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# Sperm traits in the quacking frog (*Crinia georgiana*), a species with plastic alternative mating tactics

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**Abstract** In species where males use alternative reproductive tactics and male phenotypes are confronted with different risks of sperm competition, theory predicts that between-male-type differences in sperm expenditure may evolve. In the frog *Crinia georgiana* big males can monopolize females, whereas small males often engage in polyandrous matings. Consequently, big males may experience a lower risk of sperm competition than do small males. We tested if the predictions from theoretical models can be applied to the mating system of *C. georgiana*. Our results showed that small males do not have larger testes relative to their body size compared to their larger counterparts and that the efficiency with which sperm number, size, motility, and longevity are produced by the testes does not differ between small and large males in the predicted way. These results are not in alignment with predictions from a loaded raffle model of sperm competition on sperm expenditure in males with alternative phenotypes. The plasticity in mating tactics used by *C. georgiana* males and a high intraseasonal variation in male densities may have prevented the evolution of enhanced sperm performance in smaller males. A fair raffle in the sperm

competition game played by *C. georgiana* males could also explain the observed patterns in sperm traits. Future investigations determining the parameters responsible for the deviation from theoretical predictions in this system will test the degree to which current theoretical models can indeed be applied to species with plastic reproductive tactics.

## Introduction

Sperm competition occurs whenever the sperm of two or more males compete for a given set of ova (Parker 1970). Sperm competition is widely recognized as a pervasive form of sexual selection (Birkhead and Møller 1998) and ejaculate traits can be important determinants of success in competitive situations (e.g., Birkhead et al. 1995; Stockley et al. 1996; Levitan 2000). Consequently, the evolution of sperm characteristics has been a focus of attention in recent years (Snook 2005). Across different species, sperm competition theory makes clear predictions about ejaculate size and the risk of sperm competition (Parker 1990a,b; Parker et al. 1996, 1997; Ball and Parker 1997). Species with a higher risk will have larger ejaculates often assessed as larger testis mass (e.g., Harcourt et al. 1981; Møller and Briskie 1995; Hosken 1998; Anderson and Dixson 2002; Byrne et al. 2002, 2003).

Predictions about ejaculate expenditure patterns within species are, however, more complex. Ejaculate allocation into distinct matings may depend on the presence of alternative mating behaviors, on the number of competitors present at matings, on the quality of information on risk and

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intensity of sperm competition, on the type of raffle in the sperm competition game (Parker 1998), and on mating rates. We would expect among-male variation in ejaculate expenditure in mating systems, where (1) alternative mating tactics are present, (2) males typically use one mating tactic depending on genotypic or phenotypic factors, (3) the risk of sperm competition differs between tactics, (4) males have perfect information on the number of competitors and if they are in the favored or the disfavored role in a given mating, and (5) the raffle in the game is loaded (Ball and Parker 2000). At the level of different sperm traits, this may be further complicated by genetic correlations among sperm traits (Moore et al. 2004; Birkhead et al. 2005) and by possible variation in allocation into these traits, depending on the mating strategy an individual uses (e.g., Simmons et al. 1999; Leach and Montgomerie 2000; Neff et al. 2003).

In externally fertilizing species, cryptic female choice is less likely to occur than in internally fertilizing species and the characteristics of the ejaculate may be decisive in determining the paternity share of individual males. Consequently, external fertilizers are ideal for the examination of the relationship between variation in sperm traits and alternative mating tactics. Recent studies have related within-species variation in sperm characteristics to alternative mating tactics in external fertilizers in the light of sperm competition theory (Parker 1998). These studies detected systematic variation in sperm number with the males frequently engaging in multiple male matings having larger or more concentrated ejaculates (Leach and Montgomerie 2000; Vladić et al. 2002; Neff et al. 2003), but found no difference in sperm morphology between males experiencing different levels of sperm competition (Gage et al. 1995; Schärer and Robertson 1999; Leach and Montgomerie 2000; Vladić et al. 2002).

