

THE FEMALE'S ROLE IN PRIMATE SOCIO-SEXUAL
COMMUNICATION: A STUDY OF THE VERVET MONKEY
(*Cercopithecus aethiops pygerythrus*) AND THE
CHACMA BABOON (*Papio ursinus*)

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ABSTRACT

This thesis is a study of the function of female behaviour and physical appearance, visual or olfactory, in the sexual communication of two species of Cercopithecinae. The vervet monkey, *Cercopithecus aethiops pygerythrus*, does not show appreciable changes in appearance, in relation to the ovarian cycle, nor does it exhibit unequivocal signs of cyclic, hormone-related copulatory activity. In contrast, the chacma baboon, *Papio ursinus*, exhibits a prominent sexual swelling and high levels of copulatory behaviour in relation to ovulation.

To analyse the communication system of the vervet monkey, three experiments were devised. The first experiment assessed the degree of independence, from ovarian hormones, of mating, and of female behaviour (Chapter 2). Oestradiol benzoate and testosterone propionate were administered, one at a time, to ovariectomised females who were pair-tested with males, free and restrained. The treatment of the females with oestradiol resulted in increased copulatory activity and in improved female receptivity. Female proceptive behaviour did not show signs of hormonal dependence.

The second and third experiments (Chapter 3) were devised to investigate further, in different experimental situations, any sensitivity of female proceptive behaviour to oestradiol. The two experiments were also designed to reveal whether the oestrogenic effect on copulation, found in the first experiment, was conveyed by a change in female appearance or by an undetected change in female behaviour. In one experiment, a female, either anhormonal or oestrogen-treated, could choose between a male or a female partner. In the other experiment, the male had a choice between an oestrogen-treated female and an untreated female. The two experiments showed that oestradiol had indeed an effect on female behaviour, reducing latency to choice by the female and increasing

the frequency of presents. The picture that emerged of the communication system of the vervet monkey is one in which female behaviour is the immediate modulator of sexual activity, but behavioural expression of hormonal sensitivity is under social control. Thus, sexual activity appears to be relatively independent of ovarian hormones; rather the social environment decides the timing of copulation.

To study the communication system of the chacma baboon, three experiments were devised to separate the effects on the male of the female perineal swelling from those of female behaviour, as well as to understand the role played by proceptive behaviour. The first experiment assessed the role of the perineal swelling. A group of males was exposed to the sight of an ovariectomised female, who was either wearing a plastic model of a perineal swelling or was without it (Chapter 4). Results indicated that male arousal was induced by the sight of the model.

The second experiment (Chapter 5), in which an intact female was exposed to the sight of a group of females throughout one menstrual cycle, and to the sight of a group of males during another menstrual cycle, indicated that female soliciting behaviour was used as proceptive behaviour and that it occurred with lowest levels periovulstorily.

The third experiment (Chapter 6), investigated the effectiveness of proceptive behaviour on male arousal. A group of males was exposed to the sight of a female wearing pants, so that her perineum was concealed, throughout one menstrual cycle. Female behaviour was ineffective in inducing male arousal and, as in the previous experiment, it showed a marked correlation with levels of ovarian hormones - behaviours were at their maximum level perimenstrually and at their lowest periovulstorily. It is suggested that, in the chacma baboon, behaviour is not used as a

modulator of sexual activity. Rather, it is the perineal swelling, i.e., female appearance, which controls the timing of copulation.

Only one system, either the behaviour of the female or her appearance, seems to be active in the regulation of sexual activity of the vervet monkey or the chacma baboon. Furthermore, the two systems are not equivalent; in the chacma baboon, the perineal swelling (female appearance) acts, as a releaser stimulus, directly on male physiology, whilst, in the vervet monkey, female behaviour acts as a signal, informing the male of the female's readiness to mate. The influence of ovarian hormones seems to act more stringently on the female appearance of the chacma baboon, subsequently with a more stringent effect on male response, than on female behaviour of the vervet monkey, in which the effect could be detected clearly only in an experimental situation.

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted for any degree or examination in any other University.

Rehse Piolam

4 day of August, 1989.

