Paternity data and relative testes size as measures of level of sperm competition in the Cercopithecoidea

Short Title: Sperm competition in cercopithecoids

R. Robin Baker [1,#a], Todd K. Shackelford[2*]

[1] School of Biological Sciences, University of Manchester, Manchester, UK

[2] Department of Psychology, Oakland University, Rochester, Michigan, USA

[#a] Current address: Hard Nut Books Ltd, London, UK

*Corresponding author; e-mail: shackelf@oakland.edu (TKS)

ABSTRACT

Historically, the empirical study of the role of sperm competition in the evolution of sexual traits has been problematic through an enforced reliance on indirect proxy measures. Recently, however, a procedure was developed that uses paternity data to measure sperm competition level directly in terms of males/conception (i.e., the number of males that have sperm present in a female's ampulla at conception). When tested on apes and humans (Hominoidea) this measure proved not only to correlate significantly with the traditionally-used measure of relative testes size but also to offer a number of advantages. Here we provide a second test of the procedure, this time using paternity data for the Old World monkeys (Cercopithecoidea). We calculate sperm competition levels (males/conception) for 17 species of wild and free-ranging cercopithecoids and then analyze the data against measures of relative testes size. Calculated sperm competition levels correlate strongly with relative testes size both with and without phylogenetic control at both the species and generic levels. The signal-to-noise ratios inherent in both the past measure of relative testes size and the new measure of sperm competition level from paternity data are discussed. We conclude that although both measures are appropriate for the future study of the role of sperm competition in the evolution of sexual traits, when paternity data are available they provide the more direct and meaningful analytical tool. Not least, they potentially allow a first empirical analysis of the role of sperm competition in the evolution of relative testes size that could then be compared with the wealth of theoretical analyses that already exist.

KEYWORDS

1. INTRODUCTION

Sperm competition is the competition between sperm from multiple males to fertilize the egg(s) produced by a single female (Parker, 1970). In internal fertilizers, such competition occurs only when a female "multiple-mates" (i.e. copulates with a further male or males while containing competitive sperm from an earlier but different male). To be directly involved in the production of offspring, this multiple-mating must occur when a fertilizable egg (or eggs) is already available in the female or will become available at some moment during the overlap in competitive lifetimes of the sets of sperm.

Since Parker's (1970) groundbreaking unveiling of the process of sperm competition for insects, students of sexual traits have recognized the widespread importance of the phenomenon as an evolutionary force (e.g., Smith, 1984). No matter whether the trait of interest is anatomical, physiological, behavioral, cellular, or molecular, nor whether the animal is an insect, fish, bird, mammal, or other, sperm competition is an ever-present candidate for influence. However, the empirical study of this influence has been, and still is, beset with difficulties. Prime among the problems has been the lack of means to measure sperm competition directly, forcing investigators to rely instead on indirect proxy measures as appropriate to different taxonomic groups.

For primates, two main proxy measures have been used: socio-sexual system (e.g., Harcourt, Harvey, Larson, and Short, 1981; Short 1979) and relative testes size (i.e., combined testes weight as a proportion of male body weight; for examples of use see: Anderson and Dixson, 2002; Dorus, Evans, Wyckoff, Choi, and Lahn, 2004). The adoption of socio-sexual system as a measure springs simply from the assumption that species with females living in groups containing multiple males will experience higher

levels of sperm competition than those living in groups containing only a single male (Short, 1979). In contrast, the adoption of relative testes size as a measure derives from nearly five decades of theoretical modelling.

One group of such models (review: Parker, 2016) is based on the principle that the optimum number of sperm inseminated during copulation is an evolutionary trade-off between the risk that sperm may enter into competition with sperm from another male, favoring more sperm, and the cost of sperm production, favoring fewer. In consequence, if the level of sperm competition increases during the evolution of a lineage, then natural selection should favor males that inseminate more sperm until the advantage gained via sperm competition reaches the trade-off level.

In primates, more sperm can be produced at a faster rate by larger testes (Møller, 1988). Selection to increase the number of sperm inseminated should therefore result in males investing a greater proportion of resources into testes size (Parker 1970, 1982), thus leading to greater relative testes size (i.e. absolute testes size divided by total body weight, where absolute testes size is the weight of the two testes combined). Conversely, in lineages in which the trade-off level between sperm number and production cost begins to decrease because of decreasing levels of sperm competition, male investment in testes size should decrease and relative testes size will decrease accordingly. The predicted result is that, across species, those that evolved under higher levels of sperm competition should have a greater relative testes size than others that evolved under lower levels of sperm competition. Relative testes size, therefore, should be a correlate of the level of sperm competition during a species' evolutionary history and as a consequence can be used as a proxy measure of that level.

Empirically, the primary support for the validity of both measures (socio-sexual system and relative testes size) derives from a correlation between the two (Harcourt et al. 1981; Harcourt, Purvis and Liles, 1995; Short 1979).

Recently, we argued (Baker and Shackelford, 2018) that a third source of information, paternity data, may generate more than just a proxy measure of sperm competition level. We developed a procedure and formulae that allowed the direct calculation of sperm competition level in terms of males per conception (i.e., the number of males that have sperm present in a female's ampulla at conception). So far, however, the support for the procedure and formulae developed in that article rests solely on an analysis of data for a single primate superfamily, the apes and humans (Hominoidea). Here we apply our procedure and formulae to data for the other superfamily of catarrhine primates, the Old World monkeys (Cercopithecoidea).

The hypothesis to be tested for the Cercopithecoidea in this article is the same as that tested previously for the Hominoidea (Baker and Shackelford, 2018). It is that paternity data, as processed here, can provide a measure of sperm competition that is at least as useful as relative testes size. We also take the first steps towards evaluating the accuracy of the levels of sperm competition (males/conception) calculated from paternity data and discuss whether this is a more practical or exploitable value than relative testes size to be used in future studies of the evolution of sexual traits.

2. METHODS

As all data for cercopithecoids used here are from published studies by other authors, the protocol and procedures did not require review and approval by the IACUC or other institutional ethics committees overseeing animal use in research in either the United

States of America or the United Kingdom. The study also adhered to the American

Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

2.1. Species referenced

A full list of the common and scientific names of all 28 species referenced in this article

is provided in Table 1.

2.2. Relative testes size

The relative testes size of cercopithecoids has been expressed as either: (1) the

combined weight of the paired testes as a simple percentage of male body weight

(Harcourt et al. 1981); or (2) a residual measured from the regression of combined testes

weight on body weight after log transformation of the data on both axes (Anderson and

Dixson, 2002; Harcourt et al., 1995).

Table 2 lists the combined testes weight (gm), male body weight (kg), relative

testes size (%), and residual testes size for 21 species. For nine genera it also shows the

mean generic value calculated from the species for which testes data are presented.

When data are available for only one species in a genus, the generic mean equals the

value for the single species. When there are multiple species, the value for the genus is

obtained by weighting the species-data phylogenetically. For this, we use Version 3 of

the 10kTrees Website (Arnold, Matthews, and Nunn, 2010) to generate the consensus

phylogeny, in Nexus format, of the primate species for which we have relevant data.

This phylogeny (with branch lengths) has been sampled from a Bayesian phylogenetic

analysis of genetic data. For analyses, we use version 3.0.1 (November 2017) of

BayesTraits (Pagel and Meade, 2017). Among the procedures available in BayesTraits

is the facility to estimate the value of a trait, in this case relative testes size, at particular

nodes internal to the phylogeny such as the most recent common ancestor of a specified

congeneric group of species (Pagel, Meade, and Barker, 2004). To calculate the nodal

value we use the random walk model and Markov chain Monte Carlo (MCMC) method.

2.3. Paternity

The collection of paternity data from wild populations of primates involves obtaining

genetic material from a sample of individuals and their potential parents, and then

assigning paternity. The full list of studies and study-groups plus the paternity data that

form the basis of this article is presented in Table 3. The list includes all studies known

to us of wild populations, including those populations that are habituated and/or

partially provisioned. The list also includes all studies of free-ranging populations in

their ancestral habitat, including those populations that are habituated and/or partially

provisioned as long as they are not hormonally or otherwise manipulated in ways that

could influence their sexual behavior. We exclude all studies of populations that the

authors describe as "captive". We also exclude all studies of populations introduced

outside of their ancestral geographical range.

2.4. Calculation of level of sperm competition from paternity data

The procedures and equations used here to calculate sperm competition level from

paternity data were developed, described, and discussed by Baker and Shackelford

(2018). Only a summary of the main features is provided here.

2.4.1. Main data: Designated-Male and Other-Male Paternity

The paternity of each female's offspring is expressed with respect to an individual male,

here termed the Designated Male, chosen usually by the original researchers from

within that female's range of potential mating partners. Ideally, the Designated Male has

a high (preferably ~100%) probability of having sperm present inside the female at the

moment she conceives and is usually chosen by the researchers because he is in a

recognizable behavioral or social category such as a consort or group alpha. If the

female conceives to her Designated Male, the offspring is scored as a case of

Designated-Male Paternity. All other males within a female's range of potential mating

partners are here termed Other Males. Note that the Designated Male for one female can

sometimes be an Other Male for another female. In this article we express the paternity

data for a study-group as the percentage of young with Other-Male Paternity (OMP %).

