Original Article

Concurrent effects of sperm competition and female quality on male mate choice in the Trinidadian guppy (Poecilia reticulata)

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Males are generally expected to be discriminating in their choice of mates when females vary in quality and when under sperm competition from rival males. However, how sperm competition and female quality interact to influence male mating decisions remains poorly understood. Here, we explored the concurrent effects of sperm competition and female body length on male mating decisions in the Trinidadian guppy (Poecilia reticulata) as a model system. We used female body length as a proxy for fecundity and manipulated the relative size difference of paired stimulus females concurrently with sociosexual cues (i.e., presence of rival males) that may predict sperm competition. When all else was equal, males preferred the larger female when the paired females differed considerably in body length. The presence of either 1 or 2 rival males near, and sexually interacting with, the initially preferred female reduced a focal male’s preference for that female and increased the probability that he would reverse his initial mate preference. However, focal males were more likely to reverse their initial preference when the females were similar in body length than when they differed considerably in body length after observing initially preferred females interacting with 1 rival male. Our novel results suggest that male guppies simultaneously evaluate sperm competition and female quality when making mating decisions.

Key words: body size, male mate choice, mate quality, sexual selection, social information, sperm competition.

INTRODUCTION

Although male mate choice has been documented in several taxa (Andersson 1994; Bonduriansky 2001), its evolutionary dynamics remain relatively poorly understood. Recent population genetic models of male and mutual mate choice predict that male mating preference can spread in a population if the preference is for a female phenotypic trait that indicates high fertility or viability (Servedio and Lande 2006). One such trait is female body size, as a correlate of fecundity (Andersson 1994; Galvani and Johnstone 1998; Reinhold et al. 2002). Because a male’s reproductive success can be increased by mating with a female with more fertilizable eggs (Andersson 1994), males often prefer to mate with larger more fecund females (e.g., Bisazza et al. 1989; Olsson 1993; Andersson 1994; Ptacek and Travis 1997; Basolo 2004; Hoyvak and Godin 2007) and may strategically transfer more sperm to them (Kelly and Jennions 2011). However, owing to sperm competition in particular (Simmons 2001; Wedell et al. 2002; Parker and Pizzari 2010), a female’s fecundity may not be the only factor determining how many eggs a male fertilizes. Therefore, male mating decisions may be more complicated than simply choosing a female based on a single trait.

A male’s social environment can potentially provide additional information on the reproductive value of females and influence his choice of mates (Danchin et al. 2004; Dall et al. 2005). Of particular interest here is the use of social information (sensu Danchin et al. 2004) by males in both assessing the local level of sperm competition and making mating decisions. Sperm competition could potentially lower the number of eggs a male fertilizes because he will have to compete with the sperm of one or more other males for a given set of ova (Simmons 2001; Wedell et al. 2002; Parker and Pizzari 2010).

As predicted by sperm competition theory (Simmons 2001; Parker and Pizzari 2010), males from diverse taxa have been shown to increase their ejaculate size in response to an increased probability that their sperm will compete against the sperm of another male (sperm competition risk; Kelly and Jennions 2011) but tend to decrease their ejaculate size in response to increasing numbers of competing males (sperm competition intensity), at least in some taxa studied to date (Kelly and Jennions 2011). Moreover, several studies have also reported that males adjust their mating preferences when they are observed by another male (an “audience,” sensu McGregor and Peake 2000) and discriminate against females they have recently observed in the mere presence of sexually interacting or mating with rival males (e.g., Schwagner and Parker 1990; Fuller 1998; White and Galef 1999; Simmons 2001; Dosen and Montgomerie 2004b; Plath et al. 2008; Wong and McCarthy 2009; Ziege et al. 2009; Bierbach et al. 2011; Jeswiet et al. 2011). Taken together, these results suggest that males are sensitive to sociosexual cues that predict sperm competition risk or intensity at a given mating and adjust their behavior accordingly to minimize sperm competition and maximize their reproductive success.

