

Enhanced Female Brood Patch Size Stimulates Male Courtship in *Xiphophorus helleri*

KARI E. BENSON

Females often have traits that may be useful as indicators of their reproductive status. Female Green Swordtails (*Xiphophorus helleri*) have a brood patch, a darkened region on their abdomen that is largest prior to parturition. In this field experiment, female Green Swordtails either received a control treatment or their brood patch was augmented with tattoo ink. The females were released sequentially and the number of males approaching and courting each of these females was recorded. The number of males approaching females of the sham and augmented groups was indistinguishable, but significantly more males courted the females with augmented brood patches than the females of the sham group. Male responses to female indicators of reproductive status suggest that males may make evolutionarily important mating decisions due to either time or sperm limitation.

SEXUAL characteristics in both sexes can serve as signals (Darwin, 1859). Male secondary characteristics have been widely studied (see review, Andersson, 1994). Female sexual signals can also be useful and may serve to identify species or sex, facilitate female–female competition, allow females to avoid aggressive male behavior, or either increase or decrease male courtship (Cooper and Greenberg, 1992). These signals may function by indicating female characteristics (Cooper and Greenberg, 1992). Female signals of fecundity (Katvala and Kaitala, 2001), condition (Jawor et al., 2004), and/or receptivity (Greene and Mason, 2003; McLennan, 2005) are receiving increasing attention in the literature. Female characteristics serve as signals to males via many modalities (chemical, visual, behavioral, acoustic) in a wide variety of taxa, including insects (Alcock, 1995; Carazo et al., 2004; De Cock and Matthysen, 2005), spiders (Costa et al., 2000; Papke et al., 2001; Roberts and Uetz, 2005), fish (Rowland et al., 1991; McLennan, 1994; Berglund and Rosenqvist, 2001), amphibians (see review, Houck, 1988; Marco et al., 1998), reptiles (Cuadrado, 2000; Hager, 2001; Baird, 2004), birds (Montgomerie and Thornhill, 1989; Balsby and Dabelsteen, 2002; Griggio et al., 2005), and primates (Pagel, 1994; Kuester and Paul, 1996; Nunn, 1999). Here, I focus on male response to a visual character that varies with female condition in a fish.

Reproductive indicators in females can be evolutionarily maintained in several ways. Male choice can be an adaptive explanation for female signals if quality males are limiting (Johnstone et al., 1996). With such indicators, males can avoid wasting time and resources on non-receptive females (Ryker, 1994) or focus their courtship

on weaker females (Shine et al., 2005). When quality males are abundant, females may still benefit by signaling. Reproductive indicators may increase the females' sample size of suitors by inciting courtship from more males as shown theoretically (Real et al., 1996) and empirically (Balsby and Dabelsteen, 2002; Baird, 2004). They may also enhance the females' ability to select quality males by inciting male–male competition (Cox and Le Boeuf, 1977; Montgomerie and Thornhill, 1989) or more exaggerated courtship (Wiley and Poston, 1996; Watkins, 1997). Female characters may also be beneficial because females avoid the known risks of courtship when non-receptive (Verrell, 1991; Boness et al., 1995). Courtship can be costly, as has been shown through decreased survivorship (Cordts and Partridge, 1996; Watkins, 1997), increased risk of predation or parasitism (Magnhagen, 1991; Zuk and Kollura, 1998; Mougeot and Bretagnolle, 2000), harassment of females (Schlupp et al., 2001; Andrés et al., 2002; Dadda et al., 2005), and increased energetic costs (Halliday, 1987). The preceding benefits would have to outweigh the costs of the signal for evolutionary maintenance. I test whether Green Swordtail males (family Poeciliidae) respond to a visual female trait with increased courtship behavior.

Poeciliid fishes are live-bearers with internal fertilization, copulating using a modified anal fin, the gonopodium (Rosen, 1960). Females can retain sperm for up to eight months (Kallman, 1975; Turner and Snelson, 1984), thus mating with gravid females can provide fitness benefits to the male in the female's future broods. Females of many poeciliid species have visual or chemical traits that vary with reproductive condition. For example, the anal spot in some *Poecilia* spp. and some *Gambusia* spp. coincides with sexual re-

ceptivity (Peden, 1970; Farr and Travis, 1986), and males of some species have been found to respond more vigorously to females with more pronounced anal spots (Farr and Travis, 1986), including artificially enlarged spots on fish models (Peden, 1973). In some other species, males differentially respond to reproductive pheromones indicating receptivity (Brett and Grosse, 1982), sex identification (McLennan, 2004), or species identification (Crapon de Crapona and Ryan, 1990). Finally, many poeciliid females have a brood patch, alternatively referred to as a gravidity spot in certain species. When gravid, the brood patch is visible as the dark gonoduct is exposed through the lateral aspect of the abdomen due to a split in the peritoneum (Rosen, 1960). Larger or more embryos increase the size of the brood patch (Peden, 1973). The increased size of the brood patch coincides with changes in the female's shape, where the abdomen is increasingly distended with gravidity. A causal relationship between the female brood patch and male responsiveness has not been demonstrated. I tested whether male Green Swordtails respond to the size of the brood patch by altering the patch in females and recording male responses.