2.4.2. Sampling bias and correction

None of the values of OMP % for individual studies or study-groups presented in Table

3 can be considered representative of whole species or even whole subpopulations for

two reasons: (1) in most cases the primary data are based on small samples from local

subpopulations; and (2) none of the primary samples involved structured sampling

designed to yield data representative of a wider population. We have discussed this

issue previously (Baker and Shackelford, 2018) and there employed such corrective

procedures as possible whenever these could lead to a reduction in sampling bias.

Here, when data are available, we use three factors to produce a weighted mean

for OMP % before running the calculations described below. These are: (1) sample size

(i.e. total number of paternities assigned in a study-group); (2) relative long-term

contribution of offspring to the next generation by each group studied (quantified as the

number, or mean number, of adult females in each group); and (3) relative frequency of

each type of group in the population (e.g., uni-male versus multi-male groups, or "small

groups" versus "large groups"). The full list of weighting factors and resulting weighted

means is given in Table 4.

2.4.3. Subsidiary data

Although Designated-Male Paternity and Other-Male Paternity are the primary data needed, the formulae used to calculate sperm competition level from paternity data also require values for two subsidiary variables (i.e. subsidiary in the sense that if no usable field data exist, default values can be allocated). The variables are: (1) Percentage of Other-male matings that are Multiple-matings (POM, default = 100); and (2) Fertilization Bias (FB, default = 1.0). In this article, for reasons given in the Discussion, POM is treated as a constant with a value of 100% (n.b. use of the term "Multiple-matings" in this article rather than the more traditional term "Double-matings" used in Baker and Shackelford (2018) has required the parameter POD used there to be changed to POM here).

Fertilization Bias is the ratio of observed to randomly-expected "wins" by Designated Males during sperm competition. When sperm from the average Designated Male in the sample and the average Other Male in the sample have equal chances of "winning", then FB = 1. When circumstances favor fertilization by sperm from the average Designated Male in the sample, then FB > 1. When FB < 1, it conveys that circumstances favor fertilization by sperm from the average Other Male to an extent given by 1/FB. The calculated values of Fertilization Bias for 17 species are listed in Table 5.

2.4.4. Equations

The three equations used to calculate the level of sperm competition from paternity data in this article are:

(1) FSC = {100}*{[OMP]*[POM/100]*[1+(FB/(ISC-1))]}/{DMP+OMP}

(2) ISC = [{FB}/{[((DMP+OMP)*FSC)/(OMP*POM)]-1}]+1

(3) LSC = 1+[(FSC/100)*(ISC-1)]

where: FSC is the frequency of sperm competition (i.e., the proportion of offspring,

range 0 – 100%, whose conception follows a bout of sperm competition between two or

more males); DMP is the number or percentage of Designated Male Paternities; OMP is

the number or percentage of Other Male Paternities; POM is the percentage of Other-

Male matings that are multiple-matings involving at least the Designated Male and

perhaps others; ISC is the intensity of sperm competition (i.e., the number of males,

range 2 to *n*, and including the Designated Male, that have sperm inside the female at

conception when sperm competition occurs); FB is the fertilization bias; and LSC is the

level of sperm competition (i.e., the mean number of males, range 1 to *n*, whose sperm

are present at each conception, including occasions when no sperm competition occurs).

Expressed in relation to the now-standard mathematical terms used, for example,

by Parker (2016), FSC = $q*100$, ISC = N (when FSC = 100), LSC = $1 + q$ (when FSC <

100) and LSC = N (when FSC = 100). Although Parker (2016) separates his models into

two, the "risk" model (when, in our terms, LSC < 2) and the "intensity" model (when,

in our terms, LSC $\geq$ 2), our use of LSC in this article is as a continuous variable

identical to the "Number of ejaculates in competition" shown as the *x*-axis in Parker

(2016; Figure 2).

A full account of the development and rationale of these formulae along with a

detailed exposition of caveats and other considerations is presented in Baker and

Shackelford (2018).

2.4.5. Procedure

The following procedure is that developed, discussed, and justified in Baker and

Shackelford (2018). First, use Equation (1) to calculate the frequency of sperm

competition (FSC) with intensity (ISC) set to its minimum value of two males. If the

value of FSC calculates to be less than 100%, then the frequency of sperm competition

is accepted as calculated, the intensity of sperm competition is accepted to be two

males, and the level of sperm competition (LSC, henceforth usually referenced simply

as "sperm competition level") can be calculated from Equation (3). However, if, with

ISC = 2, Equation (1) yields a value for FSC that is > 100%, an additional step is

necessary before calculating LSC. Set the value of FSC to 100 and then use Equation

(2) to calculate ISC. These are then the values of FSC and ISC used to calculate sperm

competition level from Equation (3).

Additional considerations and limitations to this procedure are discussed in

Baker and Shackelford (2018) but do not affect any of the calculations in this article. A

spreadsheet that automatically calculates frequency, intensity, and level of sperm

competition from paternity data with all constraints applied is provided as

supplementary information to Baker and Shackelford (2018).

2.4.6. Statistics

All standard parametric analyses without phylogenetic correction in this article were

generated using the Real Statistics Resource Pack software (Release 5.4; Zaiontz,

2018). Correlation analyses with phylogenetic correction were performed as described

by Pagel and Meade (2017). For the primate species for which we have relevant data we

use Version 3 of the 10kTrees Website (Arnold, Matthews, and Nunn, 2010) to generate

the consensus phylogeny, in Nexus format. We then use the Independent Contrasts

facility in version 3.0.1 (November 2017) of BayesTraits (Pagel and Meade, 2017) for

correlation analysis. The generated statistic (LogBF) is then interpreted as showing

either "no positive evidence", "positive evidence", "strong evidence" or "very strong evidence" following Raftery (1996).

3. RESULTS

3.1. Sperm competition level and relative testes size

Table 6 lists 28 species of cercopithecoids for which measures of sperm competition level and/or relative testes size are used in this article. Relative testes size is presented both as a simple percentage of body weight, and as a residual.

Phylogenetically weighted means for sperm competition level can be calculated for 10 genera (Table 6). However, for only six of these genera (if we restrict calculation to species for which a measure of relative testes size is also available), is it possible to calculate matching weighted means for relative testes size. If we relax this restriction to make maximum use of the available data we can then calculate phylogenetically weighted means for nine genera. These are the genera which contain at least one species with a measure for sperm competition level and at least one species with a measure for relative testes size, even though these species may not always be the same.

The generic means for the six genera in the column labelled residual-3 in Table 6 are residuals calculated by Anderson and Dixson (2002) from a regression of testes weight on male body weight for a wide range of primate groups, not just cercopithecoids.

3.2. Correlations between sperm competition level and relative testes size

Table 7 shows the degree of correlation (both with and without phylogenetic correction) between all equivalent measures of sperm competition level and relative testes size. All are either strongly or very strongly significant. We conclude for the Cercopithecoidea, as for the Hominoidea (Baker and Shackelford, 2018), that paternity data yield a

measure of sperm competition level (as males/conception) that correlates strongly with relative testes size (however measured) at both the species and generic levels.

3.3. Comparison with a theoretical curve from Parker (2016)

Parker (2016, Figure 2) presents a theoretical curve which shows the optimal variation in relative testes size at different sperm competition levels. In Figure 1, we show both a linear ($y = 0.07x + 0.005$: $R^2 = 0.681$; $F_{1, 8} = 17.063$; $p = 0.003$) and a log plot of our cercopithecoid data for 10 species from Table 6. Parker's theoretical curve is then superimposed on the log plot (Figure 1b). Parker's x-axis scale (number of ejaculates in competition) and our own (males/conception) are not only identical in terms of units but also span a nearly identical range (Parker: 1 to 10; Table 6: ~1 to ~9). They can therefore be matched exactly and objectively in Figure 1b. Unavoidably, however, Parker's y-axis (relative testes size) is dimensionless and so can be matched only subjectively. We opted to superimpose Parker's curve so that: a) the maximum values of the two curves are equal; and b) the minimum value on Parker's curve (where $x = 1.0$ males/conception, i.e., zero sperm competition) is positioned at a level below the smallest relative testes size plotted. Any statistical evaluation of a curve fitted to data in this subjective way would be meaningless, but visually the match between the two is at least cross-supportive, both for the data generated here and for Parker's theoretical curve itself.

3.4. Comparison of calculated and observed levels of sperm competition

Two major obstacles prevent the direct measurement of sperm competition level via simple field observation of primate mating behavior: (1) the impossibility of recording, day and night, all the males with which a given female mates; and (2) the difficulty of knowing precisely when, in terms of observation days, each female is or was in her

conceptive fertile phase. Other obstacles also exist but need not be considered here. Obstacle (1) has not yet been overcome, but a combination of the collection of hormonal and birth data has allowed some progress in circumventing obstacle (2).

