Research article

Sperm competition risk and male genital anatomy: comparative evidence for reduced duration of female sexual receptivity in primates with penile spines

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Abstract. Selection pressures influencing the way in which males stimulate females during copulation are not well understood. In mammals, copulatory stimulation can influence female remating behaviour, both via neuroendocrine mechanisms mediating control of sexual behaviour, and potentially also via effects of minor injury to the female genital tract. Male adaptations to increase copulatory stimulation may therefore function to reduce sperm competition risk by reducing the probability that females will remate. This hypothesis was tested using data for primates to explore relationships between male penile anatomy and the duration of female sexual receptivity. It was predicted that penile spines or relatively large bacula might function to increase copulatory stimulation and hence to reduce the duration of female sexual receptivity. Results of the comparative analyses presented show that, after control for phylogenetic effects, relatively high penile spinosity of male primates is associated with a relatively short duration of female sexual receptivity within the ovarian cycle, although no evidence was found for a similar relationship between baculum length and duration of female sexual receptivity. The findings presented suggest a new potential function for mammalian penile spines in the context of sexual selection, and add to growing evidence that sperm competition and associated sexual conflict are important selection pressures in the evolution of animal genitalia.

Key words: baculum, mammals, penile spines, sexual conflict, sexual selection

Introduction

Diversity in the genital anatomy of male mammals is characterised by extreme variation in penile morphology, including unexplained differences between closely related species in the relative development of traits such as the baculum or os penis, and keratinised penile spines (Eberhard, 1985; Dixson, 1987a, b, 1995, 1998). Following Eberhard (1985), much recent progress in explaining diversity in animal genitalia has come from abandoning early emphasis on the importance of genital compatibility in avoiding interspecific hybridisation, and focusing instead on the evolutionary consequences of sexual selection and

sexual conflict (Eberhard, 1985, 1996; Dixson, 1987a, b; Edwards, 1993; Arnquist, 1997, 1998). As first suggested by Eberhard (1985), cryptic female choice may be an important selection pressure in the evolution of male genital anatomy if females assess the ability of different males to stimulate them during copulation, and preferentially utilise the sperm of those males with superior stimulating capabilities (see also Eberhard, 1996; Dewsbury, 1988). Although less well studied in this context, sperm competition (Parker, 1970) may also be a significant selection pressure in the evolution of penile anatomy if females copulate with more than one male to fertilise the same set of ova, and if variation in the copulatory stimulation provided by different males affects the outcome of competition for fertilisation success. Both sperm competition and cryptic female choice can potentially result in evolutionary conflicts between the sexes – where adaptations to promote the reproductive success of one sex compromise the reproductive interests of the other (e.g. Parker, 1979; Rice and Holland, 1997; Stockley, 1997a). Sexual conflict is predicted to result in rapid coevolution of reproductive traits between the sexes (Parker, 1979; Rice, 1996; Rice and Holland, 1997), which may explain patterns of divergence in the genital anatomy of closely related species (Eberhard, 1996; Arnqvist, 1998).

Understanding the role of post-copulatory sexual selection and sexual conflict in the evolution of penile anatomy is currently less advanced for mammals than for other taxa such as insects (Eberhard, 1990, 1996; Edwards, 1993; Arnquist, 1998). For example, there is still no general consensus as to the function of the baculum, or os penis – an extremely diverse bone formed by ossification of the distal region of the corpora cavernosa (Patterson and Thaeler, 1982; Dixson, 1995, 1998). A possible function for the baculum in the context of postcopulatory sexual selection is suggested by Dixson's (1987b, 1995) reports that elongated bacula are often associated with copulatory patterns involving prolonged intromissions and/or the maintenance of intromission after ejaculation has occurred. Several hypotheses have also been put forward to explain the evolution of mammalian penile spines in the context of sexual selection (review in Harcourt and Gardiner, 1994). For example, Dixson (1987a) and Verrell (1992) showed penile structure to be more elaborate in primate species with multi-male compared to single male mating systems, and followed Eberhard (1985) in arguing that cryptic female choice was the most likely explanation for the evolution of penile spines. However, as pointed out by Harcourt and Gardiner (1994), spines are not generally more prevalent in primates with multi-male mating systems, as would be predicted under a hypothesis of cryptic female choice. They suggested instead that the spines might function in stimulating reproductive readiness and synchrony between the sexes, which fits with the observation that most primates with penile spines have dispersed or monogamous mating systems, but precludes any significant influence of sexual selection.

