Predation Intensity Does Not Cause Microevolutionary Change in Maximum Speed or Aerobic Capacity in Trinidadian Guppies (*Poecilia reticulata* Peters)

Mark Chappell[1,*]
Jason Odell[2]
[1]Biology Department, University of California, Riverside, California 92521; [2]ADInstruments, Colorado Springs, Colorado 80906

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ABSTRACT

We measured maximal oxygen consumption ($\dot{V}O_{2max}$) and burst speed in populations of Trinidadian guppies (*Poecilia reticulata*) from contrasting high- and low-predation habitats but reared in "common garden" conditions. We tested two hypothesis: first, that predation, which causes rapid life-history evolution in guppies, also impacts locomotor physiology, and second, that trade-offs would occur between burst and aerobic performance. $\dot{V}O_{2max}$ was higher than predicted from allometry, and resting $\dot{V}O_2$ was lower than predicted. There were small interdrainage differences in male $\dot{V}O_{2max}$, but predation did not affect $\dot{V}O_{2max}$ in either sex. Maximum burst speed was correlated with size; absolute burst speed was higher in females, but size-adjusted speed was greater in males. For both sexes, burst speed conformed to allometric predictions. There were differences in burst speed between drainages in females, but predation regime did not affect burst speed in either sex. We did not find a significant correlation between burst speed and $\dot{V}O_{2max}$, suggesting no trade-off between these traits. These results indicate that predation-mediated evolution of guppy life history does not produce concomitant evolution in aerobic capacity and maximum burst speed. However, other aspects of swimming performance (response latencies or acceleration) might show adaptive divergence in contrasting predation regimes.

Introduction

Intraspecific and interspecific variation in physiological performance has long been of interest to comparative physiologists. From an evolutionary perspective, heritable variation in traits affected by natural selection is the basis for Darwinian adaptation. In a mechanistic context, ANOVAs at different levels of integration (e.g., enzymes, organelles, cells, organs, organ systems, and the intact animal) can provide useful insights into the functional basis of physiological performance (Hulbert and Else 1981; Garland 1984; Bennett 1987, 1997; Bennett et al. 1989; Mangum and Hochachka 1998). These analyses can be used to predict what organs or organ systems are likely to be affected by selection on whole-organism performance or by conditioning regimes, seasonality, behavioral changes, or other factors that affect traits through phenotypic plasticity. Other studies have examined the repeatability and heritability of interindividual differences in performance, which are critical in determining how (or if) a trait can be affected by natural selection (Garland and Bennett 1990; Jayne and Bennett 1990*a*, 1990*b*).

Of special interest to both evolutionary biologists and physiologists are potential trade-offs (antagonistic pleiotropy) between genetically based traits. The concept of trade-offs is fundamental and explicit in most evolutionary models and particularly so for life-history theory (Roff 1992; Stearns 1992). Although the central tenets of comparative physiology may not incorporate trade-offs as formally and explicitly as in evolutionary theory, the trade-off concept is implicit in numerous analyses of physiological systems. Examples include the "jack-of-all-temperatures, master of none" hypothesis in the thermal biology in lizards (Huey and Hertz 1984), speed versus stamina in locomotor performance (Vanhooydonck et al. 2001), and the relationship between maximum metabolic power production and "maintenance costs" of resting metabolism (Bennett and Ruben 1979). Given the potential for trade-offs, a key question for comparative and ecological physiologists and evolutionary biologists is the extent to which selection-driven genetic change (Darwinian adaptation) in major organism-level traits affects other characters.

We explored these questions in a system that offers the possibility of particularly clear insights into microevolutionary change: the cluster of spatially separated guppy populations (*Poecilia reticulata* Peters) on the island of Trinidad. Life-history evolution in these fish has been extensively studied for several decades by David Reznick, John Endler, and their colleagues. Guppies are native to rainforest drainages throughout the mountain ranges of Trinidad and occur even in very small

* Corresponding author; e-mail: chappell@citrus.ucr.edu.

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tributaries (Reznick and Endler 1982). Local habitats range from shallow slow-moving low-volume pool-and-riffle systems (often interspersed with barrier waterfalls) to large deep fast-flowing rivers. The variation in stream topography, along with other factors, results in striking interpopulation differences in predation regimes (large piscine guppy predators occur in downstream habitats but are absent above barrier waterfalls; Reznick and Endler 1982), with concomitant differences in mortality rates (Reznick et al. 1996). In turn, differences in predation regimes are associated with large and genetically determined differences in key life-history parameters such as age at first reproduction and reproductive effort (Reznick 1982; Reznick and Bryga 1987, 1996). Moreover, experimental manipulation of predation regimes in natural habitats has revealed remarkably rapid rates of evolutionary change in life history (Reznick et al. 1997).

Given the variation in stream characteristics, striking differences in life-history parameters, and quick response to selection in Trinidadian guppies, a natural question is: has whole-animal physiological performance also evolved in these populations, and if so, do evolutionary changes in physiology result from the same environmental factor (predation) responsible for differential evolution of life-history traits? In this article we use within-population and between-population variation to examine two organism-level performance traits: aerobic capacity (the metabolic foundation of sustainable swimming and other long-duration activities) and burst speed (presumably crucial in escape from predators and other emergency responses). Both traits require the effective and coordinated functioning of a suite of enzymes, organelles, cells, tissues, organs, and organ systems, and hence are useful integrative physiological indices. Both traits can be intuitively linked to predation regime and life-history characters: intense predation by larger fishes should generate strong direct selection on burst performance (O'Steen and Bennett 1998; O'Steen et al. 2002), whereas the large differences in resource allocation between high-predation and low-predation populations—particularly in somatic versus reproductive investment—seem likely to impact the size and function of organ systems (particularly swimming muscle) responsible for locomotor physiology. Also, because different muscle fiber types are responsible for burst and aerobic swimming in fish (Jayne and Lauder 1994; Zhang et al. 1996), a trade-off between these two performance traits is a logical expectation. Finally, the amenability of guppies to laboratory culture allowed us to use laboratory-reared fish to control for environmental effects and reveal genetic differences.

Material and Methods

Animals and Collection Sites

We used second-generation and third-generation lab-born guppies reared in "common garden" conditions to minimize the possible influences of maternal effects (which would be present in F1 fish) and differential acclimatization to local environments. Ancestral fish were collected from wild populations in Trinidad (20–25 gravid females for each population), transported to University of California, Riverside, and maintained in glass aquaria as described by Reznick and Bryga (1987). Tanks contained broken pieces of terra-cotta pottery for hiding places, and water temperature was maintained at 24.5° ± 1°C. Guppies were fed liver paste and commercially available food granules (Tetra) ad lib. All aspects of animal housing, care, and measurements were approved by the University of California, Riverside, Institutional Animal Care and Use Committee.

