Physiology & Behavior xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Physiology & Behavior

journal homepage: www.elsevier.com/locate/phb

Androgen correlates of male reproductive effort in wild male long-tailed macaques (*Macaca fascicularis*): A multi-level test of the challenge hypothesis

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HIGHLIGHTS

- We studied social and ecological correlates of male androgen levels in wild macaques.
- Androgen levels rose with seasonal and social short-term reproductive challenges.
- Parity status and dominance rank of guarded females influenced male androgen levels.
- Albeit seasonal variation, high-ranking males had higher androgen levels year round.
- Androgen rise serves to enhance female monopolisation and male dominance tenure.

ARTICLE INFO

Article history:
Received 5 August 2014
Received in revised form 12 January 2015
Accepted 13 January 2015
Available online xxxx

Keywords:
Challenge hypothesis
Mammals
Mate-guarding
Male–male competition
Dominance rank
Female reproductive value

ABSTRACT

The challenge hypothesis (Wingfield et al., 1990) has been broadly utilised as a conceptual framework to study male androgen correlates of reproductive challenges in mammals. These studies mainly assessed male androgen responsiveness to a general degree of challenge over extended periods of time. Short term co-variation between the socio-sexual challenging context and androgen levels remains, however, largely understudied. We thus aim at providing a multi-level test of the challenge hypothesis by investigating the inter- and intra-individual variations in faecal androgen excretion associated to 1) breeding seasonality, 2) dominance rank, 3) mate-guarding activity and 4) value of the guarded female. We studied long-tailed macaques, a species in which males engage in highly challenging monopolisation of females over discreet periods of time. This particularity allows testing specifically the predicted increase from *level B* to *level C* in the challenge hypothesis. The study was carried out during two reproductive seasons on three groups of wild long-tailed macaques. We combined behavioural observations and non-invasive measurements of faecal androgen metabolite (fAM) levels. We found that, as predicted by the challenge hypothesis, male long-tailed macaques respond not only to seasonal but also to short term reproductive challenges by adapting their androgen levels. First, males exhibited a seasonal rise in fAM levels during the mating period which may be triggered by fruit availability as shown by our phenological data. Second, males had increased androgen levels when mate-guarding females and, across mate-guarding periods, males had higher fAM levels when monopolising high-ranking parous females than when monopolising low-ranking ones. Finally, high-ranking males had higher fAM levels than low-ranking males year round. Our study confirms that, in species with a high degree of female monopolisability, androgen may be an important physiological fitness enhancing tool for males by increasing female monopolisation efficiency (in particular with highly valuable females) and helping males to respond to rank take-over challenges.

1. Introduction

In vertebrates, androgens play an important role in priming males for the challenge of male–male competition over access to

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http://dx.doi.org/10.1016/j.physbeh.2015.01.015
0031-9384/

receptive females (reviewed in [1–3]). Androgens mediate muscle mass growth [4,5], enhance muscular performances [6] and allows for immunoredistribution of leucocytes to the periphery to prepare for potential injuries [7]. They also promote spermatogenesis (i.e. activating sperm production and enhancing sperm concentration, [4,8,9]) and are often associated with the expression of male sexual and aggressive behaviours (reviewed in [10,11]). Androgens thus affect a variety of traits that determine male–male competitive ability for successful reproduction and, by influencing male sexual behaviour and the outcome of male–male competition, greatly affects individuals' fitness [12,13]. Therefore, assessing the link between temporal fluctuation in androgen levels and male reproductive behaviours is important to understand the physiological mechanisms regulating male reproductive performance.

The "challenge hypothesis" [10] was proposed to conceptualise the relationship between males' socio-sexual behaviours and their androgen levels. This hypothesis postulates the existence of three levels of circulating androgens [10,14]: *level A*, which is the non-breeding androgen baseline, *level B*, which is the breeding baseline, sufficient for spermatogenesis to proceed and for the expression of sexual behaviours, and *level C*, which is the physiological maximum androgen level that is reached in response to specific social challenges encountered during the breeding period (e.g. male–male aggression, territory defence, female monopolisation).

Initially proposed to explain the seasonal and proximate variations of androgen levels in birds, the challenge hypothesis has meanwhile been tested in a broad range of vertebrate taxa (reviewed in [11]). These studies have largely confirmed the observation made in birds and show that the seasonal increase in androgen levels from *level A* to *level B* occurs in a diverse range of seasonally breeding vertebrates and that this elevation is often associated with an increase in aggression rate (mammals, [15–17], reptiles, [18], for a review on birds see [10, 19]). Furthermore, studies on several fish and bird species confirmed the proposed proximate male androgen responsiveness to specific social challenges (i.e. increase in androgen levels from *level B* to *level C*) using simulated territorial intrusion experiments in the presence of a fertile female [14,20]. In mammals, and in particular in primates, the challenge hypothesis has been utilised as a theoretical framework to study the relationship between male socio-sexual behaviours and androgen levels [16,17,21–23]. From these studies it is known, for example, that in a breeding context (i.e. in the presence of fertile females) primate male androgen levels correlate positively with the rate of inter-group encounters (e.g. white-faced capuchins, *Cebus capucinus* [24]), male–male aggression rates (e.g. long-tailed, *Macaca fascicularis* and Assamese macaques, *M. assamensis* [16,17]), and the occurrence of mate-guarding behaviour (e.g. savannah baboons, *Papio cynocephalus* [23]). Basing their analysis on behavioural and physiological parameters averaged per individual and/or over extended period of time (e.g. 1 month blocks), all of these studies examined male androgen responsiveness to a general degree of challenge. The pattern of intra-individual co-variation between the socio-sexual challenging context and androgen levels on a shorter term, for example daily, basis (i.e. the rise in androgens from *level B* to *level C* according to the challenge hypothesis), however, is so far largely unstudied in mammals.