In memory of

Ali, Borgia, Connie, Doris, Fran, Gretag, Helen, Joy, Lolita,
Miriana, Nirvana, Pacifica, Selvaggia, Ugo, Vincenzo, Woolie, Zeb

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TABLE OF CONTENTS

ABSTRACT	ii
DECLARATION	v
DEDICATION	vi
ACKNOWLEDGEMENTS	vii
LIST OF TABLES	xvi
LIST OF FIGURES	xix

1. GENERAL INTRODUCTION

1.1. THE PRIMATE OVARIAN CYCLE	1
1.2. FEMALE COPULATORY BEHAVIOUR	
1.2.1. Female Copulatory Behaviour Across the Order	2
1.2.2. Distribution of Female Copulatory Behaviour Across the Cycle and its Relation to Endogenous Ovarian Hormones	5
1.2.3. Female Copulatory Behaviour in Relation to Exogenous Hormones	7
1.3. FEMALE APPEARANCE	8
1.3.1. Visual Appearance	8
1.3.2. Distribution of Copulations in Relation to Size of the Perineal Swelling	8
1.3.3. Olfactory Appearance	8
1.4. DISTRIBUTION OF COPULATIONS ACROSS THE CYCLE	10
1.5. THE FUNCTION OF FEMALE COPULATORY BEHAVIOUR AND	

OF FEMALE APPEARANCE AND AIMS OF THE PRESENT STUDY	11
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2. STEROID HORMONE INFLUENCES ON THE MATING BEHAVIOUR
OF VERVET MONKEYS (*Cercopithecus aethiops pygerythrus*):
EFFECTS ON FEMALE ATTRACTIVENESS AND PROCEPTIVITY
- EXPERIMENT 1

2.1. INTRODUCTION	13
2.2. MATERIALS AND METHODS	16
2.2.1. Subjects	16
2.2.2. Housing	17
2.2.3. Transport, Test Room, Scoring and Habituation	17
2.2.4. Testing, Apparatus and Scored Categories	17
2.2.5. Behaviours Scored	21
2.2.5.1. Male Behaviours	21
2.2.5.2. Female Behaviours	22
2.2.6. Hormone Administration	23
2.2.7. Statistical Analysis	23
2.3. RESULTS	24
2.4. DISCUSSION	31

3. OESTROGEN TREATMENT INFLUENCES ON FEMALE VERVET
MONKEYS (*Cercopithecus aethiops pygerythrus*):
PROCEPTIVITY AND ATTRACTIVENESS WHEN FEMALE AND
MALE SUBJECTS HAVE A CHOICE OF PARTNER
- EXPERIMENTS 2 AND 3

3.1. INTRODUCTION	34
3.2. GENERAL METHODS	37
3.2.1. Subjects	37
3.2.2. Housing	37

3.2.3. Transport, Test Room, Scoring and Habituation	37
3.2.4. Hormone Administration	38
3.2.5. Statistical Analysis	38
3.3. EXPERIMENT 2	39
3.3.1. Methods and Procedures	39
3.3.1.1. Apparatus	39
3.3.1.2. Testing	41
3.3.1.3. Categories Scored	42
3.3.2. Results	42
3.4. EXPERIMENT 3	48
3.4.1. Methods and Procedures	48
3.4.1.1. Apparatus	48
3.4.1.2. Testing	48
3.4.1.3. Categories Scored	49
3.4.2. Results	51
3.5. DISCUSSION	57

4. THE CHACMA BABOON (*Papio ursinus*) FEMALE PERINEAL SWELLING AND ITS EFFECT ON MALE SEXUAL AROUSAL - EXPERIMENT 4

4.1. INTRODUCTION	67
4.2. MATERIALS AND METHODS	70
4.2.1. Subjects	70
4.2.2. Housing	71
4.2.3. Testing and Apparatus	71
4.2.4. Scoring	74
4.2.5. Measures Scored	74
4.2.6. Habituation	75
4.2.7. Statistical Analysis	75
4.3. RESULTS	75