We studied guppies derived from seven field populations. Six of these were upstream and downstream pairs (low- and high-predation environments, respectively) from three large river drainages (Caroni, Oropouche, and Yarra). The seventh was an unpaired upstream population (Paria) used in validation work and resting metabolic rate (RMR) measurements but excluded from population comparisons (which necessitated a 2 × 2 design). All of the third-generation fish were from the Paria drainage. Two drainages provided naturally occurring paired populations from upstream and downstream habitats: Oropouche (Quare and Oropouche sites) and Yarra (Yarra tributary and Yarra River sites). The Caroni drainage provided a downstream control population (Aripo River) and an experimental population introduced from the Aripo River site to a low-predation upstream tributary (Aripo introduction site) where guppies were previously absent (Reznick and Bryga 1987). We obtained data on stream velocity in guppy microhabitats (i.e., portions of streams where guppies were observed; 23% of randomly selected points along streams) using a Global Water flow probe resolving 3–2,000 cm/s. We also measured stream width and water depth at the sites where velocity was measured (Odell 2002); all stream data were obtained at the same time of year.

To maximize within-population diversity, only two fry were collected on any given day from a particular stock tank (this ensured roughly equal representation of each wild-caught ancestor's offspring in the test populations). Fry were reared together in population-specific 18-L tanks until they reached maturity. At 1 wk before measurements, individuals were transferred to 7.25-L tanks, where they remained isolated for the remainder of the study.

The ideal experimental design would be completely randomized (simultaneous rearing of all populations under constant conditions), but logistical constraints precluded that approach. Instead, we simultaneously reared upstream and downstream populations from the same drainage, while populations from different drainages were reared sequentially. That design allows robust comparisons between upstream and downstream (low and high predation) habitats, but even though rearing conditions were kept as identical as possible for all groups, the temporal separation in rearing fish from different drainages introduces the possibility of uncorrected "block" effects in comparisons among drainages.

Aerobic Physiology

Oxygen Consumption Measurements. We used closed-system respirometry to measure rates of oxygen consumption (O_2). The metabolic chamber was built from a small plastic (Nalgene) jar. A plastic spacer in the lid adjusted the water volume to 70 or 160 mL, depending on the size of the fish. A Teflon-coated magnetic stir bar beneath a plastic mesh false bottom circulated the water in the chamber. At low rotation rates, the stir bar mixed the water but did not induce unidirectional swimming; higher rotation rates created a current that guppies swam against. At the highest settings (average velocity of about 30 cm/s, determined from the movement of small particles in the water), no guppies were able to maintain position in the water column. An oxygen microelectrode (model 781b, Strathkelvin Instruments, Glasgow, Scotland) was inserted through the lid into the center of the swimming chamber. This arrangement exposed the microelectrode to well-mixed water and kept fish out of the central vortex created by the stir bar. The chamber was filled with aerated water (100% O_2 saturation in room air; Po_2 about 155 torr at ambient atmospheric pressure) at the beginning of each trial and maintained at 24.5° ± 0.1°C with a circulating water bath (Neslab Instruments).

Oxygen content in the sealed chamber was recorded by linking the output of the Strathkelvin meter to a Macintosh computer equipped with a data acquisition board and custom software ("LabHelper," http://warthog.ucr.edu). Oxygen concentration (percent saturation) was recorded every 5 s with multiple readings (15–20) averaged for each sample. Initial O_2 content (mL O_2) of saturated water in the respirometer was calculated from published values for O_2 solubility (Carpenter 1966) after accounting for temperature, barometric pressure, and chamber volume ("LabAnalyst," http://warthog.ucr.edu). To compute $\dot{V}o_2$, we first multiplied initial O_2 content by the fractional saturation at each time-point on the data trace and then converted fractional saturation into the cumulative amount of O_2 (μL) consumed. The time derivative of the cumulative O_2 consumption record is $\dot{V}o_2$ (μL O_2/min).

Maximum Oxygen Consumption. We used the maximal rate of oxygen consumption ($\dot{V}o_{2max}$) during intense forced exercise as our index of aerobic performance. Individual guppies were placed in the chamber and allowed to acclimate for 5 min, with a low stir bar speed setting that did not elicit directional swimming. Then the fish were subjected to 2-min step increments of stir bar speed (generating velocity increases of approximately 3–4 cm/s per step) while behavior was monitored. When a guppy lost its ability to swim against the current, speed was briefly reduced to allow the fish to regain orientation, and then speed was returned to the previous setting. Guppies were exercised until they failed to recover from three consecutive reductions of stir bar speed. At the end of a measurement, the fish was removed from the chamber, lightly anesthetized with MS-222 (USB pharmaceuticals), blotted on a tissue, weighed to the nearest milligram, and returned to its holding tank. After determining $\dot{V}o_2$ from the cumulative oxygen consumption curve as described above, $\dot{V}o_{2max}$ was computed as the highest continuous 60-s average of $\dot{V}o_2$.

Resting Metabolic Rate. Inactive metabolism (i.e., RMR) was determined by measuring $\dot{V}o_2$ over 2-h intervals in 19 males and 13 females resting at night in darkened conditions. The stir bar motor was set at the minimum possible speed, and guppies spent most of their time resting on the mesh bottom of the respirometer (fish were permitted to use the center of the chamber during these tests). Oxygen saturation remained above 85% in these experiments. As for $\dot{V}o_{2max}$ tests, $\dot{V}o_2$ was determined as the derivative of cumulative O_2 consumption over time; RMR was defined as the lowest $\dot{V}o_2$ averaged over continuous 5-min intervals. We also measured $\dot{V}o_{2max}$ for the 32 fish used for RMR data and calculated factorial aerobic scope as $\dot{V}o_{2max}$/RMR.

