Evolution, 58(3), 2004, pp. 665–669

CRYPTIC FEMALE PREFERENCE FOR COLORFUL MALES IN GUPPIES

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Abstract.—Cryptic female choice (CFC) refers to female-mediated processes occurring during or after copulation that result in biased sperm use in favor of preferred or compatible males. Despite recent empirical support for this hypothesis, evidence that CFC contributes towards the evolution of male body ornaments, in the same way that precopulatory female choice does, is currently lacking. Here, we tested the possibility that CFC selects for increased male attractiveness in the guppy *Poecilia reticulata*, a freshwater fish exhibiting internal fertilization. Specifically, we examined whether females are able to manipulate the number of sperm transferred or retained at copulation in favor of relatively attractive males. In support of this prediction, we found that following solicited copulations the number of sperm inseminated is influenced exclusively by the female's perception of relative male coloration, independent of any direct manipulation of males themselves. Because females prefer brightly colored males during precopulatory mate choice, our finding that colorful males are also favored as a consequence of enhanced insemination success indicates that cryptic female choice can reinforce precopulatory preferences for extravagant male ornaments.

Key words.—Cryptic female choice, male ornaments, *Poecilia reticulata*, postcopulatory sexual selection, sperm competition.

Received August 26, 2003. Accepted October 13, 2003.

In the majority of sexually reproducing species, sexual selection has the potential to continue beyond intromission (or spawning) in the form of sperm competition and cryptic female choice (Birkhead and Møller 1998; Birkhead and Pizzari 2002). Sperm competition is the postcopulatory equivalent of intrasexual sexual selection (male-male competition) and occurs when the ejaculates of two or more males compete for the fertilization of a given set of ova (Parker 1970). On the other hand, cryptic female choice (CFC) occurs when females themselves bias sperm use in favor of particular males (Thornhill 1983; Eberhard 1996), thus representing a subtle form of intersexual sexual selection. Despite intense interest in both of these processes (Birkhead and Møller 1998), the CFC hypothesis has received far less empirical support than sperm competition, and its importance in nature remains controversial (Telford and Jennions 1998; Birkhead and Pizzari 2002). This controversy arises partly from the debate over what exactly constitutes ''cryptic'' female choice (e.g., Eberhard 2000), especially since the term is frequently used interchangeably with ''postcopulatory female choice,'' which according to some definitions excludes female-mediated processes occurring during intromission (e.g., female control over sperm transfer). More problematic, however, is the fact that CFC is (by definition) a cryptic process and therefore not readily observed. Consequently, much of the evidence for CFC has been inferred indirectly (Eberhard 1996) with limited support derived explicitly from experimental studies (Birkhead and Pizzari 2002). Demonstrating directional CFC, where extravagant morphological (Miller and Pitnick 2002) or behavioral (Pizzari and Birkhead 2000) phenotypes are favored is especially problematic because such studies often require that the female's perception of male attractiveness is manipulated, without directly manipulating the males themselves (Pitnick and Brown 2000). Indeed, CFC can be influenced by male behavior (Edvardsson and Arnqvist 2000; Tallamy et al. 2002), and the direct manipulation of male traits makes it difficult to determine which sex ultimately influences sperm use and fertilization (see discussion by Birkhead and Pizzari 2002).

Our aim here is to determine whether females can manipulate the number of sperm transferred or retained at copulation in favor of what they perceive to be relatively attractive males. Like previous work (e.g., Andres and Rivera 2000; Eberhard 2000; Tallamy et al. 2002), we will use the term ''cryptic'' to include both copulatory (from the onset of copulation until sperm transfer is complete) and postcopulatory processes (e.g., sperm ejection). We focus on the guppy *Poecilia reticulata*, an internally fertilizing species of freshwater fish that exhibits a polyandrous, nonresource-based mating system (Houde 1997). During precopulatory mate choice, females prefer relatively colorful males exhibiting high rates of courtship. In particular, the area of carotenoid coloration (including orange, red, and yellow) consistently influences female mating decisions (Endler and Houde 1995; Houde 1997). Outside periods of female sexual receptivity, males have the potential to undermine precopulatory female choice using forced ''gonopodial thrusts'' (Pilastro and Bisazza 1999). Recent work reveals that phenotypically attractive males are more successful during sperm competition (Evans and Magurran 2001; Evans et al. 2003) and inseminate higher numbers of sperm than their less ornamented counterparts (Pilastro et al. 2002). Intriguingly, the latter study revealed that attractive males inseminated more sperm during solicited but not forced copulations, prompting us to suggest that females may influence the number of sperm inseminated in favor of phenotypically attractive males (Pilastro et al. 2002). The current study tests this hypothesis explicitly by determining whether the number of sperm transferred (or retained) during solicited copulations is influenced exclusively by the female's perception of male attractiveness, independent of any direct manipulation of the focal males themselves.

