



Research paper

Age and socially related changes in fecal androgen metabolite concentrations in free-ranging male giraffes

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ABSTRACT

In many mammal species, androgen levels in males are elevated during periods of mating activity, often to facilitate aggressive behavior between males over access to fertile females. However, this pattern might be less obvious in species with a rather low male-male aggression rate, or in those that are not strictly seasonal breeders. A complex social structure, as well as additional social and environmental factors, might add more to the complexity. Here, we applied a non-invasive method to monitor fecal androgen metabolite (fAM) levels in free-ranging giraffe bulls over a period of months to examine longitudinal patterns of androgen metabolite concentrations in relation to observed male sexual behavior in different age classes. Giraffes are non-seasonal breeders, living in a fission–fusion social system and males show a roaming strategy to search for fertile females. Our results show that season has an impact on fAM levels in free-ranging giraffes, with respective steroid concentrations being higher in summer. In the presence of females, fAM levels of bulls are significantly higher compared to when found in all-male groups, with old adult bulls showing the highest fAM levels. In contrast, young adult bulls have overall slightly higher fAM levels compared to old adult bulls when residing in all male groups. Sexual behavior increases fAM levels only in old adult bulls.

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1. Introduction

In many mammal species males undergo morphological changes during their life-history stages and when reaching puberty, the development of secondary sexual characteristics and spermatogenesis start, both of which are predominantly mediated by alterations in androgen concentrations (Saltzman et al., 2011). Further, the display of male sexual behavior is also influenced by the endocrine milieu and in most mammals spermatogenesis and male sexual activity are synchronized (Miles et al., 2007; Park and Rissman, 2011). In some species reproduction is temporarily restricted to a certain time period, often once or twice a year, to ensure that birth takes place at the most favorable time of the year,

mainly when resources are abundant to support lactation and post-weaning growth of the offspring (Revel et al., 2007).

The ‘challenge hypothesis’ predicts that especially seasonal breeding males need to balance their androgen levels between times of increased male-male competition for mating opportunities with associated elevated concentrations of androgens, and times of reduced or non-breeding occurrence, with comparatively low androgen concentrations (Wingfield et al., 1990). Elevated androgen levels are thus limited to a short period of time, as prolonged elevations in sex steroid levels can have compromising effects, including an increased mortality risk due to an overall increase in male-male aggression, which leads to a higher risk of injury (Wingfield et al., 1990). Furthermore, high androgen levels may also lead to suppressed immune function, resulting for example in a potentially higher parasite load, which in turn can have an impact on overall well-being and lifetime reproductive success (‘immunocompetence handicap hypothesis’ Folstad and Karter, 1992; Schuurs and Verheul, 1990).

Abbreviations: fAM, fecal androgen metabolites.

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Such alterations in androgen levels have even been described in non-seasonally breeding species such as chimpanzee (*Pan troglodytes schweinfurthii*), with males showing elevated androgen levels when parous females are present and therefore male-male aggression increases (Muehlenbein et al., 2004; Muller and Wrangham, 2004). Furthermore, a temporal increase in aggression related to male reproductive activity appears to be androgen mediated in African (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) (Ganswindt et al., 2005; Ghosal et al., 2013; Rasmussen et al., 2008).

However, elevations in androgen levels are of course not always primarily linked to male aggression in a reproductive context (Rose et al., 1975). In chacma baboons (*Papio hamadryas ursinus*), males show an increase in androgen levels during important life stages, for example when competing to acquire a higher dominance rank, rather than in a mating situation (Beehner et al., 2006).

However, in species with a rather low male-male aggression rate, diverse results in conjunction with the ‘challenge hypothesis’ have been described, and in a variety of species androgen levels appear to be elevated due to sexual behavior *per se* rather than associated male-male competition. In tufted capuchins (*Cebus apella nigrinus*) e.g. elevated androgen levels have been linked to female consortship rather than to intra-sexual aggressive behavior (Lynch et al., 2002). Despite a breeding season, characterized by synchronized female sexual activity, tufted capuchin monkeys seem to maintain comparable levels of androgens all year round, with the exception of a defined peak during the conception period. Thus, the expression of male sexual behavior and an increase in androgen levels seems socially mediated by higher female sexual activity and not due to increased male-male aggression (Lynch et al., 2002). A similar relationship between androgen levels and sexual activity has been found in the spotted hyena (*Crocuta crocuta*), where males show a low rate of reproductive aggression towards each other and changes in male androgen levels appears to be closely related with the presence of cycling females (Dloniak et al., 2006).