Three studies of cercopithecoids have so far yielded relevant mating data by females on days that were likely to have been within conceptive fertile phases: (1) Dixson, Bossi, and Wickings (1993) observed females of *Mandrillus sphinx* mating with an average of 1.46 males/conception (range 0 – 3); (2) Fürtbauer, Heistermann, Schülke, and Ostner (2011) recorded female *Macaca assamensis* mating with a mean of 2.2 males/conception (range 1-4): and (3) Engelhardt, Heistermann, Hodges, Nürnberg, and Niemitz (2006) observed females of *Macaca fascicularis* mating with a mean of 2.7 males/conception (range 1 – 5) if they were "monopolized" by alpha males, but with a mean of 5.2 males/conception (range 4 – 7) if they were consorted by alpha and/or other males but not monopolized (unweighted mean = (2.7+5.2)/2 = 3.95 males/conception).

As none of these authors expected or claimed to have observed all the matings by the females concerned, these three figures of 1.46, 2.20, and 3.95 males/conception would each be expected to be an underestimate of the true sperm competition level. This expectation is consistent with the figures, respectively, of 1.95, 3.26, and 5.28 males/conception calculated from paternity data (Table 6).

If the figures from paternity data in Table 6 were accurate estimates of sperm competition level, the implication would be that the field observers did not see an average of 25%, 32%, and 25%, respectively, of the females' total mating partners. Or, expressed another way, over the 5 – 6 day course of a whole conceptive fertile phase they missed a given female mating with an average of 0.49 (*Mandrillus sphinx*), 1.06 (*Macaca assamensis*), and 1.33 (*Macaca fascicularis*) additional males.

4. DISCUSSION

All scientific measurements have sources of error. These errors create a signal-to-noise ratio in the data that is less than the optimal infinity (as generated by noise = 0) (Trout, 1998). From the available evidence discussed below, however, for neither relative testes size nor sperm competition level (as calculated here) is the signal-to-noise ratio so low that the measure has no analytical value.

4.1. Signal-to-noise ratio: Relative testes size

To obtain a figure for relative testes size for a species, two measures are needed: testes weight and body weight. Noise-free measures are elusive for both, though for this discussion it is sufficient to illustrate only the one, testes weight. For a fuller discussion see Harcourt et al. (1981) and Dixson (2009). Some of the commonest sources of noise are as follows.

Some primate testes have been measured by weighing. In some cases this occurs on removal while fresh but in others much later after being preserved. Sometimes the weight of the epididymis and other accessory tissue is included and sometimes not. Most testes, however, are measured in terms of dimensions while *in situ* using calipers. These dimensions then need converting into first a volume, then a weight. Thickness of the scrotal skin and differences in the size of left and right testes are sometimes accommodated and sometimes not. Some published reports are not even clear about whether the measures refer to one testis or two (e.g., the measurement of 27.10 g for *Papio hamadryas* in Harcourt et al. (1981, 1995) is almost certainly, to judge from the measures for single testes in Jolly and Phillips-Conroy (2003), for just a single testis, not the pair). Testis size is notoriously variable (e.g., Baker and Bellis, 1995; Dahl, Gould, and Nadler, 1993) yet sample size is often small (e.g., for *Colobus guereza*, n =

1; Dixson, 1987). No samples are collected using proper sampling protocol and usually
no attempt has been made to correct for sampling bias. Noise due to season and age
(Hamada, Suzuki, Ohkura, and Hayakawa, 2005) is also usually neglected.

Despite all these known sources of error, relative testes size is widely accepted
as a proxy measure for the level of sperm competition (e.g., Anderson and Dixson,
2002; Dorus et al., 2004; Orr and Brennan, 2016). Moreover, the measure correlates not
only with other suspected correlates of sperm competition across a wide range of
animals (Simmons and Fitzpatrick, 2012) but also, for primates, with the direct measure
of sperm competition level that we introduced previously for the Hominoidea (Baker
and Shackelford, 2018). It would seem, therefore, that despite the noise in the data, the
relative testes size signal (i.e., between-species variation) is strong enough to show
through significantly in analyses.

4.2. Signal-to-noise ratio: Sperm competition level calculated from paternity data

We accept that noise is generated at each step from the field collection of paternity data
to the derivation of a figure for the sperm competition level of a species. All potential
sources of noise were appraised previously (Baker and Shackelford, 2018), and none
was considered major. This new study of the Cercopithecoidea, however, has raised
several issues that merit discussion.

**4.2.1. Noise generated by females not always containing sperm from the
Designated Male in the ampulla at conception**

The formulae developed in Baker and Shackelford (2018) are constructed to calculate
the level of sperm competition experienced by Designated Males. If these Designated
Males are chosen carefully, the mother of every young conceived in a study contains
Designated Male sperm in her ampulla at conception. The sperm competition level

experienced by Designated Males is then also the level for the sample. However, if the

proportion of sampled females containing Designated Male sperm at conception falls

below 100% then the formulae risk producing an overestimate of the sperm competition

experienced by the Designated Male. This risk can be countered by adjusting the value

of the variable POM (see Baker and Shackelford, 2018).

In almost all the field studies listed in Table 3, the females sampled can be

confidently assumed to have sperm from their Designated Male in the ampulla at

conception. This is particularly so when the Designated Male is either the only male in a

uni-male group (S, Table 3), or a fertile-phase consort (C, Table 3). It is also highly

likely when the Designated Male is a named individual because the probability of

having sperm inside sampled females was the prime criterion used in choosing that

individual as a Designated Male.

The situation in which the risk of females not containing Designated Male sperm

at conception would seem to be greatest is when the Designated Male is shown as the

group's alpha in Table 3. This is particularly so when there are many rival males in the

group and the group's multiple females have synchronous fertile phases (Altmann,

1962; Ostner, Nunn, and Schülke, 2008). The alpha male cannot guard all fertile

females against all rival males continuously and may therefore, on occasion, fail to

inseminate a given female during her fertile phase. How often this happens, however, is

far from clear, largely because (§3.4) it is impossible for field observers to observe

every mating a female performs during her usually 120 hour or so fertile phase.

Continuous observation is difficult enough by day and impossible by night (e.g.,

Mandrillus sphinx; Setchell, Charpentier, and Wickings, 2005) and matings with the

eventual sire are often missed (see Dixson et al., 1993). Some field observers even

report that despite intensive observations and many recorded matings they did not see

their target females mate even once with the male that eventually proved to be the sire,

including when this sire was the alpha (e.g., *Macaca fuscata*; Soltis, Thomsen, and

Takenaka, 2001). Failure to observe a given female mating with her Designated Male

during her conceptive fertile phase is not evidence that she did not do so. To date, we

know of no unequivocal evidence for any wild or free-ranging cercopithecoid that a

female ever conceives without containing sperm from a Designated Male (whether S, C,

α or named; Table 3). For the purposes of this article, any noise from this possibility

would seem to be minimal.

4.2.2. Noise generated by errors in the assigned proportion of Other Male

copulations that are multiple-matings

Whenever there is ~100% probability that the Designated Male has sperm in a female's

ampulla at conception it follows that any conceptive fertile phase mating by an Other

Male is inevitably a Multiple Mating. Under such circumstances the parameter POM

(percentage of Other-Male matings that are Multiple-Matings) is 100%.

So far in our studies of the Hominoidea and Cercopithecoidea only for humans

is there evidence that the Designated Male (in humans, the female's long-term partner)

does not always have sperm inside the female's ampulla at conception (see Baker and

Shackelford, 2018). After lengthy analysis and discussion we calculated a value for

POM of 95% in human societies that do not use contraception and 68% in societies that

frequently use contraception. Further data would help to refine these assessments. As

yet, however, as described above, we have found no unequivocal evidence for POM to

be less than 100% for any non-human species of catarrhine, either hominoid or

cercopithecoid. In this study, therefore, we have treated POM as a constant (= 100%),

not a variable, and conclude that any noise generated by the decision is likely to be minimal.

4.2.3. Noise generated by errors in the calculation of fertilization bias

Although there are many and varied factors involved in Fertilization Bias (see Baker and Shackelford, 2018), we can here, for simplicity of discussion, reduce these to the number of fertile sperm present in a female's ampulla at conception. This then allows Fertilization Bias to become simply the number of fertile sperm present from the Designated Male divided by the number of fertile sperm present from the average Other Male. Any noise in the estimation of Fertilization Bias then derives from two main sources: the accuracy and appropriateness of the original authors' field data, analysis, and conclusions; and the accuracy with which the relatively simple procedure we use in Table 5 converts those conclusions by other authors into appropriate values.

