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A comparison of paternity data and relative testes size as measures of level of sperm competition in the Hominoidea

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Abstract

Objectives: The phrase "level of sperm competition" is used only vaguely in the primate literature. There is also little distinction between the important elements of frequency and intensity of sperm competition, largely because the two current forms of measurement (socio-sexual system and relative testes size) are both proxies which allow neither precision nor fine distinctions. Both measures have critics, socio-sexual system in particular being branded subjective, misleading, and changeable. Testes size is considered the more reliable despite its validation resting on correlations with the other, less reliable, proxy. Recently, genetic paternity studies have been mooted to provide a potentially superior third measure of sperm competition but so far lack a formal interpretive framework. Here we use the published and relatively comprehensive genetic field studies of the Hominoidea to develop such a framework.

Materials and methods: Formulae are derived to convert paternity data into a direct measure of the frequency, intensity, and overall level of sperm competition. We then compare these measures with relative testes size at the study, species, and phylogenetic levels.

Results: A significant correlation between level of sperm competition and relative testes size was obtained at each level. These correlations provide independent support for the continuing use of testes size as a proxy measure when such a measure is sufficient. However, they also suggest that paternity data and our formulae yield a viable alternative measure.

Discussion: This alternative measure based on paternity data has a number of advantages. Not only is it a potentially direct measure of the level of sperm competition but it also allows the roles of frequency and intensity to be studied separately when of interest.

KEYWORDS
Hominoidea, paternity, relative testes size, sperm competition

1 | INTRODUCTION

Sperm competition is the competition between sperm from multiple males to fertilize the egg(s) produced by a single female (Parker, 1970). Although initially focused on insects, the potential importance of sperm competition in the evolution of both male and female sexuality was soon recognized for species across the animal kingdom, including humans (Smith, 1984a).

In internal fertilizers, competition between sperm from different males occurs only when a female "double-mates" (i.e., copulates with a second male while still containing competitive sperm from an earlier but different male; Parker, 1970). To be involved in the production of offspring, this double-mating has to occur when a fertilizable egg (or eggs) is either already available in the female or will become available at some moment during the overlap in competitive lifetimes of the two sets of sperm. It is assumed that the male with the larger number of competitively fertile sperm near the egg(s) will either fertilize more of the female's eggs or have the higher probability of fertilizing a single egg.

One group of theoretical models (Parker, 1970, 1982, 1984; Parker & Pizzari, 2010) builds on the principle that the optimum number of sperm inseminated during copulation is an evolutionary trade-off between two opposing selective pressures: (a) the risk that sperm may enter into competition with sperm from another male, favoring more

sperm; and (b) the cost of sperm production, favoring fewer. If the level of sperm competition increases during the evolution of a lineage, then natural selection should favor males that inseminate more sperm. This trend should continue until the advantage gained via sperm competition reaches the trade-off level.

More sperm can be produced at a faster rate by larger testes (e.g., primates; Møller, 1988). Selection to increase the number of sperm inseminated should therefore result in males adjusting their resource allocation in favor of an increase in sperm-producing tissue, resulting in an increase in testes size (Parker, 1970, 1982, 2016). This in turn can lead 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 (review: Parker, 2016).

A positive cross-species relationship between level of sperm competition and relative testes size has been demonstrated for many animal taxa (Simmons & Fitzpatrick, 2012) ranging from butterflies (Gage, 1994) to mammals (Ramm, Parker, & Stockley, 2005; Soulsbury, 2010), mainly species that could either freely be caught and killed in their natural habitat or raised in numbers in captivity. Inevitably, however, species for which the animals' welfare and conservation rightly took precedence proved more difficult to study in the wild. In primates, the determination of even basic parameters was problematic (Dixson, 1998).

The earliest method for assessing level of sperm competition in primates was the least invasive: to categorize the socio-sexual systems of the different species and to judge the likely level of sperm competition accordingly (Short, 1979). Species which lived in polygynandrous or polyandrous groups were assumed to experience high levels of sperm competition whereas those living in monogamous or polygynous groups were assumed to experience low levels of sperm competition. Using this approach, Short (1979) for the Hominidae (great apes) and Harcourt, Harvey, Larson, and Short (1981) for a wider range of primates, demonstrated that males of species with a likely evolutionary history of higher levels of sperm competition had a greater relative testes size than those of species with a likely history of lower levels of sperm competition. The expected links between social organization, mating system, and relative testes size have also been demonstrated for other mammals (e.g., bats; Pitnick, Jones, & Wilkinson, 2006).

Although socio-sexual system has served as a useful initial guide to level of sperm competition in primates and other mammals, its use has not been without problems. Increasingly it was shown and argued that social systems were not reliable reflections of mating system (Barelli et al., 2013; Kappeler & van Schaik, 2002; Palombit, 1994). The level of subjectivity involved in categorization and the lack of consensus about the mating system of some species led researchers to shift to relative testes size as the preferred proxy for the investigation of, for example, the role of sperm competition in the evolution of sperm mid-piece volume (Anderson & Dixson, 2002) and seminal proteins (Dorus, Evans, Wyckoff, Choi, & Lahn, 2004). However, the use of relative testes size also has its problems and critics (Mitani, Gros-Louis, & Richards, 1996; Soulsbury, 2010; van der Horst & Maree, 2014).

Difficulties exist not only in measuring testes in a standard way (Harcourt et al., 1981; Harcourt, Purvis, & Liles, 1995) but also because captive animals, which are the most often measured, can be obese or suffer from testicular degeneration (Dixson, 2009). Subjective decisions often have to be made about which measurements to use and which to reject. The use of relative testes size as a proxy has also revealed anomalies, species for which the measure does not reflect the suspected level of sperm competition (Pochron & Wright, 2002; Schülke, Kappeler, & Zischler, 2004), perhaps in part because relative testes size can be influenced by a variety of factors (Mitani et al., 1996; Ramm & Schärer, 2014). For primates, this in turn raises concern that so far relative testes size has been validated as a proxy for sperm competition only through comparison with the unreliable classification of socio-sexual system. If the use of testes size continues as it has, then its reliability needs support from additional, independent measures that are perceived to be at least equally if not more reliable than itself. Such validation, however, would then raise the possibility of using the alternative measure in addition to, or even instead of, relative testes size.

Since the development of non-invasive techniques for the collection of genetic material in the wild (Kohn, Knauer, Stoffella, Schröder, & Pääbo, 1995), the potential has existed to use paternity data to validate, complement, or replace relative testes size as the main proxy. Yet this has not yet happened. Although paternity data are often referenced in sperm competition related discussions of primates (Dixson, 2009), rarely have the data taken center stage. The exception is in the discussion of level of sperm competition in humans (Larmuseau, Matthijs, & Wenseleers, 2016), but even in this context the use of the data has been intuitive rather than formal.

A number of primate species were included among the many mammals for which Soulsbury (2010) demonstrated a cross-species correlation between relative testes size and aspects of paternity data. Three different measures were used, all still indirect: the frequency of multiple paternity of litters for species that produce several offspring at a time (see also: Firman & Simmons, 2008; Ramm et al., 2005) and the levels of both extra-group and alpha-male paternity for social animals. Each of these three measures has its limitations (Soulsbury, 2010) and, promising although the first studies appeared, no improved formal and direct use of paternity data has been developed. This is surprising, given that paternity data potentially offer one great advantage over the use of relative testes size: they could provide a direct, not a proxy, measure of level of sperm competition. Until now, however, no attempt has been made to convert paternity data into such a direct measure.

The primate superfamily, the Hominoidea (i.e., the lesser and great apes, including humans), offers a number of advantages for such a study: (a) paternity data and measures of relative testes size are available for all sub-groups and, except for gibbons, for all species in each sub-group; (b) the superfamily forms a single phylogenetic unit with a relatively recent (~17 mya) last common ancestor; (c) the phylogeny of all lineages within the superfamily are well established; and (d) the

number of extant species is small enough to permit a detailed discussion of the data for each lineage.

In this article, we assemble the paternity data collected for the Hominoidea by other authors. We then develop formulae to convert those data into direct estimates of level of sperm competition in the different samples, species, and higher phylogenetic groups. Finally, we calculate correlation coefficients between these estimates and the two commonly-used lists of relative testes size, a test that, if successful, would cross-validate both (i.e., relative testes size and paternity data) as independent measures of level of sperm competition.

Our aim of using hominoid paternity data to seek an independent validation of relative testes size as a proxy for level of sperm competition was wholly realized at all analytical levels. That success, however, in turn raises the question of whether further studies should continue to use relative testes size as the preferred measure of level of sperm competition or switch instead to the measures obtainable from paternity data. We discuss various aspects of this question and conclude that paternity data has the potential to provide greater insight into the evolution of diverse aspects of sexuality than is possible from any proxy measure, including relative testes size. Our hope is that others will now test our formulae, procedures, and suggested applications using equivalent paternity data for other groups of primates and mammals.

2 | SOURCES OF PATERNITY DATA FOR THE HOMINOIDEA

The collection of paternity data from wild populations involves obtaining genetic material from a sample of individuals (of any age, not only newly-born) and their potential parents, and then assigning paternity. In recent years, the material has been obtained almost entirely by non-invasive means through the field collection of hair or feces (Kohn et al., 1995). For humans the material has been collected by a variety of techniques, including acquisition of blood and buccal swab samples (Bellis, Hughes, Hughes, & Ashton, 2005).

The paternity of each female's offspring is expressed with respect to an individual male chosen by researchers from within that female's range of potential mating partners. In this article, we refer to this male as the Designated Male.[1] If the female conceives to the 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. If a female conceives to an Other Male, the offspring is scored as a case of Other-Male Paternity. Paternity data are usually tabulated as either the number of observed cases of Designated-Male Paternity and Other-Male Paternity or simply as the percentage of offspring that have Other-Male Paternity.

Authors can in principle designate any male as the focus for analysis. Most often, however, a male is selected whose sperm has a high (usually ~100%) probability of being present at the site of fertilization inside the female at the moment she conceives. A male that has a lower probability of having sperm present at conception could be used as a Designated Male, but further analysis is only possible if the percentage probability of that male's sperm being present is known.

In the larger studies, data are presented for a number of Designated Males, all usually characterized as forming a single social or behavioral category (e.g., consort, alpha male, territory holder, primary male, in-pair male). On occasion, however, it is of interest to express the same or overlapping sets of data with respect to two or more different categories of Designated Males (e.g., in comparing the strategic success for males of either acting as a short-term consort or of striving long-term to become an alpha male).

In presenting, analyzing, and discussing the available paternity data, we follow previous authors (e.g., Dixson, 2009; Harcourt et al., 1981) and recognize five extant groups: gibbons, orangutans, gorillas, chimpanzees, and humans. These groups, however, are of different taxonomic ranks as itemized in the section subtitles below (following Groves, 2005).

2.1 | Gibbons

2.1.1 | Family Hylobatidae

Gibbons are divided into four genera and at least 12 species (Chatterjee, 2009) and paternity data exist for three (Table 1): the white-handed gibbon, *Hylobates lar*, in Thailand (Barelli et al., 2013), Mueller's gibbon, *H. muelleri*, in Borneo (Oka & Takenaka, 2001), and the golden-cheeked gibbon, *Nomascus gabriellae*, in Vietnam (Kenyon, Roos, Binh, & Chivers, 2011).

Many gibbon populations live in a mixture of socially monogamous, polyandrous, and polygynous territorial units (Barelli, Heistermann, Boesch, & Reichard, 2008; Palombit, 1994) with the territory of each unit overlapping several neighboring territories (e.g., an average of five for *H. lar*; Barelli et al., 2013). When a female gibbon shares a territory polyandrously with more than one male, the males are socially unequal, only one of the males engaging exclusively, or almost exclusively, in singing duets with the adult female. Barelli et al. (2008) term the duetting male the "primary" male and the non-duetting male the "secondary" male.

