As the Sword Grows: Individual Variation and Ontogenetic Effects of a Sexually Selected Trait on Locomotor Performance in *Xiphophorus hellerii**

Christopher E. Oufiero[†]
Kristine Jugo
Paulina Tran
Theodore Garland Jr.
Department of Biology, University of California, Riverside, California 92521

ABSTRACT

Previous studies aimed at detecting costs of sexually selected traits have yielded mixed results partly because of variable methods. We present a novel approach: a repeated-measures design to examine individual variation in locomotor performance of male *Xiphophorus hellerii* as the sexually selected sword develops ontogenetically and to determine whether the growth of a sexually selected trait alters consistency of performance. Individual differences in sprint speed, critical swimming speed (stamina), and relative sword length were statistically repeatable over 9 wk. However, using the Akaike Information Criterion corrected for small sample sizes, the best-fit predictive models for swimming performance did not include sword length or relative sword length. Furthermore, in less supported models and within-week comparisons, there was no statistically significant effect of sword length on performance. These results suggest little effect of the sword on locomotor abilities, which is inconsistent with results from some previous experimental manipulations, possibly because compensatory traits develop ontogenetically in parallel with the sword. However, our results are consistent with correlational studies of natural variation that suggest no locomotor cost of the sword. These results do not necessarily imply a complete lack of a cost to the sword but rather lack of a functional cost for swimming performance.

Introduction

Sexual selection, driven by competition for mates or by mate choice, often results in the evolution of exaggerated behaviors or morphological structures (Andersson 1994). These traits evolve because they increase the reproductive success of the bearer and are assumed to incur a cost with respect to natural selection such that their evolutionary exaggeration will eventually stop. Detecting these putative costs has long been a goal of behavioral ecologists and evolutionary biologists (Kotiaho 2001). Costs have been examined in various taxa from several perspectives that have led to a variety of results (Kotiaho 2001; Oufiero and Garland 2007). The two most common ways to asses whether a putatively sexually selected trait is costly are to (1) experimentally manipulate the structure (Clark and Dudley 2009) and (2) compare individuals with naturally varying expressions of the trait (Wilson et al. 2010). Both approaches have led to conflicting results even within a single genus, such as *Xiphophorus* fish (Ryan 1988; Basolo and Alcaraz 2003; Royle et al. 2006; Kruesi and Alcaraz 2007; Baumgartner et al. 2011).

Xiphophorus are freshwater live-bearing fish found throughout Mexico and part of Central America. Males in several species exhibit an elongation of the lower margin of the caudal fin (sword) that is favored because of a preexisting female sensory bias (Basolo 1990, 1995), and it is one of the first examples of sexual selection proposed by Darwin (1871). Because the sword is physically linked to the thrust-producing system, several previous studies have sought to determine the energetic and locomotor costs associated with the trait. For example, completely removing the sexually selected sword through experimental manipulation in adult male *Xiphophorus montezumae* (the species with the longest sword) has suggested costs with respect to routine oxygen consumption and critical swimming speed (a measure of endurance; Basolo and Alcaraz 2003; Kruesi and Alcaraz 2007) but not for burst speed during a C-start in *Xiphophorus hellerii* (Baumgartner et al. 2011). Correlational studies of natural variation in sword length (SW) suggest no cost to endurance in *Xiphophorus nigrensis* (Ryan 1988) and that it may even be beneficial to burst speed during a C-start in *X. hellerii* (Royle et al. 2006). These discrepancies may arise for a number of reasons, including most simply a lack of consistency in species and methods used. However, the discrepancy may also be due to the fact that completely removing the trait may alter the functional relationships of various traits that affect locomotion.

The repeatability of a trait is important for several reasons (Boake 1989; Chappell et al. 1996; Dohm 2002; Garland 2010; Careau and Garland 2012). Perhaps most notably, if individual differences in behavior, performance, or any other trait are not consistent, then that trait is a "difficult" target for natural, sexual, or artificial selection. Several studies have assessed the repeatability of swimming performance in fish (Kolok 1992, 1999; Kolok et al. 1998; Reidy et al. 2000; Claireaux et al. 2007; Oufiero and Garland 2009; Handelsman et al. 2010; Marras et al. 2010, 2011) and of sexual signals in various taxa (Kotiaho et al. 1996; Jang et al. 1997). Other studies have examined the effect of sexual ornaments on swimming performance in fish (Nicoletto 1991; Basolo and Alcaraz 2003; Langerhans et al. 2005; Kruesi and Alcaraz 2007; Wilson et al. 2010; Baumgartner et al. 2011). However, no studies to date have examined the consistency of individual performance in relation to a sexually selected trait. That is, do individual differences in performance retain any statistical consistency during or after the development of a sexual ornament?

