

The turn of the sword: length increases male swimming costs in swordtails

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Sexual selection via female mate choice can result in the evolution of elaborate male traits that incur substantial costs for males. Despite increased interest in how female mating preferences contribute to the evolution of male traits, few studies have directly quantified the locomotor costs of such traits. A sexually selected trait that could affect movement costs is the sword exhibited by male swordtail fishes: while longer swords may increase male mating success, they could negatively affect the hydrodynamic aspects of swimming activities. Here, we examine the energetic costs of the sword in *Xiphophorus montezumae* by experimentally manipulating sword length and measuring male aerobic metabolism during two types of activity, routine swimming and courtship swimming. Direct measurements of oxygen consumption indicate that males with longer swords expend more energy than males with shortened swords during both types of swimming. In addition, the sword increases the cost of male courtship. Thus, while sexual selection via female choice favours long swords, males with longer swords experience higher metabolic costs during swimming, suggesting that sexual and natural selection have opposing effects on sword evolution. This study demonstrates a hydrodynamic cost of a sexually selected trait. In addition, this study discriminates between the cost of a sexually selected trait used in courtship and other courtship costs.

Keywords: sword; courtship; locomotor costs; energetics; swimming activity

1. INTRODUCTION

As recognized by Darwin (1871), traits favoured by selection in one context may be opposed by selection in an alternative context. Because male traits favoured by sexual selection are often elaborate, male investment in these traits may often reduce the amount of energy available for other activities, such as reproduction, foraging, territorial defence, predator avoidance, maturation and growth. Such trade-offs in energy allocation have widespread effects on the evolution of animal traits (Sibley & Calow 1986; Roff 1992; Stearns 1992). Morphological traits that improve male mating success via sexual selection may encumber movement and thus be energetically costly in terms of natural selection, in which case sexual selection and natural selection would be in opposition. By contrast, if traits favoured by sexual selection via female mate choice improve some component(s) of movement, natural selection and sexual selection could act in concert.

Courtship behaviour, like morphological traits, can play an important part in sexual selection. Females prefer males displaying at higher rates (Sullivan 1983; Gibson & Bradbury 1985; Nicoletto 1993; Wagner & Reiser 2000), but courtship can be energetically costly (Bennett & Houck 1983; Vehrencamp *et al.* 1989). In addition to specific courtship movements, females may base mating decisions on morphological traits exhibited during courtship, and the display of these traits may further increase the cost of courtship behaviour. Unlike many sexual signals, which are expressed only periodically, morphological traits are often not facultative, potentially encumbering males even when they are not advertising for or displaying

to females. For example, while acoustic signals have been shown to be energetically costly to produce (Taigen & Wells 1985; Prestwich 1994; Hoback & Wagner 1997), the primary cost of emitting sound is restricted to periods when individuals are advertising and displaying. By contrast, morphological traits can impose high costs even during routine activity, and thus can affect male performance in a variety of contexts. In the aquatic environment, locomotion accounts for a large part of the energy budget of fishes (Webb & Weihs 1981) and both morphology and the type of movement activity can affect swimming costs in the aquatic medium (Webb 1975). For example, larger body size and some fin shapes can improve the hydrodynamic aspects of fish movement (Beamish 1978; Webb & Corolla 1981) and explain a substantial amount of the variance in swimming costs (Boisclair & Tang 1993).

Elongated and coloured caudal fins are targets of sexual selection via female choice in freshwater poeciliid fish species, including swordtails, guppies and platyfishes (Borowsky & Kallman 1976; Reynolds *et al.* 1993; Basolo 1995). Female swordtails and unsworded platyfishes in the genus *Xiphophorus* (Basolo 1990b, 1995; Haines & Gould 1994) and females in the sister genus *Priapella* (Basolo 1996a) prefer males with swords, and female response increases with sword length (Basolo 1990a, 1998; Rosenthal & Evans 1998; Trainor & Basolo 2000). Swords consist of a set of tri-coloured basal rays originating at the proximal insertion point of the caudal rays and can extend beyond the caudal margin (Rauchenberger *et al.* 1990). Male and female swordtails have streamlined fusiform bodies typical of fast-moving fishes. However, while female swordtails have symmetric rounded caudal fins, male swordtails have asymmetric caudal fins as a result of an extended sword, which cannot be retracted

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or folded. While longer swords may increase male mating success via female mate choice, swords could negatively affect the hydrodynamic aspects of swimming activities. In this study, we report the results of respirometric experiments assessing the metabolic cost of sword length during two types of swimming in male swordtails, *X. montezumae*.