Paternity data have been collected from socially monogamous units for all three of the species above, but from socially polyandrous units only for *H. lar*. For no species has data been collected separately from the rare polygynous units. All authors for all species express their paternity data for socially monogamous units by designating the female's sole (in-pair) male partner as the Designated Male, with the Other Males being simply the males from neighboring territories. Barelli et al. (2013) express their data for socially polyandrous units by designating the primary male as the Designated Male, with Other Males being a mixture of secondary males and males from neighboring territories.

2.2 | Orangutans

2.2.1 | Family Hominidae; Subfamily Ponginae

There are two recognized species of orangutans, the Sumatran, *Pongo abelii*, and Bornean, *P. pygmaeus* (Utami, Goossens, Bruford, de Ruiter, &

[1]Although Designated Males are the focus for analysis in paternity studies, we resisted the temptation to use the term Focal Male to avoid confusion with the use of the term in observational studies (Martin & Bateson, 1993). In the behavioral literature, Focal Males are chosen at random and only then does data collection begin. Designated Males are selected non-randomly after each male's social and sexual status has been identified from existing data.

van Hooff, 2002). Both species exhibit extreme sexual dimorphism and male bimaturism. The result is that at any given time in a population there are "unflanged" males that are of female size and will remain so for a variable number of years, and "flanged" males that at some point after the age of 14 years will have rapidly grown to twice female size (Utami et al., 2002). Unflanged males are in a state of delayed maturation. However, both male morphs are fertile, sexually active, and sire offspring (Banes, Galdikas, & Vigilant, 2015; Goossens et al., 2006; Kingsley, 1982; Maggioncalda, 1995; Utami et al., 2002). They do, however, pursue different sexual strategies. Flanged males establish large territories and, in effect, sit and wait for fertile females to be attracted by their long calls, and then often consort with them. Unflanged males travel in search of females and either simply copulate or consort with them until displaced by a more dominant male, either unflanged or flanged. Even when consorting with a flanged territorially dominant male, however, females may mate with other males.

Paternity data are available (Table 1) for both species: *P. abelii* (Utami et al., 2002; see also the same data in Utami Atmoko et al., 2009); and *P. pygmaeus* (Banes et al., 2015). For *P. abelii*, the paternity data are presented in two different ways: (a) with an observed consort (flanged or unflanged) to the female as the Designated Male; and (b) with the female's local, flanged, dominant, and territorially resident male as the Designated Male. For *P. pygmaeus*, the data are presented only in way (b). Further data for *P. pygmaeus* (Goossens et al., 2006) do not allow the separation of paternities into Designated-Male and Other-Male and so cannot be used further here.

2.3 | Gorillas

2.3.1 | Family Hominidae; Subfamily Homininae; Tribe Gorillini

Gorillas are classified into two species, the eastern gorilla, *Gorilla beringei*, and the western gorilla, *G. gorilla*, each of which is also subdivided into two subspecies (eastern: *G. b. beringei* and *G. b. graueri*; western: *G. g. gorilla* and *G. g. diehli*) (Groves, 2003). With the exception of the mountain gorilla, *G. b. beringei*, all live in lowland areas.

All four subspecies live in a mixture of two types of mixed-sex groups: multi-male, multi-female and single-male, multi-female. The latter are designated as single-male not on the grounds that each group contains only one reproductively active male but on the grounds that they contain only one silverback male (>12-year old). Many such groups, however, also contain fertile and reproductively active black-backed males (8- to 12-year old) (Bradley, Doran-Sheehy, Lukas, Boesch, & Vigilant, 2004; Schaller, 1963). Whatever a group's social structure, multi-male or single-male, the group has only one dominant male at any one time.

Paternity data (Table 1) have been collected for two situations: multi-male, multi-female groups of *G. b. beringei* (Bradley et al., 2005; Rosenbaum, Hirwa, Silk, Vigilant, & Stoinski, 2015) and single-male, multi-female groups of *G. g. gorilla* (Bradley et al., 2004; Inoue et al., 2013). All authors select the group's dominant silverback to be the Designated Male. Other Males are then a mixed assortment of any other silverback or black-backed male(s) present in the group plus others (both silverback and black-backed) from outside the group, although so far no clear case of extra-group paternity has been reported (Rosenbaum et al., 2015).

2.4 | Chimpanzees

2.4.1 | Family Hominidae; Subfamily Homininae; Tribe Hominini; Subtribe Panina

Members of the two species of *Pan* (chimpanzee, *P. troglodytes*; bonobo, *P. paniscus*) copulate polygynandrously within multi-male, multi-female groups that are not only of variable size but also show fission-fusion dynamics (De Waal & Lanting, 1997; Goodall, 1986; Newton-Fisher, 2014; Tutin, 1979). Males of both species form dominance hierarchies. On occasion, also, although more in *P. troglodytes* than in *P. paniscus*, a male of any rank may attempt to separate females from other males via consortships. Females of both species also mate with males from outside the social group.

Paternity data for *P. troglodytes* have been collected in studies at various locations for variously sized groups and expressed in two ways,

TABLE 1 Summary of raw paternity data for the Hominoidea

Group	Species	Ref[a]	NS	Location	Social unit	D♂	DMP	OMP	% OMP
Gibbons	*Hylobates lar*	A	1	Thailand	1♂,1♀	IP	23	3	11.5
					2♂,1♀	P	14	1	6.7
	H. muelleri	B	1	Borneo	1♂,1♀	IP	3	0	0.0
	N. gabriellae	C	1	Vietnam	1♂,1♀	IP	9	1	10.0
Orangutans	*Pongo abelii*	D	1	Sumatra	n/a	C	4	3	42.9
					n/a	α	3	7	70.0
	P. pygmaeus	E	1	Borneo	n/a	α	9	8	47.1
					n/a	†α	9	3	25.0
Gorillas	*Gorilla beringei*	F	1	Rwanda	3♂,m♀	α	33	6	15.4

(Continues)

TABLE 1 (Continued)

Group	Species	Ref[a]	NS	Location	Social unit	D♂	DMP	OMP	% OMP
		G	2	Rwanda	6♂,11♀	α	28	5	15.2
					3♂,7♀	α	6	10	62.5
	G. gorilla	H	1	CAR/DRC	1♂,m♀	α	10	0	0.0
		I	1	Gabon	1♂,m♀	α	13	0	0.0
Chimpanzees	*Pan paniscus*	J	1	DRC	<6♂,<15♀	α	3	10	76.9
	P. troglodytes	K	1	Ivory Coast	m♂,m♀	C	1	9	90.0
		L	1	Ivory Coast	>4♂,m♀	α	8	13	61.9
					<4♂,m♀	α	10	5	33.3
		M	1	Tanzania	>4♂,m♀	α	10	23	69.7
		N	1	Guinea	1♂,m♀	α	3	1	25.0
Humans	*Homo sapiens*	O	28	N. America	1♂,1♀	IP	15637	2428	13.4
			30	Europe	1♂,1♀	IP	18437	3452	15.8
			8	Africa	1♂,1♀	IP	2880	862	23.0
			2	S. America	1♂,1♀	IP	276	56	16.9
			4	Asia	1♂,1♀	IP	220	48	17.9
			1	Oceania	1♂,1♀	IP	2774	65	2.3
			73	TOTAL			40223	6911	14.7

[a]References: A, "Extra-Pair Paternity Confirmed in Wild White-Handed Gibbons," by Barelli et al., 2013, American Journal of Primatology, 75, p. 1185; B, "Wild Gibbons' Parentage Tested by Non-Invasive DNA Sampling and PCR-Amplified Polymorphic Microsatellites," by Oka and Takenaka, 2001, Primates, 42, p. 67; C, "Extrapair Paternity in Golden-Cheeked Gibbons (*Nomascus gabriellae*) in the Secondary Lowland Forest of Cat Tien National Park, Vietnam," by Kenyon et al., 2011, Folia Primatologica, 82, p. 154; D, "Male Bimaturism and Reproductive Success in Sumatran Orang-Utans," by Utami et al., 2002, Behavioral Ecology, 13, p. 643; E, "Male Orang-Utan Bimaturism and Reproductive Success at Camp Leakey in Tanjung Puting National Park, Indonesia," by Banes et al., 2015, Behavioral Ecology and Sociobiology, 69, p. 1785; F, "Mountain Gorilla Tug-of-War: Silverbacks Have Limited Control Over Reproduction in Multimale Groups," by Bradley et al., 2005, Proceedings of the National Academy of Sciences at the United States of America, 102, p. 9418; G, "Male Rank, Not Paternity, Predicts Male–Immature Relationships in Mountain Gorillas, *Gorilla beringei beringei*," by Rosenbaum et al., 2015, Animal Behaviour, 104, p. 13; H, "Dispersed Male Networks in Western Gorillas," by Bradley et al., 2004, Current Biology, 14, p. 510, I, "Male Genetic Structure and Paternity in Western Lowland Gorillas (*Gorilla gorilla gorilla*)," by Inoue et al., 2013, American Journal of Physical Anthropology, 151, p. 583; J, "Intracommunity Relationships, Dispersal Pattern and Paternity Success in a Wild Living Community of Bonobos (*Pan paniscus*) Determined from DNA Analysis of Faecal Samples," by Gerloff et al., 1999, Proceedings of the Royal Society of London. Series B, Biological Sciences, 266, p. 1189; K, "The Chimpanzees of the Tai Forest," by Boesch and Boesch-Achermann, 2000, Oxford University Press, London, England; L, "Male Competition and Paternity in Wild Chimpanzees of the Taï Forest," by Boesch et al., 2006, American Journal of Physical Anthropology, 130, p. 103; M, "Male Dominance Rank and Reproductive Success in Chimpanzees, *Pan troglodytes schweinfurthii*," by Wroblewski et al., 2009, Animal Behaviour, 77, p. 873; N, "Paternity Discrimination and Inter-Group Relationships of Chimpanzees at Bossou," by Sugiyama et al., 1993, Primates, 34, p. 545; O, compiled from "How Well Does Paternity Confidence Match Actual Paternity? Evidence From Worldwide Nonpaternity Rates," by Anderson, 2006, Current Anthropology, 47, p. 513, and "Genetic-Genealogy Approach Reveals Low Rate of Extrapair Paternity in Historical Dutch Populations," by Larmuseau et al., 2017, American Journal of Human Biology. In press.

NS: Number of Studies (a "Study" is in most cases a unique set of data for a unique group of individuals separated from others by either location, time, or social structure. The exceptions are the data sets for each species of orangutan which for comparative purposes involve overlapping sets of individuals but in different social situations; see text for full description.).

Social unit: number (or mean number) of males and females in the social group(s) studied (n/a, not applicable; m = multi).

D♂, Designated Male (IP, in-pair male; P, primary social partner in polyandrous unit; C, consort; α, alpha/dominant male in local area or group; †α, male at peak of dominance).

DMP, number of individuals sired by Designated Males; OMP, number of individuals sired by Other Males.

with either a female's consort or the group's dominant male as the Designated Male (Table 1).

For *P. paniscus*, paternity data have been tabulated for 10 offspring tested against eight potential fathers in a single group (Gerloff, Hartung, Fruth, Hohmann, & Tautz, 1999). The paternities of three other young were also discussed, one of them most likely sired by a male from another group. These three cases can also be included here. Unfortunately, as almost all conceptions in this study occurred before the male hierarchy had been determined, rank cannot be used to separate alpha males and Other Males at the time of conception. The only identifiable male category is that of the individual, but for most males it cannot be determined with certainty whether that individual copulated with the female at a time that would ensure the presence of sperm at a particular individual's conception. Rather than exclude this study

completely, Table 1 shows data for the most successful male, MAX (table 1 in Gerloff et al., 1999), who was known to be an alpha male for several years. Not only were MAX's paternities attributed with relative certainty, but he was also very likely to have had sperm present in each female at the time of the conception of all 13-offspring tested.

