

Perineal Swellings: A Social and Endocrine Advantage for Barbary Macaque Females (*Macaca sylvanus*)

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ABSTRACT

*This study focuses the relationship between social rank, intersexual behavior, age, fecal cortisol equivalent excretion rates and perineal swelling size in contraceptive-treated *Macaca sylvanus* females. Behavioral data and fecal samples were collected during a twenty-week period from 24 females. Females were categorized with regard to perineal swelling (enlarged or reduced), and to their dominance rank (high or low); we found that swelling size was not associated with it. However, females with an enlarged perineum received more male grooming interactions, had closer spatial relations to males, and received significantly more interventions from males than did the others. Endocrinologically, females with enlarged swelling showed decreased fecal cortisol equivalent excretion rates. Multiple regression models showed a positive relationship between the extent of the swelling size and grooming, inspection and spatial relation. There was a negative relationship between the extent of swelling size and fecal cortisol equivalents. These results imply that enlarged perineal swellings among implanted Barbary macaque females have a greater impact on intersexual contact and adrenocortical activity than does social rank or age.*

Introduction

During sexually active phases, Old World monkey females frequently exhibit perineal swellings. Most species characterizing females by sexual swelling live in multi-male breeding systems¹. The larg-

est swellings are present in many macaque and baboon species and in apes². Generally, the females develop the swellings during the follicular phase of their reproductive cycle³, suggesting that they are sexual attraction signals⁴. Furthermore, these secondary sex characters

might synchronize the beginning of intersexual reproductive behavior in seasonally breeding species⁵. It has also been suggested that perineal swellings are related to female competition for males^{6,7}.

Whenever females exhibit perineal swellings, intersexual behavior changes. Males tend to develop temporary sexual bonds with females (consortships)^{8,9}, characterized by intersexual grooming and general proximity^{10–13}. Moreover, females initiate more sexual solicitation and copulate at higher frequencies when perineal swellings are largest^{14–16}.

But swellings can also appear during infertile phases. The occurrence of perineal swellings during non-reproductive phases (e.g., gestation and lactation) has been documented in lion-tailed macaques¹⁷, in rhesus macaques¹⁸, in Barbary macaques¹⁹, in sooty magabeys²⁰, and in chimpanzees²¹. The administration of oral contraceptives can also influence the degree of swelling size. In chimpanzees oral contraceptives can abolish the cyclicity of swellings^{22,23}; in contrast, levonorgestrel implanted chimpanzees show cyclic changes of the swelling size²⁴. The reason for perineal swellings during infertile phases in both female groups – untreated ones and those treated with contraceptives – remains unclear.

During their non-sexual phase, we investigated a semi-free ranging group of Barbary macaque females implanted with levonorgestrel (see the section methods). This group was characterized by a within-group variation of swelling sizes. The influence of different swelling sizes on behavioral male/female interactions and possible relationships with the fecal cortisol excretion rates, social rank and age of the focal females was studied. Therefore, our working hypothesis was: if larger swellings enhance intersexual attractiveness²⁵, females with large swellings should have more socio-positive interactions with males and therefore lower

basal cortisol excretion rates. Moreover, the intersexual behavior and the cortisol excretion rates are not related to the social rank and the age of females.

Methods

Subjects

Twenty-four adult Barbary macaque females (from a group of 45 adult females and 31 adult males) were studied for 20 weeks (1995) in Affenberg Salem, Germany. The study was conducted between March and July, during the non-sexual phase of the year. The average focal females' age was 10.5 (± 4.6 SD) years.

All females had been implanted with the contraceptive levonorgestrel (a synthetic progestin) by Norplant (control. no. 100006191; manufactured by Leiras, Turku, Finland) in order to limit population size. The tactile appearance of the sub-dermal implants was soft; the flexible opaque white elastic silicon capsules had a total length about 34 mm, with sealing plugs not less than 1 mm. Hormone column length was 28.5–31.5 mm, with an almost white levonorgestrel powder column. Each column contained 70 mg of the synthetic progestin. The mean release rate was 14 mg/day for each capsule. The capsules maintain effective contraceptive protection for five years. The interindividual range of implantation lies between one and four years.