Sperm motility and/or longevity was lower in dominant, territorial males in some studies (Gage et al. 1995; Burness et al. 2004), but not in others (Leach and Montgomerie 2000; Vladić et al. 2002; Neff et al. 2003; Burness et al. 2004). Exploring disparities among the results and relating them to differences in the reproductive biology and the reproductive environment of the studied species may yield important insights into the evolution of sperm characteristics (Hettyey and Roberts 2006). However, the low number of available studies and the fact that nothing is known about mating tactic-related differences in sperm characteristics in externally fertilizing taxa other than the three fish species studied (*Salmo salar*: Gage et al. 1995; Vladić et al. 2002; *Thalassoma bifasciatum*: Schärer and Robertson 1999; *Lepomis macrochirus*: Leach and Montgomerie 2000; Neff et al. 2003; Burness et al. 2004) currently inhibit such investigations.

In this paper we investigate sperm traits in the anuran amphibian *Crinia georgiana* (Tschudi, 1838), a species

with intensive sperm competition. In this species male size can be bimodally distributed (Smith and Roberts 2003a), but is highly variable in all populations (JDR unpublished observations), possibly a result of disruptive sexual selection (Smith and Roberts 2003a). Mating tactics adopted by different males are usually size-dependent (Byrne 2002b; Byrne and Roberts 2004). At low densities, larger males call to attract females and are more likely to be found in monandrous matings, whereas smaller males use sneak tactics and engage in multiple male matings (Byrne and Roberts 2004). Larger males adopt a conventional dorsal position in multiple male matings and enter amplexus first, while smaller males amplex in a ventral position and join a mating pair some time after the calling male enters amplexus (Roberts et al. 1999; Byrne and Roberts 2004).

At higher densities, only a low proportion of matings can be monopolized by large, calling males. Both large and small males search actively for females, and small males are largely excluded from matings by large males using sneak or search tactics (Byrne and Roberts 2004). Overall, around 50% of all matings are polyandrous and males other than the focal male gain a significant share in paternity (Roberts et al. 1999; Byrne and Roberts 2004). A comparative study indicated that high levels of sperm competition may have led to a relative testis mass four times greater in *C. georgiana* than in any other species of the genus *Crinia* (Byrne et al. 2002).

Small males almost exclusively participate in multiple-male matings, whereas large males are able to secure a significant number of monandrous matings, especially at low chorus densities (Byrne and Roberts 2004). Consequently, small and large males may both experience a high risk of sperm competition, but while small males are almost always mating in the presence of sperm competition, large males have a higher chance of mating in the absence of sperm competition. As chorus densities high enough to induce large males to use sneak tactics are relatively rare (Byrne 2002a; Byrne and Roberts 2004), on average, larger males may experience a significantly lower risk of sperm competition than smaller males. Males most probably have perfect information on the number of competitors and the role they occupy and, as the first male to enter amplexus always clasps the female in a dorsal position (Roberts et al. 1999), we assume that this position conveys some degree of advantage in situations generating sperm competition. Also, males can remate within 30 min (Roberts JD, field observations) and under laboratory conditions they can fertilize up to eight egg clutches sequentially, with no decrease in fertilization success (Byrne PG, personal communication) so that sperm depletion is unlikely.

In such a mating system, sperm competition theory predicts higher ejaculate expenditure to evolve in smaller males compared to larger males, even if alternative mating

tactics are used with some degree of plasticity (Ball and Parker 2000). Preliminary data showed no elevated relative testis mass in small vs large males, and a positive correlation between ejaculate volumes and testis mass (Byrne 2004). However, we do not know whether the efficiency of sperm production differs between small and large males, possibly resulting in different quantity and quality of available sperm (e.g., Neff et al. 2003). Another investigation concentrating on within-species variation in sperm characteristics implied that within-population variation may be related to differences in body size (Hettyey and Roberts 2006). Low per-population sample sizes, however, did not allow drawing further conclusions. Here, we specifically test a hypothesis derived from sperm competition theory (Ball and Parker 2000), that small males produce more competitive sperm in *C. georgiana*, a species with plastic alternative mating tactics.