2.5 | Humans

2.5.1 | Family Hominidae; Subfamily Homininae; Tribe Hominini; Subtribe Hominina

Anderson (2006) tabulates 67 sets of primary paternity data for over 40,000 humans from six continents. To these we can add six further Y-chromosome, genealogical-pair studies for over 5,000 humans from two continents summarized in Larmuseau et al. (2017). Methodology varies considerably, particularly between the studies listed by the two main sources, but all have three things in common: (a) the Designated Male is the female's in-pair male; (b) the percentage of (as termed here) Other-Male Paternities are provided; and (c) in most cases, the sample size is also provided. In the nine studies (in Anderson, 2006) that do not provide a total sample size, we use a token value of 100 individuals for each study. This is a conservative value, given that the median and mean sample sizes for the 58 studies for which sample sizes are known are 234 and 710 individuals respectively. In the six genealogical-pair studies, we use the total number subjected to DNA-testing, not the total number of meioses generated by the genealogies. When sample sizes are not available in Larmuseau et al. (2017), they are taken from the original publications. The level of Other-Male paternity, however, which is sometimes subjective, is taken from Larmuseau et al. (2017).

We use these published figures for Other-Male Paternity and sample sizes to calculate the number of Designated-Male and Other-Male Paternities in each of the 73 studies. These individual-study figures are used in a later analysis, but for tabulation purposes (Table 1) we instead group the data by continent: North America (data from Canada, United States, and Mexico); Europe (data from Iceland, Sweden, Denmark, Finland, Russia, Flanders, The Netherlands, United Kingdom, Germany, France, Portugal, Italy, Spain, and Switzerland); Africa (data from sub-Saharan and South Africa); South America (data from Brazil); Asia (data from Israel and India); and Oceania (data from Hawaii).

Anderson (2006) uses medians in his meta-analyses. Although not stated, the median Other-Male Paternity for the 67 studies listed in Anderson's paper is 18.0%. We prefer, for comparability with the other hominoid studies, to sum the Other-Male paternities (6,849 individuals) and express these as a percentage of the total individuals tested (42,121). This produces a slightly lower figure for Other-Male Paternities of 16.3%. When the six genealogical-pair studies from Larmuseau et al. (2017) are added, the median for the 73 studies drops to 15.3% and our procedure yields 14.7% (Table 1).

3 | SAMPLING BIAS AND CORRECTION

None of the data from the individual studies presented in Table 1 can be considered representative of whole species or even whole subpopulations for two reasons: (a) in most cases the primary data are based on small samples from local subpopulations; and (b) none of the primary samples involved structured sampling designed to yield data representative of a wider population.

To an extent, in acknowledgement of the difficulty of obtaining paternity data, these shortfalls have been tolerated in the literature, at least for the non-human groups of hominoids. After all, the same shortfalls have always been just as evident in studies involving relative testes size (perhaps more so, given that the few testes measured are often taken from captive, not wild individuals; Dixson, 2009). Also, at least in the short term, there is little that can be done about small sample sizes from just one or a few populations. For most species, however, the lack of structured sampling can at least be partially addressed.

Biased sampling of paternity at the level of the study (as defined in Table 1) is most serious when there is only one study for the species. However, as the number of studies increases, the variability and distribution of the different samples can begin to be measured and the need and nature of any required correction can begin to be assessed. Although each individual sample may be biased, the range and distribution of values from individual studies may begin to reflect the range and distribution of Other-Male paternity in the wider population as if the whole really were structured to be a random sample. If this happens then the different samples can justifiably be summated to provide paternity data representative of the wider population. Even if it does not happen, it may nevertheless still be possible to perform some form of mathematical correction that converts the distribution of study values into a distribution that does match that of the wider population.

3.1 | Gibbons

Barelli et al. (2013) obtained measures of Other-Male Paternity for *H. lar* in two social situations: monogamous and polyandrous (Table 1). The two measures were different (monogamous, 11.5%; polyandrous, 6.7%), meaning that neither could be considered representative of the wider population. However, a correction can be applied.

The population of *H. lar* studied by Barelli et al. (2013) was distributed in territorial units of which ~77% were socially monogamous, ~21% were socially polyandrous, and ~2% were socially polygynous. If we combine the monogamous and polygynous units, it follows that offspring are conceived in a 79:21 ratio to, on the one hand, females with a single male partner and, on the other hand, females with more than one male partner. A representative sample of these offspring would therefore include individuals from these units in the same ratio.

Barelli et al. (2013) assigned paternity to 26 gibbons from females with a single partner and 15 from females with multiple partners (i.e., a 63:37 ratio). Thus, although the raw data (Table 1) are not in themselves representative samples, it is possible to adjust the data appropriately and sum the results, as in Table 2.

Unfortunately, there are insufficient data to make similar adjustments to the raw data for either Mueller's gibbon, *H. muelleri* (Oka & Takenaka, 2001) or the golden-cheeked gibbon, *Nomascus gabriellae* (Kenyon et al., 2011). Nor do data exist for the remaining two genera (*Hoolock* and *Symphalangus*) and nine species. Any further analyses involving gibbons as a group, therefore, are biased by data for a

TABLE 2 Adjustment of paternity data to address sampling bias

		Total raw data (Table 1)			Adjusted data		
Group	Species	DMP	OMP	% OMP	DMP	OMP	% OMP
Gibbons	*H. lar*	37	4	9.8	36.7	4.3	10.5
	H. muelleri	3	0	0.0	3.0	0.0	0.0
	N. gabriellae	9	1	10.0	9.0	1.0	10.0
Orangutans	*P. abelii*	3	7	70.0	3.0	7.0	70.0
	P. pygmaeus	9	8	47.0	9.0	5.5	37.9
Gorillas	*G. beringei*	67	21	23.9	84.8	3.2	3.6
	G. gorilla	23	0	0.0	22.7	0.3	1.2
Chimpanzees	*P. paniscus*	3	10	76.9	3.0	10.0	76.9
	P. troglodytes	32	51	61.4	32.8	50.2	60.5
Humans	*H. sapiens*	40223	6911	14.7	38729	8405	17.8

For References and raw data, see Table 1. For rationale and methods of adjustment, see text.
DMP, number of individuals sired by Designated Males; OMP, number of individuals sired by Other Males.
For ease of comparison, the otherwise unimportant figures for DMP and OMP in "Adjusted data" have been calculated to give the same total sample size as in the "Total raw data" column. Under "Adjusted data" only the figures for % OMP are used further.

minority of extant species [as they have been in all previous studies; for example, Harcourt et al. (1981, 1995) and Anderson and Dixson (2002)].

3.2 | Orangutans

In one sense, the paternity data collected for both species of *Pongo* are unbiased insofar as all, or at least the majority of, individuals born into the study populations over a particular time period were tested in an attempt to determine their sires. Although Utami et al. (2002) separate out data for conceptions during consortship (Table 1), it is the data with the local, flanged, resident, and territorially dominant male as the Designated Male that contain all the assigned paternities, so it is these figures that approximate most closely an unbiased sample from that population (Table 2). The question of bias then shifts to how representative the sampled populations are of the wider population of orangutans.

One concern expressed by the authors of the different studies was that a proportion of the orangutans involved in each study had either been released into the wild or were the descendants of such rehabilitated individuals (Banes et al., 2015; Utami Atmoko et al., 2009). Another concern was that the dominant male which was the main focus of the study by Banes et al. (2015) received veterinary assistance for the last few years of his waning dominance. Finally, a concern was expressed that dominant males appear relatively uninterested in nulliparous females who therefore consort more with subordinate males, particularly unflanged (Utami Atmoko et al., 2009).

The various authors present their data in such a way that different subcategories can be analyzed separately if desired. However, this stretches already-small sample sizes and reveals little that can be applied to the wider population. The potential exception stems from the observation made for both species (Banes et al., 2015; Utami et al., 2002) that the flanged, territorial, and locally dominant male sires a greater proportion of offspring at the peak of his dominance than he does when that dominance is waxing or waning. As Banes et al. (2015) suspect that the waning phase of their Designated Male was unnaturally prolonged by veterinary interference, their data can be made more representative if the figures are adjusted to reflect a shorter transitional phase (Table 2).

3.3 | Gorillas

Paternity data for gorillas (Table 1) have been collected in a conspicuously biased way: in only multi-male, multi-female groups for the montane *G. b. beringei* (Bradley et al., 2005; Rosenbaum et al., 2015) and in only single-male, multi-female groups for the lowland *G. g. gorilla* (Bradley et al., 2004; Inoue et al., 2013). No data have been collected for the other two lowland subspecies, *G. b. graueri* and *G. g. diehli*.

The primary samples show a clear distinction between the two sources (Other-Male Paternity = 23.9% in the multi-male, multi-female groups of *G. b. beringei* and 0% in the single-male, multi-female groups of *G. g. gorilla*; Table 2). All sets of authors, however, attribute this difference to the social structure of the gorillas providing the two groups of samples rather than to a difference in species or subspecies. If this is correct, then the generation of representative Other-Male Paternity levels in the different subspecies and species is simply a matter of distributing the figures from the biased primary samples in a way that reflects differences in the proportions of the different social groups in each taxonomic category.

The frequency of multi-male, multi-female groups in studied populations of *G. beringei* and *G. gorilla* ranges from up to ~10% (excluding black-backed males) or ~25% (including black-backed males) in the three lowland subspecies (Bradley et al., 2004; Yamagiwa, Kahekwa, & Basabose, 2003) to up to ~50% in the mountain gorilla, *G. b. beringei* (McNeilage, Plumptre, Brock-Doyle, & Vedder, 1998). As these values are maxima and no useful medians or means are available, we adopt

mid-point figures of 5% for the three-lowland subspecies and 25% for the single montane subspecies. Using these proportions, we then reassemble the biased primary data to generate a potentially representative figure for each species, as follows.

The 95% of *G. g. gorilla* groups that live in single-male, multi-female groups are expected to experience an Other-Male Paternity rate of 0%. The remaining 5% living in multi-male, multi-female groups are expected to experience a rate of 23.9% (Table 2). The rate for the subspecies is therefore $[(95 \times 0) + (5 \times 23.9)]/100 = 1.2\%$. Although no paternity data have been collected directly, *G. g. diehli* would be expected from the frequency of multi-male, multi-female and single-male, multi-female groups in the population to return a similar figure. In which case the Other-Male Paternity rate for the species *G. gorilla*, adjusted for sampling bias, is also 1.2%, not the 0% found in the primary samples.

The comparable calculation for *G. beringei* has an additional step because the two subspecies have different proportions of multi-male, multi-female groups. The lowland subspecies, *G. b. graueri*, has a 5% frequency of multi-male, multi-female groups just like the two-lowland subspecies of *G. gorilla*. The calculated Other-Male Paternity rate for this subspecies is also therefore 1.2%. The montane subspecies, *G. b. beringei*, in contrast has a 25% frequency of multi-male, multi-female groups, so therefore the calculated Other-Male Paternity rate is $[(75 \times 0) + (25 \times 23.9)]/100 = 6.0\%$. Assuming, in the absence of data, an equal population size for the two subspecies in the relevant past (although *G. b. beringei* is now endangered; Gray et al., 2013), the Other-Male Paternity rate for the species *G. beringei*, adjusted for sampling bias, is $(1.2 + 6.0)/2 = 3.6\%$ (Table 2), not the 23.9% found in the primary samples.

3.4 | Chimpanzees

Paternity data for *P. paniscus* (Table 1) were expressed relative to a single Designated Male (MAX; in Table 1, Gerloff et al., 1999). However, the 13 bonobos tested for their sires constituted perhaps all of the young born in the study-group over several years. In the context of the group, therefore, the offspring tested were not a biased sample. How representative the group was of the wider bonobo population cannot yet be judged and until more data are available neither the necessity for adjustment nor its nature can be assessed.

For *P. troglodytes*, the data (Table 1) present two different sampling problems. First, when the Designated Male is the group's alpha male, group size appears to have an influence on the distribution of paternity (Boesch, Kohou, Néné, & Vigilant, 2006). Reassembly of the data to reflect the wider chimpanzee population needs to be based on the distribution of group sizes within that wider population. However, with no meaningful distribution of group sizes for the species or different subspecies available, there is nothing to be gained from doing anything but adding together the data for the different-sized groups. This potential lack of a representative distribution, however, should be borne in mind.

