Sexual selection and sperm diversity in primates

Guillaume Martinez, Cécile Garcia

TITLE

Sexual selection and sperm diversity in primates

AUTHORS

Guillaume MARTINEZ[1,2,*] & Cécile GARCIA[3]

AFFILIATIONS

[1] Hôpital Couple-Enfant, Centre Hospitalier Universitaire de Grenoble, UM de Génétique Chromosomique, F-38000 Grenoble, France. Mail: gmartinez@chu-grenoble.fr

[2] Genetic Epigenetic and Therapies of Infertility, Institute for Advanced Biosciences INSERM U1209, CNRS UMR5309, F-38000 Grenoble, France. Mail: gmartinez@chu-grenoble.fr

[3] UMR 7206 Eco-anthropologie, CNRS - MNHN – Université de Paris, Musée de l'Homme, 75016 Paris, France. Mail: cecile.garcia@mnhn.fr

[*] Corresponding author: gmartinez@chu-grenoble.fr

KEYWORDS: sexual selection; sperm competition; semen evaluation; testes; sperm allocation; trade-off

ABSTRACT: 150 words maximum

Many aspects of primate sperm physiology and reproductive behavior have been influenced by sexual selection, especially in taxa exposed to sperm competition where females mate with multiple partners. Primate sperm diversity reflects therefore the evolutionary divergences of the different primate species and the impact of a combination of variables exerting selection pressures on sperm form, function, and competition. Thereby, mating systems, life cycle or ecological variables are some of the important factors driving sperm diversity and explaining variation in terms of sperm morphology, parameters or male sexual characters. Here, we address primate sperm diversity through a compilation of all data available in the literature concerning primate sperm parameters and relationships between them. We then review the most important variables, e.g. seasonality, social constraints or trade-off between investments in precopulatory and postcopulatory sexual traits, which can influence primate sperm diversity and discuss also their relevance to our understanding of human reproduction.

INTRODUCTION

Mammalian spermatozoa are motile, highly differentiated and oriented haploid cells with a specific size, shape and axes of symmetry. They are composed of a head and a flagellum and of various subcellular structures adapted to the physiological processes that are essential for the reproduction of the species (capacitation, acrosomal reaction, gametic fusion). Basic head structure is a haploid nucleus containing a highly compacted chromatin, with very little cytoplasm and covered at the apical pole by the acrosome, a large secretion vesicle derived from the Golgi apparatus. The flagellum ensures cell mobility and is divided into three parts: an intermediate piece surrounded by a mitochondria sheath, a large main piece and a short terminal piece. This base structure is preserved in all mammals with specificities for some taxa such as the head sickle shape in rodents.

Primates are an order within placental mammals that includes more than 500 species. While primate sperm displays a considerable uniformity, there are still some variations between species in terms of sperm morphology and overall sperm parameters. This primate sperm diversity reflects the evolutionary divergences of the different taxa and is the result of a combination of variables exerting selection pressures on them, such as mating system variables, life cycle characteristics or ecological variables.

The first part of this review will describe primate sperm diversity through a compilation of all data available in the literature. The second part will be devoted to the most important mechanisms and factors influencing sperm form, function, and competition across primates.

1. About primate form and sh-ape

1.1. Sperm morphometry

The action of centripetal forces on spermatozoa evolution has considerably reduced morphological variations between the different species and created an overall mammalian morphometric uniformity (1980 Gould). Sperm global shape is well preserved among primates, but some interspecies variations are still observed, mainly regarding spermatozoa length. We compiled species-specific primate sperm morphometric data of 76 primates (table 1). Across all species analyzed, mean±SE total sperm length is 70.69±10 µM with a ratio of 2.4 between the shortest and longest representatives *Lepilemur mustelinus* (52 µM) and *Ateles paniscus* (124.61 µM). With a 56.15 µM total length, *Homo sapiens* is below average and also the shortest representative of Hominidae family, more than 15% less than *Pongo pygmaeus*. Head length ranged from 2.8 to 9.0 µM with a mean of 5.83±0.84 µM, accounting for 8.2 % of total sperm length. Midpiece length ranged from 3.56 to 20.7 µM with a mean of 10.07±2.13 µM, accounting for 14.3 % of total sperm length. Tail length ranged from 17.3 to 83.5 µM with a mean of 55.14±10.10 µM, accounting for 77.9 % of total sperm length. Human sperm are again under average among primates, especially regarding the midpiece length.

Sperm length is the result of a complex set of evolutionary pressures such as the female reproductive tract (2012 Higginson), metabolic requirements of sperm (2011 Gomendio) or sperm competition which can exert a positive (2009 Fitzpatrick) or negative (1997 Stockley) influence (see below in 2.1). In human, having long spermatozoa appears to be an advantage as the overall lengths of sperm components and their degree of variability within an ejaculate have been positively associated with sperm concentration and motility (2013 Mossman), which are significant fertility determinants.

Regarding the head, human sperm is similar to the chimpanzee shape (ellipticity=1.61 and elongation=0.23). However, the pleiomorphic nature of human ejaculate allows us to identify two populations similar to those observed in other great apes, albeit with smaller volumes. The first is similar to orangutans sperm with a large paddle-shaped head and thinner in the vertical dimension (ellipticity=1.40 and elongation=0.17). The second is similar to gorilla, with a shape intermediate to the previous two (ellipticity=1.38 and elongation=0.16).

1.2. Sperm parameters

We compiled literature data on sperm parameters from 43 primate species. Summarized in table 2, these data support the known high heterogeneity of primate ejaculates, both at the inter- and intra-species levels.

1.2.1. Collection method

1.2.1.1. Masturbation

Masturbation is the natural and best collection method to obtain ejaculates truly representative of testicular function. In human, semen analyses are therefore carried out on samples obtained by masturbation under specific disinfection and abstinence protocols. While the aseptic conditions of the human clinic are clearly not reproducible for other primates, it is still possible to obtain great ape masturbation samples from Gorilla (1997 Pope, 2005 O'brien, 2008 Nascimento), Pan (1988 Marson, 1993 Gould, 1995 Young, 1998 Younis, 2004 Kuehl, 2005 Agca, 2008 Nascimento, 2018 Yu) and Pongo (1995 Joslin), with higher total sperm counts and fewer abnormal forms than samples obtained via electrostimulation methods (1989 Schaffer, 1995 Gould, 1995 Young, 1996 Gould). Semen collection can be manual as part of specific training or assisted via artificial vaginas.

As male masturbation is the most frequent sexual behavior observed after copulation (2003 Thomsen, 2005 Frearson, 2012 Dixson) for primate species, another method consists in collecting the products of punctual masturbation on the ground (in Macaca (2014 Thomsen), Papio (1969 Kraemer) and Chlorocebus (1999 Hiyaoka)). This non-invasive collection method allows some precious semen analysis (2004 Dejucq-Rainsford, 2006 Thomsen, 2012 Inoue), but soil contamination prevents us from accurately assessing the quality and fertilizing potential of the male. Another pitfall associated with these samplings is the potential difficulty of quickly collecting the material prior its consumption by the male (personal observations).

1.2.1.2. Epididymal extraction

Samples obtained by epididymal extraction are numerous and are mainly collected opportunistically following castrations (2000 Gupta) or in post-mortem contexts (2001 Kusunoki, 2005 Anderson, 2008 Dong). Analysis of sperm from the tail of the epididymis allows to acquire some data on sperm morphometry or production but is not representative of an individual's ejaculate and fertility potential.

1.2.1.3. Electro-stimulation

Electro-stimulation (ES) is the most widely used method for primate semen collection (1968 Ackerman, 1978 Gould, 1980 Platz, 1983 Bader, 2002 Aslam, 2003 Amboka, 2007 Vidal, 2009 Da Silva, 2016 Oliveira, 2016 Swanson, 2017 Sampaio, 2018 Devilliers, 2019 Arakaki) including Human (1996 Nehra). Using rectal probe or penis electrodes, ES has many practical and logistical advantages (no training required, programmable in time, sleeping individuals), but this approach has also several drawbacks.

Indeed, ES is restricted to facilities with a laboratory because of the devices needed for

basic (incubator, centrifuge) or advanced sperm analysis (CASA device) and the monitoring period required at the end of the experiment due to the invasive nature of the method. Beyond the dangers associated with the capture and immobilization of an adult male in the wild, this induces a high level of stress to the subject but also to the group as a whole (2014 Thomsen), with possible negative repercussions at reintroduction time. In order to obtain consistency in physiological response, specific protocols have to be establish for each species regarding both anesthetic and stimulation phase (1990 Durrant, 1996 Morrell). Anesthesia presents significant health risks for the animals and limits the sampling frequency, whereas the stimulation phase requires trained technicians, with rectal probe placement being essential to obtain ejaculation and avoid burns. Even with robust protocols, some studies indicate that ejaculates obtained by ES tend to contain more immature sperm (1992 Matsubayashi, 1996 Morrell, 2014 Thomsen) and more coagulum formation (1986 Wildt, 1989 Schaffer) than those obtained by masturbation.

It should be noted that urethral massage is a good complement to electro-ejaculation techniques to recover residual semen and increase the volume of the sample.

Finally, ES appears to be best suited for larger primates and safer alternative methods (vaginal washing and penile vibrostimulation; see below for further details) have been developed for smaller species for which ES may be unsuitable or unsuccessful (1996 Morrell, 2000 Kuederling, 2004 Schneiders).

1.2.1.4. Vaginal washing

Vaginal washing (VW) consists of retrieving a male's ejaculate by washing a female's vagina quickly after a successful coitus. This method has been developed in small primates, such as marmosets (1996 Kuederling, 1996 Morrell, 1997 Morrell, 1998

Morrell, 2004 Schneiders) and macaques (1973 Cho), for which sedation is not required to obtain the sample. Although VW allows the collection of natural ejaculates for assisted reproduction techniques (1996 Kuderling, 1996 Morrell, 1997 Morrell, 1998 Morrell), it is less efficient for sperm parameters analysis as the sample is contaminated by secretions and some of it is lost in the female genital tract (1996 Kuderling, 1996 Morrell). VW protocols are time-consuming to set up and carry out, and have to be species-specific (2004 Schneiders). The VW is therefore effective but limited to specific applications in small species at this time.

1.2.1.4. Penile vibrostimulation

This procedure provides ejaculate through normal ejaculation via application of vibration to the penis of a restrained individual. Although there is no need to sedate the animal, it must be trained to the restriction chair. This method proved its worth in marmosets (2000 Kuederling, 2005 Hernandez-Lopez, 2005 Valtonen, 2012 Valle, 2016 Swanson, 2018 Arakaki), macaques (2000 Kholkute) and saïmiris (1997 Yeoman, 1998 Yeoman).

The main benefit of this procedure is, as with masturbation, the production of a natural ejaculate that displays a higher number of motile and total sperm versus electrostimulation (1995 Young, 1997 Yeoman, 1998 Yeoman). The main concern is that this protocol is obviously challenging to implement for great apes, but recent studies (2018 Arakaki) pointed out that, with species-specific adaptations, this technique could be very promising.

In conclusion, from a practical point of view, inter-species constraints do not allow to propose an optimal method consensus and each collection must be considered on a case-by-case basis according to the species and to the context. From a biological point of

177 view, ejaculates obtained through natural ejaculation (masturbation and
178 vibrostimulation) proved their superiority and should be favored when possible.

179 **1.2.2. Sperm motility**

180 The average primate has about two-thirds motile sperm in an ejaculate, a proportion that
181 logically correlates with vitality (measured as the percentage of intact membrane
182 sperm). It is challenging to interpret motility data because of the very high variability in
183 the percentage of motile sperm with ejaculates ranging from almost fully motile to fully
184 immobile present in all families.

185 The heterogeneity of motility data comes in part from the inherent limitations of data
186 collection protocols (discussed in section 1.3), but mostly from the existence of sperm
187 subpopulations in mammalian ejaculates (2004 Holt). Many studies concluded that
188 variations among these sub-populations have functional relevance with identified
189 associations to fertility or post-freezing survival outcomes (2001 Thurston, 2006
190 Martinez, 2008 Muino, 2009 Ortega-Ferrusola, 2010 Dorado, 2013 Ramon, 2014
191 Beracochea, 2015 Yaniz, 2016 Santaloria).

192 Although the development of computer-assisted sperm analysis (CASA) systems has
193 made it possible to bring more accuracy and depth to mobility studies, the majority of
194 the observations compiled here have been carried out manually by technicians, as these
195 systems are rarely used outside of human medicine. Among CASA parameters, average
196 straight-line velocity is recognized as a main factor in fertility (1999 Birkhead, 2005
197 Malo) and have previously been correlated with total sperm length (2009 Lupold, 2009
198 Gomez Montoto, 2011 Tourmente) and relative testes mass in mammals (2011
199 Tourmente). However, in light of the limited data available for mobility parameters in
200 the literature (table 3), it is not yet established whether these results can be reproducible

for primates alone.

Nevertheless, we can observe that human has a curvilinear velocity, a proxy for the effective sperm velocity, lower than that of other primates. This confirms conclusions of previous studies (2011 Maree) showing that sperm from polygynandrous primate species swims faster than human one. Motility percentages for *Homo* and *Gorilla* taxa are lower than those of *Pan* and *Pongo*, which suggests that sperm from polygynandrous primates swim faster than sperm from species less exposed to sperm competition in general. It is also plausible that the mobility alterations in *Homo* and *Gorilla* are only the result of the pleiotropism present in the ejaculate of these taxa, abnormal forms sperm producing lower velocities than normal form sperm. Again, the limited number of studies using CASA does not allow us to reach a robust conclusion. Other issues would also benefit from more CASA studies, for example, we still do not know if larger sperm swim faster when there is a higher risk of sperm competition in some primate species like demonstrated in rodents (2011 Montoto).

1.2.3. Sperm morphology

In human reproductive medicine, the criteria for defining normal-form sperm (NFS) have been established by averaging the observed characteristics of the sperm population that reach the oocyte (2010 Cooper). Morphological analyses of assisted reproduction centers are mostly based on the World Health Organization guidelines on semen analysis, which use very strict analysis criteria and a pathological cutoff established at 4% NFS. Based on these criteria, the species presenting the lowest and highest rates of NFS are from the Hominidae family with 23.75% and 98.5% NFS for *Gorilla gorilla* and *Pongo pygmaeus* respectively.

Of all 43 primate species studied, the spermatozoa from the ejaculate of Human and

Gorilla spp. are the only ones characterized by an extreme pleiomorphism with 23.75% and 32.22% NFS respectively. These two species also exhibit more variation in size and shape within a single ejaculate than some species between them. The pleiomorphic nature of sperm found in both species does not seem to affect their fertility, whereas when abnormal forms are found in other species, they are associated with infertility or occur outside the reproduction period (1983 Gould, 1993 Seier, 2002 Hernandez-Lopez, 2016 Pina-Aguilar). Again, these sub-populations could present functional relevance and play a key role in fertility. However, the relationship between sperm morphology and fertility is still debated and results are controversial (for review, see 2016 Garcia-Vasquez). These very low NFS rates could be explained by the lack of pressure from sperm competition. Indeed, it has been shown in other taxa that an absence of sperm competition leads to increases of abnormal sperm form in the naked mole-rat (2011 van der Horst) and of morphological variability in insects (2011 Fitzpatrick). Since gorillas and humans are considered polygynous or mildly polygynous species (2005 Marlowe), they are not supposed to be exposed to high sperm competition pressure and they may therefore allocate their resources to other parameters (see below for further details).

It is to note that the New World monkey *Callithrix penicillata* is also described with a low NFS (30,17%) but this species should not be considered as pleiomorphic, as this affirmation is based on a single study (2018 Arakaki) of four animals collected during the rainy season and the *Callithrix* genus is known for its large range of NFS (range 25% to 91.9% NFS in *Callithrix jacchus* according to data from 127 individuals among 9 studies: 1991 Cui, 1996 Cui, 1996 Morrell, 1997 Morrell, 2004 Schneiders, 2009 Da silva, 2014 Valle, 2016 Swanson, 2018 Arakaki).

1.3. Testes mass

Total testes mass of 71 primate species are compiled in table 4 and illustrate primate diversity, with a ratio of 400 between the lightest and heaviest representatives *Cebuella pygmaea* (0.16 g per testis) and *Pan paniscus* (67.6 g per testis). With an average of 21.54±2.85 g per testicle, and despite a high body weight, human testicular mass is similar to that of most Macaca species (mean Macaca: 25.23±5.44 g) and inferior to Papio species (mean Papio: 34.38±7.16 g) and some Atelidae (*Ateles paniscus*: 32.12 g, *Brachyteles arachnoides*: 39.18 g – one data point per species). Among Hominidae, humans have heavier testicles than gorillas (12.84g ±1.24 g) and orang-utans (17.65±1.2 g), but much lighter ones than Pan species.

When this mass is adjusted to body weight (figure 1), human appears to have relatively small testicles and to be closer to polygynous species like Gorilla than to polygynandrous species Pan, despite a closer common ancestor. Overall, we find that polygynandrous primates have bigger relative testes mass than those found in other mating systems, confirming results of previous studies (2016 Parker, 2018 Dixson) on the relationships between relative testes sizes and mating systems (see section 2.1. for discussion).

1.4. Limitations

While based on numerous independent sources, it should be kept in mind that all data on primate sperm should be interpreted in regard to the main sources of possible variation due to subspecies, populations, individuals, time collection and technical differences. Indeed, variations are reported at the subspecies level (2009 Steinberg), but also between populations of identical taxa but of different geographical locations (2014 Valle). Many environmental factors, such as season (2000 Gupta; 2002 Muehlenbein; 2002 Hernandez- Lopez; 2008 Hernandez-Lopez; 2009 Cerda Molina) and toxic

exposition (2007 Hung; 2011 Falzone; 2013 Nyachieo), may also play a role, as well as individual factors, such as age (2006 Sloter), sexual maturity (1988 Marson), abstinence time (1989 Marson, 2017 Alipour) and current health status. At a technical level, there is no universal standard method for the analysis of primate sperm parameters (2010 Auger). Variations may therefore be due to the use of different procedures (2005 Hernandez-Lopez), such as the sperm recovery method (1995 Young; 1998 Yeoman; 2000 Kuederling; 2004 Schneiders) or sample conditions (fresh, washed, frozen, contaminated; 1986 Katz). For example, despite the existence of WHO recommendations in humans, many different stains are still used such as, Haematoxylin/Eosin, Shorr,Papanicolaou, Bryan-Leishman, DiffQuik, Quickdip, Harris-schorr and SpermBlue (2009 van der horst, 2010 Cooper, 2010 Maree), which could explain in part the reported variations

2. Factors of sperm diversity

Here, we will review some of the most important variables (e.g. mating-system variables, life-history traits, ecological variables) influencing sperm form, function, and competition across primates.