## Materials and methods

### Data collection

In 2003, we collected male *C. georgiana* from a breeding site near Kangaroo Gully 30 km southeast of Perth (32°11′ S, 116°15′ E). We collected sexually mature males from active choruses. Mature males called, had well-developed, large forearms, and a black throat (Smith and Roberts 2003b). Collections were made on three occasions, on July 13, August 3, and August 21. We hand-collected 20 males at a time and brought them back to the laboratory. Until processing, we kept males individually in 500-ml plastic containers with 30 ml of reverse-filtered tap water at room temperature.

One, 3, and 5 days after collection, we randomly selected two small and two large males and measured their snout-vent length (SVL, to the nearest 0.5 mm) with a plastic ruler. Animals were killed by double-pithing. Any animals not used in the experiment were released at the site of collection. After weighing testes (to the nearest 0.1 mg), we crushed them and released sperm into reverse-filtered tap water. We weighed the suspensions, and pipetted 50 μl onto specially prepared microscope slides (described in Reyer et al. 2003) and recorded sperm movement for 5 min with a Hitachi HV-C20 3CCD video camera attached to a microscope at ×200 magnification for subsequent determination of sperm motility. Video recordings were always started 3 min after sperm release. An earlier start of recordings was not possible due to logistical constraints. After recording, we let slides air-dry for sperm size measurements.

Fifteen, 30, 60, and 120 min after sperm release we pipetted 50 μl of the sperm suspensions onto microscope slides and estimated the percentage of living sperm. We considered sperm to be alive if their tail-membrane was undulating and dead if there was no movement of the tail-membrane (for a detailed description of myobatrachid sperm, see Lee and Jamieson 1992). The percentage of live sperm after 60 min was used as a measure of mean sperm longevity. Data gathered at other time points were used in creating a slope of diminishing survival and to compare survival of male types separately from other sperm traits. We estimated sperm concentrations using a Neubauer chamber and calculated sperm numbers from the mass of the sperm suspension, assuming that 1 g suspension equaled 1 cm$^3$.

We measured sperm length of 20 randomly chosen sperm from each male at ×800 magnification using OPTIMAS 6.5. Measurements on sperm size proved to be highly repeatable when we compared three replicate measurements on 200 sperm originating from 20 males ($R=0.94$; SE=0.62). To further enhance reliability of sperm size data, we measured each individual sperm three times and used the average in the analysis. For estimates of sperm motility, videotapes were digitized. We measured the distance individual spermatozoa traveled between frames within the first 30 s of the recordings made on each male. Only data on sperm visible for at least 5 s were used.

This resulted in measurements on swimming speed of an average of 29 sperm (range 12–53) per male, each measured for 20 s on average. We then calculated per-male averages and these were used as measures of motility in further analyses. Testing for repeatability of sperm motility measurements by comparing two replicate measurements on 12 sperm resulted in an extremely high repeatability estimate ($R=0.99$; SE<0.001). All measurements were done in the laboratory at a constant temperature of 20°C. We recognize 20°C may be higher than average temperatures experienced in the field, but we presume that all sperm will be similarly affected and matings have been observed in the field at temperatures as high as 22.5°C (Byrne 2002a). For further details on data collection, see Hettyey and Roberts (2006).