Here, we (1) present an alternative approach to detect potential costs of sexually selected traits by comparing males with and without the trait but without experimental manipulation and (2) assess the effect of the development of a sexual ornament on individual variation in locomotor performance. Using a repeated-measures design and an information-theoretic approach to statistical model selection, we determined whether sword length is an important predictor of two forms of locomotion during ontogenetic development in male green swordtails *X. hellerii* and whether individuals are consistent in performance as the sword develops. Furthermore, unlike many exaggerated morphological structures (e.g., eye stalks of flies; Swallow et al. 2000; Husak and Swallow 2011), the sword is directly linked to the thrust-producing system and presents an opportunity to examine functional morphological relationships in a system where the trait (sword) has evolved for purposes other than locomotion. If the sword is a functional cost and increases drag or energetic burden ontogenetically, then all else being equal, we expect males to have a reduction in locomotor performance as the sword grows, similar to experimental studies that removed the trait (Basolo and Alcaraz 2003; Kruesi and Alcaraz 2007) or correlational studies examining the effect of pregnancy on swimming (Plaut 2002).

Methods

We used a total of 17 lab-born (approximately F3–4) male green swordtails (*Xiphophorus hellerii*) originating from Guatemala. Fish were fed ad lib. throughout development. At the first sign of maturation (development of the gonopodium, which is followed by development of the sword), they were removed from a 151-L stock aquarium, isolated individually in 9.46-L aquariums, and randomly assigned to either a control group ($N = 8$) or an experimental group ($N = 9$). In the control group, males were tested for sprint speed and critical swimming speed (U_{crit}) once before the sword developed and once after it was fully developed. In the experimental group, males were tested for sprint speed and U_{crit} weekly for ~9 wk after maturation. This allowed us to determine whether there were any changes in performance potentially due to sword growth and whether there were training effects in the experimental group. After each performance measure, males were anesthetized in buffered MS-222 (tricaine methanesulfonate) and had their standard length (SL; from the most anterior tip to the insertion of the caudal fin) and SW (from the most distal tip of the sword to where it met up with the edge of the caudal fin) measured to the nearest 0.01 mm using digital calipers. (Note that we also measured total length, body depth, and body mass, but we present results only for SL because it is a more commonly used size measure in fish and because preliminary model comparisons based on Akaike Information Criterion corrected for small sample sizes [AICc] showed no important differences when using the alternative size measures; $\Delta AICc < 2$, results not shown.) This method of size measurement has been shown to be repeatable in *Poecilia reticulata*, which are smaller than the fish used in this study (Oufiero and Garland 2009). After measurements, fish were returned to housing tanks. (See table A1 in the online edition of *Physiological and Biochemical Biology* for trait values per individual per week.)

Performance Methods

Before each performance measure, fish were starved for at least 24 h. Sprint speed was measured using the experimental setup and methods described in Oufiero et al. (2011). In short, sprint speed was elicited by chasing males down a racetrack (91 cm [l] × 5.5 cm [w] × 15.8 cm [h]) with 12 sets of photocells (LS10 light screen, Banner Engineering, Minneapolis) each 5 cm apart spanning the middle 60 cm of the racetrack after a 5-min acclimation toward an area of refuge. The photocells were placed 18 cm from the starting end to allow the fish room to accelerate. As males sprinted, they broke the infrared beams emitted by the photocells, and a computer recorded the timing and calculated maximum velocity. We chased each male four times during each week. We used the highest 10-cm span (a total of three consecutive photocells) as an indication of a male's sprint speed. This method has been shown to be repeatable in *Xiphophorus maculatus* in this same experimental setup (Oufiero 2010).

Critical swimming speed is defined as the maximum velocity a fish maintains for a specific period of time ending in fatigue (Brett 1964; Beamish 1978). The experimental setup and procedures used were the same used in Oufiero and Garland (2009) and Oufiero et al. (2011). Fish were acclimated to a flow tunnel for 15 min at a low flow velocity (~3 cm s⁻¹) to orient them to the direction of flow. The flow tunnel holds approximately 55 L of water, and the working area is 119.5 cm (l) × 15.3 cm (w) × 18.3 cm (h). Each fish was tested in a smaller area (12 cm [l] × 15.3 cm [w] × 11.5 cm [h]) within grating, which also served to attain laminar flow. After acclimation, the velocity of the water was increased 4.5 cm s⁻¹ every 3 min until the fish was fatigued. Fatigue was determined as the point when the fish would not remove itself from the back grating after

gently prodding with a net and tapping on the sides of the flow tunnel. U_{crit} was calculated following the formula presented by Brett (1964) and Beamish (1978). U_{crit} has been shown to be repeatable in this experimental setup in *Poecilia reticulata* (Oufiero and Garland 2009) and *X. maculatus* (Oufiero 2010).

