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PREVIEW

**SIGNAL USE IN POECILIID FISHES**

by

**Kari E. Benson**

**A DISSERTATION**

**Presented to the Faculty of  
The Graduate College of the University of Nebraska**

**In Partial Fulfillment of Requirements**

**For the Degree of Doctor of Philosophy**

**Major: Biological Sciences**

**Under the Supervision of Professors Alexandra L. Basolo and William E. Wagner**

**Lincoln, Nebraska**

**August, 1998**

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PREVIEW

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Signal Use In Poeciliid Fishes

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# SIGNAL USE IN POECILIID FISHES

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University of Nebraska, 1998

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Evaluation of conspecifics is often facilitated by signals. I examined the use of two morphological features as signals in poeciliid fishes. The first set of experiments addressed the evolution and the maintenance of the sword, a composite trait on males of some poeciliid fishes. The sword has already been shown to be used by females in evaluating prospective mates. In Chapter 2, I tested the importance of sword length and body size in male-male competition in green swordtails, *Xiphophorus helleri*. Body size, measured by lateral area, was correlated with contest success. In a manipulative test, controlling for the importance of size, males with longer artificial swords were significantly more likely to win contests than expected by chance. In Chapter Three, I present the results of two tests showing that winning males might experience increased mating success by restricting access to females. Thus, the role of the sword in competitive interactions can have evolutionary consequences. Chapter 4 shows that artificially sworded males of *Priapella olmecae* (with the ancestral condition of swordlessness) experienced increased success when matched with similarly sized males with clear attachments. These data suggest that the bias for the sworded condition in males arose prior to the sword. Chapter Five addresses the importance of a female trait as a signal. Female green swordtails possess a brood patch, an obligate feature that varies with reproductive condition. This might function as a signal of receptivity to reduce the risks associated with courtship when not receptive and increase female sampling size

of prospective mates when females are receptive. Males courted females with artificially enhanced brood patches significantly more often than they court females from a control group. These data show that this feature can serve as a signal, and be adaptive to females in a number of ways. Additional work with these fishes can address, more specifically, the adaptive value of both swords and brood patches.

PREVIEW

## Acknowledgments

I would like to thank my parents for instilling in me the spirit of philosophical inquiry, a fascination with natural history, and a deep respect for the environment. My family has been particularly supportive, both emotionally and intellectually, throughout my education. This support has made the completion of this work markedly more rewarding and successful.