Recording of data

Behavioral data were recorded using the focal animal observation method²⁶. Each focal observation unit lasted 20 min. The behaviors grooming, aggression and inspection were recorded using the one-zero time sampling method^{27–28}. For determining the right sample interval we examined the percentage difference between the true score (continuous recording) and the time sampled score for these

behaviors²⁹. As a result of this procedure we divided each minute into four 15 s intervals. To allow for variations in activity patterns, observations were conducted daily over three distinct time periods. Each animal was observed 60 times (three times per week); for all focal individuals a total 480 hours.

Five behavioral categories were recorded: (1) males *grooming* females; (2) *aggression*, including male-initiated threats, chases, and attacks with physical contact (grasping, hitting and biting) towards females^{30–31}; (3) *inspection*, defined as sexual interaction – including females' presentation of the anogenital region followed by tactile and/or olfactory inspection by the males; (4) *intervention*, in which males intervened on behalf of focal females during aggressive dyadic encounters between females (recorded *ad libitum*); (5) *spatial relations*, being the duration of relative proximity between a male and a focal female – recorded when they were continuously within 2 m during a 20 min observation session. (During spatial relation no other social interaction took place; feeding behavior was tolerated).

For purposes of analysis we also calculated a *proximity index*, by calculating the recorded frequencies of approaches and departures from focal females by adult males and vice versa within a 2 m region. The index was calculated with the formula³²:

$$(ap_f \times (ap_f + ap_m)^{-1}) \times 100 - (lv_f \times (lv_f + lv_m)^{-1}) \times 100,$$

where *ap* is approach, *lv* is leave, *f* is focal females, and *m* is adult male. The values of the index range from +100% to –100%. A positive index made the focal females responsible for maintaining the proximity, a negative one the males.

Dominance rank

The females' rank was determined during the observation period on the basis of the direction of intrasexual displacements and submissive behavior using the behavioral variables rapid flight and genital presenting in agonistic contexts³³. For each focal animal all dyadic interactions of displacement and submission were calculated with the formula³⁴:

$$displacement \times (displacement + submission)^{-1}.$$

The indices of each focal female with each female of the group were averaged and these characterized its rank index, which varied from 0 to 1. Every female having an average score of more than 0.5 was classified as high ranking. In the observed group, there were 10 high ranking and 14 low ranking females.

Swelling size measurement

A new methodology for measuring the swelling size was developed. Two conditions had to be fulfilled: first, as our interest was to compare the inter-individual dimension of this trait, we could not use established methods categorizing an individual's increasing and decreasing tumescence^{20–22,35,36}; second, as it was not possible to capture the animals, the measurements had to be optical; they were done using video.

Perineal swellings of focal animals were measured weekly – those of the other females in the group monthly – with lateral and posterior video images. As not all video images of each measurement per animal were satisfactory, we could only use 80% of all images for digital analysis. These Hi8 videocamcorder images of the individuals were transferred to hard disk (using the Macintosh software DESKTOP TV 2.1).

The lateral and posterior areas were quantified pixelwise by using the software package IMAGE SXN (Macintosh).

For each animal, we obtained two ratios – the cross section of the swelling to the body surface – once laterally and once posteriorly, per week. The sum of these two ratios was averaged for each individual, expressing the extent of the perineal swelling. The mean ratio sum for individuals with enlarged perineum (Ep) was 32.35 ± 1.37 and for individuals with reduced perineum (Rp) was 16.18 ± 1.10 . We found that the swelling size of every focal female stayed constant during the twenty weeks. The enlarged class included eight females, the reduced class 16. Four of the enlarged females were high-ranking.

