

Do faster starts increase the probability of evading predators?

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Summary

1. Nearly all fish evade predation strikes by rapidly accelerating out of the strike path, a behaviour called the fast-start evasion response. The many studies investigating morphological, behavioural and ecological correlates of fast-start performance assume that faster starts increase the probability of evasion.

2. We tested this faster-start hypothesis by measuring the effect of acceleration ability on evasion outcome (success, failure) in Guppies (*Poecilia reticulata*) evading the strike of a natural predator, the Pike Cichlid (*Crenicichla alta*).

3. Four parameters affect evasion outcome: two parameters important to the predator–prey interaction but not to the faster-start hypothesis – (1) the time required to reach the prey by the striking predator (measured by the initial distance between predator and prey and strike velocity), (2) the evasion path of the prey relative to the strike path of the predator; and two parameters relevant to the faster-start hypothesis – (1) the ability of the prey to generate rapid tangential acceleration (measured by net distance travelled, maximum velocity, and maximum acceleration), and (2) the ability of the prey to rapidly rotate during the initial stage of the fast start.

4. On average, a one standard deviation increase in fast-start performance increases the odds of surviving a predation strike 2.3-fold. These results support the assumption that faster starts increase the probability of successfully evading a predation strike.

Key-words: Fast-start performance, Guppy, predator–prey interaction

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Introduction

Animals avoid predation by many mechanisms, including behaviours that minimize encounters or attacks (Lima & Dill 1990), morphologies or behaviours that allow the successful evasion from an attack or extended chase (Webb 1977; McPeck *et al.* 1996; Van Buskirk & McCollum 2000), or morphologies that allow the animal to escape if captured (Reimchen 2000; Mikolajewski & Rolff 2004; Young *et al.* 2004). The fast-start evasion response is an antipredator mechanism that is believed to be a major factor contributing to the evolution of variation in morphology and behaviour among fishes (Webb 1978; Webb 1984b). The fast start is a rapid burst of movement away from a threatening stimulus and is highly conserved both ontogenetically and phylogenetically (Hale 1999; Wakeling *et al.* 1999; Hale *et al.* 2002).

Many aspects of the kinematics, neurophysiology, muscle physiology, biomechanics and fluid dynamics of fast starts are well studied (Domenici & Blake 1997; Wakeling & Johnston 1998; Spierts & van Leeuwen 1999; Ellerby & Altringham 2001; Hale *et al.* 2001; Verhagen 2004).

It is generally assumed that many phenotypic differences among species and closely related populations reflect the evolutionary consequence of differential selection on fast-start performance resulting from variation in the predation environment among habitats. Yet, the assumption that fast-start ability differs between populations inhabiting habitats with known differences in predation level has rarely been tested (Andraso & Barron 1995; Law & Blake 1996; Ghalambor *et al.* 2004; Langerhans *et al.* 2004).

More critically, even fewer studies have attempted to test directly the assumption that faster starts increase the probability of evasion, which we call the faster-start hypothesis. By faster, we mean the net speed of travel and not a shorter latency to respond to a threatening

stimulus. The relationship between fast-start evasion ability and survival seems nearly axiomatic but may not exist if the strike speed of larger predators is fast enough that any variation in swimming performance among smaller prey is inconsequential. Indeed, the two studies that have examined the influence of fast-start performance on evasion success in fishes reached different conclusions (Webb 1986; Katzir & Camhi 1993), but both results are confounded by uncontrolled variables (see below). Here, we directly test the hypothesis that faster starts increase the probability of successfully evading a predation strike by staging interactions between a prey fish, the Guppy, *Poecilia reticulata*, and one of its natural predators, the Pike Cichlid, *Crenicichla alta*. The *Poecilia*–*Crenicichla* system is especially relevant to test the faster-start hypothesis because of recent work demonstrating (1) a functional trade-off between a life-history strategy (increased per clutch reproductive investment in females) and fast-start acceleration ability (Ghalambor *et al.* 2004) and (2) interpopulation differences in the ability to survive in a high-predation environment (O'Steen *et al.* 2002). While the latter experiment is consistent with the faster-start hypothesis, predator preference or antipredator behaviours other than faster starts, such as increased vigilance, could be the cause of measured differences in survival rates.