In polyandrous and polygynandrous mating systems, there may often be an interaction between sperm competition and female fecundity. Larger more fecund females can have more mates than smaller less fecund ones in some taxa (e.g., Trexler et al. 1997; Becher and Magurran 2004; Herdman et al. 2004; Avise and Liu 2011), and males tend to allocate...
more sperm to more fecund females (Kelly and Jennions 2011). Nevertheless, despite receiving more sperm on average, more fecund females could still have a higher ratio of fertilizable eggs to sperm in their reproductive tract (Reinhold et al. 2002). In this case, a male may still benefit from mating with a more fecund mated female compared with a less fecund unmated female, up to a point. Therefore, if a male can simultaneously assess a female’s current fecundity, using information that he has personally gathered, and immediate sperm competition, using social information, his mate-choice decision ought to reflect a trade-off between these 2 correlates of female reproductive value. However, this largely depends on how males integrate personal (asocial) and social information when making mating decisions (Dall et al. 2005).

Here, we investigated the concurrent potential effects of sperm competition and female fecundity on male mating behavior using the Trinidadian guppy (Poecilia reticulata) as a model system. The guppy is a shoaling, internal fertilizing, Poecilia reticulata sperm competition and female fecundity on male mating behavior when making mating decisions (Dall et al. 2005).

We conducted the current study using wild adult guppies collected haphazardly by hand seining from a high-predation site in the Quare River, Trinidad, West Indies (lat 10°11’51"W) in May 2009 and May 2010. The fish were held in mixed-sex aquaria in the laboratory (see Supplementary Data) until used in the experiment. Our study population has a female-biased sex ratio (Godin 1995), adult females vary widely in body length and fecundity (Kelly et al. 1999; Herdman et al. 2004), and most (60–100%) adult females have broods that are multiply sired, with the number of sires per brood ranging from 1 to 9 (Kelly et al. 1999; Neff et al. 2008). Therefore, males in this population experience high levels of both mating and sperm competition.

**Experimental design**

Using the general protocol described below, we carried out a 3 × 2 factorial experiment testing for the concurrent effects of 2 main factors and their interaction, namely, the number of rival males present (0, 1, or 2) and the relative body length (matched or considerably different) of 2 adult stimulus females on male mating preferences. The 6 treatment combinations were carried out in random order, and each treatment combination was replicated with different focal males. The focal and rival males were matched for standard body length and body coloration (see Supplementary Data). To titrate the effect of the relative body length (= potential fecundity) of paired stimulus females, individual males were given a choice between 2 females that were either matched for body length (size difference: 0.60 ± 0.05 mm, range = 0–1; or 2.8 ± 2.0%, range = 0–5.9, n = 66) or considerably different in body length (size difference: 5.62 ± 0.06 mm, range = 4.5–6.5; or 28.5 ± 0.4%, range = 20.9–38.2, n = 95). We attempted to control for the reproductive state of paired females by visually matching the distention of their abdomen, taken as a measure of their stage of pregnancy (cf. Houde 1997). To ensure that male mate choice would not be confounded by female responses to male sexual activity, we used gravid adult females (cf. Dosen and Montgomery 2004b; Jeswiet and Godin 2011; Jeswiet et al. 2011), which are relatively unresponsive to male courtship attempts (Houde 1997).

**Experimental apparatus**

The experimental apparatus consisted of a test aquarium (40 × 20 × 25 cm; L × W × H), flanked by a clear Plexiglas container (15 × 20 × 22 cm) at either end (see Supplementary Figure S1). The central aquarium held the focal male, and vertical lines drawn on the front and back walls demarcated a 10-cm wide male mating preference zone near each of the end compartments. The 2 end compartments held the stimulus fish (1 female and either 0, 1 or 2 rival males each, depending on the treatment).

**General protocol**

The day before a trial, males were isolated into all-male pools, and small (17–22 mm, standard length) and large (23–30 mm) stimulus females were placed into separate holding aquaria without males.