### Statistical analyses

Snout-vent length, testis mass, sperm size and motility were log$_{10}$-transformed, sperm number was square-root-transformed, and survival percentage was arcsine-square-root-transformed to achieve normality and enhance homogeneity of variances (Sokal and Rohlf 1995). Two size-groups of males were used (small males: 21.5–30.5 mm SVL; large males: 31.5–42.5 mm SVL) to test for potential differences in sperm traits due to size-dependent alternative mating tactics of males. These size classes are based on observations of body size bimodality (Smith and Roberts 2003a)

and on the related dichotomy of mating tactics (Byrne and Roberts 2004; Byrne 2004; discussed above) and allow us to match our new data on longevity and motility with those on testis size reported by Byrne (2004) and mating tactics in Byrne and Roberts (2004). This resulted in 18 large and 18 small males overall.

To explore direct relationships among variables, we calculated bivariate correlations among body size, testis mass, sperm number, sperm size, sperm motility, and sperm longevity. To test more specifically for relationships between measures of sperm quality, we performed partial correlations controlling for testis mass. We investigated variation in testis size with a general linear model (GLM) analysis of covariance (ANCOVA). We entered male-size category as a fixed factor, capture date and time from collection as random factors, and soma mass (body mass–testes mass) as a covariate. To assess between-male variation in sperm number, size, motility, and longevity, we entered them into GLM ANCOVAs together with male-size category as a fixed factor, date of capture and time from collection as random factors, and testis mass as a covariate. We then compared sperm longevity among the two male size classes with repeated-measures GLM ANCOVA by entering survival at 15, 30, 60, and 120 min as the repeated-measures factor, male-size category, capture date and time from collection as fixed factors, and testis mass as a covariate. Statistics were calculated in the ANOVA-type models applying backward removal model selection. All tests were calculated using SPSS 13.0 for Windows.

## Results

The values obtained for the studied four sperm traits are presented in Table 1. Bivariate correlations among body size, testis mass, sperm number, sperm size, sperm motility, and sperm longevity indicated intercorrelations between body size, testis mass, and sperm number (Pearson correlations, body size–testis mass: $r=0.701$; $n=36$; $p<0.001$; body size–sperm number: $r=0.624$; $n=36$; $p<0.001$; testis mass–sperm number: $r=0.953$; $n=36$; $p<0.001$). All other correlations were non-significant after adjustment of á-levels according to the sequential Bonferroni correction (Rice 1989). Partial correlations controlling for effects of testis mass did not reveal any significant relationships between the sperm characteristics investigated (Table 2), confirming previous results on a lack of trade-offs between sperm traits in *C. georgiana* (Hettyey and Roberts 2006).

We found no difference in relative testis mass between large and small males (GLM ANCOVA, $F_{1, 29}=0.03$; $p=0.875$). Testis mass, however, showed a positive relationship with soma mass ($F_{1, 32}=47.78$; $p<0.001$; Fig. 1a) and differed among dates of capture ($F_{2, 32}=4.29$; $p=0.022$). The effect of time from collection was not significant ($F_{2, 30}=3.06$; $p=0.062$). All interactions were non-significant.

Relative sperm number did not differ between large and small males (GLM ANCOVA, $F_{1, 31}=0.09$; $p=0.77$). Date of capture and time from collection did not explain a significant proportion of variation in relative sperm number (date of capture: $F_{2, 32}=2.27$; $p=0.12$; time from collection: $F_{2, 29}=0.43$; $p=0.65$). Sperm number was significantly positively related to testis mass ($F_{1, 34}=333.77$; $p<0.001$; Fig. 1b). Relative sperm size showed no relationship with either male-size category (GLM ANCOVA, $F_{1, 31}=0.2$; $p=0.66$), date of capture ($F_{2, 29}=0.22$; $p=0.81$), time from collection ($F_{2, 33}=0.46$; $p=0.64$) or testis mass ($F_{1, 32}=0.09$; $p=0.77$; Fig. 1c). Relative sperm motility differed between small and large males (GLM ANCOVA, $F_{1, 31}=6.52$; $p=0.016$), with small males producing relatively slower swimming sperm. Relative motility varied independently from date of capture ($F_{2, 29}=0.43$; $p=0.66$), but