4.4. DISCUSSION	79
-----------------------	----

**5. FEMALE CHACMA BABOON CHANGES, ACROSS THE MENSTRUAL CYCLE, IN VISUAL INTERACTIVE BEHAVIOURS.
A COMPARISON BETWEEN MENSTRUAL CYCLES IN FEMALE VERSUS MALE SOCIAL ENVIRONMENTS - EXPERIMENT 5**

5.1. INTRODUCTION	84
5.2. MATERIALS AND METHODS	84
5.2.1. Subjects	84
5.2.2. Housing	85
5.2.3. Testing	86
5.2.4. Measures Scored	87
5.2.5. Habituation	87
5.2.6. Cycle Phases and Statistical Analysis	87
5.3. RESULTS	88
5.4. DISCUSSION	96

**6. FEMALE CHACMA BABOON CHANGES, ACROSS THE MENSTRUAL CYCLE, IN VISUAL INTERACTIVE BEHAVIOURS.
A COMPARISON, IN AN ALL-MALE SOCIAL ENVIRONMENT, BETWEEN NORMAL MENSTRUAL CYCLES AND CYCLES IN WHICH THE ATTRACTIVE STIMULUS IS CONCEALED
- EXPERIMENT 6**

6.1. INTRODUCTION	112
6.2. MATERIALS AND METHODS	112
6.2.1. Subjects	112
6.2.2. Housing	113
6.2.3. Testing and Apparatus	113
6.2.4. Measures Scored	115
6.2.5. Habituation	116

6.2.6. Cycle Phases and Statistical Analysis	116
6.3. RESULTS	117
6.4. DISCUSSION	132
7. GENERAL DISCUSSION AND CONCLUSIONS	151
REFERENCES	154

LIST OF TABLES

Table 1. Frequencies and durations (Means $\pm$ SEM) of male behaviours during male restraint test.	28
Table 2. Frequencies (Means $\pm$ SEM) and percentages of female behaviour during the pair mating test.	29
Table 3. Frequencies (Means $\pm$ SEM) of male behaviours in the pair mating test.	30
Table 4. Frequencies of choice by Female Subjects of Male, no choice or Female Partners (FP) before (PEB) and during (EB) oestrogen treatment.	45
Table 5. Frequencies, rates or means of Female Subjects behaviours towards Male and Female Partners as well as ejaculations received before (PEB) or during (EB) oestrogen treatment.	47
Table 6. Frequencies of choice by Males of Female Subjects (FS) or Female Partners (FP) of seven FS-FP pairs before (PEB) and during (EB) oestrogen treatment of FS.	53
Table 7. Frequencies, rates or means of Male behaviours towards Female Subjects before (PEB) and during (EB) oestrogen treatment of FS.	55

Table 8. Frequencies, rates or means of Male behaviours towards Female Partners before (PEB) and during (EB) oestrogen treatment of Female Subjects.	56
---	----

Table 9. Frequencies and rates of Female Subjects behaviours before (PEB) and during (EB) oestrogen treatment.	58
---	----

Table 10. Frequencies and rates of Female Partners behaviours before (PEB) and during (EB) oestrogen treatment of Female Subjects.	59
---	----

Table 11. Frequencies and mean values of female behaviour (presents in brackets), male responses and percentages of male responders per female preceding (PRESWELL) and during (SWELL) the application of the perineal model.	76
--	----

Table 12. Occurrences and mean values of male responses and percentage of females eliciting male response preceding (PRESWELL) and during (SWELL) the application of the perineal model.	77
---	----

Table 13. Frequencies (Means $\pm$ SD) of female Solicits across menstrual cycles, when the subject is in a female social environment (FF) and in a male social environment (FM).	96
--	----

Table 14. Frequencies (Means $\pm$ SD) of female Yawns across menstrual cycles, when the subject is in a female social environment (FF) and in a male social environment (FM).	97
---	----

Table 15. Frequencies (Means $\pm$ SD) of female Yawns
across menstrual cycles, when the female subjects are
wearing pants (PANTS) and when they are not wearing
pants (NOPANTS).126

Table 16. Frequencies (Means $\pm$ SD) of female
Presents across menstrual cycles, when the female
subjects are wearing pants (PANTS) and when they
are not wearing pants (NOPANTS).127