Individual focal males were repeatedly tested for their mating preference in 2 consecutive tests. The general protocol for each trial consisted sequentially of a 10-min acclimatization period and an initial preference test (Preference Test 1) followed immediately by a second preference test (Preference Test 2), in which an elevated level of sperm competition was simulated. At the beginning of a trial, the focal male was introduced into the central test aquarium, and one female was randomly placed in each of the 2 end compartments. The fish were allowed to swim freely for a 10-min acclimation period during which the females were blocked from the male’s view by opaque partitions. At the start of Preference Test 1, the focal male was placed in a clear Plexiglas tube in the center.
of the test aquarium and allowed to view the stimulus females in their respective end compartments for 15 min. The focal male was then released for a 15-min dichotomous choice test, during which his initial mating preference was recorded as the amount of time he spent in the preference zone adjacent to and facing (0° ± 90°) each stimulus female. This is a common measure of male mating preference in poeciliid fishes (e.g., Bisazza et al. 1989; Dosen and Montgomerie 2004b; Hoyosak and Godin 2007; Plath et al. 2008; Wong and McCarthy 2009; Ziege et al. 2009; Bierbach et al. 2011), and we previously validated that male association time with females predicts male mating preference in the guppy (Jeswiet and Godin 2011). Preference Test 2 was identical to Preference Test 1, with the exception of the viewing period during which either 0, 1 or 2 rival males were placed in the compartment of the particular female that the focal male had preferred in Preference Test 1 (i.e., had spent more than 50% of his total preference time associating with). The rival male(s) and female were thus able to freely interact physically with each other (i.e., the rival male(s) would pursue, court, and attempt copulations with the stimulus female). The rival males were then removed before the onset of the Preference Test 2 dichotomous choice test using a small dip net. We controlled for the effect of this disturbance by also similarly disturbing the paired female’s compartment with the same dip net. This procedure simulated an elevated apparent level of sperm competition associated with the initially preferred female relative to the other female using rival male numbers that correspond to the number of male guppies observed simultaneously pursuing any free-ranging female in the Quaré River (Jeswiet et al. 2011). A trial was discarded if either the focal male did not sample both preference zones in Preference Test 1, one of the stimulus females did not resume normal swimming, or the focal male appeared distressed or unhealthy. A total of 27 of 188 trials were excluded.

Each trial tested a different focal male (n = 161), and stimulus females (n = 322) were not reused. Due to the large number of fish required, some of the focal males were used in subsequent trials as rival males. These males were only used as rivals at least 2 days after they had been tested as a focal male and were never used more than once as a rival male. Twenty-nine of the 95 males tested in the treatment combinations with females that differed in body length by 28.5% on average preferred the smaller of the paired stimulus females. The rival males were then removed before the onset of the Preference Test 2 dichotomous choice test using a small dip net. We controlled for the effect of this disturbance by also similarly disturbing the paired female’s compartment with the same dip net. This procedure simulated an elevated apparent level of sperm competition associated with the initially preferred female relative to the other female using rival male numbers that correspond to the number of male guppies observed simultaneously pursuing any free-ranging female in the Quaré River (Jeswiet et al. 2011).

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Statistical analyses

To determine whether males initially preferred larger females overall, we analyzed the data from Preference Test 1 (in which rival males were not present) for all 6 treatments combined. Following Jeswiet et al. (2011), we calculated a preference score for each trial as a measure of male mating preference for the larger female (preference score [%] = [association time with the larger female/total time associating with both females] × 100). Because observed preference scores were not normally distributed, they were normalized using the arcsine transformation before analysis. Sixteen of the paired females were excluded from this analysis because they were exactly the same length.

To ascertain whether males were consistent in their expressed mating preference between the paired preference tests in the absence of rival males, we calculated the repeatability of their mating preference scores across Preference Tests 1 and 2 for the control trials (no rival male present) using the single classification Model II ANOVA, following Lessells and Boag (1987). In this analysis, the (arcSin-transformed) percentage of time individual focal males spent with the initially preferred female was the dependent variable, and male identity number was the between-subjects factor. We obtained separate estimates of repeatability for control trials in which the paired females were matched for body length and for trials in which the paired females differed considerably in length. Standard errors (SEs) for the repeatability estimates were calculated following Becker (1984).

We used separately a general linear model and a binary logistic regression model (Quinn and Keough 2002) to test for the main treatment effects of apparent sperm competition and female body size difference on male mating preference and mate-choice reversal, respectively, and their interactions. In the general linear model, the response variable was a preference difference score (preference difference score [%] = percentage of time spent near the initially preferred female in Preference Test 2 − percentage of time spent near the initially preferred female in Preference Test 1), following Jeswiet et al. (2011). A negative value denotes a reduction in the amount of time that a focal male spent with the initially preferred female in Preference Test 2. The preference difference scores were normally distributed in all of the treatment combinations (Shapiro–Wilks tests, all P > 0.05) except one, and the variances were homogeneous (Levene’s test, F2,129 = 1.092, P = 0.359). Arcsin transformation did not improve normality and actually reduced the model’s fit to the data. Therefore, there was no need to transform the response variable for the general linear model analysis (cf. Quinn and Keough 2002). The number of rival males was the fixed factor, and relative female size difference (%) (=[length of larger female − length of smaller female]/length of smaller female) × 100) was included as a covariate. In the binary logistic regression model, the dichotomous response variable was whether or not a focal male reversed his initial mating preference in Preference Test 2 (coded as Reversal = 1, No reversal = 0). Preference for a particular female was defined as a male spending more than 50% of his total preference time associating with her. Relative female size difference was treated as a continuous predictor variable. The number of rival males present was treated as a categorical predictor variable (1, 2), with the control treatment (0 rival male) selected as the reference category.