2. MATERIAL AND METHODS

The montezuma swordtail, *X. montezumae*, is a freshwater live-bearing poeciliid occurring in the Rio Panuco drainage basin, State of San Luis Potosi, Mexico. Montezuma swordtail males have the longest sword of any swordtail species (Rauchenberger *et al.* 1990). Test subjects for the respirometric experiments were maintained on a 16 L : 8 D photoperiod, and fed live brine shrimp, liver–rice cereal mixture and fish flakes daily. Test males were not fed for 24 h prior to testing to eliminate any metabolic activity associated with digestive processes (Davis *et al.* 1963; Cech 1990).

(a) *Respirometric measures of male metabolic rate*

We measured the respiratory metabolisms of nine male montezuma swordtails (mean body length of 39.9 mm, s.e. = 1.29 mm; mean sword length (from insertion of caudal rays to distal tip of sword) of 42.1 mm, s.e. = 2.1 mm; mean sword extension beyond caudal fin of 30.9 mm, s.e. = 1.8 mm) under four different trial conditions: (i) female present, intact sword; (ii) female absent, intact sword; (iii) female present, excised sword; and (iv) female absent, excised sword. For each trial, a male was placed in a cylindrical respirometric chamber (125 mm in diameter and 50 mm in height; volume of 480 ml) and a female was suspended in the water column of the cylinder in a glass tube at a height of 25 mm (each fish had a separate water system). An opaque plastic covering on the glass tube prevented the male and female from seeing each other. A gravity slow-flow system allowed water exchange to remove metabolic wastes, but did not produce a current. After a 40 min period, the covering was removed in half of the trials, exposing the female, and the chamber was closed; these constituted the female-present test trials. A water sample was taken from the respirometric chamber at this time to obtain an oxygen-concentration measurement at the beginning of each trial (YSI Model 57 dissolved O₂ meter, precision of 0.05 mg l⁻¹). After a 40 min trial period, the final oxygen concentration was obtained by again sampling water from the chamber. The chamber was then flushed to restore oxygen levels. In the other half of the trials, females remained hidden from the males; these constituted female-visually-and-chemically absent test trials (henceforth termed female-absent trials). Oxygen measurements were obtained for these trials, as detailed above for the female-present trials. After the first trial, the respirometers were flushed and the female tubes were again covered. A second 40 min acclimatization period followed. Then, for those trials in which the female had previously been hidden, the covering was removed for a female-present trial. For those trials in which females had previously been visible, the covering was left in place for a female-absent trial. Following these trials, swords were shortened by excising the portion extending beyond the caudal margin as per Basolo (1995, 1998). The males were given 3 days to recuperate, and then female-present and female-absent test trials were again conducted as described above. Each time the O₂ level in the respirometers was measured, a water sample was

taken from an identical respirometer devoid of fishes (control chamber). The temperature in the respirometers was maintained at 24 °C (± 1°). To control for possible order effects, five experimental males were run first on a female-absent trial and second on a female-present trial, and four males were run first on a female-present trial and then on a female-absent trial; the assignment of males to trial order was random. To determine whether handling and the sword-excision manipulation affected male O₂ consumption, we conducted a set of separate sham trials; there was no detectable difference in O₂ consumption either when a complete sword was present or when the sword was reduced by 1 mm (paired-*t*₇ = 1.26, *n* = 9, *p* = 0.24). Therefore, it does not appear that the experimental procedure *per se* affected male respiration.

The rate of O₂ consumption indicates the rate of aerobic energy metabolism (Beamish 1978); a higher consumption rate indicates a greater male cost. Oxygen consumption (MO₂) for each male was calculated according to Cech (1990) as: MO₂ = ([O₂i] – [O₂f])V/T, where [O₂i] and [O₂f] are the initial and final O₂ concentrations, respectively, *V* is volume and *T* is time. The male O₂ consumption measurements were corrected by subtracting the O₂ levels obtained in the control respirometer from the levels obtained for each measurement during each trial, producing a measure of the energy expended. The data for male O₂ consumption were analysed using one-way repeated-measures analysis of variance (ANOVA) followed by *post hoc* comparisons between the four different trial types (Tukey–Kramer test). The O₂ consumption data were transformed prior to analysis using an angular transformation in order to meet the assumption of normality.