Here, I argue that a further possible function of genital specialisation in male mammals may have been overlooked in the context of sexual selection – that of reducing sperm competition risk (*sensu* Parker *et al.*, 1997). Adaptations for reducing sperm competition risk have generally received less attention in mammals than have those for competing directly in sperm competition. That is, following Short's (1979) observation that male primates with multi-male or promiscuous mating systems have relatively large testes for their body size, much emphasis has been placed on explaining variation in the relative testis size, sperm production, and ejaculate characteristics of male mammals (e.g. Harcourt *et al.*, 1981; Møller, 1989; Stockley and Purvis, 1993; Hosken, 1997; Stockley, 1997b; Gage, 1998; Parker, 1998), while adaptations to reduce the probability that sperm competition will occur have been more widely studied in other taxa (see Birkhead and Møller, 1998). Such adaptations include a variety of male traits that apparently function to influence female remating behaviour, such as mate guarding (e.g. Olsson and Madsen, 1998), copulatory plugs (e.g. Shine *et al.*, 2000), and chemical substances in the ejaculate (e.g. Kubli, 1996). Although less well studied in the context of sperm competition, there is already evidence for a variety of mammals that copulatory stimulation can affect female remating behaviour, both via neuroendocrine mechanisms (review in Huck and Lisk, 1986), and/or via minor damage caused to the female genital tract during copulation (Schoot *et al.*, 1992). Hence if penile spines, or other genital specialisations of male mammals such as the presence of a large or elongated baculum, result in increased stimulation of the female tract during copulation, these traits may function ultimately to reduce sperm competition risk via an influence on female remating behaviour. Here, comparative data for primates are used to explore whether penile spines and larger bacula are associated with reduced duration of female sexual receptivity within the ovarian cycle, as predicted if they function to reduce sperm competition risk.

Methods

Data for primates on penile spines, baculum length, body mass, copulatory behaviour, duration of female sexual receptivity, total cycle length, and mating system were collated from a variety of published sources (Dixson, 1987a, b, 1991, 1998; Hrdy and Whitten, 1987; Nowak, 1991; Harcourt and Gardiner, 1994; Nunn, 1999). Dixson (1987a) and Harcourt and Gardiner (1994) each classify penile spinosity for male primates on a scale of one to five, where one corresponds to no spines and five is the most spinous. Their classifications are generally in close agreement and both datasets were therefore combined. Where disagreement occurs, it is usually by only one point on the scale, in which case a mean value of the scores was used for analysis. For fractional

differences of less than one half, figures were rounded to whole or half numbers to avoid making contrasts based on marginal differences (e.g. *Macaca* were classed as point 1 on the scale rather than 1.25). Species were excluded from the analysis where disagreement occured by more than one point on the scale (e.g. Dixson classes *Callithrix jacchus* with spinosity rating of 3, whereas Harcourt and Gardiner class it as 1). The categorical classification of Dixson (1987a) was used to quantify baculum length. This classification is also on a scale of one to five, where one is the least and five the most development of the baculum. Absolute values for baculum length were also taken from Dixson (1998). Species in which females are described as being sexually receptive throughout the ovarian cycle were assigned a duration of sexual activity equivalent to their total cycle length. This could represent an exaggeration in some cases however, since the potential for sexual activity throughout the ovarian cycle need not mean that it is maintained continuously during this time. Analyses were therefore repeated excluding species described as continuously sexually receptive.