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PREVIEW

## Chapter 1

### General Introduction

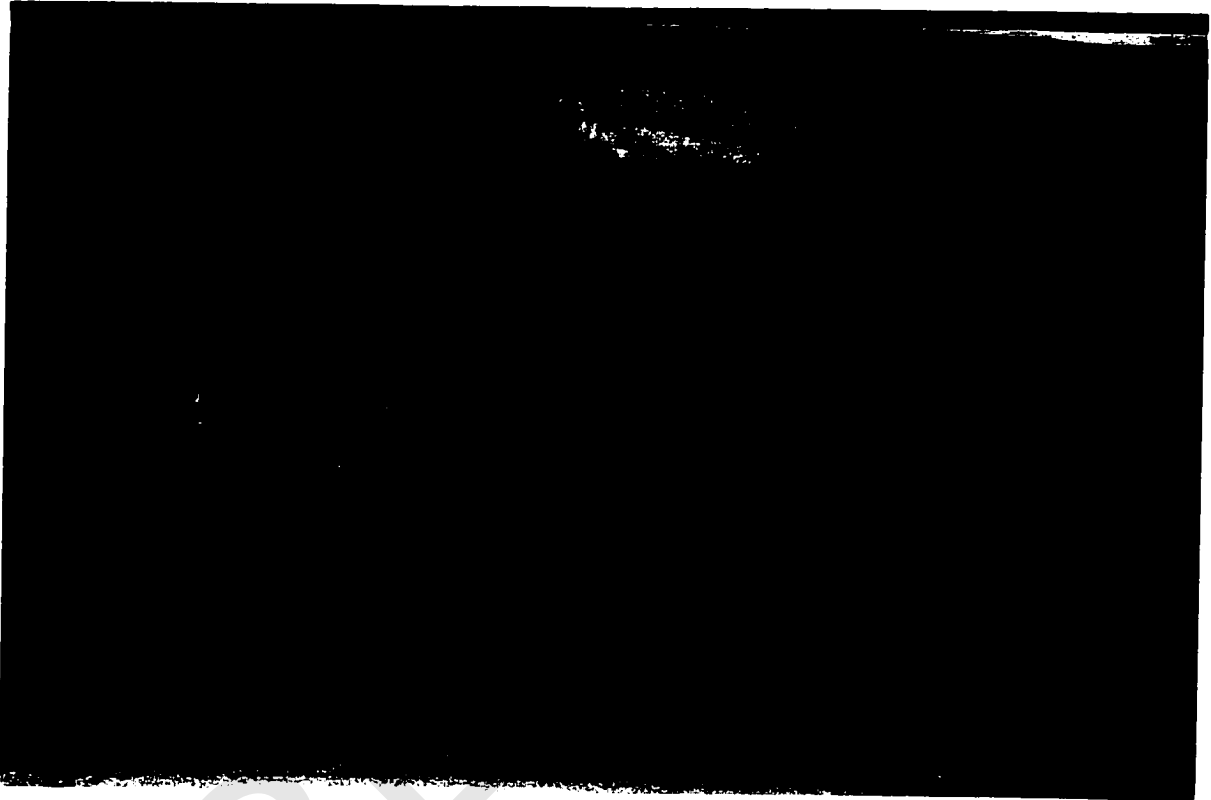


Figure 1.1: A male and a female green swordtail, *Xiphophorus helleri*. The sword, a male trait, can be seen toward the right. The female (left) has a female trait, the brood patch, which is the darkened region on the ventral aspect of the female's abdomen.

Animals interact with one another in many contexts and these interactions are facilitated by signals. Although there has been considerable debate regarding the definition of a signal (Bradbury & Vehrencamp 1998), I will operationally define a signal as an attribute of an animal that influences the response of another organism. Signals can, and often do, convey information (Dusenberry 1992). Animals signal, intentionally and incidentally, to potential predators, parasites, competitors, and conspecifics. Signals can benefit the signaler

by manipulating the behavior of receivers and may also benefit the receiver (Dawkins & Krebs 1978). Incidental transmission of signals to unintended receivers (such as cricket song received by parasitoids, Cade 1984, Wagner 1996), may enable the unintended receiver to make better decisions regarding the signaler and be costly to the signaler (Verrell 1991; Dusenberry 1992).

Visual signals can convey information quickly and over considerable distances (this topic is given considerable coverage in Bradbury & Verhencamp 1998). The distance over which a visual signal is conveyed is constrained by the medium and the environment. In aquatic organisms visual signals can only be effective within the range determined by ambient light, water clarity, the movement of the water, and the number of obstructions in the habitat (Endler 1992). Transmission speed of visual signals makes them an effective form of communication for multiple receivers or over long distances. Signaling can, however, be costly, and the costs of producing signals can vary widely depending on the nature of the signal (Dawkins & Krebs 1978; Ryan 1988).

Signals can function in a variety of contexts. Males and females often differ in their externally-observable features. Sexual dimorphism can result from natural selection if males and females differ in behavior or habitat use. Darwin (1859) proposed sexual selection as an explanation for the evolution of sexually dimorphic traits, particularly when such traits do not appear to be favored by natural selection. The role of sexual selection in the origin and maintenance of sexual dimorphism, particularly for male traits, has received considerable theoretical and empirical attention (see review, Andersson 1994). Intersexual selection, usually in the form of female choice, is important in the evolution or maintenance of many male traits (Hamilton & Zuk 1982; Andersson 1982; Møller 1988; Zuk et al. 1990). Intrasexual

selection, usually in the form of male-male competition, is important in the evolution of many male traits (Davies & Halliday 1978; Arak 1983; Adams & Caldwell 1990; Simmons & Scheepers 1996). Male-male competitive success may be evolutionarily important as competitively successful males can experience increased mating success (Dewsbury 1982). Competitive success can equate to mating success either directly by males controlling access to females or female preference for winning males, or indirectly by female preference for sites controlled by winning males or preferences for traits related to competitive success (Wiley & Poston 1996). The types of traits, or signals, favored by inter- and intrasexual selection can differ (Warner & Schultz 1992). Therefore, sexually dimorphic features can function as signals.

