

Implications of diversity in sperm size and function for sperm competition and fertility

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ABSTRACT Sperm competition is now recognised as a potent selective force shaping many male reproductive traits. While the influence of sperm competition on sperm number is widely accepted, its effects upon sperm size remain controversial. It had been traditionally assumed that there is a trade-off between sperm number and sperm size, so that an increase in sperm number would result in a decrease in sperm size, under conditions of sperm competition. Contrary to this prediction, we proposed some time ago that sperm competition favours an increase in sperm size, because longer sperm swim faster and are more likely to win the race to fertilize ova. Comparative studies between species show that in many taxa such a relationship exists, but the consequences of an increase in sperm size may vary between taxa depending on the environment in which spermatozoa have to compete. We present new evidence showing that in mammals longer sperm swim at higher speeds. We also show that mean swimming speed is highly correlated with maximum swimming speed, so even if the fastest swimming sperm are more likely to fertilize, both measures are informative. When individuals of the same species are compared, ratios between the dimensions of different sperm components, as well as the shape of the head, seem better at explaining sperm swimming velocity. Finally, we show that mean and maximum sperm swimming speed determine male fertility. Other studies have shown that in competitive contexts, males with faster swimming sperm have higher fertilization success. We conclude that the available evidence supports our original hypothesis.

KEY WORDS: *sperm head, sperm flagellum, velocity, sperm competition, fertility*

Variation in sperm size

Spermatozoa show a striking degree of variation both in shape and size among animals. Given that most sperm types share a common function (i.e. to fertilize ova), why such huge variation has arisen throughout evolution is puzzling. Two selective forces are likely to have played an important role: sperm competition and female selection (Roldan *et al.*, 1992). When spermatozoa from rival males compete to fertilize ova, there will be strong selection to enhance their competitive abilities (Parker, 1970; Birkhead and Møller, 1998; Simmons, 2001). However, what makes a spermatozoon successful at fertilizing depends to a large extent on features of the environment in which spermatozoa compete (Gomendio and Roldan, 1993). Thus, selection will favour very different sperm traits depending on whether spermatozoa are released in open water (e.g., external fertilizers), have to remain for long periods of time in female storage organs (e.g., birds and

insects), or have a short time window to fertilize after being transferred to a hostile female tract (e.g., mammals).

Sperm competition is a widespread and powerful selective force which is known to influence male reproductive traits at many levels: behavioural, physiological, cellular and molecular (Smith, 1984; Birkhead and Møller, 1998; Simmons, 2001; Gomendio *et al.*, 2006a). While the influence of sperm competition on some of these traits has received widespread recognition, its effects upon sperm size have become a controversial issue.

Comparative studies between species have demonstrated that sperm competition has favoured an increase in testes size and enhanced sperm production in taxa as diverse as mammals (reviewed in Gomendio *et al.*, 1998), birds (Briskie and

Abbreviations used in this paper: CASA, computer assisted sperm analysis; VSL, straightline velocity.

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Montgomerie, 1992), amphibians (Jennions and Passmore, 1993), fishes (Stockley *et al.*, 1997) and Lepidoptera (Gage, 1994). Microevolutionary manipulations have induced changes in testes size and sperm production by modifying the intensity of sperm competition (Hosken and Ward, 2001; Hosken *et al.*, 2001; Pitnick *et al.*, 2001) providing strong support for a causal relationship. There is ample evidence that in competitive contexts males with greater sperm numbers father more offspring (see reviews in Birkhead and Møller, 1998).

Theoretical models proposed that the increase in sperm numbers under sperm competition was achieved at the expense of a reduction in sperm size, and that this trade-off between numbers and size explained largely why sperm are tiny (Parker, 1970, 1982). Contrary to this prediction, Gomendio and Roldan (1991) found that sperm competition selects for longer sperm both in primates and rodents, and suggested that the elongation of sperm under sperm competition is adaptive because longer sperm swim faster and outcompete rival sperm in the race to fertilize ova. Given the controversy generated by this proposal, in this paper we review the information published in the last 15 years and present new evidence. Our original hypothesis includes three different relationships which need testing: (a) sperm size increases with increasing levels of sperm competition, (b) sperm size is associated with sperm swimming speed, and (c) increased swimming speed enhances fertilization success particularly in competitive contexts.