All descriptive statistics are reported as the mean ± SE (range, n). Analyses were carried out using SPSS v.18.

RESULTS

Male nonrandom choice behavior

Focal males actively sampled and chose between the 2 stimulus females in both Preference Test 1 and Preference Test 2. Overall, males (n = 132) spent on average 676.9 ± 14.3 s (87–883 s) in the preference zones during Preference Test 1 and 585.9 ± 17.7 s (143–896 s) during Preference Test 2; these values are both significantly greater than the time the males spent in the central neutral zone in each of the 2 preference tests (Wilcoxon signed-rank test: Z = −9.03, P < 0.001 and Z = −6.367, P < 0.001, respectively).
Male mating preferences based on female body length and their repeatability

In the absence of any rival male nearby (Preference Test 1 across all treatments), male guppies exhibited on average a significant preference (preference score = 61.3 ± 2.7%) for the larger of the paired stimulus females when the females differed considerably in body length (paired t-test, \( t_{14} = 4.99 \), \( P < 0.001 \)). In comparison, male guppies did not exhibit a preference (preference score = 50.3 ± 2.7%) for the larger of the paired stimulus females when the females were matched in body length (paired t-test, \( t_{40} = 0.004 \), \( P = 0.997 \)). The magnitude of a male’s preference for the larger female was positively correlated to the relative size difference of the paired females presented (linear regression: \( r^2 = 0.041 \), \( F_{1,143} = 6.070 \), \( P = 0.015 \)). However, there was considerable internmale variation in mating preference scores not explained by the difference in the body length of the paired stimulus females.

In the control treatment (0 rival male nearby), focal males were significantly consistent in their mating preference for the larger female between Preference Test 1 and Test 2 when the paired females differed considerably in body length (repeatability \( R = 0.421 \pm 0.180 \), \( F_{21,22} = 2.45 \), \( P = 0.021 \)). In comparison, when paired females were similar in body length, male mating preference strengths were not repeatable between the 2 preference tests (\( R = 0.098 \pm 0.228 \), \( F_{21,22} = 1.22 \), \( P = 0.325 \)), but the direction of their preference was consistent (nonrandom), as 19 of the 22 males preferred the same female between the 2 preference tests (Binomial test, \( P = 0.001 \)).

Male mating preferences in relation to sperm competition and female body length

Focal males significantly reduced their initial preference for a particular female after observing physical sexual interactions between her and rival males (general linear model, \( F_{2,126} = 3.379 \), \( P = 0.037 \); Figure 1a). However, the preference difference scores of males were not affected overall by the relative difference in the body length of the paired females (\( F_{1,126} = 0.872 \), \( P = 0.35 \); Figure 1a) nor was there a significant interaction between the 2 main treatment effects (\( F_{1,126} = 0.865 \), \( P = 0.42 \); Figure 1a). Nonetheless, focal males that had observed their initially preferred female interact sexually with 1 rival male subsequently exhibited a smaller reduction in their initial mating preference, as the relative size difference between the paired females increased (Figure 1a).

To complement the general linear model analysis, we also performed a binary logistic regression analysis on the frequency of mate-choice reversals. Reinforcing the above results, when a focal male had recently observed his initially preferred female interact sexually with either 1 or 2 rival males, he was significantly more likely to subsequently reverse his mating preference and to prefer the other female not seen near a rival male (Table 1, Figure 1b) compared with focal male behavior in the control treatment combinations (no rival male present). The probability of mate-choice reversal was higher overall when the number of rival males was greatest (i.e., 2 rival males vs. 1 rival male present; Figure 1b). However, the number of observed mate-choice reversals did not differ significantly between the 1 and 2 rival male treatment combinations when the paired stimulus females were matched in length (G-test: \( G_1 = 0.996 \), \( P = 0.76 \)) but tended to be greater in the 2 rival male treatment combinations when the paired females differed considerably in length (\( G_1 = 3.44 \), \( P = 0.064 \)).

