

Shift in investment between sexually selected traits: tarnishing of the silver spoon

ALEXANDRA L. BASOLO

Nebraska Behavioral Biology Group, School of Biological Sciences, University of Nebraska at Lincoln

(Received 2 January 1997; initial acceptance 11 March 1997;
final acceptance 22 July 1997; MS. number: A7805)

Abstract. Studies of resource allocation strategies have concentrated on the influence of natural selection on the evolution of life history traits. To a lesser degree, the effects of trade-offs between natural and sexual selection on the evolution of allocation strategies have also been considered. Trade-offs between sexually selected traits that are important to females but that appear to differ in cost, however, have not been considered. Female green swordtails, *Xiphophorus helleri*, prefer males with longer swords to males with shorter swords, and in this study they demonstrated a preference for larger males to smaller males. Furthermore, sexually mature males invested differentially in body and sword growth depending on resource availability; males that had an unlimited amount of food invested in both body and sword growth, but males shifted to a food-restricted regime halted investment in body growth and invested only in sword growth. These results suggest that males shift their pattern of investment in two sexually selected traits when food becomes restricted. In general, variable environmental conditions may favour such conditional investment strategies in species in which there is more than one preferred male trait and the costs of the traits differ.

© 1998 The Association for the Study of Animal Behaviour

The influence of natural selection on the evolution of resource allocation strategies has been well studied (e.g. Williams 1966; Levins 1968; Roff 1982; Clutton-Brock 1983; Warner 1984; Sibley & Calow 1989; Stearns 1992). Less well known is the influence of sexual selection on the evolution of allocation strategies. Although trade-offs between life history and sexually selected traits have been considered (e.g. Partridge & Farquhar 1981; Reznick & Endler 1982; Ryan 1985; Endler 1986), trade-offs between different sexually selected traits have received little attention.

A common tenet in life history studies is the 'silver spoon effect', which suggests that a lifetime reproductive gain is realized by individuals born in a favourable environment (Cockburn 1991). This early advantage presumably allows the individual to grow at a fast rate as well as store energy reserves. When favourable conditions are not constant, an initially abundant resource may become restricted. This change in environmental conditions encountered by an individual, a 'tarnishing of the silver spoon', may result in a shift in

investment strategy; available environmental resources may be used differently, and reserves stored early in life when conditions were favourable may be reallocated for immediate use. In terms of sexual selection by female choice, a male is faced with the dilemma of how to maximize mating success when favourable conditions become less favourable. One solution to this dilemma is to invest in less expensive traits that allow them to subvert female mating preferences, such as sneak behaviour. If conspecific females have preferences for more than one male trait, however, a second solution is to shift investment from one preferred trait to a less expensive preferred trait that is also important to females. To my knowledge, this second possibility has not been experimentally addressed.

In this study, I report the effect of experimental manipulations of food availability on sword growth and body growth in male green swordtails, *Xiphophorus helleri*. I tested whether males change their pattern of investment in two preferred traits, body size and sword length, when food becomes restricted. I found that, with a reduction in food availability, males shifted from growth in both body and sword length to growth in sword length alone.

Correspondence: A. L. Basolo, School of Biological Sciences, University of Nebraska, Lincoln, NE 68588-0118, U.S.A. (email: basolo@niko.unl.edu).

The Test Organism

The green swordtail is a freshwater livebearer that occurs at high and low elevations in streams, rivers and ponds in Central America. A characteristic feature of green swordtails is the presence of a sword in males. The sword develops in males at sexual maturity when a specific set of rays at the ventral margin of the caudal fin begins to lengthen and acquire three colour patterns (upper melanophore stripe, lower melanophore stripe and interior carotenoid and/or pterin). Darwin (1871) was the first to suggest that the sword in the green swordtail had probably evolved due to sexual selection. Female green swordtails have been shown to prefer males with longer swords and the strength of this preference increases with an increase in sword length (Basolo 1990). Although the importance of male body size to female choice has not been previously tested in *X. helleri*, body size appears to be important to females in several other members of the genus *Xiphophorus*; female pygmy swordtails, *X. pygmaeus* and female El Abra pygmy swordtails, *X. nigrensis*, have been found to prefer larger males (Ryan & Wagner 1987; Ryan et al. 1990; Morris et al. 1996). Preliminary data suggest that in the southern platyfish, *X. maculatus*, females also prefer larger males to smaller males (unpublished data).

