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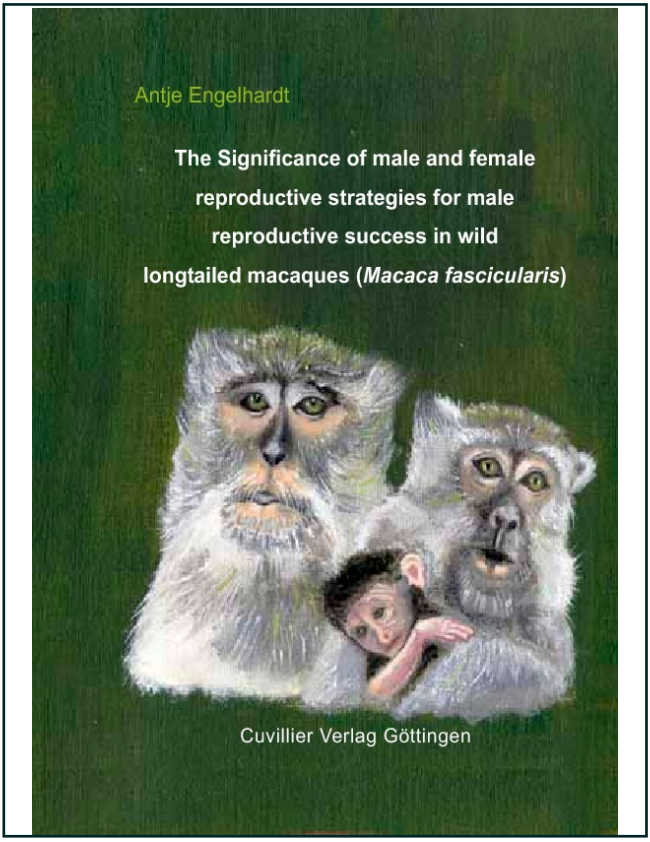
The significance of male and female reproductive strategies for male reproductive success in wild longtailed macaques (Macaca fascicularis)



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Preface

When intending to study aspects of sexual selection, there are many difficulties when choosing primates as model species: limited sample sizes due to small groups, difficulties to measure lifetime reproductive success due to longevity, a slow reproductive rate and ethical constraints on experimental manipulations limit primatological studies and generalization of results deriving from these. This probably explains why there still remains a big gap of knowledge concerning basic questions of primate sexual selection, whereas a number of extensive studies in this field have been conducted on other species by ornithologists, ichthyologists and entomologists (reviewed in Andersson 1994).

Nevertheless, since primates share a unique mixture of specific characteristics not found in other mammalian taxa and, moreover, since our own species is part of this taxon, it is sensible to take the challenge to study sexual selection in primates. In particular, the deviation from the general mammalian pattern of oestrus, i.e. the close temporal relation between female willingness to mate (behavioural receptivity) and female ability to conceive (physiological receptivity), in anthropoid primates, suggests that sexual selection may act differently on this phylogenetic group, raising particular attention of primatologists and anthropologists (e.g. Alexander & Noonan 1979; Burley 1979; Hrdy 1979; Manson 1986; Andelman 1987; Schröder 1993; Heistermann et al. 2001). The observation that female behavioural receptivity extends well over the period during which conception can actually take place, has led to numerous speculations about the ultimate causes and consequences of this phenomenon, which I will present in more detail later in the introduction. From a practical point of view, this peculiar pattern has made it difficult to study reproductive processes, and thus aspects of sexual selection, in wild groups, because the period of highest fertility within a female ovarian cycle is no longer indicated by female sexual activity in anthropoid primates. Most investigations, therefore, have for a long time either been carried out on captive primates using invasive techniques for the determination of female reproductive status, or, when conducted in the wild, been limited to behavioural observations due to a lack of appropriate methods to examine other parameters. Though useful, results obtained under artificial conditions are not necessarily transferable to natural situations and explanations of evolutionary processes can hardly be bases on these. However, in most

studies on free-living populations, information on physiological status of female primates could not be gained, so that the timing of reproductive events, such as ovulation and conception, could only be inferred by assumptions. As blood sampling for genetic paternity analysis was not practical under natural conditions either, male mating success was used as a measure of male reproductive success, although both variables need not necessarily be related to each other (Alberts et al. 2003). Hence, results of studies on free-living anthropoid orimates, too, must be assessed with great care.

Recent developments of noninvasive endocrine and genetic analyses, however, have offered new and exciting opportunities to achieve more reliable data on reproductive processes even under natural conditions. The development of genetic paternity based on the use of small amounts of hypervariable DNA (microsatellites) from faecal samples nowadays allows to reliably determine paternity in wild populations and has already been used successfully in recent field studies across all primate taxa (e.g. Constable et al. 1995; *Chlorocebus aethiops*: Newman et al. 2002; *Macaca fuscata*: Inoue & Takenata 1993, Soltis et al. 2001; *Macaca mulatta*: Nürnberg et al. 1998; *Macaca sinica*: Keane et al. 1997; *Papio hamadryas*: Yamane et al. 2003; *Pan paniscus*: Gerloff et al. 1995, 1999; *Pan troglodytes*: Vigilant et al. 2001; *Pongo pygmaeus*: Immel et al. 1999, Utami et al. 2002; *Trachypithecus entellus*: Launhardt et al. 2001). Hormone analyses from faecal samples even make it possible to distinguish the component phases of a female's ovarian cycle, particularly, ovulation and conception (Shideler et al. 1993; Whitten & Russell 1996; Heistermann et al. 1993, 1995, 1996). Recent investigations have clearly shown that faecal samples provide a valuable source for endocrine assessment of both female and male reproductive status in free-living primate populations (e.g. Wasser 1996; Brockman et al. 1998; Strier et al. 1999; Ziegler et al. 1998; Kraus et al. 1999, Heistermann et al. 2001, Deschner et al. 2003).

The aim of my thesis was, therefore, to combine detailed behavioural observations with modern non-invasive techniques of endocrine and genetic analysis in order to investigate male and female reproductive strategies and the factors determining paternity in multimale primate groups, using the long-tailed macaque (*Macaca fascicularis*) as the model species. Although it is clear that a short-term study on a single species cannot illuminate all aspects of this topic, the information obtained in this thesis will hopefully add to a better understanding of the proximate mechanisms regulating male reproductive success in primate groups with a multimale mating system and, as such, help to extend our knowledge about the effect of sexual selection on primate social systems.