Sperm size and sperm competition

In our original paper we presented data showing that in primates and rodents sperm was longer in species with high levels of sperm competition (Gomendio and Roldan, 1991). The analyses on primates were corrected for phylogenetic effects, while the analyses on rodents were not due to lack of detailed phylogenetic information at the time. This proposal stimulated a great deal of

work on several taxa. Overall, 16 studies have examined the relation between sperm size and sperm competition at the inter-specific level. The main results of these studies are summarized in Table 1.

Results from two studies on mammals seem to contradict our results. Thus, Gage and Freckleton (2003) carried out similar analyses with a larger sample (83 species) and found significant relationships between sperm competition levels and length of the head, midpiece and flagellum, which were lost after controlling for phylogenetic effects. This led to the conclusion that the apparent relationship between sperm competition and sperm size was in fact an artifact due to phylogenetic effects. However, the reason why such relationships were lost after “removing” phylogenetic effects may have to do with the fact that the phylogeny used by Gage and Freckleton (2003) is poorly resolved, so species which belong to the same genus, or sometimes to different families, share a single common node in the phylogenetic tree. Attempts to control for phylogenetic effects with unresolved phylogenies may obscure meaningful biological relationships. A study on bats (Hosken, 1997) found no relationship between sperm length and group size, which in turn is associated with testes mass (an indicator of sperm competition levels). Because bats are exceptional among mammals in that sperm must survive for long periods of time within the female tract, in this group other aspects of female reproductive physiology may exert a strong influence on sperm size, or long-term survival may be a more important sperm trait than swimming velocity.

In mammals, differences between species in sperm length are accounted mainly by differences in the length of the flagellum. The reason why increases in flagellum length may be beneficial under sperm competition is that they may lead to an increase in sperm swimming velocity, because it is the beat of the flagellum that generates the force that drives the sperm forward, and the amplitude of the waveform determines the sperm trajectory (Katz and Drobnis, 1990; Turner, 2003). Contrary to this idea, Anderson

TABLE 1

RELATION BETWEEN SPERM SIZE AND SPERM COMPETITION AMONG STUDIES COMPARING SPECIES

Taxa	Relation between sperm size and sperm competition	Sperm component	Reference
Mammals	Positive	Total length	Gomendio and Roldan (1991)
Bats	None	Total length	Hosken (1997)
Primates	Positive	Midpiece	Anderson and Dixon (2002)
Mammals	Positive	Midpiece	Anderson <i>et al.</i> (2005)
Mammals	Positive, <i>but lost after phylogenetic analysis</i>	Total length, head, midpiece, flagellum	Gage and Freckleton (2003)
Birds	Positive	Total length	Briskie and Montgomerie (1992)
Birds	Indirect relation through SST		
Birds	Positive	Total length	Briskie <i>et al.</i> (1997)
Birds	Indirect relation through SST		
Birds	Positive	Total length, head, midpiece, flagellum	Johnson and Briskie (1999)
Pheasants	None	Total length, head, midpiece, flagellum	Immler <i>et al.</i> (2007b)
	Related to duration of sperm storage		
Finches (Fringillidae)	Positive	Midpiece, flagellum	Immler and Birkhead (2007)
Old World warblers (Sylviidae)	Negative	Midpiece, flagellum	Immler and Birkhead (2007)
Frogs	Positive	Flagellum length	Byrne <i>et al.</i> (2003)
Fish	Negative	Total length	Stockley <i>et al.</i> (1997)
Fish	Positive	Total length	Balshine <i>et al.</i> (2001)
Butterflies	Positive	Total length	Gage (1994)
Moths	Positive	Total length	Morrow and Gage (2000)
Nematodes	Positive	Area (ameboid sperm)	LaMunyon and Ward (1999)

Abbreviation: SST, sperm storage tubules.

and Dixson (2002) and Anderson *et al.* (2005) suggested that sperm competition only favours an enlargement in the size of the midpiece, which contains the mitochondria, increasing in this way the amount of energy generated for sperm movement (but see below). Finally, work on rodents, which have hooks on the sperm head, has shown that sperm competition influences the shape of the hook in such a way that it facilitates the association of several spermatozoa in trains which may increase swimming velocity (Immler *et al.*, 2007a).

There are 11 additional comparative studies which have tested whether sperm competition favours an increase in sperm size in taxa other than mammals (summarized in Table 1). Increases in sperm size in species with high levels of sperm competition have been found in 8 of these studies including such diverse taxa as birds, frogs, fish, butterflies, moths and nematodes. One study has not found such a relationship in pheasants (Immler *et al.*, 2007b), while a negative relationship has been reported in fish (Stockley *et al.*, 1997). Interestingly, a recent study on passerine birds (Immler and Birkhead, 2007) has revealed that while among finches (family Fringillidae) there was a positive relationship between sperm competition and sperm length, among Old World warblers (family Sylviidae) the relation was negative.