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METHODS

Mating Trials

Guppies were first-generation descendents of wild-caught fish from the Tacarigua River, Trinidad, and were maintained as previously described (Evans and Magurran 2001; Pilastro et al. 2002). We employed a paired experimental design in which individual (focal) males copulated with two virgin females (aged six months and matched for size), once in the preferred role and once in the nonpreferred role. During rearing, virgin females were isolated both physically and visually from males and were therefore naive with respect to male phenotypic variation in the study population. Prior to the mating trials, focal males were isolated from females for three days, which is sufficient for them to replenish their sperm reserves (see below).

In each of the initial mating trials we allowed a sexually receptive virgin female to observe a focal male and a stimulus male in a dichotomous mating chamber (Fig. 1a). Stimulus males were taken at random for each trial from either a drab ($n = 19$) or colorful ($n = 11$) stimulus group, according to the experimental treatment. Focal males had intermediate levels of body coloration with respect to the two stimulus groups (see Phenotype Measurements below) and would therefore have been perceived by females to be relatively attractive or unattractive according to the treatment. An opaque screen blocked visual access between the two males (see Fig 1a). Focal males were assigned at random to the left or the right sector of the tank and their position was reciprocated during the second test (see below). Following a 30-minutes settlement period, during which visual access into the male compartments was obscured, each female was initially allowed to observe the focal and stimulus males from a distance of 10 cm, which placed her in a ''neutral'' position from which she could assess both males concurrently (Fig. 1a). During this time the two males almost invariably remained close to their respective partitions, and were therefore in full view of the female. Although focal males did not actively court the female during this period, we nonetheless noted the time that they spent within two body lengths (total length, TL) of the partition. This allowed us to determine whether the behavior of individual focal males differed between the paired mating trials. Following the initial exposure period, the intermediate divider separating the female from the two males was raised, enabling the female to inspect the two males closely for three minutes, while preventing the two males from seeing each other throughout. During this short ''close-up'' period focal males engaged in courtship, and therefore in addition to noting the position of the focal males with respect to the partition, we also recorded their courtship behavior. Courtship by focal males was estimated as the number of (sigmoid) displays (Liley 1966) performed per min during the three-minutes close-up inspection and subsequently until the pair copulated. As an index of female preference, we noted the proportion of time that females spent within two body lengths (TL) of the focal male's chamber during the three-minutes close-up period. Behavioral observations were performed behind a black cloth ''blind.''

Following the two premating assessment periods, the opaque divider in front of the stimulus male's tank was lowered, thus preventing the focal male and the female from seeing the stimulus male during the mating trial. At this point, the focal male's partition was raised, allowing him to enter the mating arena and copulate once with the female. Copulations were considered successful only if they were followed by a series of postcopulatory jerks, which signal sperm transfer (Liley 1966). After noting the time (in minutes) for the pair to copulate a single time, the male was removed from the tank and the female was isolated (again without visual access to the stimulus male) in the main mating arena for 20 minutes. The female was then captured and anaesthetized in a water bath containing MS222 (ethyl 3-aminobenzoate methanesulfonate; Sigma-Aldrich, St. Louis, MO). Following established protocols, sperm were extracted from the female's gonoduct using a glass micropipette (Pilastro et al. 2002) and counted on an 'improved Neubauer chamber' haematocyto-