2.1. Mating systems

Sperm characteristics in group-living animals, such as primates, will depend on the relative numbers of males and females mating with each other in a given social unit or population i.e. on mating systems. Four types of mating systems are commonly found among primates (2012 Dixson): monogamy (one male - one female), polygyny (one male – multifemale, also often called harem systems), polyandry (one female – multimale, mostly in cooperatively breeding primates) and polygynandry (i.e. multimale-multifemale, MMMF). Concerning polygyny, the extent and exclusiveness of

this mating system will be affected by the distribution of mating opportunities in space and time (dispersion of females and synchronicity of their fertile periods; see further details on seasonality), in interaction with female behavior, i.e. the ability to monopolize them (see below for further details on sexual monopolization and coercion). The strength of intra-sexual selection in male primates, via sperm competition, correlates with the mating system, with higher levels of selection in MMMF systems (such as macaques, baboons and chimpanzees) and then bigger relative testes size (i.e. greater investment in sperm production) and mass (figure 1) than in monogamous (e.g., owl monkeys and gibbons) or polygynous (e.g., proboscis monkeys, gorillas and geladas) mating systems (2016 Parker, 2018 Dixson). Sperm competition does seem to be the primary agent of testes size evolution in primates with large testes being adaptive under conditions where females mate with multiple partners during their fertile period (because they usually contain a greater volume of seminiferous tissue). Testes size in humans occupy an intermediate position between gorillas and chimpanzees (2014 van der Horst & Maree). As suggested by Dixson (2018), this relatively small testes size does not seem to provide evidence for a significant role of sperm competition during human evolution.

Besides testes size, some other traits have been under positive selection, via sperm competition (and/or cryptic female choice, see below), in polygynandrous primates (and more generally polygynandrous mammals): faster rates of spermatogenesis, greater capacity to sustain high sperm counts, copulatory plug formation, etc… (2018 Dixson). Indeed, increased levels of sperm competition are expected to result in increased sperm numbers (increased semen volume and sperm concentration; 1990 Parker, 2012 Montoto, 2013 Lupold), increased sperm length (figure 2), and a higher percentage of

sperm with normal morphology (figure 2), progressive motility, and viability (2009 Pitnick). For instance, ejaculate size should increase with the incidence of rapid female polyandry (i.e. the rate of mating relative to the duration of sperm survival in the female reproductive tract), such as in polygynandrous species compared to monogamous species with extra-pair matings and slower female polyandry (2016 van Schaik). Sperm length has also been linked to the intensity of sperm competition, with males producing longer (and faster swimming) sperm in species with promiscuous females, which are probably adaptations to reach the ova first (1991 Gomendio & Roldan). Other morphological parameters, such as the size of sperm midpiece (indicator of mitochondrial loading and thus motility), are larger in primate species whose females mate polyandrously and males have larger testes in relation to body weight (2004 Dixson & Anderson, 2011 Maree), with human sperm having smaller midpiece volumes than any of the 40 primate species measured by Anderson et al. (2005) (with the exception of the common marmoset). Sperm kinematic parameters (swimming characteristics) might also be related to mating systems, with sperm from MMMF primate species swimming faster and with greater force than sperm from polygynous primate species (2008 Nascimento). Nevertheless, as discussed previously (section 1.2.3.), these findings have to be taken with caution because the sample size was small and semen samples from each species were prepared using different methods. Semen quality parameters, such as the percentage of normal sperm in the ejaculate, are also related to the levels of sperm competition experienced by the different species (figure 2). The high incidence of pleiomorphism in Human and Gorilla, associated with the striking similarities between other sperm traits (e.g. ejaculate volume, sperm concentration and motility, table 2), support the view of a very low risk of sperm

competition in humans compared to other primates (2018 Dixson). Finally, there is also evidence that male copulation frequencies and frequencies of ejaculation (ejaculatory mounts and masturbation) are significantly higher in MMMF systems than in polygynous and monogamous systems, including humans (1995 Dixson) whose reproductive system does not seem to be adapted to sustain high sperm counts during periods of high sexual activity. Such findings can be interpreted as indicating that "masturbation is more likely to occur in multimale-multifemale primate groups because males possess neuroendocrine specialization for greater sexual arousal and performance in such mating systems" (2004 Dixson). However, the question of why there are so frequent masturbations in some primate species remains unresolved. One hypothesis is that regular masturbation would have a positive physiological effect on the general quality of spermatogenesis.

2.2. Interplay between pre- and post-copulatory selection

Male secondary sexual characters are traits that bias mating success because their expression influences the outcome of male-male contests over access to females (weapons) or renders males more attractive to females (ornaments). There are evidence that weapons (e.g. canines) and ornaments (e.g. the red chest patches of geladas (*Theropithecus gelada*), the red face and genital sex skin in mandrills (*Mandrillus sphinx*) and Japanese macaques (*Macaca fuscata*), the hair capes of hamadryas baboons (*Papio hamadryas*), the cheek flanges of orangutans (*Pongo* spp.), enlarged noses of proboscis monkeys (*Nasalis larvatus*), the beards of men, etc. (see 2012 Dixson)) evolved under pre-copulatory sexual selection. When these attributes do not contribute to have a better access to mates, sexual selection will be on the ability to find and reach the fertile females (mobility, sensory abilities) and/or to fertilize her. Thereby, when

females have multiple mating partners, as it is the case in many groups of primates, sexual selection will continue after mating in the form of sperm competition (1970 Parker) and through cryptic post-copulatory female choice (1996 Eberhard), i.e. females selecting sperm with particular characteristics (see section 2.4.). Theoretical models of sperm competition predict a trade-off between expenditure on the acquisition of mates (pre-mating sexual selection) and expenditure on post-copulatory traits (testes size, sperm number and quality) that promote fertilization success (post-mating sexual selection), i.e. an increased expenditure on testes and sperm should be associated with a decreased expenditure on the weapons and ornaments (2010 Parker and Pizzari).

Numerous comparative analyses have investigated the evolutionary associations between weapons and testes in a wide range of taxa (see Simmons et al. 2017 for a review). In general, the covariance between these sexual traits changes from positive to negative as male-male competition and female monopolization increase within animal taxa (2014 Lüpold, 2017 Simmons). Across primates, there is an increase in size-corrected testes mass with the number of males within breeding groups (2019 Lüpold), which is in accordance with predictions of sperm competition models (2016 Parker). Similarly, primate species characterized by a higher female monopolization show a decreased investment in testes size (2019 Lüpold). In a previous study, Lüpold et al. (2014) estimated that the proportion of species within each taxon where males monopolize females was about 20% in their primate sample (e.g. species with monogamous and multimale mating systems were classified as low monopolization while single-male mating systems were classified as high monopolization), showing that female monopolization is not very common in this Order. Given that, one should predict a general positive relationship between weapons and testes at the Order level (as shown

393 in a comparative study of gregarious primate species by Lüpold et al. 2019: testes mass
394 increases with increasing sexual dimorphism of the canines), with some taxon-specific
395 associations depending on additional life-history, ecological and mating-system
396 variables. For example, in polygynous species like gorillas, male body size/canines are
397 under very intense sexual selection and greatly exaggerated, suggesting that those very
398 costly traits will be more likely to trade off evolutionarily against investment in sperm
399 production, which could explain their relatively small testicles compared to their body
400 size.
401 Most of the studies investigating the evolutionary trade-off between pre- and post-
402 copulatory traits have focused on the associations between weapons and testes, and very
403 little attention has been paid to the patterns of covariation between ornaments and post-
404 copulatory traits. At the within-species level, studies on visual sexual signaling traits,
405 such as nose size in proboscis monkeys (2018 Koda) or face redness in mandrills (2001
406 Setchell & Dixson), showed that there was a positive relationship between the strength
407 of these ornaments and testes size. However, at the interspecific level, it has been shown
408 that species who invested most in the acoustic ornaments (enlargement of the larynx and
409 hyoid allowing males to broadcast low formant-frequency vocalizations) used during
410 male pre-mating competition in the genus Alouatta (howler monkeys), had smaller
411 testes (2015 Dunn). Moreover, a very recent comparative study in more than 100
412 primate species documented an evolutionary trade-off between pre-mating ornaments
413 (e.g. fleshy swellings, skin color, hairy traits etc) and testes mass (2019 Lüpold). The
414 authors suggested that “if male ornaments function as badges of status, with privileged
415 mating opportunities for highly ranked males similar to female monopolization by the
416 most successful males in contest competition, investment in male ornaments should also

lower the level of sperm competition and relax selection on sperm production".

Therefore, the contrasting evolutionary trajectories between weapons/testes (positive relationship) and ornaments/testes (negative relationship) reported in primates could be driven by differential selection, functional constraints or temporal patterns of metabolic investment between the different types of sexual traits (2019 Lüpold). There is a need for more research on the trade-offs between weapons/ornaments and ejaculate traits in primates (sperm number, viability, swimming speed and size; see meta-analysis by Mautz et al. 2013: positive but non-significant relation between male secondary sexual characters and ejaculate quality across taxa), as most studies until now focused almost exclusively on testes size as a proxy for post-copulatory sexual selection. Similarly, studies in sensory ecology and ecophysiology that focus on the evolutionary trade-off between ejaculate expenditure and mate-searching (linked to sensory abilities and multimodal sexual communication), rather than direct male-male contest, would be a productive avenue for future research.

2.3. From the male's perspective: Mate guarding and copulatory plugs

There is considerable evidence that males have evolved behavioral adaptations, such as mate guarding, that function to prevent competitor males from gaining access to reproductively active females (1994 Andersson), thereby limiting the extent of sperm competition (1998 Birkhead and Møller) and increasing their chances of fertilizing the egg. Mate guarding is widespread among polygynous primates, where it has been described in detail for about 20 species of New and Old World monkeys (2012 Dixson). Given the costs associated with mate guarding (e.g. reduction in foraging time, Alberts et al. 1996; physiological costs, Girard-Buttoz et al. 2014), one should expect that males would invest in mate guarding if the reproductive benefits outweigh the costs associated

441 with this activity. However, the extent to which male primates may adjust their relative
442 use of mate guarding compared to the opposite tactic, which is the engagement in sperm
443 competition through an increased expenditure on the ejaculate, remains largely
444 unexplored. In one of the rare studies examining the relationship between mate guarding
445 and ejaculate quality, Leivers et al. (2014) showed that men who performed more mate
446 guarding behaviors produced lower quality ejaculates, with a lower concentration of
447 sperm, a lower percentage of motile sperm and sperm that swam slowly and erratically.
448 Concerning male non-human primates, there is a paucity of empirical data on the costs
449 of this behavior and its effectiveness does not seem to be absolute but rather dependent
450 on its timing relative to the moment of ovulation. Moreover, whether a correlation
451 between mate guarding and ejaculate quality exists in non-human primates remains to
452 be investigated.
453 Another adaptation for the avoidance of sperm competition and an increase in male
454 fertilization success is the use of coagulated ejaculate that forms sperm plugs (also
455 called copulatory plugs). These copulatory plugs are found in many species of primates,
456 but especially in those having polygynandrous mating systems (e.g., ring-tailed lemurs,
457 muriquis, chimpanzees; 2002 Dixson and Anderson). Two main hypotheses have been
458 proposed to explain the evolution of pronounced sperm plugs in polygynandrous
459 primate species: it promotes the passage of highly motile sperm through the cervix
460 (2008 Hernandez-Lopez), buffers pH, and raises the temperature of the vagina which
461 improve sperm survival in the vagina and its transcervical transport; it obstructs semen
462 deposition and sperm transport by a second male. This second hypothesis seems less
463 supported by the empirical data, and even if plugs tend to close the entry to the female's
464 genital tract, they do not prevent her from subsequently mating with other males in

primates (2017 Parga). Indeed, several studies have shown that penile morphology, such as spines, found in different primate species may facilitate the removal or displacement of coagulated semen and plugs deposited by previous matings, and hence reduce potential sperm competition (1993 Hershkovitz, 2003 Parga). Moreover, males and females (see section 2.4. below) can also manually and/or orally remove these plugs, with semen ingestion being also reported (Garcia, personal observations in olive baboons and Japanese macaques).

2.4. Female choice & sexual conflict (sexual coercion)

Whenever polyandrous matings occur, sperm competition will inevitably arise, setting up selection on males (quantity and quality of sperm that improve their chances to fertilize the ova) but also on females to select sperm with particular characteristics and circumvent male control of reproduction (i.e. cryptic post-copulatory female choice; 1996 Eberhard). There will be also antagonistic selection on males and females due to sexual conflict.

Post-copulatory female choice is expected to occur more often in species in which females have little direct control over choice of mating partners or in which female mate choice is especially costly. This is particularly the case in species characterized by a high level of sexual dimorphism, and/or in species in which males are aggressive towards females in the context of mating (e.g. chimpanzees, pigtailed macaques, etc). In cases of sexual conflict, some traits that benefit males oppose with the female's interests and vice versa. For example, some conflicts can emerge in species where penile morphology might damage the female's genital structures during intromission (e.g. spines in galagos). They can also occur in species where females show prominent sexual swellings (e.g. chimpanzees, baboons – serving to attract multiple partners and

encourage the likelihood of mating and sperm competition; 2012 Dixson) that could influence the distance that males must cover during mating and sperm transport, and then increase the chances of being fertilized by males with longer penises. This conflict can also take the form of sexual coercion (review by Smuts & Smuts 1993 and Muller et al. 2011) with direct (females are compelled to copulate more frequently with their aggressors) and indirect coercion (females are prevented from mating with other males). Until recently, post-copulatory female choice had received little attention in the primate literature, especially because of practical difficulties of conducting such experiments in this Order, and more generally in mammals. There is therefore little evidence for differential fertilization chances of sperm of different males once inside the female reproductive tract. Nevertheless, there is ample reason to consider that, as in a number of insects and birds, there are anatomical, physiological and behavioral adaptations for post-copulatory female choice in primates. Here are a few examples of indirect evidence of possible cryptic female choice in primates.

At the anatomical level, after their deposition in the vagina during ejaculation, spermatozoa have to cross numerous barriers, such as the cervix or the uterotubal junction, before reaching the oviduct. There is a huge filtering in the number of spermatozoa from the vagina to the oviduct, with only about 200 being found in the human oviduct whereas 280 million sperm were initially released (2018 Dixson). Moreover, it seems that elongated oviducts may serve to “test” the relative fitness of gametes from rival males and thus represent a mechanism of cryptic female choice in mammals, with longer and more convoluted oviducts being associated with higher relative testes size and sperm midpiece volumes (2006 Anderson). There are unfortunately not enough data on the anatomy of these potential physical barriers in

non-human primates to assess the differential effects of the female's anatomical structures as selective filters upon sperm transport and then fertilization success and a lot more comparative studies are needed in this area of research.

At the physiological level, Hernandez-Lopez et al. (2008) have shown that there is a buffering effect of seminal fluid on vaginal pH in the spider monkey, which increased sperm motility in the vagina. Even if these results did not provide a distinct proof of female cryptic choice in this species, they still suggest that sperm selection could start as early as the vagina, with females relying on cues provided by the seminal coagulum in favoring or opposing sperm migration.

At the behavioral level, it has been suggested that female copulation calls (i.e. auditory signal occurring after mating) in Old World monkeys and apes are a form of post-copulatory female choice that encourages post-copulatory mate guarding by preferred males and minimize the probability of sperm competition by non-preferred males (2005 Maestripieri & Roney). By calling after copulation with certain males, females express their preferences for these males and their sperm; whereas by not calling after copulation with other males, they do not encourage mate guarding by these males, which leaves the possibility that other males will mate with them and engage in sperm competition. Another behavioral mechanism that could be used to choose among different males is the active manipulation of their ejaculates. It has been shown that in chickens, females can expel the sperm from matings with low-ranking roosters immediately after insemination (cited in van Schaik 2016). Nevertheless, so far, we still do not know whether primate female's behavior might actively bias the fate of spermatozoa originating from different males, and if so, how.

Therefore, the question of how the primate female's reproductive system preferentially

receives and influences processes associated with sperm transport, storage and viability remains to be investigated in more details.

2.5. Seasonality & Climatological factors

Reproductive activity of many primates is more or less seasonal, resulting in an increased frequency of matings during a relatively short period, which may select for increased sperm production, compared to year-round breeders (1977 Short). In this case, we might expect a decrease in optimal ejaculate size as sperm production rates increase. Indeed, this sperm depletion could be promoted by oestrus synchronization, which reduces the male-bias in the operational sex ratio (i.e. the ratio of the number of fertile adult males to the number of potentially fertile females in a group at a given time; definition in van Schaik 2016) during the breeding season and forces males to mate at a higher rates than if oestrus was not synchronous (2011 Stockley and Bro-Jørgensen). Different studies have reported a negative relationship between the ratio of oestrous females to males and conception rates in both geladas and hamadryas baboons (1983 Dunbar & Sharman, 1994 Zinner). Similar findings suggested some sperm limitation in gorillas (i.e. a species where males can only sustain relatively low mating rates, 1979 Short), with females receiving fewer copulations when other females were simultaneously in oestrus (1990 Watts).

Climatological factors have been invoked as causes of seasonal variation in the frequency of intercourse within human populations and could have a direct influence on human reproductive physiology and thereby on human fecundity. One of the main factors most often raised to explain these relations is temperature. Indeed, the process of spermatogenesis in primates, and mammals in general, is temperature-sensitive and optimized at temperatures slightly below the core body temperature. This temperature

561 sensitivity has been a selective force in primate evolution resulting in external testes
562 (cited in Ellison et al. 2015) and leads to ask whether high ambient temperatures, such
563 as the ones encountered by most tropical non-human primates or humans living in
564 hottest environmental places, could compromise male fecundity by affecting sperm
565 quality and/or quantity. Most studies relating heat and damage to spermatogenesis
566 focused on general seasonal variation in sperm concentration and total sperm count (e.g.
567 with summer values being much lower than the ones found during winter times; in
568 Durairajanayagam et al. 2015) or used experimental approaches with induced-
569 hyperthermia to evaluate whether different frequencies of heat exposure caused
570 different degrees of damage to spermatogenesis (2015 Rao et al.: reversible decrease in
571 sperm concentration and motility with transient scrotal hyperthermia). However, to our
572 knowledge, studies examining the effects of living in very hot environments on human
573 spermatogenesis and the resultant spermatozoa are lacking. There is also a scarcity of
574 data in non-human primates, with one study showing that high temperatures could
575 reduce 80% of the original sperm count in cynomolgus monkeys (2005 Liu). Therefore,
576 clear evidence of a relationship between high ambient temperature and defects in male
577 reproductive physiology in wild populations of primates is lacking and would deserve
578 more attention.

