Androgen levels and female social dominance in *Lemur catta*

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Morphological and behavioural traits which improve agonistic power are subject to intrasexual selection and, at the proximate level, are influenced by circulating androgens. Because intrasexual selection in mammals is more intense among males, they typically dominate females. Female social dominance is therefore unexpected and, indeed, rare. Ring-tailed lemurs (*Lemur catta*) are sexually monomorphic primates in which all adult females dominate all males. The goal of our study was to test the prediction that female dominance in this species is associated with high androgen levels. Using two captive groups, we collected data on agonistic behaviour and non-invasively assessed their androgen concentrations in faeces and saliva by enzyme immunoassay. We found that adult female *L. catta* do not have higher androgen levels than males. However, during the mating season there was a twofold increase in both the androgen levels and conflict rates among females. This seasonal increase in their androgen levels was probably not due to a general increase in ovarian hormone production because those females showing the strongest signs of follicular development tended to have low androgen concentrations. At the individual level neither the individual aggression rates nor the proportion of same-sexed individuals dominated were correlated with their androgen levels. We conclude that female dominance in ring-tailed lemurs is neither based on physical superiority nor on high androgen levels and that it is equally important to study male subordination and prenatal brain priming effects for a complete understanding of this phenomenon.

Keywords: social dominance; sex role reversal; androgens; socioendocrinology; primates

1. INTRODUCTION

Higher potential reproductive rates of male mammals lead to competition for females (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992), which is particularly intense in group-living species where access to several females can be monopolized (Emlen & Oring 1977). The ensuing intrasexual selection favours traits such as size, strength, aggression and the development of weaponry which improve male fighting ability. Sexual dimorphism and male dominance over females are considered as evolutionary by-products of this type of selection (Darwin 1871; Andersson 1994). Accordingly, so-called reversed sexual dimorphism and female dominance, defined as unconditional dominance of all adult females over all adult males, are unexpected and, indeed, rare among mammals (Ralls 1976; Richard 1987; Kappeler 1993; Jolly 1998). The evolutionary causes favouring such sex role reversals remain obscure (Young *et al.* 1990; Tilden & Oftedal 1995; Kappeler 1996a).

Female dominance was first described for ring-tailed lemurs (*Lemur catta*), a group-living primate endemic to Madagascar (Jolly 1966). All adult males of this species exhibit spontaneous submissive behaviour in all behavioural contexts towards all females (Kappeler 1990; Pereira *et al.* 1990; Pereira & Kappeler 1997). Sex has no effect on the dominance relationships among juveniles, but all females begin to dominate all males during puberty in dyadic interactions (Pereira 1993). Female

dominance has since been reported for several other lemur species (Kappeler 1993; Jolly 1998) where it may require female aggression in certain dyads and/or contexts. The spotted hyena (*Crocuta crocuta*) is the only other mammalian species in which adult females generally dominate males (Kruuk 1972; Tilson & Hamilton 1984; Frank 1996), but natal males dominate at least some females of lower ranking matriline (Frank 1986; Frank *et al.* 1989; Holekamp & Smale 1993; Smale *et al.* 1993). Female dominance is coupled with a lack of sexual size dimorphism in both lemurs and spotted hyenas (Hamilton *et al.* 1986; Kappeler 1990) and more or less pronounced masculinization of the female genitals (Matthews 1939; Petter-Rousseaux 1962).

At the proximate level, aggression and dominance in male mammals are often linked to higher levels of androgens, particularly testosterone (Bouissou 1983a; Von Holst 1989; Monaghan & Glickman 1992). However, the endocrinological basis of female dominance is still poorly known. The difference in testosterone concentrations in spotted hyenas between males and females is smaller than in brown (*Hyaena brunnea*) or striped hyenas (*Hyaena hyaena*) (Racey & Skinner 1979). The concentrations of the androgen androstenedione are higher in female spotted hyenas, particularly during the first weeks after birth and have been suggested to play a role in the virilization of females (Glickman *et al.* 1987). Circulating levels of androgens and other reproductive steroids (oestradiol and progesterone) can be strongly reduced by ovariectomy, leading to decreased aggression in females and an increase in aggression by males towards females (Glickman *et al.* 1992).

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Despite the fact that *L. catta* provides the best-known example of unconditional female dominance, the relationships between androgens and behaviour are virtually unstudied in this species. It has only been shown that, as in many other mammals, male testis size and testosterone levels increase over the mating season (Bogart *et al.* 1977; Van Horn 1980) during which there is also intense physical aggression between males. The female androgen levels in this and other lemur species have not yet been studied (but, see Kraus 1997), even though the study of a species where such a sex role reversal has occurred independently from the spotted hyena could help illuminate the general principles governing androgen-behaviour relationships.