Validation Studies. We checked for the possible influence of four factors that could affect the accuracy and reliability of $\dot{V}o_2$ measurements: chamber leakage or electrode O_2 uptake, hypoxia, feeding state, and motivation. To test for O_2 diffusion into the respirometer, the chamber was filled with hypoxic water and sealed. We rotated the stir bar at rates similar to those during $\dot{V}o_{2max}$ tests while recording O_2 saturation for 30 min (longer than any $\dot{V}o_{2max}$ test). No detectable change in O_2 saturation was detected, even at saturations as low as 65%—a much steeper O_2 diffusion gradient than during $\dot{V}o_{2max}$ and RMR measurements (where saturations were always >84%). To test for O_2 depletion by the electrode, we monitored O_2 saturation in a sealed chamber initially containing 100% saturated water. There was little or no change in saturation over 30 min; calculations based on these results and levels of electrical noise in the recorder output indicate that O_2 uptake by the electrode was at least 50-fold lower than the RMR of even the smallest guppy we tested.

Because the chamber contained a fixed initial quantity of O_2 that was depleted during experiments, we tested whether our protocol produced hypoxic conditions that suppressed $\dot{V}o_2$. We measured eight male and 10 female guppies during sustained swimming at constant speeds slightly less than maximum aerobic speed. Fish were exercised until they had reduced O_2 saturation to less than 70% (males) or 60% (females); their $\dot{V}o_2$ were compared over intervals of 10% saturation (i.e., 70%–80%, 80%–90%, 90%–100%). Repeated-measures ANCOVA revealed no effect across a 30% change in saturation ($P > 0.4$). Therefore, it is unlikely that our and $\dot{V}o_{2max}$ and RMR protocols created hypoxia-induced performance limitations.

Since metabolism can be affected by feeding state (Johnston and Battram 1993), we measured $\dot{V}o_{2max}$ in five males and five females fasted for 60 h before measurement and compared these

rates with the $\dot{V}O_{2max}$ of five males and five females fed ad lib. 6 h before measurement. Feeding state did not affect $\dot{V}O_{2max}$ (ANCOVA: $F_{1,15} = 0.011$; $P = 0.92$). Nevertheless, all fish used in the main study were fasted for a standard 24-h period before testing.

A behavioral concern was that the protocol and equipment might not motivate fish to maximal performance. A standard indicator of maximal $\dot{V}O_2$ in vertebrates is elevated levels of lactic acid, a byproduct of anaerobic power production. To test for changes in lactate status, nine guppies were subjected to an intense, 3-min exercise regime at speeds similar to those attained in our $\dot{V}O_{2max}$ protocol; a control group was rested in the dark for 30 min. All exercised fish switched from continuous swimming to a "burst and coast" gait indicative of maximal performance (Jones 1982; the same behavior occurred at the end of our $\dot{V}O_{2max}$ protocol). At the conclusion of tests, guppies were flash-frozen in liquid nitrogen and stored at −80°C. Whole-body lactate content was measured with a kit (Sigma Diagnostics 735-10, St. Louis, Mo.). Fish were homogenized in 400 μL of 6% perchloric acid, and homogenates were centrifuged at 10,000 *g* for 5 min. Absorbance at 540 nm was measured on 10 μL of supernatant. Two samples were analyzed from each fish, and mean absorbance was used to determine lactate concentration (mg/g). Whole-body lactate averaged 0.096 mg/g in rested guppies and 0.52 mg/g in exercised fish—a 5.4-fold change. This shows that the protocol forced fish to use anaerobic pathways extensively, which is consistent with attainment of $\dot{V}O_{2max}$.

Burst Performance

We used high-speed video records to measure maximal burst speed during and immediately after C-start escape responses (Eaton et al. 1977). We chose a measure of maximum velocity instead of other commonly used indices of burst performance (such as maximum acceleration or the rate of body bending during the C-start) for two reasons. First, a recent analysis (Walker 1998) shows that with typical video framing rates and resolutions, maximum velocity is less prone to estimation error than are acceleration measures. Second, we were interested in the ability of fish to accomplish a substantial forward movement of the body over a period of several milliseconds as a key element of escape behavior.

Guppies were placed individually in a 15-cm mesh enclosure in a shallow tank maintained at 25° ± 1°C. A MotionScope high-speed video camera (RedLake Instruments, San Diego, Calif.) directly above the tank recorded the escape response at 500 Hz. Video data were calibrated with *X*- and *Y*-axis scale markers on the bottom of the test tank. The camera was mounted sufficiently far above the water surface (70 cm) relative to water depth (2–3 cm) to minimize parallax errors in position determinations.

Guppies were allowed to acclimate to the tank for 2 min and then were startled when the side of the tank was tapped with a small metal object. This yielded consistent escape responses and did not disturb the water in the tank enough to distort images. After the first C-start, fish were allowed to rest for 2 min and then startled a second time. Video was saved to VHS tape and then captured to a Macintosh at the camera's resolution of 320 × 240 pixels.

Between 50 and 100 sequential frames (0.1–0.2 s) were digitized for each C-start event using custom software ("Motion Analysis," http://warthog.ucr.edu). The positions of two points on each fish were tracked: the tip of the rostrum and the body centerline at the fish's axis of bending. The latter point (approximately the center of mass) was used to avoid overestimation of forward velocity due to side-to-side motion of the snout. Preliminary measurements indicated that the bending axis was posterior to the snout by a distance of 35% of body length (measured from the video using the scale markers in the image for calibration). The software automatically located the bending axis point at 35% of body length in reference to the easily definable snout position. Digitized position data were used to determine frame-to-frame instantaneous velocity. To reduce noise from lateral motion, raw velocity data were smoothed by a three-point averaging algorithm. The 0.1–0.2 s of smoothed velocity data were scanned to find the maximum velocity (centimeters per second) of the bending axis during a continuous 10-frame (20 ms) interval. The highest value of the two tests of velocity for each fish was used as its burst speed.

Repeatability

We measured $\dot{V}O_{2max}$ twice for each fish over an interval of 1 wk ($\pm$1 d) for both sexes in two populations (Paria and Aripo downstream). In addition, Quare and Oropouche males were tested over an interval of 90 d. To minimize variation due to handling effects, we were careful to use identical procedures throughout the study. Repeatability of burst speed was determined across the 2-min interval between burst trials. For both $\dot{V}O_{2max}$ and burst speed, repeatability was calculated as the Pearson's correlation coefficient between size residuals from initial and final measurements (Hayes and Shonkwiler 1996).