Cortisol analysis

As a measure of the adrenocortical activity, we analyzed the cortisol metabolite concentrations from collected fecal samples excreted by focal animals. Once a week, feces were collected from the ground between 1:00 p.m. and 3:00 p.m. right after excretion – afternoon samples being preferred because they were then not mixed with urine – and immediately frozen to -30°C . The analyses were performed with an enzyme immunoassay; 0.5 g feces per sample were extracted with 1.5 mL water and 3 mL methanol. The intra-assay coefficient of variation for pooled samples was 9.4%, and the inter-assay coefficient of variation was 12.4%. To validate the measured cortisol concentrations, a high pressure liquid chromatography was carried out, and the concentrations of immunoreactive materials were measured in each fraction using an enzyme immunoassay for cortisol – showing that two immunoreactive substances had eluted from the column. As described elsewhere³⁷, cortisol itself could not be detected in the fecal samples. The concentrations of these substances were the variable to be analyzed statistically, which we expressed using the term cortisol equivalent. Details of the methodology are described elsewhere^{37,38}.

Statistics

The frequency of each recorded behavioral variable was averaged per individual female. The comparisons between the categories (Hr, Lr, Ep, Rp) were calculated pairwise using a *t* – test for independent samples. The relationship between age, rank and swelling size was calculated using a two-tailed Pearson correlation coefficient *r*. The (correlation) influence of rank, perineal swelling and age on the behavior variables and cortisol equivalent excretion was done using a multiple regression analysis. All values are expressed as means and reported with the standard error of the mean (S.E.M.). All results were classified as statistically significant at 95% confidence level.

Results

No relationship was found between the age, the rank and the swelling size of focal individuals (age/rank, $r = 0.33$, N.S.; age/swelling size, $r = 0.35$, N.S.; rank/swelling size, $r = 0.30$, N.S.). Furthermore, no relationship was detected between the implantation time and the extent of the swelling size ($r = 0.114$; N.S.).

Ep females received more grooming behavior by males and spent more time periods in spatial relation with males (Grooming: Figure 1; Ep vs. Rp, $t = 3.96$, $P < 0.01$; Hr vs. Lr, N. S.; Spatial relation: Ep vs. Rp, $t = 3.97$, $P < 0.01$; Hr vs. Lr, N. S.).

Males intervened more for Ep individuals, but did not discriminate their aggressive behavior between the categories (Intervention: Figure 2; Ep vs. Rp, $t = 4.76$, $P < 0.001$; HR vs. LR, $t = 1.94$, N.S.; Aggression: Ep vs. Rp, $t = 1.08$, N. S.; HR vs. LR, $t = 1.14$, N.S.). Males' sexual interest – expressed as inspection behavior – did not distinguish between females with different swelling size nor between differ-

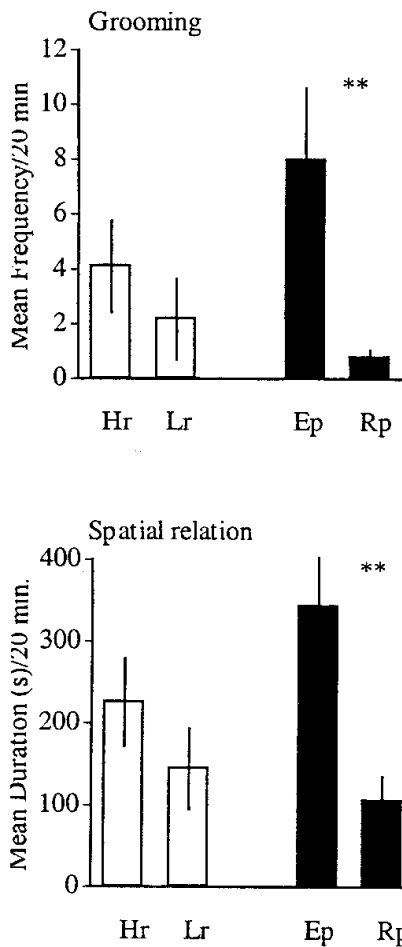


Fig. 1. Open bars: high ranking (Hr) females do not (statistically) elicit more grooming behavior and spatial relation than low ranking (Lr). Solid bars: males groom females with enlarged perineum (Ep) (statistically) more than those with reduced perineum (Rp). (Values are means \pm S.E.M.; independent *t* test; ** $P < 0.01$).

ent rank positions (Ep vs. Rp, $t = 0.11$, N.S.; HR vs. LR, $t = 1.93$, N.S.).