Table 17. Frequencies (Means $\pm$ SD) of female
Lip-smacks across menstrual cycles, when the female
subjects are wearing pants (PANTS) and when they are
not wearing pants (NOPANTS).129

Table 18. Occurrences (Means $\pm$ SD) of Male Response
across the menstrual cycles of the female subjects,
when the female subjects are wearing pants (PANTS) and
when they are not wearing pants (NOPANTS).130

LIST OF FIGURES

Figure 1. (A) The experimental cage with the transport cages attached to the extremities. The male, in the left compartment, is separated from the female by a mesh partition for the first part of the test. The subjects can still touch and sniff each other. 19

(B) The second part of the test. The mesh partition is lifted and the male may approach the female. 20

Figure 2. Schematic representation of the test situation with the restricted partner on the left of the picture. In each section of the cage, the percentage of time spent by the subject female with either a male (black bars) or a female partner (dotted bars) during the control (PEB and PTP) and treatment (EB and TP) cycles is illustrated. 25

Figure 3. (Left) Comparison of frequencies (means $\pm$ SEM) of presenting by the female subjects when paired with male and female partners during the control (PEB and PTP) and treatment (EB and TP) cycles.

(Right) Comparison of frequencies (means $\pm$ SEM) of walking by the female subjects when paired with male and female partners during the control (PEB and PTP) and treatment (EB and TP) cycles. 26

Figure 4. (A) The Female Subject (FS) in the central compartment of the cage and her two partners, female (FP) and Male. The Female Subject (FS) is looking at the Female Partner (FP) in the left compartment through the one-way mirrored window.

(B) Detail of the outside of the partition. The mirrored window before and (C) after the convex screen is applied. 40

Figure 5. (A) Entrance of the Female Subject (FS) into a partner's (FP/Male) compartment.

(B) The Female Subject is looking through the one-way mirrored window.

(C) The Female Subject is 'attempting' to open the door. 43

Figure 6. Schematic representation of the test situation of Experiment 2, with the Male in the left, the Female Subject (FS) in the middle, and the Female Partner (FP) in the right section of the cage. The percentages represent, respectively from the left, female choice of Males, female no-choice; and female choice of Female Partners. The percentages are further divided into those occurring before (PEB) and during (EB) Female Subject treatment. 44

Figure 7. Comparison of latencies (mean $\pm$ SEM) of choice by each Female Subject (FS) before (PEB) and during (EB) oestrogen treatment. 45

Figure 8. (A) The experimental cage with the Female Subject (FS) and the Female Partner (FP) ready in their lateral compartments. The Male is in the transport cage waiting to be released in the central section. The transport cage is covered with a cloth and the clear partitions are covered with cardboard sheets to prevent vision of the females by the male prior to the beginning of the test.

xx

- (B) The male is entering, and therefore choosing, the compartment of one of the two FS/FP females.
- (C) The male is 'attempting' to open the door. 50

Figure 9. Schematic representation of the test situation of Experiment 3 with the Female Subject (FS) in the left, the Male in the middle, and the Female Partner (FP) in the right sections of the cage. The percentages represent male choice of the Female Subject before (PEB) and during (EB) the hormonal treatment. 52

Figure 10. Comparison of latencies (mean $\pm$ SEM) of choice by each male before (PEB) and during (EB) oestrogen treatment of the Female Subject (FS). 54

- Figure 11. (A) One of the experimental subjects wearing the perineal model.
- (B) The perineal model and harness.
- (C) The model as it came out of the mould. 73

Figure 12. Percentage of females eliciting response in each of the male subjects during PRESWELL and SWELL. 78

Figure 13. Frequencies of female soliciting behaviour in relation to occurrence of male response during PRESWELL and SWELL. 80

- Figure 14. Swell rate and frequencies of solicits, presents, and yawns of Female 1087, across the menstrual cycle.
- (A) Female 1087 vs Females. 89
- (B) Female 1087 vs Males. 90

Figure 15. Swell rate and frequencies of solicits, presents and yawns of Female 1081, across the menstrual cycle.

(A) Female 1081 vs Females.	91
(B) Female 1081 vs Males.	92

Figure 16. Swell rate and frequencies of solicits, presents and yawns of Female 1135, across the menstrual cycle.

