

Congruence between the sexes in preexisting receiver responses

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Preexisting receiver biases have been shown to affect how females detect and respond to new conspecific traits in a mate choice context. Although preexisting biases have often been discussed in the context of female mate choice, these biases need not be sex limited. In the genus *Xiphophorus*, swordtail males possess a sexually selected trait, the sword. Here I consider evidence that the state of a bias favoring sworded conspecifics may be generally shared by the sexes in taxa in which the sword has not arisen. In three unsworded species of poeciliid fishes, both males and females prefer members of the other sex with swords. In a fourth species, males and females share the absence of a response to a sword. This congruity between the sexes suggests that response biases may not be sex limited and that the sexes could historically share common mechanisms producing shared mating responses. Alternatively, selection may tend to result in parallel changes in biases in the sexes. This work expands our understanding of receiver biases by using a phylogenetic approach to examine whether biases are historically shared by the sexes and suggests that there can be general congruence between the sexes in such biases. *Key words*: poeciliid fishes, preexisting biases, receiver biases, shared traits. [*Behav Ecol* 13:832–837 (2002)]

Receiver biases established in one context could affect fitness in other contexts (Basolo, 1990b, 2000; Endler and McLellan, 1988; Kirkpatrick, 1987; Ryan, 1990). Such correlated fitness effects may be disassociated in evolutionary time from the original context in which a trait evolved. In terms of mate choice, for example, if females have biases that cause them to be more sensitive to certain classes of environmental stimuli, and if new traits arise in males that these biases differentially recognize, females may be more likely to mate with males expressing these new traits. The same applies for biases in males for female traits. In a diverse array of animals, including fish, frogs, birds, crabs, spiders, and water mites, historical information suggests that preexisting receiver biases have played a role in the evolution of female preferences, which in turn appear to have affected the evolution of male signals (reviewed in Endler and Basolo, 1998).

Although the study of receiver biases has concentrated on females, biases need not be sex limited. Lande (1981) suggested a mechanism for the evolution of shared traits between the sexes; a trait selected in one sex can be expressed in the other sex, simply through a correlated response to selection in the other sex. This mechanism has been proposed as an explanation for shared mating tendencies of males and females within a species (Halliday and Arnold, 1987). Thus, traits shared by the sexes can result from selection on one sex within a given species. Traits may also be shared by the sexes either due to a non-sex-limited mutation being carried to a high frequency as a result of genetic drift, or due to selection acting similarly on the sexes. When a shared ancestral receiver bias is established by mutation with genetic drift, the state of the bias is not expected to differ for the sexes, unless there is a differential cost in carrying the mutation. When sensory or cognitive processing features were favored in the past due to selection acting in the same manner on both sexes, we might expect the sexes to presently share a response to a specific

stimulus. Alternatively, the sexes may respond similarly in a mating context, not due to the common descent of the response, but as a result of convergent evolution.

Shared biases that arose in an ancestor may result in the sexes exhibiting the same response to a trait in conspecifics. Alternatively, the responses of the sexes may differ because a shared bias has been co-opted by males and females in different selective contexts (e.g., intrasexual selection vs. intersexual selection; Basolo, 2000). Some studies have suggested that within a species, the sexes exhibit different responses to the same stimulus (Morton, 1990; Narins and Capranica, 1976; Rowland, 1989; Smith, 1972) as a result of differential selection. Other studies have indicated that shared biases result in similar responses by male and females (Basolo and Delaney, 2001; Jones and Hunter, 1993; Ryan and Rand, 1998). Yet we need not expect congruence between the sexes in the state of biases (Basolo, 2000). Receiver biases could change in one or both of the sexes and in one or more taxa following their appearance. And, if a trait arises in one sex that is favored by an ancestral bias, sexual selection may subsequently act differently in males and females, resulting in differences between the sexes in their responses to the trait (Basolo and Delaney, 2001).