579 **2.6. Social constraints**

580 Optimal sperm investment within species and within animal populations is expected to
581 vary predictably with respect to male roles in the society, as defined within theoretical
582 models known as sperm competition games (2010 Parker & Pizzari). Sperm
583 competition theory predicts that males should progressively invest more resources in
584 their germline as their mating costs increase. When access to fertile females is

585 determined by social dominance (e.g. dominant males being more likely to ejaculate at
586 an optimal time relative to ovulation, i.e. a favored role), allocation trade-off hypothesis
587 (soma vs. germline) predicts that semen characteristics and within-male variance in
588 sperm design should be affected by the social environment, with subordinate males (i.e.
589 the disfavored phenotype) investing more in ejaculate expenditure (1990 Parker, 1998
590 Parker). Many studies have investigated the effects of social environment and social
591 status on ejaculate characteristics in birds and some mammals, with some conflicting
592 results regarding the theoretical predictions of sperm competition (e.g. 2007 Cornwallis
593 & Birkhead and 2007 Pizzari et al.: ejaculates of lower quality and reduced swimming
594 speeds of sperm in socially dominant male fowls, who experience reduced levels of
595 sperm competition; 2009 Kruczek & Styrna: higher motility of sperm in dominant bank
596 voles; 2012 Lemaître et al.: dominant male bank voles invest more sperm per ejaculate
597 than subordinates; 2015 Burger et al.: higher sperm numbers and velocity in stallions
598 exposed to other stallions than exposed to mares; 2017 Rojas Mora et al.: ejaculates
599 with higher levels of within-ejaculate variation in sperm design in dominant house
600 sparrows compared to subordinate ones). There are much less information on the
601 influence of social status on non-human primate sperm features and sperm competition;
602 even though there has been a considerable literature on the effects of social constraints
603 on male mating and reproductive success in different primate species (1991 Cowlishaw
604 & Dunbar, 2004 van Noordwijk & van Schaik, 2005 Setchell) and a few papers on the
605 relationships between social rank and testicular physiology (e.g. smaller relative testes
606 in subordinate males than in dominant ones in mandrills or sifakas; 1992 Wickings,
607 2009 Lewis). This is even truer in human populations with very few studies venturing
608 out on this touchy topic and showing solid results. For example, Latif et al. (2018)

609 suggested that semen quality was not explained by socio-economic status, but due to the
610 limited sample size and the fact that participants did not represent the general
611 population (i.e. they were referred for infertility assessment), these results need to be
612 further confirmed in future studies. There are therefore avenues for further research on
613 the role of social status on fertilization outcomes in human and in a range of primate
614 species.
615 Besides social status, there are some other social constraints than could have an
616 influence on sperm competition and sperm features. For example, an increased
617 population density might reduce the efficiency of male-male contests in securing
618 females and increase its cumulative costs, thus leading to scramble competition (2013
619 Parker). In marine invertebrates, it has been shown that males experimentally allocated
620 to high-density groups, where sperm competition is more likely, produced longer and
621 more motile sperm that swam for longer periods of time than did males in low-density
622 treatment groups (2008 Crean). Another study in amphibians also showed that across
623 geographically isolated populations of chorusing frogs, the density of males in choruses
624 was positively associated with testes mass and sperm production (2010 Dziminski).
625 However, whether this pattern of covariation is also found in primate species and if
626 there is a phenotypic plasticity in male allocation to ejaculates in response to fluctuating
627 male densities remain to be investigated.
628 **2.7. Androgens and sperm competition**
629 Testosterone drives the process of male genital development, supports sperm production
630 (2004 Weinbauer, 2012 Dixson) and has a wide range of effects that plausibly function
631 to support male competitive behavior, for example the development and maintenance of
632 the armaments and ornaments that males employ in mating competition. The “Challenge

hypothesis", first developed from studies in birds (1990 Wingfield), states that the temporal patterns of circulating testosterone are closely associated with aggressive mating competition (2017 Muller). Observations from a range of wild primates support this hypothesis, which is also highly relevant for understanding social interactions in humans (2017 Wingfield). Mean levels of testosterone in MMMF primate species are higher than in uni-male mating systems and there is a positive correlation between testosterone levels and relative testes sizes (indicative of multiple partner matings by females and sperm competition among males) for the Order Primates, as a whole (2000 Whitten; 2004 Dixson). Muller (2017) reviewed the relationship between testosterone and mating effort in primates, with specific emphasis on the ways in which testosterone promotes male-male competition: "in both seasonally and non-seasonally breeding species, males increase testosterone production primarily when competing for fertile females. In species where males compete to maintain long-term access to females, testosterone increases when males are threatened with losing access to females […]. And when male status is linked to mating success, and dependent on aggression, high-ranking males normally maintain higher testosterone levels than subordinates, particularly when dominance hierarchies are unstable". Low testosterone levels of subordinate males have also been reported in other mammal species, with some extreme cases in which the investment in ejaculate and reproductive capabilities of subordinates could even be suppressed in the presence of dominant individuals (cited in 2012 Lemaître et al.). Regarding the correlation between testosterone levels and semen characteristics, Burger et al. (2015) found that blood testosterone levels in horses were positively correlated with both the mean sperm number (after exposure to mares but not after exposure to stallions) and curvilinear sperm velocity (after exposure to stallions),

suggesting that testosterone levels during exposure to a mare can be an indicator for a stallion's willingness to invest into costly semen production. However, to our knowledge, such studies examining the links between testosterone levels and sperm features in non-human primates are currently lacking and this topic needs further attention.

CONCLUDING REMARKS AND FUTURE DIRECTIONS

This review has discussed the different selection pressures involved in the evolution of primate sperm diversity. We considered especially how sexual selection (pre- and post-copulatory), acting via mating competition, sperm competition and cryptic female choice, has influenced the evolution of primate reproductive systems and sperm parameters. Cryptic female choice is still poorly studied in mammals and in primates in particular, and this topic deserves more attention. More detailed investigation is also required to determine the evolutionary trade-off between ejaculate expenditure and mate-searching across a broad range of primate taxa. Further studies are also needed to determine how social conditions explain variation in sperm morphology and parameters. In conclusion, further research in this field offers much exciting potential to advance our current understanding of primate reproductive system evolution.

Acknowledgments: We would like to sincerely thank Charlotte Guyot and Marlène Gandula for their assistance in bibliography recovery and their exceptional work in general. We are also grateful to Pr. Charles Coutton for his proofreading of English spelling.

Declarations of interest: The authors have declared that no competing interests exist.

Funding: This work was partially supported by the Centre National de la Recherche Scientifique (France), Projet International de Coopération Scientifique (grant number 7258) to C. Garcia.

REFERENCES

Ackerman DR, Roussel JD. Fructose, lactic acid and citric acid content of the semen of eleven subhuman primate species and of man. J Reprod Fertil. 1968;17(3):563–566. DOI:10.1530/jrf.0.0170563

Agca Y, Liu J, Mullen S, Johnson-Ward J, Gould K, Chan A, Critser J. Chimpanzee (Pan troglodytes) spermatozoa osmotic tolerance and cryoprotectant permeability characteristics. J Androl. 2005;26(4):470–477. DOI:10.2164/jandrol.04169

Alberts SC, Altmann J, Wilson ML. Mate guarding constrains foraging activity of male baboons. Anim Behav. 1996;51:1269–1277. doi: 10.1006/anbe.1996.0131.

Amann RP, Johnson L, Thompson DL Jr, Pickett BW. Daily spermatozoal production, epididymal spermatozoal reserves and transit time of spermatozoa through the epididymis of the rhesus monkey. Biol Reprod. 1976 Dec;15(5):586-92. DOI: 10.1095/biolreprod15.5.586

Amann RP. Detection of alterations in testicular and epididymal function in laboratory animals. Environ Health Perspect. 1986 Dec;70:149-58. DOI: 10.1289/ehp.8670149

Amboka JN, Mwethera PG. Characterization of semen from olive baboons. J Med Primatol. 2003;32(6):325–329. DOI:10.1046/j.1600-0684.2003.00039.x

Anderson MJ, Nyholt J and Dixson AF. Sperm competition and the evolution of sperm midpiece volume in mammals. Journal of Zoology. 2005;267: 135-142. doi:10.1017/S0952836905007284

Anderson MJ, Dixson AS and Dixson AF. Mammalian sperm and oviducts are sexually selected: evidence for co-evolution. Journal of Zoology. 2006,270:682-686. doi:10.1111/j.1469-7998.2006.00173.x

Andersson M. 1994 Sexual selection. Princeton, NJ: Princeton University Press.

Arakaki PR, Carvalho FM, Castro PHG, Muniz JAPC, Valle RDRD. Collection, Evaluation, and Coagulum Dissolution of Semen from Goeldi's Monkey, Callimico goeldii. Folia Primatol (Basel). 2017;88(4):334–343. DOI:10.1159/000480501

Arakaki PR, Nichi M, Monteiro FOB, Muniz JAPC, Guimarães MABV, Valle RDRD. Comparison of semen characteristics and sperm cryopreservation in common marmoset (Callithrix jacchus) and black-tufted-ear marmoset (Callithrix penicillata). J Med Primatol. 2019;48(1):32–42. DOI:10.1111/jmp.12388

Arakaki PR, Salgado PAB, Teixeira RHF, Rassy FB, de Barros Vaz Guimarães MA, Del Rio do Valle R. Testicular volume and semen characteristics in the endangered southern

muriqui (Brachyteles arachnoides). J Med Primatol. 2019 Aug;48(4):244-250. DOI:10.1111/jmp.12418.

Aslam H, Schneiders A, Perret M, Weinbauer GF, Hodges JK. Quantitative assessment of testicular germ cell production and kinematic and morphometric parameters of ejaculated spermatozoa in the grey mouse lemur, Microcebus murinus. Reproduction. 2002 Feb;123(2):323-32. DOI:10.1530/rep.0.1230323

Aziz N, Fear S, Taylor C, Kingsland CR, Lewis-Jones DI. Human sperm head morphometric distribution and its influence on human fertility. Fertil Steril. 1998;70(5):883–891. doi:10.1016/s0015-0282(98)00317-3

Aziz N, Said T, Paasch U, Agarwal A. The relationship between human sperm apoptosis, morphology and the sperm deformity index. Hum Reprod. 2007;22(5):1413–1419. doi:10.1093/humrep/dem016

B

Bader H. Electroejaculation in chimpanzees and gorillas and artificial insemination in chimpanzees. Zoo Biology. 1983;2(4):307-314. DOI: 10.1002/zoo.1430020407

Barnabe RC, Guimarães MA, Oliveira CA & BarnabeAH. Analysis of some normal parameters of the spermiogram of captive capuchin monkeys (Cebus apella Linnaeus, 1758). Brazilian Journal of Veterinary Research and Animal Science. 2002;39(6):331-333. https://dx.doi.org/10.1590/S1413-95962002000600010

Baumber J, Meyers SA. Hyperactivated motility in rhesus macaque (Macaca mulatta) spermatozoa. J Androl. 2006;27(3):459–468. doi:10.2164/jandrol.05107

Bennett JP. Semen collection in the squirrel monkey. J Reprod Fertil. 1967;13(2):353–355. doi:10.1530/jrf.0.0130353

Beracochea F, Gil J, Sestelo A, Garde JJ, Santiago-Moreno J, Fumagalli F, Ungerfeld R. Sperm characterization and identification of sperm sub-populations in ejaculates from pampas deer (Ozotoceros bezoarticus). Anim Reprod Sci. 2014;149(3-4):224–230. doi:10.1016/j.anireprosci.2014.07.013

Bercovitch FB, Rodriguez JF. 1993. Testis size, epididymis weight, and sperm competition in rhesus macaques. DOI:10.1002/ajp.1350300208

Birkhead TR, Møller A. Sperm competition and sexual selection. Academic press, London. 1998. Pp 826.

Birkhead TR, Martínez JG, Burke T, Froman DP. Sperm mobility determines the outcome of sperm competition in the domestic fowl. Proc Biol Sci. 1999 Sep 7;266(1430):1759-64. DOI:10.1098/rspb.1999.0843

Bogart MH, Cooper RW, Benirschke K. 1977. X. International Zoo Yearbook 17: 177-182. DOI:10.1111/j.1748-1090.1977.tb00901.x

Burger D, Dolivo G, & Wedekind C. Ejaculate characteristics depend on social environment in the horse (Equus caballus). PloS one. 2015;10(11),e0143185. DOI:10.1371/journal.pone.0143185

Butler H. The reproductive biology of a strepsirhine (Galago senegalensis senegalensis). International Review of General and Experimental Zoology. 1964, Vol1, pp241-296. DOI: 10.1016/B978-1-4831-9977-1.50012-2

C

Carvalho FM, Arakaki PR, Nichi M, Muniz JAPC, Duarte JMB, & Valle RR. Evaluation of sperm quality in successive regular collections from captive black-and-gold howler monkeys (Alouatta caraya). Animal Reproduction. 2018;11(1):11-18.

Cerda-Molina AL, Hernández-López L, Chavira-Ramírez R, Cárdenas M, Mondragón-Ceballos R. Seasonality of LH, testosterone and sperm parameters in spider monkey males (Ateles geoffroyi). Am J Primatol. 2009;71(5):427–431. DOI:10.1002/ajp.20671

Chan P, Cseh S, Corselli J, & Bailey L. Sperm characteristics after sequential semen collection and pentoxifylline treatment in the baboon (Papio anubis). Theriogenology. 1999;51(1):340.

Cho F, Honjo S. A simplified method for collecting and preserving cynomolgus macaque semen. Jpn J Med Sci Biol. 1973;26(5):261–268. doi:10.7883/yoken1952.26.261

Conradie E, Oettle EE, Seier JV. Assessment of acrosomal integrity of vervet monkey spermatozoa after cryopreservation. J Med Primatol. 1994;23(5):315–316. doi:10.1111/j.1600-0684.1994.tb00291.x

Cooper TG, Noonan E, von Eckardstein S, Auger J, Baker HW, Behre HM, Haugen TB, Kruger T, Wang C, Mbizvo MT et al. World Health Organization reference values for human semen characteristics. Hum Reprod Update. 2010;16(3):231–245. doi:10.1093/humupd/dmp048

Cornwallis CK, & Birkhead TR. Changes in sperm quality and numbers in response to experimental manipulation of male social status and female attractiveness. The American Naturalist. 2007;170(5):758-770. Doi:10.1086/521955

Cowlishaw G, & Dunbar RI. (1991). Dominance rank and mating success in male primates. Animal Behaviour. 1991;41(6):1045-1056. DOI:10.1016/S0003-3472(05)80642-6

Cranfield MR, Kempske SE, & Schaffer N. The use of in vitro fertilisation and embryo transfer techniques for the enhancement of genetic diversity in the captive population of the Lion-tailed macaque Macaca silenus. International Zoo Yearbook. 1988;27(1):149-159. DOI:10.1111/j.1748-1090.1988.tb03208.x

Crean AJ, & Marshall DJ. Gamete plasticity in a broadcast spawning marine invertebrate. Proceedings of the National Academy of Sciences. 2008;105(36):13508-13513. Doi:10.1073/pnas.0806590105

Cseh S, Chan PJ, Corselli J, Bailey LL. Electroejaculated baboon (Papio anubis) sperm requires a higher dosage of pentoxifylline to enhance motility. J Assist Reprod Genet. 2000;17(8):449–453. doi:10.1023/a:1009469319596

Cui KH, Flaherty SP, Newble CD, Guerin MV, Napier AJ, Matthews CD. Collection and analysis of semen from the common marmoset (Callithrix jacchus). J Androl. 1991;12(3):214–220. PMID: 1917685

Cui KH. The effect of stress on semen reduction in the marmoset monkey (Callithrix jacchus). Hum Reprod. 1996;11(3):568–573. doi:10.1093/humrep/11.3.568

D

da Silva Verona CE, de Souza FF, Toniollo GH, Garcia JM, & Esper CR. Colheita e avaliação do sêmen de sagui-de-tufo-branco (Callithrix jacchus). Ciência Animal Brasileira. 2009;10(2):544-552.

de Araújo LL, de Lima JS, Oliveira KG, Muniz JAPC, Valle RDR, & Domingues SFS. Use of coconut water solution at 37° C as extender of captive Cebus apella (capuchin monkey) semen. Ciência Animal Brasileira. 2009;10(2):588-594.

Dejucq-Rainsford N, Jégou B. Viruses in semen and male genital tissues--consequences for the reproductive system and therapeutic perspectives. Curr Pharm Des. 2004;10(5):557–575. doi:10.2174/1381612043453225

Denis LT, Poindexter AN, Ritter MB, Seager SW, Deter RL. Freeze preservation of squirrel monkey sperm for use in timed fertilization studies. Fertil Steril. 1976;27(6):723–729. PMID: 819313

de Villiers C. A comparison between the semen and sperm parameters from the captive-bred Vervet monkey (Chlorocebus aethiops) and Rhesus monkey (Macaca mulatta). J Med Primatol. 2018;10.1111/jmp.12349. doi:10.1111/jmp.12349

Dixson AF. Observations on the evolution of the genitalia and copulatory behaviour in male primates. 1987. DOI:10.1111/j.1469-7998.1987.tb03718.x

817 Dixson AF. Sexual selection and ejaculatory frequencies in primates. Folia Primatol
818 (Basel). 1995;64(3):146–152. doi:10.1159/000156845

819 Dixson AF, Anderson MJ. Sexual behavior, reproductive physiology and sperm
820 competition in male mammals. Physiol Behav. 2004 Nov 15;83(2):361-71.
821 DOI:10.1016/j.physbeh.

822 Dixson BJ, Vasey PL. Beards augment perceptions of men's age, social status, and
823 aggressiveness, but not attractiveness, Behavioral Ecology. 2012;23(3):481-490.
824 DOI:10.1093/beheco/arr214

825 Dixson AF. Primate sexuality. 2012. Oxford University Press, Oxford

826 Dixson AF. Copulatory and Postcopulatory Sexual Selection in Primates. Folia Primatol
827 (Basel). 2018;89(3-4):258–286. doi:10.1159/000488105

828 Dong Q, Rodenburg SE, Huang C, Vandevoort CA. Cryopreservation of rhesus monkey
829 (Macaca mulatta) epididymal spermatozoa before and after refrigerated storage. J
830 Androl. 2008;29(3):283–292. doi:10.2164/jandrol.107.003921

831 Dong Q, Correa LM, VandeVoort CA. Rhesus monkey sperm cryopreservation with
832 TEST-yolk extender in the absence of permeable cryoprotectant. Cryobiology.
833 2009;58(1):20–27. doi:10.1016/j.cryobiol.2008.09.014

834 Dorado J, Molina I, Muñoz-Serrano A, Hidalgo M. Identification of sperm
835 subpopulations with defined motility characteristics in ejaculates from Florida goats.
836 Theriogenology. 2010;74(5):795–804. doi:10.1016/j.theriogenology.2010.04.004

837 Dubaut JP, Gurung S, Trammell MR, Myers D, Reuter D, Preno A, Zavy MT, & Papin
838 JF. Semen parameters during ZIKA virus infection in the olive baboon (Papio anubis).
839 Fertility and Sterility. 2017;108(3):e52-e53. DOI: 10.1016/j.fertnstert.2017.07.168

840 Dunbar RIM & Sharman M. Female competition for access to males affects birth rate in
841 baboons. BEAS. 1983;13:157-159. doi:10.1007/BF00293805

842 Dunn JC, Halenar LB, Davies TG, Cristobal-Azkarate J, Reby D, Sykes D, Dengg S,
843 Fitch T, Knapp LA. Evolutionary trade-off between vocal tract and testes dimensions in
844 howler monkeys. Curr Biol. 2015;25(21):2839–2844. doi:10.1016/j.cub.2015.09.029

845 Durairajanayagam D, Agarwal A, Ong C. Causes, effects and molecular mechanisms of
846 testicular heat stress. Reprod Biomed Online. 2015;30(1):14–27.
847 doi:10.1016/j.rbmo.2014.09.018

848 Durrant BS. Semen collection, evaluation and cryopreservation in exotic animal
849 species: maximizing reproductive potential. Ilar News 1990;32:2–9.
850 DOI:10.1093/ilar.32.1.2

Dziminski MA, Roberts JD, Beveridge M, and Simmons LW. Among population covariation between sperm competition and ejaculate expenditure in frogs. Behav. Ecol. 2010;21:322-328. Doi:10.1093/beheco/arp191

E

Eberhard WG (1996). Female Control: Sexual Selection by Cryptic Female Choice. Princeton, Princetown University Press.