Body size, or length, has a strong genetic component in the genus *Xiphophorus* (Schreibman & Kallman 1978; Bao & Kallman 1982; Kallman 1983) and male body growth rate decreases at sexual maturity as a correlated effect of maturation. With sexual maturation, body growth rate in male green swordtails is greatly reduced. It is a general principle of life history theory that with the onset of reproduction, there is often a correlated decrease in investment in further body growth and diversion of resources from somatic to reproductive growth (Cockburn 1991); growth in body size in male green swordtails after sexual maturation appears to adhere to this principle. Female green swordtails, however, continue to grow after sexual maturity (in many cases doubling and tripling body size), with growth slowly decreasing with age (unpublished data).

An incremental increase in sword length involves the elongation and coloration of seven to eight caudal fin rays, but an incremental increase in body length involves increasing muscle, connective, nerve and epithelial tissues. Furthermore, an

increment of body length growth (even at the narrowest part of the body, the caudal peduncle) is well over 100-fold more mass than an increment of sword growth. Therefore, it is a reasonable assumption that a millimetre increment of sword length growth is energetically less expensive to produce relative to a millimetre increment of body length growth. Because both body length and sword length may be important to female choice, we might predict that in a food-limited environment, male swordtails may change their pattern of growth by increasing their relative investment in sword growth, while reducing their relative investment in body growth, to maximize their relative attractiveness to females.

METHODS

Test subjects were offspring from fish collected in the northern Belize River drainage, Belize, Central America. Test subjects were collected at birth and housed as juveniles in communal aquaria (37.5 litre). When sex was discernible, immature females were removed to female-only aquaria (37.5 litre). Unless stated otherwise, all fish were fed three times daily: liver pabulum once in the morning, live brine shrimp nauplii in the early afternoon and TetraMin[®] fish flakes in the late afternoon. All fish were maintained on a 16:8 h light:dark cycle with natural and fluorescent light provided during the daylight hours. Water temperature was maintained at $24.5 \pm 0.5^\circ\text{C}$.

Female Preference for Male Body Size

To test for female preference for male body size, males were removed from communal male-only aquaria 4–6 days prior to testing and isolated in 6-litre aquaria. When sexually mature, females were exposed to males for 24–48 h, then placed in 37.5-litre aquaria with other sexually mature females. Females that were not noticeably gravid were drawn without replacement from these communal tanks for testing. The method I used to test for female preference for body size (standard length measured from the anterior tip of the mouth along the lateral line to the point immediately posterior to the caudal vein) was identical to that used to test for female preference for the sword (Basolo 1990). In short, this protocol compares the summed amount of time females spend with males in two 10-min observation periods.

To determine whether female *X. helleri* prefer larger males to smaller males, each of five pairs of males differing in body length (standard length) by at least 4.4 mm was tested. Although males were not always matched for sword length in these tests, the smaller male always had a sword of equal or longer length than the larger male with which it was paired. I analysed the results of female preference tests by comparing the amount of time females spent with each male in each of the five pairs. Because different females were used in each test, each pair of males represents an independent data point.

Investigating the Effect of Food on Growth

I tested the hypothesis that swordtails change their pattern of growth in response to environmental conditions by raising swordtails under two feeding regimes: ad libitum and restricted. Specifically, the effect of differences in food availability was tested for: (1) growth in body length; (2) growth in sword length; and (3) the growth in sword length compared to the growth in body length.