**Table 1** Absolute values of the four measured sperm traits

| Variables | Male size | $n$ | Minimum | Maximum | Mean | SD |
|---|---|---|---|---|---|---|
| Sperm number | Small | 18 | 454,613 | 50,561,235 | $1.34\times10^7$ | $1.3\times10^7$ |
| (pcs.) | Large | 18 | 973,8055 | 93,908,425 | $4.41\times10^7$ | $2.56\times10^7$ |
| | Overall | 36 | 454,613 | 93,908,425 | $2.88\times10^7$ | $2.54\times10^7$ |
| Sperm size | Small | 18 | 67.6 | 72.4 | 70.1 | 1.38 |
| (μm) | Large | 18 | 65.5 | 73.6 | 70 | 2.4 |
| | Overall | 36 | 65.5 | 73.6 | 70.1 | 1.93 |
| Sperm motility | Small | 18 | 4.95 | 14.94 | 9.46 | 2.93 |
| (μm/s) | Large | 18 | 2.49 | 19.48 | 10.72 | 4.19 |
| | Overall | 36 | 2.49 | 19.48 | 10.09 | 3.62 |
| Sperm longevity | Small | 18 | 9 | 70 | 34.5 | 16 |
| (%) | Large | 18 | 13 | 80 | 45.8 | 20.2 |
| | Overall | 36 | 9 | 80 | 40.2 | 18.9 |

Sperm size and sperm motility are also presented on the basis of individual males, not on individual sperm. Sperm survival is the percentage of active sperm 60 min after sperm activation. Data are presented for male-size categories separately and for all males together.

**Table 2** Results of partial correlations among the four measured sperm characteristics while controlling for testis mass

| Variables | | (2) | (3) | (4) |
|---|---|---|---|---|
| Sperm number | (1) | $r=0.037$ $p=0.83$ | $r=-0.288$ $p=0.09$ | $r=-0.200$ $p=0.25$ |
| Sperm size | (2) | | $r=-0.067$ $p=0.70$ | $r=-0.152$ $p=0.38$ |
| Sperm motility | (3) | | | $r=0.369$ $p=0.03$ |
| Sperm longevity | (4) | | | |

Sample size is 36 throughout. The correlation between sperm motility and longevity is non-significant after adjustment of $\alpha$ ($p>0.008$) according to the sequential Bonferroni correction (Rice 1989).

showed a decrease with time from collection ($F_{2, 31}=4.68$; $p=0.017$). Motility was negatively related to testis mass ($F_{1, 31}=8.12$; $p=0.008$; Fig. 1d). All interactions were non-significant.

The number of active sperm decreased over the time period of our investigation (repeated-measures GLM ANCOVA, $F_{3, 32}=9.75$; $p<0.001$; Fig. 2). We found no difference in relative sperm longevity according to male-size category ($F_{1, 29}=0.15$; $p=0.7$), date of capture ($F_{2, 30}=$
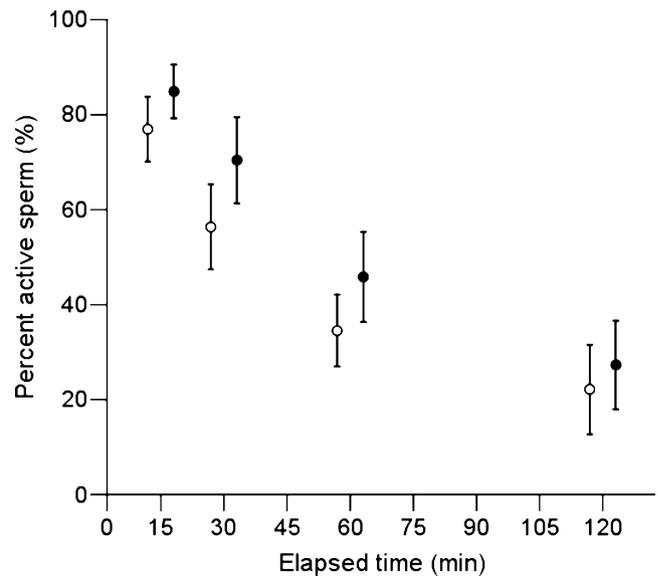