Swordtails and unsworded platyfish are poeciliid fishes that compose the genus *Xiphophorus* (Rosen, 1979; Rosen and Bailey, 1963). Male swordtails possess a sword, a colored extension of the lower caudal fin, except for three species in which sword components appear to have been secondarily lost (Basolo, 1996; Rauchenberger et al., 1990; Rosen, 1979; Rosen and Bailey, 1963). Based on the available phylogenetic evidence (Borowsky et al., 1995; Haas, 1993; Meyer et al., 1994; Rosen, 1979), it appears that this sword arose after the divergence of the sister genera *Priapella* and *Xiphophorus*. Evidence also suggests that a female mating bias for males with swords was present before the divergence of the two clades; females of four species in the *Xiphophorus/Priapella* clade favor conspecific males with swords, including the green swordtail, *X. helleri* (Basolo, 1990a; Rosenthal and Evans, 1998; Trainor and Basolo, 2000), the variable platyfish, *X. variatus* (Basolo, 1990c, 1995a; Haines and Gould, 1994), the southern platyfish, *X. maculatus* (Basolo, 1990b), and the guayacón olmeca, *Priapella olmeca* (Basolo, 1995b). Males of two of these species have been tested for a response to sworded females as

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Received 9 October 2001; revised 12 April 2002; accepted 13 April 2002.

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well; *Pr. olmecae* males prefer sworded females, but *X. helleri* males discriminate against sworded females (Basolo and Delaney, 2001). Thus, the sister genera *Priapella* and *Xiphophorus* appear to share a bias in females favoring sworded males, but not a bias in males favoring sworded females. Although the results for females suggest that a bias was present before the appearance of a sword in swordtails, the ancestral condition for males is unclear.

Although a number of studies have investigated whether conspecific males and females share similar responses to specific signals, a phylogenetic approach has not previously been used to investigate whether a response to a trait is historically shared between the sexes. Here, to test whether the sexes generally share receiver responses for traits not present in their evolutionary history, a receiver bias favoring a sword is further investigated by testing the sword response in male *X. maculatus*, in male and female sailfin mollies, *Poecilia latipinna*, and in male and female Mexican mollies, *Poecilia mexicana*. The results of this study are combined with the results of previous studies to assess whether there is general congruence or noncongruence between the sexes in the state of preexisting receiver responses. It appears that in species in which the sword has not arisen, there is congruence between the sexes in their responses to sworded conspecifics of the other sex.

MATERIALS AND METHODS

The test fish were either field collected or first- or second-generation offspring of field-collected fish. The *P. mexicana* originated from Reptile Pond, Belize. This species was collected under a permit awarded by the Fisheries Ministry of Belize. The *X. maculatus* originated from the Rio Palma, Vera Cruz, Mexico. This species was collected under a permit awarded by the Secretaria de Relaciones Exteriores and the Secretaria de Medio Ambiente Recursos Naturales y Pesca, Mexico. The *P. latipinna* originated from a canal in Harvey, Louisiana, under a collection permit awarded by the Department of Wildlife and Fisheries, State of Louisiana.

Five choice experiments were conducted: (1) male preference for sworded female *X. maculatus*, (2) male preference for sworded female *P. mexicana*, (3) female preference for sworded male *P. mexicana*, (4) male preference for sworded female *P. latipinna*, and (5) female preference for sworded male *P. latipinna*. For each of these five experiments, a set of conspecific individuals were paired for sex, body size, and morphology. One member of each pair received a surgically attached plastic sword consisting of an upper stripe, a lower stripe, internal coloration, and elongation, typical of male green swordtails. The other member of each pair received a clear attachment of equal length that simulated the visual absence of a sword, but controlled for the effect of the attachment on behavior. (Details concerning this procedure have previously been described in Basolo, 1990b, 1995b.) For each of the five mate choice experiments, a set of conspecific test fish was given a choice between paired individuals of the other sex. For each experiment, test fish and test pairs were used only once.

Mating preferences were tested using a general method for poeciliid fish species (Basolo, 1995b; Bischoff et al., 1985; Morris et al., 1995; Ryan and Wagner, 1987; Schlupp et al., 1991). This general method was first used by Bischoff et al. (1985) to test the response of female guppies, *Poecilia reticulata*, to males differing in coloration; they found that their measure of female preference, amount of time a female spent in association with males, accurately predicted male reproductive success based on number of offspring. This general design has also been used to show that male *P. latipinna* prefer conspecific females to heterospecific females (Schlupp et