Male test subjects were housed with conspecifics and fed ad libitum until sexual maturity. With the appearance of a fully developed gonopodium and the development of a sword 22 ± 2.0 mm (measured from the point immediately posterior to the caudal vein on the ventral side of the body to the distal tip of the sword), male test subjects were moved and housed individually in 5.5-litre aquaria and alternately placed on either an ad libitum or a restricted diet. Ad libitum-treatment males received an unlimited amount of TetraMin[®] flakes; restricted-treatment males received a weekly portion of 0.05 g of flakes, fed daily (roughly 25% of that fed to ad libitum-males). Aquaria containing males on the two treatments were interspersed on shelves, and all males were in visual contact with other males throughout the experiment. For the 8-month experimental period, test males were scored monthly for body length and sword length.

RESULTS

Female Preference for Male Body Size

In all five tests investigating female preference for male body size, females spent more time, on

Table I. Preference of females based on male body size in the green swordtail, *X. helleri*

Test	Difference in male size (mm)	Number of females spending more time with	
		Larger male	Smaller male
1	10.0	10	0
2	8.0	11	3
3	5.7	9	6
4	5.5	14	0
5	4.4	3	2

average, with the larger male than the smaller male (one-tailed binomial test: $P=0.03$; mean difference: test 1=530 s, test 2=302 s, test 3=293 s, test 4=313 s and test 5=141 s; Table I). This result suggests that body length, like sword length, is a target of female choice in the green swordtail.

Effect of Food Availability on Growth

The data presented include only fish that survived and that were scored over the entire 8-month period. Survivorship did not differ between the males in the two treatment groups (survivorship: ad libitum=12 of 19, restricted=14 of 19; G -test: $G_1=0.49$, $P<0.40$). This survivorship rate is within the normal range for mature males in a laboratory situation. For two of these males, one from each treatment group, a monthly scoring period was inadvertently missed, so they were not included in the results.

Body growth

At the beginning of the experiment, body length did not differ between the males in the two groups (two-tailed t -test: $t_{22}=0.36$, $P=0.73$; restricted treatment: $\bar{X} \pm SE=47.0 \pm 1.55$ mm, $N=13$; ad libitum treatment: $\bar{X} \pm SE=46.2 \pm 1.68$ mm, $N=11$).

The body length of males in the ad libitum group increased significantly (two-tailed paired t -test: $t_{10}=2.92$, $P=0.015$; Fig. 1) a mean $\pm SE$ of 1.58 ± 0.54 mm, or an average increase after 8 months of 3.4% (range=0–13.4% increase).

In contrast, body length in males on the restricted treatment decreased significantly (two-tailed paired t -test: $t_{12}=3.55$, $P=0.004$) mean of 0.57 ± 0.16 mm, or an average decrease of 1.2% after 8 months (range=0–3.3%). Not surprisingly,

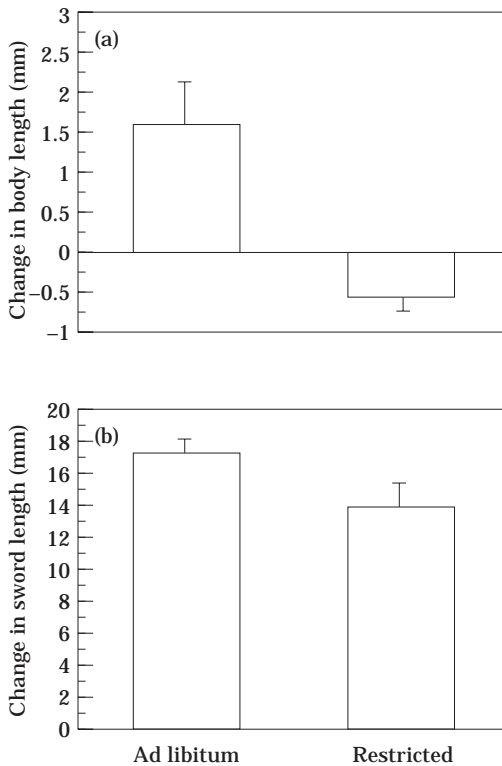


Figure 1. (a) Mean \pm SE change in body length for ad libitum-treatment and restricted-treatment males at the end of the 8-month experimental period. (b) Mean \pm SE change in sword length for ad libitum-treatment and restricted-treatment males at the end of the 8-month experimental period.

the difference between the two groups in the changes in body length was significant (two-tailed paired t -test: $t_{22}=4.09$, $P<0.001$).

