss of top predators drives trophic evolution and ecology of prey. *PLoS ONE* **6**, e18879.
- Rice, A. N.** (2008). Coordinated mechanics of feeding, swimming, and eye movements in *Tautoga onitis*, and implications for the evolution of trophic strategies in fishes. *Mar. Biol.* **154**, 255-267.
- Rice, A. N. and Westneat, M. W.** (2005). Coordination of feeding, locomotor and visual systems in parrotfishes (Teleostei: Labridae). *J. Exp. Biol.* **208**, 3503-3518.
- Tran, H. Q., Mehta, R. S. and Wainwright, P. C.** (2010). Effects of ram speed on prey capture kinematics of juvenile Indo-Pacific tarpon, *Megalops cyprinoides*. *Zoology* **113**, 75-84.

- Van Leeuwen, J. L.** (1984). A quantitative study of flow in prey capture by rainbow trout, *Salmo gairdneri* with general consideration of the actinopterygian feeding mechanism. *Trans. Zool. Soc. Lond.* **37**, 171-227.
- Wainwright, P. C. and Day, S. W.** (2007). The forces exerted by aquatic suction feeders on their prey. *J. R. Soc. Interface* **4**, 553-560.
- Wainwright, P. C., Ferry-Graham, L. A., Waltzek, T. B., Carroll, A. M., Hulsey, C. D. and Grubich, J. R.** (2001). Evaluating the use of ram and suction during prey capture by cichlid fishes. *J. Exp. Biol.* **204**, 3039-3051.
- Wainwright, P. C., Carroll, A. M., Collar, D. C., Day, S. W., Higham, T. E. and Holzman, R. A.** (2007). Suction feeding mechanics, performance, and diversity in fishes. *Integr. Comp. Biol.* **47**, 96-106.
- Wainwright, P. C., McGee, M. D., Longo, S. J. and Patricia Hernandez, L.** (2015). Origins, innovations, and diversification of suction feeding in vertebrates. *Integr. Comp. Biol.* **55**, 134-145.
- Walker, J. A., Ghalambor, C. K., Griset, O. L., McKenney, D. and Reznick, D. N.** (2005). Do faster starts increase the probability of evading predators? *Funct. Ecol.* **19**, 808-815.
- Willing, E.-M., Bentzen, P., Van Oosterhout, C., Hoffmann, M., Cable, J., Breden, F., Weigel, D. and Dreyer, C.** (2010). Genome-wide single nucleotide polymorphisms reveal population history and adaptive divergence in wild guppies. *Mol. Ecol.* **19**, 968-984.
- Zandonà, E., Auer, S. K., Kilham, S. S., Howard, J. L., López-Sepulcre, A., O'Connor, M. P., Bassar, R. D., Osorio, A., Pringle, C. M. and Reznick, D. N.** (2011). Diet quality and prey selectivity correlate with life histories and predation regime in Trinidadian guppies. *Funct. Ecol.* **25**, 964-973.
- Zandonà, E., Dalton, C. M., El-Sabaawi, R. W., Howard, J. L., Marshall, M. C., Kilham, S. S., Reznick, D. N., Travis, J., Kohler, T. J., Flecker, A. S. et al.** (2017). Population variation in the trophic niche of the Trinidadian guppy from different predation regimes. *Sci. Rep.* **7**, 5770.