al., 1991); the results from this experiment are in agreement with the results obtained by using male mating attempts in *P. latipinna* and *P. mexicana* (Ryan et al., 1996) as the measure of male preference. Male mating preferences in *P. reticulata* have also been measured using a similar design (Benz and Leger, 1993) and verify results from the field and laboratory that indicate that males prefer larger females (Endler and Houde, 1995; Houde, 1997; Reynolds and Gross, 1992). For the five experiments reported here, mate choice trials were performed for each species by presenting a matched pair of conspecifics to other sex test fish in a divided tank that did not allow chemical or physical cues between the test subjects. The time that a test fish spent showing mating interest to each of the paired stimulus fish was recorded. Mating interest was defined as being within three body lengths of a stimulus fish while attending to the stimulus fish and interacting by exhibiting mating behavior. The behaviors observed for the five tests conducted here (e.g., circling, backing toward a conspecific, unison swim, presenting a flexed flank) are attributed to mating behavior in the literature for poeciliids (Basolo, 1995b; Clark et al., 1954; Farr, 1989; Franck, 1964; Hemens, 1966; Houde, 1997; Schlosberg et al., 1949); the aggressive behaviors that have been described do not include these behaviors. Mating interest was preceded by the test subject ceasing other activities (e.g., swimming around the tank foraging on the bottom, swimming vertically up and down the front of the aquarium, positioned near the companion fish, hanging motionless at the surface), looking over at one of the paired individuals, then swimming directly toward that individual. To control for the potential effect of association behavior on the measurement of male and female choice used here, the test fish could also interact with the companion fish of the same sex in a tank adjacent to the center section (as described in Basolo, 1995b, 2002). For each of the five different choice experiments, I summed and compared the amount of mating interest time for two 10-min test periods for each test subject (Basolo, 1995b) using a Wilcoxon matched-pairs signed-rank test.

I calculated the statistical power of the nonsignificant analyses using NCSS Pass 2000 software. These power calculations are approximations that use the asymptotic relative efficiency of the Wilcoxon matched-pairs signed-rank tests relative to the paired *t* test (per Lehmann, 1975). The average effect size was calculated separately for each sex using those comparisons in which there was a significant difference. For the comparisons that were not significantly different (both sexes of one species), the power to detect the average effect size observed for that sex in the four other species was calculated (e.g., Bee, 2002).

RESULTS

Male *X. maculatus* spent significantly more time with sworded females than with unsworded females (Wilcoxon matched-pairs signed-rank test: $n = 15$, $p = .03$, Figure 1a). Thus, in this unsworded species, males prefer conspecific females with swords to those with clear attachments.

Female sailfin mollies, *P. latipinna*, spent significantly more time with sworded males than unsworded males (Wilcoxon matched-pairs signed-rank test: $n = 15$, $p = .04$; Figure 1b). Likewise, male sailfin mollies spent significantly more time with sworded conspecific females than with unsworded females (Wilcoxon matched-pairs signed-rank test: $n = 17$, $p = .04$; Figure 1b). Thus, in this unsworded species, females and males preferred conspecifics of the other sex with swords to those with clear attachments.

Female Mexican mollies, *P. mexicana*, did not discriminate between sworded males and unsworded males based on mat-

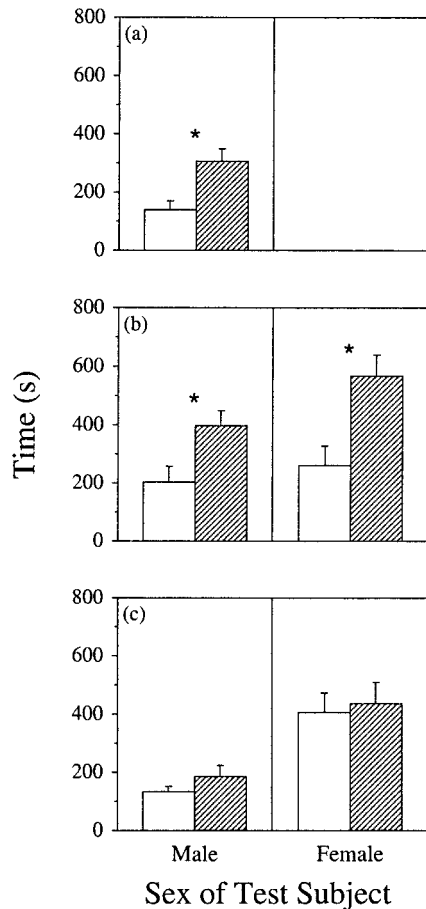


Figure 1

The amount of time (\pm SE) males and females spent with either unsworded (open bars) or sworded (hatched bars) conspecifics of the other sex. (a) Response of males to sworded *Xiphophorus maculatus* females. (b) Response of males to sworded *Poecilia latipinna* females and the response of females to sworded *P. latipinna* males. (c) Response of males to sworded conspecific *P. mexicana* females and the response of females to sworded *P. mexicana* males.