(A) Female 1135 vs Females.	93
(B) Female 1135 vs Males.	94

Figure 17. Female solicits to Females vs to Males. 99

Figure 18. Female solicits to Females vs to Males with phases 1, 2 and 4, 5 averaged. 100

Figure 19. (A) The pants. The buckle goes on the dorsum of the female. Below the buckle is the slit that allows space for the tail.

(B) and (C) One of the experimental subjects wearing the pants. It can be seen that mobility of the hind limbs is not hindered by the garment. 114

Figure 20. Swell rate and frequencies of solicits, presents and yawns of Female Q-436, across the menstrual cycle.

(A) Female Q-436 - NOPANTS.	118
(B) Female Q-436 - PANTS.	119

Figure 21. Swell rate and frequencies of solicits, presents and yawns of Female 83, across the menstrual cycle.

(A) Female 83 - NOPANTS.	120
(B) Female 83 - PANTS.	121

Figure 22. Swell rate and frequencies of solicits, presents and yawns of Female DB-9, across the menstrual cycle.

(A) Female DB-9 - NOPANTS.	122
(B) Female DB-9 - PANTS.	123

Figure 23. Female Q-436 - Body weight across two menstrual cycles.

Figure 24. Female presents during PANTS cycles vs during NOPANTS cycles.

Figure 25. Female lip-smacks during PANTS vs during NOPANTS cycles.

Figure 26. Female solicits during PANTS cycles vs during NOPANTS cycles.

Figure 27. Female solicits during PANTS and NOPANTS cycles with phases 1 and 2 averaged.

Figure 28. Occurrence of male response in relation to body weight and swell rate of Female Q-436, across the menstrual cycle.

(A) Female Q-436 - NOPANTS.	136
(B) Female Q-436 - PANTS.	137

Figure 29. Occurrence of male response in relation to body weight and swell rate of Female 83, across the menstrual cycle.

(A) Female 83 - NOPANTS.	130
(B) Female 83 - PANTS.	139

Figure 30. Occurrence of male response in relation to body weight and swell rate of Female DB-9, across the menstrual cycle.

(A) Female DB-9 - NOPANTS.	140
(B) Female DB-9 - PANTS.	141

Figure 31. Male response during PANTS cycles vs during NOPANTS cycles.

	142
--	-----

Figure 32. Female solicits vs male response during PANTS cycles.

	143
--	-----

Figure 33. Female solicits vs male response during NOPANTS cycles.

	144
--	-----

Figure 34. Female solicits for all menstrual cycles combined.

	146
--	-----

1. GENERAL INTRODUCTION

1.1. THE PRIMATE OVARIAN CYCLE

Before discussing the role of the female in primate sexual communication, it is necessary to understand the hormonal mechanisms that assist the female in becoming a successful, reproductive being. The present work will focus, however, only on reproductively mature females and on the hormonal mechanisms underlying the ovarian cycle.

The ovarian cycle of primates has three phases. The first, the follicular or proliferative, phase, usually variable in length, is characterized by the development of the maturing follicle. The second phase, which is very brief, is the ovulatory event. It starts with the mid-cycle surge of the luteinizing hormone (LH), which is followed by the follicular rupture and the extrusion of a mature oocyte. The third phase, termed luteal or secretory, consists of the formation and the lifespan of the corpus luteum and, with respect to the follicular phase and within the order, is rather constant in length (Hodges, 1987).

The overall cycle length in primates is species-typical and ranges from very short, 9 to 16 days for some New World monkeys, through a medium-length cycle of 28 days for most of the Old World monkeys, to longer cycles, which exceed 30 days, characteristic of prosimians and of those species of the Anthropoidea that show perineal swellings (Hodges, 1987; Hrdy and Whitten, 1987).

Despite differences among species in the absolute hormone levels and in duration of each phase of the cycle, a common trait is the rise in oestrogens during the follicular phase, a

preovulatory surge in oestrogens and in gonadotropins (LH and follicle-stimulating hormone, FSH) and the rise in progesterone during the luteal phase (Hodges, 1987). In some primates, rises in oestrogens have been found to be paralleled by rises in ovarian testosterone (Dixon, 1983a).

