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SHORT COMMUNICATION

Geographic variation in sperm traits reflects predation risk and natural rates of multiple paternity in the guppy

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cryptic female choice;
polyandry;
promiscuity;
sexual selection;
sperm competition.

Abstract

Guppies (Poecilia reticulata) are models for understanding the interplay between natural and sexual selection. In particular, predation has been implicated as a major force affecting female sexual preferences, male mating tactics and the level of sperm competition. When predation is high, females typically reduce their preferences for showy males and engage more in antipredator behaviours, whereas males exploit these changes by switching from sexual displays to forced matings. These patterns are thought to account for the relatively high levels of multiple paternity in high-predation populations compared to low-predation populations. Here, we assess the possible evolutionary consequences of these patterns by asking whether variation in sperm traits reflects differences in predation intensity among four pairs of Trinidadian populations: four that experience relatively low levels of predation from a gape-limited predator and four that experience relatively high levels of predation from a variety of piscivores. We found that males in high-predation populations had faster swimming sperm with longer midpieces compared to males in low-predation populations. However, we found no differences among males in high- and low-predation populations with respect to sperm number, sperm head length, flagellum length and total sperm length.

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Introduction

The impressive diversity in sperm number, velocity and morphology across species is thought to be primarily a result of strong evolutionary pressure from sperm competition, the competition between the ejaculates of two or more males for the fertilization of a single set of ova (Parker, 1970; Birkhead & Moller, 1998; Simmons, 2001; Pizzari & Parker, 2009). The probability of encountering sperm competition (i.e. sperm competition risk; sensu Parker et al., 1997) and the average number of ejaculates competing for each fertilization (i.e. sperm competition intensity; sensu Parker et al., 1996) varies broadly among species and ecological gradients. Ecological variables can shape mating behaviour, which in turn affects sperm competition. For example, the frequency of extrapair paternity, and hence sperm competition risk, in birds can be affected by breeding density (Richardson & Burke, 2001), territory quality (Rubenstein, 2007) and food availability (Vaalav et al., 2003).

One ecological variable that has received little attention in studies of sperm competition is predation. It has long been recognized that particular reproductive behaviours can increase the risk of predation (Lima & Dill, 1990; Magnhagen, 1991; Sih, 1994). As a result, predation risk can shape reproductive strategies (Magurran & Seghers, 1990; Sih, 1994; Candolin, 1998), the frequency and duration of reproduction (Sih et al., 1990; Candolin, 1997; Rohr & Madison, 2001) and operational sex ratios (Lo de et al., 2004), all of which can affect sperm competition risk and intensity (Birkhead & Moller, 1998; Simmons, 2001). For example, in the agile frog (Rana dalmatina), elevated levels of predation lead to a reduced probability of multiple mating by females, and thus a lower risk of sperm competition (Lo de et al., 2004).
Reproductive behaviour and predation intensity are closely integrated in the guppy, Poecilia reticulata (Luyton & Liley, 1985; Magurran & Seghers, 1990; Darden & Croft, 2008). Guppies are small, live-bearing fish found in streams throughout the northern mountainous range of Trinidad (Houde, 1997). These streams vary in ecological conditions and are isolated from one another, making this system ideal for studying the effects of various ecological factors on behaviour (Liley & Seghers, 1975; Magurran, 2005). For example, in lowland streams guppies typically face high levels of predation pressure because they co-exist with a number of large piscivores. These include members of the Characidae family, such as Hoplias malabaricus and species belonging to the Cichlidae, such as Crenicichla frenata (Liley & Seghers, 1975). However, waterfalls and rapids can act as barriers that preclude the upstream migration of these large predators into smaller tributaries. Consequently, guppies that inhabit upstream streams typically face low levels of predation because they co-exist only with a smaller gape-limited predator, Rivulus hartii of the family Cyprinodontidae, which is incapable of consuming large adult guppies, but is a significant predator of juveniles (Liley & Seghers, 1975).