ing interest (Wilcoxon matched-pairs signed-rank test: $n = 14$, $p = .98$; Figure 1c). Likewise, male Mexican mollies did not discriminate between sworded females and unsworded females (Wilcoxon matched-pairs signed-rank test: $n = 14$, $p = .36$; Figure 1c). Thus, in this unsworded species, neither females nor males appear to prefer conspecifics of the other sex with swords to those with clear attachments.

The power to detect the average effect size observed in the other four species was calculated for *P. mexicana*. The mean effect size for females for the other four species was 1.44, and the power to detect this expected effect size in female *P. mexicana* was > 0.99 . The mean effect size for males for the other four species was 0.67, and the power to detect this expected effect size in male *P. mexicana* was 0.61.

DISCUSSION

Male and female responses to sworded conspecifics of the other sex have now been examined in four related poeciliid species that lack a sword, and in one species with sworded males. In the four historically unsworded species, there appears to be congruence between the sexes in response to a sword (Fig-

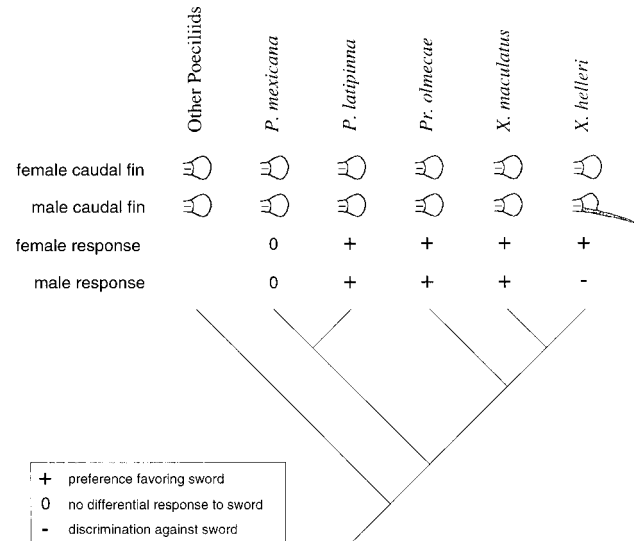


Figure 2

Response of males and females in one sworded and four unsworded species in the tribe Poeciliini to sworded conspecifics of the other sex. Female caudal fin indicates the normal caudal fin condition for females in each species. Male caudal fin indicates the normal caudal fin condition for males in each species. Female response indicates the response of females to sworded conspecific males. Male response indicates the response of males to sworded conspecific females.

ure 2). In one of the unsworded species, *P. mexicana*, neither sex exhibited a differential response to sworded conspecifics, suggesting that a bias favoring a sword is absent in both sexes. The power to detect the expected effect size was modest for male *P. mexicana* and high for females. In the other three unsworded species, both females and males prefer sworded conspecifics of the other sex. The results from the experiments presented here, combined with previous findings, suggest that there is general congruence between the sexes in the state of a bias when the trait is not present (Figure 2). Although there does not appear to be an intersexual difference in the state of the bias within the two *Poecilia* species, there was an interspecies difference in the state of the bias; male and female *P. latipinna* responded positively to sworded individuals of the other sex, while male and female *P. mexicana* did not respond differentially to sworded individuals of the other sex. This result suggests that biases can change over time in both sexes, possibly with simultaneous change in males and females. However, as indicated by previous findings for the green swordtail, *X. helleri*, when the trait is currently present in males, congruence may not exist between the sexes.

