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The orang-utan mating system and the unflanged male: A product of increased food stress during the late Miocene and Pliocene?

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Abstract

The orang-utan is unique among apes in having an unusually long male developmental period and two distinct adult male morphs (flanged and unflanged), which generally, but not exclusively, employ different reproductive strategies (call-and-wait vs. sneak-and-rape). Both morphs have recently been shown to have roughly similar levels of reproductive success in the one site where such a study has been conducted. This is in stark contrast to the unimale polygynous gorilla, in which dominant males sire almost all infants. Despite this, evidence on sexual dimorphism, life history, diet, and socioecology of extant and extinct apes, as well as the ontogeny, reproductive morphology, and physiology of extant apes, all indicate that the orang-utan's present-day mating system most likely evolved from a gorilla-like base, with one dominant male guarding a harem of females. The available evidence indicates that, due chiefly to the likely onset of the El Niño Southern Oscillation (generally regarded as the trigger for mast fruiting in dipterocarps) approximately 3–5 Ma, southeast Asian forests would have begun to experience longer and more severe periods of low food availability. This change in food availability would have meant that full-time gregariousness was no longer energetically tolerable and, as a result, females dispersed more widely in search of food and adult/flanged males were no longer able to effectively guard a harem of females. A niche for a quiet, quick, opportunistic "sexual predator" (i.e., the unflanged male) then became available. This finding implies that, despite being anatomically quite chimpanzee-like, the ancestral hominoid probably had a social and mating system more similar to the gorilla than any other living ape.

Keywords: Orang-utan; Male bimaturism; Sexual dimorphism; Mating systems; Paleoclimate; Sociality

Introduction

The orang-utan (*Pongo* spp.) male is unusual in having two distinct adult morphs, which generally, but not exclusively, pursue two distinct reproductive strategies (Galdikas, 1981, 1985; Rodman and Mitani, 1987; Kingsley, 1988; Maggioncalda et al., 1999; Maggioncalda et al., 2000; Maggioncalda et al., 2002; Utami et al., 2002), depicted in Fig. 1. Flanged males possess large cheek pads, a large throat sac, are twice the size of unflanged males, and produce loud "long calls" to advertise their presence (Rodman, 1973; MacKinnon, 1974; Rijksen, 1978). Unflanged males are about the same size as females, lack the secondary sexual characteristics possessed by flanged males (Galdikas, 1985; Kingsley, 1988) and, until recently, were thought to have limited reproductive success.

These physical differences are largely paralleled by differences in the two morphs' reproductive strategies. Flanged males are considered to be the preferred mate choice (Galdikas, 1985; Schurmann and van Hooff, 1986; Nadler, 1988; van Schaik and van Hooff, 1996), with many researchers suggesting that females seek out the dominant male when they are most fertile (Galdikas, 1981; Delgado and van Schaik, 2000; Utami et al., 2002). This is supported by Delgado's (2003) playback experiments, which indicate that females approach long-calling dominant males. Correspondingly, most matings involving flanged males are cooperative (Schurmann and van

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Fig. 1. (a) Flanged and (b) unflanged male Bornean orang-utans. Note the flanged male's cheek pads, throat sac, large body size, and long hair at the base of the back. These features are absent in the unflanged male. Photographs by A. Gibson (1a) and H. Morrogh-Bernard (1b).

Hooff, 1986; Fox, 1998), whereas most matings involving unflanged males are forced (MacKinnon, 1974; Galdikas, 1985; Mitani, 1985a). While the proportion of cooperative and forced matings involving the two different morphs varies between sites (being twice as high in Borneo relative to Sumatra; Delgado and van Schaik, 2000), there is universal agreement that unflanged males engage in more forced and less cooperative matings than flanged males. Flanged males do not tolerate other flanged males in the area and long call regularly to ward them off (Mitani, 1985b). Encounters between flanged males are always aggressive, with the loser fleeing (Rijksen, 1978; Mitani, 1985a; Rodman and Mitani, 1987). In contrast, unflanged males are generally quite tolerant towards one another (Galdikas, 1985; van Schaik, 2004). This type of social system has been termed "roving male polygyny" (van Schaik and van Hooff, 1996) or "dispersed harem polygyny" (Maggioncalda et al., 2002), and it creates a selective pressure for alternative mating strategies among subordinate (i.e., unflanged) males (Maggioncalda et al., 2002). Unflanged males also suffer little energetically from association compared to flanged males (Mitani, 1989), allowing them to spend more time in association with females (Galdikas, 1985). It has even been suggested that females may seek out flanged males for protection from harassment by unflanged males (Fox, 2002).

In captivity, all male orang-utans eventually develop into flanged males and it is believed that this is also true in the wild (Kingsley, 1988; Delgado and van Schaik, 2000). Like gorillas (*Gorilla gorilla*), the switch from the undeveloped (i.e., unflanged) to the developed (i.e., flanged) state in orang-utans is irreversible (Utami Atmoko and van Hooff, 2004). Orang-utans are unusual, however, in that males can arrest their development for a variable period between one and twenty-five years of age (Galdikas, 1985; te Boekhorst et al., 1990; van Schaik, 2004; Wich et al., 2004b), which probably depends on the presence or absence of flanged males in the area (Maggioncalda et al., 1999). After this period of arrest, male orang-utans then develop rapidly into flanged males, often within the space of a year (Brandes, 1939; Ulmer, 1958; M.E. Harrison, pers. obs.). One hypothesis, which remains untested, is that unflanged males monitor the presence of flanged males in the area by listening to their long calls, allowing them to continue their development when the chances of becoming dominant are higher (Maggioncalda et al., 1999). Although unflanged males possess insufficient concentrations of testosterone, luteinizing hormone, and dihydrotestosterone for the development of secondary sexual characteristics, concentrations are sufficient for the development of functional testes and fertility (Maggioncalda et al., 1999). Analysis of testes size in flanged and unflanged males supports this (Dahl et al., 1993).

Moreover, recent genetic analyses have shown that, in a population of Sumatran orang-utans (*Pongo abelii*), unflanged males fathered 6 out of 10 offspring born over a 15-year period for which paternity could be determined (Utami et al., 2002), although it should be noted that four of these unflanged male conceptions occurred during a period of instability in male rank when dominant males were not present. The absence of dominant males in this study may not actually be that rare an event—studies in Tanjung Putting (Galdikas, 1979, 1981), Kutai (Mitani, 1985a), and Suaq Balimbing (Singleton and van Schaik, 2001) all report that the only resident/frequently present flanged male was the dominant male. Should he die or leave the area for whatever reason, it is likely that a period of time where no dominant flanged male is resident will follow. This could happen quite regularly if no flanged male is obviously stronger than the