Variation in the level of predation has been implicated as an important determinant of male behavioural and morphological traits, including mating behaviour (reviewed in Endler, 1995; Houde, 1997). Individual male guppies employ two distinct mating tactics interchangeably, a courtship behaviour called the sigmoid display, and a form of sneaky mating called the gonopodial thrust (Houde, 1997). Under elevated risk of predation, females become increasingly unresponsive to male courtship (Godin & Briggs, 1996; Gong, 1997), typically increase their vigilance and antipredator behaviours (Magurran, 2005) and actively select areas of high-predation risk to reduce sexual harassment by males (Darden & Croft, 2008). For their part, males exploit these changes in female behaviour by switching from courtship to forced sneaky mating attempts (Evans et al., 2002). Consequently, sneaky mating is more prevalent in high-predation populations than in low-predation ones (Luyton & Liley, 1985; Magurran & Seghers, 1990), and these differences in the relative levels of forced matings among populations are thought to account for the relatively higher levels of multiple paternity in high-predation locations (as measured by the mean number of sires per brood) (Neff et al., 2008). Consequently, the level of sperm competition is thought to be higher in populations experiencing high levels of predation (Neff et al., 2008).

One possible mechanism of sperm competition, the ‘fair raffle’ model, occurs when the male who enters the most tickets (i.e. contributes the most sperm) is most likely to succeed in fertilizing the majority of a female’s ova (Parker et al., 1990). The fair raffle principle predicts that males will respond to sperm competition by increasing ejaculate size and overall sperm production, and this has been supported in comparative (e.g. Stockley et al., 1997) and intraspecific studies (e.g. Gage et al., 1995). Nevertheless, previous work on guppies indicates that populations inhabiting high-risk locales had lower sperm reserves (as estimated by manually stripping ejaculates) than their low-risk counterparts (Evans & Magurran, 1999), which, although based on a relatively small sample (n = 5 populations) is inconsistent with the idea that selection imposed through sperm competition favours elevated sperm production. Instead, selection may favour the evolution of traits that influence the quality of ejaculates, independent of numbers. For example, in many species, there are several sperm traits in addition to number that can influence fertilization efficiency, creating a ‘loaded raffle’ (Parker et al., 1990; Snook, 2005; Pizzari et al., 2008a). These sperm traits are collectively referred to as ‘sperm quality’ and may include traits such as viability (e.g. García-González, 2005), velocity (e.g. Birkhead et al., 1999; Gage et al., 2004) and morphology (e.g. LaMunyon & Ward, 1998; Oppliger et al., 2003). In guppies, sperm competition appears to follow such a ‘loaded raffle’ mechanism (Neff & Wahl, 2004). Indirect evidence linking sperm swimming velocity to competitive fertilization success comes from the association between relative paternity success and the area of orange in the male’s colour pattern (Evans et al., 2003a) – a trait positively correlated with sperm velocity (Locatello et al., 2006; Pitcher et al., 2007; but see Skinner & Watt, 2007). There also appears to be a positive relationship between sperm velocity and the combined length of the sperm’s head and midpiece (Pitcher et al., 2007; Skinner & Watt, 2007). Overall, variation in morphology and velocity appears to vary among individuals, and these traits are all implicated in mediating competitive fertilization success. These sperm traits therefore presumably face distinct selection pressure because of variation in the ecological conditions that occur among populations of guppies.

In this study, we exploited the variation in predation intensity among natural guppy populations to determine whether sperm quality exhibits consistent variation across eight populations differing in the level of predation. We predicted that because of the expected asymmetry in the level of sperm competition between high- and low-predation populations (Neff et al., 2008), coupled with the recently established direct (C. Boschetto, C. Gasparini & A. Pilastro, personal communication) and indirect (Evans et al., 2003a; Locatello et al., 2006; Pitcher et al., 2007) associations between sperm quality and competitive fertilization success, that populations of guppies facing high-predation intensity would have higher sperm velocity (and consequently relatively longer sperm heads and midpieces, because these measures are correlated with sperm velocity; Pitcher et al., 2007) than populations experiencing lower predation intensity. We also compare sperm counts (as estimated from stripped ejaculates) among populations to compare...
our results with those obtained from a more limited sample by Evans & Magurran (1999).