Species cannot be regarded as statistically independent for the purpose of comparative analyses because closely related taxa are likely to share characteristics of common ancestors (Harvey and Pagel, 1991). It is particularly important to control for phylogenetic effects in the comparative analyses presented here because several of the traits examined are unevenly distributed among taxa in the dataset. For example, penile spines are common in prosimian primates (12/13 genera), but are relatively unusual among anthropoids (3/19 genera, see also Harcourt and Gardiner, 1994), and the duration of female sexual activity is generally shorter in prosimians than in other primates because sexual receptivity in anthropoid primates is less rigidly influenced by ovarian hormones (Dixson, 1998). The primate phylogeny of Purvis (1995) was therefore used to identify independent contrasts within the dataset. Burt's (1989) comparative method was used to test for effects of categorical traits (penile spinosity, baculum length) on a continuous variable (duration of female sexual receptivity), and to control for variation in mating system (see below). Using this method, independent contrasts were produced by pairing each species in the dataset with its closest relative differing with respect to the category under investigation, with the proviso that no species was used more than once. Where alternative contrasts were possible within the dataset, mean values were used for closely related species with the same categorical variables. Wilcoxon signed rank tests were used to test results of the paired contrasts.

The CAIC (Comparative Analysis by Independent Contrasts, version 2.0) software package (Purvis and Rambaut, 1995) was also used to repeat analyses performed using Burt's method, and to look for evidence of evolutionary relationships between continuous variables in the dataset (baculum length, duration of female sexual receptivity, body size). The CAIC program generates a

series of independent contrasts by identifying nodes in the phylogeny where changes have occurred in the independent variable, quantifying the extent of these changes in a given direction, and calculating associated changes in the extent and direction of the dependent variable(s) for comparison. All continuous data were log transformed prior to analysis. Branch lengths were set at equal in the phylogeny (Purvis *et al.*, 1994). The BRUNCH algorithm was selected to test for relationships between categorical and continuous variables, and the CRUNCH algorithm, by default, was used for continuous variables. Relationships between hypothesised independent and dependent continuous variables were tested using linear regression analysis, forced through the origin (Harvey and Pagel, 1991).

Some consideration of mating systems is important in the analyses presented because penile anatomy tends to be more specialised among primate species in which females typically mate with more than one male (Dixson, 1987a, 1991; Verrell, 1992). Misleading results might therefore result if the duration of female receptivity is generally shorter in species with multi-male mating systems than in those with single-male mating systems, for reasons unrelated to variation in copulatory stimulation. A separate comparative analysis was therefore performed using Burt's method to control for mating system. In this case, each species in the dataset was matched with its closest relative that has a comparable mating system, but differs with respect to the category under investigation.

Body mass is a further potential confounding factor in the analyses presented if it explains variation in both the duration of female sexual receptivity and the intensity of stimulation provided by males. For example, females of small-bodied species might typically be sexually receptive for shorter periods because they are more vulnerable to predation. Such a scenario appears unlikely, however, since there is no evidence for a relationship between female body mass and duration of sexual receptivity in the present dataset (CAIC analysis: $n = 41$; $r^2 = 0.005$, $F = 0.21$, n.s.). Further, previous analyses demonstrate no evidence of a relationship between body mass and penile spinosity within either the prosimian or anthropoid primates (Harcourt and Gardiner, 1994). Hence any relationship between penile spinosity and duration of female sexual receptivity is unlikely to be confounded by body size.

Results

Data on two or more key variables (penile spines, baculum length, and duration of female sexual receptivity) were collated for 49 species from 36 genera (Appendix A).

A significant negative association was found between degree of penile spinosity and duration of female sexual receptivity within the ovarian cycle. In

Table 1. Independent contrasts between penile spinosity and duration of female sexual receptivity within the ovarian cycle, identified using Burt's method (see methods)