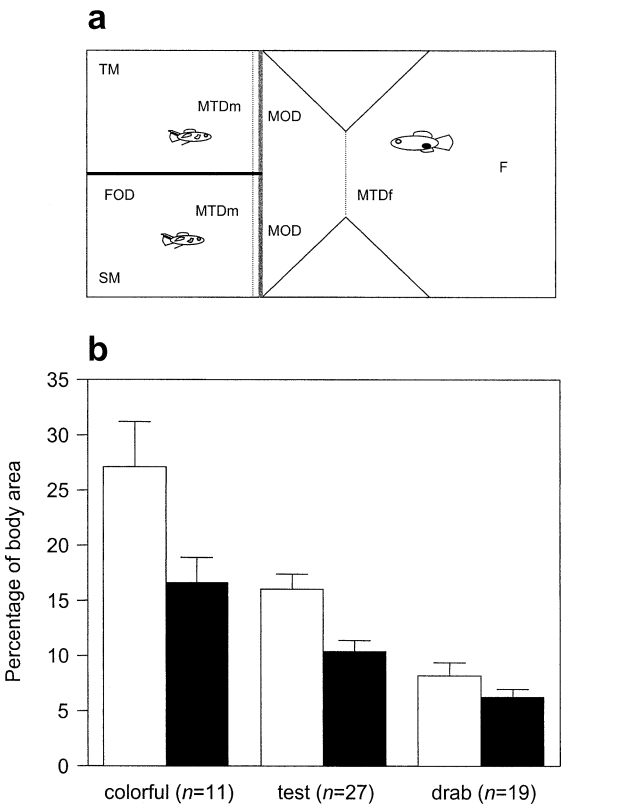

FIG. 1. Experimental conditions and comparison of male phenotype. The experimental tank (*a*) depicts the female (F) and the male (stimulus male, SM; test male, TM) sectors. A fixed opaque divider (FOD) prevented the two males from seeing each other. Mobile opaque (MOD) and transparent dividers (MTDm), which could be raised and lowered from a remote location, allowed the female to assess both males during the two premating assessment periods (see Methods). A narrow gap between the female and male sections, closed off by a mobile transparent divider (MTDf), ensured that during the initial 10-minutes assessment period the female was able to assess both males concurrently. As the focal male entered the mating arena (F), the stimulus male's MOD divider was lowered, preventing visual access into his compartment from the mating arena. The comparison of male phenotype (*b*) confirms that the focal males had intermediate mean (± SE) values of pigmented area (as a percentage of total body area) relative to the two stimulus groups (drab and colorful). Open bar, total pigmented spots; filled bar, carotenoid spots.

meter (Matthews et al. 1997). After participating in their first mating trial, focal males were isolated for a further three days to replenish their sperm reserves, before being tested again in the other treatment with a second virgin female (as above). In preliminary trials we found that the mean number of sperm stripped from males that had been manually stripped of sperm three days earlier ($5935 \times 10^3 \pm 549$ SE, $n = 50$) were not significantly different from the mean number of sperm stripped from rested males (i.e., that were not previously stripped) ($5211 \times 10^3 \pm 798$ SE, $n = 22$; t-test, $t_{70} = 0.75$, $P = 0.46$, after log-transformation, authors' unpubl. data). This indicates that focal males would have had fully replenished sperm reserves before participating in the mating trials. Furthermore, this result is in agreement with previous work showing that the number of sperm obtained from males that were stripped daily does not decline significantly over a 10-day period (Kuckuck and Greven 1997). We performed 27 paired trials ($n = 54$ mating trials) in which the order of presentation of focal males was randomized (focal males copulated first in the preferred role in 14 trials, and first in the nonpreferred role in 13 trials). Sperm extractions of a subsample of the paired trials ($n = 6$ pairs, $n = 12$ extractions) and all sperm counts were done blind of the experimental group.

Phenotype Measurements

After participating in the two (paired) mating trials, focal males were anaesthetized and photographed using a digital camera. Image analysis software (Scion Corporation, available at http://www.scioncorp.com) was used to measure male standard length and analyze body coloration of focal and stimulus males. Three components of these patterns were considered: (1) the area of carotenoid pigmentation (including orange, red and yellow), (2) melanistic black spots, and (3) the iridescent structural colors, which include blue and green. The group of focal males comprised individuals with intermediate levels of color pigmentation (carotenoid and total pigmented area) with respect to the two stimulus groups (proportion of carotenoid spots: ANOVA: $F_{2,54} = 12.92$, $P < 0.0001$, proportion of total pigmented area: $F_{2,54} = 20.63$, $P < 0.0001$, arcsine transformation; all groups significantly different at $P < 0.05$, Tukey post hoc test; Fig. 1b).

RESULTS

Our results revealed that focal males inseminated significantly more sperm when they were paired with relatively drab stimulus males (mean ejaculate size = $1521.3 \times 10^3 \pm 188.4$ SE) than with relatively attractive males ($905.5 \times 10^3 \pm 159.5$ SE; paired t-test, $t_{26} = 3.50$, $P = 0.0017$; Fig. 2). Similar results were obtained when considering only the trials in which sperm extractions were performed blind of the experimental group (preferred role, mean ejaculate size = $1376.4 \times 10^3 \pm 160.2$ SE; nonpreferred role, mean ejaculate size = $534.4 \times 10^3 \pm 170.3$ SE; Wilcoxon signed ranks test: $z = 2.20$, $P = 0.03$, $n = 6$). There was no effect of the order of presentation on ejaculate size (repeated-measures ANOVA: stimulus male phenotype: $F_{1,25} = 12.87$, $P = 0.0014$; order of presentation: $F_{1,25} = 0.05$, $P = 0.83$; interaction: $F_{1,25} = 1.66$, $P = 0.21$). The difference in the number of sperm inseminated by the test male under the two conditions (preferred minus nonpreferred) was positively correlated with the difference in the extension of colored body area between the two stimulus males ($r = 0.39$, $P = 0.048$, $n = 27$), indicating that the greater the difference between the phenotype of the test males and the stimulus males, the greater the difference in the test male's insemination success between the two conditions.

