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Sexual dimorphism of body size in an African fossil ape, *Nacholapithecus kerioi*

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ABSTRACT

Sexual size dimorphism in the African fossil ape *Proconsul nyanzae* (18 million years ago, 18 Ma) has been previously documented. However, additional evidence for sexual dimorphism in Miocene hominoids can provide great insight into the history of extant hominoid mating systems. The present study focused on body mass (BM) sexual dimorphism in *Nacholapithecus kerioi* from the Middle Miocene (16–15 Ma) in Africa. Bootstrap analysis revealed that *P. nyanzae* BM sexual dimorphism was lower than that in *Pan troglodytes*, which exhibits moderate sexual dimorphism, as reported previously. The same simulation revealed that BM sexual dimorphism of *N. kerioi* was comparable with that in *Gorilla* spp.; i.e., the males were approximately twice as large as the females. High sexual dimorphism in extant apes is usually indicative of a polygynous social structure (gorilla) or solitary/fission-fusion social system (orangutan). However, because of the high proportion of adult males in this fossil assemblage, the magnitude of dimorphism inferred here cannot be associated with a gorilla-like polygynous or oranguran-like solitary/fission-fusion social structure, and may reflect either taphonomic bias, or some other social structure. Extant hominoids have a long evolutionary history owing to their deep branching, comprising only a few existing members of the original highly successful group. Therefore, it is not surprising that the mating systems of extant hominoids fail to provide fossil apes with a perfect "model". The mating systems of extinct hominoids may have been more diverse than those of extant apes.

1. Introduction

Among extant primate groups, hominoids are unusual in having highly diverse social structures despite a limited number of species. Hylobatids are monogamous (single-male single-female: Tenaza, 1975; Mitani, 1984, 1987; Palombit, 1996; Brockelman et al., 1998; Bartlett, 2008); chimpanzees and bonobos are polygynandrous (multi-male multi-female: Goodall, 1986; Fleagle, 1999; Nishida, 2011); orangutans have a (semi-) solitary social system (territory of one male covers that of several females) or fission-fusion society (Galdikas, 1985, 1988; van Schaik, 1999; Delgado and van Schaik, 2000; Setia et al., 2009; Singleton et al., 2009); gorillas are usually polygynous (single-male multi-female), but groups of mountain gorillas frequently include more than two silverbacks in Bwindi and Virungas, Congo (Yamagiwa, 1987; Yamagiwa et al., 1993, 2009;

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McNeilage et al., 2001; Parnell, 2002; Kalpers et al., 2003), similar to a polygynandrous group. The evolutionary history of the social structure in hominoids is of particular interest with regard to the origin of pair-bonding mating systems and cooperative breeding in humans.

BM (body mass) and canine size sexual dimorphism are the most common traits used to infer the mating system of fossil primates. In living primates, correlations between these measures and the intensity of male–male aggression for mating have been studied extensively, and primate species with high levels of male–male competition, with a marked dominance hierarchy or unequal breeding access among the males, generally show a high degree of sexual dimorphism in BM and canine size (Clutton-Brock et al., 1977; Leutenegger and Kelley, 1977; Harvey et al., 1978; Leutenegger and Cheverud, 1982; Gaulin and Sailer, 1984; Plavcan and van Schaik, 1992; Leigh and Shea, 1995; Mitani et al., 1996; Plavcan and van Schaik, 1997; Plavcan, 2001; Smith and Cheverud, 2002; Leigh et al., 2005; Plavcan, 2011, 2012; Grueter et al., 2012). Among living apes, sexual differences in BM and canine size are the lowest in hylobatids, followed by chimpanzees and bonobos, and highest in orangutans and gorillas (Table 1).

Sexual dimorphism of BM and canine size is actually influenced by multiple factors in addition to social structure, such as predation, substrate preference, phylogeny, reproductive strategy, foraging, and diet (Leutenegger and Kelley, 1977; Leutenegger and Cheverud, 1982; Gaulin and Sailer, 1984; Plavcan and van Schaik, 1992; Plavcan, 2001, 2011, 2012). For example, terrestrial primates are generally more dimorphic than closely related arboreal species, which has been explained as a consequence of selection for larger male size associated with male predation-defence (Clutton-Brock et al., 1977; Harvey et al., 1978; Leutenegger and Cheverud, 1982; Cheverud et al., 1985; Plavcan and van Schaik, 1997). Females are generally more responsive to nutritional resource insufficiency than males owing to the higher energetic burden of reproduction (Ralls, 1976; Emlen and Oring, 1977; Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Mitchell et al., 1991; van Hooff and van Schaik, 1992; Isbell and Pruetz, 1998) and such pressure would also influence female body size evolution (Gordon, 2004). Since the major function of canines is generally weaponry in most primates, it is possible that canine size is influenced by selection for protection against predators, in addition to mating competition (Leutenegger and Kelley, 1977; Harvey et al., 1978; Leutenegger and Cheverud, 1982; Plavcan and van Schaik, 1992, 1997; Kelley, 1995b; Plavcan, 2001).