In contrast, the separate data available for the two different categories of Designated Males (consort and alpha-male; Table 1) does allow an adjustment to be made. The proportion of young conceived via consortship (only 10% of which are attributable to the consort; Table 1) can be estimated to be around 9% (see Boesch & Boesch-Achermann 2000; Newton-Fisher, 2014). The data for consort and summed non-consort samples can therefore be assembled mathematically to reflect the 9:91 ratio found in the wider population (Table 2).

3.5 | Humans

The 73 primary samples for humans used in this article show Other-Male Paternity levels in individual samples ranging from 0.4% to 55.6%. The question then becomes, as for the other hominoids, whether this range and distribution of values for individual cohorts is an accurate reflection of the range and distribution of cohorts found in the human population. If it is, then the 73 samples can simply be summated to produce an unbiased estimate of Other-Male Paternity for humans. If it is not, then some form of correction needs to be made. Just as for gibbons (with some samples from monogamous and some from polyandrous groups) and gorillas (with some samples from polygynandrous and some from polygynous groups), it is not important that each individual sample is unrepresentative of the wider population. What is important is whether those samples as a whole are representative or, if not, whether they can be reassembled in a representative way.

Every one of the 73 primary samples can be claimed to be in some way unrepresentative of the worldwide human population. All were collected with some sort of bias (Bellis et al., 2005). For example, Anderson (2006) categorized the 67 primary surveys listed in his article in terms of whether the offspring were born into circumstances of high paternity confidence (22 studies, ~20,000 individuals), low paternity confidence (31 studies, ~18,000 individuals), or unidentifiable paternity confidence (14 studies, ~4,000 individuals). High confidence studies were conducted on families that most likely agreed to take part because both the mother and the putative father were confident that the result would not compromise them. In contrast, the low confidence studies were conducted primarily on families in which paternity was being disputed for financial reasons. All 53 of these high and low confidence studies were therefore thought to be biased in one direction or another and this suspicion was reinforced by the results. The median levels of Other-Male Paternity recorded were 1.85% (range: 0.4–11.8) for high confidence, 29.8% (range: 14.3–55.6) for low confidence, and 16.7% (range: 2.0–32.0) for unknown confidence.

Anderson (2006) proposed treating populations as a mixture of high and low paternity-confidence conceptions. To this end, on the grounds that the unidentified-confidence samples were unlikely to be low-confidence samples, he combined the high and unknown paternity-confidence samples into an enlarged set of high paternity-confidence samples. On this basis, 31 of the studies listed by Anderson are of low paternity confidence cohorts and 36 are of high. To these 36 can be added all six of the Y-chromosome, genealogical pair studies summarized in Larmuseau et al. (2017). In terms of individuals, this gives a high:low paternity confidence ratio for the 73 studies of 28,906:18,228 (i.e., 61% of births have high paternity confidence). The question then becomes whether this figure is an acceptable reflection of the worldwide human population over recent decades. If it is, the

primary studies can simply be summated. If it is not, then some form of correction needs to be applied. Unfortunately, we know of only three publications that illuminate this question.

For the female Ache, forest hunter-gatherers of eastern Paraguay, Hill and Hurtado (1996, p. 273) report that "sexual relations with multiple men before the birth of a child was a common occurrence" and (p. 444) that around 63% of people from the forest period claimed to have more than one father. This is unlikely to mean that all of the remaining 37% had high paternity confidence but this is the figure used below. Similarly, of 421 Himba children in Namibia, 36% could be classed as having low paternity confidence (22% conceived "out of wedlock" and 14% while the mother was mating with a man or men other than her social partner; Scelza, 2011). Paternity confidence is generally low anyway and the men make little investment in their wives' children, so the remaining 64% of children may not all have been born into a high paternity confidence situation. Nevertheless, 64% is the figure used below.

The only study to attempt to determine the proportion of high paternity confidence offspring in a modern industrial population using a quasi-random sample is that in Albuquerque, New Mexico, United States (Anderson, Kaplan, & Lancaster, 2006, 2007; Kaplan, Lancaster, & Anderson, 1998). Over 1,300 men were recruited while attending a New Mexico Motor Vehicle Division for purposes unrelated to the study and asked to list all pregnancies that had been attributed to them. They were then asked to categorize each pregnancy with respect to paternity confidence. Out of 3,360 pregnancies, high paternity confidence was claimed for 95.5%, although Anderson et al. (2006) note that their methodology could have led to this figure being artificially high.

The figures for the percentage of high paternity confidence births produced by these three studies (median = 64%; mean = 65.5%) are marginally higher than the 61% of individuals in the primary paternity data. However, given that the figures for Albuquerque, the Ache, and Himba are all maxima, this is more of a match than a mismatch. Naturally, we accept that these three studies are far from being a representative sample of paternity confidence levels worldwide. Many more studies are needed worldwide before any final decision can be made. Nevertheless, for the moment, there seems more reason simply to summate the primary samples than there is to make any adjustments. The same cannot be said, however, with respect to geographical distribution.

Although most of the human population (60%) lives in Asia, with Africa (~13%), Europe (~12%), North America (~8%), South America (~6%), and Oceania (~1%) being home to the rest (United Nations Department of Economic, 2007), the primary studies are biased toward Europe (47% of total individuals tested) and North America (38%) with the other four continents combined providing only 15%; Table 1). This biased geographical distribution of the primary data can be adjusted by calculating the proportion of Other-Male Paternities (Table 2; retaining for easier comparison a total sample size of 47,134 individuals) that would have been found if the numbers tested on each continent had proportionally reflected the continental distribution of the human population in the year 2000 CE (from: United Nations Department of Economic, 2007). The calculated level of Other-Male Paternity rises from 14.7% to 17.8% (Table 2).

4 | FROM PATERNITY DATA TO LEVEL OF SPERM COMPETITION: DEVELOPMENT OF A FORMULA

Despite the early detailed formulations by Parker (1990), the phrase "level of sperm competition" has been used only vaguely in the primate literature, qualified simply as low, high, trivial, significant, and so on, with little reference to the important distinction between risk and intensity (Parker, Ball, Stockley, & Gage, 1996). Re-phrased in our own terms, "risk" refers to the probability that the sperm inseminated into a fertile-phase female by a Designated Male will face competition from sperm inseminated by at least one Other Male. "Intensity" refers (*when* competition occurs) to the number of males (ranging from two to many and including the Designated Male) that simultaneously have competitive sperm inside the female while the Designated Male's sperm are also competitive. "Level" of sperm competition is then some mathematical combination of risk and intensity as described later.

In this article, we do not overtly measure the risk of sperm competition that faces a male when he inseminates a fertile-phase female. Instead we begin by calculating sperm competition frequency. In part, this is because paternity data are always collected and expressed as frequencies. Primarily, however, it is because the initial target in the study of sperm competition in primates is to determine the frequency, expressed as a percentage, with which conception follows a bout of sperm competition (e.g., a conclusion may be that 10% of young are conceived via sperm competition). We note, however, that once this percentage has been calculated it can if required be transformed (by converting the percentage into a probability) into a measure of the mean risk of one male's sperm encountering another male's sperm inside a given fertile-phase female (e.g., in the above example the risk is 0.1).

As we now show, paternity data can be used to measure both the frequency (and hence also the risk) and the intensity of sperm competition in field situations. First, we show in four steps how paternity data can be used to calculate the frequency of sperm competition in terms of the proportion of young (range 0–100%) that are conceived through sperm competition between two or more males. Next, we rearrange the formula to calculate the intensity of sperm competition (range 2–*N* males). Finally, we combine the frequency and intensity of sperm competition to calculate a single value for level of sperm competition (mean number of males, range 1–*N*, whose sperm are present at a single conception).

It should be noted that the logic used in the development of the following equations applies only if the female gives birth to just one offspring per reproductive cycle, not a litter. Among mammals, therefore, the formulae can be applied not only (see Ernest, 2003) to the majority of primates, the larger herbivores, and cetaceans but also (see Kunz & Feton, 2005) to most bats. However, further development of the formulae would be needed before they could be applied to species that produce litters.

It should also be noted that, at every step, our formulation allows the field-obtained values of Designated-Male Paternity and Other-Male Paternity to be entered either: (a) both as raw counts; or (b) both as percentages.

4.1 | Frequency of sperm competition

4.1.1 | Step one

Suppose that the mother of each individual processed in the collection of paternity data has always copulated with a Designated Male before conception. Suppose also that: (a) the mother, while fertile, never copulated with more than two different males (i.e. one Designated Male and one Other Male); (b) all matings with the Other Male are double-matings (thus generating sperm competition); and (c) that the chances of the Designated Male or Other Male fertilizing the egg via sperm competition are equal.

In such a situation, for every case of Other-Male Paternity that results from sperm competition there will also be a case of Designated-Male Paternity resulting from sperm competition. Any remaining cases of Designated-Male Paternity will not be the result of sperm competition. The total number of young conceived via sperm competition in the sample can therefore be calculated by multiplying the percentage of Other-Male Paternities by a factor of 2. If DMP represents the percentage (or raw count) of Designated-Male Paternities and OMP represents the percentage (or raw count) of Other-Male Paternities then the frequency of sperm competition (FSC) for the sample can be calculated (as a percentage, no matter whether the data are entered as percentages or raw counts) as:

$$\mathrm{FSC}=\{100\}*\{[\mathrm{OMP}]*[2]\}/\{\mathrm{DMP}+\mathrm{OMP}\}$$

For example, paternity data with OMP = 10% yield FSC = 20%.

On occasion (e.g., at the present step, whenever OMP > DMP), the formula will yield a value for frequency of sperm competition >100% which is unacceptable biologically. The further treatment of data that yield a frequency of sperm competition >100% is elaborated in a later section.

4.1.2 | Step two: Introduction of variable "POD"

Not all matings of a female with an Other Male are necessarily double-matings because at conception the female may no longer have sperm from both males present at the site of fertilization. Described simply, variable POD is the percentage of matings by Other Males that are double-matings. A more precise definition, however, is necessary. Let *x* be the number of female fertile phases that include at least one mating with an Other Male (whether or not the female also mates with a Designated Male) and let *y* be the number of fertile phases that include at least one double-mating involving an Other and the Designated Male. Now let POD be the percentage of these fertile phases that include at least one such double-mating. Thus POD = 100 × (*y*/*x*). Then:

$$\mathrm{FSC}=\{100\}*\{[\mathrm{OMP}]*[\mathrm{POD}/100]*[2]\}/\{\mathrm{DMP}+\mathrm{OMP}\}$$

For example, with circumstances as in Step 1, but with POD = 50%, then paternity data with OMP = 10% yield a frequency of sperm competition of 10%.

4.1.3 | Step three: Introduction of variable "ISC"

Females can double-mate with more than one Other Male in addition to the Designated Male so that the mean intensity of sperm competition (ISC) for the sample is > 2 males. We still assume at this step that each individual male has an equal chance of paternity. The logic then is as follows.

Of Other-Male progeny, [OMP] × [POD/100] result from double matings (from Step Two). With just one Other Male competing against the Designated Male, then twice this number gives the number of progeny from double matings (see Step One). If vast numbers of Other Males compete against a Designated Male, virtually all of [OMP] × [POD/100] progeny will be from Other Males, that is, increasing sperm competition intensity causes [OMP] × [POD/100] more closely to reflect FSC. With ISC males competing, the probability that an Other Male wins is (ISC-1)/ISC. Hence in ISC double mating events, an Other Male wins (ISC-1) times, so the ratio of double mating events to Other-Male wins is ISC:(ISC-1). To obtain FSC we therefore need to multiply [OMP] × [POD/100] by ISC/(ISC-1). Note that the term ISC/(ISC-1) = 1 + 1/(ISC-1); we use the latter term in preference to the former because it facilitates Step Four.

So now:

$$\mathrm{FSC}=\{100\}*\{[\mathrm{OMP}]*[\mathrm{POD}/100]*[1+(1/(\mathrm{ISC}-1))]\}/\{\mathrm{DMP}+\mathrm{OMP}\}$$

For example, if ISC = 3 males, then for every two cases of Other-Male Paternity that result from sperm competition there will be one case of Designated-Male Paternity. Other-Male Paternity now needs to be multiplied by 3/2 (not 2/1 as in Step 1) to include the instances of sperm competition leading to Designated-Male Paternity. So, with POD = 100% and ISC = 3 males, then paternity data with OMP = 10% yields FSC = 15%.

