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Seasonal and social influences on fecal androgen and glucocorticoid excretion in wild male long-tailed macaques (*Macaca fascicularis*)

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ABSTRACT

Whereas it is well known that in strictly seasonal breeding primates (income breeders), alike other vertebrates, males show pronounced changes in testicular and adrenal hormone levels concurrent with reproductive activity, hormonal patterns in males of non-strictly seasonal breeding primate species (capital breeders) and their relation to seasonal and social correlates remain largely unknown. In the present study, we examined the annual pattern of fecal androgen and glucocorticoid excretion and their relationship to environmental (rainfall, temperature) and social factors (number of cycling females, male aggression and copulation rates, male dominance rank) in a group of wild long-tailed macaques (*Macaca fascicularis*), a species with a moderate degree of reproductive seasonality and classified as capital breeder. The study was carried out in the Gunung Leuser National Park, North Sumatra, Indonesia over a period of ten months encompassing the conception and the birth season. Our results show that male long-tailed macaques exhibit a distinct annual variation in both androgen and glucocorticoid levels. Androgen (but not glucocorticoid) levels were significantly elevated during the conception period in association with elevated rates of male–male aggression and copulatory activity, both strongly related to the number of cycling females in the group. Neither glucocorticoid nor androgen levels were related to male dominance rank or to the environmental parameters investigated. Interestingly, levels of both hormones started to increase in the late birth season and thus 1–2 months prior to the mating season, suggesting that male long-tailed macaques go through pre-breeding hormonal changes in preparation for prospective challenges. Our data thus provide the first evidence that males of a non-strictly seasonal breeding species/capital breeder show endocrine patterns generally similar to those found in strictly seasonal/income breeders.

1. Introduction

For males, the mating season is a particularly challenging period in which they compete with each other for access to sexually receptive females. In order to cope with the increased physical and energetic demands of male–male competition at this time, male vertebrates often undergo pronounced changes in body mass and physiology concurrent with changes in reproductive activity (e.g. mammals, [1,2]; reptiles, [3]; and amphibians, [4]). Specifically, males of seasonally breeding species often show an increase in body and testes size and a marked rise in testosterone levels during the mating season in association with an increase in aggression rate (e.g. mammals: [5]; birds: [6]; reptiles: [7,8], see also the "challenge hypothesis": [9]). In addition, males of these species often show an elevation in glucocorticoid levels during the mating season (e.g. mammals: [10]; amphibians and reptiles: [8,11]; for a review see [12]), which is typically linked to an increase in aggression rates [13,14] and higher energetic expenditures ("energy mobilization hypothesis": [12]) associated with increased competition for mate acquisition. In many of these species, male physiology during the mating season, however, varies inter-individually and is often influenced by dominance rank (e.g. [10,15,16]).

Seasonal reproductive activity is characteristic of many primate species, although there is large variation, ranging from species that only breed during restricted times of the year with sharply delineated periods of mating (and thus birth) (strictly seasonal breeders, for definition of primate reproductive seasonality see [17]) to a complete non-seasonal reproduction with mating and births being distributed broadly throughout the year ([18,19]). Given that environmental factors (such as photoperiod, climate and diet) as well as social factors (such as degree of male–male competition) are known to modulate male hormone secretion (e.g. [20–22]), it should be expected that primate species differ in their physiological and behavioral response to seasonal changes in environment depending on whether they exhibit a high or low degree of seasonality in breeding. In this respect and in an attempt to further our understanding of seasonality and

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reproductive function in primates, Brockman and van Schaik [23] have developed the concept of "income" vs. "capital" breeders [24] as a framework for explaining patterns of seasonal breeding and the proximate mechanisms regulating them. Accordingly, strictly seasonally breeding species are classified as income breeders, which are expected to rely principally on external cues such as photoperiod and climate to activate reproductive activity, whereas less strictly seasonally (and aseasonally) reproducing capital breeders are expected to rely more on internal factors (e.g. fat stores, energy balance) for regulating onset and acceleration of reproduction. Concerning endocrine responses in males, the model predicts that males of income (strictly seasonal) breeders should show a marked seasonal variation in testosterone levels in response to predominantly external cues. In contrast, males of capital (non-strictly seasonal or aseasonal) breeders are predicted to show less seasonal or no annual variation in testosterone levels. In these species, male endocrine physiology is also expected to respond more to female reproductive state and food abundance, rather than to photoperiod and climate changes.