MATERIALS AND METHODS

Green Swordtails, *Xiphophorus helleri*, live in streams and lakes from central Mexico to southern Belize and Guatemala (Rosen, 1960). I conducted this experiment in May of 1997 at Laguna Azul, a small, clear impoundment at Los Tuxtlas Biological Station in the state of Veracruz, Mexico. The water temperature was 24 C, and the water clarity allowed visibility greater than five meters. The Green Swordtail, *Xiphophorus helleri*, was found primarily on a rocky bottom in the shallow end of the lake. *Xiphophorus helleri* males often approached females laterally. After approaching a female, males courted females following only 45% of approaches (pers. obs.). Green Swordtail courtship behavior is characterized by forward and backward swimming and sigmoid displays (Clark et al., 1954; Hemens, 1966; Farr, 1989). While adjacent to females, males were also observed to swing their gonopodium forward in an arc (pers. obs.). This behavior was characterized as gonopodial swinging. Gonopodial swinging is out of range of the gonopore, thus distinct from gonopodial thrusting.

I collected female Green Swordtails and selected subjects haphazardly from those collected. Each female was measured in a petri dish while covered with Stress Coat™. Female stan-

dard length, total length, and greatest body depth were measured using calipers. The female's existing brood patch was assigned a score (0—negligible, 1—intermediate, 2—prominent). An artificial brood patch was generated using a small amount of black tattoo ink and a hypodermic syringe. Black tattoo ink injected under the scales (approx. 0.05 ml, through a 28-gauge needle) on both sides of the female provided an enhanced brood patch, which would have been scored as "prominent," but within the natural range of variation. In preliminary laboratory tests, these marks faded in one to four weeks. Each female was either control (needle loaded with ink was inserted under the scales of the natural brood patch location and no ink was injected) or treated (brood patch was augmented by inserting the needle under the scales on each side and releasing a small amount of ink). Treatment assignments were alternated for consecutive trials.

I released each female individually after marking or control handling. Different release locations ensured that a large number of males were observed responding to the females. Approximately 1 m separated each release point from the previous release location. After each release, I snorkeled to observe male response to the female for 3 min. I recorded the number of times males approached the female (direct approach within 5 cm to the lateral aspect of the female) and the number of times that these approaches escalated to courtship behavior (continued courtship by one male was recorded as one instance). Each time a male approached a female was counted as one approach and was not recounted as long as the male remained within approximately 15 cm of the female. If a male that had approached a female proceeded to court a female as defined by sigmoid displays or front and back swimming, it was noted as one instance of courtship as long as the male remained in the female's proximity, even if the courtship behavior was not continuous. In cases where the subject female was lost during the three-minute interval (eight trials), the trial was excluded and repeated with a different female. Excluding those trials where the subject was lost, there were 21 three-minute trials (ten control, 11 augmented).

RESULTS

Female selection for the alternating treatments was haphazard, so I tested whether there were any systematic differences in either body size or natural brood patch score between treatments. The brood patch score was independent of the

treatment group (Chi-square contingency test: $\chi^2 = 2.39$, $P = 0.30$). Body size measurements in the two groups did not differ: standard length ($t = 1.25$, $P = 0.23$, $n = 21$), total length ($t = 0.91$, $P = 0.37$, $n = 21$), and body depth ($t = 0.01$, $P = 0.89$, $n = 21$).

Males actively responded to the females with the augmented brood patches. There was no difference in the number of approaches by males between females of the treated ($\bar{x} \pm 1SE = 8.6 \pm 3.85$) and the control ($\bar{x} \pm 1SE = 6.8 \pm 4.6$) groups (Wilcoxon rank sum test: $Z = -0.92$, $P = 0.36$). The treated females received significantly more courtship responses ($\bar{x} \pm 1SE = 3.9 \pm 4.1$) than did the control ($\bar{x} \pm 1SE = 0.1 \pm 0.31$) groups (Wilcoxon rank sum test: $Z = -2.94$, $P = 0.003$).