Ellison PT, Valeggia C, Sherry DS. Seasonality in Primates: Human birth seasonality. In Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates, ed. Diane K. Brockman and Carel P. van Schaik. 2005. Cambridge University Press.

F

Feradis AH, Pawitri D, Suatha IK, Amin MR, Yusuf TL, Sajuthi D, Budiarsa IN, Hayes ES. Cryopreservation of epididymal spermatozoa collected by needle biopsy from cynomolgus monkeys (Macaca fascicularis). J Med Primatol. 2001;30(2):100–106. doi:10.1034/j.1600-0684.2001.300205.x

Fitzpatrick JL, Montgomerie R, Desjardins JK, Stiver KA, Kolm N, Balshine S. Female promiscuity promotes the evolution of faster sperm in cichlid fishes. Proc Natl Acad Sci U S A. 2009;106(4):1128–1132. doi:10.1073/pnas.0809990106

Fitzpatrick JL, Baer B. Polyandry reduces sperm length variation in social insects. Evolution. 2011;65(10):3006–3012. doi:10.1111/j.1558-5646.2011.01343.x

Flechon J E, Hafez E SE. Scanning electron microscopy of human spermatozoa. Human Semen and Fertility Regulation in Men, E SE Hafez. C.V. Mosby, St. Louis 1976; 76–82.

Flores-Herrera H, Acuña-Hernández DG, Rivera-Rebolledo JA, González-Jiménez MA, Rodas-Martínez AZ, Swanson WF. Effect of increasing trypsin concentrations on seminal coagulum dissolution and sperm parameters in spider monkeys (Ateles geoffroyi). Theriogenology. 2012;78(3):612–619. DOI:10.1016/j.theriogenology.2012.03.007

Frearson C. Masturbation in male primates: taxonomic distribution, proximate causes and potential evolutionary functions. 2005. In: MSc thesis. University College London, Dept of Anthropology, UK

G

Gadea J, Toledano-Díaz A, Navarro-Serna S, Jiménez-Movilla M, Soriano P, Matás C, Santiago-Moreno J. Assessment and preservation of liquid and frozen-thawed Black

crested mangabey (Lophocebus aterrimus) spermatozoa obtained by transrectal ultrasonic-guided massage of the accessory sex glands and electroejaculation. Anim Reprod Sci. 2019;210:106176. doi:10.1016/j.anireprosci.2019.106176

Gagliardi C, Myers L, Kubisch HM. Postthaw survival of rhesus macaque sperm: variation in the response of individual males to different freezing protocols. Am J Primatol. 2008;70(11):1093–1096. doi:10.1002/ajp.20598

Gago C, Pérez-Sánchez F, Yeung CH, Tablado L, Cooper TG, Soler C. Morphological characterization of ejaculated cynomolgus monkey (Macaca fascicularis) sperm. Am J Primatol. 1999;47(2):105–115. doi:10.1002/(SICI)1098-2345(1999)47:2<105::AID-AJP2>3.0.CO;2-L

García-Vázquez FA, Gadea J, Matás C, Holt WV. Importance of sperm morphology during sperm transport and fertilization in mammals. Asian J Androl. 2016;18(6):844–850. doi:10.4103/1008-682X.186880

Girard-Buttoz C, Heistermann M, Rahmi E, Marzec A, Agil M, Fauzan PA, & Engelhardt A. Mate-guarding constrains feeding activity but not energetic status of wild male long-tailed macaques (Macaca fascicularis). Behavioral ecology and sociobiology, 2014;68(4):583-595. doi:10.1007/s00265-013-1673-8

Gomendio M, Roldan ER. Sperm competition influences sperm size in mammals. Proc Biol Sci. 1991;243(1308):181–185. doi:10.1098/rspb.1991.0029

Gomendio M, Tourmente M, Roldan ER. Why mammalian lineages respond differently to sexual selection: metabolic rate constrains the evolution of sperm size. Proc Biol Sci. 2011;278(1721):3135–3141. doi:10.1098/rspb.2011.0275

Gould KG, & Kling OR. Fertility in the male gorilla (Gorilla gorilla): Relationship to semen parameters and serum hormones. American Journal of Primatology. 1982;2(3):311-316. DOI:10.1002/ajp.1350020310

Gould KG, & Styperek RP. Improved methods for freeze preservation of chimpanzee sperm. American Journal of Primatology. 1989;18(4):275-284. DOI:10.1002/ajp.1350180402

Gould KG, Young LG, Smithwick EB, & Phythyon SR. Semen characteristics of the adult male chimpanzee (Pan troglodytes). American Journal of Primatology. 1993;29(3):221-232. DOI: 10.1002/ajp.1350290307

Gupta G, Maikhuri JP, Setty BS, Dhar JD. Seasonal variations in daily sperm production rate of rhesus and bonnet monkeys. J Med Primatol. 2000;29(6):411-414. DOI:10.1111/j.1600-0684.2000.290605.x

H

Hall-Craggs ECB. The testis of Gorilla gorilla beringei. Proceedings of the Zoological Society of London. 1962 Volume 139, Issue 3. DOI:10.1111/j.1469-7998.1962.tb01845.x

Harcourt AH, Harvey PH, Larson SG, Short RV. Testis weight, body weight and breeding system in primates. Nature. 1981;293(5827):55-57. DOI:10.1038/293055a0

Harcourt AH. Sperm competition and the evolution of nonfertilizing sperm in mammals. Evolution. 1991;45(2):314-328. DOI: 10.1111/j.1558-5646.1991.tb04406.x.

Harcourt AH, A. Purvis A, Liles L. Sperm Competition: Mating System, Not Breeding Season, Affects Testes Size of Primates. 1995 Functional Ecology. Vol. 9, No. 3, pp. 468-476. DOI:10.2307/2390011

Hardin CJ, Liebherr G & Fairchild O. Artificial insemination in chimpanzees. International Zoo Yearbook. 1975;15(1):132-134. DOI:10.1111/j.1748-1090.1975.tb01376.x

Harrison Matthews L. 1946. Notes on the Genital Anatomy and Physiology of the Gibbon (Hylobates). DOI:10.1111/j.1096-3642.1946.tb00126.x

Hernández-López L, Parra GC, Cerda-Molina AL, Pérez-Bolaños SC, Díaz Sánchez V, Mondragón-Ceballos R. Sperm quality differences between the rainy and dry seasons in captive black-handed spider monkeys (Ateles geoffroyi). Am J Primatol. 2002;57(1):35–41. DOI:10.1002/ajp.1086

Hernández-López L, Umland N, Mondragón-Ceballos R, Nayudu PL. Comparison of the effects of Percoll and PureSperm on the common marmoset (Callithrix jacchus) semen. J Med Primatol. 2005;34(2):86–90. DOI:10.1111/j.1600-0684.2005.00095.x

Hernández-López L, Cerda-Molina AL, Páez-Ponce LD, Mondragón-Ceballos R. Seasonal emission of seminal coagulum and in vivo sperm dynamics in the black-handed spider monkey (Ateles geoffroyi). Theriogenology. 2008;69(4):466–472. DOI:10.1016/j.theriogenology.2007.10.016

Hershkovitz P. Male external genitalia of the non-prehensile tailed South American monkeys. 1. Subfamily Pithecinae, family Cebidae. Fieldiana Zoology. 1993;73:1–17. doi:10.5962/bhl.title.3265

Higginson DM, Miller KB, Segraves KA, Pitnick S. Female reproductive tract form drives the evolution of complex sperm morphology. Proc Natl Acad Sci U S A. 2012;109(12):4538–4543. doi:10.1073/pnas.1111474109

Hill WCO. 1960. Primates Comparative Anatomy and Taxonomy IV. Cebidae Part A. Edinburgh: Edinburgh University Press.

Hill WCO. (1966). Primates Comparative Anatomy and Taxonomy VI—Catarrhini Cercopithecoidea: Cercopithecinae. Edinburgh Univ Pubs Science & Maths, No 3f.

Hill WCO. (1970). Primates Comparative Anatomy and Taxonomy VIII—Cynopithecinae (Papio, Mandrillus, Theropithecus). Edinburgh Univ Pubs Science & Maths, No 3h.

Hiyaoka A, Cho F. [A Method for Collecting Semen by Fingers in the African Green Monkey (Cercopithecus Aethiops) and Properties of the Semen Collected]. Jikken Dobutsu. 1990;39(1):121–124. doi:10.1538/expanim1978.39.1_121

Holt WV, Van Look KJ. Concepts in sperm heterogeneity, sperm selection and sperm competition as biological foundations for laboratory tests of semen quality. Reproduction. 2004;127(5):527–535. doi:10.1530/rep.1.00134

Hoskins DD, Patterson DL. Prevention of coagulum formation with recovery of motile spermatozoa from rhesus monkey semen. J Reprod Fertil. 1967;13(2):337–340. doi:10.1530/jrf.0.0130337

Hrdlička A. Weight of the brain and of the internal organs in American monkeys. With data on brain weight in other apes. 1925. DOI:10.1002/ajpa.1330080207

Hung PH, Baumber J, Meyers SA, VandeVoort CA. Effects of environmental tobacco smoke in vitro on rhesus monkey sperm function. Reprod Toxicol. 2007;23(4):499–506. doi:10.1016/j.reprotox.2007.03.005

I

Inoue E. Male masturbation behaviour of Japanese macaques in the Arashiyama E troop. In: Leca JB, Huffman MA, Vasey PL (eds) The monkeys of stormy mountain: 60 years of primatological research on the Japanese macaques of Arashiyama. Cambridge University Press, Cambridge. 2012. pp 204–220

J

Jeyendran RS, Schrader SM, van der Ven HH, Burg J, Perez-Pelaez M, Al-Hasani S, Zaneveld LJD. Association of the in-vitro fertilizing capacity of human spermatozoa with sperm morphology as assessed by three classification systems. Hum Reprod. 1986;1(5):305–308. doi:10.1093/oxfordjournals.humrep.a136410

Joslin JO, Weissman WD, Johnson K, Forster M, Wasser S, & Collins D. In vitro fertilization of Bornean orangutan (Pongo pygmaeus pygmaeus) gametes followed by embryo transfer into a surrogate hybrid orangutan (Pongo pygmaeus). Journal of Zoo and Wildlife Medicine. 1995:32-42.

K

Katz DF, Overstreet JW, Samuels SJ, Niswander PW, Bloom TD, Lewis EL. Morphometric analysis of spermatozoa in the assessment of human male fertility. J Androl. 1986;7(4):203–210. doi:10.1002/j.1939-4640.1986.tb00913.x

Kennard MA, Willner MD. Findings at autopsies of seventy anthropoid apes. Endocrinology. 1941a;28:967–976. DOI:10.1210/endo-28-6-967

Kennard MA, Willner MD. Weights of brains and organs of 132 new and old world monkeys. Endocrinology. 1941b;28:977-984. DOI:10.1210/endo-28-6-977

Kholkute SD, Gopalkrishnan K, Puri CP. Variations in seminal parameters over a 12-month period in captive bonnet monkeys. Primates. 2000;41(4):393–405. doi:10.1007/BF02557650

Kinsky M. [Quantitative studies on Ethiopian mammals. (II. Absolute and relative weight of the testes of Ethiopian apes)]. Anatomischer Anzeiger. 1960;108:65-82. PMID: 14409245

Koda H, Murai T, Tuuga A, Goossens B, Nathan SKSS, Stark DJ, Ramirez DAR, Sha JCM, Osman I, Sipangkui R, Seino S, Matsuda I. Nasalization by Nasalis larvatus: Larger noses audiovisually advertise conspecifics in proboscis monkeys. Sci Adv. 2018;4(2):eaaq0250. doi:10.1126/sciadv.aaq0250

Kraemer DC, Vera Cruz NC. Collection, gross characteristics and freezing of baboon semen. J Reprod Fertil. 1969;20(2):345–348. doi:10.1530/jrf.0.0200345

Kruczek M & Styrna J. Sperm quantity and quality correlate with bank voles males' social status. Behav. Proc. 2009;82:279–285. Doi:10.1016/j.beproc.2009.07.009

Kuederling I, Morrell JM, Nayudu PL. Collection of semen from marmoset monkeys (Callithrix jacchus) for experimental use by vaginal washing. Lab Anim. 1996;30(3):260–266. DOI:10.1258/002367796780684845

Kuederling I, Schneiders A, Sønksen J, Nayudu PL, Hodges JK. Non-invasive collection of ejaculates from the common marmoset (Callithrix jacchus) using penile vibrostimulation. Am J Primatol. 2000;52(3):149–154. doi:10.1002/1098-2345(200011)52:3<149::AID-AJP4>3.0.CO;2-B

Kuehl TJ, Bowsher T, Perlman J, Lefever RL, Dye JL, & Brown ML. Cryo-banking of great ape spermatozoa using human protocols and variation among males. Fertility and Sterility. 2004;82:S326. DOI:10.1016/j.fertnstert.2004.07.881

Kusunoki H, Daimaru H, Minami S, Nishimoto S, Yamane KI, & Fukumoto Y. Birth of a chimpanzee (Pan troglodytes) after artificial insemination with cryopreserved epididymal spermatozoa collected postmortem. Zoo biology. 2001;20(3):135-143. DOI:10.1002/zoo.1015

Kyaligonza KJ. Semen analysis and induction of acrosome reaction in spermatozoa of tana mangabey (ercocebus galeritus) and De Brazza's (Cercopithecus neglectus) monkeys'. 1998. University of Nairobi. Thesis.

L

Lanzendorf SE, Gliessman PM, Archibong AE, Alexander M, Wolf DP. Collection and quality of rhesus monkey semen. Mol Reprod Dev. 1990;25(1):61–66. doi:10.1002/mrd.1080250111

Latif T, Lindahl-Jacobsen R, Mehlsen J, Eisenberg ML, Holmboe SA, Pors K, Brinth L, Skouby SO, Jørgensen N and Jensen TK. Semen quality associated with subsequent hospitalizations – Can the effect be explained by socio-economic status and lifestyle factors?. Andrology. 2018;6:428-435. doi:10.1111/andr.12477

Leão DL, Miranda SA, Brito AB, Lima JS, Santos RR, Domingues SF. Efficacious long-term cooling and freezing of Sapajus apella semen in ACP-118(®). Anim Reprod Sci. 2015;159:118–123. doi:10.1016/j.anireprosci.2015.06.005

Leibo SP, Kubisch HM, Schramm RD, Harrison RM, VandeVoort CA. Male-to-male differences in post-thaw motility of rhesus spermatozoa after cryopreservation of replicate ejaculates. J Med Primatol. 2007;36(3):151–163. doi:10.1111/j.1600-0684.2006.00194.x

Leivers S, Rhodes G, Simmons LW. Sperm competition in humans: mate guarding behavior negatively correlates with ejaculate quality. PLoS One. 2014;9(9):e108099. doi:10.1371/journal.pone.0108099

Lemaître JF, Ramm SA, Hurst JL, & Stockley P. Sperm competition roles and ejaculate investment in a promiscuous mammal. Journal of evolutionary biology. 2012;25(6):1216-1225. doi:10.1111/j.1420-9101.2012.02511.x

Lewis RJ. Chest staining variation as a signal of testosterone levels in male Verreaux's sifaka. Phys¬iology and Behavior. 2009;96:586–592. doi:10.1016/j.physbeh.2008.12.020

Li YH, Cai KJ, Su L, Guan M, He XC, Wang H, Kovacs A, Ji WZ. Cryopreservation of cynomolgus monkey (Macaca fascicularis) spermatozoa in a chemically defined extender. Asian J Androl. 2005a;7(2):139–144. doi:10.1111/j.1745-7262.2005.00039.x

Li YH, Cai KJ, Kovacs A, Ji WZ. Effects of various extenders and permeating cryoprotectants on cryopreservation of cynomolgus monkey (Macaca fascicularis) spermatozoa. J Androl. 2005b;26(3):387–395. doi:10.2164/jandrol.04147

Lima JS, Leão DL, Oliveira KG, Brito AB, Sampaio WV, Santos RR, Queiroz HL Domingues SF. Seminal coagulation and sperm quality in different social contexts in

captive tufted capuchin monkeys (Sapajus apella). Am J Primatol. 2017;79(6). doi:10.1002/ajp.22643

Liu YX. Control of spermatogenesis in primate and prospect of male contraception. Archives of Andrology. 2005;51(2):77-92. doi: 10.1080/01485010490485768

Lüpold S. Ejaculate quality and constraints in relation to sperm competition levels among eutherian mammals. Evolution. 2013;67(10):3052–3060. doi:10.1111/evo.12132

Lüpold S, Tomkins JL, Simmons LW, Fitzpatrick JL. Female monopolization mediates the relationship between pre- and postcopulatory sexual traits. Nat Commun. 2014;5:3184. doi:10.1038/ncomms4184

Lüpold S, Simmons LW, Grueter CC. Sexual ornaments but not weapons trade off against testes size in primates. Proc Biol Sci. 2019;286(1900):20182542. doi:10.1098/rspb.2018.2542

M

Maestripieri D, Roney JR. Primate copulation calls and postcopulatory female choice, Behavioral Ecology. 2005;16(1):106–113. https://doi.org/10.1093/beheco/arh120

Mahony MC, Oehninger S, Doncel G, Morshedi M, Acosta A, Hodgen GD. Functional and morphological features of spermatozoa microaspirated from the epididymal regions of cynomolgus monkeys (Macaca fascicularis). Biol Reprod. 1993;48(3):613–620. doi:10.1095/biolreprod48.3.613

Mahony MC, Lanzendorf S, Gordon K, Hodgen GD. Effects of caffeine and dbcAMP on zona pellucida penetration by epididymal spermatozoa of cynomolgus monkeys (Macaca fascicularis). Mol Reprod Dev. 1996;43(4):530–535. doi:10.1002/(SICI)1098-2795(199604)43:4<530::AID-MRD16>3.0.CO;2-2

Mahony MC, Rice K, Goldberg E, Doncel G. Baboon spermatozoa-zona pellucida binding assay. Contraception. 2000;61(3):235–240. doi:10.1016/s0010-7824(00)00093-7

Maree L, du Plessis SS, Menkveld R, van der Horst G. Morphometric dimensions of the human sperm head depend on the staining method used. Hum Reprod. 2010;25(6):1369–1382. doi:10.1093/humrep/deq075

Maree, L. Sperm mitochondria: species specificity and relationships to sperm morphometric features and sperm function in selected mammalian species. Thesis. 2011.