Male signals may function in female choice, male-male competition, or in both. Female choice may favor male traits or signals regardless of whether these traits are informative regarding a male's genotypic or phenotypic quality (Kirkpatrick 1982). Male traits, however, can be honest signals of a male's attributes (Kodric-Brown & Brown 1984). Female choice could favor male traits that are indicators of a male's genetic quality, ability to procure resources, or other attributes of a male's potential (Zahavi 1977, 1991, Hamilton & Zuk 1982, Pomiankowski 1987, 1988, Grafen 1990a, Andersson & Iwasa 1996). Traits that directly enhance a male's ability to fight (for example, antlers used as weapons) can also serve as signals in male-male competition (Clutton-Brock 1982). Males that evaluate competitors can avoid fighting if the outcome can be predicted (Parker 1974). Thus, a trait that is not useful as a weapon can be favored by male-male competition if it facilitates assessment of competitors.

Male competitive signals can convey honest information about ability (Kodric-Brown

& Brown 1984). Size is often a reliable indicator of a male's fighting ability that males use to evaluate competitors (Morton 1977; Maynard Smith & Brown 1986). Thus, a male trait that increases apparent size could be favored (Dawkins & Krebs 1978). A trait that deceptively provokes a response in other males by exploiting the male sensory or perceptual system will, initially, be strongly favored (Christy 1995). However, in male-male competition, if a trait is not an accurate indicator of a male's ability to fight, male response to this trait would be selected against (Dawkins & Krebs 1978; Grafen 1990a; Zahavi 1991; Hasson 1994). Populations are susceptible to dishonest signals if males using the dishonest signals do not incur costs due to their dishonesty (Owens & Hartley 1991). If there are sufficient costs associated with the signal itself, the signal may become correlated with ability (Hasson 1994). The evolution of signals used in fighting has received considerable theoretical attention (Maynard Smith 1974, 1982, Parker 1974, Zahavi 1977, Dawkins & Krebs 1978, Maynard Smith & Brown 1986, Enquist & Leimar 1987, Gardner & Morris 1989, Grafen 1990a, Michod & Hasson 1990, Owens & Hartley 1991, Johnstone & Norris 1993, Hasson 1994). Although manipulations can be effective (Davies & Halliday 1978; Arak 1983; Grether 1996a), explicit tests of the use of visual signals have been problematic due to difficulties with manipulations of these signals (Grether 1996a,b) and the relationship between intra- and intersexual selection (Moore 1990a; Warner & Schultz 1992).

Females can also have sexually dimorphic traits and these traits may be favored by male choice (Sargent et al. 1986; Berglund et al. 1993) or by female-female mate competition (Berglund & Rosenqvist 1993). However, these mechanisms are only predicted in cases where quality males are a limited resource (Emlen & Oring 1977; Johnstone et al. 1996). There are other adaptive explanations for female signals. Female traits often coincide with



reproductive status and signal receptivity and can be adaptations to avoid harassment (Boness et al. 1995), to avoid increased predation risk due to courtship when not receptive (Verell 1991; Magnhagen 1995), or to increase a female's sample size of prospective mates when receptive (Real et al. 1996). For a female trait to be adaptive in any of these contexts, males must differentially respond to females dependent on the expression of the trait.

I examined the use of two different morphological features as signals in poeciliid fishes, the sword in males and the brood patch in females (Figure 1.1). By manipulating these visual signals, I examined how male and female poeciliid fishes use these morphological attributes in evaluating conspecifics. In Chapter Two, I test how differences in the strength or exaggeration of the male trait influences male-male competition in addition to the known female preferences for longer sworded males (Basolo 1990b). In Chapter Three, I examine the relationship between male competitive success and mating success with respect to the sword. In Chapter Four, I address the evolutionary history of male response to the sword. In Chapter Five, I present some findings on male responsiveness to the female trait, the brood patch. In Chapter Six, I review my empirical findings and propose several research topics that would logically extend these results.