Materials and methods

Fish collections

We collected male guppies from both downstream and upstream populations of four river systems (Aripo, Tacarigua, Quare and Turure) in Trinidad’s Northern Mountain Range. For Tacarigua, the Tunapuna stream was the upstream sampling site. As is typical of rivers in the Northern Mountain Range, upstream locations exhibited low-predation intensity, and downstream locations exhibited high-predation intensity (Houde, 1997; Magurran, 2005). All sampling sites have been extensively surveyed for predators (Magurran & Seghers, 1994; Endler & Houde, 1995) and subsequently monitored by other researchers (e.g. Evans et al., 2003b, T.E. Pitcher, personal observations). We collected 25 males from each population; however, for some males, sperm degraded prior to analysis or the video recordings were not of sufficient quality for velocity analysis (see below) so fewer individuals were used.

Sperm trait assessment

Males were isolated for 3 days after capture from the wild to allow sperm reserves to replenish (Kuckuck & Greven, 1997). We collected sperm from males from each of the eight populations, following Matthews et al. (1997). Individuals were placed under a dissecting microscope, and sperm were then extracted by swinging the gonopodium forwards and applying pressure to the side of the abdomen with a blunt probe until all spermatozeugmata (i.e. sperm bundles) were released. Initially, a fixed number of sperm (25 bundles) were drawn up in a pipette and added to 250 µL of Courtland’s saline, which contained bovine serum albumin at 1% v/v (hereafter saline solution) (Evans et al., 2003a). The resulting solution was drawn repeatedly into the pipette to break the sperm bundles and activate the sperm for velocity analysis (see below). Remaining sperm bundles were then collected and diluted in saline solution, as outlined earlier, for sperm number and sperm morphology analyses (see below). Finally, we took a digital photograph of the left side of each male, which was later used to measure total body length (from the tip of the mouth to the base of the caudal fin, along the central axis) using IMAGEJ software (available at http://rsbweb.nih.gov/ij/).

Sperm numbers at rest (hereafter sperm number) were calculated by counting sperm cells in an ‘improved Neubauer chamber’ haemocytometer under 400x magnification (see Pitcher et al., 2003). The distribution of sperm cells across the haemocytometer was checked visually for evenness before counts commenced. If the sperm were unevenly distributed across the haemo-

...
Statistical analyses

We analysed variation in sperm traits (log transformed sperm number and sperm morphology metrics) between predation regimes using linear mixed effects models fitted via restricted maximum likelihood (nlme package, R Development Core Team, 2009). In these analyses, sperm-related traits were entered as response variables, with predation as a fixed factor (2 levels, high- and low-predation). However, as predation level varied between upstream and downstream locations within rivers, river and predation level within river were treated as random effects (see Schielzeth & Forstmeier, 2009). Thus, our analyses incorporate the random effects of river (treated as random intercepts) and predation (treated as random slopes) to account for variation in the effect of predation both within and between rivers. To test the between-group effect of predation within streams, we calculated intraclass correlation coefficients (ICC), reflecting the proportion of variance attributable to each level of the model (see Raudenbush & Bryk, 2002). For example, when modelling sperm velocity as a function of predation, the estimated ICC was <1%, indicating minimal between-group effect (i.e. negligible variation in the effect of predation on sperm velocity between rivers) suggesting that there is no need to retain the random effect of predation in the model. However, for additional models in our analyses, estimates of ICC were considerably higher (e.g. for the model reflecting the effect of predation on midpiece length, the ICC was considerably higher at ~35%). Therefore, to avoid overconfident estimates from our mixed models (see Schielzeth & Forstmeier, 2009), we retained the random effect of predation within each model.

To compare sperm number across predation levels, we first tested the relationship between sperm number and adult body size (i.e. body length), which are often found to covary within populations (see Pitcher & Evans, 2001). In this study, we found that sperm number was indeed correlated with body length ($r^2 = 0.10, P < 0.001$), so we added body size as a covariate to analyses involving sperm number. To ensure that we constructed models that produce unambiguous and unbiased estimates of within- and between-subject effects when covariates are employed, we applied group centering to evaluate whether the modelled relationship captured the effect both within subjects (stream section within rivers) and between subjects (rivers) (see van de Pol & Wright, 2009). In our case, when comparing sperm number across predation levels, the effect of the centred value was not significant ($P = 0.46$) indicating the modelled relationship was similar within and between groups.