The timely restricted mate-guarding behaviour seen in many mammalian species may be a very suitable behaviour for testing the androgen rise from *level B* to *level C* predicted by the challenge hypothesis. In primates, mate-guarding is commonly defined as a "close, persistent following of a female by a male that involves exclusion of other males from access to the female" (cf. [25]). It is a highly challenging and costly behaviour for male primates since during mate-guarding, males face a decrease in feeding time [25–29] and an elevation in physiological stress levels [30,31], aggression rates [30,32] and vigilance time [30]. These costs are outweighed by the fact that mate-guarding significantly increases male reproductive success (rhesus macaques, *M. mulatta* [33,34], long-tailed macaques [35,36]; Japanese macaques, *M. fuscata* [28]; mandrills, *Mandrillus sphinx* [37]), and a recent revision of the "challenge hypothesis" predicts a stronger androgen response to challenges associated with high fitness benefits [14]. Since males do not monopolise females continuously during the entire breeding season but mate-guard over discreet periods of a few hours up to a month (reviewed in [38]), this behaviour specifically allows to test the prediction of androgen responsiveness to specific social challenges (i.e. rise from *level B* to *level C*) as postulated by the challenge hypothesis.

Beyond the general difference between mate-guarding and non-mate-guarding periods, the level of challenge can also vary across different mate-guarding periods depending on the value of the mate-guarded female. In primates, the reproductive value of females often varies with dominance and parity status. High-ranking and/or parous females often produce more offspring and offspring of better quality (i.e. more likely to survive until adulthood) than low ranking and/or nulliparous females [39–43]. In turn, males preferentially mate-guard and/or mate with high-ranking parous females than with low-ranking nulliparous ones (e.g. Barbary macaques, *Macaca sylvanus* [44]; long-tailed macaques [35], chimpanzees [45]; mandrills [46]; savannah baboons [47]). In some species, males also exhibit mating preferences towards females with whom they have strong social bonds, independent of female rank, parity or fertility status (e.g. rhesus macaques [48]; Japanese macaques [49]; savannah baboons [47]). This overall mate-choice towards females with higher reproductive and social value can also be expressed at the level of the investment and thoroughness with which males mate-guard the females. In long-tailed macaques, males are more aggressive towards other males when mate-guarding high-ranking females and/or females with whom they have strong social bonds than when mate-guarding other females [50]. This latter example highlights how the level of challenge faced by the male during mate-guarding depends on the value of the female. This thus may add an additional dimension of analysis to the "challenge hypothesis", i.e. androgen responsiveness in relation to differences in the quality of the females being mate-guarded, that remains to be investigated.

In our study we aimed to provide a multi-level test of the challenge hypothesis. Specifically we aimed to investigate the inter- and intra-individual variations in faecal androgen metabolite (fAM) excretion associated to 1) breeding seasonality, 2) male dominance rank, 3) mate-guarding effort and 4) value of the female monopolised. Inter-individual variations refer to variations in fAM levels across individuals, which can be attributed to consistent inter-individual differences in other parameters (e.g. dominance rank). Intra-individual variations refer to variation in fAM levels within the same individual across time in response to specific seasonal and/or social challenges (e.g. mating period, mate-guarding effort). We used long-tailed macaques as a model species. In original primary rainforests, this species lives in medium sized (10–50 individuals) multi-male multi-female groups, which contain around 2–8 adult males and 4–18 adult females [39]. Males leave their natal group as sub-adults to reach maturity in a new group [40]. Overall, males migrate several times during their lifetime, whereas females remain life-long in their natal group where they form matrilines. Long-tailed macaques are non-strictly seasonal breeders, i.e. females can conceive year round [51]. There are nevertheless periods of 4–7 months during which the number of receptive females and subsequent births (in the wild on average 163 days after conception [36]) is increased, the timing of which depends on inter-annual variation in seasonality of fruit abundance [51]. Females undergo 1–3 ovarian cycles before conceiving and are sexually active almost throughout the whole ovarian cycle and additionally during the first and second trimester of pregnancy [36,52]. During both periods of sexual activity, females mate on average once per hour during peak times (i.e. the fertile phase of the ovarian cycle an days 48 to 52 after conception) and with a variety of males, but are also intensively and for a number of subsequent days mate-guarded by specific males [36,52]. During ovarian cycles, only high ranking males (alpha- and beta-males) invest extensively into mate-guarding, and particularly the alpha-male mate-guards females throughout the fertile phase [35,36]. Consequently,

Please cite this article as: C. Girard-Buttoz, et al., Androgen correlates of male reproductive effort in wild male long-tailed macaques (*Macaca fascicularis*): A multi-level test of the challenge hypothesis..., Physiol Behav (2015), http://dx.doi.org/10.1016/j.physbeh.2015.01.015