In this study, we therefore tested the prediction that, compared to males, female ring-tailed lemurs show elevated androgen levels. We measured their androgen concentrations in faeces and saliva before and during the mating season using non-invasive sampling methods. Hormone measurements in faeces are an established approach to studying the interaction of hormones and behaviour in lemurs (Brockman *et al.* 1998; Cavigelli 1999; Kraus *et al.* 1999). In addition, we examined the relationship between androgen levels and female rank within the female hierarchy, rates of conflicts and rates of aggression, respectively. We complete our analyses of these socioendocrinological traits by also presenting data on male hormonal and reproductive status.

2. MATERIAL AND METHODS

(a) Animals

The study was conducted from August to December 1998 on two captive groups of *L. catta* kept at the Tierpark Hellabrunn, Munich, Germany (group 1: seven adult (less than two years), three subadult (18 months) and one infant (six months) females, and two adult, two subadult and two infant males) and at the Parc Zoologique de Thoiry, France (group 2: five adult, three subadult and two infant females, and 11 adult and three infant males). Group 1 was kept in a large indoor-outdoor run and group 2 was semi-free-ranging in a safari park. Individuals were recognized based on their external characteristics such as tail length, ear notches and facial patterns.

(b) Behavioural observations

Observations of agonistic behaviour were conducted in August (non-mating season) and in October and November (mating season) for more than 200 h by N.v.E. A combination of focal animal and focal behaviour sampling (Altmann 1974) was used to record the frequency and direction of exchanges of aggressive and submissive acts and signals using the definitions provided by Pereira & Kappeler (1997). Only the direction of agonistic interactions was recorded during *ad libitum* observations in group 2. The data on these agonistic interactions were entered into a matrix in order to determine the dominance relationships between dyads. Only decided conflicts, which were defined as interactions in which only one animal exhibited submissive behaviour (see Pereira & Kappeler 1997), were used to calculate a dominance index following Bramblett (1981). This index reflects the proportion of all same-sexed group members dominated by a given individual (see also Bentley-Condit & Smith 1999).

(c) Sample collection and hormone analysis

A total of 568 faecal samples (one to 22 per animal for the non-mating season and two to six per animal for the mating season) and 268 salivary samples (one to eight per animal for the non-mating season and two to four per animal for the mating season) were collected in parallel with the behavioural observations. The faecal samples were collected directly after defecation. The saliva samples were collected by using cotton swabs and salivettes according to the method described by Kirschbaum & Hellhammer (1994). Cotton swabs were tossed in icing sugar and then attached to a piece of wire so that an animal could chew on it from a distance. The moist swab was transferred into the salivette. The samples were collected either in the morning or afternoon and were frozen within 2 h of collection. The possible influences of diurnal changes in their androgen levels were minimized for statistical analysis by using only one mean value per individual based on all morning and afternoon samples collected from an individual during one season.

Following centrifugation, saliva could be taken directly from the salivette for hormone analysis. The faecal samples were freeze-dried, pulverized and 0.04–0.05 g of faecal powder was extracted with 3 ml methanol (80%) according to the method described by Heistermann *et al.* (1995). The extraction efficiency, as determined by the recovery of *ca.* 30,000 cpm ^{14}C -testosterone added to a subset of faecal samples before extraction, was $98.0 \pm 4.3\%$ ($n = 40$).

The faecal and saliva samples were measured for immunoreactive testosterone by microtitreplate enzyme immunoassays following previously established methods (Kraus *et al.* 1999). Two different antisera were used, one of which was purchased from Dr E. Möstl (Veterinary University of Vienna, Austria) and the second (BioClin) from BioClinical Services Ltd (Cardiff, UK). The Möstl antibody was used for the faecal analysis, while the BioClin antiserum was taken for the saliva analysis. Two antisera were chosen as serial dilutions of the faecal extracts and saliva showed a parallel displacement of the testosterone standard only with the use of the respective antiserum. However, the values for samples measured in both assays were highly correlated for both faeces and saliva, indicating that the use of a single assay would have provided qualitatively similar results. The specificities of the two antibodies for various androgens were as follows.

- (i) Möstl: testosterone 100%, 5 α -dihydrotestosterone 23.7%, 5 β -dihydrotestosterone 12.3%, 4-androsten-3 β , 17 β -diol 7.6%, 5 α -androsten-3 α , 17 β -diol 5.5% and five others < 2%.
- (ii) BioClin: testosterone 100%, 5 α -dihydrotestosterone 16.0%, 5 α -androsten-3 α , 17 β -diol 5.8%, 5 α -androsten-3 β , 17 β -diol 3.7% and three others < 0.1%.