Methods

Guppies from several sources were used in order to increase interindividual variation in fast-start ability. These sources included both second and third generation (F2–F3), lab-reared Guppies from wild collected grandmothers from three high-predation ($N = 33$) and two low-predation streams ($N = 12$) and domestic Guppies acquired through the aquarium trade ($N = 10$) that presumably are many generations removed from the wild. Guppies were maintained in a 1175-l flow through an aquarium system fitted with six 113.5-l community aquaria (Guppies from different sites of origin were kept separately). Two wild-caught Trinidadian Pike Cichlids (total length: 13.5 cm, 13.3 cm; mass: 19.88, 21.5 g) were maintained in separate 113.5-l aquaria that were also part of the larger system.

The predator–prey interactions were filmed in arenas submerged within each cichlid tank. Three arena designs were used. The original design was simply a 43 cm × 45 cm region of the cichlid tank partitioned from the rest of the tank with egg crate covered with insect screen. The second design was a trapezoidal arena (45 cm long, 40 cm long base, 22 cm short base) made with acrylic sheets. The third design was a 35 cm diameter circular, plastic arena. All arenas were 15 cm high. Cichlids entered each arena through a tunnel (25 cm L × 15 cm H × 15 cm W) made of screened egg-crate side-walls and a PVC 'half-pipe' top. The glass aquarium bottom formed the floor of the cichlid tunnel. The tunnel was glued to the edge of a doorway cut into the egg crate (design one), the short base of the trapezoidal arena,

or the circular arena. Each arena had a lid made of white acrylic and a floor formed by the glass aquarium bottom. The cichlids almost invariably hovered in the tunnel and would emerge from the tunnel into the arena only when striking a Guppy. The tunnels were substantially larger than the cichlids and did not at all limit the ability of a cichlid to form the S-shape characteristic of the strike fast start.

Cichlids were starved the day prior to filming. Guppies were either placed directly into the arena while a door to the cichlid tunnel was in a closed position or entered on their own through a 2.5 cm hole cut into the arena's ceiling. If a strike failed, the cichlid would most often voluntarily return to the tunnel allowing us to recover the Guppy. After a short rest period (15–30 min) we would reintroduce the Guppy. We recorded only a single successful strike per cichlid per day although up to two additional failed strikes per cichlid were recorded. Following an experiment, we fed the cichlid two or three additional Guppies.

The staged predator–prey interactions were filmed using a Phantom 4.0 high-speed digital video camera (Vision Research, Inc., Wayne, NJ) with a frame rate of 1000 Hz and resolution of 512 × 512 pixels. To avoid distortion of the images due to surface waves, we filmed a ventral view using a mirror mounted below the arena. The white, acrylic top containing a centimetre scale provided a uniform background. Halogen lights above the acrylic top were used to backlight the arena. Because the staged interaction arena was part of the larger cichlid tank, which was, in turn, part of the larger flow-through system, water temperature in the arena was not significantly affected by the lights and easily maintained at the system temperature (22 ± 1 °C).

Of the approximately 100 digital films, only 55 met the following screening criteria. First, to control for the initial distance of the predator to the prey, the predator's snout had to be in view at the initiation of the start. Second, the prey had to be sufficiently away from a wall (more than about two body lengths) to avoid wall effects on either predator or prey behaviour (see below for test of wall effects). Third, the prey behaviour had to be a fast start from rest (on rare occasions the cichlid would strike a Guppy that was swimming rapidly past the tunnel or a fleeing Guppy). Fourth, the predator had to present an actual strike, including an S-start and buccal expansion (occasionally early evasion responses by the prey caused the predator to abandon either or both the S-start and buccal expansion). One sequence was not analysed because the Guppy fast started, unexpectedly stopped and paused, and was then promptly captured by the cichlid.