Statistical Analyses

To test for training effects on performance, we used repeated-measures ANCOVA comparing the first and last measure of the experimental group with the first and last measure of the control group. Training effects should cause higher values in the experimental group at the end of the experiment, evidenced by a week × group interaction. The repeated-measures model included SL, SW, and temperature as covariates; group, week, and the week × group interaction as fixed effects; individual as the within-subjects effect; and individual nested within group as a random effect (SAS PROC MIX, SAS, ver. 9.2).

We used a repeated-measures design to determine how size, SW, and performance change over time and whether SW affected performance. In all repeated-measures analyses, week was included as a fixed effect and individual fish (ID) as a random within-subjects effect. We first examined changes in SL and SW/SL (relative SW) with ID and week included as listed above. We then evaluated two models for SW using AICc (Burnham and Anderson 2002) to determine whether including the week × SL interaction gave a better-fitting model.

To determine whether performance changed over time and any effects of SL, relative SW (SW/SL), or SW, we first evaluated several candidate repeated-measures models using AICc based on maximum likelihood (ML) estimates (table A2 in the online edition of *Physiological and Biochemical Zoology*). If a trait (SL, SW, etc.) is important to changes in performance over time, then we would expect it to be retained in the best-fitting models. These models varied in the predictors (week, SL, SW, or SW/SL) and interactions that were included, but all included individual as a random within-subject effect and temperature as a fixed effect. AICc was calculated as

$$AICc = -2[\ln{(\text{likelihood})}] + 2k \times \left(\frac{N}{N-k-1}\right),$$

where k = the number of parameters in the model and N = the sample size. To calculate AICc, we used a sample size of 76 (77 for SW): nine individuals over 9 wk result in 81 individual × week samples, but we had missing data for five individual × week (table A1), resulting in a sample size of 76 (Olea 2009).

To test for the consistency of individual performance during the development of the sword, we tested the significance of the effect of individuals in the models through likelihood ratio tests (LRT) based on models estimated by restricted maximum likelihood (REML; table A3 in the online edition of *Physiological and Biochemical Zoology*). Therefore, for each statistical model presented in table A4 in the online edition of *Physiological and Biochemical Zoology*, we analyzed three variants: (1) a model

with ID as the random repeated measure with REML estimation to obtain estimates of the effects of the predictors presented in tables 1 and A4 as well as the −2 log likelihood with ID included presented in table A3 to estimate the effect of including individual in the model presented in tables 1 and A4; (2) a model with the random repeated-measure effect of ID excluded with REML estimation to obtain the −2 log likelihood without ID as presented in table A3 to determine the effect of including individual in the model as presented in tables 1 and A4; and (3) a model with the random repeated-measure effect of ID

Table 1: Results from repeated-measures ANOVAs and ANCOVAs examining the experimental group ($N = 9$ individuals) throughout sword development

Trait and effect	F (df) or LRT	P
SL:		
Week	**24.65 (8, 60)**	**<.0001**
ID	**LRT = 120.6**	**<.0001**
SW/SL:		
Week	**35.91 (8, 60)**	**<.0001**
ID	**LRT = 107.8**	**<.0001**
SL:		
Week	**4.10 (8, 59)**	**<.0001**
SL	**23.02 (1, 59)**	**<.0001**
ID	**LRT = 60.9**	**<.001**
U_{crit}:		
SL	.89 (1, 65)	.3479
Temperature	**9.23 (1, 65)**	**.0034**
ID	**LRT = 9.7**	**.0078**
U_{crit}:		
Week	**2.42 (8, 58)**	**.0250**
Temperature	**17.90 (1, 58)**	**<.0001**
ID	**LRT = 8.8**	**.0123**
U_{crit}:		
Week	**2.60 (8, 57)**	**.0171**
SL	2.26 (1, 57)	.1380
Temperature	**16.55 (1, 57)**	**.0001**
ID	**LRT = 7.4**	**.0247**
Sprint speed:		
SL	2.95 (1, 65)	.0907
Temperature	1.25 (1, 65)	.2681
ID	**LRT = 8.8**	**.0123**

Note. U_{crit} = critical swimming speed; SL = standard length; SW = sword length. The best-fit models based on Akaike Information Criterion corrected (see table A2 in the online edition of *Physiological and Biochemical Zoology*) are presented for SW, U_{crit}, and sprint speed. LRT indicates likelihood ratio test for significance of individual fish (ID) included as a random effect (see table A3 in the online edition of *Physiological and Biochemical Zoology* for details). For all traits, the effect of individual is statistically significant, thus demonstrating some consistency of individual differences across this period of ontogenetic development. Significant predictors are shown in bold.

with ML estimation to calculate the AICc scores as presented in table A2. We also used Kendall's coefficient of concordance (e.g., Bennett 1980), which uses the rank order of individual values across all measures, to determine whether traits were repeatable over the 9 wk.

We present the effects of the predictors for best models based on AICc in the main text of the article and the effect of candidate predictors in all models in table A4. We also obtained residuals for each performance within each week and examined multiple regression of residual performance on relative SW (SW/SL) and temperature to determine whether SW is affecting performance within each week.