Such noise can manifest itself in two ways. First, it can cloud existing differences in Fertilization Bias between species. Table 5, for example, concludes that the strongest Fertilization Bias in favor of the Designated Male is found in *Macaca fascicularis* and the weakest (in fact a bias in favor of the average Other Male) in *M. mulatta* and *M. sylvanus*. If these differences between species are misrepresentative then the signal-to-noise ratio in the complete set of calculated sperm competition levels will be reduced. Secondly, if the values of Fertilization Bias are inaccurate, they will reduce the accuracy of the calculated sperm competition level for each given species.

Although we cannot yet assess the level of noise generated by errors in our calculation of Fertilization Bias directly, we can assess them indirectly from the performance of the final estimates of sperm competition level shown in Tables 6 and 7 that use them. On this basis, anticipating the outcome of the discussions below in §4.2.4

and §4.4, we conclude that whatever the level of noise generated by the estimation of

Fertilization Bias in the different species it is insufficient to destroy either the overall

signal or the accuracy of the estimate for the individual species.

4.2.4. Signal-to-noise ratio

Whatever the total level of noise generated by the procedures and formulae used here to

calculate sperm competition level, the evidence presented in §3 suggests that the signal

remains strong enough to power an analytical tool. The primary evidence is that

calculated levels of sperm competition correlate with levels of relative testes size. This

is true for both the Cercopithecoidea (Table 7) and previously for the Hominoidea

(Baker and Shackelford, 2018). Such strong or very strong correlations could not occur

unless the signal-to-noise ratio for both measures is not only strong enough but also

similar enough for such correlations to emerge. The two measures cross-validate each

other, at least as independent proxies for sperm competition. Secondarily, the

comparison of calculated and theoretical data (Figure 1b) and of calculated and field

data (§4.4) also add support to this conclusion.

4.3. Comparison of paternity data and relative testes size as measures of level of

sperm competition

Until relatively recently, paternity data were scarce and primatologists had little choice

but to use relative testes size as a proxy measure for level of sperm competition. Now,

though, that situation has changed. Although paternity data may not yet be more

available than measures of relative testes size, they are at least equally accessible.

Availability is no longer a factor.

If the use of relative testes size has any advantage as a measure of level of sperm

competition, it is that testes size has evolved over the same or similar period as any

other sexual characteristic that may invite assessment as an evolutionary product of sperm competition. Paternity data, on the other hand, can generate only the level of sperm competition at the time and place at which the data are collected. Therefore, if level of sperm competition has changed markedly in the recent past as has been suggested, in the Hominoidea, for gorillas (Stoinski et al., 2009) and humans (Dupanloup et al., 2003; van der Horst and Maree, 2014), then paternity data may not illuminate the evolutionary past as well as might relative testes size.

The data presented here and in Baker and Shackelford (2018) suggest that this potential advantage of relative testes size may not be as great in practice as it appears in principle, at least not for the Cercopithecoidea and Hominoidea. If there were a major mismatch in the information embedded within relative testes size and paternity data, the correlations between the two (Cercopithecoidea: Table 7. Hominoidea: Baker and Shackelford, 2018) would not be significant, or at least not as strongly as they are.

Against this uncertain but potential advantage of relative testes size, the advantages of the more direct measure of level of sperm competition yielded by paternity data are much more apparent. As detailed in Baker and Shackelford (2018) the two main advantages of the measures from paternity data are that: (1) they are explicit and meaningful (e.g., males/conception) compared with the fairly inscrutable measures for relative testes size (e.g., % of body weight or residuals after log transformation; Table 2); and (2) varying as they do (see study-group values for OMP, Table 4) they can potentially be used to identify differences in sperm competition level between subpopulations and even socio-sexual groups in situations in which relative testes size varies little or not at all.

4.4. Accuracy of calculated sperm competition level

Relative testes size is a proxy measure of sperm competition level, the values reflecting the relative sperm competition levels for a range of species but otherwise, as noted in § 4.3, having little meaning. A value of 0.06 (%) or 0.0 (residual) could for example, reflect a low, medium, or even high level of sperm competition.

At a minimum, the values generated from paternity data by the procedures used here could be viewed as similarly proxy measures. We have claimed (Baker and Shackelford, 2018), however, that when our procedure generates a figure of, say, 2.1, it means that at conception the sperm from a mean of 2.1 males are present in the female's ampulla at the moment of conception. The Cercopithecoidea have allowed a first opportunity to judge the accuracy of these figures.

As shown in §3.4, three field studies of female mating behavior during the conceptive fertile phase yielded observed numbers of males mating with a female during her conceptive fertile phase that were between 25% and 32% lower than our estimates of males/conception from paternity data. On average, this difference was roughly equivalent to the field workers missing females mating with a single male individual (range 0.49 to 1.33 missed males) per conceptive fertile phase. The absence of eventual sires from the list of observed mating partners (e.g., *Mandrillus sphinx*, Dixson et al., 1993; *Macaca fascicularis*, Engelhardt et al., 2006; *Macaca fuscata*, Soltis et al., 2001) verifies that this level of error frequently occurs in the field. On this basis, therefore, while acknowledging that the field data are limited, we contend that our calculated values are currently consistent with the mating events seen (and missed) in the field.

Further studies on a range of primates and other non-litter producing animals are necessary to evaluate the accuracy of our procedure further. However, on current

evidence, we suggest that our method has the potential to become a powerful tool in future studies of the role of sperm competition in the evolution of sexual traits. Not least, it would allow a first empirical analysis of the role of sperm competition in the evolution of relative testes size that could then be compared with the wealth of theoretical analyses that already exist (Parker 2016). It could also be used to provide further analysis for such traits as sperm mid-piece volume (Anderson and Dixson, 2002) and seminal protein change (Dorus et al., 2004) for which suitable data already exist and for which conclusions so far have been based solely on proxy measures.

The hypothesis that this investigation was designed to test for the Cercopithecoidea was that paternity data, when processed as described, can provide a measure of sperm competition that is at least as useful as relative testes size. Insofar as the two measures showed a strong to very strong correlation, this hypothesis would seem to have been supported. Equally the similarities and differences between the calculated levels of sperm competition and the best figures that have so far been obtained from direct field observation of mating behavior were also reassuring given the known problems that exist with such field observations. We tentatively suggest, therefore, that when paternity data are available they offer a more practical or exploitable measure than relative testes size for future studies of the evolution of sexual traits.

CONFLICTS OF INTEREST

The authors declare no conflicts on interest.

REFERENCES

Alberts, S. C., Buchan, J. C., & Altmann, J. (2006). Sexual selection in wild baboons: from mating opportunities to paternity success. *Animal Behaviour*, *72*, 1177–1196. DOI: 10.1016/j.anbehav.2006.05.001

Altmann, S. A. (1962). A field study of the sociobiology of rhesus monkeys, Macaca mulatta. *Annals of the New York Academy of Sciences*, *102*, 338-435. DOI: 10.1111/j.1749-6632.1962.tb13650.x

Altmann, J., & Alberts, S. C. (2003). Variability in reproductive success viewed from a life□history perspective in baboons. *American Journal of Human Biology*, 15, 401–409. DOI: 10.1002/ajhb.10157

Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., ... & Wayne, R. K. (1996). Behavior predicts genetic structure in a wild primate group. *Proceedings of the National Academy of Sciences of the United States of America*, 93, 5797–5801. DOI: 10.1073/pnas.93.12.5797

Anderson, M. J., & Dixson, A. F. (2002). Sperm competition: motility and the midpiece in primates. *Nature*, 416, 496–496. DOI: 10.1038/416496a

Arnold, C., Matthews, L. J., & Nunn, C. L. (2010). The 10kTrees Website: A New Online Resource for Primate Phylogeny. *Evolutionary Anthropology*, 19, 114–118. DOI: 10.1002/evan.20251

Baker, R. R., & Bellis, M. A. (1995). *Human sperm competition: copulation, masturbation, and infidelity*. London, England: Chapman and Hall.

Baker, R. R., & Shackelford, T. K. (2018). A comparison of paternity data and relative testes size as measures of level of sperm competition in the Hominoidea. *American Journal of Physical Anthropology*, 165, 421–443. DOI: 10.1002/ajpa.23360

Brauch, K., Hodges, K., Engelhardt, A., Fuhrmann, K., Shaw, E., & Heistermann, M.

    (2008). Sex-specific reproductive behaviours and paternity in free-ranging Barbary

    macaques (Macaca sylvanus). *Behavioral Ecology and Sociobiology*, 62, 1453–1466.

    DOI: 10.1007/s00265-008-0575-7

Bulger, J. B. (1993). Dominance rank and access to estrous females in male savanna

    baboons. *Behaviour*, 127, 67–103. DOI: 10.1163/156853993X00434

Charpentier, M., Peignot, P., Hossaert-McKey, M., Gimenez, O., Setchell, J. M., &

    Wickings, E. J. (2005). Constraints on control: factors influencing reproductive

    success in male mandrills (Mandrillus sphinx). *Behavioral Ecology*, 16, 614–623.