The ventral midlines of the fast-starting Guppies and the tip of the snout of the striking cichlid were digitized from the frame prior to the initial head movement of the Guppy to the 30th frame following the initial head movement (if available) using a modification of the public domain NIH Image program (developed at the US National Institutes of Health and available on

the Internet at <http://rsb.info.nih.gov/nih-image/>) for the Apple Macintosh (the modification is available from the author upon request). All linear performance measures of the Guppy fast start are based on the displacement of the measured centre of mass. To estimate the position of the stretched-straight centre of mass, a cubic spline algorithm was fit to the mid-line points and the centre of mass (COM) was estimated as the interpolated point located some constant distance from the tip of the snout (along the midline) that moved the least during the response. A mean-square error quintic spline (Woltring 1985) was used to smooth the COM displacement and to estimate its velocity and acceleration. For estimates of fast-start performance, this algorithm was shown to have a small bias and standard error relative to other numerical differentiation algorithms (Walker 1998).

Four performance measures were compared: $d_{\text{net}(t)}$, $v_{\text{max}(t)}$, $a_{\text{max}(t)}$ and $\bar{\omega}_{(s1)}$. $d_{\text{net}(t)}$, the net distance travelled by the centre of mass through time, t , is simply the straight-line distance between the location of the centre of mass in the frame prior to the initial head movement of the prey and the location of the centre of mass in some later frame. The frame prior to the initial head movement of the prey is F_0 and the time associated with this frame is t_0 . $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$ are the maximum velocity and acceleration occurring any time between t_0 and t . $\bar{\omega}_{(s1)}$ is the average rotational velocity of the head during stage 1 of the fast start and is computed as stage 1 rotation angle divided by stage 1 duration (stage 1 ends at the end of the first lateral stroke of the tail, that is, when the fish is 'C'-shaped. Stage 2 ends at the end of the return stroke. For the purposes of this paper, stage 3 ends at the end of the third stroke, that is, when the tail is to the same side of the body as at the end of stage 1. See Weihs (1973) for details).

The estimates of $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$ were biased by the number of frames in the sequence, that is, the numerical differentiation algorithm undersmoothed shorter sequences and the magnitude of the effect increased with the shortness of the sequence. Because short sequences were invariably the sequences in which the Guppy was captured, the failed evasions were associated with artificially high $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$. In order to fairly compare successful and failed evasions, all sequences were limited to 13 frames (12 ms), which allowed the comparison of 53 of the 55 sequences (in the two discarded sequences, the Guppies were captured prior to frame 13). Stage 1 in most sequences was complete by 12 ms (the average stage 1 duration was 10.6 ms and the maximum duration was 14 ms). In general, peak accelerations occurred during stage 1. Because of the reduction in the number of frames, the resulting $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$ are biased upwards, but there should not be any differential bias between successful and failed evasions. However, for comparisons with other studies, both the upwards-biased $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$, and the $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$ computed from the full 30 frames for the successful evasion sequences, are reported.