In the binary logistic regression model, the relative size difference of paired females did not significantly affect the probability of a male reversing his initial mating preference (Table 1). However, there was a significant interaction between the main effects of relative female size difference and rival males in the treatment combinations with 1 rival male present (Table 1, Figure 1b). That is, focal males were less likely to reverse their initial mating preference when paired stimulus females differed considerably in body length than when they were similar in length in situations where 1 rival male was present compared with situations when rival males were absent (Table 1, Figure 1b). No such significant interaction occurred when 2 rival males were present.

**Figure 1**  
Mean (±SE) mating preference difference scores (a) and probability of reversal of initial mating preferences (b) of focal males after they had observed physical sexual interactions between their initially preferred female and either 0 (triangles, solid line), 1 (circles, dashed line) or 2 (diamonds, dotted line) rival males in relation to the mean (±SE) relative difference in the body length of paired stimulus females presented as potential mates. The fitted lines depicted were obtained from a general linear model (a) and a binary logistic regression model (b), respectively. Where SEs overlap, only the upper or lower error bars are shown.

**DISCUSSION**

The current study demonstrated that wild-caught male Trinidadian guppies were able to differentiate between 2 simultaneously presented stimulus females that differed in body length by approximately 29% on average and preferentially and consistently associated with the larger (and presumably more fecund) female. Preferring large females appears to be adaptive, as larger female guppies are more fecund (Reznick and Endler 1982) and mating with a larger more fecund female could increase the reproductive success of a male when...
everything else is equal (Andersson 1994). As noted above, a preference by males to mate with larger more fecund females is widespread taxonomically (e.g., Bisazza et al. 1989; Olsson 1993; Andersson 1994; Puucek and Travis 1997; Basolo 2004; Hoyos and Godin 2007; Avise and Liu 2011). When paired females were similar in body length (≤1 mm difference), male guppies still showed an initial preference for one or the other female, irrespective of the absolute length of the preferred female. However, although males were consistent in their preference for a particular female between the 2 consecutive preference tests, the strength of their preference was not. These results corroborate previous studies showing that male guppies prefer the larger female when given a choice between 2 females of unequal body length (Dosen and Montgomery 2004a; Herdman et al. 2004).

In addition, our results showed that male guppies can use sociosexual cues to assess the apparent sperm competition associated with a particular female and tended to avoid females with the relatively higher apparent level of sperm competition. Consistent with the results of previous studies using poeciliid fish (e.g., Dosen and Montgomery 2004b; Plath et al. 2008; Wong and McCarthy 2009; Ziege et al. 2009; Jeswiet et al. 2011) and other taxa (e.g., Schwagmeyer and Parker 1990; White and Galef 1999), male guppies here tended to reduce their preference for females they had recently observed interacting with rival males and instead chose to associate with the other female that they had observed alone. Females in our study population (Quaré River) are often pursued by 1 or 2 males (Jeswiet et al. 2011), which may signal to other nearby males watching such sexual interactions that the pursued female has recently mated or is about to mate. Here, we showed that male guppies from this population can use the presence of 1 or 2 rival males in close proximity to, and sexually interacting with, a female as a predictor of sperm competition and prudently reduce their preference for these females. However, for polyandrous and polygynandrous species with internal fertilization, such as the guppy, it is difficult to know whether such sociosexual cues are used by males as a reliable predictor of sperm competition risk or intensity because having information on the number of rival males interacting with a female is not necessarily the same as knowing exactly how many competing ejaculates exist (cf. Engqvist and Reinhold 2005). Interestingly, increasing the number of rival males from 1 to 2 in the current study did not appear to significantly affect the mate-choice behavior of focal males when females were matched for body length (i.e., fecundity). We expected that the tendency for males to avoid females that they had observed sexually interacting with rival males would be greater when the number of rival males was increased from 1 to 2, regardless of whether the increase indicated an elevated sperm competition risk or intensity. Contrary to our expectation, when the paired females were matched for body length, the magnitude of the reduction in preference and the probability of a male reversing his mating preference were similar after he had observed his initially preferred female interacting with either 1 or 2 rival males. This suggests that the focal males estimated the probability of competing with all other males to be low and that adding a second rival male in our experiment represented too small of an increase in either sperm competition risk or intensity to influence the focal male’s mating behavior when differences in female body length were negligible.