## Chapter 2

### **The role of the sword in male-male competition in the green swordtail, *Xiphophorus helleri*.**

<sup>1</sup> Green swordtails (*Xiphophorus helleri*) are sexually dimorphic; mature males have a composite trait called a sword. Sexual dimorphism can arise through natural selection and through sexual selection. Intersexual selection, in the form of female choice, has previously been shown to favour longer sworded males. However, the role of the sword as a signal in intrasexual selection, specifically male-male competition, has received little attention. The role of body size and natural sword length were examined in a study in which males were randomly paired and allowed to compete. Body size and sword length were positively correlated, and body size had an important effect on competitive success. Sword length manipulations were used to examine the importance of sword length in determining competitive success. Males were matched for similar body size and swords were replaced with artificial sword attachments of different lengths. In this test, males with longer attachments did not win significantly more often than expected by chance. In a second experiment, controlling for variation in body size, males were given artificial attachments of equal length that appeared to be swords of different lengths. Males with longer appearing swords won contests significantly more often than expected by chance. These data suggest that, controlling for body size, longer sworded males experience greater competitive success, indicating that longer swords may be evolutionarily favoured by male-male competition as well as by female choice.

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<sup>1</sup>This chapter is formatted for submission to *Animal Behaviour*.

## Introduction

Sexually dimorphic traits can arise due to natural selection in which males and females experience different environmental constraints (Darwin 1871; Merilaita & Jormalainen 1997) or due to sexual selection. Darwin (1859) proposed sexual selection as an explanation for the evolution of sexually dimorphic traits, particularly when such traits are elaborate or showy. The role of sexual selection in the origin and maintenance of sexual dimorphism has received considerable attention (for review, see Andersson 1994). Female choice, a form of intersexual selection, is important in many species as a mechanism for the exaggeration and maintenance of male traits (Andersson 1982; Hamilton & Zuk 1982; Møller 1988; Zuk et al. 1990). Male-male competition, a form of intrasexual selection, can play an important role in the evolution of sexually-selected traits (Davies & Halliday 1978; Arak 1983; Adams & Caldwell 1990; Simmons & Scheepers 1996). The focus here is on the role of male-male competition in the maintenance of a sexually dimorphic trait.

Males are expected to compete for mating success in many mating systems (Emlen & Oring 1977; Johnstone et al. 1996). If female quality is variable, males can compete for the higher quality females. Even if female quality does not vary, because males often maximize reproductive success with an increase in the number of mates and often spend little time with individual mates, the resulting biased operational sex ratio can favour male-male competition. Male-male competition can result from differences in search abilities (Wiklund & Fagerström 1977; Gaulin & FitzGerald 1986; Carroll & Salamon 1995), as well as from direct male conflict. Competitive interactions have been found to be important in many taxa including insects (Moore 1990a,b, Lederhouse & Scriber 1996), spiders (Miyashita 1993), mites, (Saito 1995); fishes, (Gorlick 1976); birds, Ligon et al. 1990, Mateos & Carranza

1997), and mammals (Clutton-Brock 1982, Manson 1996).

Traits favoured by females might also be important in male-male competition as a means of evaluating prospective competitors. For example, male and female dragonflies use the same attributes to evaluate males (Moore 1990a). However, in other circumstances, either males and females use different traits, or they weigh the importance of traits differently when making assessments (Cote & Hunte 1989; Warner & Schultz 1992; Wiltenmuth 1996). Signals that males use in competitive interactions are thought to be constrained to reliable indicators (Maynard Smith 1982). But, it is evolutionarily stable for females to favour traits that are not reliable indicators due to a sensory bias (Hasson 1994). Thus, inter- and intrasexual selection can evolutionarily favour different types of characteristics.

Traits favoured by male-male competition often directly determine contest outcomes (Parker 1974). For example, size can provide an advantage in contests and is a determinant of success in male-male contests (Davies & Halliday 1978; Arak 1983; Beaugrand et al. 1991; Madsen & Shine 1993; Bisazza et al. 1996). In addition to size, many other traits are also useful in competitive interactions. Some traits that may be used as weapons are favoured by intrasexual selection. In red deer, the use of sexually dimorphic traits such as antlers as weapons is well documented (Clutton-Brock 1982). Intrasexual selection has also been documented in traits that traditionally had been thought to have resulted from natural selection. Male giraffes possess longer necks than females and these have traditionally been considered an adaptation for giraffe feeding strategies. Recent evidence, however, suggests that males use their exaggerated necks as weapons in male-male competitive interactions (Simmons & Scheepers 1996). Morphological features are commonly used in contests and these traits influence competitive success (Clutton-Brock 1982).