A one-tailed, multiple logistic regression was used to test the directional hypothesis that faster starts increase the probability of evasion success. The combination of $\bar{\omega}_{(s1)}$, $d_{\text{net}(t)}$, $v_{\text{max}(t)}$ or $a_{\text{max}(t)}$ were tested in separate models. Both Δt_{close} , the time taken by the predator to swim the distance separating predator and prey at the onset of the prey response, and θ , the direction of the net prey escape path relative to the striking predator, may confound the ability to measure fast-start performance effects on evasion success. Δt_{close} is a function of both the initial distance, D_{pred} , from predator to prey at t_0 and the average swimming speed, \bar{v}_{pred} , of the predator while traversing this distance. While it is Δt_{close} that ultimately influences evasion outcome, D_{pred} and \bar{v}_{pred} were included in the model, in place of Δt_{close} , because these two variables are of more interest to behavioural biologists and functional morphologists (the P -values with D_{pred} and \bar{v}_{pred} in the model are slightly higher than with Δt_{close}). D_{pred} was measured as the distance between the tip of the predator's snout and the prey's estimated centre of mass at t_0 . \bar{v}_{pred} was estimated by $0.75D_{\text{pred}}/\Delta t_{\text{close}(0.75)}$, where $\Delta t_{\text{close}(0.75)}$ is the duration between F_0 and the frame in which the predator's snout traversed $0.75D_{\text{pred}}$. Because the predator failed to swim the full D_{pred} in the sequences in which the prey swam in the direction of the predator, $0.75D_{\text{pred}}$ was used instead of D_{pred} . Initial flight angle, θ , was measured as the angle between the strike path and the escape path, where the strike path is the chord linking the position of predator's snout and the prey's centre of mass in F_0 and the escape path is the chord linking the prey's centre of mass in F_0 and in the last frame (frame 13). A Bonferroni procedure to control α over multiple tests was not employed because the focal measures of this study (the linear performance measures $d_{\text{net}(t)}$, $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$ at $t = 5$ ms and $t = 10$ ms) are all estimates of the same phenomenon (ability to accelerate away from a starting location) and are therefore highly correlated with each other. Finally, while the response latency should be an important parameter on survival outcome, we did not measure it because our films do not record when the predator started its movement toward the prey nor do we know how to infer when the prey became aware of the predator or the potential threat of the predator. Regardless, the response latency, while interesting in its own right, is not a confounding variable to test the main hypothesis. Summary definitions of all parameters are given in Table 1.

We specifically emphasize the effect size instead of P -values in our interpretation of the results. The effect size in a logistic regression is the odds ratio, which is most often scaled as $\exp(\beta)$, where β is the multiple regression coefficient. The odds ratio scaled as $\exp(\beta)$ gives the multiple increase or decrease in the odds of an event occurring given a one unit increase in the independent variable (the odds of an event is the ratio of the probability of the event to the probability of not the event). Given that our independent variables typically vary far less or far more than one unit, we find

Table 1. Definitions of symbols used in text and tables

Parameter	Definition
F_0	The frame immediately prior to the first detectable movement of the prey
D_{pred}	Distance from predator's snout to prey centre of mass at F_0
\bar{v}_{pred}	The average speed of the predator between F_0 and the frame in which the predator has travelled $0.75D_{\text{pred}}$
Δt_{close}	The time taken by the predator's snout to cover the distance between its location in F_0 and the location of the prey's centre of mass in F_0
θ	The angle subtended by the strike path and the net evasion path at F_{13}
$d_{\text{net}(t)}$	The net distance travelled after t ms
$v_{\text{max}(t)}$	The maximum velocity occurring at any time during the first t ms
$a_{\text{max}(t)}$	The maximum acceleration occurring at any time during the first t ms
$\bar{\omega}_{(s1)}$	The mean rotational velocity of the anterior body of the prey during stage 1

Table 2. Mean and standard errors of parameters that potentially affect the ability of prey to successfully evade a predation strike. The analysis in the 12 ms sequence was limited to 13 frames, in order to equalize the bias in the estimate of the linear performance measures $d_{\text{net}(t)}$, $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$ across both successful and failed evasions. The multiple logistic regression (Table 3) is based on the 12-ms sequence analysis. The symbols are defined in Table 1

Performance	12-ms sequences		Full sequences	
	Escaped ($N = 36$)	Captured ($N = 18$)	Escaped ($N = 36$)	Captured ($N = 18$)
D_{pred} (cm)	5.2 ± 0.4	3.1 ± 0.2		
\bar{v}_{pred} (cm s ⁻¹)	137.1 ± 6.8	150.4 ± 10.0		
θ (deg)	112.4 ± 7.5	77.1 ± 10.0		
$d_{\text{net}(5)}$ (cm)	0.125 ± 0.009	0.093 ± 0.010	0.12 ± 0.008	0.09 ± 0.010
$v_{\text{max}(5)}$ (cm s ⁻¹)	56.5 ± 3.2	51.8 ± 4.7	52.1 ± 2.6	0.49 ± 3.1
$a_{\text{max}(5)}$ (m s ⁻²)	155 ± 16	114 ± 21	97 ± 8	97 ± 13
$d_{\text{net}(10)}$ (cm)	0.244 ± 0.015	0.207 ± 0.022	0.24 ± 0.09	0.21 ± 0.024
$v_{\text{max}(10)}$ (cm s ⁻¹)	71.7 ± 3.2	72.4 ± 6.3	67.1 ± 2.5	67.6 ± 6.6
$a_{\text{max}(10)}$ (m s ⁻²)	189 ± 20	141 ± 23	105 ± 9	110 ± 17
$\bar{\omega}_{(s1)}$ (deg s ⁻¹)	9777 ± 220	9155 ± 405		