To investigate whether the measure of male O₂ consumption was affected by habituation to the respirometer over the duration of these experiments, an analysis was conducted (unpaired *t*-test) to determine whether order affected male O₂ consumption. We compared the O₂ consumptions of males in trials where females were absent. First, we compared the O₂ consumptions of males with intact swords that had their female-absent trial preceding or following their female-present trial. Second, we compared the O₂ consumptions of males with excised swords that had their female-absent trial preceding or following their female-present trial. We also compared the O₂ consumptions of males in trials where females were present. First, we compared the O₂ consumptions of males with intact swords that had their female-present trial preceding or following their female-absent trial. Second, we compared the O₂ consumptions of males with excised swords that had their female-present trial preceding or following their female-absent trial.

(b) *Routine versus courtship activity*

Male swordtail reproductive behaviour can involve a number of active behaviours performed in close proximity to a female, with the sword bending as the male manoeuvres around the female (Schlosberg *et al.* 1949; Clark *et al.* 1954; Hemens 1966). These behaviours include a male: (i) swimming underneath a female; (ii) swimming beneath a female to position his mouth near to the female gonopore; (iii) swimming rapidly back and forth in a tight figure-of-eight in front of a female; (iv) performing a lateral presentation in front of the female and flexing his body and sword to form a sigmoid shape; and (v) circling a female. These behaviours can conclude with a backward swim, with the male curving his body and sword along the female flank, ending in an insemination position.

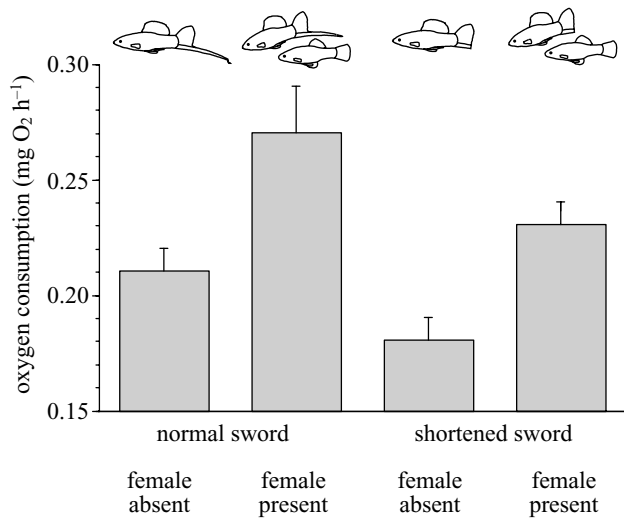


Figure 1. Mean (+ s.e.) O₂ consumptions for males with intact (normal) swords and shortened (excised) swords in the absence and presence of females. Female-absent results represent male routine swimming. Female-present results represent male courtship swimming.

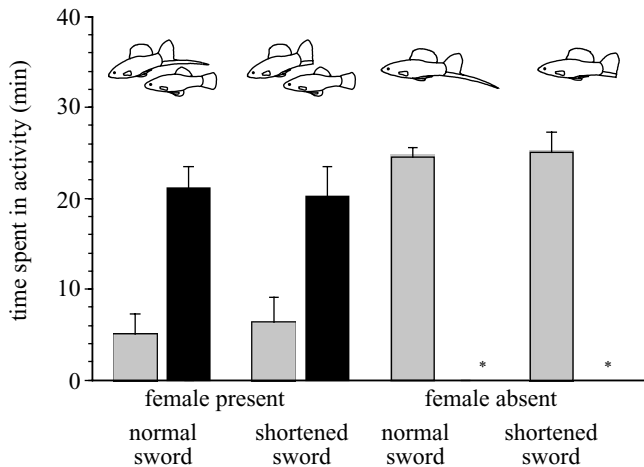


Figure 2. Mean (+ s.e.) times spent in routine (grey bars) swimming activity and courtship (black bars) activity by males with intact (normal) and shortened (excised) swords, in the absence and presence of females. The asterisks indicate the lack of courtship behaviour when females were not present.