Furthermore, no statistically significant relation was found between who maintained the proximity to males and the categorized focal females (Ep vs. Rp, $t = 1.13$, N.S.; HR vs. LR, $t = 1.01$, N.S.). The fecal cortisol equivalent excretion was significantly decreased in Ep females (Figure 3; Ep vs. Rp, $t = 2.55$, $P < 0.05$; HR vs. LR, N. S.).

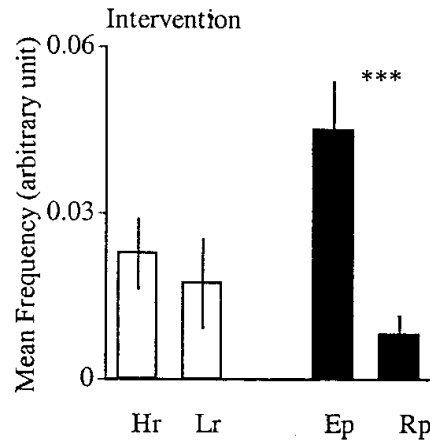


Fig. 2. Open bars: males do not differentiate in their intervention behavior between high (Hr) and low (Lr) ranking females. Solid bars: males do intervene on behalf of females with enlarged perineal swellings (Ep) significantly more than for those with reduced swellings (Rp). (Values are means \pm S.E.M.; independent *t* test; *** $P < 0.001$.) Frequencies were recorded ad libitum (see text).

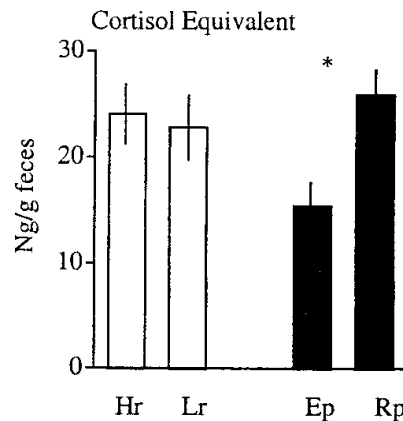


Fig. 3. Open bars: high (Hr) and low (Lr) ranking individuals have no distinctive fecal cortisol equivalent excretions. Solid bars: females with enlarged perineal swellings (Ep) exhibit lower cortisol equivalent excretions than those with reduced swellings (Rp). (Values are means \pm S.E.M.; independent *t* test; * $P < 0.05$).

The multiple regression model in Table 1 showed a positive relationship between the swelling size and the variables grooming ($P < 0.05$) and intervention ($P <$

TABLE I
 MULTIPLE REGRESSION BETWEEN THE INDEPENDENT VARIABLES, AGE, RANK, SWELLING SIZE, AND THE DEPENDENT VARIABLES GROOMING (G), INTERVENTION (I), SPATIAL RELATION (S), CORTISOL EQUIVALENT (C), INSPECTION (IS), AGGRESSION (A), AND THE PROXIMITY INDEX (P).

		age	rank	swelling size
	R ²	b _k	b _k	b _k
g	0.370*	0.129	0.210	0.449*
i	0.428*	0.103	-0.039	0.621**
s	0.506**	0.019	0.236	0.602**
c	0.425*	0.448*	-0.045	-0.653**
is	0.235 N.S.	-	-	-
a	0.288 N.S.	-	-	-
p	0.178 N.S.	-	-	-

* P < 0.05; ** P < 0.01

R² coefficient of multiple determination
 b_k standard partial regression coefficient

0.01). Furthermore, the cortisol equivalent excretion was positively correlated with the individuals age ($P < 0.05$), but negatively with the extent of the swelling size ($P < 0.01$). The dependent variables inspection, aggression and the proximity index showed no relationship to the independent variables, age, rank and swelling size.