4.1.4 | Step four: Introduction of variable "FB"

In Steps 1–3, we assumed that all males participating in a bout of sperm competition have an equal chance of winning. This is rarely likely to be the case; some form of bias almost certainly exists. In our terms, this is a "fertilization bias"; in the terms of Parker (1990), it is a "loaded" raffle.

We express fertilization bias (FB) as the ratio of observed:randomly-expected "wins" by Designated Males during sperm competition. Let DW be the percentage of wins by Designated Males recorded for a sample. Then, with ISC as the mean intensity for that sample, FB = DW/(100/ISC) = (DW × ISC)/100.

Note that FB applies only to that portion of Designated-Male Paternities that prevailed in sperm competition, not to the total Designated-Male Paternities for the sample as a whole. Note also that, calculated as here, FB quantifies the chances of sperm from the Designated Male "winning" a bout of sperm competition against sperm from the average Other Male, not the chances of sperm from the Designated Male winning against the total Other Male sperm in the female.

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, circumstances favor fertilization by sperm from the average Other Male to an extent given by 1/FB.

Now, the formula for the calculation of frequency of sperm competition becomes:

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

For example, suppose that ISC = 2 males and POD = 100% and that the paternity data show OMP = 10%. Let FB = 2, meaning that for every fertilization achieved by an Other Male, two fertilizations will be achieved by a Designated Male. As 10% of total conceptions are cases of Other-Male Paternity via sperm competition, then 20% (OMP × FB) will be cases of Designated-Male Paternity via sperm competition. Total number of conceptions resulting from sperm competition in the sample is now 10% + 20% = 30%, meaning that to yield the frequency of sperm competition the measured level of Other-Male Paternity needs to be multiplied by a factor of 3.0 (i.e., [1+(FB/(ISC – 1))] = [1+(2/(2 − 1))] = 1 + 2 = 3). Similarly, if FB = 2 and ISC = 4, then OMP needs to be multiplied by 1.67, and so on.

4.2 | Intensity of sperm competition

Mathematically, the formula developed for the calculation of the frequency of sperm competition (FSC) can be re-arranged to calculate the intensity of sperm competition (ISC) as follows:

$$ISC=[\{FB\}/\{[((DMP+OMP)*FSC)/(OMP*POD)]-1\}]+1$$

In practice, however, the calculation of ISC can only proceed if the value of FSC is already known. Yet FSC can be calculated only if the value of ISC is itself already known. Our procedural solution to this potential stalemate involves two steps, with the resulting caveats expounded and assessed in the Discussion.

Step 1: The frequency of sperm competition is calculated first with the intensity of sperm competition 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 and the intensity is accepted to be two males. No further calculation can be made. However, if, with ISC = 2, the formula for FSC yields a value > 100% a further step is possible.

Step 2: A value for FSC > 100% may simply indicate a frequency of sperm competition that is near 100% but which has calculated higher due to sampling error in the paternity data. However, the apparent anomaly can also be an alert that along with a value for frequency of sperm competition of ~100% the paternity data indicate a value for intensity of sperm competition that is > 2 males. In these cases, after setting the value of FSC at 100, it becomes possible to use the rearranged formula to calculate a value for ISC.

4.3 | Level of sperm competition

The frequency and intensity of sperm competition can be combined mathematically to give a single measure for level of sperm competition (LSC) as follows:

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

This expression gives a figure for level of sperm competition (range 1.0 to many) that is the mean number of males whose sperm compete to fertilize an egg. A figure of 1.0 (i.e., only one male's sperm present at conception) signifies the absence of sperm competition. However, as LSC increases toward 2.0 it shows (primarily) an increasing probability that the average offspring will be conceived following a bout of sperm competition. For example, a figure of 1.5 indicates that an average of 1.5 males' sperm are present at conception or, expressed another way (if the intensity of sperm competition is two males), that on average 50% of offspring are conceived as the result of sperm competition. Then, as LSC becomes increasingly > 2, it reflects primarily that sperm from an increasing number of males are involved in each conception (e.g., LSC = 4.0 indicates that the average offspring is the result of competition between the sperm from four males).

4.4 | Biological constraints in the use of formulae

So far, to maintain biological reality, two constraints have been applied to the use of the formulae developed in this article: (a) intensity of sperm competition should never be set nor accepted with a value of less than two males; and (b) frequency of sperm competition should never be set nor accepted with a value greater than 100%. Constraint (a) is inviolable, but constraint (b) needs further qualification.

The maximum constrained value for the calculated frequency of sperm competition is 100% only when the value of the variable POD (proportion of Other-Male matings that are double matings) is also 100%. If POD is less than 100%, then allowance has to be made for the fact that some Other-Male progeny are not the result of sperm competition. The maximum constrained frequency of sperm competition (mcFSC) must therefore also be less than 100%. The value of mcFSC (as a percentage) can be calculated from the formula:

$$mcFSC=\{100\}*\{[DMP+OMP]-[OMP*((100-POD)/100)]\}/\{DMP+OMP\}$$

For example, if DMP = 2, OMP = 8, and POD = 50%, then frequency of sperm competition should neither be set nor accepted > 60%.

This constraint has repercussions for the calculation of the intensity of sperm competition in the two-step procedure described earlier which, for ease of description, assumed that mcFSC = 100%. However, if, in situations when mcFSC < 100, Step 1 of that procedure (with ISC set to 2) yields a value for FSC that is > mcFSC, then Step 2 can proceed but only if the term FSC is set to the value of the mcFSC instead of 100.

Although this constraint on the calculable level of sperm competition frequency is presented here for completeness, in practice it will rarely need to be applied. Designated males are usually chosen by researchers to be those who virtually always have sperm inside the studied females at conception. As a result, when any Other Male mates with a female, sperm competition almost always ensues, hence POD approximates to 100%. In this article, for example, none of the calculations needed constraining. The only situation in which it *could* have been necessary is for human populations that practice contraception for which POD can be much less than 100%, as described in the next section. In none of such populations analyzed here, however, does the

calculated frequency of sperm competition reach the maximum constrained level and so enforcement of the constraint was unnecessary.

A spreadsheet (S1_Calculator.xlsx) provided as Supporting Information with this article not only uses all of the above formulae to generate the values of frequency, intensity, and level of sperm competition from input paternity data but also automatically accommodates all constraints and procedures.

5 | SUBSIDIARY VARIABLES: FIELD ASSESSMENT

Although Designated-Male Paternity and Other-Male Paternity are the primary data needed for the calculation of the frequency, intensity, and level of sperm competition, the formulae developed here require values for two other variables: FB and POD.

5.1 | Variable FB (fertilization bias) in the Hominoidea

5.1.1 | Biological basis

Fertilization bias derives from inequalities in the competitiveness of sperm from the mean Designated Male and mean Other Male at the site and time of fertilization. In hominoids, this site and time is the ampulla of an oviduct in the moments surrounding the arrival of an egg.

Sperm reach the ampulla at the end of a journey that begins by departing the inseminate in the vagina and then continues by negotiating, in sequence, the cervix, uterus, uterotubal junction, and the isthmus of the oviduct (review: Suarez & Pacey, 2006). Progress through the tract is staggered with some sperm passing through within hours or even minutes of insemination, others taking days. The staggering is achieved by sperm spending variable amounts of time en route in first the cervical crypts (Höglund & Odeblad, 1977; Insler, Glezerman, Zeidel, Bernstein, & Misgav, 1980; Mortimer, 1983) and later in the isthmus (Suarez & Pacey, 2006).

The vast majority of sperm inseminated into a female die before reaching the ampullae, although full details are known only for humans. We assume, as do others (e.g., Barelli et al., 2008) that the following can be extrapolated (in principle, but not numerically) to other hominoids.

In humans, only ~25,000 sperm from an inseminate of ~300 million (i.e. < .01%) ever pass through an oviduct (Ahlgren, 1975). At any one time, only 250 sperm (range 80–1,400) are present in the two oviducts (Williams et al., 1993). While acknowledging the scope for numerical vicissitudes from such a huge decline in numbers, we assume in our derivations of fertilization bias that the more sperm that enter the cervix from any one insemination, the more will later pass through the oviducts. Trends observed during artificial insemination are weakly consistent with this assumption (Williams et al., 1993). When, as is usual, the number entering the cervix is not known, we similarly adopt the general assumption that the more sperm a male inseminates, the more will later pass through the oviducts. However, this last assumption we expect to be justified only on average. On any single occasion, the relationship can be distorted by factors such as female ejection of sperm (Baker & Bellis, 1993b,1995), sperm age (Baker, 1997), and semen displacement by subsequent males (Baker & Bellis, 1995; Gallup & Burch, 2004; Gallup, Burch, Tracy, & Mitchell, 2006; Gallup et al., 2003).

The number of sperm passing through each oviduct increases gradually to a peak 2 days after insemination (Settlage, Motoshima, & Tredway, 1973) and then steadily declines, the last fertile sperm evidently not leaving the ampullae until 5 days after insemination (Wilcox, Weinberg, & Baird, 1995). In total, therefore, there are potentially 6 days in the human menstrual cycle on which a single insemination can lead to fertilization (Wilcox et al., 1995). Insofar as is known, the pattern and timing in the non-human groups of hominoids is similar [e.g., gibbons (Barelli et al., 2008), and orangutans, (Knott, Thompson, Stumpf, & McIntyre, 2010)], although the length may be a day or two shorter in gorillas (Robbins, 1999).

Individual sperm do not remain in an ampulla for long but pass through in a stop-start procession (Suarez & Pacey, 2006), finally exiting into the female body cavity where they die (Mortimer, Leslie, Kelly, & Templeton, 1982). When sperm from two or more males are present, the ratio of sperm numbers in the ampullae from Designated and Other Males will be constantly changing as traffic from the inseminates of the two (or more) males asynchronously builds, then declines. However, the Designated Male:Other Male ratio of sperm numbers is not the only factor to influence sperm competitiveness and thus fertilization bias.

At any one time, between only 2–12% of the sperm present in the two oviducts are capable of fertilizing an egg, individual sperm possessing this ability for only 1–4 hr (Cohen-Dayag, Tur-Kaspa, Dor, Mashiach, & Eisenbach, 1995). However, as some sperm lose the ability to fertilize and exit into the body cavity, others arrive in the oviduct, gain the ability to fertilize, and perform their own traverse.

5.1.2 | Formula

Sperm competitiveness, C, can be expressed as $N \times P$ where N is the total number of sperm from a given male present in the ampulla at an instant and P is the proportion (range 0 to 1) of those sperm capable of fertilizing an egg at that instant. Let C_D be the competitiveness of sperm from the Designated Male and C_O be the summed competitiveness of sperm from all (ISC-1) of the Other Males. However, due to the way that the formulae for the calculation of the frequency and intensity of sperm competition are constructed, the fertilization bias (FB) at the moment an egg "ripe" for fertilization arrives in an ampulla needs to be given by the ratio of C_D to the *mean* competitiveness of the total sperm from all of the Other Males ($FB = C_D/[C_O/(ISC - 1)] = [C_D \times (ISC - 1)]/C_O$).

5.1.3 | Field assessment

Although $[C_D \times (ISC - 1)]/C_O$ would be the ideal estimate of fertilization bias for use in calculating the frequency and intensity of sperm competition, it cannot, at present, be estimated using all factors. Beyond identifying potential examples of sterility (e.g., gibbons, Barelli et al., 2013), little progress has been made in quantifying differences between individual males in hominoids in the proportion of sperm capable of fertilizing an egg at that instant. Thus, in this article, the mean proportion is assumed to be equal for Designated and Other

Males and the parameter is considered no further. This leaves estimates of the number of sperm (*N*) from different males present in the ampulla at the time of fertilization as the only possibility for assessing potential values for fertilization bias. In which case if N_D = the number of sperm from the Designated Male in the ampulla at the moment of fertilization and N_O = the number of sperm from all Other Males at the same moment then FB = $[N_D \times (ISC - 1)]/N_O$. In the simplest case, when the intensity of sperm competition (ISC) = 2, then FB = N_D/N_O.