In summary, the majority of studies comparing species have found an increase in sperm size under sperm competition. Several reasons may account for the lack of relation or the existence of a negative one in the remaining studies. First, in some studies data have been collected from the literature and the quality of such data may not be entirely reliable. Second, in some taxa spermatozoa are stored in specialized organs in the female tract. In these cases, sperm size is often associated with the size of the sperm storage organ (Immler *et al.*, 2007b; review in Snook, 2005). The use of an experimental approach in *Drosophila* has revealed that male fertilization success is determined by an interaction between sperm size and the size of the female sperm storage organ, so that when the female storage organ is long, long sperm are more successful, but there is no effect of sperm size when the female storage organ is short (Miller and Pitnick, 2002). Sperm-female coevolution is likely to be widespread, and suggests that the influence of the size of female storage organs needs to be taken into account for any effects of sperm competition on sperm size to be detected.

The fact that an increase in sperm size under sperm competition has been favoured in many diverse taxa is surprising given that sperm differ greatly in shape and structure. While in mammals increases in sperm length are achieved mainly through increases in the length of the flagellum, in birds such increases are accounted for largely by increases in the midpiece. Thus, the consequences of increases in sperm size under sperm competition, in terms of sperm function, may differ between taxa.

Much of the controversy about the role of sperm competition in determining sperm size comes from studies which have looked at differences within species. At the intraspecific level, males which face higher levels of sperm competition (e.g., males following alternative mating strategies among fish or insects) do not always have longer sperm (e.g., Simmons *et al.*, 1999). We will not attempt to review this literature here because it falls outside the scope of this paper, but just wish to draw attention to the fact that the degree of differences between males of the same species in sperm size may be smaller than those between species, so at the