The investigation of the relationship between androgens and male reproductive behavior is a growing field, but the potential role of contributing social and environmental factors are still less understood. This is especially true in species that are not strictly seasonal breeders and live in a complex social structure, respective patterns are difficult to extract, with the influence of extrinsic factors adding to the complexity. One reason why our current knowledge is still limited in this regard might be the result of logistical challenges of longitudinal monitoring of androgen levels in free-ranging populations. In many studies concerning wild animals, it is not possible to collect blood samples on a regular basis, which has resulted in the development of non-invasive methods to collect samples without disturbing the animals under investigation. In this regard, fecal sampling as a non-invasive alternative for hormone monitoring has proven to be most suitable for determining the endocrine milieu in a variety of species (Schwarzenberger, 2007). Feces can be collected easily, animals are usually not disturbed during sample collection, thus sampling is safe and feedback-free due to the absence of capture and handling (Möstl and Palme, 2002). Furthermore blood hormone levels are usually affected by circadian or pulsatile hormone release, whereas fecal steroid concentrations give an overview over the hormone secretion during a longer timeframe and therefore reduces the influence of short-term fluctuations (Möstl and Palme, 2002).

In our study, we frequently collected fecal samples to examine longitudinal patterns of androgen metabolite concentrations for free-ranging male giraffes in relation to observed male sexual behavior for different age classes. Giraffes occur in a highly flexible fission-fusion system which is characterized by the splitting and reunion of subgroups within a population on a daily basis

(Bercovitch and Berry, 2013; Dagg, 2014; Kummer, 1971). Male giraffes assume a more solitary lifestyle once they reach adulthood at an age of about 5 years, and adopt a roaming strategy to search for fertile females (e.g. Dagg, 1971; Pratt and Anderson, 1982). When males encounter cows they start to stimulate the anogenital region of the female to stimulate urination. After the female has urinated, the male tests the urine by taking it into his mouth and displays so called “flehen” behavior (Bercovitch et al., 2006).

Giraffes do not have a strict mating season, but birth peaks within the rainy season have been reported from different locations (e.g. Bercovitch and Berry, 2010; Dagg, 1971; Pratt and Anderson, 1982). It has also been shown that androgen levels in male giraffes are not only age dependent, but also show a seasonal pattern and appear to be linked to sexual activity (Seeber et al., 2013). This seasonal pattern in androgen levels seem to also be influenced by differences in group structure occurrence found between winter and summer months (Wolf et al., 2017, submitted for publication).

2. Material and methods

2.1. Study site and animals

Data collection took place in an approximately 70 km² fenced Game Reserve in Kwazulu-Natal, South Africa. The reserve mainly consists of acacia & marula woodland and mixed acacia woodland, with an average annual rainfall of 400–600 mm, occurring mostly in summer (between September and March) (Shannon et al., 2006). A giraffe population of 80 individuals (27 males, 41 females, and 12 infants of unknown sex) was observed over a period of 12 months (November 2014 – October 2015). Giraffes were individually identified by their unique pelage pattern, and assigned to respective age classes following Langman (1977). Infants are defined as individuals younger than 3 months and still accompanied by their mothers, juveniles younger than 1.5 years, sub-adults up to about 4 years of age, and adult individuals over the age of 4 years. From observations in captive populations male giraffes are assumed to become sexually mature at an age of about three years (Hall-Martin et al., 1978; Reuther, 1961).

Initially, we classified adult bulls into three age classes A, B, and C (Pratt and Anderson, 1982). Class A bulls were the oldest and tallest, with massive muscular on the base of the neck, big ossicones, and well developed bone structure on the forehead as described by Pratt and Anderson (1982). Class B bulls were younger, had less stout neck muscles, and developed bone structure on the forehead, whereas class C show only slight muscular on the neck and no or little additional bone mass on the skull. However, while in our study it was not possible to clearly distinguish between B and C bulls, we subsequently assigned only two age classes, old bulls (Ad1, n = 5) – formerly Class A) and younger bulls (Ad2, n = 6 – formerly class B and C). Subadult and juvenile individuals were categorized as young (n = 8).

2.2. Social and behavioral data

Giraffe groups were categorized either as ‘all-male groups’ (comprising only bulls) or ‘mixed sex groups’ (comprising all groups in which at least one female was present). All-male groups were encountered 75x in winter and 30x in summer, whereas mixed sex groups were observed 147x in winter and 203x in summer (Wolf et al., 2017, submitted for publication).

A male was considered to be sexually active if it emitted any of the following behaviors towards a female: courtship behavior, investigation of the females anogenital region, urine testing, mating and mate guarding (Seeber et al., 2013). Conversely, a bull

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