Sword growth

At the beginning of the experiment, sword length did not differ between the two treatment groups (two-tailed t -test: $t_{22}=0.099$, $P=0.922$; restricted treatment: 21.87 ± 0.27 mm, $N=13$; ad libitum treatment: 21.83 ± 0.33 mm, $N=11$).

At the experiment's end, however, ad libitum males had significantly longer swords (two-tailed paired t -test: $t_{10}=19.596$, $P<0.00$; Fig. 1), with an average increase of 17.27 ± 0.88 mm and an average increase after 8 months of 79% (range=62–103% increase).

Sword length in males on the restricted treatment also increased significantly (two-tailed

paired t -test: $t_{12}=10.24$, $P<0.00$) a mean \pm SE of 14.05 ± 1.37 mm, an average increase after 8 months of 65% (range=30–116% increase). At the end of the experiment, growth in sword length did not differ significantly between the two treatment groups (two-tailed paired t -test: $t_{22}=1.89$, $P=0.072$). Despite a lower level of available food, restricted-treatment males appear to have maintained investment in the sword at a rate not significantly different from that of ad libitum males. Although there was not a significant difference in sword growth between the two treatment groups after 8 months, the rate of sword growth in ad libitum-treatment males tended ($P=0.07$) to outdistance that of restricted-treatment males; the average sword growth for ad libitum-treatment males was 3.22 mm greater than that for restricted-treatment males.

Field data suggests that sword length is positively correlated with body length (A. L. Basolo and W. E. Wagner, Jr, unpublished data; $r=0.71$, $N=31$, $P<0.001$). Because food affects body length, and sword length is correlated with body length, variation among treatment groups in sword growth may be a correlated consequence of the effect of food on body growth. Sword growth was not significantly correlated with body growth for subject males, however, either in the ad libitum treatment ($r=0.24$, $N=11$, $P=0.48$) or the restricted treatment ($r=0.28$, $N=13$, $P=0.36$).

DISCUSSION

The results suggest that when food is a plentiful resource, male green swordtails invest in both body growth and sword growth; with a reduction in food availability, however, males shift their growth pattern and invest solely in sword growth. Clearly, body size is a condition-dependent trait. Although there was not a significant difference in sword growth between the two groups, there was a trend for ad libitum males to show greater sword growth than restricted males.

Sword growth and body growth may not 'compete' measurably for available energy when food is not limited, but they apparently do so when food becomes limited. In fact, restricted-treatment males decreased in body length over the experimental period, suggesting that reserves stored in body tissue prior to the change in food availability were subsequently used by restricted-treatment

males when food became limited. Whether these reserves were reallocated to sword growth, or whether available food was allocated to sword growth, was not addressed in this study. Although investment in body size was retractable to a small degree, investment in sword growth does not appear to be retractable; energy invested in sword tissue was not reallocated, but the results suggest that a portion of energy invested in body tissue can be reclaimed.

The difference in growth patterns between the treatment groups suggests that a shift in the allocation strategy occurs with a change in food availability. Although not specifically tested in this study, one explanation for the shift of investment pattern is to maximize attractiveness to females as expediently and inexpensively as possible. Because both body size and sword length are important to female swordtails in terms of mate choice, investment in sword growth may increase overall length at a lower cost to males. A shift in growth pattern may allow males in poor condition to enhance their mating success, because females prefer not only larger males, but also males with longer swords. If a unit (millimetre) investment in sword growth for males on a restricted diet increases their attractiveness to females but costs less than a unit investment in body growth, then sexual selection by female choice will favour increased investment in the sword by males in poorer condition. Thus, individuals experiencing a shift from 'good' to 'poor' environmental conditions may change their pattern of energy allocation to growth to compensate for this environmental change, thereby optimizing the likelihood of mating in a poor environment.