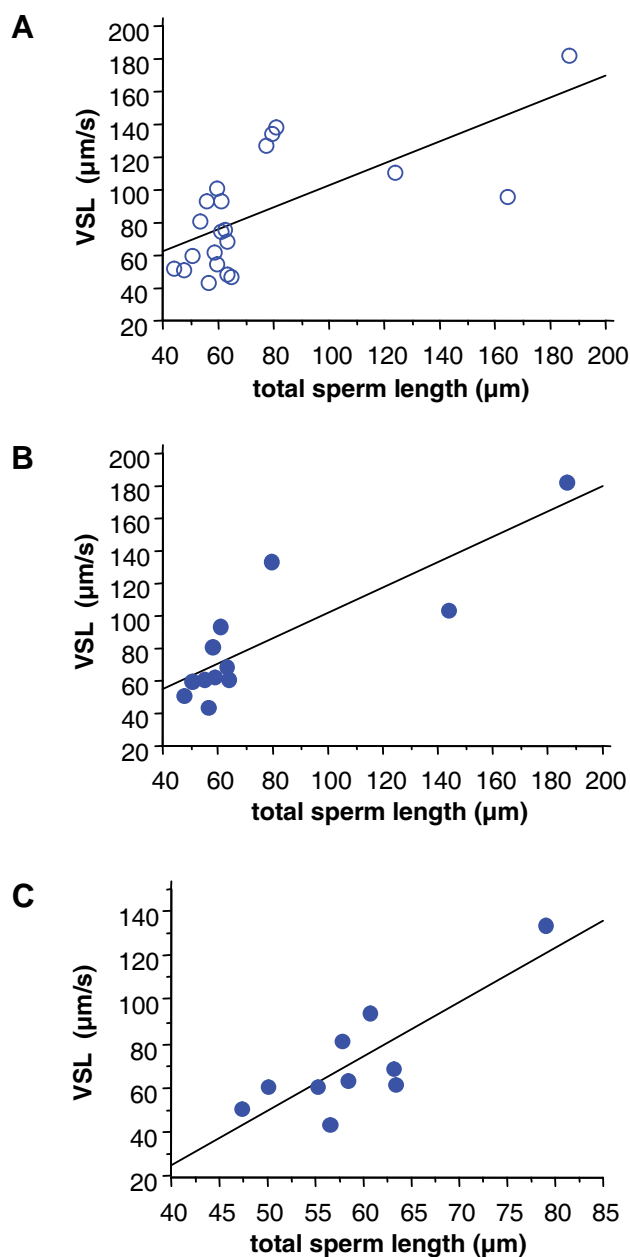


Fig. 1. Relation between total sperm length and sperm velocity in eutherian mammals. (A) Relation among 21 species belonging to 12 families ($r^2 = 0.45$, $F = 15.544$, $p = 0.0009$). **(B)** Relation among 12 families ($r^2 = 0.668$, $F = 20.161$, $p = 0.0012$). **(C)** Relation among 10 families; the two rodent families for which data were available were excluded ($r^2 = 0.582$, $F = 11.15$, $p = 0.0102$). Analyses were carried out with log-transformed variables. Data for straightline velocity (VSL) were obtained from the literature (Mortimer and Mortimer, 1990; Stachecki *et al.*, 1993, 1994; Shivaji *et al.*, 1995; Mahony *et al.*, 1996; Moore and Akhondi, 1996; Trimeche *et al.*, 1996, 1999; Patil *et al.*, 1998; van der Horst *et al.*, 1999; Castellini *et al.*, 2000, 2006; Jayaprakash *et al.*, 2001; Kawaguchi *et al.*, 2004; Lavara *et al.*, 2005; Miró *et al.*, 2005; Baumber and Meyers, 2006; Cox *et al.*, 2006; Slotter *et al.*, 2006; Aurich *et al.*, 2007; Grzmil *et al.*, 2007; Holt *et al.*, 2007; Hung *et al.*, 2007; Immler *et al.*, 2007a; Rijsselaere *et al.*, 2007) and our own unpublished observations. Data for total sperm length were obtained from Cummins and Woodall (1985), Cassinello *et al.* (1998), Gage and Freckelton (2003) and Malo *et al.* (2006).

intraspecific level more subtle measures such as ratios between different sperm components may be more strongly related to differences in sperm swimming velocity. In addition, other factors such as seminal fluid components, or the amount of energy available, may also play an important role. Similarly, microevolutionary manipulations have rendered contradictory results, so that experimentally altered levels of sperm competition in a species in some cases leads to changes in sperm size (La Munyon and Ward, 2002), but not in others (Hosken *et al.*, 2001; Pitnick *et al.*, 2001). Studies differ in the experimental regimes used to alter levels of sperm competition and number of generations, so more work is needed to obtain a clear picture.

Sperm size and sperm swimming speed

Sperm length and sperm velocity at the inter-specific level

The adaptive significance of the increase in sperm size under sperm competition is perhaps the least understood question due to lack of robust evidence. We originally proposed (Gomendio and Roldan, 1991) that in mammals an increase in sperm length may result in faster swimming speed, and thus in a competitive advantage when competing against rival sperm. This was supported by the few data available back then, with a strong positive relation found between total sperm length and maximum straightline velocity in 5 eutherian species.

Studies carried out after our original work was reported have focused on analyses at the intraspecific level and they have generated contradictory results. For example, a relation at the intraspecific level between sperm size and velocity has been found in some studies (LaMunyon and Ward, 199) but this relationship is not always present (Gage *et al.*, 2002). Furthermore, larger sperm achieve higher fertilization success at the intraspecific level in some taxa (Radwan, 1996; Oppliger *et al.*, 2003) but not in others (Morrow and Gage, 2001; Gage and Morrow, 2003; Simmons *et al.*, 2003; Garcia-Gonzalez and Simmons, 2007). This has led some authors to conclude that there is no relationship between sperm size and swimming speed (Snook, 2005). However, no other study has addressed differences between species where sperm length shows a larger degree of variation and thus may have a stronger influence on sperm swimming speeds.

Another line of argument has suggested that looking for relations between sperm length and velocity is “naïve” because it ignores processes of biochemical activation and switching mechanisms and, thus, that little or no relation between sperm length and fertility should be expected (Holt and van Look, 2004). Surprisingly, this view ignores all the evidence showing that hydrodynamic designs are more efficient, which means that the design of spermatozoa would influence velocity, much in the same way as the design of a car is linked to its performance (Birkhead and Immler, 2007). Thus, major differences in the design and structure of spermatozoa may impose constraints on sperm swimming velocity which will define the range of swimming velocities which are potentially achievable; within this range, actual swimming velocity will be influenced by other external regulators such as those present in the male and female tracts. Such modulators of sperm velocity come into play after spermatozoa are produced in the testis, first repressing its expression and then causing an activation and further hyperactivation; these are