Results

We found no differences between the control group and the experimental group for SL, SW, SW/SL, or performance values (table A5; fig. A1 in the online edition of *Physiological and Biochemical Zoology*). Therefore, the experimental procedure did not cause substantial training effects.

In the experimental group, males grew approximately 15% in SL (figs. 1*A*, 2*A*) over 9 wk (32.69 ± 0.63 to 38.75 ± 0.76 mm, mean ± SE), while their swords increased to a much greater extent (from 1.60 ± 0.34 to 15.78 ± 1.20 mm; figs. 1*B*, 2*B*). Comparison of two repeated-measures models for SW indicated that a model with week and SL was the best fit based on AICc (tables 1, A2). Furthermore, both the LRT for the effect of individual and Kendall's coefficient of concordance (W) were significant for SL ($W = 0.8660$, $P < 0.0001$), relative SW ($W = 0.7471$, $P < 0.0001$), and SW ($W = 0.6646$, $P < 0.0001$; fig. 2; tables 1, A3).

Evaluating candidate models for U_{crit} revealed three supported models ($\Delta AICc < 2$; tables 1, A2). In all three models, neither SW nor relative SW was included, performance increased after week 3 (fig. 1*C*), and individual fish varied significantly ($W = 0.4243$, $P = 0.0018$; table 1; fig. 2*D*). For sprint speed (figs. 1*D*, 2*E*), the best-fit model included only SL and temperature (table 1) with a significant individual effect ($W = 0.3372$, $P = 0.0096$; fig. 2*E*) and nonsignificant size effect (table 1; fig. 3*B*). Similar results were obtained for less supported models (table A4).
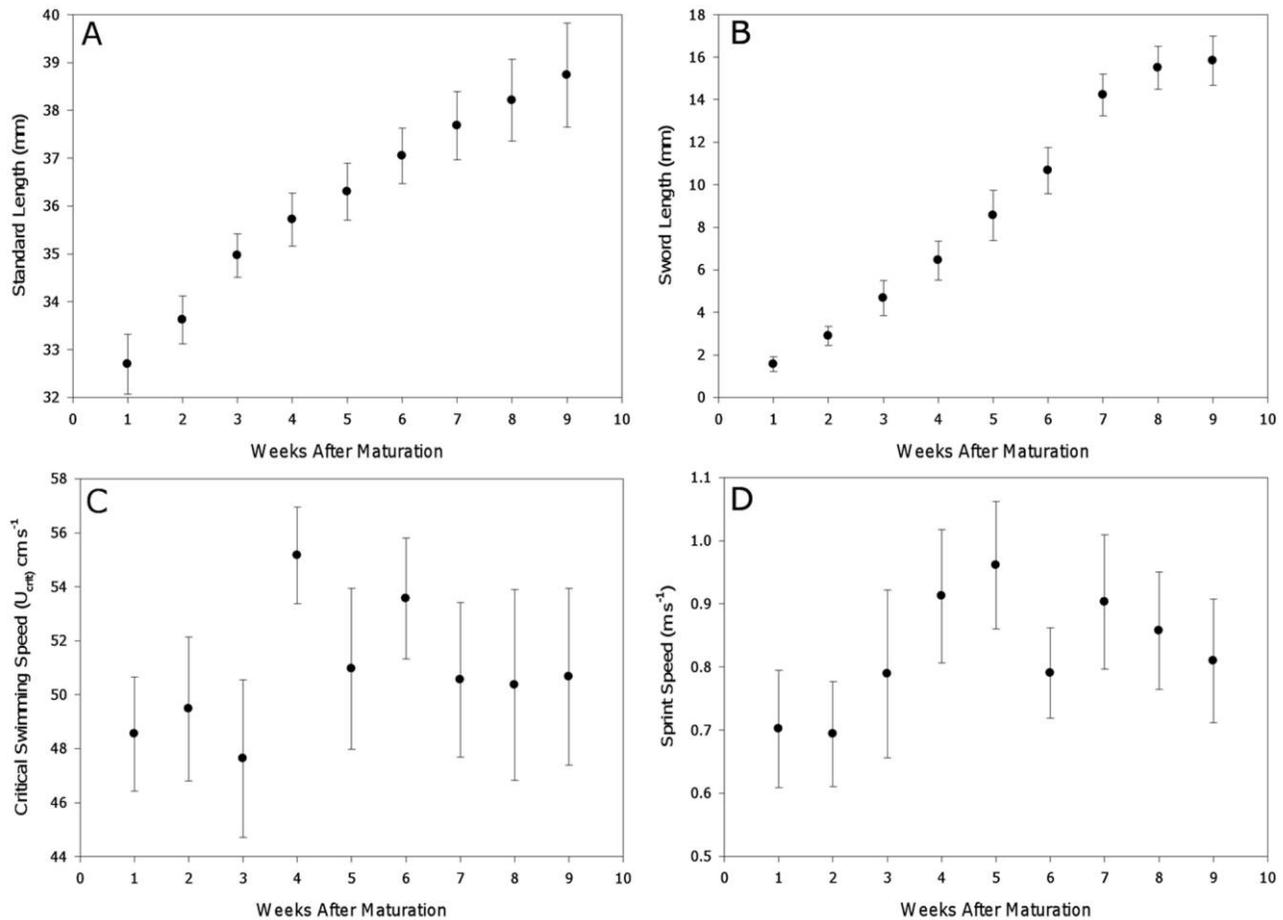