that scaling the odds ratios by the standard deviation of the variable ($[\exp(\beta)]^s$, where s is standard deviation) provides a more intuitive interpretation. With this scaling, an odds ratio of 3, for example, indicates that an increase of one standard deviation increases the odds of the event three times. Importantly, odds ratios are exponential, a $2s$ increase in the independent variable increases the odds not six times but $[\exp(\beta)]^{2s}$ times.

Results

In staged laboratory interactions, *Poecilia reticulata* successfully evaded 36 of 55 (65%) *Crenicichla alta* predation strikes. Many of the successful evasions were nearly unsuccessful as the prey avoided contact with the predator in only 24 of 55 (44%) strikes. The striking predator typically travelled the initial predator distance, D_{pred} , within 33 ms (the closing time, Δt_{close}) of the Guppy's initial movement. In general, the predator could make small adjustments to its strike trajectory although this was only conspicuous in the longer interactions. For failed evasions, Δt_{close} averaged 21.7 (± 1.8) ms ($N = 18$) while for successful evasions Δt_{close} averaged 39.6 (± 2.6) ms ($N = 34$), a difference that is significant ($P < 0.0001$). The Δt_{close} for a failed evasion was 36 ms. The minimum Δt_{close} for a successful evasion

was 15 ms. The average time to contact was 22.9 (± 1.9) ms in successful evasions and 17.5 (± 1.5) ms in failed evasions, suggesting that increased escape speed contributed to successful evasions. A startled Guppy, on average, completed fast-start stage 2 within 21.9 (± 0.1) ms. 73% of the contacts between predator and prey occurred before the end of stage 2 and 92% occurred before stage 3. Only two contacts and one failed evasion occurred after stage 3. These contact data highlight the importance of the initial stages of the fast start (stages 1 and 2) in evasion success.

Neither initial prey distance from a wall ($P = 0.37$, including Δt_{close} and θ in the model) nor arena geometry ($P = 0.81$, including Δt_{close} and θ in the model) had an effect on evasion outcome and these variables were excluded from all further analyses. Mean performance traits (Table 2) suggest that successful evasions were associated with both long predator distances at the start of the evasion response (D_{pred}) and low predator strike velocities (\bar{v}_{pred}), increased initial flight angles ($d_{\text{net}(t)}$, $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$), increased accelerations (reflected in the linear performance measures $d_{\text{net}(t)}$, $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$) and increased stage 1 turning velocities ($\bar{\omega}_{(s1)}$). Table 2 also gives the estimates of the linear performance measures for the full sequences. Values for the 12 ms sequences are biased upwards but this

Table 3. Summary of regression coefficients (β), one-tailed probabilities (P) and odds ratio from the seven multiple logistic regression analyses. Each analysis included one of the seven performance parameters as the main effect and D_{pred} , \bar{v}_{pred} and θ as covariates. β and P for the covariate parameters D_{pred} , \bar{v}_{pred} and θ are averaged over the seven analyses. The odds ratio is scaled by the standard deviation, s , as $[\exp(\beta)]^s$ (see text for interpretation). Parameter abbreviations as in Table 1