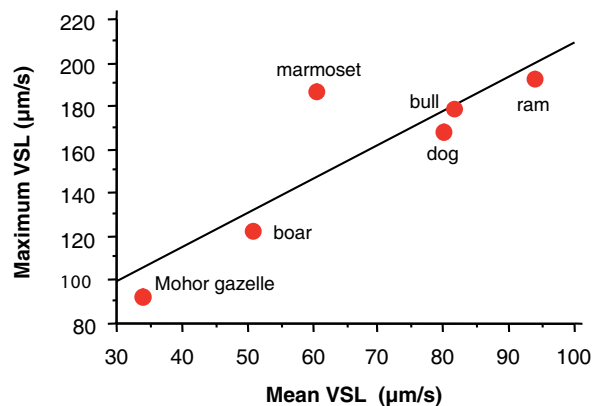


Fig. 2. Relation between mean and maximum straightline velocity (VSL) among eutherian mammals. Data are from Table 2 in Holt *et al.* (2007), with the exclusion of values for the grey short-tail opossum (see text for explanation). Values for the dog were calculated from their Fig. 1B since they were not included in the table. The graph shows nontransformed data with analyses carried out using log-transformed values ($r^2 = 0.753$, $F = 12.226$, $p = 0.025$).

likely to determine actual swimming velocity within the limits imposed by sperm design and structure.

To further examine links between sperm length and velocity, we compiled more information on mammals and carried out comparative analyses. Data from a total of 21 species (12 families) of eutherians were collected and analyzed. We deliberately left out marsupials because of their different sperm structure and the fact that, in many species, spermatozoa swim in pairs. For some species, several studies were available and, in these cases, information was pooled. Some results were regarded as inadequate (e.g., swimming velocity from refrigerated or frozen-thawed spermatozoa) and they were not included. Care was taken to identify sperm swimming results that corresponded to fresh, non-capacitated spermatozoa. We employed information on average straightline velocity (VSL; i.e., velocity calculated using the straight-line distance between the beginning and end of the sperm track), because information on maximum VSL was not always available. Nevertheless, average VSL is a very good measure of sperm swimming velocity and it significantly correlates with maximum VSL (see below). Earlier studies have also found strong relations between VSL and the other two descriptors of swimming velocity (curvilinear velocity, VCL, and average path velocity, VAP) (e.g., Malo *et al.*, 2005). To remove possible phylogenetic effects we carried out comparative analyses by independent contrasts (CAIC) using log-transformed data (Purvis and Rambaut, 1995) and testing the relations between contrasts by regression analyses forcing the regression through the origin. Analyses were done using both a “morphological tree” (Springer *et al.*, 2004; Ferguson-Smith and Trifonov, 2007) and a “molecular tree” (Springer *et al.*, 2004) for mammalian orders, with relationships within Cetartiodactyla resolved based on Hernández Fernández and Vrba (2005) and Ropiquet and Hassanin (2005). Comparisons were done at both the species and the family levels.

Analyses using data from the 21 species revealed a strong positive relation between total sperm length and straightline velocity ($r^2 = 0.45$, $p = 0.0009$) (Fig. 1A) and this result remained statistically significant after controlling for phylogenetic effects

with CAIC using both the morphological tree ($r^2 = 0.27$, $p = 0.02$) and the molecular tree ($r^2 = 0.27$, $p = 0.02$). In order to further minimize phylogenetic effects analyses were carried out comparing families. When data from the 12 families were analyzed, again a highly significant relation between total sperm length and straightline velocity was found ($r^2 = 0.668$, $p = 0.001$) (Fig. 1B), which remained significant after removing each family, including rodents ($r^2 = 0.582$, $p = 0.01$) (Fig. 1C). The relation among families was also statistically significant after controlling for phylogenetic effects with CAIC using both the morphological tree ($r^2 = 0.42$, $p = 0.03$) and the molecular tree ($r^2 = 0.44$, $p = 0.03$).

Thus, our early suggestion that sperm length confers an advantage because it results in faster swimming speed is supported by analyses including a larger number of species representing a wider range of taxa among eutherian mammals.