Figure 1. Ontogenetic changes in (*A*) standard length, (*B*) sword length, (*C*) critical swimming speed, and (*D*) sprint speed. Note that the pattern of change in performance does not parallel the change in either body size or standard length. Points represent means ± 1 SE.
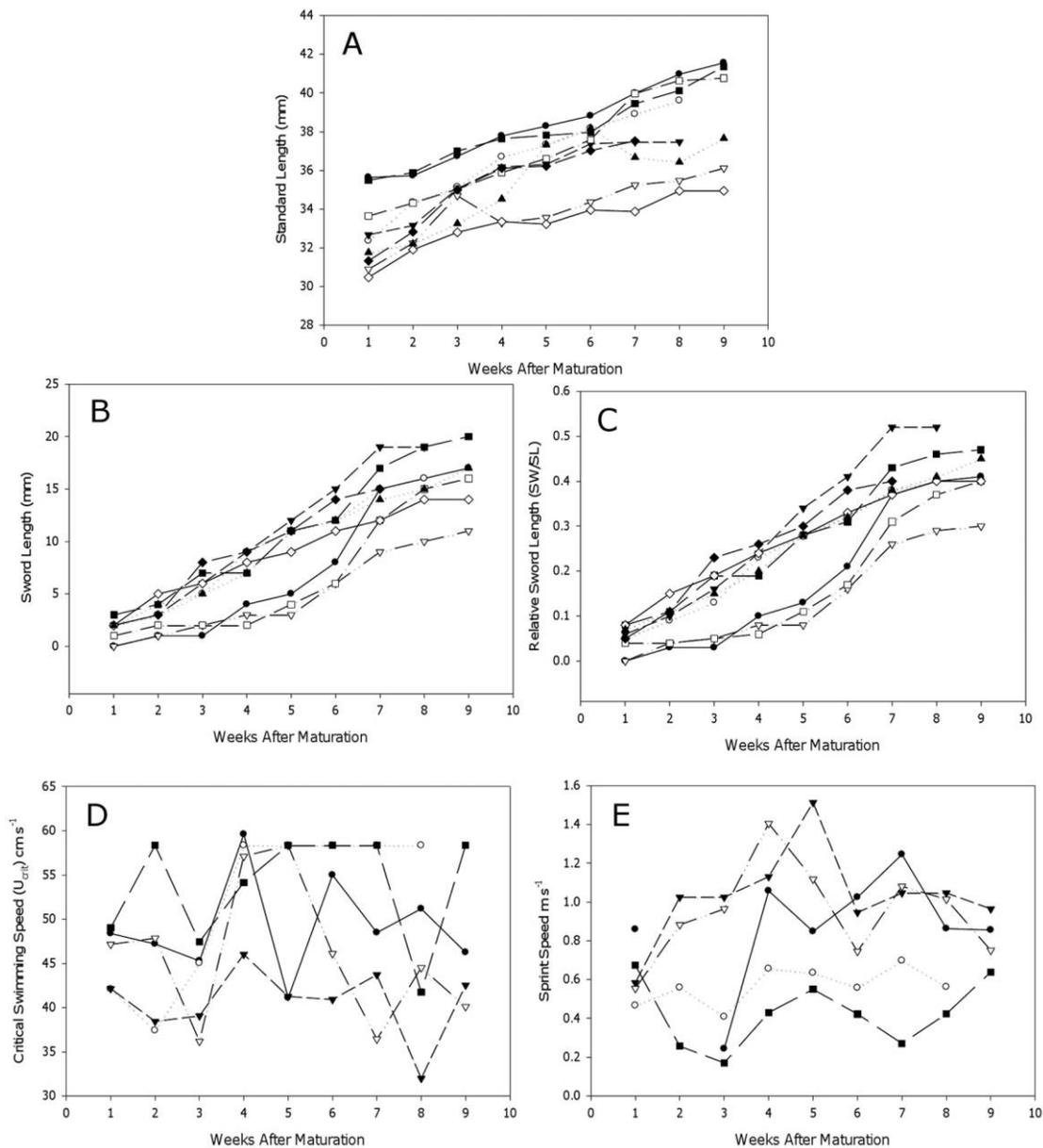
Figure 2. Ontogenetic changes in (A) standard length (SL), (B) sword length (SW), (C) relative sword length (SW/SL), (D) critical swimming speed (U_{crit}), and (E) sprint speed within individuals. A, B, and C show changes in SL, SW, and SW/SL among all individuals in the experimental group. For clarity, D and E show individual variation only among five individuals (same individuals in each plot). All traits were significantly repeatable over the 9 wk based on Kendall's coefficient of concordance (SL: 0.8660, $P < 0.0001$; SW: 0.6646, $P < 0.0001$; SW/SL: 0.7471, $P < 0.0001$; U_{crit}: 0.4243, $P = 0.0018$; sprint speed: 0.3372, $P = 0.0096$).