During the respirometry trials, male behaviour in the female-absent trials involved routine swimming activity, while the female-present trials involved both routine and courtship swimming. In the female-absent trials, males exhibited three behaviours: (i) motionless on the bottom; (ii) motionless in the water column; and (iii) routine swimming around the respirometer. For the female-present trials, males exhibited the same three behaviours as well as the following courtship behaviours: (iv) back and forth swimming in front of the female, with repeated presentations of the sword and body to the female; (v) circling the female; (vi) swimming beneath the female and touching his mouth to the glass near the female gonopore; and (vii) swimming underneath the female. Both routine and courtship swimming can involve slow wide turns, and courtship behaviour may involve rapid movements and turns as males manoeuvre into position to display to and inseminate females.

Thirty-six respirometry trials were videotaped and scored for the total amount of time each male spent performing each of the seven behaviours described above. The summed data for the time males spent motionless at the bottom and motionless in the water column, as well as the data for routine swimming were analysed using one-way repeated-measures ANOVA followed by *post hoc* comparisons between the four different tests (Tukey–Kramer test). Because there was no courtship behaviour when females were absent, the data for courtship behaviour could not be analysed using repeated-measures ANOVA. Instead, the time spent in courtship was compared between trials using paired *t*-tests. The paired *t*-tests were adjusted for the experiment-wide error rate using a Bonferroni procedure (critical value of $p=0.017$). Finally, paired *t*-tests were used to compare the amounts of time spent in routine and courtship swimming within trials.

3. RESULTS

There was significant variation in metabolic rate among the four treatment groups ($F_{3,24} = 22.01$, $p < 0.001$). When females were absent, the metabolic rate of males with intact swords was 19.4% higher than that of males whose swords had been shortened (Tukey–Kramer *post hoc* test: $p < 0.05$; figure 1). In the absence of females, there was no difference in the time spent in routine swimming between males with intact swords and those with shortened swords (Tukey–Kramer *post hoc* test: $p > 0.05$; figure 2). These combined results suggest that the significant difference in male metabolic rate was not caused by a difference in male behaviour between the tests, but can be attributed to sword costs incurred during routine activity not involving courtship.

When females were present, the metabolic rate of males with intact swords was 18.6% higher than that of males whose swords had been shortened (Tukey–Kramer *post hoc* test: $p < 0.05$; figure 1). In the presence of females, there was no difference between males with intact and shortened swords in the time spent in courtship (paired- $t_8 = 0.43$, $p = 0.68$; figure 2). These combined results indicate that the difference in metabolic rate was not caused by a difference in male courtship activity between the tests, and thus that sword length increases the amount of energy expended during courtship.

The metabolic rate of males with intact swords was 29.9% higher when females were present than when females were absent (Tukey–Kramer *post hoc* test: $p < 0.05$; figure 1). Males with intact swords spent more time courting when females were present than when females were absent (paired- $t_8 = 9.01$, $p < 0.01$; figure 2). Thus, the higher metabolic rate of males with long swords in the presence of females appears to be the result of increased courtship activity.

The metabolic rate of males with shortened swords was 30% higher when females were present than when females were absent (Tukey–Kramer *post hoc* test: $p < 0.05$; figure 1). Males with shortened swords spent more time courting when females were present than when females were absent (paired- $t_8 = 6.08$, $p < 0.01$; figure 2). Thus, the higher metabolic rate of males with shortened swords in the presence of females appears to be the result of courtship activity.

There were no significant differences among the four treatment groups in the amounts of time spent motionless at the bottom ($F_{3,24} = 1.44$, $p = 0.26$) or motionless in the water column ($F_{3,24} = 0.15$, $p = 0.93$). There was, however, a significant variation among the groups in routine swimming behaviour ($F_{3,24} = 26.6$, $p < 0.001$). Males spent more time in routine swimming behaviour when females were absent than when females were present (Tukey–Kramer tests: all $p < 0.05$). However, there were no significant differences in the times spent in routine swimming behaviour by males with normal and shortened swords in either the presence or the absence of females (Tukey–Kramer tests: both $p > 0.05$).