Naturally, no direct measure has yet been attempted for the total number of sperm (N_D and N_O) present in a female's ampulla from a Designated Male (from 1 or more inseminations) and all Other Males, respectively. The best that can be done at present is to generate an indirect estimate of the N_D:N_O ratio using field measurements for as many of the following as possible:

1. Number of female fertile-phase copulations with Designated and Other Males;
2. Mean number of sperm inseminated per fertile-phase copulation by each;
3. Proportion of sperm the female retains from each;
4. Timing of Designated and Other Male copulations relative to day of ovulation;
5. Copulation sequence (e.g., first male, second male, last male);
6. Proportion of sperm from a previous male that is removed by the next male to copulate.

Field data exist that enable some assessment of fertilization bias for all of the hominoid groups. In orangutans, gorillas and *Pan* spp these data are either minimal or very indirect. Those for gibbons, however, are more detailed and for humans consist of a range of early attempts to measure most of the six elements in the above list.

Although a default value of 1.0 for fertilization bias (meaning that the chances of the average Designated Male and average Other Male in a sample have equal chances of "winning" a bout of sperm competition) might at first sight seem reasonable, from an evolutionary perspective it seems less so, depending on the nature of the Designated Male. Some categories of Designated Male expend considerable energy and resources in attaining a position that should tip the fertilization bias in their favor (FB > 1). Consorts, alpha males and territory holders are expected examples and it seems unlikely that such behavior would evolve unless the investment did result in FB > 1. The data summarized in the next few sections are generally consistent with such an expectation.

5.1.4 | Gibbons: Designated male = the female's sole or primary male partner

Barelli et al. (2008) tabulate copulation rates with Designated and Other Males by female *H. lar* on particular days near to ovulation. They also link these copulation rates with the probability of conception on different days as provided for humans by Wilcox et al. (1995). These data are here reorganized in Table 3 in a way that allows calculation of fertilization bias.

The following assumptions are made: (a) sperm longevity, fertility, and passage through the female tract are similar in humans and *H. lar* (see Barelli et al., 2008); (b) probability of conception for each day that insemination occurs is proportional to the number of fertile sperm from that insemination that will be present in the female's ampulla when an egg arrives on the day of ovulation; (c) Designated Males and Other

TABLE 3 Calculation of fertilization bias (FB) for the white-handed gibbon, *H. lar*

Day of cycle (0 = ovulation)	Col. A Probability of conception	Col. B ♀ copulation rates/day With D-male	Col. C ♀ copulation rates/day With O-male(s)	(Col. A×B×100) D-male	(Col. A×C×100) O-male(s)
−6	0.00	0.59	0.00	0.00	0.00
−5	0.08	0.62	0.00	4.96	0.00
−4	0.17	0.63	0.30	10.71	5.10
−3	0.08	0.60	0.00	4.80	0.00
−2	0.36	0.75	0.00	27.00	0.00
−1	0.34	0.85	0.00	28.90	0.00
0	0.36	1.05	0.15	37.80	5.40
+1	0.00	1.10	0.00	0.00	0.00
	Total			114.17	10.50
	Adjusted total			114.17	16.80
	Fertilization bias			6.80	

Day of cycle: Negative numbers indicate days before ovulation.
Column A from "Timing of Sexual Intercourse in Relation to Ovulation—Effects on the Probability of Conception, Survival of the Pregnancy, and Sex of the Baby," by Wilcox et al., 1995, The New England Journal of Medicine, 333, p. 1517; Columns B and C from "Mating Patterns and Sexual Swellings in Pair-Living and Multimale Groups of Wild White-Handed Gibbons, *Hylobates lar*," by Barelli et al., 2008, Animal Behaviour, 75, p. 991.
D-male = Designated Male; O-Male = Other Male. For rationale behind calculation, see text.

Males inseminate the same number of sperm per copulation and the number inseminated at each copulation does not vary with day of cycle; (d) the intensity of sperm competition is two males (one Designated, one Other); and (e) "total" values calculated in Table 3 reflect the relative numbers of sperm from the Designated and Other Male present in the ampulla when an egg arrives for fertilization.

As the total value for Other Males in Table 3 includes zeros from three (out of eight) females that were never seen to copulate with an Other Male (Barelli et al., 2008), the figure for Other Males needs adjusting (multiplying by 8/5) to relate specifically to females that contained sperm from both categories of males, not to the female population as a whole.

The calculated fertilization bias is 6.8, meaning that the population of sperm in the ampullae at the time of fertilization is biased such that the average Designated Male has 6.8 times the chances of fertilizing the egg than the average Other Male. In the absence of comparable data for the other gibbon species for which paternity data are available (Table 1), the same figure of 6.8 is applied to all three gibbon species in later analysis (Table 4).

5.1.5 | Orangutans: Designated male = the local flanged, dominant territory holder

Variation in female copulation rate with males of different categories (Knott et al., 2010; Utami Atmoko et al., 2009) suggests a modest overall bias in favor of Designated Males that should be even more extreme if limited to matings in the days before ovulation. However, the only hormonal study that could separate out fertile-phase matings (Knott et al., 2010) recorded few (i.e., 7) mating occasions by an unspecified number of females (maximum = 4) over an unspecified number of menstrual cycles. These observations suggest a minimum value for fertilization bias of 3.0, which is broadly consistent with the impressions presented by Utami Atmoko et al. (2009). This is the value used for both dominant territory holders and consorts in later calculations (Table 4).

5.1.6 | Gorillas: Designated male = a group's dominant silverback male

Mating frequency figures presented by Robbins (1999) for estrous mountain gorilla females mating with Designated and Other Males suggest a fertilization bias of ~4.6. In our analyses (Table 4), we use this figure for the studies by Bradley et al. (2005) and for the 2003–2004 study by Rosenbaum et al. (2015). However, the latter authors observed in their 2011–2012 study that the age structure of their study population had changed and that reproductive skew had become less extreme. No mating data are available from the time that allow fertilization bias to be estimated, but in acknowledgement of this observation we reduce the fertilization bias for this study alone by fifty percent to 2.3 (Table 4).

5.1.7 | Chimpanzees: Designated male = a group's alpha male

Field data for *Pan paniscus* that allow the copulation rate for the alpha male to be divided by the mean rate for all lower-ranked males generate values for fertilization bias of 2.44 (Surbeck, Mundry, & Hohmann, 2011; Table 2) and 2.12 (Kano, 1996; table 10.3). Both sets of data, however, were for bonobo matings across estrus, not just during the 5–6 days of fertility. Extrapolation from the behavior of *P. troglodytes* suggest that fertilization bias for alpha bonobos will in fact be higher than is suggested by these figures.

Alpha *P. troglodytes* males show an 11-fold increase in mating with females that are at peak fertility, whereas lower-ranked males do not change their copulation rate significantly (Deschner, Heistermann, Hodges, & Boesch, 2004). If the alpha:mean-Other-Male copulation rate ratio across estrous is similar to bonobos (i.e., ~2.3), then during peak fertility the ratio should be considerably higher. However, not all evidence points unequivocally in this direction. Although individual female *P. troglodytes* show preferences for mating with particular males during peak fertility, not all females necessarily favor the current alpha male (Stumpf & Boesch, 2005).

From these figures and considerations, we adopt a fertilization bias of 3.0 in favor of alpha males for both *Pan* species in our analyses below (Table 4). However, we expect future field data to show this figure to be a considerable underestimation. In the absence of targeted data, we use the same figure for consort males.

5.1.8 | Humans: Designated male = female's in-pair male

To judge from changes in the probability of conception from a single insemination (Wilcox et al., 1995), the fertilization potential of a single human inseminate stays high and constant for Days 0, 1, and 2 (where Day 0 is the day of insemination) then decreases through Days 3–5 before reaching zero on Day 6. Potentially, this pattern reflects changes in the number of fertile sperm that are passing through the female's ampullae on each day after insemination. The implication is that if an in-pair male inseminates his social partner at least once every 3 days, then sperm traffic through the ampullae will remain relatively constant. In part, this constancy is the result of in-pair males adjusting the number of sperm they inseminate into their main social partner as a function of hours since their last copulation (Baker & Bellis, 1993a). The total number inseminated over the course of a full menstrual cycle varies little whether the pair copulates 5, 10, or 20 times. Increasing the copulation rate above once every 3 days similarly fails to increase the probability of conception (Wilcox et al., 1995).

Although a male inseminates significantly fewer sperm in a single copulation when acting as an Other Male instead of an in-pair male (Baker, 1997), a higher proportion (Baker & Bellis, 1995), and essentially equal numbers (Baker, 1997) of those sperm are retained by the female. Initially, therefore, we assume that roughly equal numbers of sperm from an in-pair male's inseminate and an Other Male's inseminate are likely to gain access to the cervix, uterus, and eventually ampullae.

Suppose that an in-pair male copulates with his partner at least every 72 hr during her 6-day fertile phase and so achieves a constant traffic of fertile sperm through the ampullae throughout that phase. The competitiveness (C_D) of those sperm on any given day can be expressed as the probability of conception for the cycle (0.37; Wilcox

TABLE 4 Calculated levels of sperm competition in the Hominoidea

			Variables		Level of sperm competition (males/conception)			
						Species, from:		
Group	Species		POD	FB	Studies	Raw totals	Adjusted totals	Group
Gibbons	*H. lar*		100	6.80	1.90	1.76	1.82	1.53
			100	6.80	1.52			
	H. muelleri		100	6.80	1.00	1.00	1.00	
	N. gabriellae		100	6.80	1.78	1.78	1.78	
Orangutans	*Pongo abelii*		100	3.00	3.25	8.00	8.00	5.42
			100	3.00	8.00			
	P. pygmaeus		100	3.00	3.67	3.67	2.83	
			100	3.00	2.00			
Gorillas	*G. beringei*		100	4.60	1.86	2.44	1.22	1.15
			100	4.60	1.85			
			100	2.30	4.83			
	G. gorilla		100	4.60	1.00	1.00	1.08	
			100	4.60	1.00			
Chimpanzees	*P. paniscus*		100	3.00	11.00	11.00	11.00	8.30
	P. troglodytes		100	3.00	28.00	5.78	5.59	
			100	3.00	5.88			
			100	3.00	2.50			
			100	3.00	7.90			
			100	3.00	2.00			
Humans	*H. sapiens*	NA	68	2.25	1.30[a]	1.32	1.39	1.39
		Eu	68	2.25	1.35[a]			
		Af	68	2.25	1.51[a]			
		SA	68	2.25	1.37[a]			
		As	68	2.25	1.40[a]			
		Oc	68	2.25	1.05[a]			

Abbreviations: POD, percentage of Other Male Matings that are double-matings (see text); FB, fertilization bias.
For References and raw data, see Table 1. Order of studies as in Table 1.
"Studies" are in most cases unique sets of data for unique groups of individuals separated either by location, time, or social structure. The exceptions are the data sets for each species of orangutan which involve overlapping sets of individuals but in different social situations. In calculating the level of sperm competition for orangutans as a group, however, only one, the least biased, study is used for each species as evident from the figures (see text for full descriptions).
Level of Sperm Competition, calculated from paternity data in Table 1 (for individual studies) and Table 2 (for Species, both raw and adjusted data). Group values are the means of the "adjusted" species-values.
To improve clarity, only the level of sperm competition (LSC) is shown, not the frequency (FSC) or intensity (ISC). In this table, however, most values of FSC and ISC can quickly be calculated from the value of LSC. If LSC $\geq$ 2.0, then FSC = 100% and ISC = LSC males; if LSC $<$ 2.0 then FSC = (LSC-1) $\times$ 100 and ISC = 2 males. Only for gorillas does this simplified calculation not work for reasons given in the Discussion. For this group, ISC = 2.44 for all subspecies and FSC = 25% for the montane *G. b. beringei* and 5% for the three lowland subspecies.
[a]For tabulation, the 73 studies of humans have been collected together by continent: NA, North America; Eu, Europe; Af, Africa; SA, South America; As, Asia; Oc, Oceania).

et al., 1995). If an Other Male also manages to inseminate the female twice, 72 hr apart, during the fertile days, then $C_D = C_O$ on each day and over the whole phase FB = 1. However, if, as is perhaps more likely (but depending on efficiency of mate guarding), the Other Male only inseminates the female on one occasion during those 6 days, the fertilization bias changes in favor of the in-pair male.