Within-week multiple regressions (table 2) revealed no significant or consistent negative effect of relative SW (SW/SL) on either performance measure except during week 4 for sprint speed. Similar results were obtained in multiple-regression models with SW instead of relative SW included (results not shown). Therefore, throughout development, SW does not seem to be consistently detrimental to locomotor performance.

Discussion

Ontogenetic changes in locomotor performance can be the result of any number of factors, including simply increases in body size (Garland and Else 1987; Bennett et al. 1989; Carrier 1996). Based on allometric relationships in fish, performance should increase ontogenetically in a fairly consistent fashion
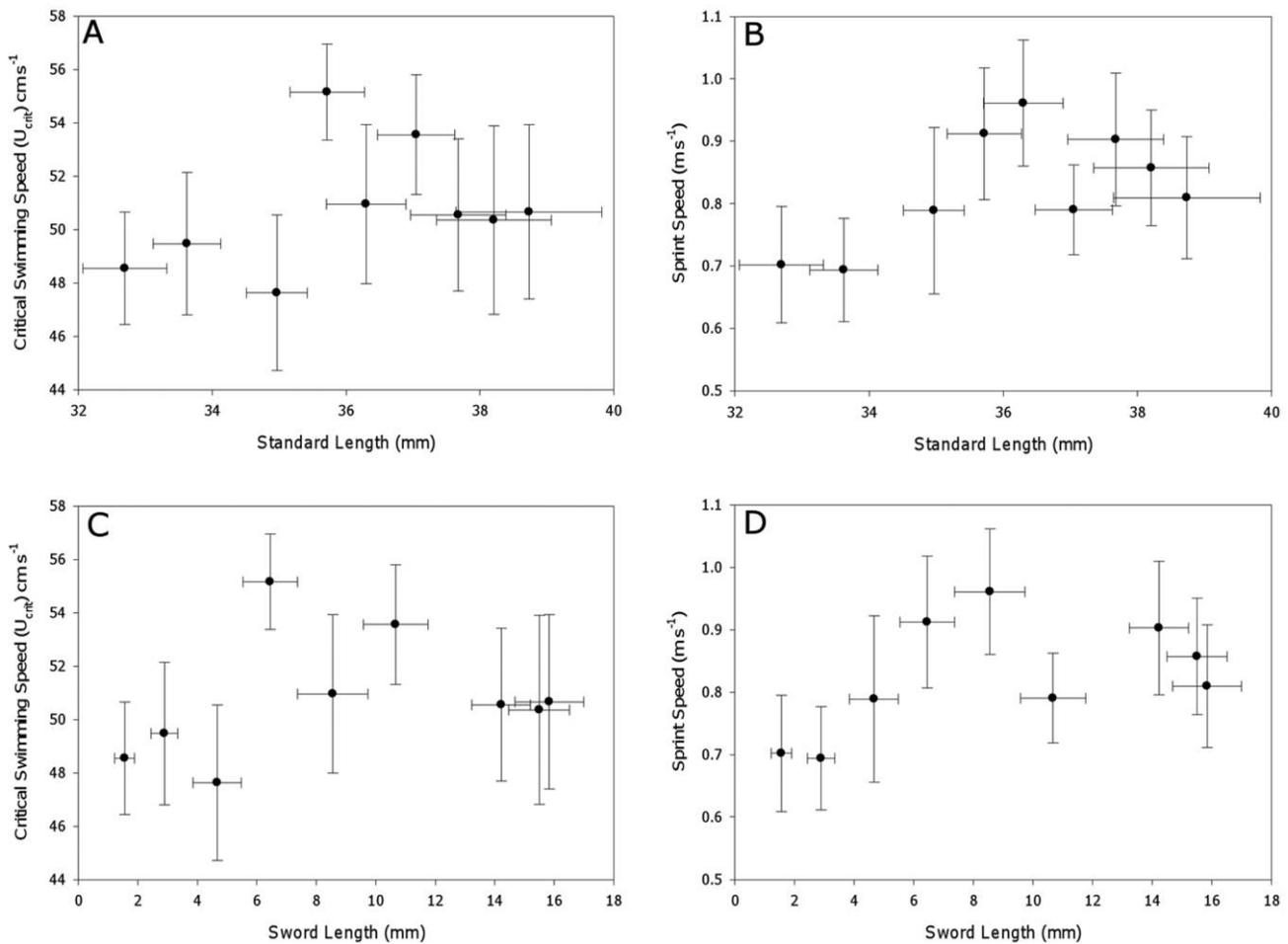
Figure 3. Relationships of standard length to (*A*) critical swimming speed (U_{crit}) and (*B*) sprint speed and of sword length to (*C*) U_{crit} and (*D*) sprint speed. Points represent means for each week ± SE for each trait.