No significant effect of order on O_2 consumption was detected. Oxygen consumption during routine swimming activity did not differ significantly between males in which routine swimming trials were first and routine swimming trials were second (with normal sword: $t_7 = 1.07$, $p = 0.32$; with shortened sword: $t_7 = 1.84$, $p = 0.11$). Similarly, O_2 consumption for courtship swimming did not differ significantly between males in which courtship swimming trials were first and courtship swimming trials were second (with normal sword: $t_7 = 0.627$, $p = 0.55$; with shortened sword: $t_7 = 0.34$, $p = 0.74$). Thus, male O_2 consumption does not appear to have been affected by the sequence of exposure to the experimental conditions.

4. DISCUSSION

Increased sword length in the montezuma swordtail appears to increase the energetic costs of both routine and courtship swimming activities: males expended more energy performing both activities when swords were intact than when swords were shortened. Additionally, the results indicate that courtship activity itself is expensive. The combined effect of a long sword and courtship is a substantial increase in male energy expenditure. This increased energy expenditure is meaningful because males continually pay the locomotor costs of a sword while moving.

What might explain the hydrodynamic costs of the sword during these swimming activities? Fish morphological traits can affect the energetic cost of swimming by contributing to thrust production or inducing drag forces (Webb 1982). The elongation of the lower caudal rays results in an overall increase of surface area, which could increase drag forces and thus swimming costs. In addition, turning increases swimming costs (Boisclair & Tang 1993; Webb & Gerstner 2000), thus multi-directional swimming is energetically costlier than forward swimming at similar velocities. Additionally, while both routine and courtship swimming involve turning, some male courtship manoeuvres in swordtails involve rapid successive changes in direction, with the flexible sword arcing with movement. A long sword, combined with the extra rigidity of sword rays, could add to the angular resistance as males turn, potentially contributing to the cost of the sword. Furthermore, a fish swimming forwards can create a wake (Lighthill 1969), leaving a hydrodynamic trail that persists for several minutes (Dehnhardt *et al.* 2001). Thus, courtship behaviour such as the repeated figure-of-eight manoeuvre in front of a female could result in a male swordtail repeatedly turning into his own turbulent trail,

which could further add to the costs of courtship swimming. Because males develop swords at maturation, sword-length swimming costs would continue throughout a male's adult lifetime.

It appears that there are both benefits and costs of the sword in terms of mating: longer swords are preferred by females, yet longer swords are energetically costlier during courtship swimming. In addition to courting females, male *X. montezumae* perform a suite of other swimming activities under natural conditions. These include maintaining a position in a current, foraging around rocks for algae and detritus, darting away from predators, defending foraging females from intruding males by displaying to and chasing them, and swimming to the defended foraging areas of other males (A. L. Basolo, personal observation). Although fish fin shape can affect movement through the water in a number of fish species (Beamish 1978; Webb & Corolla 1981), in tests investigating the effect of caudal-ray length in guppies, *Poecilia reticulata*, and swordtails, *X. nigrensis*, caudal-ray extension was not found to affect male swimming against a current (Ryan 1988; Nicoletto 1991). Likewise, no effect of sword length on swimming endurance was detected in *X. helleri*, even after prolonged swimming trials (A. L. Basolo, unpublished data). These results mirror those for other fishes. Partial caudal-fin excision in salmonids does not appear to affect swimming at steady speeds (Breder 1926; Gray 1968). In addition, swimming speed and O_2 consumption in the sockeye salmon, *Oncorhynchus nerka*, are not affected when either the upper or the lower portion of the caudal fin is excised (Webb 1973). Thus, it does not appear that the sword is costly when swimming in a current. Such sustained swimming activities do not involve repeated or rapid turns to change direction. Several swordtail activities other than courtship, however, do require sharp turns and rapid acceleration. As there is predicted to be a trade-off between locomotor performance and fish manoeuvrability (Domenici & Blake 1993), hydrodynamic costs of the sword may be incurred during these other activities. For example, the sword could be energetically costly when escaping predators and chasing male competitors. However, such costs of the sword have yet to be directly tested. In addition to these potential energetic costs, long swords could hinder escape from predators or make males more conspicuous to predators. Winemiller *et al.* (1990) have demonstrated that, in poeciliids, more conspicuous males are more likely to be attacked by predators than less conspicuous males. Rosenthal *et al.* (2001) found that the predatory tetra, *Astyanax mexicanus*, orientates more towards high-backed pygmy swordtail, *X. multilineatus*, males with long swords than males with shortened swords. Thus, a longer sword could not only be more attractive to females, but could also attract predators. In *X. helleri* swordtail populations that occur sympatrically with predatory fishes, swords are relatively shorter than in populations that lack these predatory fishes (A. L. Basolo and W. E. Wagner Jr, unpublished data). This suggests that longer swords increase male predation risk. Finally, increased predation risk as well as the energetic costs of sword length during routine swimming and courtship swimming could explain the secondary loss (Rauchenberger *et al.* 1990) of the elongation component of the sword in several extant swordtail species.