In terms of the natural history of green swordtails in Belize, large bodies of water can be reduced to small ponds in the transition from wet season to dry season, with a concurrent shift from low densities to high densities of swordtails (personal observation). By shifting limited resources from a trait that is important to mating but is more costly to produce, such as body size, to another preferred trait that is relatively less costly to produce, such as sword length, males could maximize their attractiveness to females. As the present laboratory results suggest, reallocation of investment from body to sword growth would allow food-limited males to maintain a level of expression of the less expensive trait equivalent to

the expression of males that are not food-limited. Males may not be able to maintain a high rate of investment in sword growth indefinitely, however, because by the eighth month, the rate of sword growth in ad libitum-treatment males tended to outdistance that of restricted-treatment males.

If females prefer both sword length and body length, and sword length is cheaper to increase than body length, why then do males in favourable conditions not invest in sword growth to a greater degree? There are a number of possible answers to this question; although not inclusive, some possible explanations follow. First, the strength of the female preference for these two male traits may differ. That is, the strength of the preference for body length may be greater than that for sword length; thus, an incremental increase in body length would be relatively more attractive to females than an incremental increase in sword length. Second, body size may be important in competition between males. Male size has been suggested to be important in *X. helleri* in terms of intra-sexual selection; [Beaugrand et al. \(1984\)](#) concluded that larger individuals may have an advantage in male-male interactions, but that sword length does not play a role. [Ribowski & Franck \(1993\)](#) found a significant relationship between weight and fighting success for *X. helleri* males. Weight did not always predict fight outcome, however, and, when prior size assessment was allowed, encounters between males of differing sizes were less likely to escalate than encounters between males that were size-matched. Third, the sword may decrease a male's fitness in terms of natural selection; for example, longer swords may reduce a male's swimming ability, or increase his conspicuousness to predators. Fourth, there may be an advantage to larger male size in relation to predator avoidance (larger males may exceed the gape limits of a predator) or in some other natural selection context. Thus, when food is plentiful, males may invest in increasing body size because body size is important in terms of both natural and sexual selection, but males experiencing less favourable conditions may be making 'the best of a bad situation' by switching to sword investment only.

The results reported here suggest the presence of different strategies of energy allocation depending on food availability. When food is limited, males appear to use energy stored in body tissues

to support maintenance, yet still continue to invest in sword growth. The observed shift in growth pattern by food-stressed males may be a facultative strategy to maximize attractiveness to females, given the available resources. Although there is a wealth of information addressing the trade-offs between life history and sexually selected traits, the investigation of trade-offs between sexually selected traits has so far been limited to male strategies that attempt to subvert female preferences (Barlow 1967; Le Boeuf 1974; Gross 1982; Robertson 1986). The alternative strategy addressed in this paper, that is, a shift to investment in a less expensive trait, has not been previously demonstrated. In an organism in which there is more than one trait under selection by female choice such as the green swordtail, selection may favour facultative changes in relative resource allocation: because sword growth is probably less expensive than body growth, food-stressed males appear to channel energy to growth of the less expensive sexually selected trait. However, the hypothesis that female choice has favoured this reallocation strategy remains to be verified.

ACKNOWLEDGMENTS

I thank the Fisheries Ministry of Belize for awarding collecting permits, K. Kallman for sharing his expertise on *Xiphophorus*, J. Gardner, F. Pfertner and R. Traylor for their assistance with fish measurement, female choice tests and fish maintenance, J. E. Endler for his encouragement of this work and J. E. Endler, C. St Mary, K. Benson, B. Trainor, W.E. Wagner, Jr and R. Warner for comments on the manuscript. Support for this research was provided by an NSF Doctoral Dissertation Improvement Grant. Support was provided by NIMH-B/START grant MH55288 and NSF-RPG grant IBN9509211 during manuscript preparation.