    DOI: 10.1093/beheco/ari034

Cords, M., Mitchell, B. J., Tsingalia, H. M., & Rowell, T. E. (1986). Promiscuous

    mating among blue monkeys in the Kakamega forest, Kenya. *Ethology*, 72, 214–226.

Dahl, J. F., Gould, K. G., & Nadler, R. D. (1993). Testicle size of orang-utans in

    relation to body size. *American Journal of Physical Anthropology*, 90, 229–236.

    DOI: 10.1002/ajpa.1330900209

De Ruiter, J. R., Van Hooff, J. A., & Scheffrahn, W. (1994). Social and genetic aspects

    of paternity in wild long-tailed macaques (Macaca fascicularis). *Behaviour*, 129,

    203–224.

Dittus, W. P. (1988). Group fission among wild toque macaques as a consequence of

    female resource competition and environmental stress. *Animal Behaviour*, 36, 1626–

    1645.

Dixson, A. F. (1987). Observations on the evolution of the genitalia and copulatory

    behaviour in male primates. *Journal of Zoology*, 213, 423–443. DOI:

    10.1111/j.1469-7998.1987.tb03718.x

Dixson, A. F. (2009). *Sexual selection and the origins of human mating systems*.

Oxford, England: Oxford University Press.

Dixson, A. F., Bossi, T., & Wickings, E. J. (1993). Male dominance and genetically

determined reproductive success in the mandrill (Mandrillus sphinx). *Primates*, 34,

525–532.

Dorus, S., Evans, P. D., Wyckoff, G. J., Choi, S. S., & Lahn, B. T. (2004). Rate of

molecular evolution of the seminal protein gene SEMG2 correlates with levels of

female promiscuity. *Nature Genetics*, 36, 1326–1329. DOI: 10.1038/ng1471

Dupanloup, I., Pereira, L., Bertorelle, G., Calafell, F., Prata, M. J., Amorim, A., &

Barbujani, G. (2003). A recent shift from polygyny to monogamy in humans is

suggested by the analysis of worldwide Y-chromosome diversity. *Journal of

Molecular Evolution*, 57, 85–97. doi: 10.1007/s00239-003-2458-x

Engelhardt, A., Heistermann, M., Hodges, J. K., Nürnberg, P., & Niemitz, C. (2006).

Determinants of male reproductive success in wild long-tailed macaques (Macaca

fascicularis)—male monopolisation, female mate choice or post-copulatory

mechanisms? *Behavioral Ecology and Sociobiology*, 59, 740–752. DOI:

10.1007/s00265-005-0104-x

Fox, S. (2015). The Effect of Potential and Actual Paternity on Positive Male-Infant

Behaviour in Ursine Colobus (Doctoral dissertation, University of Calgary). Calgary,

Alberta, Canada. DOI: 10.5072/PRISM/28090

Fürtbauer, I., Heistermann, M., Schülke, O., & Ostner, J. (2011). Concealed fertility and

extended female sexuality in a non-human primate (Macaca assamensis). *PloS one*,

6, e23105. DOI: 10.1371/journal.pone.0023105

Groves, C. P. (2005). Primates. In D. E. Wilson & D. M. Reeder (Eds.), *Mammal*

species of the world: a taxonomic and geographic reference (Vol. 1) (3rd ed.).

Baltimore, MD: John Hopkins University Press.

Guo, S., Ji, W., Li, M., Chang, H., & Li, B. (2010). The mating system of the Sichuan

snub☐nosed monkey (Rhinopithecus roxellana). *American Journal of Primatology*,

72, 25–32. DOI: 10.1002/ajp.20747

Hall, K. R. L. (1962). The sexual, agonistic and derived social behaviour patterns of the

wild chacma baboon, Papio ursinus. *Proceedings of the Zoological Society of London*,

139, 283–327. DOI: 10.1111/j.1469-7998.1962.tb01831.x

Hamada, Y., Suzuki, J., Ohkura, S., & Hayakawa, S. (2005). Changes in testicular and

nipple volume related to age and seasonality in Japanese macaques (Macaca fuscata),

especially in the pre-and post-pubertal periods. *Primates*, 46, 33–45. DOI:

10.1007/s10329-004-0099-3

Harcourt, A. H., Harvey, P. H., Larson, S. G., & Short, R. V. (1981). Testis weight,

body weight and breeding system in primates. *Nature*, 293, 55–57.

Harcourt, A. H., Purvis, A., & Liles, L. (1995). Sperm competition: mating system, not

breeding season, affects testes size of primates. *Functional Ecology*, 9, 468–476.

DOI: 10.2307/2390011

Harding, R. S., & Olson, D. K. (1986). Patterns of mating among male patas monkeys

(Erythrocebus patas) in Kenya. *American Journal of Primatology*, 11, 343–358.

DOI: 10.1002/ajp.1350110405

Hayakawa, S. (2008). Male–female mating tactics and paternity of wild Japanese

macaques (Macaca fuscata yakui). *American Journal of Primatology*, 70, 986–989.

DOI: 10.1002/ajp.20580

Heistermann, M., Ziegler, T., Van Schaik, C. P., Launhardt, K., Winkler, P., & Hodges, J. K. (2001). Loss of oestrus, concealed ovulation and paternity confusion in free-ranging Hanuman langurs. *Proceedings of the Royal Society of London, Series B*, 268, 2445–2451. DOI: 10.1098/rspb.2001.1833

Huchard, E., Alvergne, A., Féjan, D., Knapp, L. A., Cowlishaw, G., & Raymond, M. (2010). More than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma baboons. *Behavioral Ecology and Sociobiology*, 64, 769–781. DOI: 10.1007/s00265-009-0894-3

Huchard, E., Charpentier, M. J., Marshall, H., King, A. J., Knapp, L. A., & Cowlishaw, G. (2013). Paternal effects on access to resources in a promiscuous primate society. *Behavioral Ecology*, 24, 229–236. DOI: 10.1093/beheco/ars158

Jolly, C. J., & Phillips-Conroy, J. E. (2003). Testicular size, mating system, and maturation schedules in wild anubis and hamadryas baboons. *International Journal of Primatology*, 24, 125–142. DOI: 10.1023/A:1021402730111

Keane, B., Dittus, W. P. J., & Melnick, D. J. (1997). Paternity assessment in wild groups of toque macaques Macaca sinica at Polonnaruwa, Sri Lanka using molecular markers. *Molecular Ecology*, 6, 267–282.

Kummer, H. (1968). *Social organization of hamadryas baboons* (Vol. 89). Chicago, IL: University of Chicago Press.

Kümmerli, R., & Martin, R. D. (2005). Male and female reproductive success in Macaca sylvanus in Gibraltar: no evidence for rank dependence. *International Journal of Primatology*, 26, 1229–1249. DOI: 10.1007/s10764-005-8851-0

Launhardt, K., Borries, C., Hardt, C., Epplen, J. T., & Winkler, P. (2001). Paternity

analysis of alternative male reproductive routes among the langurs (Semnopithecus

entellus) of Ramnagar. *Animal Behaviour*, 61, 53–64. DOI: 10.1006/anbe.2000.1590

Le Roux, A., Snyder-Mackler, N., Roberts, E. K., Beehner, J. C., & Bergman, T. J.

(2013). Evidence for tactical concealment in a wild primate. *Nature

Communications*, 4, 1462. DOI: 10.1038/ncomms2468

Liu, Z., Huang, C., Zhou, Q., Li, Y., Wang, Y., Li, M., ... & Takenaka, A. (2013).

Genetic analysis of group composition and relatedness in white□headed langurs.

Integrative Zoology, 8, 410–416. DOI: 10.1111/1749-4877.12048

Luetjens, C. M., & Weinbauer, G. F. (2012). Functional assessment of sexual maturity

in male macaques (Macaca fascicularis). *Regulatory Toxicology and Pharmacology*,

63, 391–400. DOI: 10.1016/j.yrtph.2012.05.003

Møller, A. P. (1988). Ejaculate quality, testes size and sperm competition in primates.

Journal of Human Evolution, 17, 479–488. doi: 10.1016/0047-2484(88)90037-1

Nystrom, P. (1992). Mating Success of Hamadryas, Anubis and Hybrid Male Baboons

in a Mixed Social Group in the Awash National Park, Ethiopia. PhD thesis,

Washington University. St. Louise, MO, USA.

Ohsawa, H., Inoue, M., & Takenaka, O. (1993). Mating strategy and reproductive

success of male patas monkeys (Erythrocebus patas). *Primates*, 34, 533–544. DOI:

10.1007/BF02382664

Orr, T. J., & Brennan, P. L. (2016). All features great and small—the potential roles of

the baculum and penile spines in mammals. *Integrative and Comparative Biology*,

56, 635–643. DOI: 10.1093/icb/icw057

Ostner, J., Nunn, C. L., & Schülke, O. (2008). Female reproductive synchrony predicts
skewed paternity across primates. *Behavioral Ecology*, 19, 1150-1158. DOI:
10.1093/beheco/arn093

Pagel, M., & Meade, A. (2017). BayesTraits
(www.evolution.rdg.ac.uk/BayesTraitsV3.0.1/BayesTraitsV3.0.1.html), Reading,
UK.