Parameter	β	P	Odds ratio
D_{pred} (cm)	1.418	2.3×10^{-6}	26.0
\bar{v}_{pred} (cm s ⁻¹)	-0.0486	0.0010	0.087
θ (deg)	0.0189	0.0010	2.44
$\bar{\omega}_{(s)}$ (deg s ⁻¹)	0.000691	0.0241	2.74
$d_{\text{net}(5)}$ (cm)	30.4	0.0017	4.70
$v_{\text{max}(5)}$ (cm s ⁻¹)	0.0342	0.0592	1.94
$a_{\text{max}(5)}$ (m s ⁻²)	0.0115	0.0115	2.94
$d_{\text{net}(10)}$ (cm)	8.920	0.0307	2.29
$v_{\text{max}(10)}$ (cm s ⁻¹)	0.0372	0.0333	2.26
$a_{\text{max}(10)}$ (ms ⁻²)	0.00779	0.0211	2.42

bias is uniform across both successful and unsuccessful evasions. In contrast, only failed evasion sequences are biased upwards in the full sequence analysis because of their shorter number of frames. While differences in $d_{\text{net}(t)}$ between successful and failed evasions are suggested by the full sequence analysis, differences in $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$ are not, which simply reflects the stronger bias in the derivatives (Walker 1998).

Odds ratios from the multiple logistic regression (Table 3) support the strong effect of D_{pred} and \bar{v}_{pred} on the probability of escape. The odds ratio of D_{pred} (26.0) indicates that a one standard deviation increase in initial predator distance increases the odds of survival 26 times while the odds ratio of \bar{v}_{pred} (0.087) indicates that a one standard deviation increase in \bar{v}_{pred} decreases the odds of survival 11.5 times. D_{pred} reflects a contribution from both predator stealth and prey boldness but these factors cannot be separated. \bar{v}_{pred} is potentially determined by both swimming speed and the speed of jaw protrusion, two components that are discussed in more detail in Nemeth (1997).

The initial flight path relative to the direction of the predator (θ) is an important component of evasion success; one standard deviation increase in θ increases the odds of survival 2.44 times (Table 3). While it is obvious that small θ should lead to increased evasion failure, it is not clear if the optimal flight path should be closer to 90° (normal to the predator's strike path) or 180° (directly away from the predator's strike path). To examine this, θ was binned into six (30°) or eight (20°) intervals and the frequency of successful evasions in each interval was computed (Table 4). Both linear and quadratic regressions of frequency against interval number were then computed. Regardless of the binning procedure, the linear component was significant (20°: $P = 0.0063$; 30°: $P = 0.0012$) while the quadratic component was not (20°: $P = 0.1358$; 30°: $P = 0.2575$). These data, then, suggest an optimal flight path near 180°.

Table 4. Frequency of successful and failed evasions as a function of escape angle, θ

θ	Success	Failure	Total	% Success
(a) 20° bins				
0–20	0	2	2	0
20–40	3	3	6	50
40–60	1	1	2	50
60–80	5	4	9	55.6
80–100	6	5	11	54.5
100–120	6	1	7	85.7
120–140	4	0	4	100
140–160	4	2	6	66.7
160–180	7	1	8	87.5
(b) 30° deg bins				
0–30	1	3	4	25
30–60	3	3	6	50
60–90	8	7	15	53.3
90–120	9	3	12	75
120–150	7	2	9	77.8
150–180	8	1	9	88.9

The direction of the differences in $\bar{\omega}_{(s)}$, $d_{\text{net}(t)}$, $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$ between successful and failed evasions when holding D_{pred} , \bar{v}_{pred} and θ constant are consistent with the *a priori* hypothesis that faster starts increase the probability of survival (Table 3). Note that this is not true for $\bar{v}_{\text{max}(10)}$ when not holding the other variables constant (Table 2). All performance variables have effectively the same effect size, indicated by the odds ratios scaled by the parameter's standard deviation (Table 3). The geometric mean odds ratio for the seven performance measures ($\bar{\omega}_{(s)}$ and $d_{\text{net}(t)}$, $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$ at 5 and 10 ms) is 2.29, indicating that a one standard deviation increase in fast-start performance increases the odds of survival about 2.29 times.