Discussion

The data collected in this study shows that females with enlarged perineal swellings have more socio-positive interactions with males, are more supported by males and have lower fecal cortisol equivalent excretion than individuals with reduced expression of this trait. These beneficial aspects take place independently of the female's rank. Furthermore, the swelling size showed neither a significant relation with the female's rank nor her age.

In this population all females had been administered the contraceptive levonorgestrel. Normally, the swelling size increases with increasing levels of estra-

diol during the follicle phase and decreases with increasing levels of progesterone during the luteal phase³⁹. Our data does not clarify whether these enlarged signals are influenced by this treatment or not. The variation of the signal within the population may be compatible with the data found in chimpanzees with orally administered contraceptives, where some individuals exhibited occasional swellings whereas others maintained permanent swellings²³. In contrast, levonorgestrel implanted chimpanzees show cyclic changes in swelling size²⁴. During the virtual breeding season, the implanted females of our study group show more tumescence of the perineum combined with heightened sexual activity (Wallner, pers. obs.). In women, a continuously decreasing release of levonorgestrel into the blood system during the first 18 months was reported by Wyeth Laboratories²⁴. Our initial working hypothesis of a correspondence between the implantation time and the swelling extent is not confirmed by the correlation coefficient. In a study of subdermally levonorgestrel implanted women, Shoupe et al.⁴⁰ reported similar preovulatory serum estradiol peaks in control groups, yet decreased progesterone levels. We suspect that levonorgestrel could influence the secretion patterns of gonadal steroids in our study group in a similar way, possibly acting on individual estradiol/progesterone ratios and resulting, therefore, in different extents of swelling size.

However, these different swelling sizes have an interesting behavioral and physiological impact on females. Ovariectomized *Papio ursinus* females wearing an artificial swelling prosthesis (reproducing a fully swollen female) became more attractive and elicited greater male response to their presenting behavior²⁵. While the frequency of the presenting behavior did not change, the males' response to it did, as evidenced by a daily

occurrence of coagulated seminal emissions. In our study male sexual interest was measured by male inspection of the presented anogenital region (as the only expression of sexuality). We could not detect any difference between enlarged and reduced swollen females or between the different ranks. Our results show greater similarities to Gust's²⁰ findings in sooty mangabeys, where males inspect the perineal area of post-conception swollen females less frequently than during the fertile period.

But males still maintain a social interest in 'attractive females'. In artificial menstrual cycling rhesus monkeys, the expression of partner preferences appeared to be a better predictor for male interest in grooming females than the females' dominance, quite the opposite to male initiated proximity⁴¹. The results presented in this study of male grooming behavior is likewise independent of the females' dominance rank and, moreover, positively related to their swelling size. Furthermore, our findings indicate that the spatial relation between the sexes seems to be also a function of the 'female attractiveness' and not of her rank. The increased grooming interactions and spatial relations of enlarged swollen females can not be equated with the occurrence of these variables, as shown, for example, in baboons outside or during the mating activity^{11,12,42,43}. We could not find a dyadic partner bond or partner preference between enlarged swollen females and males. Eight males performed 60% of the social contacts with these attractive females, the remaining interactions were distributed among all adult males. Our data seems to be compatible with Taub's number of consociations during the sexually active phase of free ranging Barbary macaques⁴⁴. He also found that the estrous females were responsible for terminating the consociations. We note that our calculated proximity index cannot describe a

statistically significant difference in who is maintaining proximity to whom. Accepting Hill's definition³² that the absolute value of the proximity index being less than 10% defines the focal individual, the females in our study that were responsible for maintaining proximity had an index between -10% and zero. Indeed, our results can be interpreted as supporting to Taub's data. Both, the means of low ranking and of enlarged swollen females indicate a male maintaining the proximity. Whereas the latter category seems to be reasonable, the interpretation of males' interest in the low ranking females seems to be difficult to interpret and/or substantiate.