Pagel, M., Meade, A., & Barker, D. (2004). Bayesian estimation of ancestral character
states on phylogenies. *Systematic biology*, 53, 673–684. DOI:
10.1080/10635150490522232

Palombit, R. A. (2003). Male infanticide in wild savanna baboons: adaptive significance
and intraspecific variation. In C. B. Jones (Ed.), *Sexual selection and reproductive
competition in primates: new perspectives and directions*, (pp. 3 –47). Norman, OK:
The American Society of Primatologists.

Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the
insects. *Biological Reviews*, 45, 525–567. 10.1111/j.1469-185X.1970.tb01176.x

Parker, G. A. (1982). Why are there so many tiny sperm? Sperm competition and the
maintenance of two sexes. *Journal of Theoretical Biology*, *96*, 281–294. doi: 10.1016/0022-
5193(82)90225-9

Parker, G. A. (2016). The evolution of expenditure on testes. *Journal of Zoology*, 298,
3–19. DOI: 10.1111/jzo.12297

Raftery, A. E. (1996). Hypothesis testing and model selection. In W. R. Gilks, S.
Richardson, S., & D. J. Spiegelhalter (Eds.), *Markov chain Monte Carlo in practice*,
(pp. 163 – 188). London: Chapman & Hall.

Roberts, S. J., & Cords, M. (2015). Life as a bachelor: quantifying the success of an

   alternative reproductive tactic in male blue monkeys. *PeerJ*, 3, e1043. DOI:

   10.7717/peerj.1043

Roberts, S. J., Nikitopoulos, E., & Cords, M. (2014). Factors affecting low resident

   male siring success in one-male groups of blue monkeys. *Behavioral Ecology*, 25,

   852–861. DOI: 10.1093/beheco/aru060

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance

   reproductive success in male macaques. *Current Biology*, 20, 2207–2210. DOI:

   10.1016/j.cub.2010.10.058

Setchell, J. M., Charpentier, M., & Wickings, E. J. (2005). Mate guarding and paternity

   in mandrills: factors influencing alpha male monopoly. *Animal Behaviour*, 70, 1105–

   1120. DOI: 10.1016/j.anbehav.2005.02.021

Short, R. V. (1979). Sexual selection and its component parts, somatic and genital

   selection, as illustrated by man and the great apes. *Advances in the Study of*

   Behavior, 9, 131–158. DOI: 10.1016/S0065-3454(08)60035-2

Simmons, L. W., & Fitzpatrick, J. L. (2012). Sperm wars and the evolution of male

   fertility. *Reproduction*, 144, 519–534. DOI: 10.1530/REP-12-0285

Smith, R. L. (Ed.) (1984). *Sperm competition and the evolution of animal mating*

   systems. London, England: Academic Press.

Snyder-Mackler, N., Alberts, S. C., & Bergman, T. J. (2012). Concessions of an alpha

   male? Cooperative defence and shared reproduction in multi-male primate groups.

   Proceedings of the Royal Society of London, Series B, 279, 3788–3795. DOI:

   10.1098/rspb.2012.0842

Soltis, J., Thomsen, R., & Takenaka, O. (2001). The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, Macaca fuscata. *Animal Behaviour*, 62, 485–494. DOI: 10.1006/anbe.2001.1774

Stoinski, T. S., Vecellio, V., Ngaboyamahina, T., Ndagijimana, F., Rosenbaum, S., & Fawcett, K. A. (2009). Proximate factors influencing dispersal decisions in male mountain gorillas, *Gorilla beringei beringei*. *Animal Behaviour*, 77, 1155-1164. doi: 10.1016/j.anbehav.2008.12.030

Sukmak, M., Wajjwalku, W., Ostner, J., & Schülke, O. (2014). Dominance rank, female reproductive synchrony, and male reproductive skew in wild Assamese macaques. *Behavioral Ecology and Sociobiology*, 68, 1097–1108. DOI: 10.1007/s00265-014-1721-z

Swedell, L. (2006). *Strategies of sex and survival in hamadryas baboons: through a female lens*. Upper Saddle River, NJ: Pearson Prentice Hall.

Swedell, L., & Saunders, J. (2006). Infant mortality, paternity certainty, and female reproductive strategies in hamadryas baboons. In L. Swedell & S. R. Leigh (Eds.), *Reproduction and fitness in baboons: Behavioral, ecological, and life history perspectives* (pp. 19–51). Boston, MA: Springer. DOI: 10.1007/978-0-387-33674-9_2

Teichroeb, J. A., & Sicotte, P. (2010). The function of male agonistic displays in ursine colobus monkeys (Colobus vellerosus): male competition, female mate choice or sexual coercion? *Ethology*, 116, 366–380. DOI: 10.1111/j.1439-0310.2010.01752.x

Teichroeb, J. A., Wikberg, E. C., Ting, N., & Sicotte, P. (2013). Factors influencing male affiliation and coalitions in a species with male dispersal and intense male–

male competition, Colobus vellerosus. *Behaviour*, 151, 1045-1066. DOI:

10.1163/1568539X-00003089

Trout, J. D. (1998). *Measuring the intentional world: Realism, naturalism, and*

quantitative methods in the behavioral sciences, Oxford, England: Oxford University

Press.

van der Horst, G., & Maree, L. (2014). Sperm form and function in the absence of

sperm competition. *Molecular Reproduction and Development*, 81, 204–216. doi:

10.1002/mrd.22277

Van Noordwijk, M. A., & Van Schaik, C. P. (1985). Male migration and rank

acquisition in wild long-tailed macaques (Macaca fascicularis). *Animal Behaviour*,

33, 849–861. DOI: 10.1016/S0003-3472(85)80019-1

Wang, B. S., Wang, Z. L., Tian, J. D., Cui, Z. W., & Lu, J. Q. (2015). Establishment of

a microsatellite set for noninvasive paternity testing in free-ranging Macaca mulatta

tcheliensis in Mount Taihangshan area, Jiyuan, China. *Zoological Studies*, 54, 8.

DOI: 10.1186/s40555-014-0100-9

Xiang, Z. F., Yang, B. H., Yu, Y., Yao, H., Grueter, C. C., Garber, P. A., & Li, M.

(2014). Males collectively defend their one☐male units against bachelor males in a

multi☐level primate society. *American Journal of Primatology*, 76, 609–617. DOI:

10.1002/ajp.22254

Yamane, A., Shotake, T., Mori, A., Boug, A. I., & Iwamoto, T. (2003). Extra-unit

paternity of hamadryas baboons (Papio hamadryas) in Saudi Arabia. *Ethology*

Ecology & Evolution, 15, 379–387. DOI: 10.1080/08927014.2003.9522664

Zaiontz, C. (2018) Real Statistics Using Excel. www.real-statistics.com (downloaded

02/15/2018).

Table 1. Taxonomic list of all species of Cercopithecoidea referenced

Taxon	Common English name	Scientific name	Authority
Superfamily	Old World Monkeys	Cercopithecoidea	
Family		Cercopithecidae	
Subfamily		Colibinae	
	King colobus	*Colobus polykomos*	Zimmermann, 1780
	Mantled guereza	*Colobus guereza*	Rüppell, 1835
	Ursine colobus	*Colobus vellerosus*	I. Geoffroy, 1834
	Golden snub-nosed monkey	*Rhinopithecus roxellana*	Milne-Edwards, 1870
	Northern plains gray langur	*Semnopithecus entellus*	Dufresne, 1797
	White-headed langur	*Trachypithecus poliocephalus*	Pousargues, 1898
	Dusky leaf monkey	*Trachypithecus obscurus*	Reid, 1837
	Silvery lutung	*Trachypithecus cristatus*	Raffles, 1821
Subfamily		Cercopithecinae	
Tribe		Cercopithecini	
	Red-tailed monkey	*Cercopithecus ascanius*	Audebert, 1799
	Blue monkey	*Cercopithecus mitis*	Wolf, 1822
	Patas monkey	*Erythrocebus patas*	Schreber, 1775
Tribe		Papionini	
	Assam macaque	*Macaca assamensis*	McClelland, 1840
	Toque macaque	*Macaca sinica*	Linnaeus, 1771
	Stump-tailed macaque	*Macaca arctoides*	I. Geoffroy, 1831
	Bonnet macaque	*Macaca radiata*	É. Geoffroy, 1812
	Southern pig-tailed macaque	*Macaca nemestrina*	Linnaeus, 1766
	Japanese macaque	*Macaca fuscata*	Blyth, 1875
	Crab-eating macaque	*Macaca fascicularis*	Raffles, 1821
	Rhesus macaque	*Macaca mulatta*	Zimmermann, 1780
	Barbary macaque	*Macaca sylvanus*	Linnaeus, 1758
	Mandrill	*Mandrillus sphinx*	Linnaeus, 1758
	Drill	*Mandrillus leucophaeus*	F. Cuvier, 1807
	Gelada	*Theropithecus gelada*	Rüppell, 1835