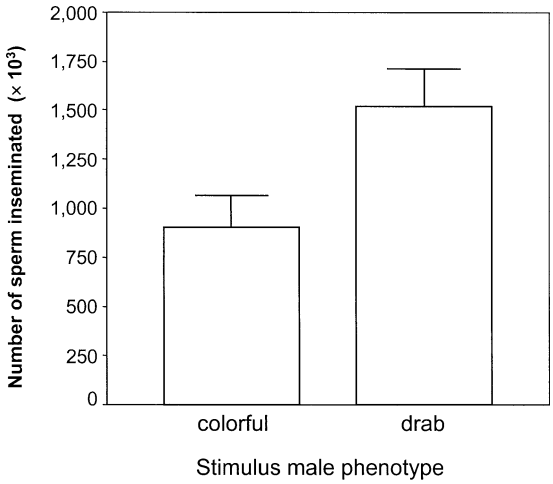

FIG. 2. The mean number of sperm (± SE) delivered by individual male guppies (focal males, $n = 27$) during solicited copulations is compared between treatments: colorful (where stimulus males are relatively attractive) and drab (where stimulus males are less colorful).

Behavioral data recorded during the premating assessment periods (Table 1) revealed that focal males did not differ significantly between treatments in the time spent close to the partition (Wilcoxon signed ranks test: $z = 0.92$, $P = 0.38$, $n = 27$). Furthermore, there was no effect of treatment on the rate of male courtship, estimated as the number of sigmoid displays per minute during the three-minutes close-up period and subsequently until copulation occurred (see Mating Trials, Wilcoxon signed ranks test: $z = 0.03$, $P = 0.99$, $n = 23$). Where focal males copulated within 10 seconds of the start of a trial ($n = 4$), observations were excluded from the analysis of male courtship to avoid spurious estimates of behavior (the inclusion of these trials did not result in significant differences in mating behavior between the two treatments). The time taken for pairs to copulate tended to be shorter when the focal male mated in the preferred role (Table 1), although this difference was not statistically significant (paired t-test: $t_{26} = 1.55$, $P = 0.13$, log-transformation). The 95% confidence limits for the two means (preferred role: 0.1–9.2 min, range = 9.1 min; nonpreferred role: 2.7–11.2 min, range = 8.5 min) had two largely overlapping distributions and were much larger than the observed difference between the two means (2.27 min), suggesting that the observed difference of time to copulate between treatments was biologically nonsignificant (Colegrave and Ruxton 2003). A similar figure is obtained using the log-transformed data (95% confidence limits for the mean: preferred role, 0.63–1.43, range = 0.80 min; nonpreferred role, 0.96–1.86 min, range = 0.90 min; difference between the means = 0.38). Taken together,

TABLE 1. Male and female behavior during the assessment and mating periods.

	Colorful stimulus (mean ± SD, $n = 27$)	Drab stimulus (mean ± SD, $n = 27$)
Assessment period		
Female—proportion of time within two body lengths from the MTDf divider (Fig. 1a)[1]	0.517 ± 0.266	0.566 ± 0.233
Female—proportion of time in front of the focal male[2]	0.421 ± 0.398	0.508 ± 0.357
Male—proportion of time within two body lengths from the divider[3]	0.952 ± 0.100	0.909 ± 0.210
Mating trials		
Male—sigmoid display rate (displays min^{-1})[4]	2.23 ± 2.47	2.89 ± 3.62
Time to mating (min)	6.94 ± 10.70	4.67 ± 11.43

[1] Calculated over the first 10 min of the assessment period (see Methods; paired *t*-test, $t_{26} = 0.74$, $P = 0.47$).
[2] Calculated as the proportion of time close to the mobile transparent divider (MTDm, Fig. 1a) in front of the focal male compartment (TM) over three min after the first 10 min of assessment (paired *t*-test, $t_{26} = 1.02$, $P = 0.32$).
[3] Over both premating assessment periods (13 min).
[4] Calculated only for the cases in which mating time was greater than 10 sec ($n = 23$).

these results indicate that the behavior of individual males was not influenced by the treatment.