We found that males show no differences in distributed aggression towards the different categories of females. Usually, males tend to attack estrous females more than anestrus ones^{11,45-47}. Dominant rhesus females were also more often attacked by males during artificial menstrual cycles⁴⁸. In the Barbary macaques we have studied, advertising attractiveness outside the mating period does not increase, in any way, male aggressiveness toward the females.

To summarize: the effects of enlarged swellings in terms of socio-positive intersexual interactions seem obvious; moreover, attractive females benefit more, because males intervene more for them. Only the category enlarged swollen females showed decreased fecal cortisol excretion. This latter point should be crucial for the female's condition. The effects of prolonged increases in cortisol levels lead to serious consequences for the organism. Elevated cortisol secretion can interact negatively with numerous systems within the body; for example: the suppression of gonadal functions, the inhibition of the thyroid and growth axis⁴⁹. Glucocorticoids can act negatively on fat tissue catabolism, bone and muscle anabolism⁵⁰ and reduce immunological func-

tions⁵¹. We therefore conclude that attractiveness that is independent of social dominance could be interpreted as a sign of female quality. The positive correlation of cortisol equivalent with age on the one hand contrasts sharply with the negative correlation of cortisol equivalent with the swelling size on the other hand; we infer that this finding corroborates our hypothesis. Although interpretations of the effects of normal aging on the baseline hypothalamic-pituitary-adrenocortical function is controversial in both rats and humans, we point out that in rats a relationship between aging, glucocorticoids and stress has been proposed⁵².

The results of this study can neither explain the inter-individual variance of perineal swellings, nor the physiologically proximate causes for their occurrence during the non-reproductive phase

among implanted Barbary macaque females. But it should be obvious that these perineal swellings are expressed independently of the social rank and the age of the individual and therefore can influence the behavior and physiology in a positive way. Future investigations under semi-free or free conditions with untreated females, exhibiting this signal during the infertile phase could perhaps contribute further clarifications to such questions.

Acknowledgements

We thank W. Angst and A. Paul for their support, J. Kuester for valuable suggestions regarding the disposition of the monkeys, and J. Dittami for valuable discussions. The first author thanks K. Schaefer for sharing this inspiring time.

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OTOK PERINEALNOG TKIVA: SOCIOLOŠKE I ENDOKRINOLOŠKE PREDNOSTI KOD ŽENKI *Macaca sylvanus*

SAŽETAK

Ova se studija usredotočuje na odnos društvenog poretka, ponašanja među spolovima, dobi, ekvivalenta stope ekskrecije fekalnog kortizola i veličine otoka perinealnog tkiva kod ženki *Macaca sylvanus* tretiranih kontraceptivnim sredstvima. Podaci o ponašanju i fekalnim uzorcima sakupljeni su tijekom 20 tjedana i obuhvatili su 24 ženke. Ženke su kategorizirane s obzirom na otok perinealnog tkiva (povećan ili smanjen) i dominantnost (visoka ili niska); pronašli smo kako veličina otoka i dominantnost nisu bili povezani. Međutim, ženke s povećanim perinealnim otokom najviše su privlačile mužjake, imale su bliže prostorne odnose s mužjacima te su imale više odnosa s njima nego druge ženke. Endokrinološki, ženke s povećanim perinealnim otokom imale su niže ekvivalente stope ekskrecije fekalnog kortizola. Modeli multipne regresije pokazali su pozitivan odnos veličine otoka, privlačnosti i prostornih odnosa. Uočen je negativan odnos veličine otoka i ekvivalenta fekalnog kortizola. Navedeni rezultati ukazuju da je povećani otok perinealnog tkiva kod implantiranih ženki *Macaca sylvanus* imao veći utjecaj na kontakt među spolovima i adrenokortikalnu aktivnost nego što to imaju društveni poredak i dob.