Congruence between the sexes in a response bias is expected to exist as a result of one of four evolutionary scenarios. First, a bias could arise simultaneously in the sexes and evolve simultaneously in both via drift. Second, a bias could simultaneously evolve in both sexes via selection because selection should often act similarly on the sensory and cognitive systems of both sexes. Third, the sexes may have similar, but nonhomologous biases. This would be the case if different sources of selection independently favor the same type of response in both sexes or if genetic drift results in the establishment of similar mutations in the sexes. Fourth, a bias could evolve in one sex via selection and evolve in the other sex as a correlated effect (Basolo, 1996; Halliday and Arnold, 1987; Lande and Arnold, 1985); this assumes that there is little cost

to the trait being carried along in the sex in which the bias is not selected.

Natural selection can favor sensory and cognitive systems to process data in certain ways, and this results in biases toward certain kinds of signals and signal properties (Endler and Basolo, 1998). If the bias favoring a sword is homologous for the sexes, there are two equally parsimonious hypotheses for the evolutionary history of the sword response in the five species of poeciliid fishes discussed here. First, assuming that *P. mexicana* males really do not have a bias toward swords, the bias could have arisen in a common ancestor of all five, with a single evolutionary event resulting in the lack of a response in *P. mexicana* and a second change resulting in the negative response exhibited by *X. helleri* males (Figure 3a). Alternatively, there may have been two independent origins of a sword bias, one in *P. latipinna* and one in an ancestor of the *Priapella/Xiphophorus* clade, with a subsequent change in the bias in *X. helleri* males (Figure 3b). These alternative hypotheses would both require three independent evolutionary events. It is also possible that the responses for the five species are not homologous or that the responses are not homologous for the sexes. However, if the response to a sword is not homologous for the sexes, a minimum of five evolutionary events is required to explain the distribution of the bias. If parsimony (Hennig, 1966) is assumed, then a shared, homologous bias is one explanation for the congruence between the sexes in the response to the sword.

Given the female preference for swords, why might male *X. maculatus*, *P. latipinna*, and *Pr. olmecae* lack swords? Regardless of the context in which a bias originates, it may be specific, or it may be general for the types of traits it can subsequently influence. Depending on the types of variation that arise after a bias has been established, different lineages could have different traits that have evolved as a result of the same general ancestral bias (Basolo, 2000). If this is the case, then the same ancestral bias could have contributed to the evolution of the sword in male swordtails, the elongated, colorful dorsal fins in male *P. latipinna*, the orange gonopodium, caudal fin and dorsal fin expressed by male *Pr. olmecae*, and the red, yellow, orange, and black fins expressed by male *X. maculatus*. This possibility is intriguing, but further investigation in both sexes across the clade using surgical manipulations or altered video presentations (Rosenthal and Evans, 1998; Trainor and Basolo, 2001) are needed to explore the bases of the bias favoring a sword.

It seems clear why female green swordtails do not presently have swords; males discriminate against sworded females. But why do female *X. maculatus*, *P. latipinna*, and *Pr. olmecae* lack swords when sworded females are preferred by males? This question may be addressed by considering potential costs to females of producing and maintaining a sword or swordlike structures and colors. Although female *Pr. olmecae* express light yellow fins and some female *X. maculatus* express red, yellow, orange, and black fins, expression of these colors is usually weaker than expression in males. Investment in a sword can include extending the length of lower caudal fin rays as well as allocating pterin, melanin, and carotenoid pigments to these rays. Allocation to sword components may be costly to younger females at a time when they are under pressure to mature and reproduce. In addition, if the sword affects swimming ability, changes in the caudal fin may be particularly costly to gravid females in terms of capturing prey or avoiding predators (gestation of young results in a change in shape, producing a less streamlined body). In such cases, a sword combined with the temporary change in female body shape might impede rapid maneuvers used in capture and escape. Finally, although males prefer sworded females, the strength of the preference may differ for the sexes. Tests investigating