(Goolish 1991). However, the development of a sexually selected trait, such as the sword of male *Xiphophorus hellerii*, could alter the expected ontogenetic scaling. To our knowledge, no previous study has used longitudinal sampling to examine the development of locomotor performance in relation to a sexually selected trait that might impose a cost; however, this approach is similar to studies examining the effects of pregnancy on locomotor performance (Plaut 2002).

Following sexual maturation, our experimental fish grew continuously in body size across the 9-wk study period (fig. 1*A*), and sword size increased for approximately eight of those weeks (fig. 1*B*), reaching sizes consistent with previous studies with the same species (Baumgartner et al. 2011). All else being equal, body size and sword size, as developmental traits, should have positive and negative effects on locomotor performance, respectively. Both U_{crit} (fig. 1*C*) and sprint speed (fig. 1*D*) increased across the study period, but the patterns of increase were more complicated than for body size or SW. Although this pattern of increase suggests that SW may be altering allometric relationships, results from AICc suggest that SW is

not an important predictor of either performance (table A2). Furthermore, repeated-measures analyses did not indicate any effect of SL (fig. 3*A*, 3*B*), SW (fig. 3*C*, 3*D*), or relative SW on either performance measure (table 1). Finally, results from within-week comparisons revealed no consistent significant negative effect of SW on swimming performance (table 2). Overall, these results suggest that as the sword develops, it does not cause an important decrease in locomotor abilities either across weeks as fish grow or within weeks at the level of individual variation.

As noted in the "Introduction," the repeatability of locomotor performance and potential effects of body size have been documented for various species of fish in previous studies (Kolok 1992, 1999; Kolok et al. 1998; Reidy et al. 2000; Claireaux et al. 2007; Oufiero and Garland 2009; Handelsman et al. 2010; Marras et al. 2010, 2011). We found statistically significant consistency of individual differences for both performance traits as evidenced by a significant difference in model fit with and without the individual effect (tables 1, A3) and the separation of individual ontogenetic trajectories shown in figure 2

Table 2: Multiple regressions for each week separately to determine the effect of relative sword length (sword length/standard length [SW/SL]) on residual critical swimming speed (U_{crit}) and sprint speed, with temperature included as an additional independent variable

Week and trait	Partial regression coefficient	F	df	P
Residual U_{crit}:				
1:				
Temperature	1.398	.076	2, 7	.794
SW/SL	−103.351	2.066		.210
2:				
Temperature	−2.225	1.489	2, 8	.268
SW/SL	−51.917	.701		.435
3:				
Temperature	−2.909	2.238	2, 8	.185
SW/SL	−38.815	1.059		.343
4:				
Temperature	−2.186	4.428	2, 8	.080
SW/SL	−46.060	4.824		.070
5:				
Temperature	−3.510	5.185	2, 8	.063
SW/SL	12.136	.186		.682
6:				
Temperature	**−4.757**	**16.438**	2, 8	**.007**
SW/SL	−47.860	5.294		.061
7:				
Temperature	−2.737	5.211	2, 8	.063
SW/SL	37.128	1.620		.250
8:				
Temperature	−1.665	.775	2, 7	.419
SW/SL	−42.663	.423		.544
9:				
Temperature	−1.530	2.759	2, 5	.195
SW/SL	3.272	.016		.908
Residual sprint speed:				
1:				
Temperature	.059	.240	2, 8	.642
SW/SL	4.378	.608		.465
2:				
Temperature	.108	3.236	2, 7	.132
SW/SL	−.655	1.231		.318
3:				
Temperature	.110	1.486	2, 8	.269
SW/SL	.540	.069		.801
4:				
Temperature	−.030	.747	2, 8	.421
SW/SL	**−2.982**	**10.546**		**.018**
5:				
Temperature	.062	2.024	2, 8	.205
SW/SL	.288	.093		.771
6:				
Temperature	.015	.028	2, 8	.872
SW/SL	−1.104	.918		.375
7:				
Temperature	−.019	.370	2, 8	.565
SW/SL	−1.573	2.675		.153

Table 2 (*Continued*)

Week and trait	Partial regression coefficient	F	df	P
8:				
Temperature	−.015	.187	2, 7	.684
SW/SL	−1.232	.535		.497
9:				
Temperature	.045	2.677	2, 5	.200
SW/SL	−1.791	1.504		.308

Note. Similar results obtained from models with sword length. Significant predictors ($P < 0.05$, unadjusted for multiple comparisons) are in bold.