Predictions made for the impact of season on endocrine patterns in male primates have largely been confirmed for strictly seasonal/income breeders (e.g. rhesus macaques, *Macaca mulatta*: [25]; Japanese macaques, *Macaca fuscata*: [26]; squirrel monkeys, *Saimiri boliviensis*: [27]; tufted capuchin monkeys, *Cebus apella nigritus*: [28], golden lion tamarins, *Leontopithecus rosalia*: [29]; ring-tailed lemurs, *Lemur catta*: [22]; Verreaux's sifakas, *Propithecus verreauxi*: [30,31]; redfronted lemurs, *Eulemur fulvus rufus*: [32,33], lesser mouse lemur, *Microcebus murinus* [34]; and muriqui monkeys, *Brachyteles arachnoides* [35]). Here, the data generally show clear circannual fluctuations in male testosterone and/or cortisol levels with marked elevations of either or both hormones during the mating season in association with heightened male–male aggression and sexual activity (but see [35]). The temporal relationship, magnitude and duration of these changes, however, vary between species. In this respect, in some species, such as the sifaka [30,31,36], squirrel monkey [27], rhesus macaque [25] and Japanese macaque [21,26], male hormonal changes associated with breeding readiness precede the actual onset of the mating season (and thus of reproduction and male–male competition) for up to 3 months. Given the various promoting effects of testosterone and cortisol on bodily functions (e.g. sperm production, development of secondary sexual characters, facilitation of sexual and aggressive behavior, promotion of muscle gain and fat storage [27,37–42]), such an early rise in both sex and adrenal steroids has been attributed to physiological preparations in anticipation of the behavioral and energetic demands of male reproduction [40,43]. The observed time lag between the elevation of hormones and the onset of the breeding season in these species supports the prediction [23] that in income breeders, males rely on external cues when getting prepared for the upcoming reproductive period.

By comparison, the impact of season on male physiology and the relationship between male behavioral patterns and endocrine status are less clear in non-strictly seasonally/capital breeding primate species where the distinction between breeding and non-breeding periods is less extreme and birth can occur year-round. To our knowledge the only studies carried out in this respect so far either found no seasonal variation in male testosterone levels or testicular parameters (stumptailed macaque, *Macaca arctoides*: [44]; Hanuman langur, *Semnopithecus entellus*: Lohiya et al. [45]) or results were inconsistent (long-tailed macaques, *Macaca fascicularis*: [46,47]). Furthermore, all of these studies were conducted in captivity, an environment which has often been demonstrated to substantially influence seasonal effects on reproductive physiology and behavior when compared to the situation in the wild (see [23]). Information on seasonal endocrine patterns in primate males of capital breeders living in the wild under natural ecological and social conditions is conspicuously absent.

Thus, in order to further our understanding on the impact of season on male physiology and the relationship between male endocrine state and reproductive behavior in a wild-living, non-strictly seasonally breeding primate species, we conducted a study on the long-tailed macaque, a species classified by Brockman and van Schaik [23] as capital breeder. Although female long-tailed macaques can conceive year-round [48], birth peaks occur [48–50], the timing of which seems to depend primarily on availability of food [48]. Whether and to what extent such moderate reproductive seasonality is associated with changes in male endocrine status and variation in sexual activity and aggression rate and, assuming endocrine seasonal changes occur, whether these are related to external climatic conditions or are primarily socially mediated is, however, unknown. Studies conducted on males of this species in captivity so far generated inconsistent results, either showing an annual change in male testosterone levels [46] or not [47]. In the present study we therefore set out to examine the following questions under completely natural conditions: (i) what are the endocrine (androgen and glucocorticoid) and behavioral (aggression, sexual activity) changes across seasons in males of a non-strictly seasonal primate, the long-tailed macaque, (ii) what are the temporal relationships involved, (iii) assuming that males show a seasonal variation in endocrine status, what are the cues involved? In this respect and according to Brockman and van Schaik [23] conceptual framework mentioned above, we posed the following predictions: (i) male long-tailed macaques exhibit a seasonal variation in androgen and glucocorticoid levels which should, however, be less pronounced than in income breeders; (ii) endocrine profiles are not related to external factors (e.g. rainfall, temperature) but can be alternatively explained by endogenous factors related to the degree of reproductive competition (number of cycling females, level of male–male aggression, level of sexual behavior). If the latter applies and as postulated by the challenge hypothesis [9], we further predict that (iii) androgen levels are significantly elevated during the period when conceptions occur, the period when male contest for reproduction should be most pronounced and thus (iv) that male aggression and copulation rates are elevated during the conception period and strongly related to the number of cycling females.

Since male endocrine status can significantly be influenced by social status [36,51–54], particularly in a species like the long-tailed macaque where male reproductive success is clearly rank-related and high-ranking males engage heavily in energy-costly mate-guarding of fertile females compared to low-ranking males [49,55], we also investigate the impact of rank on male physiology and predict that high-ranking males exhibit significantly higher androgen and glucocorticoid levels during the conception period.

2. Materials and methods

2.1. Animals and study site

The study was carried out from February to November 2000 on long-tailed macaques living around the Ketambe Research Station (3°41′N, 97°39′E), Gunung Leuser National Park, North Sumatra, Indonesia. The study area consists of primary lowland rainforest and has been described by Rijksen [56] and van Schaik and Mirmanto [57]. The long-tailed macaques in the area have been studied since 1979. In this population, most births occur in the months July to November with the mating season usually starting in December/January [48,58].

We focused on group HA, since it had a size representative for this species out of three groups (HA, HB and HD) originating from a split of one large group (House group) prior to the onset of the study. All group members of group HA were individually known and well habituated to observers. The group consisted of eight adult females, five adult males and several subadults/juveniles and, at the beginning of the study, two infants. Seven infants were conceived between February and June 2000. The home range of group HA overlapped with