In the current study, male guppies appeared to have incorporated both the information they personally gathered on a female’s fecundity (presumably via the correlate of body length) and social information predicting sperm competition in making their mating decisions. For the treatment combinations wherein the focal male observed his initially preferred female interacting with 1 rival male, there was a strong trend for focal males to show a greater reduction in their preference and a higher probability of mate-choice reversal when the paired females were matched in body length compared with when they differed considerably in body length. Therefore, when females differed considerably in size, males were consistent and maintained their preference for larger females despite social information indicating a higher level of sperm competition associated with that particular female. However, when the number of rival males was increased to 2, the decrease in mate preference and the likelihood of mate-choice reversal were insensitive to the difference in the body length of the paired females. As discussed above, it is unknown whether the focal males associated 2 rival males with a higher sperm competition risk or intensity compared with 1 rival male. In either case, the cost of mating with a female previously seen interacting sexually with 2 rival males may have outweighed the potential benefit of mating with a larger female. Therefore, it appears that male guppies in the current study concurrently evaluated female fecundity (= body length) and sperm competition and accepted the potential cost of sperm competition when choosing to mate with the larger more fecund female until the risk or intensity of sperm competition became too high.

An interesting direction for future research would be to investigate additional cues, such as chemical cues or pheromones (Thomas 2011), that may be perceived by males as reliable predictors of sperm competition on their mating preferences. Female-borne chemical cues indicating a female’s mating status (virgin vs. mated) may more reliably predict sperm competition than sociosexual cues and may interact with, and potentially override, the latter in influencing male mate-choice decisions.

### Table 1

Results of the binary logistic regression analysis on the number of males that reversed their initial mating preference between the paired preference tests in each of 6 experimental treatment combinations of number of rival males present (3 levels) and difference in the relative body length of paired stimulus females.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\beta$ (SE)</th>
<th>Wald statistic</th>
<th>df</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rival males</td>
<td></td>
<td>11.738</td>
<td>2</td>
<td>0.003</td>
</tr>
<tr>
<td>Rival males (1)</td>
<td>2.562 (0.85)</td>
<td>9.181</td>
<td>1</td>
<td>0.002</td>
</tr>
<tr>
<td>Rival males (2)</td>
<td>2.737 (0.85)</td>
<td>10.570</td>
<td>1</td>
<td>0.001</td>
</tr>
<tr>
<td>Female size difference</td>
<td>0.039 (0.031)</td>
<td>1.546</td>
<td>1</td>
<td>0.21</td>
</tr>
<tr>
<td>Female size difference × Rival males</td>
<td>5.495</td>
<td>2</td>
<td>0.064</td>
<td></td>
</tr>
<tr>
<td>Female size difference × Rival males (1)</td>
<td>-0.094 (0.040)</td>
<td>5.486</td>
<td>1</td>
<td>0.019</td>
</tr>
<tr>
<td>Female size difference × Rival males (2)</td>
<td>-0.060 (0.038)</td>
<td>2.471</td>
<td>1</td>
<td>0.12</td>
</tr>
<tr>
<td>Constant</td>
<td>-2.012 (0.70)</td>
<td>8.382</td>
<td>1</td>
<td>0.004</td>
</tr>
</tbody>
</table>

df, degrees of freedom.
This proposition could be tested using the guppy, as males can distinguish virgin from non-virgin females using chemical cues that are emitted by females in this species (Guevara-Fiore et al. 2009).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

FUNDING


We thank the Director of Fisheries, Ministry of Agriculture, Land and Marine Resources of Trinidad and Tobago for permission to collect guppies from the Quare River, I.W. Ramnarine for logistical support, K. McGrath for quantifying male guppy coloration patterns, T.N. Sherratt for statistical advice, and T.N. Sherratt and 2 anonymous reviewers for their constructive comments on the manuscript. This research was approved by the Institutional Animal Care Committee at Carleton University (protocol number B09-14) and thus adheres to the animal use and care guidelines of the Canadian Council on Animal Care and the laws of Canada.

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