Marlowe, F. W. Hunter-gatherers and human evolution. Evolutionary Anthropology: Issues, News, and Reviews. 2005;14(2):54-67. Doi: 10.1002/evan.20046

1092 Marson J, Meuris S, Moysan F, Gervais D, Cooper RW, Jouannet P. Cellular and
1093 biochemical characteristics of semen obtained from pubertal chimpanzees by
1094 masturbation. J Reprod Fertil. 1988;82(1):199–207. doi:10.1530/jrf.0.0820199

1095 Marson J, Gervais D, Meuris S, Cooper RW, Jouannet P. Influence of ejaculation
1096 frequency on semen characteristics in chimpanzees (Pan troglodytes). J Reprod Fertil.
1097 1989;85(1):43–50. doi:10.1530/jrf.0.0850043

1098 Martínez IN, Morán JM, Peña FJ. Two-step cluster procedure after principal component
1099 analysis identifies sperm subpopulations in canine ejaculates and its relation to
1100 cryoresistance. J Androl. 2006;27(4):596–603. doi:10.2164/jandrol.05153

1101 Mastroianni L, Manson WA. Collection of monkey semen by electroejaculation. Proc
1102 Soc Exp Biol Med. 1963;112:1025–1027. doi:10.3181/00379727-112-28242

1103 Matsubayashi K. Comparison of the two methods of electroejaculation in the Japanese
1104 monkey (Macaca fuscata). Jikken Dobutsu. 1982;31(1):1–6.
1105 doi:10.1538/expanim1978.31.1_1

1106 Mautz BS, Møller AP, Jennions MD. Do male secondary sexual characters signal
1107 ejaculate quality? A meta-analysis. Biol Rev Camb Philos Soc. 2013;88(3):669–682.
1108 doi:10.1111/brv.12022

1109 Mdhluli MC, Seier JV, van der Horst G. The male vervet monkey: sperm characteristics
1110 and use in reproductive research. Gynecol Obstet Invest. 2004;57(1):17–18. PMID:
1111 14971416

1112 Middleton CC, Rosal J. Weights and measurements of normal squirrel monkeys (Saimiri
1113 sciureus). Lab Anim Sci. 1972;22(4):583-586. PMID:4340308

1114 Montoto LG, Arregui L, Sánchez NM, Gomendio M, Roldan ER. Postnatal testicular
1115 development in mouse species with different levels of sperm competition.
1116 Reproduction. 2012;143(3):333–346. doi:10.1530/REP-11-0245

1117 Morland HS. Reproductive activity of ruffed lemurs (Varecia variegata variegata) in a
1118 Madagascar rain forest. Am J Phys Anthropol. 1993;91(1):71-82.
1119 DOI:10.1002/ajpa.1330910105

1120 Moreland RB, Richardson ME, Lamberski N, Long JA. Characterizing the reproductive
1121 physiology of the male southern black howler monkey, Alouatta caraya. J Androl.
1122 2001;22(3):395–403. DOI:10.1002/j.1939-4640.2001.tb02195.x

1123 Morrell JM, Küderling I, Hodges JK. Influence of semen collection method on ejaculate
1124 characteristics in the common marmoset, Callithrix jacchus. J Androl. 1996;17(2):164–
1125 172. PMID: 8723441

Morrell JM. CASA as an aid to selecting sperm suspensions for artificial insemination in Callithrix jacchus. Int J Androl. 1997;20(5):287–296. DOI:10.1046/j.1365-2605.1997.00072.x

Morrell JM, Nubbemeyer R, Heistermann M, Rosenbusch J, Kuderling I, Holt W, Hodges JK. Artificial insemination in Callithrix jacchus using fresh or cryopreserved sperm. Anim Reprod Sci. 1998;52(2):165–174. DOI:10.1016/s0378-4320(97)00092-4

Mortimer ST, Mortimer D. Kinematics of human spermatozoa incubated under capacitating conditions. J Androl. 1990;11(3):195–203. DOI:10.1016/s0378-4320(97)00092-4

Mossman JA, Pearson JT, Moore HD, Pacey AA. Variation in mean human sperm length is linked with semen characteristics. Hum Reprod. 2013;28(1):22–32. doi:10.1093/humrep/des382

Muiño R, Tamargo C, Hidalgo CO, Peña AI. Identification of sperm subpopulations with defined motility characteristics in ejaculates from Holstein bulls: effects of cryopreservation and between-bull variation. Anim Reprod Sci. 2008;109(1-4):27–39. doi:10.1016/j.anireprosci.2007.10.007

Muller MN, Thompson ME, Kahlenberg SM, Wrangham RW. Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. Behav Ecol Sociobiol 2011;65:921–933. DOI:10.1007/s00265-010-1093-y

Muller MN. Testosterone and reproductive effort in male primates. Hormones and behavior. 2017;91:36-51. doi:10.1016/j.yhbeh.2016.09.001

N

Nagle, C. A., & Denari, J. H. (1983). The cebus monkey (Cebus apella). In Reproduction in new world primates (pp. 39-67). Springer, Dordrecht.

Nakazato, C., Yoshizawa, M., Isobe, K., Kusakabe, K. T., Kuraishi, T., Hattori, S., ... & Kiso, Y. Morphological characterization of spermatozoa of the night monkey. Journal of Mammalian Ova Research, 2015;32(1):37-41. DOI: 10.1274/jmor.32.37

Nascimento JM, Shi LZ, Meyers S, Gagneux P, Loskutoff NM, Botvinick EL, Berns MW. The use of optical tweezers to study sperm competition and motility in primates. J R Soc Interface. 2008;5(20):297–302. doi:10.1098/rsif.2007.1118

Nehra A, Werner MA, Bastuba M, Title C, Oates RD. Vibratory stimulation and rectal probe electroejaculation as therapy for patients with spinal cord injury: semen parameters and pregnancy rates. J Urol. 1996;155(2):554–559. PMID: 8558659

Nyachieo A, Spiessens C, Chai DC, Kiulia NM, Mwenda JM, D'Hooghe TM. Separate and combined effects of caffeine and dbcAMP on olive baboon (Papio anubis) sperm. J Med Primatol. 2010;39(3):137–142. DOI:10.1111/j.1600-0684.2010.00401.x

Nyachieo A, Spiessens C, Chai DC, Kiulia NM, Mwenda JM, D'Hooghe TM. Baboon spermatology: basic assessment and reproducibility in olive baboons (Papio anubis). J Med Primatol. 2012;41(5):297–303. DOI:10.1111/j.1600-0684.2012.00555.x

Nyachieo A, Kiraithe MM, Spiessens C, Chai DC, Kiulia NM, D'hooghe TM, Mwenda JM. Short-term effects of high-dose khat on sperm parameters and reproductive hormonal levels in olive baboons (Papio anubis). Gynecol Obstet Invest. 2013;75(2):109–114. DOI:10.1159/000345308

O

O'Brien JK, Hollinshead FK, Evans KM, Evans G, Maxwell WM. Flow cytometric sorting of frozen-thawed spermatozoa in sheep and non-human primates. Reprod Fertil Dev. 2003;15(7-8):367–375. DOI:10.1071/RD03065

Oliveira KG, Miranda SA, Leão DL, Brito AB, Santos RR, Domingues SF. Semen coagulum liquefaction, sperm activation and cryopreservation of capuchin monkey (Cebus apella) semen in coconut water solution (CWS) and TES-TRIS. Anim Reprod Sci. 2011;123(1-2):75–80. doi:10.1016/j.anireprosci.2010.11.002

Oliveira KG, Leão DL, Almeida DV, Santos RR, Domingues SF. Seminal characteristics and cryopreservation of sperm from the squirrel monkey, Saimiri collinsi. Theriogenology. 2015;84(5):743–749.e1. DOI:10.1016/j.theriogenology.2015.04.031

Oliveira KG, Santos RR, Leão DL, Brito AB, Lima JS, Sampaio WV, Domingues SF. Cooling and freezing of sperm from captive, free-living and endangered squirrel monkey species. Cryobiology. 2016a;72(3):283–289. doi:10.1016/j.cryobiol.2016.03.004

Oliveira KG, Santos RR, Leão DL, Queiroz HL, Paim FP, Vianez-Júnior JLDSG, Domingues SFS. Testicular biometry and semen characteristics in captive and wild squirrel monkey species (Saimiri sp.). Theriogenology. 2016b;86(3):879–887.e4. doi:10.1016/j.theriogenology.2016.03.009

Ombelet W, Bosmans E, Janssen M, Cox A, Vlasselaer J, Gyselaers W, Vandeput H, Gielen J, Pollet H, Maes M, Steeno O, Kruger T. Semen parameters in a fertile versus subfertile population: a need for change in the interpretation of semen testing. Hum Reprod. 1997;12(5):987–993. doi:10.1093/humrep/12.5.987

Ortega-Ferrusola C, Macías García B, Suárez Rama V, Gallardo-Bolaños JM, González-Fernández L, Tapia JA, Rodríguez-Martinez H, Peña FJ. Identification of sperm subpopulations in stallion ejaculates: changes after cryopreservation and comparison

with traditional statistics. Reprod Domest Anim. 2009;44(3):419–423. doi:10.1111/j.1439-0531.2008.01097.x

P

Parga JA. Copulatory plug displacement evidences sperm competition in Lemur catta. International Journal of Primatology. 2003;24(4):889-899. doi:10.1023/A:1024637024088

Parga JA. (2017). Copulatory Plug. In The International Encyclopedia of Primatology (eds Bezanson M, MacKinnon KC, Riley E, Campbell CJ, Nekaris K, Estrada A, Di Fiore AF, Ross S, Jones-Engel LE, Thierry B, Sussman RW, Sanz C, Loudon J, Elton S, Fuentes A). doi:10.1002/9781119179313.wbprim0223

Parker GA. Sperm competition and its evolutionary consequences in the insects. Biological Reviews. 1970;45:525–567. doi:10.1111/j.1469-185X.1970.tb01176.x

Parker GA. Sperm competition games: raffles and roles. Proc. R. Soc. Lond. B. 1990;242:120-126. Doi: 10.1098/rspb.1990.0114

Parker GA. Sperm competition and the evolution of ejaculates: towards a theory base. Sperm competition and sexual selection, 1998;3-54. DOI:10.1016/B978-0-12-100543-6.X5022-3

Parker GA, Lessells CM, and Simmons LW. Sperm competition games: a general model for precopulatory male-male competition. Evolution. 2013;67:95-109. Doi:10.1111/j.1558-5646.2012.01741.x

Parker GA. The evolution of expenditure on testes. J Zool. 2016;298:3-19. doi:10.1111/jzo.12297

Parker GA, Pizzari T. Sperm competition and ejaculate economics. Biol Rev Camb Philos Soc. 2010;85(4):897–934. doi:10.1111/j.1469-185X.2010.00140.x

Petter-rousseaux A. Reproductive physiology and behavior of the Lemuroidea In Buettner-Janusch J., editor.(Ed.), Evolutionary and genetic biology of primates. 1964; 91–132. DOI:10.1016/B978-0-12-395562-3.50009-6

Pitnick S, Dobler R, Hosken DJ. Sperm length is not influenced by haploid gene expression in the flies Drosophila melanogaster and Scathophaga stercoraria. Proc Biol Sci. 2009;276(1675):4029–4034. doi:10.1098/rspb.2009.1208

Pizzari T, Cornwallis CK, Froman DP. Social competitiveness associated with rapid fluctuations in sperm quality in male fowl. Proc Biol Sci. 2007;274(1611):853–860. doi:10.1098/rspb.2006.0080

Platz CC, Wildt DE, Bridges CH, Seager SW, Whitlock BS. Electroejaculation and semen analysis in a male lowland gorilla,Gorilla gorilla gorilla . Primates. 1980;21:130–132. doi:10.1007/BF02383831

Poches RA, Brieva CI & Jiménez C. Caracteristicas seminales del Titi gris (Saguinus leucopus) bajo condiciones de cautiverio, obtenidas por estimulacion vibratoria del pene (EVP). Revista de la Facultad de Medicina Veterinaria y de Zootecnia, 2013;60(I):11-22. ISSN: 0120-2952

Pope CE, Dresser BL, Chin NW, Liu JH, Loskutoff NM, Behnke EJ, ... & Cameron KN. Birth of a western lowland gorilla (Gorilla gorilla gorilla) following in vitro fertilization and embryo transfer. American journal of primatology, 1997;41(3):247-260. DOI:10.1002/(SICI)1098-2345(1997)41:3<247::AID-AJP6>3.0.CO;2-X

Pudritz S. (2000). Untersuchungen zu Kapazitierung und Akrosomreaktion der Spermatozoen des Weißb€ uschelaffen (Callithrix jacchus) in vitro.[Characterization and regulation of sperm capacitation and acrosome reaction in vitro in the marmoset monkey (Callithrix jacchus)] (Doctoral dissertation, PhD thesis)–Faculty of Biology, University of Marburg, Marburg).

R

Ramakrishna PA, Prasad MR. Changes in the male reproductive organs of Loris tardigradus lydekkerianus (Cabrera). Folia Primatol (Basel). 1967;5(3):176-89. DOI:10.1159/000161945

Ramesh V, Ramachandra SG, Krishnamurthy HN, Rao AJ. Electroejaculation and seminal parameters in bonnet monkeys (Macaca radiata). Andrologia. 1998;30(2):97–100. doi:10.1111/j.1439-0272.1998.tb01153.x

Ramón M, Pérez-Guzmán MD, Jiménez-Rabadán P, Esteso MC, García-Alvarez O, Maroto-Morales A, Anel-López L, Soler AJ, Fernández-Santos MR, Garde JJ. Sperm cell population dynamics in ram semen during the cryopreservation process. PLoS One. 2013;8(3):e59189. doi:10.1371/journal.pone.0059189

Rao M, Zhao XL, Yang J, Hu SF, Lei H, Xia W, Zhu CH. Effect of transient scrotal hyperthermia on sperm parameters, seminal plasma biochemical markers, and oxidative stress in men. Asian J Androl. 2015;17(4):668–675. doi:10.4103/1008-682X.146967

Rojas Mora A, Meniri M, Ciprietti S, Helfenstein F. Social dominance explains within-ejaculate variation in sperm design in a passerine bird. BMC Evol Biol. 2017;17(1):66. doi:10.1186/s12862-017-0914-2

Roussel JD, Austin CR. Preservation of primate spermatozoa by freezing. J Reprod Fertil. 1967;13(2):333–335. doi:10.1530/jrf.0.0130333

Roussel JD & Austin CR. Improved electroejaculation of primates. J. Inst. Anim. Tech. 1968;19(1):22.

S

Sampaio WV, Oliveira KG, Leão DL, Caldas-Bussiere MC, Queiroz HL, Paim FP, Santos RR, Domingues SFS. Morphologic analysis of sperm from two neotropical primate species: comparisons between the squirrel monkeys Saimiri collinsi and Saimiri vanzolinii. Zygote. 2017;25(2):141–148. doi:10.1017/S0967199416000411

San Diego Zoo Global Library Sperm Atlas. 2020 San Diego Zoo Global. Last Updated: Dec 31, 2019 7:19 PM https://ielc.libguides.com/sdzg/databases/spermatlas

Sánchez-Partida GL, Maginnis G, Dominko T, Martinovich C, McVay B, Fanton J, Schatten G. Live rhesus offspring by artificial insemination using fresh sperm and cryopreserved sperm. Biol Reprod. 2000;63(4):1092–1097. doi:10.1095/biolreprod63.4.1092

Sankai T, Terao K, Yanagimachi R, Cho F, Yoshikawa Y. Cryopreservation of spermatozoa from cynomolgus monkeys (Macaca fascicularis). J Reprod Fertil. 1994;101(2):273–278. doi:10.1530/jrf.0.1010273

Santolaria P, Soler C, Recreo P, Carretero T Bono A, Berné JM, Yániz JL. Morphometric and kinematic sperm subpopulations in split ejaculates of normozoospermic men. Asian J Androl. 2016;18(6):831–834. doi:10.4103/1008-682X.186874

Schaffer N, Cranfield M, Meehan T, & Kempske S. Semen collection and analysis in the conservation of endangered nonhuman primates. Zoo Biology. 1989;8(S1):47-60. DOI: 10.1002/zoo.1430080507

Schaffer N, Jeyendran RS, & Beehler B. Improved sperm collection from the lowland gorilla: recovery of sperm from bladder and urethra following electroejaculation. American Journal of Primatology. 1991;24(3-4):265-271. DOI:10.1002/ajp.1350240312|

Schneiders A, Sonksen J, Hodges JK. Penile vibratory stimulation in the marmoset monkey: a practical alternative to electro-ejaculation, yielding ejaculates of enhanced quality. J Med Primatol. 2004;33(2):98–104. DOI:10.1111/j.1600-0684.2004.00058.x

Schultz AH. The relative weight of the testes in primates. 1938. DOI:10.1002/ar.1090720310

Seager SWJ, Wildt DE, Schaffer N, & Platz CC. Semen collection and evaluation in Gorilla gorilla gorilla. American Journal of Primatology. 1982;3(S1 S1):13-13. DOI: 10.1002/ajp.1350030506

Setchell JM, Dixson AF. Changes in the secondary sexual adornments of male mandrills (Mandrillus sphinx) are associated with gain and loss of alpha status. Horm. Behav. 2001;39:177–184. doi:10.1006/hbeh.2000.1628

Setchell JM, Charpentier M, & Wickings EJ. Sexual selection and reproductive careers in mandrills (Mandrillus sphinx). Behavioral Ecology and Sociobiology. 2005;58(5):474-485. DOI: 10.1007/s00265-005-0946-2

Seuanez HN, Carothers AD, Martin DE, Short RV. Morphological abnormalities in spermatozoa of man and great apes. Nature. 1977;270(5635):345–347. doi:10.1038/270345a0

Short RV. (1977). Sexual selection and the descent of man. In Reproduction and evolution: 3–19. Calaby, J.H. & Tyndale-Biscoe, C.H. (Eds). Canberra: Australian Academy of Sciences.