It is not necessary that sexually dimorphic traits be directly valuable as weapons to influence contest success. Even when not used as weapons, males with more exaggerated traits can experience greater contest success. This relationship has been reported in several diverse taxa (dragonflies, Moore 1990, Grether 1996a; northern swordtails, Morris et al. 1992; spiders, Miyashita 1993; frogs, Davies and Halliday 1978, Arak 1983). In these circumstances, the traits may serve as signals (Berglund et al. 1996). Sexually dimorphic traits can act as signals of intent (Maynard Smith 1982), past success (Grafen 1990b), or indicate vigour (Zahavi 1977), size (Parker 1974), or age (Burk 1988). By enabling evaluation of prospective competitors without a contest, these signals allow males to avoid unnecessary injury, unnecessary energy expenditure, or increased predation risk incurred by fighting (Maynard Smith & Parker 1976; Maynard Smith & Brown 1986). Signaling in competitive interactions can be cooperative in that both prospective losers and prospective winners benefit by avoiding a contest if they are disparate in abilities (Parker 1974; Hurd 1997).

To be informative in male-male competition, male signals have to be correlated with attributes of fighting ability (Zahavi 1977, 1991, Grafen 1990, Dawkins & Guilford 1991). This relationship has been found in correlational studies (Rohwer 1975; Veiga 1993; Kodric-Brown 1996) and in manipulative experiments. For example, Veiga (1993, 1995) found that artificially augmenting badges on house sparrows did not alter their competitive or mating success, though natural badges were indicative of status. Likewise, comb manipulations in jungle fowl did not alter male competitive success (Ligon et al. 1990). However, manipulations of signals have influenced male competitive success in a frog (Davies & Halliday 1978; Arak 1983), a bird (Rohwer & Rohwer 1978), and a dragonfly, (Grether 1996a). Whether

manipulations are effective or not may be due to the cost of assessing the honesty of the signal (Dawkins & Guilford 1991). The investment in assessment depends on the cost of escalating a contest (Gardner & Morris 1989). Manipulations can indicate whether a male trait is a signal in male-male competitive interactions. Here, I manipulate a signal, the sword, in male swordtail fishes to evaluate whether it is used as a signal in male-male competition.

### The Study Organism

Green swordtails, *Xiphophorus helleri* (Haeckel), are livebearing fishes in the Family Poeciliidae and are widespread in the Atlantic tributaries of Northern Central America (Rosen & Bailey 1963, Figure 2.1). Male green swordtails have a composite morphological trait, the sword, which consists of the a tri-coloured elongation of several ventral caudal fin rays (Rauchenberger et al. 1990, Figure 2.2). Basolo (1990a) has shown that female green swordtails prefer longer sworded males. Thus, due to female choice, longer sworded males presumably achieve greater reproductive success than shorter sworded males. Further, Basolo (1990c, 1995a, b, 1996) has shown that a preexisting bias in the females of this taxa may have been important in the origin of this trait.

In addition to intersexual selection, male-male competition may be a source of sexual selection that favoured the origin or the maintenance of the sword. Male green swordtails have well-studied competitive interactions. In field observations, winners of contests appeared to retain access to particular sites and dominance hierarchies were reported (Franck & Ribowski 1989). In laboratory tests, previous contest success, size, and previous experience at a given location are important determinants of current contest success in the green swordtail (Beaugrand & Beaugrand 1991; Beaugrand et al. 1991; Franck & Ribowski