Contrast	High penile spines	PS	SR	Low penile spines	PS	SR
1.	*Lemur catta*	4	2–10 h	*Varecia variegata*	1	4–24 h
2.	*Galago senegalensis*	5	1–3 d	*Otolemur crassicaudatus*	4.5	2–10 d
3.	*Arctocebus calabarensis*	4	Few hours	*Loris tardigradus*	2	2 d
4.	*Propithecus verreauxi*	3	12–36 h	*Nycticebus coucang*	2	1–2.5 d
	Cheirogaleus medius	3	1 d	*Perodicticus potto*	2	2 d (1.9 d)
	Microcebus murinus	3	3 d (1.6 d)			
5.	*Leontopithecus rosalia*	2	3–5 d	*Saguinus oedipus*	1	23 d[a]
6.	*Saimiri sciureus*	2.5	1 h–2 d	*Cebus apella*	1	5–6 d
7.	*Tarsius bancanus*	3	1 d	*Aotus trivirgatus*	1	16 d[a]
				Aloutta	1	3–4 d
				Ateles paniscus	1	8–10 d (9.5 d)
8.	*Hylobates lar*	3	~4 d	*Pongo pygmaeus*	1	31 d[a]
				Pan troglodytes	1	14 d
				P. paniscus	1	15 d
				Homo sapiens	1	28 d[a]
				Gorilla gorilla	1	3–4 d (18.3 d)

Key: PS – penile spinosity score: 1 – no spines, 5 – highly spinous; SR – duration of sexual receptivity within the ovarian cycle.
[a] Indicates classification as sexually active throughout the ovarian cycle.

each of eight independent contrasts produced using Burt's method, the species with the higher score for penile spinosity also has a shorter duration of female sexual receptivity (Table 1; Wilcoxon signed ranks test, $p = 0.01$). Females of several species included in the dataset are classed as being continuously sexually receptive throughout the ovarian cycle (see Methods and Appendix A). Exclusion of these species did not significantly alter the outcome of the analysis (Wilcoxon signed ranks test, seven negative contrasts, $p < 0.02$). The same relationship between penile spinosity and duration of sexual receptivity was found when the CAIC program was used to identify independent contrasts (eight negative contrasts, sign test $p < 0.05$), and when species were paired according to mating system using Burt's method (Table 2; seven negative contrasts, Wilcoxon signed ranks test $p < 0.02$).

Further analyses where carried out to investigate whether penile spines are associated with patterns of copulatory behaviour likely to increase female stimulation or injury. This does not appear to be the case with respect to single versus multiple intromissions, because most prosimians (but relatively few anthropoid primates) have penile spines, and also have single rather than

Table 2. Independent contrasts between penile spinosity and duration of female sexual receptivity within the ovarian cycle, identified using Burt's method, with control for mating system (see methods)

	High penile spines	MS	PS	SR	Low penile spines	MS	PS	SR
1.	*Lemur catta*	M	4	2–10 h	*Propithecus verreauxi*	M	3	12–36 h
2.	*Galago senegalensis*	D	5	1–3 d	*Otolemur crassicaudatus*	D	4.5	2–10 d
3.	*Arctocebus calabarensis*	D	4	Few hours	*Loris tardigradus*	D	2	2 d
4.	*Tarsius bancanus*	D	3	1 d	*Nycticebus coucang*	D	2	1–2.5 d
					Perodicticus potto	D	2	2 d (1.9 d)
5.	*Leontopithecus rosalia*	P	2	3–5 d	*Aotus trivirgatus*	P	1	16 d
6.	*Saimiri sciureus*	M	2.5	1 h–2 d	*Cebus apella*	M	1	5–6 d
7.	*Hylobates lar*	P	3	~4 d	*Pongo pygmaeus*	D	1	31 d

Key: MS – mating system: M – multi-male; D – dispersed; P – paired; PS – penile spinosity score: 1 – no spines, 5 – highly spinous; SR – duration of sexual receptivity within the ovarian cycle.

multiple intromission patterns of copulation (review in Dixson 1998). Only two species in the dataset (*Saimiri sciureus* and *Leontopithecus rosalia*) have both spines and multiple intromissions, and it is likely that copulatory patterns are constrained by both phylogenetic and ecological factors (see Dixson 1991). To investigate whether species with penile spines are also more likely to stimulate females by behavioural means during copulation, I therefore looked for evidence of an association between penile spinosity and number of thrusts per copulation. Overall, there was no significant relationship between penile spinosity and number of thrusts per intromission. Increases in penile spinosity were associated with increased thrusting in only one out of five independent contrasts produced using CAIC, and in all four of the contrasts produced forprosimians and New World monkeys, the species with higher penile spinosity has fewer thrusts per copulation (Wilcoxon signed ranks test, $p = 0.07$, n.s.).