REFERENCES

- Barlow, G. W. 1967. Social behaviour of South American leaf fish, *Polycentrus schomburgkii*, with an account of recurring pseudofemale behavior. *Am. Midl. Nat.*, **78**, 215–234.
- Bao, I. & Kallman, K. 1982. Genetic control of the hypothalamus-pituitary axis and the effect of hybridization on sexual maturation (*Xiphophorus*, Pisces, Poeciliidae). *J. exp. Zool.*, **220**, 297–309.
- Basolo, A. L. 1990. Female preference for male sword length in the green swordtail, *Xiphophorus helleri* (Pisces, Poeciliidae). *Anim. Behav.*, **40**, 332–338.
- Beaugrand, J. P., Caron, J. & Comeau, L. 1984. Social organization of small heterosexual groups of green swordtails (*X. helleri*, Pisces, Poeciliidae) under conditions of captivity. *Behaviour*, **91**, 24–60.
- Clutton-Brock, T. E. 1983. The cost of reproduction to red deer hinds. *J. Anim. Ecol.*, **52**, 367–384.
- Cockburn, A. 1991. *An Introduction to Evolutionary Ecology*. Oxford: Blackwell Scientific.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: Murray.
- Endler, J. E. 1986. *Natural Selection in the Wild*. Princeton, New Jersey: Princeton University Press.
- Gross, M. T. 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Z. Tierpsychol.*, **60**, 1–26.
- Kallman, K. 1983. The sex-determining mechanism of the poeciliid fish, *Xiphophorus montezumae*, and the genetic control of sexual maturation process and adult size. *Copeia*, **1983**, 755–769.
- Le Boeuf, B. J. 1974. Male–male competition and reproductive success in elephant seals. *Am. Zool.*, **14**, 163–176.
- Levins, R. 1968. *Evolution in a Changing Environment*. Princeton, New Jersey: Princeton University Press.
- Morris, M. R., Wagner, W. E. Jr & Ryan, M. J. 1996. A negative correlation between trait and mate preference in *Xiphophorus pygmaeus*. *Anim. Behav.*, **52**, 1193–1203.
- Partridge, P. & Farquhar, M. 1981. Sexual activity reduces lifespan of male fruitflies. *Nature, Lond.*, **294**, 580–582.
- Reznick, D. & Endler, J. E. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution*, **36**, 160–177.
- Ribowski, A. & Franck, D. 1993. Demonstration of strength and concealment of weakness in escalating fights of male swordtails (*Xiphophorus helleri*). *Ethology*, **93**, 265–274.
- Robertson, J. G. M. 1986. Male territoriality, fighting and assessment of fighting ability in the Australian frog, *Uperolia rugosa*. *Anim. Behav.*, **34**, 763–772.
- Roff, D. 1982. The evolution of life history parameters in teleosts. *Can. J. Fish. Aquat. Sci.*, **41**, 989–1000.
- Ryan, M. 1985. *The Tungara Frog: A Study in Sexual Selection and Communication*. Chicago: The University of Chicago Press.
- Ryan, M. J. & Wagner, W. E., Jr. 1987. Asymmetries in mating preferences between species: female swordtails prefer heterospecific males. *Science*, **236**, 595–597.
- Ryan, M. J., Hewes, D. K. & Wagner, W. E., Jr. 1990. Sexual selection on alleles that determine body size in the swordtail *Xiphophorus nigrensis*. *Behav. Ecol. Sociobiol.*, **26**, 231–237.
- Schreibman, M. & Kallman, K. 1978. The genetic control of sexual maturation in the teleost,

- Xiphophorus maculatus* (Poeciliidae). *Anns Biol. anim. Biochim. Biophys.*, **18**, 957–962.
- Sibley, R. & Calow, P. 1989. A life-cycle theory of responses to stress. *Biol. J. Linn. Soc.*, **37**, 101–116.
- Stearns, S. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Warner, R. R. 1984. Deferred reproduction as a response to sexual selection in a coral reef fish: a test of the life historical consequences. *Evolution*, **38**, 148–162.
- Williams, G. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. *Am. Nat.*, **100**, 687–690.