



Androgens in a female primate: Relationships with reproductive status, age, dominance rank, fetal sex and secondary sexual color



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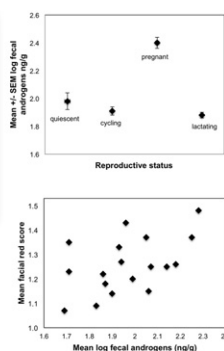
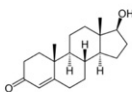
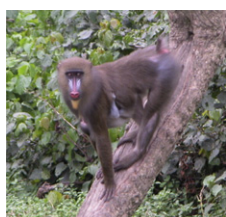
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HIGHLIGHTS

- Far less is known about the biological significance of androgens in females than in males.
- Fecal androgens are not related to rank in female mandrills.
- Readiness to conceive and offspring sex are unrelated to fecal androgens.
- Facial color increases with fecal androgens across females.
- However, the relationship between color and androgens is negative within females.

GRAPHICAL ABSTRACT



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ABSTRACT

A comprehensive understanding of the role of androgens in reproduction, behavior and morphology requires the examination of female, as well as male, hormone profiles. However, we know far less about the biological significance of androgens in females than in males. We investigated the relationships between fecal androgen (immunoreactive testosterone) levels and reproductive status, age, dominance rank, fetal sex and a secondary sexual trait (facial color) in semi-free-ranging female mandrills (*Mandrillus sphinx*), using samples collected from 19 reproductively mature females over 13 months. Fecal androgens varied with reproductive status, being highest during gestation. Fecal androgens began to increase at 3 months of gestation, and peaked at 5 months. This pattern is more similar to that found in a platyrrhine than in other cercopithecine species, suggesting that such patterns are not necessarily phylogenetically constrained. Fecal androgens did not vary systematically with rank, in contrast to the relationship we have reported for male mandrills, and in line with sex differences in how rank is acquired and maintained. Offspring sex was unrelated to fecal androgens, either prior to conception or during gestation, contrasting with studies of other primate species. Mean facial color was positively related to mean fecal androgens across females, reflecting the same relationship in male mandrills. However, the relationship between color and androgens was negative within females. Future studies of the relationship between female androgens and social behavior, reproduction and secondary sexual traits will help to elucidate the factors underlying the similarities and differences found between the sexes and among studies.

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1. Introduction

Androgens are traditionally viewed as male hormones. The effects of androgens on male behavior, morphology and physiology are well studied, including the relationships with the expression of sexual behavior, stereotypically male behaviors such as aggression and display, and the development of secondary sexual characters [23]. Like males, females produce androgens in the gonads and adrenal glands, and the two sexes share many mechanisms of androgenic action [76]. Thus, a comprehensive understanding of the role of androgens in reproduction, behavior and morphology requires the examination of female, as well as male, hormone profiles. However, the biological significance of androgens has received far less attention in females than in males.

Reproductive status is probably the best-documented influence on female androgen levels. For example, testosterone is elevated during gestation in mammals [16,37,49,83], including primates (e.g., [11,30]). Testosterone also rises at ovulation in many mammal species (e.g., [37,49]), suggesting a possible link with sexual behavior and motivation, although this is less well understood [23]. Few studies, however, have investigated patterns of androgens across the conceptive period, gestation and lactation in detail for wild or semi-free-ranging primates [30].

The influence of age on female androgen levels is less well studied than that of reproductive status. In male primates, testosterone begins to increase at reproductive maturity and matches the age-profile of reproduction (e.g., [63]). Testosterone decreases with age in women (*Homo sapiens*, e.g., [22]) and female baboons older than 16 years also had lower testosterone levels than younger females [11].

Dominance rank has important implications for female primates, with higher-ranking females enjoying higher reproductive success than lower-ranking females in many studies (review in [53]). In male primates, androgens increase in the winner of an aggressive encounter, but decrease in the loser (testosterone: [12,59]). If the same is true for females, then higher-ranking females may have higher androgen levels than lower-ranking females. Studies of how testosterone relates to dominance rank among females in group-living primates show mixed findings. Higher-ranking females show higher serum testosterone and androstenedione levels than lower-ranking females in captive talapoin (*Miopithecus talapoin* [8]), fecal testosterone is higher in dominant than in subordinate hybrid baboons (*Papio hamadryas hamadryas* × *Papio hamadryas anubis* [11]), and fecal 17 β -OH-androgens are higher in dominant than in subordinate Barbary macaques (*Macaca sylvanus* [34]). However, there is no relationship between rank and fecal testosterone in female yellow baboons (*Papio cynocephalus* [2]), between rank and fecal and salivary testosterone in ring-tailed lemurs (*Lemur catta* [27]), or between rank and fecal 5 α -androstano-17 α -ol-3-one in bonobos (*Pan paniscus* [60]).