**Fig. 2** Sperm survival as a function of time in small and large males (*empty circles*: small males; *full circles*: large males). The apparent effect of male-size category is caused by the larger size of testes in large males (see "Results"). Means ± 2SE of untransformed data are shown



**Fig. 1** Relationships between soma mass and testis mass (**a**), testis mass and sperm number (**b**), testis mass and sperm size (**c**), and testis mass and sperm motility (**d**) in small and large males (*empty circles*: small males; *full circles*: large males). Displayed values are untransformed data for the ease of interpretation
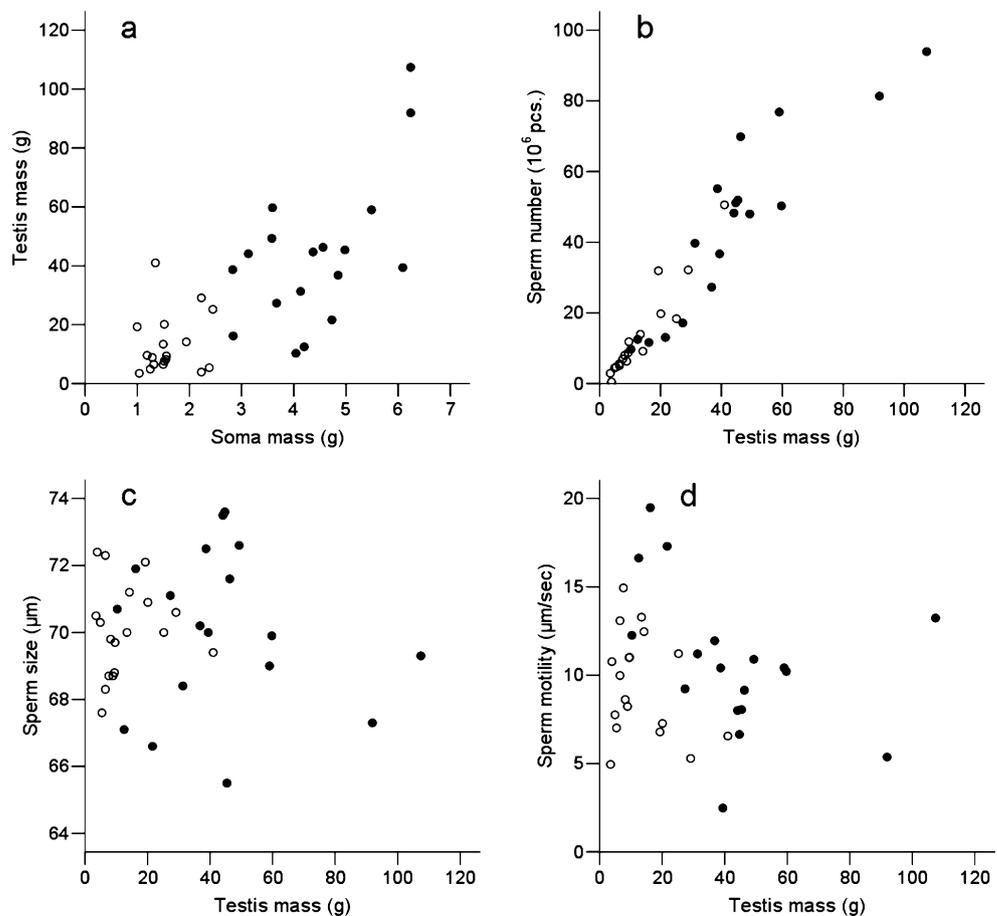
1.13; $p=0.34$) or time from collection ($F_{2, 32}=1.67$; $p=0.21$). Longevity was positively related to testis mass ($F_{1, 34}=8.51$; $p=0.006$). All interactions were non-significant.