Statistics

Within species and over a wide range of taxa, metabolism scales allometrically with mass (Fig. 1; Bartholomew 1982), leading to confounding effects when comparing between groups with different masses. Burst performance also scales with size (Fig. 2). Hence, mass residuals of $\dot{V}O_{2max}$ and burst speed or ANCOVA with mass as the covariate were used in many analyses. Nonsignificant interaction terms were removed from final models. A 2 × 2 design was used to test for differences between populations as a function of drainage and stream ecology (predation regime). Because male guppies are considerably smaller

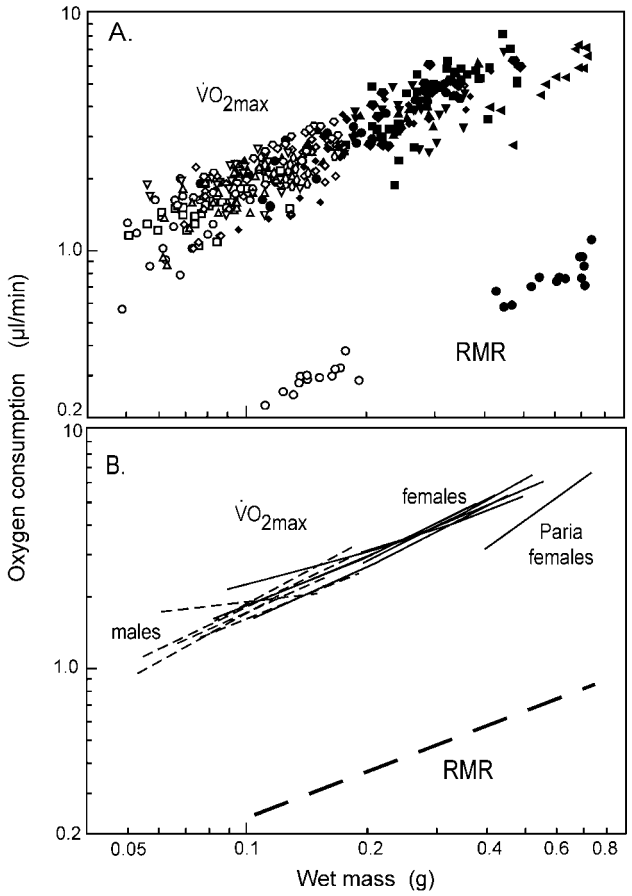

Figure 1. *A*, Log-log plot of wet mass versus maximum oxygen consumption rates ($\dot{V}o_{2max}$) and resting metabolic rates (RMR) for 176 male (*open symbols*) and 159 female (*filled symbols*) guppies from seven populations. *B*, Least-squares regressions for each population and the regression line for RMR. Females from the Paria drainage were significantly different than all other populations of females, but there were differences between males and females in the other six populations.

than females (with little size overlap; Fig. 1), the sexes were analyzed separately. Statistics were performed using JMP software for Macintosh (SAS, Cary, N.C.) and Statistica/Mac (Statsoft, Tulsa, Okla.).

Results

Size

Body size (expressed as both mass and standard length) was strongly affected by sex and to a lesser extent by drainage and predation regime (Table 1). Females averaged 34% longer and more than twice as heavy as males (Figs. 1, 2). In our samples, females from high-predation sites were larger than females from low-predation sites (0.300 ± 0.091 g and 0.244 ± 0.107 g, respectively; $P = 0.00089$), but the reverse was true for males (0.0997 ± 0.0248 g and 0.114 ± 0.0367 g, respectively; $P = 0.00306$). Mass differences among drainages were smaller and often contrasted between sexes; means ranged from 0.247 g (Oropouche) to 0.289 g (Yarra) in females and 0.0875 g (Caroni) to 0.120 g (Yarra) in males (on average, the largest fish came from the Yarra drainage).

Oxygen Consumption and Aerobic Performance

Unsurprisingly, $\dot{V}o_{2max}$ was tightly correlated with body mass in all tested populations and for both sexes (Fig. 1). ANCOVA indicated that Paria females had significantly lower $\dot{V}o_{2max}$ than Paria males. However, there were no sex differences in the other six populations, which contained a 3.6-fold mass range in males (0.053–0.193 g), a 6.7-fold mass range in females (0.082–0.553 g), and a 10.4-fold mass range overall. Excluding Paria fish (which were older and hence larger than fish from the other populations), $\dot{V}o_{2max}$ averaged 3.57 µL/min in 147 females (mean mass 0.271 ± 0.103 g) and 1.77 ± 0.52 µL/min in 168 males (mean mass 0.107 ± 0.032 g). In the pooled data from the six paired populations and both sexes, mass explained 82% of the variation in aerobic capacity ($\dot{V}o_{2max} = 9.65 \times \text{mass}^{0.764}$; $r = 0.908$).

Guppy RMR was also tightly correlated to mass (Fig. 1; these 32 fish were from the Paria population). RMR averaged 0.726 µL/min in females (mean mass 0.679 g) and 0.284 µL/min in males (mean mass 0.147 g). Mass explained nearly all of the variation in RMR (resting $\dot{V}o_2 = 0.929 \times \text{mass}^{0.628}$; $r = 0.99$).

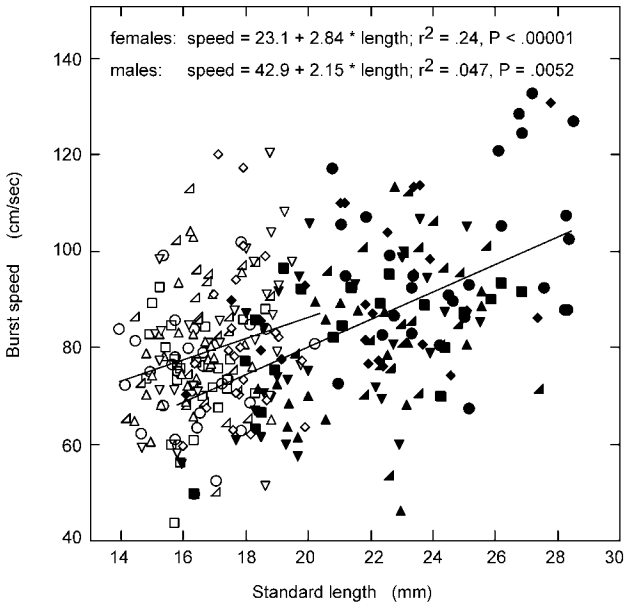

Figure 2. The relationship between size (standard length) and maximum burst speed in guppies. Different symbols indicate fish from different populations; filled symbols indicate females, and open symbols indicate males.