One possible explanation for the differences found across studies in the relationship between female rank and androgens is differences in the exact androgens measured, and in how androgens are metabolized and excreted [46]. However, species differences in how rank is attained, and maintained, may also influence the relationship between rank and androgens. Where male primates actively contest their rank, androgens are higher in higher-ranking males than in lower-ranking males (e.g., [10,15,61,68]). In contrast, where rank is stable, androgen levels often show no consistent relationship with rank (e.g., [7,15,33]). The same may also be true for females. For example, rank is inherited maternally in yellow baboons [38], where there is no relationship between rank and fecal testosterone, while the hybrid population may have more potential to contest their position, and show a relationship between rank and fecal testosterone [11]. However, ring-tailed lemurs contest their rank position, yet there is no relationship between rank and testosterone, measured either in feces or in urine [27]. Thus, there is as yet no comprehensive understanding of the link between dominance rank and androgens in female primates.

Female androgen levels may also relate to the sex of the offspring, both pre- and post-conception. For example, preconception androgens are higher in females that subsequently bear male offspring than it is in those that subsequently bear females in ibex (*Capra nubiana* [73]), field voles (*Microtus agrestis* [39]), and Barbary macaques (*Macaca sylvanus* [34]), offering a possible mechanism by which females may influence offspring sex [34]. Post-conception, gestational androgens are derived from multiple sources, both maternal (ovaries, corpus luteum, and adrenal glands) and fetal (testes and adrenals) [75]. In rhesus macaques (*Macaca mulatta*) the fetal testes secrete androgens throughout gestation, peaking at days 40–75 (trimesters 1–2) then declining, with another increase around day 140 (trimester 3) [82]. In line with this, females carrying male fetuses have higher androgen levels in some species, including humans (*Homo sapiens* [45]), elephants (*Elephas maximus* [26]), Assamese macaques (*Macaca assamensis* [30]), and yellow baboons [1], although not in others, such as red-fronted lemurs (*Eulemur fulvus* [50]).

Finally, the expression of many secondary sexual traits is related to androgens in males [4], such that these traits act as ‘badges of status’ or signals of competitive ability [58]. Androgen-dependent traits may also signal the ability to withstand the costs of high testosterone to potential mates [28]. Females also possess secondary sexual traits, but these are less understood than those of males [18]. Female traits may represent a by-product, or correlated response, of selection for ornaments in males, particularly where females are muted by comparison to males [20,43,44]. However, they may also have adaptive explanations in their own right, such as a role in contest competition or mate choice [3,18,19]. Studies of the similarities and differences between hormone profiles and secondary sexual traits in males and females can shed light on the evolution of ornaments. Experimental administration of testosterone increases the expression of sexual ornaments in female birds (e.g., [42,56]) and lizards [40,54]. However, such experiments involve androgen levels greater than the levels females naturally experience. Very few studies have examined the relationship between natural variation in androgens and female ornamentation [41,47,48], with none, to our knowledge, in female mammals.

In this study, we investigated the relationships between female androgens and reproductive status, dominance rank, fetal sex and secondary sexual color in mandrills (*Mandrillus sphinx*), a large, group-living, primate found in the rainforests of central Africa [36]. We investigated the correlates of fecal measures of immunoreactive testosterone over 13 months in 19 female mandrills living in a large, semi-free-ranging group in Gabon. As in other non-invasive studies, it is very likely that our testosterone assay cross-reacts with metabolites of dehydroepiandrosterone, so we discuss our results in terms of female androgens, rather than testosterone specifically. Mandrills in our study population breed moderately seasonally, with 63% of peri-ovulatory periods occurring between July and September, and only 6% between December and April [72] and a corresponding birth peak in January to March [66]. Females show inherited, stable dominance relationships, and higher-ranking females have a reproductive advantage relative to lower-ranking females, experiencing their first sexual cycles on average 6 months earlier, giving birth for the first time at a younger age and undergoing shorter inter-birth intervals [62,72]. Like male mandrills, females exhibit bright pink and red facial coloration, which varies extensively between females, and across the female reproductive cycle, peaking post-parturition ([70]). Female coloration is more muted than in adult males, although ranges overlap. Male coloration is linked to fecal testosterone [68], but this relationship has not yet been investigated in females.

Based on the results of previous studies, we predicted that:

1. Reproductive condition would influence female androgen levels, as in other cercopithecines. Specifically, pregnant females would experience higher fecal androgen levels than either cycling or lactating females.
2. Androgen levels would decrease with age, as female baboons show a decrease in fecal testosterone measures with age [11].

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