## Discussion

In accordance with a game-theoretical model (Ball and Parker 2000) and previous empirical work on fish (Gage et al. 1995; Schärer and Robertson 1999; Leach and Montgomerie 2000; Vladić et al. 2002; Neff et al. 2003; Burness et al. 2004) we hypothesized that sperm characteristics of smaller males may be different from those of larger males in ways that would enhance competitiveness in situations involving sperm competition, as small males generally experience higher risks of sperm competition (Byrne 2002b; Byrne and Roberts 2004; see "Introduction"). This is not what we found. Our study confirms previous results (Byrne 2004) on the lack of difference in soma mass–corrected testis mass between small and large males in *C. georgiana*. Relative sperm number, size, and longevity did not parallel differences in male body size either, whereas relative sperm motility was lower in small males. Based on our gross measures of performance (see Burness et al. 2004) it appears, that small *C. georgiana* males cannot compensate for behavioral dominance of large males by means of enhanced sperm production efficacy of testes resulting in superior abilities at the level of sperm competition.

Theoretical models are unequivocal about their predictions of how sperm number should change with mating tactic related differences in the risk of sperm competition within a species (Parker 1993; Ball and Parker 1996). Predictions are well supported by empirical studies on species with genotypically or phenotypically fixed non-random roles (Leach and Montgomerie 2000; Vladić et al. 2002; Neff et al. 2003). In *C. georgiana* only the extended "almost constant roles" model applies, which was developed for a mating system where male types experience some probability of mating in both roles (Ball and Parker 2000). The observed differences in sperm number between males of different sizes did not fit predictions of the Ball and Parker (2000) model. Our result that relative sperm number was not associated with male body size may be viewed as a result of no change in relative testicular investment with body size and implies that, in this species, testes of different-sized males produce sperm numbers with similar efficacy.

No model has explicitly investigated how sperm size should change with the risk of sperm competition within a species (Parker 1998). However, Parker (1998) argued that when given males employ different mating tactics, they may have different sperm size optima depending on the

conditions they face. In our study, sperm size was neither related to testis mass, nor to body size of males and thus did not reflect differences in sperm competition risk faced. Other within-species studies have come to a similar conclusion (Gage et al. 1995; Schärer and Robertson 1999; Leach and Montgomerie 2000; Vladić et al. 2002) and the effect of sperm competition on the evolution of sperm size remains enigmatic.

Theoretical models analyzing within-species differences in sperm motility or longevity according to different risks of sperm competition are lacking (Parker 1998). Ball and Parker (1996) modeled how sperm number, speed, and longevity should be optimized at different intensities of sperm competition across species. Their model was based on the assumption that these sperm characteristics trade off each other and concluded that longevity is insignificant when sperm competition is intense, whereas sperm speed always seemed important, independently from sperm competition intensity. In cases, however, where motility and longevity do not trade off each other or with other sperm characteristics, as in *C. georgiana*, it seems reasonable to assume that increased motility, and sometimes also longevity, should enhance competitive ability of sperm. This is indeed what has been found in some within-species studies (e.g. Levitan 2000; Gage et al. 2004).

We thus expected both sperm motility and sperm longevity to increase with the risk of sperm competition. Empirical studies, however, do not support this prediction unequivocally (Gage et al. 1995; Leach and Montgomerie 2000; Vladić et al. 2002; Neff et al. 2003; Burness et al. 2004) and our results do not fit with the predictions of this hypothesis either. Relative sperm motility showed, contrary to our expectations, a positive relationship with body size. This relationship cannot be attributed to a link between testis mass and sperm motility, as these were negatively related. We thus conclude that testes of large males are more efficient in producing faster-swimming sperm. Considering the lack of difference in relative sperm longevity between small and large males together with no change in relative testicular investment with body size and the positive relation between longevity and testis mass implies that testes of different-sized males produce long-lived sperm with similar efficacy.