While sexual selection via female mate choice appears to favour the evolution of longer swords (Basolo 1990a, 1998), natural selection arising from energetic costs appears to oppose the evolution of longer swords. Few studies have shown that morphological traits preferred by females increase male locomotor costs. One of the few systems in which movement costs of a preferred trait have been extensively considered is tail morphology in birds (Norberg 1994; Møller & Nielsen 1997; Buchanan & Evans 2000; Matyjasiak *et al.* 2000; Park *et al.* 2001). The energetic costs and benefits of elaborate bird tails during flight, however, have not been directly tested; studies thus far have primarily relied on aerodynamic models rather than direct testing of metabolic costs (Rayner 2001). Swords in swordtails can be likened to elaborate tail morphology in birds: one has the potential to affect hydrodynamic aspects of swimming, the other may affect aerodynamic aspects of flight. The initial source of selection favouring elaborate tail morphology in birds has been debated, with some researchers arguing that sexual selection has played the major part (Smith & Montgomerie 1991; Matyjasiak *et al.* 2000), and others maintaining that natural selection arising from aerodynamic benefits plays a strong part in tail evolution (Norberg 1994; Buchanan & Evans 2000; Park *et al.* 2001). For swordtails, phylogenetic information combined with experimental evidence indicates that there was an adaptive field in the form of a female bias favouring a sword when it arose in male swordtails (Basolo 1990b, 1996b). Thus, an original source of selection on male swords was sexual selection via female mate choice as a result of a pre-existing receiver bias (this conclusion does not preclude other sources of selection subsequently affecting sword evolution). Thus, it appears that sexual selection via female mate choice has contributed to the evolution of long male swords, despite opposing selection resulting from sword swimming costs.

5. CONCLUSIONS

Because male swordtails spent more time in courtship and used more energy in the presence than in the absence of females, there appears to be a cost of courtship manoeuvring. In addition, because male swordtails with intact swords used more energy than males with excised swords, both in the presence and in the absence of females, there are costs of the sword in both routine and courtship swimming. Thus, while caudal-ray extension may not be costly during some types of swimming, such as forward swimming in a current, it is clear from our study that, during routine and courtship swimming activities involving turning and backward swimming, there are significant costs imposed by longer swords. This is the first demonstration, to our knowledge, that a sexually selected trait affects the hydrodynamic cost of locomotion in fishes. The results presented here suggest that there were probably hydrodynamic costs countering the evolution of long swords when they arose in swordtails, but, despite the hydrodynamic costs, many extant species of swordtail exhibit long swords. Finally, our results suggest that the common assumption that swimming in fishes is an inexpensive activity relative to running, flying and swimming in other animals (Alexander 1999) is probably not valid when sex-

ually selected morphological traits such as the sword are present.