1.2. FEMALE COPULATORY BEHAVIOUR

1.2.1. Female Copulatory Behaviour across the Order

In female primates, copulation is generally preceded, and accompanied, by a variety of behaviours that, although species-typical in the type of display or in the frequency of use (Zumpe and Michael, 1983; Bernstein and Gordon, 1979), have similar characteristics.

Behaviours that serve to maintain contact with the male, like approaching, following, sitting or standing next to the male, have been noticed in a number of species across the two suborders: among the prosimians, the ruffed lemur, *Lemur variegatus* (Shideler *et al.*, 1983), the thick-tailed bushbaby, *Galago crassicaudatus* (Girolami and Bieleert, unpublished), the lesser bushbaby, *G. senegalensis* (Girolami *et al.*, unpublished); among the New World monkeys, the howler monkey (Jones, 1985); among the Old World monkeys, the patas monkey, *Erythrocebus patas* (Rowell and Hartwell, 1978), the long-tailed macaque, *Macaca fascicularis* (Emory *et al.*, 1980), the lion-tailed macaque, *M. silenus* (Lindburg *et al.*, 1985), the rhesus macaque, *M. mulatta* (Carpenter, 1942; Loy, 1971; Cochran, 1979; Lindburg, 1983), and a Japanese macaque, *M. fuscata* (Enomoto *et al.*, 1979; Wolfe, 1984); and, among the apes, the gorilla (Hess, 1973; Nadler *et al.*, 1983; Mitchell *et al.*, 1985), the chimpanzee (Young and Orbinson, 1944), and the orangutan (Nadler, 1977). Staring at the male or the seeking of eye-contact

is also widely diffused. It is noted in the stump-tailed macaque, *N. arctoides* (Linnankoski *et al.*, 1981; Linnankoski and Leinonen, 1985); in the Celebes macaque, *N. nigra* (Dixson, 1977; in the common marmoset *Callithrix jacchus* (Dixson, 1986); in the gorilla (Hess, 1973); in the chimpanzee (Wallis, 1982); and in the baboon (Bielert, 1986, which includes a thorough review on distribution of eye-contact across the order).

Similarly diffused are female behaviours which involve physical contact with the male. Among these are the touching or fondling of his genitals as in the long-tailed macaque (Emory and Payne, 1980), in the vervet monkey, *Cercopithecus aethiops* (Rowell, 1971), and in the chimpanzee and gorilla (Wallis, 1982; Hess, 1973), or the grabbing or pulling of the male as in the clutching reaction of the rhesus, stump-tailed and Japanese macaques (Carpenter, 1942; Loy, 1971; Lindburg, 1983; Linnankoski *et al.*, 1981; Enomoto *et al.*, 1979; Wolfe, 1984), the woolly spider monkey, *Brachyteles arachnoides* (Milton, 1985), and the gorilla (Hess, 1973), or, eventually, the mounting of the male and/or rubbing of the female's genitals on him, as occurs in the Japanese macaque (Hanby *et al.*, 1971; Wolfe, 1984;), the orangutan (Nadler, 1977) and the gorilla (Nadler, 1975).

Other behaviours consist of the display of the body, or part of it, and they may involve a reiteration or a stereotypy of the movement. To this category belong the parading display, as in the Celebes macaque (Dixson, 1977), the approach-withdrawal sequence, seen in the long-tailed macaque (Emory and Payne, 1980), the samango monkey, *Cercopithecus albogularis*, (Girolami, unpublished), and gorilla (Hess, 1973), the stiff-legged jumping of the lion-tailed macaque (Lindburg *et al.*, 1985), the rhythmic micturation of the slender loris, *Loris tardigradus malabaricus* (Izard and Rasmussen, 1985), the rolling and rubbing of the ruffed lemur (Shideler *et al.*, 1983), the head-shuddering of the langurs

(Hrdy and Whitten, 1987), and the head-bob, head-duck and hand-slap of the rhesus, Japanese and lion-tailed macaques (Cochran, 1979; Enomoto *et al.*, 1979; Lindburg *et al.*, 1985). Among the female behaviours which display a part of the body is the exhibition of the genital area, which may take the form of presentation of the rump ("present") which is widespread among primates, or the form of rhythmic rubbing of the genitals in front of the male, as shown by the patas monkey (Rowell and Hartwell, 1978), the orangutan (Nadler, 1977) and the gorilla (Hess, 1973).