The samples were diluted in assay buffer for the hormone assay (for details see Kraus *et al.* 1999) and 50 μl aliquots of standards, controls and unknowns were pipetted in duplicate into the microtitreplate wells. Fifty microlitres biotinylated testosterone label and 50 μl antiserum were added and the plates incubated overnight at 4 °C. Following incubation, the plates were washed four times, 150 μl (20 ng) streptavidin-peroxidase added and the plates incubated in the dark on a shaker at room temperature for 30 min. After a further washing, 150 μl substrate solution was added and the plates incubated in the dark for another 45 min before the reaction was terminated by adding 50 μl of 2 mol l $^{-1}$ H $_2$ SO $_4$ and the absorbance measured at 450 nm. The sensitivity at 90% binding was 0.1 pg per well for

both assays. The intra- and interassay coefficients of variation for the faecal and saliva pool samples were 5.5% ($n = 25$) and 11.0% ($n = 17$) (faeces) and 5.0% ($n = 13$) and 18.6% ($n = 7$) (saliva), respectively.

Individual means were calculated for each animal for a comparison of the faecal and salivary immunoreactive testosterone ('androgen') levels for the two observation periods. The correlation coefficients were significant for both periods (Pearson correlation, non-mating season $n = 36$, $r = 0.4$ and $p < 0.02$ and mating season $n = 36$, $r = 0.72$ and $p < 0.001$). The data are shown in nanograms per gram of dry weight (dw) for faeces and picograms per millilitre for saliva.

(d) Genital status

The reproductive status of females was assessed on a nearly daily basis during the mating season from the appearance of their external genitalia (Jolly 1966). The labia of females turn red during the follicular phase, i.e. when females approach oestrus. The day after oestrus the labia return to their former black appearance (Evans & Goy 1968). Three categories were used for this classification: 'black', 'some red' and 'strongly red'. Thus, although no detailed documentation of individual females' cycles was available, a rough distinction of the three cycle stages was possible by visual inspection of the females' genitalia. One female copulated on the first day of the second observation period and was excluded from these analyses. Male genital status could only be assessed in group 2. Once during the mating season, the maximal length of both testes was measured using callipers and the mean was used to calculate their relative testis sizes by dividing by the grand mean testis length of all males.

3. RESULTS

(a) Differences in the androgen levels between sexes and seasons

We found no evidence of increased androgen levels in adult, female ring-tailed lemurs. The mean androgen concentrations in the faeces were lower in adult females than in males in both seasons (figure 1a). In addition, the mean values for adult females did not differ significantly from those of subadults and infants during the non-mating season (figure 1a). During the mating season, the faecal androgen levels of adult females and those of adult and subadult males increased significantly (figure 1a). These results were confirmed by the analyses of the androgen levels in their saliva (figure 1b). Therefore, in the analyses below (§§ 3(b) and (c)), we only present data on the faecal androgen levels because they can be directly compared with values obtained in other studies.

(b) Aggression, social status and androgens

Quantitative data on agonistic behaviour were only taken for group 1. During the mating season, the conflict rates between the females of that group increased to almost twice the rates observed during the non-mating season (mean hourly rate $\pm$ s.d., non-mating season $3.27 \pm 1.11 \text{ h}^{-1}$ and mating season $5.87 \pm 1.7 \text{ h}^{-1}$) (t -test, d.f. = 6, $t = 3.61$ and $p < 0.05$). This change parallels the twofold increase in their androgen concentrations. To examine possible interrelationships between individual differences in their aggression rates, social status and androgen concentrations, the data for both groups were

Figure 1. Androgen immunoreactivity in different sex and age classes before and during the mating season in (a) faeces and (b) saliva. (a) An ANOVA on the log-transformed values revealed a significant effect of sex ($F_{1,31} = 90$ and $p < 0.001$), age ($F_{2,31} = 36$ and $p < 0.001$) and season ($F_{1,31} = 16$ and $p < 0.001$) and a significant interaction of sex and age ($F_{2,31} = 15$ and $p < 0.001$) for the faecal measurements. Post-hoc analyses using least significant differences (LSD) revealed that the adult females had significantly lower androgen concentrations than the adult males in both seasons (LSD, non-mating $p < 0.001$ and mating $p < 0.001$) and did not differ from those of subadult females and infants during the non-mating season. The androgen concentrations increased during the mating season in adult animals of both sexes and subadult males (LSD, adult females $p < 0.001$, adult males $p < 0.001$ and subadult males $p < 0.001$). (b) The same pattern was found in saliva: there was a significant effect of sex ($F_{1,25} = 42$ and $p < 0.001$) and a significant interaction of sex and season ($F_{1,25} = 5.5$ and $p < 0.05$) and age and season ($F_{2,25} = 4.8$ and $p < 0.05$). Again, adult females had significantly lower androgen concentrations than males in both seasons (LSD, non-mating $p < 0.05$ and mating $p < 0.001$) and the androgen concentrations increased during the mating season only in adult males (LSD, males $p < 0.001$ and females $p = 0.37$).