If a single Other Male copulation occurs on the day of ovulation (Day 0) or on either of the 2 days previously (Day -1 or -2) then both

in-pair and Other Males are likely to have equal numbers of sperm passing through the ampullae at ovulation and FB is again ~1. However, if the Other Male copulation occurs on any of the days before Day −2, then FB is likely to be 2.18 from a copulation on day −4 (i.e., 0.37/0.17; see Wilcox et al., 1995; Table 1) and 4.63 from a copulation on Day −3 or −5 (i.e., 0.37/0.08).

In the absence of data for the incidence of Other Male copulations on different days of the 6-day fertile phase, we assume that the event occurs at some random point during these days. Then, based on the probability of conception on each day of the phase (Wilcox et al., 1995), mean fertilization bias during the human fertile phase can be calculated as $FB = [(3 \times 1) + (1 \times 2.18) + (2 \times 4.63)]/6 = 14.44/6 = 2.41$. This figure, however, can be further refined in the light of other adaptations known to be shown by in-pair and Other Males.

Although an Other Male does not inseminate more sperm during a single copulation than an in-pair male, he does inseminate significantly younger sperm (in the sense that time since last ejaculation, whether copulatory or masturbatory, is 28 hr shorter for Other Males than in-pair males; Baker, 1997). Suppose, therefore, that the traffic of fertile sperm through the ampullae from a single Other Male inseminate stays at its high plateau for a full day longer than from a single in-pair male inseminate. The calculation then becomes $FB = [(4 \times 1) + (1 \times 2.18) + (1 \times 4.63)]/6 = 10.81/6 = 1.8$. The Other Male's putative strategy of inseminating younger sperm could thus reduce the in-pair male's fertilization advantage by ~25%. However, in-pair males have a counter-strategy.

The less time an in-pair male (and/or his family network, as in the Dogon; Strassmann et al., 2012) spends with his partner between copulations, the more likely is her last copulation to be with an Other Male (Baker & Bellis, 1993a, 1995). In-pair males respond to this risk factor by adjusting the number of sperm that they inseminate: the less time an in-pair male spends with his partner between copulations, the more sperm he inseminates at the next copulation (Baker & Bellis, 1989, 1995). This response remains significant even after controlling for factors such as hours since last ejaculation and lifestyle variables such as alcohol consumption and smoking (Baker, 1997). It has also been demonstrated to be shown by individual males from one copulation to the next (Baker & Bellis, 1993a, 1995).

For present purposes, suppose that the data collected for in-pair males by Wilcox et al. (1995) are for males spending 50% of their time with their partner. Suppose also that in any 6-day fertile window that a female copulates with an Other Male, then the in-pair male has spent only 25% of his time in her company. The consequence would be an increase in the number of sperm inseminated by the in-pair male of ~25% (Baker, 1997; figure 4, with mean inseminate = 300 million sperm). The fertilization bias would then be given by $FB = [(4 \times 1.25) + (1 \times 2.73) + (1 \times 5.79)]/6 = 13.52/6 = 2.25$.

All of these role-responses by in-pair and Other Males appear to be adaptations that could influence the outcome of any given bout of sperm competition by changing fertilization bias. So, too, could other adaptations such as semen displacement (Baker & Bellis, 1995; Gallup & Burch, 2004; Gallup et al., 2003, 2006) on those relatively rare, but certainly not evolutionarily-insignificant (Pham & Shackelford, 2014), occasions that a female conceives after mating with two or more males within the space of a maximum of two hours (Baker, 2016). Without data that allow the scale of this factor to be judged, however, we adopt in our later analyses (Table 4) a value of FB = 2.25 for humans.

5.2 | Variable POD in the Hominoidea

Described simply, variable POD is the percentage of matings by Other Males that are double-matings. In the context of the formulae for calculation of the frequency and intensity of sperm competition, however, POD is expressed in terms of female fertile phases (i.e., the percentage of fertile phases involving an Other-Male mating that also involve sperm competition with the Designated Male).

In all non-human species for which information is available and the Designated Male is a member of one of the usual categories (e.g., consort, group alpha, territorial dominant) all females seem to copulate with this male within the fertile window (e.g., gibbons, Barelli et al., 2008; orangutans, Knott et al., 2010; gorillas, Robbins, 1999; and *Pan* spp, Tutin, 1979). Thus, there will virtually always be such Designated-Male's sperm passing through the ampullae at ovulation. Hence, any fertile-phase insemination by an Other Male automatically leads to sperm from both males being present in the ampulla at the critical time. POD can confidently be set to 100% when applying the formulae developed here.

Humans, in the absence of contraception, also appear to have a POD that approaches 100%. Females not trying to avoid becoming pregnant almost always copulate with their in-pair male during their 6-day fertile window as determined by hormonal assay (Wilcox et al., 1995). Over the course of 625 menstrual cycles, the female failed to copulate with the in-pair male during the 6-day fertile window in only 31 cycles (i.e., ~5%). On a random model, therefore, the value of POD would be 95%, because in 5% of fertile phases an Other Male's sperm will not encounter sperm from a Designated Male. This figure (95%) is therefore used for human societies that do not practice contraception.

In the presence of contraception, the value of POD changes, although the type of contraception is important. Permanent or long-term contraceptives such as hormonal or IUDs act on the female to prevent conception and/or implantation (Guillebaud, 2016) and provide a zero in paternity data for both Designated-Male Paternity and Other-Male Paternity equally. Such contraceptives, therefore, do not introduce bias. However, one-off contraceptives such as barrier and post-coital methods (e.g., "morning after" pill) have the potential to affect one copulation but not another. For example, if a "Designated followed by Other" or "Other followed by Designated" mating sequence within the 6-day fertile window involves the use of contraception on one but not the other occasion, then any child that results will appear in paternity data. Yet no sperm competition was involved. Whichever male gains paternity, the Other Male copulation was not a double-mating.

The only direct studies of the involvement of contraception in sperm competition were conducted in Britain and Spain (Baker, 1997; Baker & Bellis, 1995; Bellis & Baker, 1990). These showed that, during the fertile-phase (defined as days 5–14 of the menstrual cycle), nulliparous younger women with current but short-term partners showed a greater use of contraceptives during matings with Other-Males. The

likely result would be to reduce the chances of Other-Male Paternity (Baker, 1997). In contrast, older females at the stage of first reproduction or later showed a different pattern (Baker & Bellis, 1995; Bellis & Baker, 1990). For these women, fertile-phase Other-Male matings were nearly twice as likely to be "unprotected" as fertile-phase in-pair matings, potentially leading to Other-Male Paternity without sperm competition.

Two studies combined have helped to obtain a value for POD for populations that use contraceptives. First, in a study of United Kingdom females in the late 1980s, Baker and Bellis (1995) found that 50% of "unprotected" fertile-phase Other-Male matings had been preceded within the previous 5 days by "unprotected" in-pair male matings. Second, Gallup et al. (2006) in a study of United States college students found that 35.9% of Other-Male matings were followed over the next 2 days by in-pair matings. Unfortunately, neither the phase of cycle nor contraceptive use was recorded in the latter study. The two study groups also differed in location and age. Nevertheless, we combine the two studies to obtain a value for POD of $[50+(50 \times 35.9/100)] = \sim 68\%$ which we then apply to societies that practice contraception.

6 | LEVEL OF SPERM COMPETITION AND RELATIVE TESTES SIZE

6.1 | Level of sperm competition

Table 4 shows the levels of sperm competition for the Hominoidea calculated by applying the formulae developed in this article to the paternity data in Tables 1 and 2. The results are tabulated at several different levels: individual studies (using data from Table 1); individual species (using both raw and adjusted data; Table 2); and higher taxonomic groups (using data in Table 4). For humans, although levels of sperm competition were calculated for each of the 73 studies and used in the correlation analysis of "Individual studies" below, they are not tabulated individually in Table 4. Instead, the levels are presented separately for each continent (with the conservative assumption that the majority of individuals tested in each continent practiced contraception; hence, in Table 4, POD is listed as 68%, not 95%).

6.2 | Relative testes size

The first major list of relative testes sizes to include measures for the five groups of hominoids was published by Harcourt et al. (1981) and showed testes weight as a simple proportion of body weight. Harcourt and colleagues later enlarged and updated this dataset and switched to expressing relative testes size in terms of residuals from regression analyses of testes size on body weight after log transformation of the data (Harcourt et al., 1995). Anderson and Dixson (2002) then performed their own regression analysis on a further dataset and produced a separate set of residuals. Rather than choose between these two sets of residuals (Table 5), we use them both in our analyses.

Currently, residuals are available only for the five major taxonomic groups of the hominoids, not for individual species, subpopulations, or studies. Analyses at these levels are therefore limited to a single group measure of relative testes size (e.g., for "gibbons," "gorillas," and so on) that is the same for each species or study.

TABLE 5 Two measures of relative testes size for the Hominoidea

	Relative testes size (residuals)	
Group	Harcourt et al. (1995)	Anderson and Dixson (2002)
Gibbons	−0.57	−1.1
Orangutans	−0.04	−0.8
Gorillas	−0.73	−1.4
Chimpanzees	1.54	0.8
Humans	0.12	−0.4

6.3 | Correlation between relative testes size and the level of sperm competition as calculated from paternity data

Pearson's correlation coefficient, r, is calculated for levels of sperm competition against the two published lists of relative testes size (Table 6). The results are shown separately for the different levels of: individual studies ($n = 92$); species, using raw data ($n = 10$); species, using adjusted data ($n = 10$) and higher taxonomic groups ($n = 5$). In every case, the correlation is significant (p (1-tailed) $< .05$) and in some cases p (1-tailed) $< .001$.

7 | DISCUSSION

7.1 | Paternity data and relative testes size as independent measures of sperm competition

One aim of this article, using the relatively extensive paternity data available for the Superfamily Hominoidea, was to attempt an independent validation of relative testes size as a proxy for level of sperm competition. To the extent that the figures generated from paternity data at different levels, all correlate significantly with two separate measures of relative testes size (Table 6), that aim would seem to have been realized.

Naturally, it has to be accepted that the existence of a significant correlation between any two measures does not in itself prove that either is accurate. What the correlations do show, however, is that if one measure is considered a valid and useful measure, as has relative testes size for the past three decades, then the other measure should be considered as a candidate too. So although Table 6 provides independent support for the continuing use of testes size as a proxy measure for sperm competition, it also suggests that the conversion of paternity data using the formulae developed in this article can provide a viable alternative.

7.2 | Paternity data vs. Relative testes size: advantages and disadvantages

Until the beginning of the 21st century, paternity data were a rarity and primatologists had little choice but to use relative testes size as a

TABLE 6 Relative testes size and paternity data as independent measures of level of sperm competition

Level of sperm competition from paternity data		Measures of relative testes size	
		Harcourt et al. (1995)	Anderson and Dixson (2002)
	n	Pearson's *r*	
Individual studies	92	.505****	.430****
Species (raw totals)	10	.770***	.725***
Species (adjusted totals)	10	.778***	.740***
Groups	5	.864*	.806*

Correlation coefficients calculated from data in Tables 4 and 5.
p-values (1-tailed): *< .05; ***< .01; ****< .001.

proxy measure for level of sperm competition. Now, however, as we have illustrated for the Hominoidea, that situation has changed. Although paternity data may not yet be much more available than measures of relative testes size, they are at least equally accessible. Availability is no longer a factor.

If there is any continuing advantage to using relative testes size as a measure of level of sperm competition, it is that testes size has evolved, in principle at least, over the same (or a similar) period as any other sexual characteristic that an author may want to assess as a product of level 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 for gorillas (Stoinski et al., 2009) and humans (Dupanloup et al., 2003; van der Horst & Maree, 2014), then paternity data may not illuminate the evolutionary past as well as relative testes size.