Sperm length and sperm velocity at the intra-specific level

Efforts to identify which sperm phenotypic traits determine swimming velocity have not always been successful when individuals of the same species have been compared (Gage *et al.*, 2002; Birkhead *et al.*, 2005). One possibility is that rather crude measures (e.g. total sperm length), which can explain differences between species in swimming velocity, may not be as informative within species due to the smaller degree of variation found at this level. In a study of natural populations of red deer (Malo *et al.*, 2006), we reasoned that the size and shape of the head will represent the degree of resistance or drag, and that ratios between the components of the flagellum may give a better idea than the size of each component of the optimal balance needed to propel the spermatozoon forward. We found that sperm with elongated heads swim faster, and that the effect of head shape upon sperm hydrodynamics is considerable. Contrary to expectations, we found that the size of the midpiece shows a negative relationship with swimming speed, suggesting that it is not a major determinant of the energy needed to achieve higher swimming speeds. Finally, the length of the principal plus terminal piece in relation to the rest of the flagellum influences sperm swimming velocity and, in particular the straightness of the trajectory, suggesting that the roles played by the midpiece and the rest of the flagellum should be considered jointly. In addition to the influence that size of the rest of the flagellum may have in generating the force needed for sperm movement, it may also determine the amount of energy generated. Recent studies show that most of the energy required for sperm motility is generated by glycolysis, rather than oxidative phosphorylation. Glycolysis depends on a sperm-specific glycolytic enzyme which is tightly bound to the fibrous sheath (Miki *et al.*, 2004; Miki, 2007), a cytoskeletal structure that extends along the principal piece of the flagellum (Turner, 2003; Eddy, 2007). Thus, actual swimming speed will be the result of the combined design of different sperm components.

Mean and maximum sperm velocity

It has been argued that mean values of velocity descriptors provided by computer-assisted sperm analysis (CASA) systems are not representative of a sperm popu-

lation, because there are sperm subpopulations which may be more meaningful biologically, and that there is no relationship between mean and maximum values of sperm swimming velocity casting doubt on their significance (Holt *et al.*, 2007).

Detailed analysis of the data presented in support of this claim reveals several problems. Frequency distribution of VSL values in a sample of common marmoset (*Callithrix jacchus*) epididymal spermatozoa was presented to illustrate a lack of normal distribution and to argue that the use of mean VSL values would be inadequate for this sample; analyses of other individuals apparently showed similar results with no normal distribution (Holt *et al.*, 2007). It is not clear how generalized this phenomenon is. Our analyses of frequency distribution of sperm motility descriptors in Iberian deer from natural populations revealed a normal distribution of VSL values at both the inter-individual (Fig. 1D in Gomendio *et al.*, 2007) and intra-individual level (unpublished results). Thus, in this case the use of mean values is informative and captures the variation found both between and within individuals.

With regards to relations between mean and maximum VSL values across mammals, Holt *et al.* (2007) concluded that «there is no simple linear relationship between the mean VSL value and