Short RV. Sexual selection and its component parts, somatic and genital selection, as illustrated by man and the great apes. Advances in the Study of Behavior. 1979;9:131–158. doi:10.1016/S0065-3454(08)60035-2

Si W, Zheng P, Tang X, He X, Wang H, Bavister BD, Ji W. Cryopreservation of rhesus macaque (Macaca mulatta) spermatozoa and their functional assessment by in vitro fertilization. Cryobiology. 2000;41(3):232–240. doi:10.1006/cryo.2000.2283

Silva KSM, Ribeiro HFL, Valle RR, Sousa JS, Silva AO, & Barbosa EM. Efeitos do trimetilaminoetano (TES) e ringer lactato em sêmen de macacos-aranha mantidos em cativeiro (Ateles paniscus e A. marginatus). Arquivo Brasileiro de Medicina Veterinária e Zootecnia. 2013;65(3):934-937. DOI:10.1590/S0102-09352013000300044

Simmons LW, Lüpold S, Fitzpatrick JL. Evolutionary Trade-Off between Secondary Sexual Traits and Ejaculates. Trends Ecol Evol. 2017;32(12):964–976. doi:10.1016/j.tree.2017.09.011

Sloter E, Schmid TE, Marchetti F, Eskenazi B, Nath J, Wyrobek AJ. Quantitative effects of male age on sperm motion. Hum Reprod. 2006;21(11):2868–2875. doi:10.1093/humrep/del250

Smuts BB, Smuts RW. Male Aggression and Sexual Coercion of Females in Nonhuman Primates and Other Mammals: Evidence and Theoretical Implications. Advances in the Study of Behavior. 1993;22:1-63.

Soini P. 1993. The ecology of the pygmy marmoset, Cebuella pygmaea: some comparisons with two sympatric tamarins. In Marmosets and Tamarins: Systematics, Behaviour, and Ecology, ed. A. B. Rylands, pp. 252-72. Oxford: Oxford University Press. DOI:10.1002/ajpa.1330970413

Soler C, de Monserrat JJ, Gutiérrez R, Nuñez J, Sancho M, Pérez-Sánchez F, Cooper TG. Use of the Sperm-Class Analyser for objective assessment of human sperm morphology. Int J Androl. 2003;26(5):262–270. doi:10.1046/j.1365-2605.2003.00422.x

Sparman ML, Ramsey CM, Thomas CM, Mitalipov SM, Fanton JW, maginnis GM, Stouffer RL, Wolf DP. Evaluation of the vervet (Clorocebus aethiops) as a model for the assisted reproductive technologies. Am J Primatol. 2007;69(8):917–929. doi:10.1002/ajp.20413

Srivastava PN, Farooqui AA, Gould KG. Studies on hydrolytic enzymes of chimpanzee semen. Biol Reprod. 1981;25(2):363–369. doi:10.1095/biolreprod25.2.363

Steinberg ER, Sestelo AJ, Ceballos MB, Wagner V, Palermo AM, Mudry MD. Sperm Morphology in Neotropical Primates. Animals (Basel). 2019;9(10):839. DOI:10.3390/ani9100839

Stockley P, Gage MJ, Parker GA, Møller AP. Sperm competition in fishes: the evolution of testis size and ejaculate characteristics. Am Nat. 1997;149(5):933–954. doi:10.1086/286031

Stockley P, & Bro-Jørgensen J. Female competition and its evolutionary consequences in mammals. Biological Reviews. 2011;86(2):341-366.

Swanson WF, Valle RR, Carvalho FM, Arakaki PR, Rodas-Martínez AZ, Muniz JAPC, García-herreros M. Sperm Morphology Assessment in Captive Neotropical Primates. Reprod Domest Anim. 2016;51(4):623–627. doi:10.1111/rda.12711

T

Thilagavathi J, Venkatesh S, Kumar R, Dada R. Segregation of sperm subpopulations in normozoospermic infertile men. Syst Biol Reprod Med. 2012;58(6):313–318. doi:10.3109/19396368.2012.706361

Thomsen R, Soltis J, Teltscher C. Sperm competition and the function of male masturbation in non-human primates. In: Jones CB (ed) Sexual selection and reproductive competition in primates: new perspectives and directions. ASP-Book Series, Special Topics in Primatology. 2003;3:436–453

Thomsen R, Soltis J, Matsubara M, Matsubayashi K, Onuma M, Takenaka O. How costly are ejaculates for Japanese macaques?. Primates. 2006;47(3):272–274. doi:10.1007/s10329-005-0171-7

Thomsen R. Non-invasive collection and analysis of semen in wild macaques. Primates. 2014;55(2):231–237. doi:10.1007/s10329-013-0393-z

Thomson JA, Iliff-Sizemore SA, Gliessman PM, & Wolf DP. Collection and fertilization potential of sperm from the Sulawesi crested black macaque (Macaca nigra). American Journal of Primatology. 1992;28(4):289-297. DOI: 10.1002/ajp.1350280407

Thurston LM, Watson PF, Mileham AJ, Holt WV. Morphologically distinct sperm subpopulations defined by Fourier shape descriptors in fresh ejaculates correlate with variation in boar semen quality following cryopreservation. J Androl. 2001;22(3):382–394. PMID: 11330638

Tollner TL, VandeVoort CA, Overstreet JW, Drobnis EZ. Cryopreservation of spermatozoa from cynomolgus monkeys (Macaca fascicularis). J Reprod Fertil. 1990;90(2):347–352. doi:10.1530/jrf.0.0900347

V

Valerio DA, Leverage WE, Munster JH. Semen evaluation in Macaques. Lab Anim Care. 1970;20(4 Pt 1):734–740. PMID: 4247970

Valle RR, Guimarães MA, Muniz JA, Barnabe RC, Vale WG. Collection and evaluation of semen from captive howler monkeys (Alouatta caraya). Theriogenology. 2004;62(1-2):131–138. DOI:10.1016/j.theriogenology.2003.08.004

Valle RDRD, Zacarias FC, Miranda RP, Muniz JAPC, Carvalho RAD, & Ribeiro HF. Evaluation of Howler monkeys (Alouatta caraya) semen after cooling at 4 C using two different extenders. In: Internal congress on animal reproduction, 15; 2004, Porto Seguro.

Valle RR, Valle CM, Nichi M, Muniz JA, Nayudu PL, Guimarães MA. Validation of non-fluorescent methods to reliably detect acrosomal and plasma membrane integrity of common marmoset (Callithrix jacchus) sperm. Theriogenology. 2008;70(1):115–120. doi:10.1016/j.theriogenology.2008.03.011

Valle RR, Carvalho FM, Muniz JA, Leal CL, García-Herreros M. Differential distribution of sperm subpopulations and incidence of pleiomorphisms in ejaculates of captive howling monkeys (Alouatta caraya). Naturwissenschaften. 2013;100(10):923–933. DOI:10.1007/s00114-013-1092-8

Valle Rdel R, Valle CM, Nichi M, Muniz JA, Nayudu PL, Guimarães MA. Semen characteristics of captive common marmoset (Callithrix jacchus): a comparison of a German with a Brazilian colony. J Med Primatol. 2014;43(4):225–230. doi:10.1111/jmp.12111

Valtonen-André C, Olsson AY, Nayudu PL, Lundwall A. Ejaculates from the common marmoset (Callithrix jacchus) contain semenogelin and beta-microseminoprotein but not prostate-specific antigen. Mol Reprod Dev. 2005;71(2):247–255. DOI:10.1002/mrd.20257

van Der Horst G, Seier JV, Spinks AC, Hendricks S. The maturation of sperm motility in the epididymis and vas deferens of the vervet monkey, Cercopithecus aethiops. Int J Androl. 1999;22(3):197–207. doi:10.1046/j.1365-2605.1999.00171.x

van der Horst G, Maree L, Kotzé SH, O'Riain MJ. Sperm structure and motility in the eusocial naked mole-rat, Heterocephalus glaber: a case of degenerative orthogenesis in the absence of sperm competition?. BMC Evol Biol. 2011;11:351. doi:10.1186/1471-2148-11-351

van der Horst G, Maree L. Sperm form and function in the absence of sperm competition. Mol Reprod Dev. 2014;81(3):204–216. doi:10.1002/mrd.22277

Vandevoort CA, Neville LE, Tollner TL, & Field LP. Noninvasive semen collection from an adult orangutan. Zoo Biology. 1993;12(3):257-265. DOI: 10.1002/zoo.1430120303

VandeVoort CA. High quality sperm for nonhuman primate ART: production and assessment. Reprod Biol Endocrinol. 2004;2:33. Published 2004 Jun 16. doi:10.1186/1477-7827-2-33

van Noordwijk, M.A., van Schaik, C.P., 2004. Sexual selection and the careers of primate males: paternity concentration, dominance acquisition tactics and transfer decisions. In: Kappeler, P.K., van Schaik, C.P. (Eds.), Sexual Selection in Primates: New and Comparative Perspectives. ambridge University Press, Cambridge, pp. 208–229.

Van Schaik CP. The primate origins of human nature. John Wiley & Sons. 2016. DOI:10.1002/9781119118206

van Schaik J, Kerth G. Host social organization and mating system shape parasite transmission opportunities in three European bat species. Parasitol Res. 2017;116(2):589–599. doi:10.1007/s00436-016-5323-8

Vidal FD, Luz MS, de Pinho TG, & Pissinatti A. Coleta de sêmen em mico-leão-de-cara-dourada (Leontopithecus chrysomelas)(Kuhl, 1820) através da eletroejaculação Callitrichidae–primates. Revista Brasileira de Ciência Veterinária. 2007;14(2).

W

Warner H, Martin DE, Keeling ME. Electroejaculation of the great apes. Ann Biomed Eng. 1974;2(4):419–432. doi:10.1007/bf02368098

Watts DP. Mountain gorilla life histories, reproductive competition, and some implications for captive husbandry. Zoo Biology. 1990;9:185–200. Doi:10.1002/zoo.1430090302

Weinbauer GF, Niehaus M, Nieschlag E. The role of testosterone in spermatogenesis. In: Nieschlag E, Behre HM, editors. Testosterone: Action, Deficiency, Substitution. Cambridge University Press; Cambridge: 2004. pp. 173–206.

Weisbroth S, Young FA. The collection of primate semen by electro-ejaculation. Fertil Steril. 1965;16:229–235. doi:10.1016/s0015-0282(16)35530-3

Whitten PL. Evolutionary endocrinology of the cercopithecoids. In:Whitehead PF, Jolly CJ, editors. Old world monkeys. Cambridge, U.K. Cambridge University Press; 2000. p. 269– 97.

Wickings EJ, Nieschlag E. Seasonality in endocrine and exocrine testicular function of the adult rhesus monkey (Macaca mulatta) maintained in a controlled laboratory environment. Int J Androl. 1980;3(1):87–104. doi:10.1111/j.1365-2605.1980.tb00099.x

Wickings EJ, Dixson AF. Testicular function, secondary sexual development, and social status in male mandrills (Mandrillus sphinx). Physiol Behav. 1992;52(5):909-16. DOI:10.1016/0031-9384(92)90370-h

Wildt DE: Spermatozoa: collection, evaluation, metabolism, freezing, and artificial insemination. In: Comparative Primate Biology, Volume 3: Reproduction and Development. Dukelow & Erwin (eds). New York: Alan R. Liss, Inc., 1986.

Wingfield JC, Hegner RE, Dufty AM Jr, Ball GF. The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. Am. Nat. 1990;136:829–846. www.jstor.org/stable/2462170.

Wingfield. The challenge hypothesis: Where it began and relevance to humans. Hormones & Behaviour. 2017;92: 9-12. Doi:10.1016/j.yhbeh.2016.11.008

Y

Yang S, Ping S, Ji S, Lu Y, NIU Y, Wang H, Ji W, Si W. The positive effects of seminal plasma during the freezing process on cryosurvival of sperm with poor freezability in the rhesus macaque (Macaca mulatta). J Reprod Dev. 2011;57(6):737–743. doi:10.1262/jrd.11-056n

Yeoman RR, Ricker RB, Williams LE, Sonksen J, Abee CR. Vibratory Stimulation of Ejaculation Yields Increased Motile Spermatozoa, Compared with Electroejaculation, in Squirrel Monkeys (Saimiri boliviensis). Contemp Top Lab Anim Sci. 1997;36(1):62–64.

Yeoman RR, Sonksen J, Gibson SV, Rizk BM, Abee CR. Penile vibratory stimulation yields increased spermatozoa and accessory gland production compared with rectal electroejaculation in a neurologically intact primate (Saimiri boliviensis). Hum Reprod. 1998;13(9):2527–2531. doi:10.1093/humrep/13.9.2527

Young LG, Smithwick EB, & Gould KG. Characteristics of chimpanzee (Pan troglodytes) ejaculates collected by rectal probe electrostimulation and by artificial vagina. American Journal of Primatology. 1995;35(4):293-304. DOI:10.1002/ajp.1350350405

Younis AI, Rooks B, Khan S, Gould KG. The effects of antifreeze peptide III (AFP) and insulin transferrin selenium (ITS) on cryopreservation of chimpanzee (Pan troglodytes) spermatozoa. J Androl. 1998;19(2):207–214. PMID: 9570745

Yu JF, Lai YH, Wang TE, Wei YS, Chang YJ, Li SH, Chin SC, Joshi R, Chang HW, Tsai PS. The effects of type I collagenase on the degelification of chimpanzee (Pan troglodytes) semen plug and sperm quality. BMC Vet Res. 2018;14(1):58. doi:10.1186/s12917-018-1389-0

Z

Zamboni L, Conaway CH, Van Pelt L. Seasonal changes in production of semen in free-ranging rhesus monkey. Biol Reprod. 1974;11(3):251–267. doi:10.1095/biolreprod11.3.251

Zainuddin Z, Kang YC, Tarmizi MRM, Ahmad AH & Payne JB. Seminal evaluation and cryopreservation of sperms from the pig-tailed macaque, Macaca nemestrina. Journal of Sustainability Science and Management. 2019;14(3):92-99.

Zinner D, Schwibbe MH & Kaumanns W. Cycle synchrony and probability of conception in female hamadryas baboons Papio hamadryas. Behavioral Ecology and Sociobiology. 1994;35:175–183. doi:10.1007/BF00167957

FIGURE LEGENDS

Figure 1. Relative testes mass to body mass for 71 primate species displayed by family (A) or mating system (B). Each dot refers to a single species. If several data were available, mean is presented.

References : Aotidae : 1938 Schultz, 1981 Harcourt, 2004 Dixson ; Atelidae : 1925 Hrdlicka, 1938 Schultz, 1981 Harcourt, 1998 Parker, 2004 Dixson, 2019 Arakaki ; Callitrichidae : 1925 Hrdlicka, 1981 Harcourt, 1987 Dixson, 1993 Soini, 1999 Birkhead, 2004 Dixson 2004 ; Cebidae : 1960 Hill, 1972 Middleton, 1981 Harcourt, 1998 Parker, 1999 Birkhead 1999, 2004 Dixson ; Cercopithecidae : 1938 Schultz, 1941b Kennard, 1960 Kinsky, 1966 Hill, 1970 Hill, 1976 Amann, 1981 Harcourt, 1986 Amann, 1987 Dixson, 1991 Harcourt, 1992 Wickings, 1993 Bercovitch, 1998 Parker, 1999 Birkhead, 2000 Gupta, 2004 Dixson ; Cheirogaleidae : 1964 Petter-Rousseaux, 1998 Parker, 2002 Aslam, 2004 Dixson ; Galagidae : 1964 Butler, 1987 Dixson, 1998 Parker, 2004 Dixson ; Hominidae : 1938 Schultz, 1962 Hall-Craggs, 1981 Harcourt, 1986 Amann, 1998 Parker, 1999 Birkhead, 2004 Dixson ; Hylobatidae : 1938 Schultz, 1941a Kennard, 1946 Harrison-Matthews, 1981 Harcourt, 1998 Parker, 1999 Birkhead, 2004 Dixson ; Indriidae : 1964 Petter-Rousseaux ; Lemuridae : 1964 Petter-Rousseaux, 1977 Bogart, 1993 Morland, 1998 Parker, 2004 Dixson ; Lorisidae : 1967 Ramakrishna, 1981 Harcourt ; Pitheciidae : 1960 Hill, 1995 Harcourt.

Figure 2. Relationships between total sperm length, abnormal morphology and mating system of 66 primate species. Total sperm length is presented according to the species mating system (A) and percentage of sperm with normal morphology is presented according to the mean total sperm length of the species (B) or mating system (C). Each dot refers to a single species with data presented as mean if several sources. Black

horizontal line is the mean of each mating system. *_Gorilla gorilla_ and **_Callithrix penicillata_.

References : Aotidae : 2015 Nakazato ; Atelidae : 2001 Moreland, 2002 Hernandez-Lopez, 2004a Valle, 2004b Valle, 2012 Flores-Herrera, 2013 Valle, 2016 Swanson ; Callitrichidae : 1991 Cui, 1996 Cui, 1996 Morrell, 1997 Morrell, 2004 Schneiders, 2007 Vidal, 2009 Da Silva, 2013 Poches, 2013 Valle, 2014 Valle, 2016 Swanson, 2017 Arakaki, 2018 Arakaki ; Cebidae : 1968 Ackerman, 2002 Barnabe, 2011 Oliveira, 2015 Leao, 2015 Nakazato, 2015 Oliveira, 2016a Oliveira, 2016b Oliveira, 2017 Sampaio ; Cercopithecidae : 1968 Ackerman, 1980 Wickings, 1988 Cranfield, 1989 Schaffer, 1992 Thomson, 1998 Kyaligonza, 1999 Chan, 1999 Gago, 2000 Cseh, 2000 Kholkute, 2004 Mdhluli, 2012 Nyacheio, 2014 Thomsen, 2019 Zainuddin ; Hominidae : 1968 Ackerman, 1977 Seuanez, 1980 Platz, 1982 Gould, 1982 Seager, 1983 Bader, 1986 Jeyendran, 1988 Marson, 1997 Ombelet, 1997 Pope, 1998 Aziz, 2001 Kusunoki, 2003 Soler, 2005 O’brien, 2007 Aziz, 2010 Cooper, 2012 Thilagavathi, 2018 Yu ; Hylobatidae : 1968 Ackerman.

TABLES

Table 1. Sperm morphometric data of 76 primate species.