Many studies have attempted to clarify the mating system of fossil apes and their evolutionary implications on the basis of sexually dimorphic skeletal traits. Since teeth are comparatively abundant in the primate fossil record, canines are the preferred material for this purpose: *Proconsul* (or *Ekembo*) (Greenfield, 1972; Kelley and Pilbeam, 1986; Pickford, 1986; Kelley, 1986a, 1995a, 1986b; Teaford et al., 1988; Cameron, 1991; Walker et al., 1993), *Nacholapithecus* (Ishida et al., 1991), *Sivapithecus* (Kay, 1982; Wu and Oxnard, 1983a, 1983b; Kelley, 1988, 1995a; Scott et al., 2009), *Lufengpithecus* (Kelley and Pilbeam, 1986; Wu and Wang, 1987; Kelley and Etler, 1989; Kelley and Xu, 1991; Kelley, 1993, 1995a; Kelley and Plavcan, 1998; Scott et al., 2009) and *Ouranopithecus* (Kelley, 1995a; Schrein, 2006; Scott et al., 2009; Koufos et al., 2016). Among these fossil apes, *Proconsul* has been most extensively studied in this regard. Kelley (1986a, 1986b) demonstrated that sexual dimorphism of canine size (crown height and basal crown area) in *Proconsul nyanzae* was comparable to or beyond that of *Gorilla* spp. (Table 1). However, some *Proconsul heseloni* canine specimens used in Kelley's analysis (see Walker et al., 1993) were misclassified as *P. nyanzae* and, therefore, canine dimorphism was exaggerated. Nevertheless, a recent revision supported very strong canine sexual dimorphism in *P. nyanzae* (Pickford et al., 2009).

Use of only canine size to characterize dimorphism to infer social or mating systems for a species may be misleading. For example, Pitheciinae have large and laterally splayed canines, which, together with procumbent incisors, are used to puncture the pericarp of hard fruits (Kinzey, 1992; Martin et al., 2003). Pithecine-like dental features in the middle Miocene *Afropithecus* and *Equatorius* have been explained as an adaptation for sclerocarpic feeding (McCrossin, 1994; Leakey and Walker, 1997; Palmer et al., 1999;

Table 1

Ratios of male to female in African Miocene hominoids, extant apes, highly sexual size dimorphic cercopithecines, and colobines; body mass and the canine size in maxilla and mandible. Basal area is the product of mesiodistal length and buccolingual breadth.

Species	Body mass[a]	Maxilla		Mandible	
		Crown height[d]	Basal area[g]	Crown height[d]	Basal area[g]
Nacholapithecus kerioi	2.0–2.1[b]	1.6[e]	2.3[e]	1.5[e]	2.5[e]
Proconsul nyanzae	1.4[c]	1.8[f]	2.1[f]–2.2[h]	1.5[f]	2.0[f]–2.3[h]
Proconsul heseloni			1.9[h]		1.8[h]
Gorilla spp.	1.7–2.5	1.7	2	1.6	2
Pongo spp.	1.9–2.3	1.7	1.6–1.8	1.5–1.6	1.5–1.8
Pan paniscus	1.2–1.3	1.4	1.6	1.3	1.3–1.7
Pan troglodytes	1.1–1.3	1.4	1.5–1.6	1.3	1.5–1.6
Hylobates spp.	1.0–1.1	1.0–1.2	1.1–1.2	1.0–1.2	1.1–1.2
Papio cynocephalus	1.8–1.9	2.9	2.6	2.3	2.4
Papio hamadryas	1.7–2.3	2.7	2.6	2.2	2.7
Mandrillus sphinx	2.2–2.9	5.2	5.6	3.3	5
Nasalis larvatus	2.0–2.1	2.2	1.7	1.9	1.4
Colobus guereza	1.2–1.3	1.5	1.3	1.4	1.3
Colobus polykomos	1.2–1.3	1.8	1.2–1.7	1.7	1.2–1.6
Procolobus verus	1.1	2.0	1.7	1.8	1.7
Pliocolobus badius	1.0–1.4	1.9	1.5–1.9	1.7	1.6–2.1

[a] Extant species data from Ruff (2003), Delson et al. (2000), Plavcan (1990) and Smith and Jungers (1997).

[b] Male-mean/female-mean was calculated (Table 2).

[c] Calculated by the median values of 35–38 kg in estimated males and 26–28 kg in estimated females (Ruff et al., 1989).

[d] Extant species data from Plavcan (1990).

[e] Ishida et al. (1991).

[f] Kelley (1986a,b).

[g] Extant species data from Plavcan (1990), Mahler (1973), and Swindler (2002).

[h] Pickford et al. (2009)

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