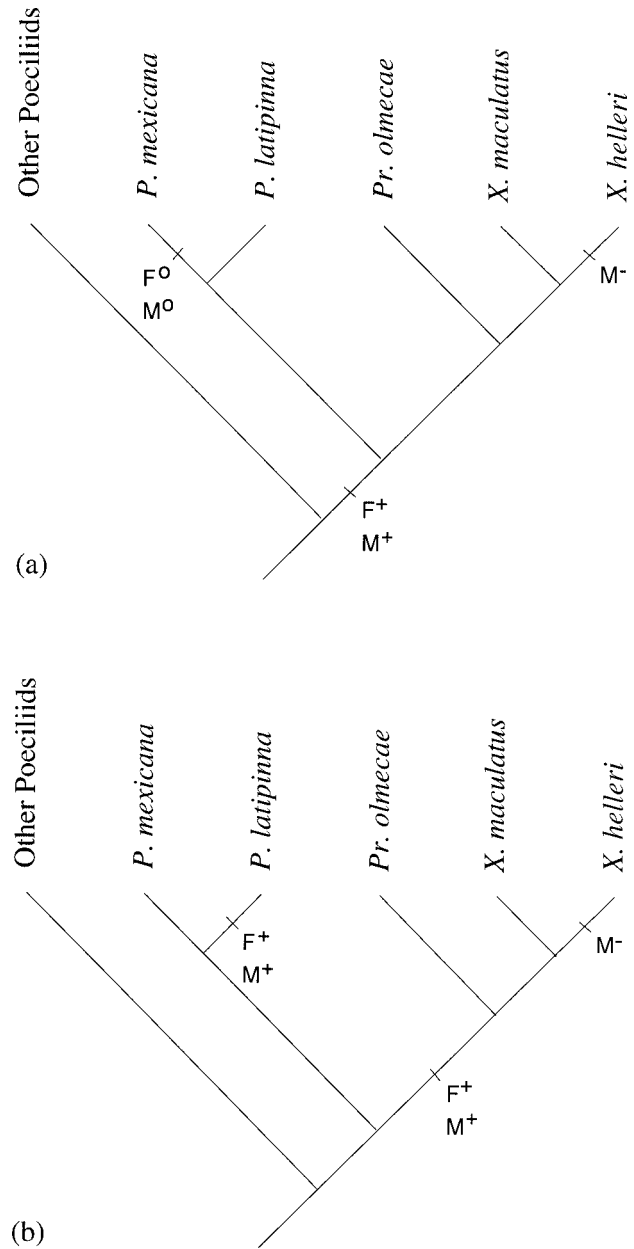


Figure 3
Equally parsimonious hypotheses for the evolutionary history of the response to a sword. F[°] indicates the lack of a female response to sworded males. M[°] indicates the lack of a male response to sworded females. M⁺ indicates the presence of a bias in males favoring sworded females. F⁺ indicates the presence of a bias in females for sworded males. M⁻ indicates the loss of a bias favoring sworded females.

the preference functions (Wagner, 1998) in both sexes could establish whether males and females differ in the strength of this sword preference; a weaker male preference would provide another explanation for the lack of swords in females.

Although this work includes only five species, the results are provocative. For either evolutionary scenario (Figure 3), the combined evidence suggests that the female ancestral state for these taxa is a receiver bias that results in a sword preference; the same ancestral bias could explain the preference found in males as well. In one species that exhibits no differential response to a sword, the sexes share this response. Only in a

species that presently possesses a sword is there a negative response to the sword in a mate choice context, and only in this species were the sexes found to differ in their response to a sword. If the ancestral state for males is a favorable response to a sword, it appears that somewhere along the receiver signal processing/response system, there has been a change in the bias in male *X. helleri*; males do detect the sword, but they respond negatively to sworded conspecific females. The sword currently appears to play a role in female mate choice in swordtails, and the sword could function in alternative contexts in males, such as sex recognition, maturation status, or male–male competition (Basolo, 2000). Such other evolved functions could preclude the co-option of the bias in an intersexual context in swordtail males, suggesting that once a bias has been co-opted by a sex in one context, there may be constraints on its co-option in a different context. The work presented here adds to our growing understanding of receiver biases, but it remains to be determined whether congruence between the sexes in the state of receiver biases extends to more distantly related species.

I thank W. E. Wagner, Jr. for insightful input during the course of these experiments, J. A. Endler, D. Leger, S. Louda, and W. E. Wagner, Jr. for comments on various manuscript versions, A. Aspbury and K. Delaney for assistance with the fish, D. Westneat and two anonymous reviewers for constructive criticism of earlier drafts, and the Fisheries Ministry of Belize, the Secretaria de Relaciones Exteriores, the Secretaria de Medio Ambiente Recursos Naturales y Pesca, Mexico, and the Louisiana Department of Wildlife and Fisheries for permission to collect fish. This work was supported by National Science Foundation grant IBN9629318.

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