Species	Head									Flagellum				Total length (µM)
	Length (µM)	Width (µM)	Perimeter (µM)	Area (µM²)	Volume (µM³)	Ellipticity (L/W)	Elongation (L-W)/(L+W)	Roughness (4π(A/P²))	Regularity (π(LW/4A))	Midpiece length (µM)	Principal piece length (µM)	Terminal piece (µM)	Flagellum length (µM)	
Aotidae family														
Aotus lemurinus	2.8	4.7	-	-	19.3	0.60	-0.25	-	-	6.60	-	-	45.70	55.10
Atelidae family														
Alouatta caraya	4.8	3.1	13.2	12.3	37.5	1.57	0.22	0.88	132.6	3.56	-	-	-	55.01
Ateles belzebuth	5.2	2.7	-	-	38.2	1.93	0.32	-	-	6.56	-	-	-	70.83
Ateles chamek	5.2	3.3	-	-	45.6	1.58	0.22	-	-	7.34	-	-	-	64.09
Ateles geoffroyi	4.5	2.8	-	-	29.6	1.62	0.24	-	-	-	-	-	-	-
Ateles paniscus	5.8	3.3	-	-	45.0	1.56	0.22	-	-	8.71	-	-	48.50	124.61
Mean Aotidae	5.1	3.0	13.2	12.3	39.2	1.7	0.2	0.9	132.6	6.5	-	-	48.5	78.6
Callitrichidae family														
Callimico goeldii	5.0	3.1	14.3	14.8	40.3	1.57	0.21	0.90	181.0	-	-	-	-	-
Callithrix geoffroyi	5.0	2.5	-	-	32.7	2.00	0.33	-	-	6.00	-	-	62.00	73.00
Callithrix jacchus	5.2	3.3	14.6	15.2	44.1	1.55	0.21	0.89	214.9	4.15	-	-	47.22	52.31
Cebuella pygmaea	5.3	4.0	-	-	53.9	1.50	0.20	-	-	7.75	-	-	42.95	58.00
Leontopithecus rosalia	5.5	4.0	-	-	63.4	1.38	0.16	-	-	5.00	-	-	68.00	78.00
Saguinus fuscicollis	5.6	3.2	-	-	52.5	1.73	0.27	-	-	-	-	-	55.16	60.74
Saguinus leucopus	4.9	3.3	-	9.7	41.9	1.51	0.20	-	123.1	-	-	-	58.62	64.88
Saguinus midas	5.3	-	-	-	36.2	-	-	-	-	9.10	-	-	40.20	
Saguinus oedipus	5.1	3.3	-	-	42.9	1.67	0.25	-	-	11.20	-	-	49.17	64.96
Mean callitrichidae	5.2	3.3	14.4	13.2	45.3	1.6	0.2	0.9	173.0	7.2	-	-	52.9	64.6
Cebidae family														
Cebus albifrons	9.0	-	-	-	59.4	-	-	-	-	13.20	-	-	58.20	-
Saimiri boliviensis	5.9	4.0	-	-	74.0	1.47	0.19	-	-	11.35	-	-	62.00	74.10
Saimiri collinsi	6.2	4.2	-	-	84.5	1.48	0.19	-	-	-	-	-	70.50	76.80
Saimiri sciureus	5.4	3.5	-	-	46.3	1.46	0.19	-	-	9.83	55.34	-	58.08	71.42
Saimiri vanzolinii	6.8	4.8	-	-	116.2	1.42	0.17	-	-	-	-	-	69.20	76.10
Sapajus apella	7.5	3.5	-	-	60.5	1.64	0.24	-	-	10.96	-	-	64.00	75.97
Sapajus cay	6.1	3.9	-	-	77.0	1.57	0.22	-	-	8.67	-	-	-	65.06
Sapajus libidinosus	5.9	3.7	-	-	67.1	1.58	0.22	-	-	8.53	-	-	-	67.26
Sapajus nigritus	6.3	4.1	-	-	85.1	1.53	0.21	-	-	9.35	-	-	-	66.27
Mean Cebidae	6.6	4.0	-	-	74.5	1.5	0.2	-	-	10.3	55.3	-	63.7	71.6
Cercopithecidae family														
Allenopithecus nigroviridis	5.6	3.3	-	-	54.9	1.69	0.26	-	-	9.32	-	-	57.54	66.49
Cercocebus galeritus	6.8	-	-	-	-	-	-	-	-	13.30	-	-	73.00	93.10
Cercopithecus lhoesti	4.0	2.5	-	-	20.9	1.60	0.23	-	-	9.00	-	-	41.00	54.00
Cercopithecus nictitans	5.3	-	-	-	46.2	-	-	-	-	12.30	-	-	40.50	-
Cercopithecus petaurista	5.7	3.0	-	-	41.4	1.67	0.25	-	-	9.60	-	-	38.95	73.00

Cercopithecus wolfi	5.0	4.0	-	-	52.4	1.25	0.11	-	-	-	-	-	68.00	73.00
Chlorocebus aethiops	5.8	3.3	14.0	13.3	44.0	1.60	0.23	0.86	161.9	11.40	52.26	2.87	65.10	77.32
Erythrocebus patas	7.7	-	-	-	63.2	-	-	-	-	13.55	-	-	69.90	89.50
Lophocebus albigena	5.8	-	-	-	37.2	-	-	-	-	11.10	-	-	17.30	-
Lophocebus aterrimus	5.2	3.8	15.2	16.6	53.4	1.36	0.15	0.90	256.6	8.51	4.54	-	-	-
Macaca arctoides	5.9	3.4	-	-	52.5	1.64	0.24			10.52	61.46	-	64.10	77.61
Macaca fascicularis	5.7	3.7	15.0	16.7	58.7	1.54	0.21	0.93	296.9	11.15	57.04	-	58.60	77.97
Macaca mulatta	5.3	3.3	15.9	17.1	51.7	1.71	0.26	0.85	280.5	11.19	57.88	2.97	62.58	75.86
Macaca nemestrina	7.4	-	-	-	48.7	-	-	-	-	13.50	-	-	69.25	90.40
Macaca radiata	5.5	-	-	-	-	-	-	-	-	10.50	50.00	-	75.00	-
Macaca silenus	5.7	3.2	-	-	49.7	1.50	0.20	-	-	10.83	-	-	29.93	60.04
Macaca sinica	-	-	-	-	-	-	-	-	-	-	-	-	-	69.10
Macaca sylvanus	5.5	-	-	-	49.5	-	-	-	-	12.80	-	-	62.10	-
Macaca thibetana	6.0	3.5	-	-	64.9	1.72	0.26	-	-	11.98	-	-	62.01	79.96
Mandrillus leucophaeus	4.5	3.0	-	-	31.3	1.33	0.14	-	-	12.10	-	-	36.30	70.00
Mandrillus sphinx	6.1	4.1	-	-	64.4	1.40	0.17	-	-	11.63	55.80	-	51.65	69.63
Papio anubis	4.8	3.1	-	-	45.3	1.56	0.22	-	-	8.40	-	-	67.48	75.30
Papio cynocephalus	4.7	3.9	-	-	47.7	1.23	0.10	-	-	10.02	58.03	3.50	64.07	75.40
Papio hamadryas	6.5	-	-	-	47.2	-	-	-	-	12.70	-	-	58.00	-
Papio ursinus	5.6	3.5	15.4	16.3	56.3	1.60	0.23	0.86	248.2	9.97	58.02	3.37	70.92	76.49
Piliocolobus badius	-	-	-	-	-	-	-	-	-	-	-	-	-	84.00
Pygathrix nemaeus	4.3	-	-	-	44.7	-	-	-	-	11.50	-	-	23.50	-
Theropithecus gelada	6.8	-	-	-	61.9	-	-	-	-	12.20	-	-	68.80	87.30
Trachypithecus cristatus	6.0	3.0	-	-	56.5	2.00	0.33	-	-	11.00	-	-	42.00	59.00
Trachypithecus francoisi	5.0	3.0	-	-	39.3	1.67	0.25	-	-	10.00	-	-	45.00	60.00
Mean Cercopithecidae	5.6	3.4	15.1	16.0	49.4	1.6	0.2	0.9	248.8	12.3	50.6	3.2	53.7	74.5
Cheirogaleidae family														
Microcebus murinus	7.3	-	-	-	38.7	-	-	-	-	13.70	-	-	66.74	86.65
Microcebus myoxinus	8.1	-	-	-	-	-	-	-	-	-	-	-	-	93.60
Daubentoniidae family														
D. madagascariensis	6.3	-	-	-	-	-	-	-	-	-	-	-	-	55.80
Galagidae family														
Galago senegalensis	4.7	4.0	-	-	44.4	1.23	0.10	-	-	9.65	46.00	-	53.43	61.20
Otolemur crassicaudatus	5.6	3.8	-	-	62.4	1.47	0.19	-	-	9.50	45.30	-	48.47	60.30
Hominidae family														
Gorilla gorilla	8.8	7.1	-	-	258.2	1.38	0.16	-	-	12.23	40.97	-	41.99	61.17
Homo sapiens	4.9	3.1	12.9	11.5	40.3	1.61	0.23	0.80	147.6	4.51	43.25	5.62	49.05	56.15
Pan paniscus	4.7	2.8	-	-	30.1	1.68	0.25	-	-	6.79	-	-	52.25	59.30
Pan troglodytes	4.8	2.9	-	-	32.8	1.61	0.23	-	-	6.62	46.42	-	51.42	61.54
Pongo pygmaeus	5.2	3.8	-	-	50.3	1.40	0.17	-	-	8.97	52.27	-	53.42	66.58
Mean Hominidae	5.7	3.9	12.9	11.5	82.3	1.5	0.2	0.8	147.6	7.8	45.7	5.6	49.6	60.9
Hylobatidae family														
Hylobates lar	7.1	-	-	-	66.3	-	-	-	-	8.40	-	-	48.00	63.50
Hylobates syndactylus	7.5	-	-	-	55.2	-	-	-	-	8.20	-	-	53.20	-
Lemuridae family														

Eulemur fulvus	5.6	-	-	-	35.1	-	-	-	-	11.00	-	-	62.30	-
Eulemur macaco	6.5	4.5	-	-	89.9	1.58	0.22	-	-	10.68	37.30	-	45.10	54.90
Eulemur mongoz	6.0	-	-	-	43.2	-	-	-	-	13.50	-	-	43.20	55.30
Lemur catta	4.9	4.6	-	-	55.7	1.13	0.06	-	-	11.27	42.10	-	52.20	55.87
Varecia variegata	7.5	3.6	-	-	106.0	2.08	0.35	-	-	20.70	76.60	-	83.50	104.87
Mean Lemuridae	6.1	4.2	-	-	66.0	1.6	0.2	-	-	13.4	52.0	-	57.3	67.7
Lepilemuridae family														
Lepilemur mustelinus	-	-	-	-	-	-	-	-	-	-	-	-	-	52.00
Lorisidae family														
Nycticebus coucang	7.7	5.6	-	-	152.4	1.52	0.21	-	-	13.63	67.90	-	72.28	90.00
Tarsiidae family														
Cephalopachus bancanus	9.0	-	-	-	-	-	-	-	-	9.90	-	-	-	-
Mean primates	**5.8**	**3.6**	**14.5**	**14.4**	**56.6**	**1.5**	**0.2**	**0.9**	**204.3**	**10.1**	**50.4**	**3.7**	**55.1**	**70.7**

All measurements are presented uncritically and as mean when multiple sources. References: Aotidae : 1938 Schultz, 1981 Harcourt, 2004 Dixson ; Atelidae : 1925 Hrdlicka, 1938 Schultz, 1981 Harcourt, 1998 Parker, 2004 Dixson, 2019 Arakaki, 2019 Steinberg ; Callitrichidae : 1925 Hrdlicka, 1981 Harcourt, 1987 Dixson, 1993 Soini, 1999 Birkhead, 2004 Dixson, 2019 San Diego Zoo ; Cebidae : 1960 Hill, 1972 Middleton, 1981 Harcourt, 1998 Parker, 1999 Birkhead, 2004 Dixson ; Cercopithecidae : 1938 Schultz, 1941 Kennard, 1960 Kinsky, 1966 Hill, 1970 Hill, 1976 Amann, 1981 Harcourt, 1986 Amann, 1987 Dixson, 1991 Harcourt, 1992 Wickings, 1993 Bercovitch, 1998 Parker, 1999 Birkhead, 2000 Gupta, 2004 Dixson, 2019 San Diego Zoo ; Cheirogaleidae : 1964 Petter-Rousseaux, 1998 Parker, 2002 Aslam, 2004 Dixson ; Galagidae : 1964 Butler, 1987 Dixson, 1998 Parker, 2004 Dixson ; Hominidae : 1938 Schultz, 1962 Hall-Craggs, 1981 Harcourt, 1986 Amann, 1998 Parker, 1999 Birkhead, 2004 Dixson, 2019 San Diego Zoo ; Hylobatidae : 1938 Schultz, 1941 Kennard, 1946 Harrison-Matthews, 1981 Harcourt, 1998 Parker, 1999 Birkhead, 2004 Dixson ; Indriidae : 1964 Petter-Rousseaux ; Lemuridae : 1964 Petter-Rousseaux, 1977 Bogart, 1993 Morland, 1998 Parker, 2004 Dixson ; Lorisidae : 1981 Harcourt, 1967 Ramakrishna ; Pitheciidae : 1960 Hill, 1995 Harcourt, 2019 San Diego Zoo.

1543 Table 2. Semen analysis of 43 primate species.

			Semen analysis									
Species	Collection method	n	pH	Mean volume (µL)	Volume range	Mean concentration (10^6/mL)	Concentration range	Mean motility (%)	Motility range (%)	Mean intact membrane (%)	Mean intact acrosome (%)	Normal morphology (%)
Aotidae family												
Aotus lemurinus	EE	3	-	-	-	-	-	-	-	-	-	67.1
Atelidae family												
Alouatta caraya	ES	41	7.97	88.4	10-218	748.4	7-5400	74.43	5-95	57.84	58.96	59.45
Ateles geoffroyi	ES	21	-	3300	210-8000	102.48	18-301	62.2	7-65	53.8	-	62.83
Brachyteles arachnoides	ES	5	7.7	353	303-402	144	-	82.5	70-95	64.5	81	-
Callitrichidae family												
Callimico goeldii	ES	16	7.61	26.9	-	143.18	-	83.33	-	36.38	66	47.8
Callithrix jacchus	ES	48	7.56	35.1	8-200	139.2	0.1-710	47.7	10-90	76.48	-	50.4
Callithrix jacchus	EE	26	-	-	-	28	2.2-85.8	57.47	43.5-90	83.21	74.5	89.83
Callithrix jacchus	PVS	107	7.54	26.62	2-78	492.62	32.4-3557	65.52	20-95	67.22	80.44	44.33
Callithrix jacchus	VW	12	-	-	-	19	0.3-114	71.65	20-95	84.4	-	91.9
Callithrix penicillata	PVS	10	7.53	16.83	-	1.47	-	56.67	-	62.83	76.67	30.17
Leontopithecus chrysomelas	ES	10	-	11.9	-	-	-	-	-	-	-	67.29
Saguinus leucopus	PVS	-	7.5	24	-	87.62	-	97.1	-	93.7	-	69.3
Cebidae family												
Saimiri boliviensis	ES	20	-	202.5	200-205	2.8	-	57.05	44.1-70	-	-	-
Saimiri boliviensis	EE	1	-	-	-	-	-	-	-	-	-	98.3
Saimiri boliviensis	PVS	20	-	418	400-436	77.1	-	80.2	79.8-80.6	-	-	-
Saimiri cassiquiarensis	ES	10	-	120	60-180	-	-	61.5	43-80	76	-	86
Saimiri collinsi	ES	48	7.43	285.97	10-1100	92.64	20-121	73.67	16-100	65.88	-	75.32
Saimiri macrodon	ES	10	-	500	-	-	-	90	-	98	-	93
Saimiri sciureus	ES	12	-	243.68	37-500	298.24	0.1-847.1	65.85	20-90	70.3	-	57
Saimiri vanzolinii	ES	18	-	168.37	-	-	-	89	-	74.33	-	92
Sapajus apella	ES	74	-	911.4	200-2600	791.85	38.7-1810	52.51	15-83	64.57	-	64.8
Cercopithecidae family												
Cercocebus galeritus	ES	4	8.3	57.4	20-150	1989	100-4100	89.8	-	-	-	83.8
Cercopithecus neglectus	ES	3	8.4	39.2	3.6-80	64.1	15-180	76.8	-	-	-	71
Chlorocebus aethiops	EE	1	-	-	-	230.7	-	32	-	-	-	-
Chlorocebus aethiops	ES	81	7.82	700	600-1200	134.69	0.2-280	56.11	28-80	63.13	57.39	64.02
Chlorocebus aethiops	M	5	-	1540	1300-1900	3.14	2.3-3.9	46.4	30-67	-	-	-
Erythrocebus patas	ES	8	-	-	-	226.2	6.5-445.9	45	5-56	45.5	-	59.5
Lophocebus aterrimus	ES	1	-	337.5	50-750	1.45	0.3-3	62.5	30-90	78.85	83.79	-
Macaca arctoides	ES	6	-	-	-	264	11-509	35	5-60	49	-	70
Macaca fascicularis	EE	24	-	-	-	23	-	75.33	64-82	78.9	63.5	-
Macaca fascicularis	ES	31	-	576.25	50-3000	551.46	10-2430	75.15	35-91	67.72	91.09	74.75
Macaca fascicularis	VW	4	-	530	300-800	275	120-870	-	-	82.4	-	-
Macaca fuscata	ES	2	-	-	-	-	-	50	40-55	-	-	-
Macaca fuscata	M	32	7.1	2200	100-5000	529.4	12.5-990	-	-	59.6	-	94.4
Macaca mulatta	ES	117	7.25	411	20-7200	433.75	6-4040	74.24	30-98	73.15	88.59	60.94
Macaca mulatta	EE	19	-	-	-	920	9-218	83	50-95	-	-	-

Macaca nemestrina	ES	10	7.82	1298.5	80-2600	168.15	4-705	77.43	44-90	82.01	-	70.57
Macaca nigra	ES	4	-	-	-	31.15	3.6-57.6	71.3	58-82.2	-	-	96.95
Macaca radiata	ES	7	-	780	200-3000	249	116-799	78.3	60-94	78	91.4	87.2
Macaca silenus	ES	23	8.5	900	10-4000	144.2	38-800	58.35	30-95	-	-	50
Papio anubis	ES	54	7.53	413.65	150-3220	65.21	0.2-239.2	57.59	0.1-98	72.25	53.88	63.99
Papio cynocephalus	ES	2	-	4000	3000-5000	840	600-1080	75	70-80	-	-	-
Papio hamadryas	EE	2	-	-	-	-	-	42.5	-	-	59.5	-
Papio ursinus	ES	10	-	900	-	212.5	-	73.4	-	-	-	
Theropithecus gelada	ES	1	-	-	-	-	104	-	20	22	-	81
Cheirogaleidae family												
Microcebus murinus	ES	16	-	-	-	-	-	48.4	37-64	66.4	-	-
Hominidae family												
Gorilla gorilla	ES	57	8.3	548.33	10-1850	111.33	0.1-1300	25.33	0-90	45	-	42.5
Gorilla gorilla	M	2	-	2100	-	91.7	-	-	-	-	-	23.75
Homo sapiens	M	2580	7.8	2500	1400-6000	39	12-200	32	0-90	58	-	32.22
Pan paniscus	ES	1	-	-	-	-	-	-	-	-	-	98
Pan troglodytes	ES	34	-	1860	100-5400	493.45	1-2900		0-84	52	-	81.9
Pan troglodytes	EE	2	-	-	-	-	-	87.5	82.5-89.5	96.95	88.73	95.5
Pan troglodytes	M	69	-	2471.43	100-4400	775.88	61-11300	73.5	3-93.2	72.13	82.75	69.58
Pongo abelli	M	1	-	6100	-	164	6-312	60	38-70	-	-	-
Pongo pygmaeus	ES	4	-	1100	200-3200	61	10-128	47	32-62	59	-	98.5
Pongo pygmaeus	M	1	-	2000	-	60	-	-	-	-	-	-
Hylobatidae family												
Hylobates lar	ES	3	-	-	-	293	34-552	10	5-15	29.5	-	55.5

All measurements are presented uncritically and as mean when multiple sources. EE: epididymal extraction (aspiration or dissection) ; ES: Electrostimulation (rectal probe or electrods) ; M: Masturbation (manual or artificial vagina) ; PVS : penile vibrostimulation ; VW: vaginal washing (flushing or pipetting) ; n: number of individuals (as some authors did not give the number of individuals included in their studies, these numbers should be considered as minima).