We also used linear mixed effects models (nlme package, R Development Core Team, 2009) to examine whether potential trade-offs existed between sperm number and sperm size metrics. Here, as earlier, our analyses incorporated the random effects of river and predation but did not include the covariate of adult body length.

**Results**

Our analyses revealed significant differences among populations in male sperm traits (see Table 1 for descriptive statistics), which in turn were attributable to variation in the level of predation at each site (Table 2). High-predation males possessed significantly faster sperm (Fig. 1) and sperm with longer midpieces than their low-predation counterparts (Table 2). Finally, sperm number, flagellum length and total sperm length did not differ significantly between high- and low-predation populations (Table 2).

We found a weak but significant negative relationship between sperm number and sperm head length ($t_{55} = 5.46, P = 0.04$). There was no relationship between sperm number and midpiece length ($t_{55} = 2.11, P = 0.15$), flagellum length ($t_{55} = -0.93, P = 0.35$) or total sperm length ($t_{55} = -1.19, P = 0.24$). Finally, there was no relationship between sperm number and sperm size metrics when we examined high- ($n = 27$ males) and low-predation ($n = 35$ males) populations separately (all $P > 0.10$).

### Table 1

Mean ± standard deviation and sample sizes for body size, sperm number, sperm velocity, sperm head length, midpiece length, flagellum length and total sperm length of guppies (*Poecilia reticulata*). Values presented for sperm morphology traits are back-transformed from log-transformed values used in the analyses (see Materials and methods).

<table>
<thead>
<tr>
<th>Population</th>
<th>Predation intensity</th>
<th>Body length (mm)</th>
<th>Sperm number ($\times 10^5$)</th>
<th>n</th>
<th>Sperm velocity (PC1)</th>
<th>n</th>
<th>Head length ($\mu$m)</th>
<th>Midpiece length ($\mu$m)</th>
<th>Flagellum length ($\mu$m)</th>
<th>Total sperm length ($\mu$m)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower Aripo</td>
<td>High</td>
<td>16.14 ± 1.06</td>
<td>3.19 ± 1.50</td>
<td>18</td>
<td>0.58 ± 1.24</td>
<td>14</td>
<td>4.26 ± 1.02</td>
<td>6.15 ± 1.06</td>
<td>44.75 ± 1.03</td>
<td>55.18 ± 1.02</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper Aripo</td>
<td>Low</td>
<td>18.34 ± 1.05</td>
<td>4.13 ± 1.75</td>
<td>20</td>
<td>-0.33 ± 0.70</td>
<td>14</td>
<td>4.18 ± 1.02</td>
<td>5.64 ± 1.05</td>
<td>45.60 ± 1.01</td>
<td>55.44 ± 1.01</td>
<td>10</td>
</tr>
<tr>
<td>Tacarigua</td>
<td>High</td>
<td>15.91 ± 1.06</td>
<td>2.02 ± 0.73</td>
<td>20</td>
<td>-0.10 ± 0.44</td>
<td>14</td>
<td>4.28 ± 1.03</td>
<td>6.22 ± 1.03</td>
<td>43.49 ± 1.01</td>
<td>53.99 ± 1.01</td>
<td>10</td>
</tr>
<tr>
<td>Tunapuna</td>
<td>Low</td>
<td>18.04 ± 1.07</td>
<td>3.83 ± 1.86</td>
<td>20</td>
<td>-0.99 ± 0.46</td>
<td>11</td>
<td>4.38 ± 1.05</td>
<td>6.03 ± 1.12</td>
<td>44.05 ± 1.02</td>
<td>54.50 ± 1.01</td>
<td>10</td>
</tr>
<tr>
<td>Lower Quare</td>
<td>High</td>
<td>17.22 ± 1.06</td>
<td>5.84 ± 3.15</td>
<td>19</td>
<td>1.22 ± 0.88</td>
<td>6</td>
<td>4.20 ± 1.03</td>
<td>6.00 ± 1.08</td>
<td>43.27 ± 1.02</td>
<td>53.49 ± 1.02</td>
<td>10</td>
</tr>
<tr>
<td>Upper Quare</td>
<td>Low</td>
<td>16.60 ± 1.05</td>
<td>3.91 ± 1.72</td>
<td>22</td>
<td>0.55 ± 1.33</td>
<td>14</td>
<td>3.91 ± 1.04</td>
<td>4.75 ± 1.09</td>
<td>41.82 ± 1.02</td>
<td>50.50 ± 1.02</td>
<td>8</td>
</tr>
<tr>
<td>Lower Turure</td>
<td>High</td>
<td>16.86 ± 1.05</td>
<td>2.75 ± 1.05</td>
<td>18</td>
<td>0.19 ± 0.61</td>
<td>14</td>
<td>4.37 ± 1.02</td>
<td>6.03 ± 1.06</td>
<td>44.03 ± 1.04</td>
<td>54.45 ± 1.03</td>
<td>10</td>
</tr>
<tr>
<td>Upper Turure</td>
<td>Low</td>
<td>17.78 ± 1.07</td>
<td>3.11 ± 1.38</td>
<td>22</td>
<td>-0.42 ± 0.65</td>
<td>18</td>
<td>4.33 ± 1.02</td>
<td>5.81 ± 1.07</td>
<td>45.56 ± 1.02</td>
<td>55.73 ± 1.01</td>
<td>10</td>
</tr>
</tbody>
</table>
Discussion