Table 1: Effects of gender, drainage, and predation regime on body size expressed as wet mass and standard length

Effect	*F* (Mass)	*P* (Mass)	*F* (Length)	*P* (Length)
Predation	5.98	.015	4.97	.027
Drainage	4.72	.0096	6.82	.0013
Sex	429	<.00001	627	<.00001
Predation × drainage	11.0	.000023	6.1	.0025
Predation × sex	19.1	.000017	29.5	<.000001
Drainage × sex	3.81	.023	9.00	.00016
Predation × drainage × sex	3.15	.044	1.10	.33

Note. $N = 315$ fish (147 females, 168 males).

Within the RMR test group, factorial aerobic scope was not affected by sex (ANOVA: $F_{1,30} = 0.22$; $P = 0.65$) and averaged 7.2 ± 0.4 (range 2.8–12.6).

Burst Performance

In all populations, absolute burst speed was positively correlated with body size (expressed either as mass or standard length), although variance was high (Fig. 2). Burst speed ranged from 46.3 to 132.9 cm/s in females (mean 86.8 ± 16.5 cm/s) and from 43.8 to 120.4 cm/s in males (mean 79.1 ± 13.4 cm/s). After accounting for size effects, males were 9.5% faster than females (ANCOVA: $F_{1,307} = 8.8$; $P = 0.0032$). A commonly used size-compensated index of maximal swimming speed in fish is body lengths per second (Wardle 1975; Domenici and Blake 1997). When burst speed is expressed this way, male guppies are substantially faster than females (47.3 ± 10.2 vs. 38.7 ± 6.5 lengths/s, respectively; $F_{1,311} = 60.4$; $P < 0.000001$).

Variation and Repeatability

For convenience in comparisons, we plotted variation in burst speed and $\dot{V}O_{2max}$ as measured values as a percentage of values predicted from mass regressions (Fig. 3). Variation was similar among populations; the pooled variation in $\dot{V}O_{2max}$ (across seven populations) was 19.4% in males and 18.6% in females (Fig. 3*A*). Variation in burst performance was 16.5% in both males and females (Fig. 3*B*).

Over 2 min, maximum burst speed was significantly repeatable (Pearson's $r = 0.805$; $P < 0.0001$); $\dot{V}O_{2max}$ was significantly repeatable over 7-d intervals in all groups tested (86 males and females from two populations) and in the pooled data (Table 2). Over 90-d intervals (60 males from two populations), $\dot{V}O_{2max}$ repeatability was substantially lower but remained statistically significant in one population (Table 2) and for the pooled data.

Performance Comparison among Populations

We tested for performance differences across populations as a function of two main effects: predation regime (presence or absence of large predatory fishes, particularly pike cichlids, *Crenicichla alta*; Reznick 1982) and drainage (to account for other biotic or abiotic differences or genetic drift between stream systems). We included only data from the three drainages with matched high/low predation pairs (Oropouche, Yarra, Caroni). In all three drainages, high-predation sites were downstream of low-predation sites (and had greater depth and width); therefore, to account for any effects of stream hydro-

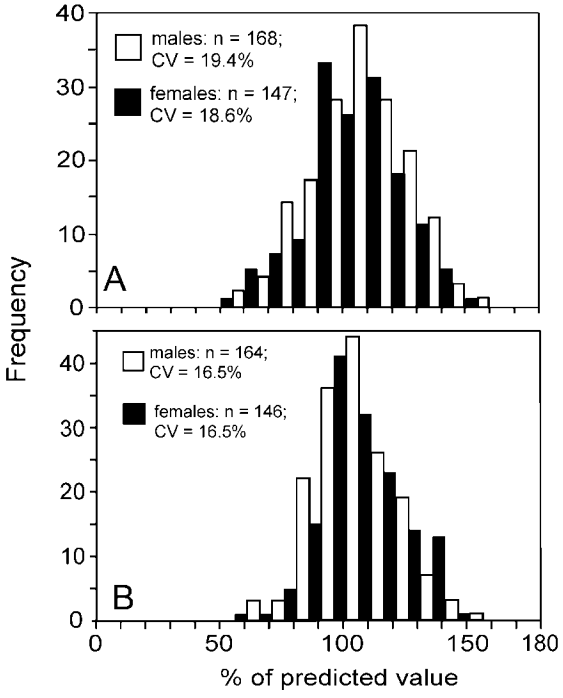

Figure 3. Mass-independent variation in (*A*) $\dot{V}O_{2max}$ and (*B*) burst speed in guppies. Data shown as percentage of values predicted by regression on wet mass (i.e., 100% indicates equality of observed and predicted values). Open bars are data for males, and filled bars are for females. *CV* = variation.

Table 2: Repeatability (r) of $\dot{V}O_{2max}$

Locale	Sex	Interval (d)	N	r	P
Paria	Male	7	17	.73	.0008
Paria	Female	7	13	.61	.0265
Aripo control	Male	7	27	.64	.0003
Aripo control	Female	7	29	.56	.0015
Quare	Male	90	30	.24	.202
Oropouche	Male	90	30	.36	.0491
Pooled	Both	7	86	.58	<.0001
Pooled	Male	90	60	.30	.021

Note. $\dot{V}O_{2max}$ = maximal oxygen consumption.

dynamic differences among populations, we included stream velocity as a covariate.

There was a significant (but small) positive relationship between $\dot{V}O_{2max}$ and stream velocity in males, but a similar effect was not found for females. Relationships between performance, sex, drainage, and predation environment had few clear patterns, and both burst and aerobic performance had complex interactions between sex and drainage (Tables 3, 4). Male (but not female) $\dot{V}O_{2max}$ varied significantly by drainage, but there was no apparent effect of predation regime on either male or female $\dot{V}O_{2max}$ (Fig. 4; Table 3). Absolute burst speed differed significantly by drainage in female guppies but not in males (Fig. 4; Table 4), but predation regime did not explain the variation in burst speed among sites for either sex. Finally, burst speed expressed as body lengths per second was not affected by either drainage or predation regime ($P = 0.17$ and $P = 0.77$, respectively).

Our experimental design (simultaneous rearing and testing of upstream and downstream population pairs within drainages; sequential rearing and testing of populations from different drainages) allowed rigorous testing of the effects of low- (upstream) predation and high- (downstream) predation regimes. Therefore, the observed absence of differences between low-predation and high-predation populations seems to be a robust and unambiguous result. However, there is less certainty in our findings of differences between drainages (and interactions between sex and drainage): as far as we can determine, rearing and testing procedures were identical for all groups, but the temporal separation of populations from different drainages introduces the possibility of uncontrolled "block" effects.