The linear performance variables $d_{\text{net}(t)}$, $v_{\text{max}(t)}$ and $a_{\text{max}(t)}$ are each associated with a different power to test the fast-start hypothesis because of different levels of measurement error (Walker 1998). While the error associated with estimating the centre of mass at any t is low relative to the error in the centre of mass derivatives, the estimate of $d_{\text{net}(t)}$ is dependent on identifying the precise frame in which head movement begins, which is not trivial given the very subtle initial head movements with 1000 Hz data. Regardless of the variation in error variance, our data indicate that inference of performance effects on survival is not necessarily dependent on the linear performance measure (displacement, velocity or acceleration). This result may be due to the choice of the MSE quintic spline as the numerical differentiation algorithm, which has reduced error variance relative to many other available algorithms (Walker 1998).

Comparisons of performance between wild and domestic Guppies or among Guppies from high and low-predation sites are difficult with these data because of the variation in arena designs and prey introduction, and the non-random order in which the prey were introduced over the course of the experiments. Nevertheless,

interpopulation comparisons are interesting because these give a sense of the sensitivity of the results to the different source populations. Wild Guppies successfully evaded 66.7% of the strikes while domestic Guppies evaded 60% of the strikes, which suggests a domestication effect. Indeed, when holding D_{pred} , \bar{v}_{pred} and θ constant, the odds of wild Guppies surviving a prey strike are three times that of domestic Guppies ($\exp(\beta) = 0.315$, $P = 0.066$). Differences in fast-start ability between wild and domestic Guppies average 0.47 standard deviation units across all seven performance measures, and consequently, wild Guppies have about 1.65 times increased odds of survival over domestic Guppies owing to this increased performance. Despite variation in performance between wild and domestic Guppies, the inclusion of the domestic Guppies in the experiment has little influence on the outcome of performance ability on the probability of survival. The geometric mean of the odds ratios of the seven performance measures is 2.29 in the analyses including the domestic Guppies and 2.55 excluding them while the geometric mean of the associated one-tailed P -values is 0.030 with the domestic Guppies and 0.052 without.

Within the wild Guppies, those from high-predation sites evaded 63.6% of the strikes while those from low-predation sites evaded 75% of the strikes. However, when holding D_{pred} , \bar{v}_{pred} and θ constant, Guppies from high-predation sites are 1.3 times more likely to survive ($\exp(\beta) = 1.3$), an effect that is not nearly significant ($P = 0.645$). Eight of the 12 low-predation individuals are from a population that was experimentally transplanted from a high-predation to a low-predation site in 1976. Evasion success was 87.5% in the transplanted low-predation fish and 50% in the natural low-predation fish. Unfortunately, the sample used to compute these evasion success frequencies is too small to draw any conclusions about evasion ability differences among Guppies from high and low-predation environments.

Discussion

A comprehensive, ecomorphological model of fish body and fin shape variation based on simple hydrodynamic models of fish propulsion has developed over many years (Aleev 1969; Lighthill 1969; Weihs 1973, 1989; Blake 1981; Webb 1982; Webb 1984a; Walker 1997). The model is commonly used to explain body and fin shape variation among both closely related populations and distantly related species. These hypotheses of adaptive divergence in body shape implicitly assume that faster starts directly influence the ability to successfully evade predators. The results of this study support this assumption.

Three studies measuring an indirect relationship between fast-start ability and predator-induced mortality in laboratory selection experiments are also consistent with the higher swimming performance equals increased survival hypothesis. In separate experiments, Swain (1992a,b) showed that Threespine Sticklebacks

(*Gasterosteus aculeatus*) with an optimal ratio of abdominal to caudal vertebrae had both faster starts and were more likely to survive laboratory predation from Sunfish (*Lepomis gibbosus*) compared with sticklebacks with suboptimal vertebral ratios. Similarly, *Menidia menidia* with slower growth rates had faster starts (Billerbeck *et al.* 2001) and were more likely to survive laboratory predation (Lankford *et al.* 2001) than *M. menidia* with faster growth rates. Finally, Guppies from high-predation streams had higher probabilities of survival than those from low-predation streams in laboratory selection experiments with the predator, *Crenicichla alta* (O'Steen *et al.* 2002). While all of these experiments are consistent with the hypothesis that faster starts increase the probability of evading a predation strike, fast-start performance during an actual predator-prey interaction was not directly measured in any of these experiments. Consequently, the alternative hypothesis, that faster starts do not matter, cannot be rejected.