pooled (where possible) (see §2(b)) and analysed by partial correlations. Neither the individual aggression rates nor dominance indices were correlated with the androgen concentrations within both observation periods

Table 1. *Partial correlations (r) between the aggression rate, rank index and androgen levels for adult females*
(The number of animals is given in parentheses.)

	aggression rate versus rank index (n = 7)		aggression rate versus androgen levels (n = 7)		rank index versus androgen levels (n = 12)	
	r	p	r	p	r	p
non-mating	0.89	0.02	− 0.80	0.06	0.78	0.07
mating	0.95	< 0.01	− 0.44	0.37	0.41	0.41

Figure 2. The androgen concentrations for females in different reproductive states. The faecal androgen immuno-reactivity tended to be lower in females with increased genital activity (Kruskal–Wallis ANOVA, d.f. = 2, $H = 5.6$ and $p = 0.06$).

after controlling for the dominance index and aggression rate, respectively (table 1).

(c) *Reproductive status and androgens*

As an increase in androgen production during the follicular phase is seen in many other mammals, we examined whether the seasonal increase in androgen concentration could be attributed to follicular development. Contrary to our expectations, females whose genital stage indicated follicular development tended to have lower androgen levels than those with little change in the appearance of their genitalia (figure 2). Among males, their dominance rank was negatively correlated with their androgen concentrations during the non-mating season (figure 3*a*), which was due to a single outlier and there was no correlation during the mating season (figure 3*b*). Their rank indices but not androgen concentrations were significantly correlated with their relative testis size (figure 3*c*).

4. DISCUSSION

The most important result of this study is that female ring-tailed lemurs do not have higher androgen levels than males, despite being the dominant sex and showing higher rates of aggression during most times of the year. Androgens are known to be positively related to rates of aggression and dominance status in male mammals

Figure 3. Interrelationships between the rank indices, androgen concentrations and relative testis size. Each point represents the mean of all samples collected for a male for the given period. (a) The rank indices were negatively correlated with the androgen concentrations in the faeces during the non-mating season ($n = 13$, $r = -0.62$ and $p < 0.05$). (b) There was no correlation between the rank indices and androgen concentrations during the mating season ($n = 12$, $r = 0.50$ and $p = 0.10$). (c) Only the rank indices and not the androgen concentrations were correlated with the relative testis size (stepwise forward multiple regression, rank index $b = 0.25 \pm 0.08$ and $p < 0.05$, and androgen concentration $b = 0.00 \pm 0.00$ and n.s.).

(Bouissou 1983*a*; Von Holst 1989; Monaghan & Glickman 1993). The observation that, in many female mammals, including primates, testosterone treatment can lead to higher aggressiveness and dominance rank (Joslyn 1973;

Bouissou 1983*a,b*; Floody 1983) and that high-ranking females can have higher androgen concentrations (Batty *et al.* 1986; Faulkes & Abbott 1997) suggested that female dominance in lemurs may be associated with increased levels of testosterone or other androgens. Even though the ranges of androgen levels in female ring-tailed lemurs appear high in relation to male levels (cf. faeces, women 7–30 ng g⁻¹ and men 25–570 ng g⁻¹ (Sobolik *et al.* 1996), female domestic cat (*Felis catus*) < 0.4 µg g⁻¹ and male domestic cat 400 µg g⁻¹ (Brown *et al.* 1996), female sifaka (*Propithecus verreauxi*) 30–170 ng g⁻¹ and male sifaka 150–6000 ng g⁻¹ (Kraus 1997), and saliva, women 5–30 pg ml⁻¹ and men 50–80 pg ml⁻¹ (Swinkels *et al.* 1992; Granger *et al.* 1999)), our results indicate that quantitative sex differences in their androgen levels are not the main proximate mechanism behind female dominance in ring-tailed lemurs.