DISCUSSION

The results from this experiment provide support for the hypothesis that cryptic female choice has the potential to contribute towards the evolution of male ornaments by reinforcing precopulatory female mating preferences. The color components measured in this study, and in particular the area of carotenoid pigmentation, consistently predict female mating preferences in guppies (Endler and Houde 1995; Houde 1997), including the population chosen for this study (authors' unpubl. data). On average, males inseminated 68% more sperm when they were perceived to be relatively attractive, a finding that cannot be explained by male identity because individual focal males were tested under both conditions (without direct manipulation). Recent evidence from guppies confirms that highly ornamented males are more successful than their drab counterparts during sperm competition when ejaculate size is experimentally controlled using artificial insemination (Evans et al. 2003). Our present finding that females influence the number of sperm transferred in favor of relatively attractive males suggests that cryptic female choice may refine this fertilization bias in favor of colorful males. Taken together, these studies highlight the importance of both male and female roles during postcopulatory sexual selection.

Importantly, our experimental design avoided the direct manipulation of male phenotype (e.g., through the use of dyes or artificial ornaments). We employed this design because direct manipulation may have had an unpredictable effect on the ability (or willingness) of males to inseminate females (Birkhead 2000; Pitnick and Brown 2000; Birkhead and Pizzari 2002), or influenced the handling of sperm by females as a consequence of the interaction between male and female behaviors (Edvardsson and Arnqvist 2000). Indeed, we were careful to ensure that the focal males were unaware of their test status, and thus did not perceive themselves to be relatively attractive or unattractive with respect to the stimulus males. Our behavioral data supported this view by confirming that male behavior (display intensity and the time spent close to the partition) was not affected by treatment. Nonetheless, we cannot entirely rule out the possibility that males allocated fewer sperm when they perceived that females were less willing to copulate with them. Such an influence on the male's insemination strategy would still constitute an important female-mediated effect as it would depend exclusively on the perception of relative male quality rather than the male's identity per se.

In a recent review, Birkhead and Pizzari (2002) suggest that CFC is more likely to evolve when mate choice is costly, or when the success of coupling depends not only on male phenotype, but also on genetic compatibility or similarity. According to this view, females rely on postcopulatory sexual selection to ensure against infertility, temporary sperm depletion, genetic incompatibility, or genetic similarity (Jennions and Petrie 2000; Evans and Magurran 2000; Tregenza and Wedell 2002; Blomqvist et al. 2002). Even in the absence of such effects, however, CFC may evolve in species where females encounter males sequentially (as in guppies) rather than simultaneously (as in lekking birds). Thus, it may pay females to accept even a little sperm from unattractive males if there is a risk of not encountering a more attractive male during their short periods of sexual receptivity (Houde 1997). An interesting direction for future work is to determine whether costs associated with precopulatory mate choice differ among populations (Endler and Houde 1995) and are correlated with the strength of postcopulatory female preferences.

A question resulting from our study is how females influence the insemination success of particular males. One possibility is that they selectively eject part of the ejaculate when they perceive that males are relatively unattractive (Pizzari and Birkhead 2000). Alternatively, they may influence the number of sperm inseminated, for example by manipulating the duration of copulation (Andres and Rivera 2000; Elgar et al. 2000). Notwithstanding the mechanisms underlying female control of sperm transfer or retention, which remain to be investigated, the current study clearly demonstrates that cryptic female preferences can be directed towards male characters that function in precopulatory sexual selection, and complement recent evidence from the feral fowl *Gallus gallus domesticus* (Pizzari and Birkhead 2000) in which females differentially retain the sperm from subdominant and dominant males. At even more cryptic levels of sexual selection, recent evidence from *Drosophila* reveals that male fertiliza-

tion success depends on the interaction between sperm length and female tract morphology, and thus that CFC can select for elongated sperm tails, the postcopulatory equivalent of exaggerated sexually selected male ornaments (Miller and Pitnick 2002). Collectively, these studies highlight the important role that females play in influencing the fertilization dynamics of particular males.

Acknowledgments

We thank T. Birkhead, R. Brooks, W. Brown, S. Griffith, J. Kelley, S. Pitnick, T. Pizzari, and an anonymous referee for comments on an earlier draft of the manuscript, and M. Dadda and C. Gasparini for their help with the trials. This work was supported by a Marie Curie Independent Fellowship to JPE (contract no. HPMF-CT-2000-00479), and grants from the Italian Research Ministry (Cofin2001 and Cofin2003) and Institutional Research Grants from the University of Padova to AP and AB (ex60% 2000–3).

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