No relationship was found between baculum length and the duration of female sexual receptivity within the ovarian cycle. Baculum length was tested both as a categorical and a continuous variable, with control for male body mass (changes in baculum length did not correlate with female body mass: $n = 30$; $r^2 = 0.05$, $F = 1.61$, n.s.). Greater development of the baculum was associated with decreased duration of female sexual receptivity in only four of 10 independent contrasts produced using the categorical classification (sign test, n.s.). There was no evidence either for shorter duration of female sexual receptivity in species where males have a relatively long baculum for their body mass (contrasts of residual baculum length versus duration of female sexual receptivity: $n = 29$; $r^2 = 0.01$, $F = 0.30$, n.s.).

Discussion

Results of these comparative analyses provide evidence that relatively high penile spinosity of male primates is associated with relatively short duration of female sexual receptivity within the ovarian cycle. Although caution is required in interpreting correlational evidence, these results indicate that penile spines might function to reduce sperm competition risk via a mechanism involving increased or exaggerated copulatory stimulation. Vaginal-cervical stimulation during copulation in mammals has several important reproductive functions, including stimulation of the male to ejaculate, facilitation of sperm transport by the female, and stimulation of ovulation and/or secretion of progesterone via the initiation of complex neuroendocrine reflexes (reviewed in Dewsbury, 1988). Importantly in the present context, studies of diverse species, including both induced and spontaneous ovulators, have shown that vaginal-cervical stimulation also commonly inhibits subsequent female sexual activity (e.g. Goldfoot and Goy, 1970; Carter and Schien, 1971; Hardy and DeBold, 1972; Romano and Benech, 1996; Ramos and deBold, 1999; review in Huck and Lisk, 1986). Hence, if females mate multiply, an effect of copulatory stimulation on oestrus duration is likely to have significant consequences for male fertilisation success (Huck and Lisk, 1986), and males should be selected to increase copulatory stimulation where this leads to a reduction in sperm competition risk.

In addition to potential effects of increased stimulation via neuroendocrine mechanisms, it is also possible that penile spines could affect female remating behaviour by causing short-term local damage to the female genital tract, making continued sexual activity painful or aversive. This effect has previously been suggested to occur in rats, a species with penile spines and multiple intromissions, where oestrus duration was abbreviated following frequent intromissions (Schoot et al., 1992). More severe damage caused to the female reproductive tract by male penile spines has also recently been demonstrated to occur in invertebrates, with resultant long-term fitness consequences for females (Crudgington and Siva Jothy, 2000; see also Johnstone and Keller, 2000). However, selection on males to cause damage to their mates may be more constrained in mammals, where harm caused to the female might ultimately influence survival of the male's offspring. No evidence was found here that male primates with penile spines show increased levels of thrusting during copulation, which might be expected if the spines function primarily to damage the female reproductive tract. Indeed, there is a non-significant trend for thrusting to decrease with increasing penile spinosity in the prosimian and New World primates. It is important to note, however, that ecological factors or constraints are likely to be important in explaining overall patterns of diversity in the copulatory behaviour of male mammals. It is known, for example, that copulatory patterns consisting of prolonged single intromissions are particularly

common among arboreal prosimians and New World monkeys (Dixson, 1991, 1998). Perhaps then, in such species, penile spines might provide an alternative means of increasing copulatory stimulation when thrusting is constrained by ecological or other factors. Alternatively, in these species the spines may be designed primarily to cause minor damage to the female genital tract on with-drawal – they are sharp and often distally pointed (Dixson, 1987a). Whatever the mechanism involved, the relationship between penile spinosity and duration of female sexual receptivity presented here appears worthy of more detailed investigation, both in primates and in other mammalian taxa with penile spines.