Relationship between $\dot{V}O_{2max}$ and Burst Speed

We tested for the possibility that aerobic capacity and burst velocity are correlated traits by computing Pearson's product-moment correlations of residual burst speed and residual $\dot{V}O_{2max}$. We found no significant correlation between $\dot{V}O_{2max}$ and burst speed in either males ($r = 0.028$; $P = 0.76$; Fig. 5) or females ($r = 0.147$; $P = 0.076$). ANCOVA revealed no significant drainage or predation regime differences in the relationship between residual burst speed and residual $\dot{V}O_{2max}$ in females, but in males there was a significant effect of drainage ($F_{2,160} = 15.3$; $P < 0.00001$) and a significant predation × drainage interaction ($F_{2,160} = 3.57$; $P = 0.030$).

Discussion

The main goal of this study was to examine the impacts of predation regime and associated life-history evolution on two highly integrative whole-animal performance traits, burst speed, and maximal aerobic capacity. For both traits, we found little or no evidence of predation effects. To put those findings into an appropriate context, it is useful to compare guppy locomotor physiology to that of other species and to examine the degree of variance and its repeatability in burst and aerobic performance.

Comparative Locomotor Performance

Although they do not seem specialized for intense sustained swimming, wild guppies frequently swim against currents for substantial periods when foraging or traveling (J. Odell, unpublished data). Hence, aerobic activity is a normal component of their behavior. We used data in FishBase (http://www.fishbase.org; Froese and Pauly 2003; Appendix) to construct an allometric equation for $\dot{V}O_2$ during high-speed swimming (speeds ≥ 4 body lengths/s). This equation ($\dot{V}O_2$ in μL/min = $10.96 \times \text{mass}^{1.03}$; mass in g; $N = 71$, $r^2 = 0.90$; data from seven teleost species corrected to a temperature of 24.5°C with a Q_{10} of 2.4) predicted an exercise $\dot{V}O_2$ of 1.10 μL/min for male guppies (mean mass 0.107 g) and 2.86 μL/min for females (mean mass 0.271 g). Our measured $\dot{V}O_{2max}$ values are 61% higher (1.77 μL/min) for males and 25% higher (3.57 μL/min) for females (excluding Paria fish). There are some potentially confounding differences in methodology: the data in FishBase were obtained primarily during fast but steady state swimming, often in laminar flow conditions (and hence may

Table 3: Drainage, predation, and sex effects on $\dot{V}O_{2max}$

Effect	df	F value	P
Predation	1, 312	.210	.65
Drainage	2, 311	7.26	.00083
Sex	1, 312	.01	.92
Predation × drainage	2, 308	3.63	.028
Predation × sex	1, 310	.01	.91
Drainage × sex	2, 308	5.02	.0071
Predation × drainage × sex	2, 302	.24	.79

Note. $\dot{V}O_{2max}$ = maximal oxygen consumption. ANCOVA with mass as the covariate; log values used for both $\dot{V}O_{2max}$ and mass.

Table 4: Drainage, predation, and sex effects on burst speed

Effect	df	*F* value	*P*
Predation	1, 307	.30	.59
Drainage	2, 306	1.34	.26
Sex	1, 307	9.08	.0028
Predation × drainage	2, 303	2.40	.092
Predation × sex	1, 305	.16	.69
Drainage × sex	2, 303	5.52	.0044
Predation × drainage × sex	2, 297	3.45	.033

Note. ANCOVA with standard length as the covariate.

not be maximal rates), whereas our measurements were intended to push fish beyond their maximal aerobic speed.

We used data for 76 teleost species in FishBase to compute an equation for RMR ($\dot{V}O_2$ in μL/min = 4.343 × mass$^{0.878}$; $N = 1{,}004$; $r^2 = 0.86$; mass in g; corrected to 24.5°C with a Q_{10} of 2.4). Our measured RMR (0.284 μL/min in 0.147-g males and 0.726 μL/min in 0.679-g females) are 65%–77% lower than predicted (0.807 and 3.09 μL/min for males and females, respectively). Nevertheless, our data may be elevated above "true" RMR for two reasons: little time was allowed for acclimation to the chamber, and small currents created by the slowly spinning stir bar may have disturbed the fish. Therefore, our value of 7.2 for factorial metabolic scope ($\dot{V}O_{2max}$/RMR) may be an underestimate, but it is considerably higher than the metabolic scope (3.4) measured in stressed zebrafish (*Brachydanio rerio*; Lucas and Priede 1992) and the scope predicted for guppies from FishBase-derived equations for exercise $\dot{V}O_2$ and RMR (3.4 for males and 3.5 in females).

The maximum burst speeds we measured for guppies (79–87 cm/s in males and females) are remarkably high for such small fish but are not without precedent. Johnson et al. (1998) reported a maximum speed of 71 cm/s in lab-raised Trinidadian guppies measured at 20°C. Their fish (mean standard length, 2.0 ± 0.2 cm) were the same size as ours (mean standard length, 1.94 ± 0.36 cm), and although they measured maximum speed in a slightly different manner, the two data sets show considerable similarity. Most other studies of burst speed in fish found length-specific velocities substantially lower than the 39–47 body lengths/s we found in guppies (e.g., 4–27 lengths/s in a variety of species; Domenici and Blake 1997), but results of Johnson et al. for guppies (about 35.5 lengths/s) are similar to our data. Allometric analysis indicates that high length-specific speed in guppies is simply a function of their small size compared with most species for which burst velocity has been determined (Fig. 6).

Variation and Repeatability

The amount of variation in aerobic capacity and burst speed in guppies (roughly 10%–20% mean differences between observed and predicted values; Fig. 3) is consistent with data for similar traits in other vertebrates (Huey and Dunham 1987; van Berkum et al. 1989; Hayes and Chappell 1990; Chappell and Bachman 1995; Chappell et al. 1996, 1999; Hammond et al. 2000; Reidy et al. 2000).

In guppies, as in other species (Austin and Shaffer 1992; Chappell et al. 1995, 1996), repeatability declined as measurement intervals increased. Nevertheless, repeatabilities for guppy $\dot{V}O_{2max}$ are comparable to those reported for $\dot{V}O_{2max}$ in reptiles, mammals, and birds (Hayes and Chappell 1990; Friedman et al. 1992; Chappell et al. 1995, 1996); to our knowledge there are no reports of $\dot{V}O_{2max}$ repeatability in fish, but other indices of aerobic metabolism are repeatable, for example, RMR in juvenile Atlantic salmon (*Salmo salar*; McCarthy 2000) and $\dot{V}O_2$ during intense but submaximal swimming in Atlantic cod (*Gadus morhua*; Reidy et al. 2000). Repeatability for burst speed in guppies is similar to that for Atlantic cod (Reidy et al. 2000) and for sprint speed in reptiles (Huey and Dunham 1987; van Berkum et al. 1989), but a caveat is that our initial and final measurements were done across a much shorter time interval than for the other species.