Females also have lower circulating testosterone concentrations than males (females 0.5 ng ml⁻¹ and males 2–4 ng ml⁻¹) in spotted hyenas although their androstendione concentrations are clearly higher (Glickman *et al.* 1987, 1992) and the female testosterone levels are also much closer to the male levels than in brown or striped hyenas (females 0.5 ng ml⁻¹ and males 5–20 ng ml⁻¹) (Racey & Skinner 1979). Previous research on this species has identified prenatal hormone effects as a possible mechanism for reconciling the lack of higher female androgen levels with female dominance (Glickman *et al.* 1993). Specifically, large amounts of androstendione produced by pregnant hyenas are converted into testosterone by the placenta which in turn appears responsible for the masculinization of the foetus (Glickman *et al.* 1992; Licht *et al.* 1992; Yalcinkaya *et al.* 1993). More recent work has shown that treatment with anti-androgens or juvenile gonadectomy do not prevent masculinization, indicating that androgen-independent mechanisms must also be involved (Drea *et al.* 1998; Glickman *et al.* 1998; Licht *et al.* 1998). Androgens during early development are responsible for differentiation of the genitals in other mammals and have an organizing effect on the brain which can lead to higher aggressiveness in adult animals without the need for increased androgens (Goy & McEwen 1980; Breedlove 1992; Monaghan & Glickman 1992). Possible prenatal androgen effects as well as studies of androgen receptor densities are therefore a promising area for future research into the proximate basis of female dominance in lemurs.

Even though adult, female ring-tailed lemurs do not exhibit higher androgen levels than males, some of our results indicate that androgens nevertheless affect their aggressive behaviour. Their androgen concentrations increased during the mating season, paralleling the increasing rates of conflicts and targeted aggression. During periods of targeted aggression, (coalitions of) females routinely attack and eventually evict other co-resident females (Vick & Pereira 1989; Pereira 1993). The individual rates of aggression did not correlate with their androgen concentrations, but this is also the case in other species because individuals respond differently to similar circulating concentrations of androgens (Michael *et al.* 1984; Von Holst 1989). Year-round parallel monitoring of changes in aggressiveness, social status and hormone levels should contribute to a better understanding of the role of androgens in female aggression. In particular, we

predict an increase in androgen levels during the birth season, a second period which is characterized by heightened levels of targeted aggression (Pereira 1993).

Social and behavioural mechanisms may also play an important role in generating systems with female dominance. Maternal rank inheritance, active female interventions and coalitions and male dispersal promote the stability of existing dominance relationships in spotted hyenas, including female dominance (Smale *et al.* 1993; Jenks *et al.* 1995). In fact, these behavioural mechanisms are also responsible for exceptions from female dominance in that sons of high-ranking females can sometimes dominate adult females from a lower ranking matriline (Smale *et al.* 1993). In contrast, ring-tailed lemurs do not inherit the rank of their mothers and there are rarely interventions in conflicts in order to support offspring (Pereira 1995; Pereira & Kappeler 1997). In addition, adult males ranking high in the male hierarchy of their natal group become subordinate to pubertal females (Pereira 1995). Thus, neither androgen-dependent behaviours, physical superiority nor social coalitions appear to be proximately responsible for female dominance in ring-tailed lemurs.

The behaviour and physiology of males may therefore hold at least a partial answer to the question of determinants of female dominance (Richard 1987; Kappeler 1992). Spontaneous submission of males in the absence of aggression from females is common among lemurs (Pollock 1979; Kappeler 1993; Pereira 1995). Male ring-tailed lemurs are among the mammals which compete most fiercely for access to females during a short mating season (Jolly 1967), yet they are neither bigger than the females (Kappeler 1991) nor do they have substantially larger canines (Kappeler 1996*b*). Even though males maintain a dominance hierarchy year round (Pereira & Kappeler 1997), their rank was not strongly and consistently related to their androgen concentrations in this study. We could only confirm a previously noted seasonal increase in their androgen levels and found a correlation with their relative testis size during the mating season (see also Brockman *et al.* 1998; Kraus *et al.* 1999). Our sampling schedule was not detailed enough for documenting possible short-term androgen fluctuations as they have been documented in other lemur species (Bogart *et al.* 1977; Aujard & Perret 1998). Indications that the androgen levels in male ring-tailed lemurs are correlated with their aggression rates only during the mating season (S. Cavigelli and M. Pereira, unpublished data) have suggested that ring-tailed lemurs may opportunistically increase their androgen levels and aggression rates which would explain the lack of correlation with rank in our study. Similarly, male baboons exhibited a correlation between steroids and rank only when a challenge was under way in the troop (Sapolsky 1993). In conclusion, these preliminary data from an exceptional species call into question the notion that male dominance is an automatic, passive side-effect of intense reproductive competition among males.

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