Our findings support the prediction that some aspects of sperm quality reflect the level of predation and therefore possibly the level of sperm competition among natural populations of Trinidadian guppies. Guppy sperm were faster and had longer midpieces in high-predation populations compared to those inhabiting low-predation populations. However, sperm numbers and other sperm morphological traits did not differ between low-predation and high-predation populations.

We found that on average sperm velocity was greater in high-predation compared to low-predation populations. There is now increasing evidence that sperm number does not fully explain sperm competition success, and that instead of a ‘fair raffle’ mechanism, in many species sperm competition proceeds on the basis of a ‘loaded raffle’ mechanism, where traits other than sperm number influence competitive fertilization success (Parker et al., 1990; Snook, 2005). In guppies, there is increasing evidence for such a ‘loaded raffle’ mechanism. For example, Neff & Wahl (2004) used Pitcher et al.’s (2003) paternity estimates to evaluate the mechanistic basis of sperm precedence in guppies. Their mathematical model incorporated Pitcher et al.’s estimates of relative ejaculate size to examine the relationship between fertilization success and the number of sperm competing for fertilization. A nonlinear relationship between paternity and relative ejaculate size would be indicative of a loaded raffle mechanism. Their analysis hinted at last-male sperm precedence with diminishing reproductive returns for increased sperm production, thereby supporting a loaded raffle mechanism. This conclusion has been supported by studies documenting nonrandom paternity biases when the number of sperm from each male is regulated through artificial insemination. For example, in a recent unpublished study, Boschetto, Gasparini & Pilastro (personal communication) used artificial insemination to transfer controlled amounts of sperm to female guppies and found that both relative ejaculate size and sperm velocity were the primary determinants of paternity. This supports findings from a similar experiment conducted by Evans et al. (2003a), who found that male paternity was related to the amount of orange colouration, a trait which has been linked to sperm velocity (Locatello et al., 2006; Pitcher et al., 2007; but see Skinner & Watt, 2007).

Functionally, the increase in velocity in high-predation compared to low-predation populations may be because of differences in midpiece length, which were signifi- cantly longer in high-predation populations compared to low-predation populations. Pitcher et al. (2007) previously demonstrated that in guppies, sperm head length

<table>
<thead>
<tr>
<th>Sperm trait</th>
<th>Predation Intensity</th>
<th>Mean ± SE*</th>
<th>n</th>
<th>Δt</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sperm number (× 10⁶)</td>
<td>High</td>
<td>3.81 ± 0.80</td>
<td>75</td>
<td>-0.09</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>3.82 ± 0.75</td>
<td>84</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sperm velocity (PC1)</td>
<td>High</td>
<td>0.73 ± 0.17</td>
<td>48</td>
<td>4.37</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>-0.29 ± 0.31</td>
<td>57</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head length (µm)</td>
<td>High</td>
<td>4.28 ± 1.05</td>
<td>38</td>
<td>0.96</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>4.20 ± 1.03</td>
<td>38</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Midpiece Length (µm)</td>
<td>High</td>
<td>6.10 ± 1.10</td>
<td>38</td>
<td>2.0</td>
<td>0.048</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>5.54 ± 1.05</td>
<td>38</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flagellum length (µm)</td>
<td>High</td>
<td>44.10 ± 1.01</td>
<td>38</td>
<td>-0.57</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>44.24 ± 1.02</td>
<td>38</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total length (µm)</td>
<td>High</td>
<td>54.25 ± 1.04</td>
<td>38</td>
<td>0.25</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>54.00 ± 1.02</td>
<td>38</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Mean values (estimated from the mixed model) and their standard errors (± SE) for sperm number, velocity, head length, midpiece length, flagellum length and total length. n denotes number of individuals sampled.