Two studies have measured fast-start performance during actual evasion responses. Webb (1986) found that the probability of evasion success for four prey species attacked by Largemouth Bass (*Micropterus salmoides*) was not a function of prey acceleration ability but that higher acceleration starts did increase the probability of an aborted strike. For several reasons, we believe Webb's analysis was not sufficient to unambiguously conclude that prey acceleration ability does not influence the probability of evasion success. First, acceleration varied among the four prey species but the effect of species on evasion success or predator strike velocity was not analysed (mean strike velocities for each species were reported and the predator appeared to modulate its attack velocity based on prey acceleration ability). Variation in predator strike velocity (\bar{v}_{pred}) and initial predator distance (D_{pred}) were combined into the variable Apparent Looming Threshold (ALT). No ALT effect on evasion success was found, but it seems unlikely that \bar{v}_{pred} and especially D_{pred} could have no effect on evasion success. Second, both predator and prey responses included several behaviours in addition to a simple predation strike and prey fast-start evasion response. Predator behaviours included aborted strikes and strikes without buccal expansion. Prey behaviours included short duration (<500 ms), postfast-start sprints. Importantly, both fast-start and postfast-start behaviour varied among the four prey species.

Katzir & Camhi (1993) found that evasion success of Black Mollies (*Poecilia sphenops*) from striking Pied Kingfishers (*Ceryle rudis*) was associated with both prey swimming speed and the time necessary for the predator to reach the prey (closing time), but, importantly, the affect of swimming speed holding closing time constant was not reported. Consequently, high evasion speed could be associated with successful escapes not because the high speed allowed the escape but because a long closing time allowed both an escape and time for the prey to accelerate to a high speed.

In contrast to these previous studies, our data provide strong support for the hypothesis that faster starts increase the probability of successfully evading a predation strike. The magnitude of the effect is strong; a one standard deviation increase in fast-start performance increases the odds of survival by about 2.3 times. Three aspects of our design augmented our ability to find this association. First, we controlled for the highly influential and confounding factors D_{pred} , \bar{v}_{pred} and θ . Second, for our measures of velocity and acceleration, we limited the sequences to an equal number of frames, which equalized the bias between both outcome groups (success, failure). Third, we compared performance within the range of t that is relevant to the outcome of the predator–prey interaction. The dynamics of the interactions in this study suggest that measures of fast-start performance in Guppies should be confined to t less than the duration through stage 2 (~22 ms). Importantly, however, we do not know how the relevant range of t varies with predator or habitat, or how the range scales with prey size.

A common concern of artificially stimulated evasion responses is our lack of confidence that these responses are maximal. In a companion study (J. A. Walker, K. Ghalambor and D. N. Reznick, in preparation), we measured the maximum (of three) fast starts for 112 F2, lab-reared, male Guppies from the same streams as those in this study. The fast starts in this companion study were induced by a tennis ball falling against the side of the experimental aquarium. Perhaps reassuringly, there is no difference in $d_{\text{net}(10)}$ between the predator-stimulated and ball-stimulated fast starts (predator: $\bar{d}_{\text{net}(10)} = 0.23 \pm 0.01$ cm; ball: $\bar{d}_{\text{net}(10)} = 0.22 \pm 0.007$ cm; $F = 1.5$, $P = 0.22$). Although one may be tempted to use a predator stimulus instead of an artificial stimulus when investigating the functional ecology of fast-start performance variation within and among populations, our analysis suggests that, not only is a predator stimulus not necessary to induce a maximal response, but will also produce upwards biased results, at least for the shorter, failed evasion sequences.

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