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REFERENCES

- Alexander, R. M. 1999 Bioenergetics: one price to run, swim or fly? *Nature* **397**, 651–652.
- Basolo, A. L. 1990a Female preference for male sword length in the green swordtail, *Xiphophorus helleri* (Pisces, Poeciliidae). *Anim. Behav.* **40**, 331–338.
- Basolo, A. L. 1990b Female preference predates the evolution of the sword in swordtail fish. *Science* **250**, 808–810.
- Basolo, A. L. 1995 A further examination of a pre-existing bias favoring a sword in the genus *Xiphophorus*. *Anim. Behav.* **50**, 365–375.
- Basolo, A. L. 1996a Phylogenetic evidence for the role of a preexisting bias in sexual selection. *Proc. R. Soc. Lond. B* **259**, 307–311.
- Basolo, A. L. 1996b The phylogenetic distribution of a female preference. *Syst. Biol.* **4**, 290–307.
- Basolo, A. L. 1998 Evolutionary change in a receiver bias: a comparison of female preference functions. *Proc. R. Soc. Lond. B* **265**, 2223–2228. (DOI 10.1098/rspb.1998.0563.)
- Beamish, F. W. H. 1978 Swimming capacity. In *Fish physiology*, vol. VII (ed. W. S. Hoar & P. P. Randall), pp. 101–187. New York: Academic Press.
- Bennett, A. F. & Houck, L. D. 1983 The energetic cost of courtship and aggression in a plethodontid salamander. *Ecology* **64**, 979–983.
- Boisclair, D. & Tang, M. 1993 Empirical analysis of the influence of swimming pattern on the net energetic cost of swimming in fishes. *J. Fish Biol.* **42**, 169–183.
- Borowsky, R. L. & Kallman, K. D. 1976 Patterns of mating in natural populations of *Xiphophorus*. I. *X. maculatus* from Belize and Mexico. *Evolution* **30**, 693–706.
- Breder, C. M. 1926 The locomotion of fishes. *Zoologia* **4**, 159–256.
- Buchanan, K. L. & Evans, M. R. 2000 The effect of tail streamer length on aerodynamic performance in the barn swallow. *Behav. Ecol.* **11**, 228–238.
- Cech Jr, J. J. 1990 Respirometry. In *Methods for fish biology* (ed. C. B. Schreck & P. B. Moyle), pp. 335–362. Bethesda, MD: American Fisheries Society.
- Clark, E., Aronson, L. R. & Gordon, M. 1954 Mating behavior patterns in two sympatric species of *Xiphophorus* fishes. Their inheritance and significance in sexual isolation. *Bull. Am. Mus. Nat. Hist.* **103**, 135–226.
- Darwin, C. 1871 *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. London: John Murray.
- Davis, G. E., Foster, J., Warren, C. E. & Doudoroff, P. 1963 The influence of oxygen concentration on the swimming performance of juvenile Pacific salmon at various temperatures. *Trans. Am. Fish. Soc.* **92**, 111–124.
- Dehnhardt, G., Mauck, B., Hanke, W. & Bleckman, H. 2001 Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). *Science* **293**, 102–104.