References: Aotidae : 2015 Nakazato ; Atelidae : 2001 Moreland, 2002 Hernandez-Lopez, 2004a Valle, 2004b Valle, 2008 Hernandez-Lopez, 2009 Cerda Molina, 2012 Flores-Herrera, 2013 Valle, 2013 Silva, 2014 Carvalho, 2016 Swanson, 2019 Arakaki ; Callitrichidae : 1991 Cui, 1996 Cui, 1996 Kuederling, 1996 Morell, 1997a Morell, 1997b Morell, 2000 Kuederling, 2000 Pudritz, 2003 O'brien, 2004 Schneiders, 2005 Hernandez-Lopez, 2005 Valtonen, 2007 Vidal, 2008 Valle, 2009 Da silva, 2013 Poches, 2013 Valle, 2014 Valle, 2016 Swanson, 2017 Arakaki, 2018 Arakaki ; Cebidae : 1967 Bennett, 1968 Ackerman, 1976 Denis, 1983 Nagle, 1997 Yeoman, 1998 Yeoman, 2002 Barnabe, 2009 Araujo,2011 Oliveira, 2015 Leao, 2015 Nakazato, 2015 Oliveira, 2016a Oliveira, 2017 Lima, 2017b Oliveira ; Cercopithecidae : 1963 Mastroianni, 1965 Weisbroth, 1967 Hoskins, 1967 Roussel, 1968 Ackerman, 1968 Roussel, 1969 Kraemer, 1970 Valerio, 1973 Cho, 1974 Zamboni, 1976 Fléchon, 1980 Wickings, 1988 Cranfield, 1989 Schaffer, 1990 Lanzendorf, 1990 Tollner, 1992 Thomson, 1993 Mahony, 1994 Conradie, 1994 Sankai, 1996 Mahony, 1998 Kyaligonza, 1998 Ramesh, 1999 Chan, 1999 Gago, 1999 Hiyaoka, 1999 van der Horst, 2000 Cseh, 2000 Kholkute, 2000 Mahony, 2000 Sanchez-Partida, 2000 Si, 2001 Feradis, 2003 Amboka, 2003 O'brien, 2004 Mdhluli, 2004 Vandevoort, 2005a Li, 2005b Li, 2007 Hung, 2007 Leibo, 2007 Sparman, 2008 Gagliardi, 2008 Dong, 2009 Dong, 2010 Nyachieo, 2011 Maree, 2011 Yang, 2012 Nyachieo, 2013 Nyachieo, 2014

Thomsen, 2017 Dubaut, 2018 Devilliers, 2019 Gadea, 2019 Zainuddin ; Hominidae: 1967 Roussel, 1968 Ackerman, 1974 Hardin, 1974 Warner, 1977 Seuanez, 1980 Platz, 1981 Srivastava, 1982 Gould, 1982 Seager, 1983 Bader, 1986 Jeyendran, 1988 Marson, 1989 Gould, 1989 Marson, 1991 Schaffer, 1993 Vandevoort, 1993 Gould, 1995 Young, 1995 Joslin, 1997 Ombelet, 1997 Pope, 1998 Aziz, 1998 Younis, 2001 Kusunoki, 2003 O'brien, 2003 Soler, 2004 Kuehl, 2005 Agca, 2005 O'brien, 2006 Sloter, 2007 Aziz, 2010 Cooper, 2010 Maree, 2011 Maree, 2012 Thilagavathi, 2013 Mossman, 2018 Yu ; Hylobatidae : 1968 Ackerman.

Table 3. Computer assisted sperm analysis of 9 primate species.

Species	VAP (μM)	VCL (μM)	VSL (μM)	ALH (μM)	References
Callitrichidae family					
Callithrix jacchus	97.5	125.2	82.7	6.2	1996 Morell, 1997 Morell, 1998 Morell, 2004 Schneiders, 2005 Hernandez-Lopez
Cercopithecidae family					
Chlorocebus aethiops	227.7	201.5	167.8	3.8	1999 van der Horst, 2004 Mdhluli, 2011 Maree
Macaca fascicularis	-	152.7	140.0	6.3	1990 Tollner, 1993 Mahony, 1996 Mahony
Macaca mulatta	182.0	222.1	163.9	4.6	2006 Baumber, 2007 Hung, 2011 Maree
Papio ursinus	357.2	367.7	337.8	3.4	2011 Maree
Cheirogaleidae family					
Microcebus murinus	-	145	20.2	-	2002 Aslam
Hominidae family					
Homo sapiens	75.2	98	69.9	2.7	1990 Mortimer, 2006 Sloter, 2011 Maree
Pan troglodytes	138.0	110.3	34.3	5.2	1993 Gould, 1998 Younis, 2018 Nascimiento, 2018 Yu

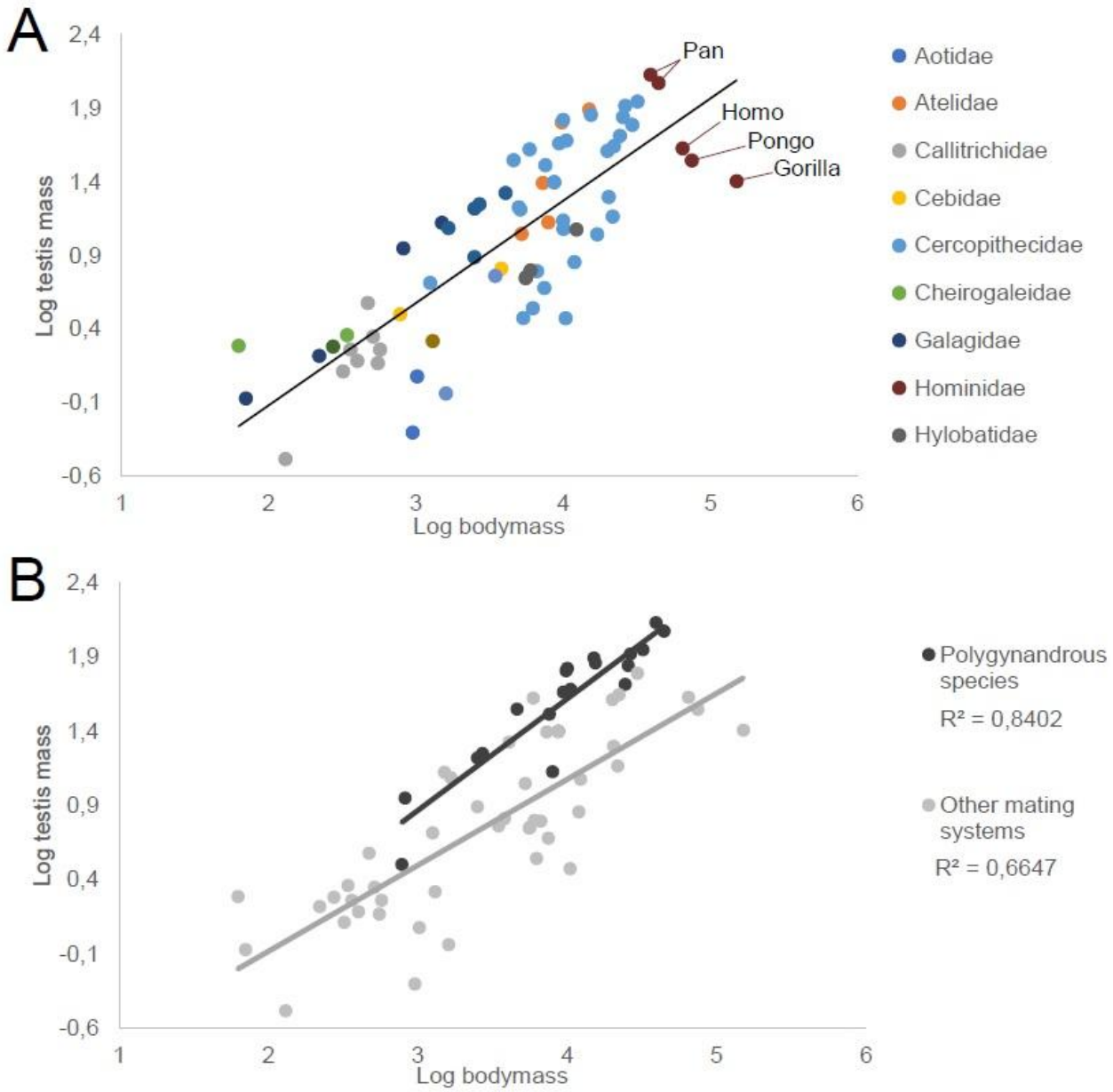
All measurements are presented uncritically and as mean when multiple sources. VAP: average path velocity; VCL: curvilinear velocity; VSL: straight-line velocity; ALH: head lateral amplitude.

1568 Table 4. Mean total weight of both testis for 71 primate species.

Species	Total weigth (gr)	References
Aotidae family		
Aotus lemurinus	0.500	2004 Dixson
Aotus trivigatus	1.200	1938 Schultz, 1981 Harcourt
Atelidae family		
Alouatta palliata	24.950	1925 Hrdlicka, 1981 Harcourt
Ateles geoffroyi	13.400	1938 Schultz, 1981 Harcourt
Ateles paniscus	64.230	1998 Parker
Brachyteles arachnoides	78.350	2019 Arakaki
Lagothrix lagotricha	11.200	1938 Schultz, 1981 Harcourt
Mean Atelidae	38.426	
Callitrichidae family		
Callithrix jacchus	1.300	1981 Harcourt, 1999 Birkhead, 2004 Dixson
Cebuella pygmaea	0.330	1993 Soini
Leontopithecus rosalia	1.480	1987 Dixson
Mico argentatus	1.830	1987 Dixson
Saguinus fuscicollis	1.530	2004 Dixson
Saguinus midas	1.830	1987 Dixson
Saguinus nigricollis	3.800	1987 Dixson
Saguinus oedipus	2.440	1925 Hrdlicka, 1981 Harcourt, 1999 Birkhead
Mean callitrichidae	1.818	
Cebidae family		
Saimiri sciureus	3.185	1972 Middleton, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
Sapajus apella	6.870	1960 Hill, 1998 Parker, 2004 Dixson
Cercopithecidae family		
Allenopithecus nigroviridis	16.960	1966 Hill
Cercocebus atys	25.100	1966 Hill
Cercocebus torquatus	25.100	1941 Kennard
Cercopithecus ascanius	3.000	1966 Hill
Chlorocebus aethiops	16.800	1960 Kinsky, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
Colobus guereza	2.980	1987 Dixson
Colobus polykomos	12.200	1960 Kinsky, 2004 Dixson
Erythrocebus patas	7.200	1991 Harcourt, 1998 Parker, 2004 Dixson
Lophocebus aterrimus	13.780	1966 Hill
Macaca arctoides	48.200	1981 Harcourt, 1999 Birkhead, 2004 Dixson
Macaca fascicularis	35.450	1938 Schultz, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
Macaca fuscata	72.300	2004 Dixson
Macaca mulatta	49.565	1938 Schultz, 1976 Amann, 1981 Harcourt, 1986 Amann, 1993 Bercovitch, 1999 Birkhead, 2000 Gupta, 2004 Dixson
Macaca nemestrina	66.700	1938 Schultz, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
Macaca radiata	38.950	1938 Schultz, 1981 Harcourt, 2000 Gupta, 2004 Dixson
Macaca silenus	42.000	1998 Parker, 2004 Dixson
Mandrillus leucophaeus	41.050	1970 Hill
Mandrillus sphinx	61.907	1992 Wickings, 1998 Parker, 2004 Dixson
Miopithecus talapoin	5.200	1987 Dixson
Nasalis larvatus	14.700	1938 Schultz
Papio anubis	83.447	1981 Harcourt, 1998 Parker, 2004 Dixson
Papio cynocephalus	52.000	1981 Harcourt
Papio hamadryas	49.700	1960 Kinsky, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
Papio papio	88.900	1981 Harcourt
Papio ursinus	69.760	1981 Harcourt, 2004 Dixson
Presbytis rubicunda	3.500	1938 Schultz, 1981 Harcourt
Semnopithecus entellus	11.100	1981 Harcourt, 2004 Dixson
Theropithecus gelada	20.033	1960 Kinsky, 1970 Hill, 1999 Birkhead
Trachypithecus cristatus	6.250	1938 Schultz, 1981 Harcourt
Trachypithecus obscurus	4.800	1981 Harcourt
Mean Cercopithecidae	32.954	
Cheirogaleidae family		
Cheirogaleus major	2.300	1964 Petter-Rousseaux
Microcebus murinus	2.098	1964 Petter-Rousseaux, 1998 Parker, 2002 Aslam, 2004 Dixson
Galagidae family		
Galago senegalensis	1.660	1964 Butler
Galagoides demidovii	0.850	1987 Dixson
Otolemur crassicaudatus	13.320	1998 Parker, 2004 Dixson
Otolemur garnetti	8.930	2004 Dixson
Mean Galagidae	6.190	

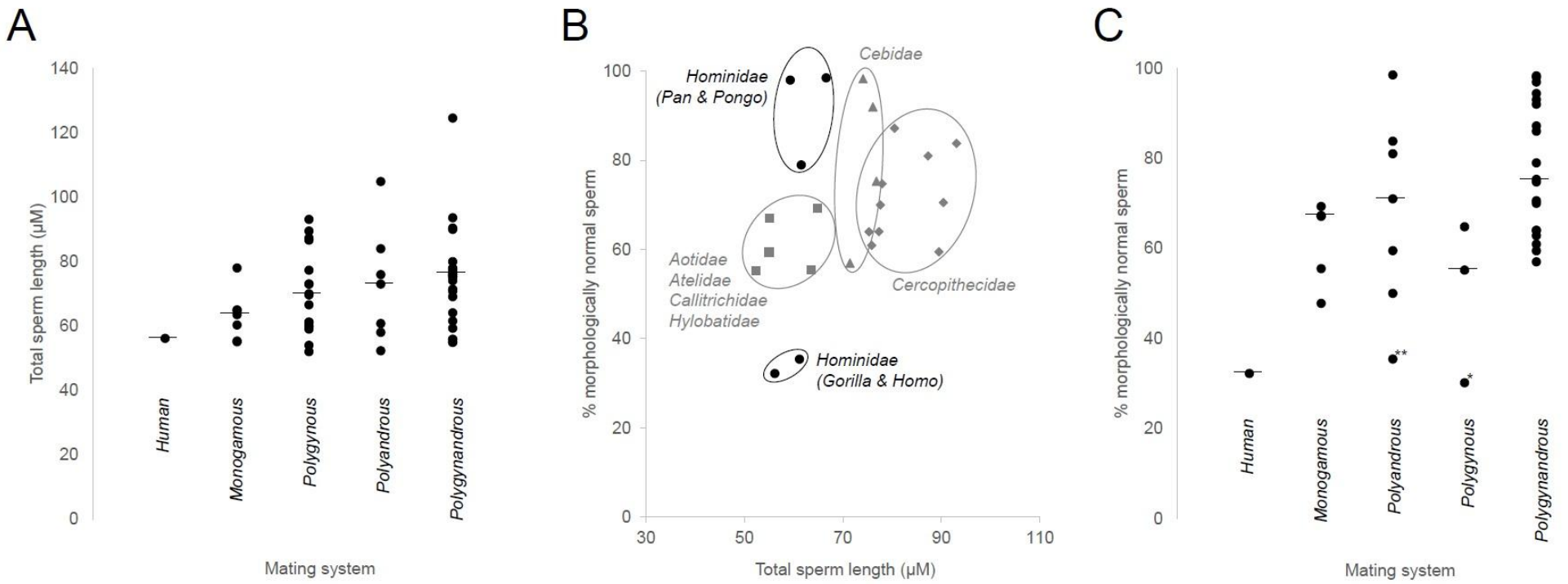
Hominidae family		
Gorilla gorilla	25.673	1962 Hall-Crags, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
Homo sapiens	43.080	1938 Schultz, 1981 Harcourt, 1986 Amann, 1999 Birkhead, 2004 Dixson
Pan paniscus	135.200	1998 Parker, 2004 Dixson
Pan troglodytes	118.800	1938 Schultz, 1999 Birkhead, 2004 Dixson
Pongo pygmaeus	35.300	1938 Schultz, 1999 Birkhead, 2004 Dixson
Mean Hominidae	71.611	
Hylobatidae family		
Hylobates agilis	6.320	1946 Harrison-Mattews
Hylobates lar	5.705	1941 Kennard, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
Hylobates moloch	5.600	1938 Schultz, 1981 Harcourt
Hylobates syndactylus	11.950	1998 Parker, 2004 Dixson
Mean Hylobatidae	7.394	
Indriidae family		
Avahi laniger	2.090	1964 Petter-Rousseaux
Lemuridae family		
Eulemur fulvus	7.780	1964 Petter-Rousseaux
Eulemur macaco	16.650	1977 Bogart, 1998 Parker, 2004 Dixson
Eulemur mongoz	12.250	1998 Parker, 2004 Dixson
Lemur catta	17.800	1998 Parker, 2004 Dixson
Varecia variegata	21.735	1993 Morland, 2004 Dixson
Mean Lemuridae	15.243	
Lorisidae family		
Loris tardigradus	1.920	1967 Ramakrishna, 1981 Harcourt
Pitheciidae family		
Cacajao calvus	5.800	1995 Harcourt
Pithecia pithecia	0.920	1960 Hill
Mean primates	**24.096**	

All measurements are presented uncritically and as mean when multiple sources.


A
2,4
1,9
1,4
0,9
0,4
-0,1
-0,6
Log testis mass
1
2
3
4
5
6
Log bodymass
Pan
Homo
Pongo
Gorilla
Aotidae
Atelidae
Callitrichidae
Cebidae
Cercopithecidae
Cheirogaleidae
Galagidae
Hominidae
Hylobatidae
B
2,4
1,9
1,4
0,9
0,4
-0,1
-0,6
Log testis mass
1
2
3
4
5
6
Log bodymass
Polygynandrous species
R² = 0,8402
Other mating systems
R² = 0,6647

1572

1573


A
Total sperm length (μM)
140
120
100
80
60
40
20
0
Human
Monogamous
Polygynous
Polyandrous
Polygynandrous
Mating system
B
% morphologically normal sperm
100
80
60
40
20
0
30
50
70
90
110
Total sperm length (μM)
Hominidae
(Pan & Pongo)
Cebidae
Aotidae
Atelidae
Callitrichidae
Hylobatidae
Cercopithecidae
Hominidae
(Gorilla & Homo)
C
% morphologically normal sperm
100
80
60
40
20
0
Human
Monogamous
Polyandrous
Polygynous
Polygynandrous
**
*
Mating system

1574