(and Kendall's coefficient of concordance reported in the legend). Thus, despite growth of the sword and increases in SL, both U_{crit} and sprint are significantly repeatable, consistent with previous studies of fishes that have examined short-term repeatability (see Oufiero and Garland 2009 for references). Furthermore, although SL was retained in the best-fit models for both performance measures, suggesting it is important to individual variation in performance, it was not a statistically significant predictor of performance based on partial F-tests (table 1). The lack of a significant effect of size on performance is consistent with previous studies on both performance measures in fish intraspecifically and may be due to a relatively small variation of size in males used in this study. For example, using the same experimental procedure and apparatus, Oufiero and Garland (2009) and Oufiero et al. (2011) found no statistical effect of SL on U_{crit} within either *Poecilia reticulata* or *Rivulus hartii*. Others have also found a lack of a size effect on U_{crit} in other species of fish (Kruesi and Alcaraz 2007; Handelsman et al. 2010). Although Oufiero et al. (2011) found a significant size effect on sprint speed using the same setup and apparatus as here, their size range of fish was larger (34.07–77.78 mm in Oufiero et al. 2011 vs. 30.47–43.18 mm in this study). Furthermore, Handlesman et al. (2010) found no statistical effect of size on sprint speed in *Dicentrarchus labrax*. Therefore, individual differences in locomotor performance can generally be demonstrated within populations of fish, and there seem to be minimal effects of body size on performance when the range of body sizes is small.

Because the sword is directly linked to the thrust-producing system, it has the potential to alter functional (mechanistic) relationships and affect locomotor performance. However, one of the interesting results regarding the cost of the sexually selected sword in *Xiphophorus* is that experimental manipulations demonstrate a cost to aerobic performance (Basolo and Alcaraz 2003; Kruesi and Alcaraz 2007), but natural variation (Ryan 1988) and our ontogenetic study do not. Although the discrepancy may be attributable to differences in species or methods (Kotiaho 2001; Oufiero and Garland 2007), it may also be an indication of how the trait is interacting with other aspects of the organism. Removing the sword may decrease routing oxygen consumption (Basolo and Alcaraz 2003) and increase U_{crit} (Kruesi and Alcaraz 2007); however, in backward stepwise regression analysis, Kruesi and Alcaraz (2007) found that SW

was not retained in the models and that there was no significant negative effect of the sword on U_{crit}, similar to our ontogenetic results (tables 1, 2). These results suggest that compensatory traits may be developing in conjunction with the sword, thus enabling males to avoid a performance decrement (Kirkpatrick 1987; Oufiero and Garland 2007; Husak and Swallow 2011). Such compensatory traits might include heart size or rate, muscle size or fiber-type composition, innervation, or any factor that altered tail-beat frequency or kinematics. However, when the sword is removed, males may perform better because they are accustomed to swimming with the structure and may essentially be "training"; therefore, when it is completely removed, they are freed from its burden. In fact, this type of "resistance" training is often used and has proven to increase performance in human athletes (Bird et al. 2005).

Our results regarding sprint speed are consistent with both experimental reductions of SW on burst speed during a C-start (Baumgartner et al. 2011) and natural variation in SW and burst speed (Royle et al. 2006). Therefore, results to date suggest that even if the sword is increasing drag, the effect is not large enough to reduce anaerobic locomotor performance to a measurable extent.

Although our results suggest no developmental cost of the sword with respect to locomotor abilities, other costs may exist. For example, males may have a reduced survival compared with females due to increased conspicuousness and not due to a reduction in locomotor performance. In fact, studies have demonstrated a repeated correlation of sword reduction with the presence of predators (Basolo and Wagner 2004) and that females as well as predators prefer males with longer swords (Rosenthal et al. 2001). Costs may also occur through increased metabolic demands throughout life and via shorter life spans in males with longer swords. However, no study has yet examined these types of costs. Therefore, a lack of locomotor costs does not necessarily translate into a lack of fitness costs.

One of the most common assumptions across hypotheses for the evolution and maintenance of sexually selected traits is that they entail a cost (Kotiaho 2001). Although costs can be examined in various ways (Oufiero and Garland 2007), few studies have examined the ontogenetic effects of sexually selected traits via repeated measures of individuals. Such an approach allows the comparison of males with and without the structure but without the use of experimental manipulation

and may be particularly useful in cases where the trait cannot be physically altered. Using this approach, we found that as the sword develops in the swordtail *X. hellerii*, it does not adversely affect either U_{crit} or sprint speed and that individual differences in performance are statistically consistent in spite of variable sword development.

Acknowledgments

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