DISCUSSION

Males approached females from both treatment groups equally often. Thus, males apparently did not use the brood patch to discriminate between females until in close proximity. Males performed significantly more courtship solicitations to females with augmented brood patches than they did to females in the control group. The patch is clearly visible to the human observer from more than a meter away, but the males altered only their courtship response and not the rate at which they approached the females. It is possible that males evaluate the brood patch in conjunction with some other signals (such as chemicals). Males in other poeciliid species have been shown to respond to female chemicals (Brett and Grosse, 1982; McLennan and Ryan, 1997). Artificially augmented females, however, would not have had the appropriate chemical signals in conjunction with the visual signal. Thus, male response to these females appears to result from the visual trait itself.

Males may increase their fitness by vigorously courting females with high fecundity (Trexler et al., 1997). Males may be responding to the brood patch as a signal of fecundity or investment in offspring. Males that mate with large-patched females have selected females either with many offspring or with larger offspring (Peden, 1970), either of which may enhance male fitness. Males are not, however, selectively courting receptive females. Brood patch expression does not directly coincide with receptivity; receptivity lags temporally after the most prominent expression of the patch (Peden, 1970). Males of other taxa have been shown to alter their courtship rate to females depending on reproductive signalling; however, typically this signalling indicates receptivity. In multiply mated female poeciliids, there is a high degree of last male sperm precedence; though

several males can be represented, the last male to copulate with a female fertilizes most of the offspring in a brood, at least partially due to cryptic female choice (Constantz, 1984; Pitcher et al., 2003). The effect of precedence in the Sailfin Molly is magnified if the last male mates with the female at the peak of receptivity (Farr and Travis, 1986). In Sailfin Mollies, multiple paternity is more common in larger and more fecund females (Trexler et al., 1997).

It is not clear how the brood patch enhances female fitness; however, diminished expression may serve to deter harassment or courtship when sperm is least likely to be useful. The benefits may result from their ability to avoid harassment or courtship when sperm is least likely to be useful. That is, the benefit in harassment avoidance would accrue during the time where the brood patch is least prominent, when the female is least gravid. Harassment and courtship risks have been found to be costly in other poeciliids (Magurran and Seghars, 1994; Brewster and Houde, 2003; Dadda et al., 2005) and are suggested to be important in this species (Basolo, 2004). Alternatively, females may benefit by obtaining more information about the quality of available mates, either directly through increased courtship or by inciting male-male competition. Males compete vigorously in this species, and males have been shown to use similar traits for assessment in competition as females use to assess males (Benson and Basolo, 2006). Thus, competitively successful males would possess traits favored by females. Further, competitively successful males obtain increased mating opportunities (Morris et al., 1992). Although female Green Swordtails are known to be choosy (Basolo, 1990), the adaptive value of the brood patch trait may stem from some combination of female choice, male-male competition, and male choice.

Rather than considering which species might be choosy, it has been suggested that we might consider the relative availability of quality mates for either sex and the advantages to advertising to either sex in these conditions, rather than considering one sex as limiting and the other as competing (Berglund et al., 2005). Male choice may be important in either the origin or maintenance of the gravidity spot. Males have been shown to respond differentially to females based on another characteristic, size, in swordtails, guppies, and other livebearers (Bisazza, 1997; Basolo, 2004; Dosen and Montgomerie, 2004). However, male choice alone is not sufficient for selection on females (Itzkowitz et al., 1998). Alternatively, male coercion could be important; coercion is thought to be an impor-

tant facet of male reproductive success in another poeciliid (Bisazza et al., 2001). Coercion may play a role in *X. helleri*, but coercion is thought to be more important in poeciliids in which there are more sneak matings and limited or no courtship (Peden, 1972; Ptacek and Travis, 1998).

Presumably, females must benefit in some way, as this sort of trait is typically associated with costs. For example, colorful displays on female sticklebacks indicating receptivity may increase their visibility to predators (Rowland et al., 1991). Similarly, the brood patch may reduce the effects of counter-shading, thereby reducing crypticity (Ruxton et al., 2004). Breeding coloration is widespread across taxa, however the indicator in this species is unusual as it does not correspond with receptivity. Additional work in this species, or in similar taxa, using this or similar techniques can clarify the factors important in the origin and maintenance of this and other female traits.

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SCHOOL OF SCIENCES, LYNCHBURG COLLEGE, 1501 LAKESIDE DRIVE, LYNCHBURG, VIRGINIA 24501. E-mail: benson@lynchburg.edu. Submitted: 22 April 2005. Accepted: 9 Nov. 2006. Section editor: S. F. Fox.