Olive baboon	*Papio anubis*	Lesson, 1827
Hamadryas baboon	*Papio hamadryas*	Linnaeus, 1758
Guinea baboon	*Papio papio*	Desmarest 1820
Yellow baboon	*Papio cynocephalus*	Linnaeus, 1766
Chacma baboon	*Papio ursinus*	Kerr, 1792

Nomenclature from Groves (2005)

Table 2. Relative testes size

| | WEIGHTS | | RELATIVE TESTES SIZE | | | |
| | Testes | Body | Species | | Genus (weighted) | |
	(gm)	(kg)	(%)	Residual	(%)	Residual
CERCOPITHECOIDEA						
COLIBINAE						
Colobus polykomos	10.70	10.25	0.104	–0.232	0.070	–0.501
Colobus guereza	2.98	10.40	0.029	–0.795		
Semnopithecus entellus	11.10	17.00	0.065	–0.490	0.065	–0.490
Trachypithecus obscurus	4.80	7.45	0.064	–0.408	0.083	–0.331
Trachypithecus cristatus	6.20	6.58	0.094	–0.230		
CERCOPITHECINAE						
Cercopithecini						
Cercopithecus ascanius	3.00	5.36	0.056	–0.435	0.056	–0.435
Erythrocebus patas	7.20	10.00	0.072	–0.391	0.072	–0.391
Papionini						
Macaca arctoides	48.20	10.51	0.459	+0.408	0.503	+0.393
Macaca radiata	48.20	8.65	0.557	+0.513		
Macaca nemestrina	66.70	9.98	0.668	+0.577		
Macaca fuscata	84.40	14.20	0.594	+0.489		
Macaca fascicularis	36.20	6.30	0.575	+0.560		
Macaca mulatta	46.40	9.20	0.504	+0.463		
Mandrillus sphinx	68.00	35.00	0.194	–0.092	0.212	–0.045
Mandrillus leucophaeus	41.05	20.00	0.205	–0.009		
Theropithecus gelada	17.10	20.40	0.084	–0.400	0.084	–0.400
Papio anubis	98.98	22.71	0.436	+0.304	0.256	+0.034
Papio hamadryas	58.62	20.78	0.282	+0.125		
Papio papio	88.90	31.98	0.278	+0.073		
Papio cynocephalus	52.00	24.32	0.214	–0.012		
Papio ursinus	72.00	31.75	0.227	–0.015		

Data shown only for genera for which paternity data are also available. **WEIGHTS:**

Testes, combined weight of both testes (gm); **Body**, male body weight (kg). Data from

Hamada et al. (2005), Harcourt et al. (1981, 1995), Jolly and Phillips-Conroy (2003),

Luetjens and Weinbauer (2012). When mean values for a species occur in more than

one publication the most recent is used. **RELATIVE TESTES SIZE: %**, testes weight

as a percentage of male body weight; **Residual**, measured from the regression of

combined testes size on body weight after log transformation of the data on both axes

(+, testes heavier than expected; –, testes lighter than expected). **Genus (weighted):**

Phylogenetically weighted means of all species in genus that are listed.

Table 3. Paternity data

	Ref	Location	W/FR	D♂	DMP	OMP	OMP%
Cercopithecoidea							
Colobus vellerosus	1	Ghana	W/FR	α	6	1	14.3
	2		W/FR	α	4	4	50.0
	2		W/FR	S	1	3	75.0
Rhinopithecus roxellana	3	China (Qinling)	W	S	9	12	57.1
	4	China (Shennongjia)	FR	S	8	0	0.0
Semnopithecus entellus	5	S. Nepal	W	S	13	0	0.0
	5		W	α	17 †	13 †	43.1
Trachypithecus poliocephalus	6	China	W	S	20	1	4.8
Cercopithecus mitis	7	Kenya	W	R	67	54	44.6
Erythrocebus patas	8	Cameroon	W	S	2	2	50.0
	8		W	R	4	1	20.0
Macaca assamensis	9	Thailand	W	C	7 †	4 †	36.0
	9		W	α	11	27	71.1
Macaca sinica	10	Sri Lanka	W	S	7	0	0.0
	10		W	PF	6	12	66.7
Macaca fuscata	11	Yakushima Island	W	α	2	7	77.8
	12		W	(α+β)/2	1	7	87.5
Macaca fascicularis	13	N. Sumatra	W	S	12	1	7.7
	13		W	α	8	3	27.3
	13		W	α	12	9	42.9
	14		W	HA	2	4	66.7
Macaca mulatta	15	China (Jiyuan)	W/FR	α	1	7	87.5
Macaca sylvanus	16	Gibraltar	W	α	1	17	94.4
	17		W	Thoran	4	8	66.7
Mandrillus sphinx	18	Gabon	FR	α	147	46	23.8
Theropithecus gelada	19	Ethiopia	W	S	47	0	0.0
	19		W	α	24	5	17.2
Papio cynocephalus	20	E. Africa	W	Radi	22	5	18.5
	21		W	α	49	96	66.2
Papio hamadryas	22	Saudi Arabia	W	S	1	6	85.7
	22		W	S	1	5	83.3
	22		W	S	1	2	66.7
Papio ursinus	23	Namib Desert	W	α	5	7	58.3
	23		W	α	8	1	11.1

References: 1, Teichroeb et al. (2013); 2, Fox (2015); 3, Guo et al. (2010); 4, Xiang et al. (2014); 5, Launhardt et al. (2001); 6, Liu et al. (2013); 7, Roberts et al. (2014); 8, Ohsawa et al. (1993); 9, Sukmak et al.(2014); 10, Keane et al. (1997); 11, Soltis et al. (2001); 12, Hayakawa (2008); 13, De Ruiter et al. (1994); 14, Engelhardt et al. (2006); 15, Wang et al. (2015); 16, Kümmerli and Martin (2005); 17, Brauch et al. (2008); 18, Charpentier et al. (2005); 19, Snyder-Mackler et al. (2012); 20, Altmann et al. (1996); 21, Alberts et al. (2006); 22, Yamane et al. (2003); 23, Huchard et al. (2010, 2013). **W/FR:** W, Wild; FR, free-ranging; W/FR, in natural habitat with some degree of restriction of movement due to isolated or fragmented habitats. **D♂,** Designated Male: α, alpha male of multi-male, multi-female group; S, sole male in a uni-male, multi-female group; R, resident male in a group that is sometimes uni-male and sometimes multi-male; β, beta male; C, consort; PF, previous father (i.e. sire of a female's previous infant); IP, in-pair male; P, primary male; HA, Thoran, Radi, MAX, named individuals. **DMP**, Designated-Male Paternities; **OMP**, Other-Male Paternities; **OMP%**, percentage Other-Male Paternities. †, rounded integers for studies in which the original authors, through uncertainty, either divided some paternities among males or gave a rounded value for OMP% that did not convert precisely into integers.

Table 4. Other-Male Paternity: Calculation of weighted means

	Study	Weighting Factor Values				Weighted mean
	OMP (%)	Sample size	♀♀	Proportion	(type)	OMP (%)
Colobus vellerosus	14.3	7	8.8	0.63/2	♂♂	34.8
	50.0	8	5.0	0.63/2	♂♂	
	75.0	4	3.5	0.37	♂	
Rhinopithecus roxellana	57.1	21	5.6	—		43.8
	0.0	8	4.5	—		
Semnopithecus entellus	0.0	13	4.8	0.28	♂	38.6
	43.1	29	7.2	0.72	♂♂	
Trachypithecus poliocephalus	4.8	—	—	—		4.8
Cercopithecus mitis	44.6	—	—	—		44.6
Erythrocebus patas	50.0	4	—	0.50	♂	33.3
	20.0	5	—	0.50	♂♂	
Macaca assamensis	36.0	11	—	0.79	C	53.0
	71.1	38	—	0.21	OM	
Macaca sinica	0.0	7	3.5	0.38	♂	61.5
	66.7	18	10.0	0.62	♂♂	
Macaca fuscata	77.8	9	15.0	—		79.6
	87.5	8	4.0	—		
Macaca fascicularis	7.7	13	3.0	0.05	Sg1	51.7
	27.3	11	4.5	0.08	Sg2	
	42.9	21	12.0	0.15	Lg	
	66.7	6	8.0	0.72	Mog	
Macaca mulatta	87.5	—	—	—		87.5
Macaca sylvanus	94.4	18	9.0	—		79.6
	66.7	12	15.5	—		
Mandrillus sphinx	23.8	—	—	—		23.8
Theropithecus gelada	0.0	47	5.1	0.67	♂	4.7
	17.2	29	6.3	0.33	♂♂	
Papio cynocephalus	18.5	27	16.7	—		58.1
	66.2	145	15.2	—		
Papio hamadryas	85.7	7	5.0	—		82.1
	83.3	6	2.0	—		
	66.7	3	3.0	—		
Papio ursinus	58.3	12	16.0	—		44.3
	11.1	9	9.0	—		

Order of studies and reference sources as in Table 3, plus supplementary information for weighting factors from references in Table 5. **Weighting factor values:** Sample size, number of paternities assigned; ♀♀, mean number of females in the study-group; Proportion (type), either the proportion of the wider population that is of the studied type or (as appropriate) the proportion of young conceived that are from this source. ♂, uni-male group; ♂♂, multi-male group; C, consortships; OM, opportunistic mating; Sg1, small group with 1-2 males; Sg2, small multi-male (3-4) group; Lg, large multi-male (>8) group; Mog, modal-sized multi-male (5-7) group; —, indicates a value is either unavailable or unnecessary and so the factor is not used in weighting. **Weighted mean:** Mean value of OMP (%) for each species.