- Domenici, P. & Blake, R. W. 1993 The effect of size on the kinematics and performance of angelfish (*Pterophyllum eimekei*) escape responses. *Can. J. Zool.* **71**, 2319–2326.
- Gibson, R. M. & Bradbury, J. W. 1985 Sexual selection in lekking sage grouse: phenotypic correlates of male mating success. *Behav. Ecol. Sociobiol.* **18**, 117–123.
- Gray, J. 1968 *Animal locomotion*. London: Weidenfield and Nicolson.
- Haines, S. & Gould, J. 1994 Female platys prefer long tails. *Nature* **370**, 512.
- Hemans, J. 1966 The ethological significance of the sword-tail in *Xiphophorus helleri* (Haekel). *Behaviour* **27**, 290–315.
- Hoback, W. W. & Wagner Jr, W. E. 1997 The energetic cost of calling in the variable field cricket, *Gryllus lineaticeps*. *Physiol. Entomol.* **22**, 286–290.
- Lighthill, M. 1969 Hydromechanics of aquatic and animal propulsion: a survey. *A. Rev. Fluid Mechanics* **44**, 265–301.
- Matyjasiak, P., Jablonski, P. G., Olejniczak, I. & Boniecki, P. I. 2000 Imitating the initial evolutionary stage of tail ornament. *Evolution* **54**, 704–711.
- Møller, A. P. & Nielsen, J. T. 1997 Differential predation costs of a secondary sexual character: sparrowhawk predation on barn swallows. *Anim. Behav.* **54**, 15 454–15 551.
- Nicoletto, P. F. 1991 The relationship between male ornamentation and swimming performance in the guppy, *Poecilia reticulata*. *Behav. Ecol. Sociobiol.* **28**, 365–370.
- Nicoletto, P. F. 1993 Female sexual response to condition dependent ornaments in the guppy, *Poecilia reticulata*. *Anim. Behav.* **46**, 441–450.
- Norberg, R. A. 1994 Swallowtail streamer is a mechanical device for self-deflection of tail leading edge, enhancing aerodynamic efficiency and flight maneuverability. *Proc. R. Soc. Lond. B* **257**, 227–233.
- Park, K. J., Buchanan, K. L. & Evans, M. R. 2001 Sexy streamer? The role of natural and sexual selection in the evolution of hirundine tail streamers. *Evolution* **55**, 445–446.
- Prestwich, K. N. 1994 The energetics of acoustic signaling in anurans and insects. *Am. Zool.* **34**, 625–643.
- Rauchenberger, M., Kallman, K. D. & Morizot, D. C. 1990 Monophyly and geography of the Panuco Basin swordtails (genus *Xiphophorus*) with descriptions of four new species. *Am. Mus. Nat. Hist. Novitates* **2974**, 1–41.
- Rayner, J. M. 2001 Fat and formation in flight. *Nature* **413**, 685–686.
- Reynolds, J. D., Gross, M. R. & Coombs, M. J. 1993 Environmental conditions and male morphology determine alternative mating behavior in Trinidadian guppies. *Anim. Behav.* **45**, 145–152.
- Roff, D. A. 1992 *The evolution of life histories: theory and analysis*. London: Chapman & Hall.
- Rosenthal, G. G. & Evans, C. S. 1998 Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proc. Natl Acad. Sci. USA* **95**, 4431–4436.
- Rosenthal, G. G., Martinez, T. Y. F., de Leon, F. J. G. & Ryan, M. J. 2001 Shared preferences by predators and females for male ornaments in swordtails. *Am. Nat.* **158**, 146–154.
- Ryan, M. J. 1988 Phenotype, genotype, swimming endurance and sexual selection in a swordtail (*Xiphophorus nigrensis*). *Copeia* **1988**, 484–487.
- Schlosberg, H., Duncan, M. C. & Daitch, B. H. 1949 Mating behavior of two live-bearing fish, *Xiphophorus maculatus* and *Platyepocilus maculatus*. *Physiol. Zool.* **22**, 128–155.
- Sibley, R. M. & Calow, P. 1986 *Physiological ecology of animals: an evolutionary approach*. Oxford: Blackwell Scientific.
- Smith, H. G. & Montgomerie, R. 1991 Sexual selection and the tail ornaments of North American barn swallows. *Behav. Ecol. Sociobiol.* **28**, 195–201.
- Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.
- Sullivan, B. K. 1983 Sexual selection in Woodhouses' toad (*Bufo woodhousei*). II. Female choice. *Anim. Behav.* **31**, 1011–1017.
- Taigen, T. L. & Wells, K. D. 1985 Energetics of vocalizations by an anuran amphibian. *J. Comp. Physiol.* **155**, 163–170.
- Trainor, B. & Basolo, A. L. 2000 An evaluation of video playback using *Xiphophorus helleri*. *Anim. Behav.* **59**, 83–89.
- Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M. 1989 The energetic costs of display in male sage grouse. *Anim. Behav.* **38**, 885–896.
- Wagner Jr, W. E. & Reiser, M. G. 2000 The importance of calling song and courtship song in female mate choice in the variable field cricket. *Anim. Behav.* **59**, 1219–1226.
- Webb, P. W. 1973 Effect of partial caudal-fin amputation on the kinematics and metabolic rate of underyearling sockeye salmon (*Oncorhynchus nerka*) at steady swimming speeds. *J. Exp. Biol.* **59**, 565–581.
- Webb, P. W. 1975 Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 1–159.
- Webb, P. W. 1982 Locomotor patterns in the evolution of actinopterygian fishes. *Am. Zool.* **22**, 329–342.
- Webb, P. W. & Corolla, R. T. 1981 Burst swimming performance of northern anchovy, *Engraulis mordax*. *Fish. Bull.* **79**, 143–150.
- Webb, P. W. & Gerstner, C. L. 2000 Fish swimming behavior: predictions from physical principles. In *Biomechanics in animal behavior* (ed. P. Domenici & R. W. Blake), pp. 59–77. Oxford: BIOS Scientific Publishers.
- Webb, P. W. & Weihs, D. 1981 Optimization of locomotion. In *Fish biomechanics* (ed. P. W. Webb & D. Weihs), pp. 339–371. New York: Praeger.
- Winemiller, K. O., Leslie, M. A. & Roche, R. 1990 Phenotypic variation in male guppies from natural inland populations: corroboration of Haskin's sexual selection/predation hypothesis. *Environ. Biol. Fish.* **29**, 179–191.