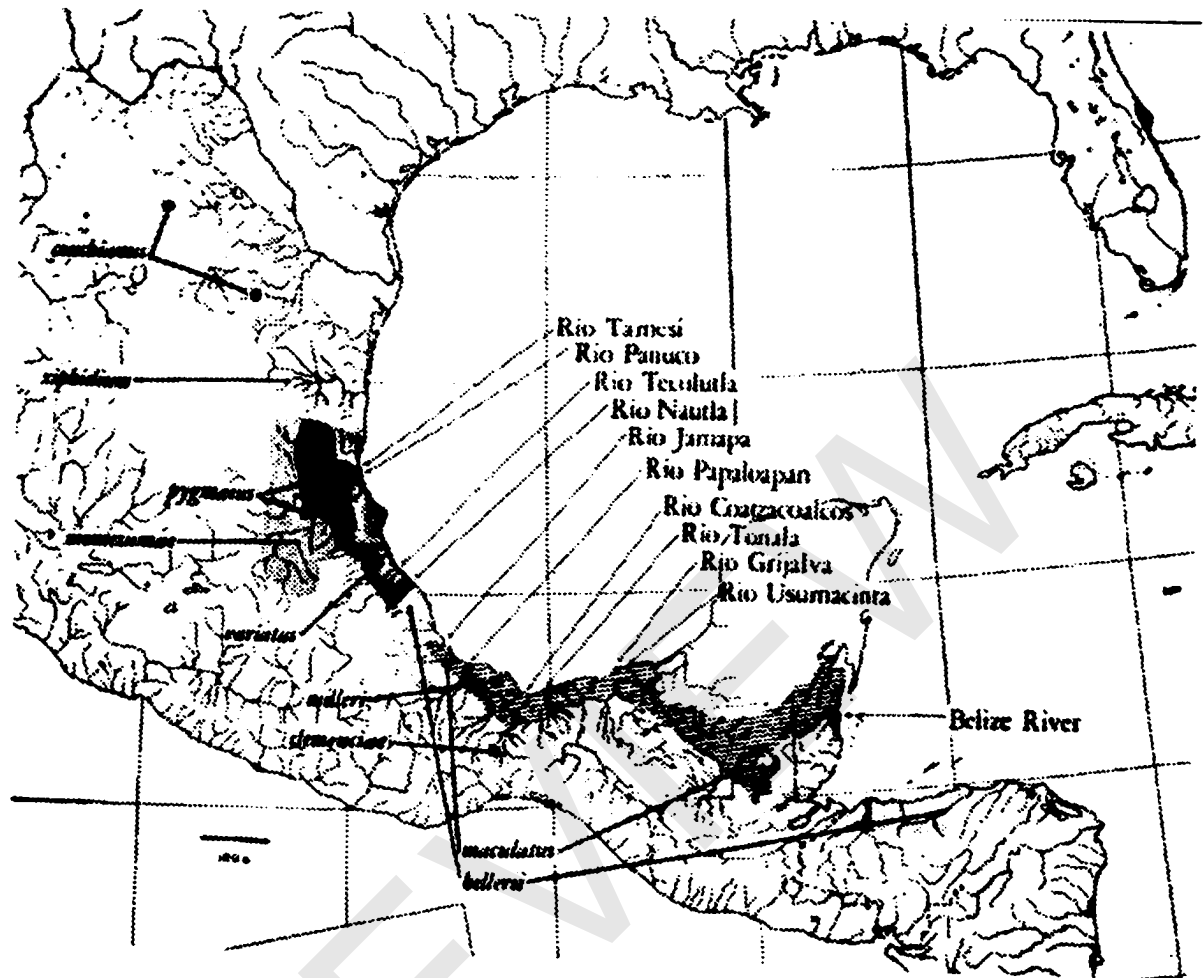


Figure 2.1: This map shows the natural distribution of several *Xiphophoran* fish species.

1993; Beaugrand et al. 1996). In early experimental manipulations of the sword, males behaved more aggressively toward males with swords than to de-sworded males (Hemmens 1966; Franck & Hendricks 1973).