Table 5. Assessment of fertilization bias from observational and paternity data

| | Field evidence | | |
	Overt	Cryptic	FB
Colobus vellerosus	0		1.0
Rhinopithecus roxellana	++	–	2.0
Semnopithecus entellus	0		1.0
Trachypithecus poliocephalus			1.0
Cercopithecus mitis	+		2.0
Erythrocebus patas	+	–	1.0
Macaca assamensis	+		2.0
Macaca sinica			1.0
Macaca fuscata	+		2.0
Macaca fascicularis	++	+	4.0
Macaca mulatta	+	– –	0.5
Macaca sylvanus	0	–	0.5
Mandrillus sphinx	++		3.0
Theropithecus gelada	++	–	2.0
Papio cynocephalus	++	0	3.0
Papio hamadryas	++	– –	1.0
Papio ursinus	++	0	3.0

Field evidence from references in Table 3 with additional data on behavior for: *Colobus vellerosus* (Teichroeb and Sicotte, 2010); *Semnopithecus entellus* (Heistermann et al., 2001); *Cercopithecus mitis* (Cords et al., 1986; Roberts and Cords, 2015); *Erythrocebus patas* (Harding and Olson, 1986); *Macaca assamensis* (Fürtbauer et al., 2011; Schülke et al., 2010); *Macaca sinica* (Dittus, 1988); *Macaca fascicularis* (van Noordwijk and van Schaik 1985); *Mandrillus sphinx* (Dixson et al., 1993; Setchell et al., 2005); *Theropithecus gelada* (Le Roux et al., 2013); *Papio cynocephalus* (Altmann and Alberts, 2003); *Papio hamadryas* (Kummer, 1968; Nystrom, 1992; Swedell, 2006; Swedell and Saunders, 2006); *Papio ursinus* (Bulger, 1993; Hall 1962; Palombit, 2003). **Overt** (++, strong observed skew in mating frequency in favor of Designated Male; +, weak observed skew in favor of Designated Male; 0, no observed skew); **Cryptic** (+, skew in paternity even more strongly in favor of Designated Male than mating frequency; 0, paternity skew matches mating frequency skew; –, paternity skew less strongly in favor of

Designated Male than mating frequency skew; – –, paternity skew much less strongly in favor

of Designated Male than mating frequency skew). Empty cells indicate no relevant data. **FB**,

fertilization bias. Each plus in the Overt and Cryptic columns is given a value of +1, each 0 and

empty cell a value of 0, and each minus a value of –1. When the sum (S) of the cell values is

positive, FB = 1+S. When S is negative, FB = –1/(–1+S).

Table 6. Data for comparison of sperm competition level and relative testes size

Species	Sperm Competition Level Males/conception	Relative Testes Size %	residual
Colobus vellerosus	1.697	—	—
Colobus polykomos	—	0.104	−0.232
Colobus guereza	—	0.029	−0.795
Rhinopithecus roxellana	2.556	—	—
Semnopithecus entellus	1.772	0.065	−0.490
Trachypithecus poliocephalus	1.100	—	—
Trachypithecus obscurus	—	0.064	−0.408
Trachypithecus cristatus	—	0.094	−0.230
Cercopithecus mitis	2.612	—	—
Cercopithecus ascanius	—	0.056	−0.435
Erythrocebus patas	1.667	0.072	−0.391
Macaca arctoides	—	0.459	+0.408
Macaca assamensis	3.256	—	—
Macaca radiata	—	0.557	+0.513
Macaca sinica	2.600	—	—
Macaca nemestrina	—	0.688	+0.577
Macaca fuscata	8.824	0.594	+0.489
Macaca fascicularis	5.283	0.575	+0.560
Macaca mulatta	4.500	0.504	+0.463
Macaca sylvanus	2.951	—	—
Mandrillus sphinx	1.953	0.194	−0.092
Mandrillus leucophaeus	—	0.205	−0.009
Theropithecus gelada	1.141	0.084	−0.400
Papio anubis	—	0.436	+0.304
Papio hamadryas	5.600	0.282	+0.125
Papio papio	—	0.278	+0.073
Papio cynocephalus	5.165	0.214	−0.012
Papio ursinus	3.388	0.227	−0.015

Genus	SCL-1	SCL-2	%-1	%-2	residual-1	residual-2	residual-3
Colobus	—	1.697	—	0.070	—	−0.501	—
Rhinopithecus	—	2.556	—	—	—	—	—
Semnopithecus	1.772	1.772	0.065	0.065	−0.490	−0.490	—
Trachypithecus	—	1.095	—	0.083	—	−0.331	—
Cercopithecus	—	2.612	—	0.056	—	−0.435	−0.18
Erythrocebus	1.667	1.667	0.072	0.072	−0.391	−0.391	−1.25

	SCL-1	SCL-2	%-1	%-2	residual-1	residual-2	residual-3
Macaca	4.574	4.031	0.511	0.503	+0.400	+0.393	+0.84
Mandrillus	1.953	1.953	0.194	0.212	−0.092	−0.045	+0.37
Theropithecus	1.141	1.141	0.084	0.084	−0.400	−0.400	−0.75
Papio	4.257	4.257	0.259	0.256	+0.038	+0.034	+0.54

Sperm competition level: males/conception. **Relative testes size: %**, combined testes weight as percentage of male body weight; **residual,** measured from the regression of combined testes size on body weight after log transformation of the data on both axes (+, testes heavier than expected; –, testes lighter than expected). **Species:** Sperm Competition level (SCL) – calculated from the data in Tables 3, 4 and 5 using the procedures and formulae in Baker and Shackelford (2018) with POM = 100; Relative Testes Size – from Table 2. **Genera:** Values for both Sperm Competition and Relative Testes Size are phylogenetically weighted means; —, missing values.

SCL-1, %-1, residual-1: Generic means calculated using only species for which data are available for both sperm competition level and relative testes size; **SCL-2, %-2, residual-2**; Generic means calculated using all species for which data are available; **residual-3**; Generic means from Anderson and Dixson (2002).

Table 7. Correlations between sperm competition level and relative testes size

Correlation:	Without phyl. corr.			With phyl. corr.		
	Pearson's r			Independent Contrasts		
	n	*r*	*P*	*n*	*logBF*	strength
			(1-tailed)			*(2-tailed*)
Species						
SCL v RTS (%)	10	0.825	0.002	10	7.5	'strong'
SCL v RTS (residual)	10	0.820	0.002	10	7.6	'strong'
Genus						
SCL-1 v RTS (%)	6	0.884	0.010	6	9.7	'strong'
SCL1 v RTS (residual-1)	6	0.896	0.008	6	10.6	'very strong'
SCL-2 v RTS (%)	9	0.773	0.007	9	7.3	'strong'
SCL-2 v RTS (residual-2)	9	0.771	0.008	9	7.8	'strong'
SCL-2 v RTS (residual-3)	6	0.796	0.029	6	6.7	'strong'

Correlation analysis, without and with phylogenetic correction (phyl. corr.), using data from

Table 6. SCL, sperm competition level (males/conception) (SCL-1, SCL-2 as defined in Table

6); RTS, relative testes size (%, residual, residual-1, residual-2; residual-3; see Table 6)

Figure 1. Linear and log plots of relative testes size on sperm competition level for 10 species of cercopithecoids

Data from Table 6. **1,** *Theropithecus gelada*; **2,** *Erythrocebus patas*; **3,** *Semnopithecus entellus*; **4,** *Mandrillus sphinx*; **5a**, *Papio ursinus*; **5b,** *Papio cynocephalus*; **5c,** *Papio hamadryas*; **6a,** *Macaca mulatta*; **6b,** *Macaca fascicularis*; **6c,** *Macaca fuscata*. In (b) the black curve is the logarithmic fit to the data and the gray curve is a superimposed theoretical curve taken from Parker (2016).