In contrast to the results for penile spinosity, no evidence was found for an association between baculum length in primates and the duration of female sexual receptivity within the ovarian cycle. The baculum, or os penis, is found in several mammalian orders including primates, rodents, insectivores, carni-vores and bats (Dixson, 1995, 1998; Hosken *et al.*, 2001). Although its function is uncertain, Dixson (1998) has shown that primates with copulatory patterns involving single prolonged intromissions have significantly longer bacula than those with single or multiple brief intromissions, and are also more likely to maintain intromission into the post-ejaculatory period. Well-developed bacula are also commonly found in primates with dispersed or multi-male mating systems, in which prolonged intromissions may function as a type of mate guarding behaviour by the male (Dixson, 1998). Coupled with the present findings, these results suggest a role in supporting the penis during prolonged intromissions to be a more likely function of the baculum than increasing copulatory stimulation of the female to reduce subsequent sexual receptivity, although other functions are also possible (reviewed in Dixson, 1998; Hosken *et al.*, 2001).

If, as suggested here, penile spines function in some way to limit female remating behaviour, variation in male genital anatomy may have important fitness consequences for females. In general, internal fertilisation offers sig-nificant opportunities for sexual conflict where the reproductive interests of males and females differ (Rice and Holland, 1997), and there is growing evi-dence that costs for females associated with male adaptations to sperm com-petition may often outweigh any potential fitness benefits for their offspring associated with cryptic female choice (e.g. Rice, 1996; Holland and Rice, 1998). Hence, particularly if male copulatory stimulation causes damage to the female reproductive tract, a role for cryptic female choice in the evolution of increased stimulation appears less likely. Furthermore, if multiple mating is beneficial for females in contexts other than promotion of post-copulatory competition, sexual conflict may result from male attempts to restrict female mating be-haviour (review in Stockley, 1997a).

In conclusion, much remains to be discovered concerning mechanisms of male stimulation and female response during copulation, and the ecological

Appendix A.
Species included in the dataset and details of variables used in the analyses

	PS	BD	BL	MBM	FBM	NI	NT	SR	TDOC	MS
Lemuroidea										
Indriidae										
Propithecus verreauxi	3	2	7.6	3.7	3.5	S	40	12–36 h		M
Lemuridae										
Lemur catta	4	3	11.5	2.9	2.5	S	6–35	2–10 h	39	M
Varecia variegata	1		12.3			M?		4–24 h	40	P
Lorisoidea										
Cheirogaleidae										
Cheirogaleus medius	3	5	14.0			S	2–3	1 d	50	D?
Microcebus murinus	3	5	11.0	0.08	0.08	SP		3 d	48–55	D
Galagidae										
Galago senegalensis	5	5	16.7			SP	None	1–3 d	30–37	D
Galagoides demidoff	5	5	13.1	0.06	0.06	SP				D
Otolemur crassicaudatus	4/5	5	22.4	1.51	1.26	SP	5–6	2–10 d	34–44	D
Lorisidae										
Arctocebus calabarensis	4			0.31		SP		Few hours	36–45	D
Perodicticus potto	2	5	21.0	1.02	1.08			2 d	37–38	D
Loris tardigradus	2	5	14.2	0.29	0.26	SP		2 d	29–40	D
Nycticebus concang	2	4		0.68	0.63	SP		1–2.5 d	42	D
Tarsiidae										
Tarsius bancanus	3					S		24 h	24	D
Ceboidea										
Callitrichidae										
Callithrichinae										
Leontopithecus rosalia	2	1	3.0	0.56	0.55	M		3–5 d	14–21	P?
Saguinus oedipus	1	1	1.7	0.50	0.51	S	3–20	23 d	23	M
Callithrix jacchus	1/3	1	2.0	0.31	0.29	S	7–10	15–17 d	15–17	P
Atelidae										
Atelinae										
Aloutta	1	1				M	12	3–4 d	11–24	M