This paper addresses the role of the sword in male-male competitive success. First, I present a correlational study that investigates the importance of body size (measured by lateral area) and natural sword length as determinants of competitive success in pairwise contests. A relationship between sword length and competitive success could result from some genetically or phenotypically correlated effect, and not be due to variation in sword

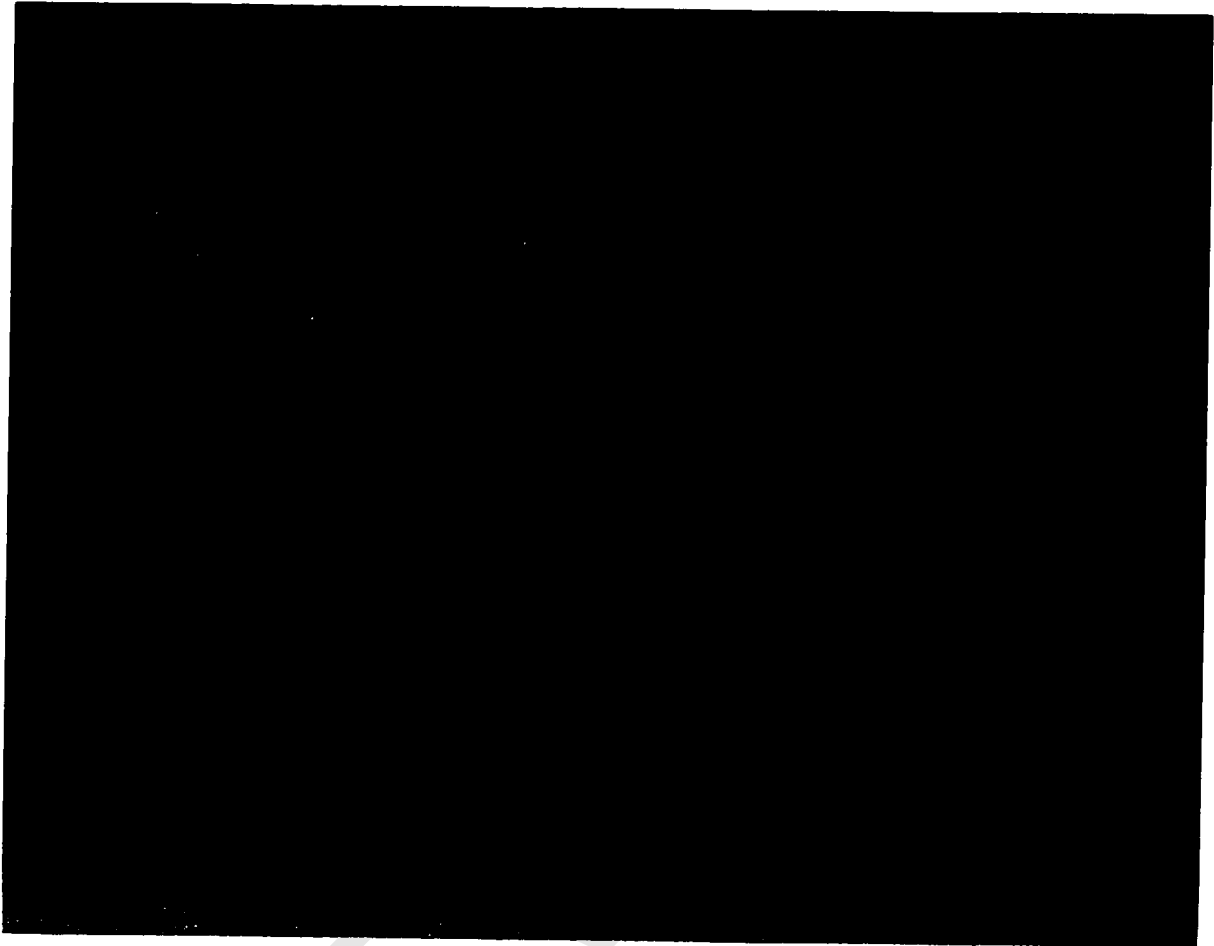


Figure 2.2: A male with a natural sword consisting of four components including upper and lower black stripes, extension, and internal colouration.

length. I address this possibility using sword manipulations. Pairs of males were matched for body size and given artificial sword attachments of different lengths. In these contests, only the length of the swords differs systematically between partners.

### Methods

Subjects were male descendants of green swordtails, *X. helleri*, collected from Savannah Stream near Mile Marker 28, Western Highway in Belize during 1993 and 1994. Fish were housed in treated water (distilled water treated with Novaqua™, Instant Ocean™, and Start Right™) and maintained at approximately 26°C, on a 14h:10h light:dark photoperiod. Fish