*Values presented are back-transformed from log-transformed values used in the analyses (see Materials and methods).
(a measure that included the midpiece) was positively correlated with sperm velocity. Skinner & Watt (2007) found a similar pattern using sperm midpiece area. The midpiece is the component of the sperm containing the mitochondria, which provide energy for the beating of the flagellum (Baccetti & Afzelius, 1976). Thus, a larger midpiece could potentially provide more energy for locomotion, resulting in faster sperm, although this possibility has yet to be thoroughly investigated and other components of sperm morphometry, including scaling relationships between the sperm’s head and flagellum (see Humphries et al., 2008), need to be incorporated into future analyses that link sperm swimming velocity to sperm size.

Sperm competition is predicted to select for greater sperm number through a ‘fair raffle’ mechanism, whereby males with greater numbers of sperm are able to enter more ‘tickets’ into the contest for fertilization and are therefore likely to outcompete males with fewer sperm (Parker et al., 1990). It follows that males facing increasing risk or intensity of sperm competition invest in producing greater numbers of sperm (Gage et al., 1995; Stockley et al., 1997). Instead, unlike Evans & Magurran (1999), we did not find that sperm number (after controlling for body size) differed significantly between low-predation and high-predation populations. This finding may indicate that total sperm number at rest may not be a trait selected for by sperm competition, perhaps because total sperm number is not representative of ejaculate size. Alternatively, investment in sperm production may be constrained by investment in sperm quality. Interestingly, in a recent multivariate analysis of sexual selection on precopulatory and post-copulatory traits in guppies, Head et al. (2008) reported that selection actually favoured males with lower sperm reserves, prompting them to speculate that components of sperm quality may be traded off against sperm production. Our results similarly suggest that sperm quality may be traded off to some extent against sperm quantity, because we found a very weak but significant negative relationship between sperm number and sperm head size, albeit not when we examined high- and low-predation populations separately. Nevertheless, experimental and/or quantitative genetic approaches are needed to properly test the basis for such relationships.

Our comparative analyses revealed variation in sperm traits reflect differences in predation intensity and concordant rates of multiple paternity among populations of Trinidadian guppies. We found that males in high-predation populations had faster swimming sperm with longer midpieces, but there were no differences in sperm number, flagellum length and total sperm length among high- and low-predation populations. Although our results appear to be consistent with the idea that components of sperm quality account for the variation in sperm traits we observed, we interpret this relationship cautiously because in addition to sperm competition, other variables that differ among the high- and low-predation populations may also explain some of the variation we found in sperm traits. For example, effective population size, sex ratio, food availability, population density and longevity differ between high- and low-predation populations (reviewed in Houde, 1997; Magurran, 2005). Although all of these variables may in theory affect sperm production to some extent, the most biologically relevant variable is possible age differences between the males in the high- and low-predation populations. Because of high levels of predation on adult guppies, the males we sampled from high-predation populations were likely younger on average compared to low-predation populations. It is therefore plausible that, rather than sperm competition per se, senescence might account for some of the results we report in this study (Radwan, 2003; Pizzari et al., 2008b). For example, the result that males from high-predation populations produce sperm of higher velocity might be explained by the fact that a random sample of these males will be closer to their reproductive prime than a random sample of males from low-predation populations, which are expected to be older on average. Although we do not possess any data to directly test this hypothesis, it seems unlikely that age differences among males from high- and low-predation populations could explain our main result because Gasparini et al. (2010) found that older male guppies actually produced slower sperm, more sperm and longer sperm compared to younger males.

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