Appendix A. Continued

	PS	BD	BL	MBM	FBM	NI	NT	SR	TDOC	MS
Ateles paniscus	1	1				SP		8–10 d	24–27	M
Lagothrix lagothricha	2	1		6.8	5.8	S			23–36	M
Cebidae										
Cebinae										
Cebus apella	1	2	8.5	2.86	2.1	M		5–6 d	16–20	M
Saimiri sciureus	2/3	3		0.75	0.58	S/M	1–15	1h–2 d	7–25	M
Aotinae										
Aotus trivirgatus	1	1	2.2			S	3–4	16 d	16	P
Cercopithecoidea Cercopithecidae Cercopithecinae										
Erythrocebus patas	1	3	15.8	10.0	5.6	M	10	12 d	32	S,M
Miopithecus talapoin	1	3	9.5	1.4	1.1	S		11 d	33	M
Cercopithecus aethiops	1	3	16.5	4.75	3.56	S	9.5	7–13 d	33	M
Cercopithecus mitis	1	3	16.3	7.6	4.4	M		4–5 d	30	S,M
Macaca sylvanus	1/1.5	3		11.2	10.0	S		14 d	31	M
M. sinica	1/1.5	4	20.0	6.5	3.4	S		14 d	29	M
M. radiata	1/1.5	4		6.6	3.7	S	14–23	5 d	25–36	M
M. silenus	1/1.5	3		6.8	5.0	M		18 d	40	M,S
M. nemestrina	1/1.5	3	21.7	10.4	7.8	M	12	13 d	32	M
M. fascicularis	1/1.5	3	13.1	5.9	4.1	M	4–29	15 d	31	M
M. mulatta	1/1.5	3	17.0	11.2	8.2	M	1–15	9 d	29	M
M. arctoides	1.5/3	5	53.1			SP	1–170	31 d	31	M
M. fuscata	1/1.5	3	19.0	11.7	9.1	M	1–8	11 d	28	
M. nigra	1/1.5	3	23.8			M		9 d	34	M
M. maurus	1/1.5	3						15 d		M
Cercocebus spp	1	3				M		5 d	30–32	M
Papio anubis	1	3	30.0	21.0	12.0	S	6	15–20 d	31–35	M
P. hamadryas	1	3	21.6	21.5	9.4	M		5 d	31–35	S
Theropithecus gelada	1	3	26.0	20.5	13.6	S	14	9 d	35	S

Appendix A. Continued

	PS	BD	BL	MBM	FBM	NI	NT	SR	TDOC	MS
Colobinae										
Colobus badius	1	3		10.5	5.8	M				M
Presbytis entellus	1			18.4	11.4	M		6 d	27	S,M
Hominoidea Hylobatidae										
Hylobates lar	3	2	8.5	5.7	5.3	S	30	Several days	30	P
Pongidae Ponginae										
Pongo pygmaeus	1	3	13.5	70	37	SP		31 d[a]	31	D
Paninae										
Gorilla gorilla	1	2	12.6	205	105	S		3–4 d	31	S
Pan troglodytes	1	1	6.9	41.6	31.1	S	3–30	14 d	37	M
P. paniscus	1	1	8.5	45.0	33.2	S	2–54	15 d	28–37	M
Hominidae										
Homo sapiens	1		–	75	52	S		28 d	28	S

Penile spinosity scores (PS: 1 – no spines, 5 – highly spinous); baculum development (BD; 1 – least development, 5 – maximum development), baculum length (mm) (BL); male body mass kg (MBM); female body mass kg (FBM); number of intromissions per copulation (NI: single (S), single prolonged (SP), multiple (M); number of thrusts per intromission (NT); duration of female sexual receptivity in the ovarian cycle (SR); total duration of ovarian cycle, days (TDOC); and mating system (MS: dispersed (D), multi-male (M), single-male (M), single-male (S) and paired (P). Sources are listed in the methods section.
[a] Forcible matings may occur through cycle.

and phylogenetic constraints involved in the evolution of penile morphology and copulatory behaviour. Results of the present study suggest that more direct tests of patterns of stimulation and response, and the mechanisms underlying them, would offer significant potential to advance current understanding of mammalian reproductive diversity.

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