Interestingly, substantial variance persisted in our test guppies despite at least two generations of laboratory culture in constant, controlled conditions, and the amount of variance in

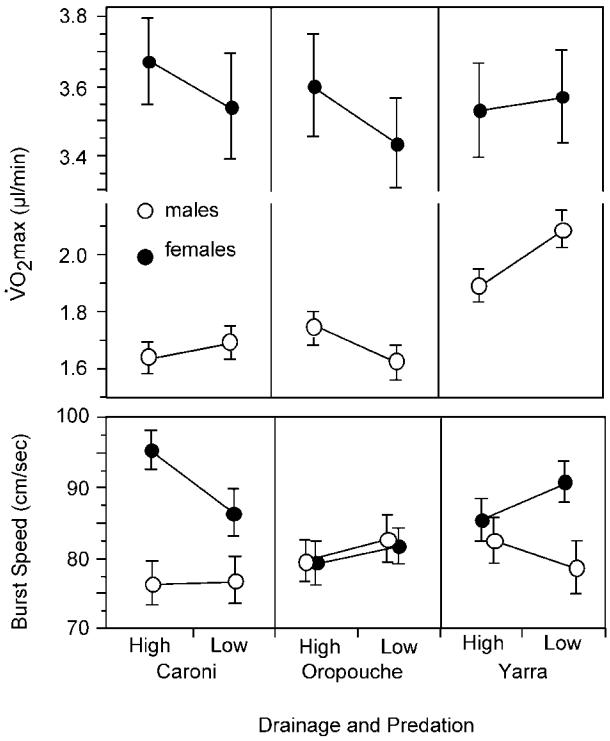

Figure 4. Independent means ± standard error of burst and aerobic performance among populations of guppies. Data are sorted by drainage and predation environment.

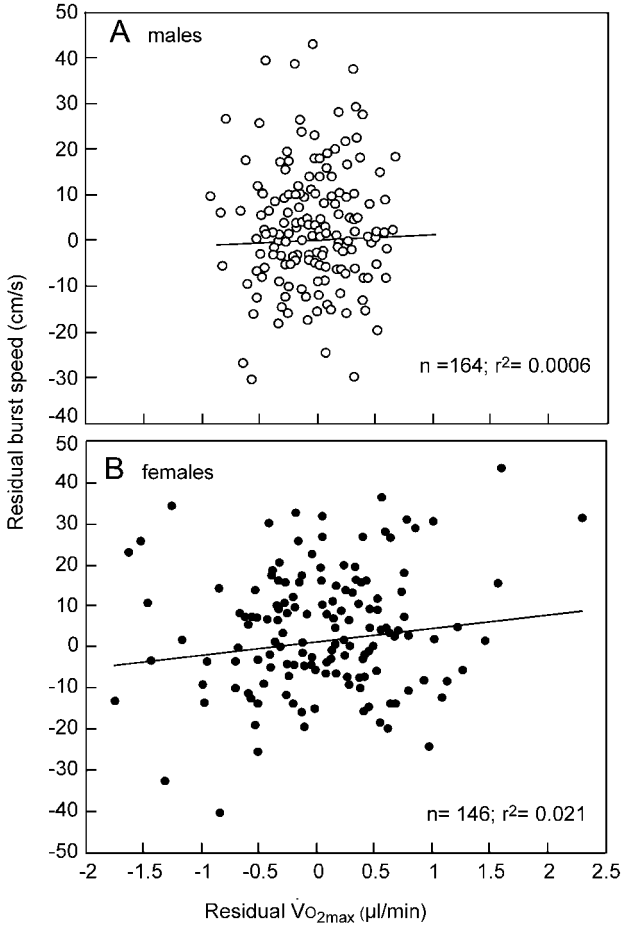

Figure 5. Relationship of mass-corrected performance variables in (*A*) males and (*B*) females. Neither relationship was significant at the 0.05 level.

our populations was similar to that found in wild-caught individuals of other species (Huey and Dunham 1987; van Berkum et al. 1989; Chappell and Bachman 1995; Chappell et al. 1999). Persistence of variance despite constant "common garden" environmental conditions, along with significant repeatability of both aerobic performance and burst speed, is consistent with (but does not conclusively demonstrate) a genetic basis for variation in these traits.

Microevolution of Locomotor Performance

The main purpose of this study was to test two related evolutionary predictions. The first hypothesis is that guppy locomotor performance would evolve in concert with life-history traits, either because of direct selection on burst speed by predators or indirectly through differential resource allocation among somatic versus reproductive tissues in high-predation versus low-predation populations. This hypothesis would be supported by consistent performance contrasts between high-predation and low-predation populations in each of the three drainages, with the expectation that burst speed would be higher in high-predation sites. The second hypothesis is that there would be a trade-off between burst speed and aerobic capacity because of differential allocation of muscle tissue to either fast-twitch glycolytic fibers (used in burst swimming) or to slow-twitch oxidative fibers (used for sustainable aerobic swimming). That hypothesis would be supported if we found negative correlations between burst and aerobic performance both within and between populations.

Somewhat unexpectedly, neither hypothesis was supported by our results: there were no consistent associations between either aerobic or burst performance and predation regime (Fig. 4), and no evidence of trade-offs between burst and aerobic performance (Fig. 5). Our findings could be evidence of lack of selection on locomotor performance, although that seems surprising given the rapid predation-mediated evolution of life history in guppies. Alternately, lack of divergence in burst speed and aerobic capacity could reflect strong but balanced selection. For example, burst speed is intuitively expected to undergo positive selection in fish from high-predation populations (e.g., O'Steen et al 2002); mechanistically, higher burst speed would likely be accomplished by increases in the mass of swimming muscle or perhaps the fraction of muscle comprised of fast-twitch glycolytic fibers. However, guppies from high-predation habitats also undergo selection for greater reproductive effort