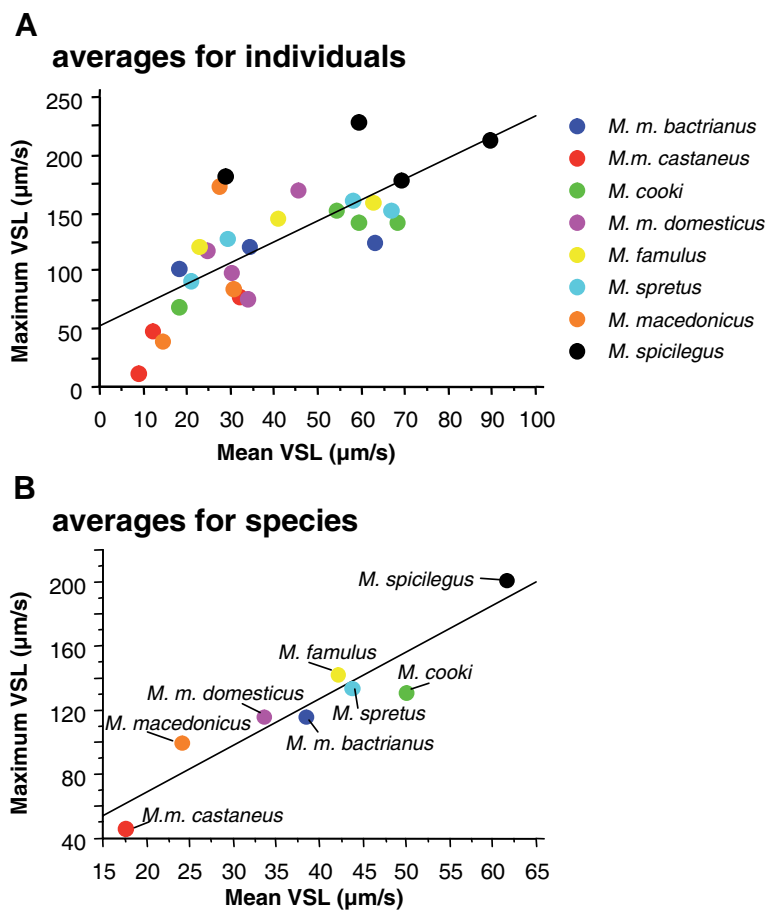


Fig. 3. Relation between mean and maximum straightline velocity (VSL) among mouse species (genus *Mus*). (A) Relation between mean and maximum VSL among individuals of eight species of *Mus* ($r^2 = 0.636$, $F = 45.501$, $p < 0.0001$). (B) Relation between mean and maximum VSL between average values for eight species of *Mus* ($r^2 = 0.872$, $F = 40.788$, $p = 0.0007$). The graph shows nontransformed data with analyses carried out using log-transformed values.

the maximum possible value.» However, it is clear that one of the species included in their analysis (the grey short-tail opossum) stands out as an outlier for two very important reasons. First, it is the only marsupial among various eutherian species included in the analysis and, second, sperm structure and function in this species are clearly different with sperm swimming in pairs. If data

from this species are not included in the analysis, there is a good relation between medium VSL and maximum VSL among eutherian species (Fig. 2). Thus, contrary to the conclusion by Holt *et al.* (2007), there is a significant relation between both mean and maximum VSL values across taxa.

We examined this relation further by looking first at mouse spermatozoa in a group of closely related species deriving from natural populations and kept under controlled conditions, and then in natural populations of red deer from Spain. The aim of these analyses is to examine possible relations between velocity descriptors and, furthermore, a possible relation between mean and maximum VSL with fertility.

In mice, a comparison of mean and maximum VSL reveals that there is a significant positive relation between both parameters among different individuals of eight different species of the genus *Mus* (Fig. 3A). When mean values for the different species are compared, again, a highly significant positive relation is observed (Fig. 3B).

Among Iberian red deer, mean VSL and maximum VSL for individual males were plotted and a significant positive relation was found (Fig. 4A). In fact, previous studies had already shown that all descriptors of sperm swimming velocity are closely associated (Malo *et al.*, 2005). Thus, although fertilization may be achieved by the fastest moving spermatozoa in a sperm population (since they will be able to better negotiate barriers in the female tract and establish a sperm reservoir in the oviduct from which they will swim actively towards the ovum), mean values for a sperm population are representative and meaningful.

Swimming speed and fertilization success with and without sperm competition

The evidence gathered so far shows that sperm competition does select for an increase in sperm size in a wide range of taxa and that, at least in mammals, such increases lead to an increase in sperm swimming velocity. The final question that we need to address is whether increases in sperm swimming velocity do enhance fertilization success and competitive ability. The evidence in this respect is limited but clear-cut. Sperm swimming velocity is a major determinant of male fertilization success in non-competitive contexts (Froman *et al.*, 1999; Levitan, 2000), which becomes the best predictor of competitive success when rival ejaculates compete (Birkhead *et al.*, 1999; Gage *et al.*, 2004). This work was carried out on birds and fish so we decided to explore the matter further with mammals.

Previous studies by our research group (Malo *et al.*, 2005; Gomendio *et al.*, 2006b, 2007) had already uncovered a relation between mean sperm velocity descriptors (VCL, VSL, VAP) and male fertility in the absence of sperm competition. These data thus represent a good opportunity to test relations between both mean VSL and maximum VSL and fertility after artificial insemination trials (performed with constant numbers of spermatozoa and identical time-intervals of insemination in relation to oestrus synchronization). These new analyses reveal that there is a significant relation between mean VSL and fertility (Fig. 4B), as reported previously, and also between maximum VSL values and fertility (Fig. 4C). Thus, sperm swimming velocity is also a main determinant of fertility in mammals, and all measures of velocity seem to convey the same kind of information about sperm