Deviations from the predictions of theory on the level of distinct sperm characteristics may be due to trade-offs among sperm traits (*sensu* Hettyey and Roberts 2006). Such trade-offs have often been described (e.g., Pitnick 1996; Levitan 2000; Gage et al. 2002). However, as in *C. georgiana*, there do not seem to be negative correlations among sperm characteristics (Hettyey and Roberts 2006; this study), and as we investigated four sperm traits instead of concentrating on one, this hypothesis cannot explain the inconsistency between theoretical predictions and empirical results.

An explanation for the observed patterns in sperm characteristics may be deduced from the lack of fixed size-dependent mating strategies. On nights with high densities, large males are also engaging in multiple male matings at a high frequency, using sneak tactics (Byrne and Roberts 2004). Also, there is large intraseasonal variation in male densities, which determines the number of multiple male matings and the number of males participating in polyandrous matings (Byrne 2002a; Byrne and Roberts 2004). A high relative abundance of males applying sneak tactics, especially on peak nights, may decrease the disparity in gametic expenditure (Parker 1990b; Gage et al. 1995; Simmons et al. 1999). Consequently, it is possible that differences in risk and intensity of sperm competition experienced by small and large males are not consistent enough to result in adaptations (sensu Sasaki and Ellner 1997).

Theory predicts the evolution of between-male differences in sperm performance in the case of fixed alternative mating tactics (Parker 1990b), but also if mating tactics are applied with some degree of plasticity (Ball and Parker 2000). As we did not detect higher ejaculate expenditure in small males, we may, however, conclude that the probabilities of C. georgiana males employing the mating tactic that is atypical for them, is too high to result in differences in sperm traits due to adaptations to sperm competition. Our results underline the importance of a more rigid segregation of male phenotypes if evolution resulting in different sperm trait optima is to take place.

It is also possible that our assumption on the type of raffle is not correct. Males in the dorsal position may not have a consistent advantage over other males in polyandrous matings. Consequently, paternity share may not depend on the position of amplexing males, and the raffle in the sperm competition game may be fair. In such a scenario, theory predicts no difference in ejaculate expenditure to evolve (Ball and Parker 2000). This could be resolved by detailed analyses of male position, time in amplexus, and fertilization success, which we are currently conducting.

Finally, the presence of alternative life histories could explain the coexistence of alternative mating tactics and the observed patterns in sperm traits as well. Alternative strategies (sensu Gross 1996) are viewed as Evolutionary Stable Strategy (Maynard Smith 1982) and occur widely in vertebrates (e.g., Lank et al. 1995; Sinervo and Lively 1996; Garant et al. 2003). In the case of C. georgiana, some males may live and grow for several years, potentially facing high mortality rates, but achieving high reproductive success due to their superior competitive ability. Others may be genetically predisposed to reproduce as early as possible, experiencing lower mortality rates until reaching sexual maturity, but achieve low reproductive success due to their competitive inferiority. Few males survive to reproduce over two breeding seasons (Smith and Roberts 2003a): trading reproductive success against survival may be a viable strategy. Differences in mortality and reproductive success may outweigh each other and lead to the coexistence of the two life histories (as in Salmo salar, Fleming 1998) with frequency-dependent mechanisms stabilizing random fluctuations (Gross 1996).

As we do not have quantitative data on these hypotheses, it remains impossible to say what maintains the extreme variation in body size in male C. georgiana and why differences in their sperm characteristics do not parallel predictions of sperm competition models (Ball and Parker 2000) that seem to fit their mating system best. The inconsistency between theoretical predictions and observed patterns, however, presents a good opportunity to put assumptions and predictions of sperm competition theory to the test and emphasizes the need for further studies exploring the evolutionary background of the mating system of this species.

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