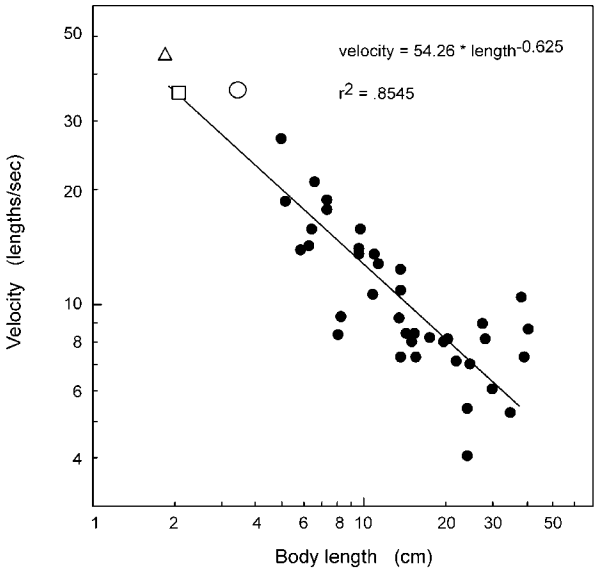

Figure 6. Relationship between body size (standard length) and maximum burst velocity (expressed as body lengths per second) in several species of fish. Open symbols are results for guppies: the triangle and circle represent males and females, respectively, from this study, and the square represents pooled data from both sexes from Johnson et al (1998). The filled symbols are data from Domenici and Blake (1997).

(Reznick 1982), which may mean less resource investment in somatic tissue and more investment in offspring—a response that could counteract selection for increased size of the swimming motor.

The lack of differentiation in burst speed is particularly surprising, given two pieces of seemingly contradictory data. First, Cullum and Bennett (1995) reported different C-start performance in wild-caught guppies from high-predation and low-predation populations. However, as we report here, burst speed differences did not persist in laboratory-reared fish (A. J. Cullum, personal communication), which implies phenotypic but not genetic selection (i.e., performance variance is not genetically based, but predators remove guppies with low burst performance from natural populations) or conditioning responses to predation (phenotypic plasticity) in natural habitats.

Second, a recent article by O'Steen et al. (2002) reported that in staged encounters with pike cichlids (a major guppy predator in Trinidad), guppies from high-predation habitats are better at escaping attacks than are guppies from low-predation habitats. These differences in escape ability—which make intuitive sense—were large and consistent in wild-caught fish from several populations and persisted (albeit with reduced magnitude) in laboratory-reared guppies (F2 generation), implying a genetic basis. O'Steen and her colleagues did not measure the kinematics of escape behavior, and it is possible that factors other than burst speed account for the escape ability differences among populations.

In that context, even though we found no predation-related differences in the maximum speed attained during the first 100–200 ms of the escape response, we urge caution in interpreting our results as evidence for the absence of any adaptive differences. An important consideration for studies of burst performance is the timing of measurements during the escape sequence. Recent work suggests that genetic differences between high-predation and low-predation poulations do exist in velocity and acceleration during the early stages (first 22 ms) of the C-start response of female guppies, and these performance shifts are influenced by reproductive status (C. Ghalambor and D. Reznick, unpublished data). Thus, fish from high-predation populations may accelerate more rapidly, but their maximum speed over slightly longer intervals does not differ from that of fish from low-predation environments. It is also possible that guppies from high-predation habitats may respond more quickly to attacks than their low-predation compatriots, perhaps because of better sensory acuity or other dissimilarities in neurobiology or behavior (e.g., vigilance, approach tolerance) that would not be apparent in our measures of maximum burst velocity. Some studies (e.g., Reidy et al. 2000) have shown that acceleration and maximum burst velocity may be poorly (or negatively) correlated, even within a species. The precise components of the C-start response that affect the success or failure of an attack are controversial and probably vary interspecifically with both predator and prey (Domenici and Blake 1997).

The absence of trade-offs between burst speed and aerobic performance is less surprising than the absence of predation effects. Although fast-twitch "white" glycolytic fibers (used in burst swimming) and slow-twitch "red" oxidative fibers (used in sustained aerobic swimming) are usually spatially separated in swimming muscle (Jayne and Lauder 1994; Zhang et al. 1996), most of the muscle in a typical fish is comprised of glycolytic fibers. Hence, even if a trade-off existed, it could be difficult to identify, in part because of the proportionately small change in white muscle content and in part because aerobic enzymes that are abundant in red muscle are also found (albeit in lower concentrations) in white muscle (Dickson et al. 1993; Dickson 1995). For other species, the evidence for burst versus aerobic performance trade-offs is mixed. In house mice (Dohm et al. 1996) and several lizard species (Vanhooydonck et al. 2001), aerobic performance and sprinting appear to be negatively correlated (consistent with a trade-off). However, trade-offs between sprinting and endurance do not occur in garter snakes (Garland 1988; Jayne and Bennett 1990*a*, 1990*b*) or salamanders (Bennett et al. 1989). In Atlantic cod, aerobic performance is negatively associated with burst acceleration but associates positively with maximum sprint speed (Reidy et al. 2000).

In summary, the most interesting result of this study is that despite major differences in stream predators and consequent striking evolutionary divergence of life histories among Trinidadian guppy populations, integrative whole-animal physiological performance remains relatively unchanged. We did find some small performance differences between populations, and the "common garden" experimental design makes it likely that these have a genetic basis. However, the pattern of these microevolutionary changes is matched to stream pairs (drainages) and not to predation regime (or life history). Guppy populations within drainages are assumed to be more closely related than populations from different drainages (D. Reznick, personal communication), suggesting that the observed divergence of locomotor performance is due to genetic drift (founder effects). Alternately, performance commonalities within drainages could result from drainage-specific biotic or abiotic factors other than predation (conceivably they could also result from uncontrolled "block" effects, given the experimental design). In either case, our results demonstrate that the Darwinian evolution of large shifts in major life-history traits do not necessarily engender substantial concomitant pleiotropic changes in integrative whole-animal physiological systems.

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Appendix

Table A1: Species used to calculate an allometric equation for $\dot{V}O_2$ during high-speed swimming

Species	Temperature (°C)	Speed (BL/s)	*N*
Rhinomugil corsula	30	4.2–4.3	5
Oreochromis mossambicus	30	4.25	9
Oncorhynchus nerka	15	4.1–6.65	4
Oncorhynchus mykiss	10–20	4.1–5.6	28
Liza aurata	20	4.3–5.05	11
Kuhlia sandvicensis	23	4.0–4.1	3
Carassius auratus	15–30	4.0–7.75	11

Note. Speeds ≥ 4 body lengths/second (BL/s). The data are from FishBase (http://www.fishbase.org; Froese and Pauly 2003). Only data from normoxic conditions were used.

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