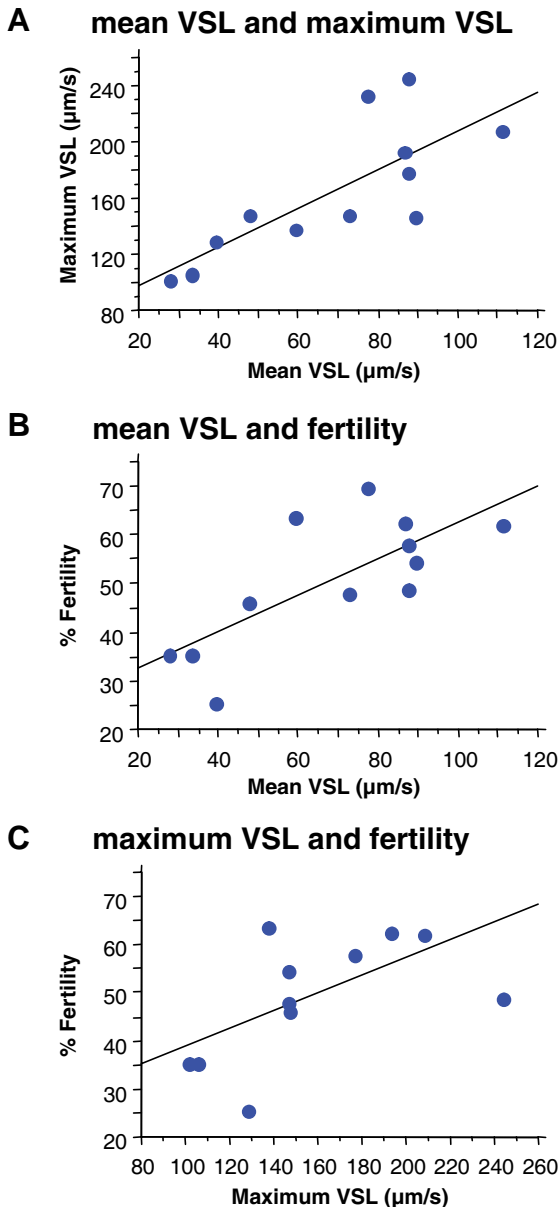


Fig. 4. Relation between mean and maximum straightline velocity (VSL), and with fertility, among male Iberian deer. (A) Relation between mean and maximum VSL among individual males of Iberian deer ($r^2 = 0.705$, $F = 23.938$, $p = 0.0006$). **(B)** Relation between mean VSL and fertility among Iberian deer ($r^2 = 0.589$, $F = 14.348$, $p = 0.0036$). **(C)** Relation between maximum VSL and fertility among Iberian deer ($r^2 = 0.467$, $F = 8.769$, $p = 0.0143$). Fertility corresponds to percentage of females giving birth after artificial insemination with a constant number of spermatozoa and a similar time interval after oestrus synchronization. The graph shows nontransformed data with analyses carried out using log-transformed values.

performance. While it seems clear that sperm velocity is important when sperm have to win the race to reach the ova against rival sperm, it is not entirely clear why it also determines fertility when there is no competition between males. In this case, swimming speed may be a good indicator of the ability of spermatozoa to overcome physical barriers in the female tract, to penetrate ova vestments, or simply spend less time exposed to a hostile female tract.

Conclusions

Sperm competition does seem to favour an increase in sperm size in a wide range of taxa, but the adaptive significance of such changes may vary between taxa. We present new evidence showing that in mammals increases in sperm length are associated with increases in swimming speed. Average swimming speed is strongly related to maximum swimming speed so both measures are good indicators of a male's competitive ability. Sperm swimming velocity is an important determinant of fertility in non-competitive contexts, which determines fertilization success when rival males compete. Some of these relationships are not as clear at the intraspecific level, suggesting that the selective forces may operate differently at the macroevolutionary and microevolutionary level.

Acknowledgements

We are very grateful to Julián Garde and Aurelio Malo for data and analyses of deer sperm size and function and to José Benavent-Corai for phylogenetic analyses. We also thank Ana Soler, Andrés García, Concepción Magaña, María R. Fernández-Santos, Milagros C. Esteso, Bárbara Lang-Lenton and Raquel Lorensu for their valuable help with field and laboratory work. Analyses of sperm swimming velocities in rodents were carried out using a Hobson Sperm Tracking system through the generosity of W.V. Holt (Institute of Zoology, London). Funding was provided by Ministerio de Educación y Ciencia, Instituto Nacional de Investigación y Tecnología Agraria and Junta de Comunidades de Castilla-La Mancha, all from Spain, and the European Regional Development Fund. ERSR is a recipient of a Royal Society Wolfson Research Merit Award.

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