The data presented here suggest that this potential advantage of relative testes size may not be as great in practice as it appears in principle. If there were such a mismatch in the information embedded within relative testes size and the level of sperm competition generated by paternity data, the correlation between the two (Table 6) should not be significant, or at least not as strongly as it is.

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. Not least, they are explicit and meaningful: frequency measures as the percentage of conceptions resulting from sperm competition; intensity as the mean number of males involved in each bout of sperm competition; and level as the mean number of males whose sperm compete for each conception. By comparison, the measures of relative testes size are virtually inscrutable. For example, variation in relative testes size may be able to establish that variation in an aspect of sexuality [e.g., sperm mid-piece volume (Anderson & Dixson, 2002); seminal proteins (Dorus et al., 2004)] might relate evolutionarily to level of sperm competition, but it cannot go further. It cannot, for example, establish whether a mid-piece volume that matches a seemingly low relative testes size value [such as −1.1 on Anderson & Dixson's (2002) scale] has evolved under a near-zero, simply low, or even moderate level of sperm competition.

Another advantage of paternity data is the ability to identify differences in the level of sperm competition between subpopulations and even between types of behavior in situations in which relative testes size might be expected to be invariable. Examples in this article (Table 4) are differences between: monogamous and polyandrous situations in gibbons; consorts versus territorial dominants in orangutans; polygynandrous versus polygynous groups of gorillas; and the influence of group size in *Pan* species. Unless relative testes size also varies in all the same situations, paternity data would seem to provide a much more versatile measure.

7.3 | Paternity data vs. Mating data

Our conversion of paternity data into a measure of sperm competition requires a generous input from field observations of mating behavior. Both fertilization bias (FB) and the proportion of Other-Male matings that are double-matings (POD) are variables that depend on such data if their field values are to be calculated. So why not use just mating behavior and forego the need for paternity data altogether?

An extreme illustration of the answer is provided by the female *Pan troglodytes* at Ngogo that Watts (2007) reported mating 65 times with 17 different males in a single day and by the other females that copulated with up to 38 different males during a single estrous cycle. Rarely is such a wealth of information available for female primates, yet even this much information cannot generate a direct numerical measure for level of sperm competition. The reason is that inside the female a quite different scenario almost certainly emerges. Failure of males to ejaculate, the success and failure of copulatory plugs, lack of female retention of sperm from some males, displacement of one male's sperm by another, and/or differences in timing of copulation of only a few hours could all rule out some, or even most, males' sperm from being present when the contest for fertilization reaches its climax. An endoscope is needed, and in a sense, this is what paternity data provide.

Mating behavior is an important element in the calculation of fertilization bias, and sometimes as described in earlier sections it is all that is currently available. Ideally, however, as illustrated by the derivation of a figure for fertilization bias in humans, other data (on sperm) should also be involved. Nevertheless, even with such extra data, fertilization bias is still only one part of the formula, just one element in the translation of paternity data into a level of sperm competition.

At best, mating data on their own can provide only a proxy measure of sperm competition. As a contributor to the measure of fertilization bias, however, such data provide a means by which paternity data can measure what happens inside the female.

7.4 | Problems in the calculation of level of sperm competition from paternity data

Naturally, we accept that more and wider-ranging paternity data are needed for all species to improve the accuracy of the figures listed in Table 4. We also accept that calculation of the contributing parameters, particularly fertilization bias, needs further refinement (and inevitably also more data). Such problems, however, are universal and hopefully will diminish with time. There was, though, one problem that we encountered that may not have a solution: the need for a value for either the frequency or the intensity of sperm competition before we could calculate the other.

We circumvented this problem by assuming the intensity of sperm competition to have the minimum value of two males unless the resulting value of frequency of sperm competition was greater than the maximum constrained value (usually 100%). Only then could we set frequency of sperm competition at its maximum constrained value and actually calculate intensity of sperm competition. The consequence was that all studies or species that yielded values for frequency of sperm competition less than the maximum constrained value had to be allocated a value for intensity of sperm competition of two males.

In the final analysis, this problem did not impact our handling of the data for gorillas. Only males living in multi-male, multi-female groups appear to experience sperm competition (Table 4). As the frequency of sperm competition in such groups was calculated to be 100%, then the intensity could be calculated (as 2.44 males) and not simply allocated. With the intensity of sperm competition, a factor only when sperm competition occurs, 2.44 then became the value that had to be used for each of the subspecies and species. No procedural artefact was involved. The only taxonomic groups affected by our protocol, therefore, were gibbons and humans, but even for these two groups the consequences appear to be minor.

For gibbons, although a female will occasionally copulate with up to four different males in a short length of time (Palombit, 1994), within a single fertile period most females probably copulate with just their one or two social partners plus, if they copulate with another male at all, with an occasional territorial neighbor (Barelli et al., 2013). Modal intensity of sperm competition is likely to be two and the mean is likely to be only a little higher and almost certainly nearer to two than to three.

For modern humans, females who copulate with more than one male in the days leading to conception are also in most cases likely to copulate with only two (i.e., one in-pair male + one Other Male). This does not mean that group-sex (both consensual and coercive), prostitution, and other short-interval female copulations with more than two males is too rare to be of evolutionary significance (Baker & Bellis, 1995; Gallup et al., 2006; Pham & Shackelford, 2014; Smith, 1984b). The occurrence must at times lead to conception while sperm from more than two males are in the ampullae. Nevertheless, the frequency with which this occurs is unlikely to be high enough to generate a population mean for intensity of sperm competition that is nearer to three males than to two. Even the forest-period, hunter-gatherer Ache of eastern Paraguay, who on 63% of occasions claimed between two and 10 potential fathers for a child, still had a modal and median claim of two males (Hill & Hurtado, 1996). The mean claim of 2.5 males (from data in Hill & Hurtado, 1996; fig. 13.4) was still not quite nearer to three males than to two.

It seems, therefore, that although a value of two males for the intensity of sperm competition for gibbons and humans is a byproduct of our procedure rather than a direct calculation, the figure still appears to be realistic. This may indicate that in lineages in which the frequency of sperm competition is less than 100% (or the maximum constrained value), the mean value for intensity is unlikely to be much higher than two males anyway. Perhaps not until frequency approaches the maximum constrained value does mean intensity start to rise significantly higher.

7.5 | Levels of sperm competition in the Hominoidea

7.5.1 | Gibbons

The relative testes size of −1.1 from Anderson and Dixson (2002) quoted above was for gibbons, negative values being considered to represent a "low" level of sperm competition. Early field studies had concluded that all four genera of extant Hylobatidae were sexually monogamous (Gittins & Raemaekers, 1980) and all analyses since have assumed a "low" level of sperm competition for this hominoid Family (e.g., Dixson, 1998; Harcourt et al., 1981). The calculated relative testes size value of −1.1 seemed wholly appropriate.

More recent field studies, however, have challenged the assumption of a low level of sperm competition (Barelli et al., 2013; Palombit 1994; Reichard, 1995), a challenge that now receives further support from Table 4. There, the mean level of sperm competition for three gibbon species is calculated to be 1.53 males per conception. Expressed another way (using frequency), 53% of conceptions involve sperm competition. In terms of natural selection, this represents a substantial selective pressure. The figure calculated for level of sperm competition would be even higher if the small, three-paternity, study of *Hylobates muelleri* were excluded (thereby giving 1.80 males per conception) or weighted less.

Such levels of sperm competition add further weight to the argument (Barelli et al., 2013) that the general lack of investment by male gibbons in the offspring of their social partner indicates low paternal confidence. Even the siamang, *Symphalangus syndactylus*, the only gibbon species that does show a degree of male investment (the carrying of infants older than 12 months) appears to do so for sexual, not parental, reasons (Lappan, 2008).

Low although a relative testes size of −1.1 might appear on Anderson and Dixson's (2002) scale, it might nevertheless still represent a substantial level of sperm competition.

7.5.2 | Orangutans

The position of the orangutans was unclear in the earliest analyses of sperm competition in primates. At first, the subfamily was aligned with gibbons, gorillas, and humans as having a "single-male" mating system with the expectation of a low level of sperm competition (Harcourt et al., 1981; Short, 1979). Later, however, Harcourt et al. (1995) and Dixson (1998) endowed the Ponginae with a "dispersed" socio-sexual system that was tentatively aligned more with the multi-male, multi-female breeding systems of chimpanzees. Now, no matter how the social system is subjectively categorized, Table 4 suggests that sperm competition in orangutans is considerable, with sperm from an average of 5.42 males competing for the prize of fertilization in each fertile window. The calculated figure is higher for *P. abelii* (8.0 males/conception) than *P. pygmaeus* (2.83 males) and perhaps lowest of all (2.0 males) for territorial males of *P. pygmaeus* at the peak of their dominance.

Such figures allow the building and testing of hypotheses in ways that a proxy measure such as relative testes size never could, not least, for example, because a male at the peak of his dominance presumably has the same relative testes size as when his dominance is waxing or waning.

7.5.3 | Gorillas and chimpanzees

All past studies of the Hominoidea based on both mating systems and relative testes size have concurred that level of sperm competition is lowest in gorillas and highest in chimpanzees (e.g., Dixson, 1998, 2009; Harcourt et al., 1981, 1995; Short, 1979; van der Horst & Maree, 2014). Table 4 provides further independent support for this conclusion while at the same time adding potential values for more focused interpretation (gorillas = 1.15 males/per conception; chimpanzees = 8.30).

Despite this clear overall difference, we note that any male gorilla that finds itself in a polygynandrous group will still experience a frequency and intensity of sperm competition of 100% and 2.44 males, respectively (Table 4), and that in the mountain gorilla, such high levels impact up to 50% of males (McNeilage et al., 1998). This is a higher level of sperm competition (2.44 males/conception; Table 4) than is calculated for a male chimpanzee in a small social group at Bossou in Guinea (2.0 males/conception; Table 4).

7.5.4 | Humans

For humans, the use of relative testes size has had little success in generating a consensus over evolutionary levels of sperm competition. The earliest studies concluded a level that was likely to be intermediate between that of gorillas and chimpanzees (Harcourt et al., 1981). More recently, however, Dixson (2009) has argued that he can see nothing unusual about the relative testes size of humans (–0.4 on Anderson and Dixson's (2002) scale; Table 5) and sees no evidence of anything other than a trivial level of sperm competition. Other authors have concurred (Larmuseau et al., 2017; van der Horst & Maree, 2014).

The levels shown for humans in Table 4 are 1.32 males per conception using total primary data from >47,000 individuals and 1.39 when the samples are adjusted for the distribution of the human population across the world. These levels will undoubtedly be thought high by many authors, especially those whose focus is firmly on the high paternity confidence sectors of the modern industrial world. These figures, however, are based on data from six continents and a range of social situations, low paternity confidence sectors as well as high. Moreover, even if the proportion of children born worldwide into circumstances of high paternity confidence is as high as around 60–65%, then these levels of sperm competition would still be an acceptable reflection of the wider human population. If the proportion with high paternity confidence is lower, then the adjusted figures would generate a level of sperm competition that is even higher. For the moment, however, beyond noting that the use of relative testes size and paternity data are in significant accord (Table 6) over the level of sperm competition in the human lineage as it relates to other hominoids, we consider that the potentially extensive discussion of the evolutionary levels of sperm competition in humans is beyond the scope of this article.

7.6 | Conclusion

Although this article adds strong support for the continuing use of relative testes size as a valid proxy for level of sperm competition, we suggest that the generation of direct measures of frequency, intensity, and level of sperm competition from paternity data using the formulae developed in this article has much greater potential. The procedure could, as the above discussion illustrates, provide greater insight into the evolution of diverse aspects of sexuality than is possible from any proxy measure. Among the most intriguing possibilities is an appraisal of the evolution of relative testes size itself, an appraisal that was impossible for as long as relative testes size was the only available measure of sperm competition.

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SUPPORTING INFORMATION

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