Presents may occur in various forms: a low crouch as in vervet monkeys (Gartlan, 1969), a casual stance as in the samango monkey (Rowell, 1971), or as a more stereotyped posture, with orientation of the perineum and slight flexion of the hind limbs, as in the baboon (Bialert, 1986). Differences in the posture can be species-typical (for discussions of "presenting", see Rowell, 1972; Dixon, 1977), can depend on the context in which they are performed (Hausfater and Takacs, 1987) and, finally, may depend on individual preferences (Yerkes, 1939). Presents have not been observed in nocturnal primates, such as some prosimians (see Van Horn and Eaton, 1979, for a review) nor in the owl monkey, *Aotus trivirgatus* (Dixon, 1983b). However, presentation of the rump is described for diurnal prosimians, namely the ring-tailed lemur, *Lemur catta* (Jolly, 1966; Evans and Goy, 1968) and the sifaka, *Propithecus varrauxi* (Richard, 1974).

Certain behaviours may also be the source of acoustic signals besides the obvious visual ones. These include: pursing of the lips, as in the blue and samango monkeys (Rowell, 1971; Girolami, unpublished), and the gorilla (Hess, 1973); smacking of the lips, as in the Celebes macaque (Dixon, 1977), the rhesus (Carpenter, 1942) and the Japanese macaque (Wolfe, 1986); flicking of the tongue, as in the marmoset (Dixon, 1986) and the howler monkey (Jones, 1985); chattering of the teeth in the stump-tailed macaque

(Linnankoski *et al.*, 1981); and blowing of the cheeks, as in the petas monkey (Rowell and Hartwell, 1976).

Precopulatory vocalizations seem to occur in the Japanese (Hanby *et al.*, 1971; Enomoto *et al.*, 1979) and lion-tailed macaques (Lindburg *et al.*, 1985), whereas copulatory vocalizations are well-known in the chacma baboon, *Papio ursinus* (Saayman, 1970; Hamilton and Arrowood, 1978; Bielert, 1982) and in the long-tailed macaque (van Noordwijk, 1985).

Female copulatory behaviours are also reviewed by Dixon (1983a) and by Erdy and Whitten (1987).

1.2.2. Distribution of Female Copulatory Behaviour across the Cycle and Its Relation to Endogenous Ovarian Hormones

In a number of primate species, the expression of female copulatory behaviours is influenced by ovarian hormones. Perioviulatory increases in female behaviours have often been reported and, when levels of endogenous oestrogens were measured, behavioural increases were found to be correlated with the hormonal levels.

In prosimians, female behaviour seems to be under strict hormonal control. This is visible as a drastic change from refusal to acceptance of the male seen in concomitance with vaginal oestrus (see Van Horn and Eaton, 1979, for a review). In the ring-tailed lemur (Evans and Goy, 1968; van Horn and Resko, 1977) and in the thick-tailed bushbaby (Eaton *et al.*, 1973), female acceptance of the male is related to high levels of circulating oestrogens.

Among the New World monkeys, tongue flicks peak around the time of ovulation in the common marmoset (Kendrick and Dixon, 1983) and in the howler monkey (Jones, 1985). In the rhesus macaque, increases in approaches and proximity to the male, during the follicular phase of the cycle, have been elucidated by Pomerantz

and Goy (1983) and by Czaja and Bielewicz (1973). Also the time with which the female sought male contact was found to be shorter during mid-cycle (Bonsall *et al.*, 1978). Hand-slap, threaten away, head-bob, head-duck, and reach-back were found to increase with increasing levels of follicular hormones (Ball and Hartman, 1955; Gordon, 1981; Wallen *et al.*, 1984). Erikson (1967) found also that female inclination to vaginal stimulation would increase around ovulation. Female solicits peak during the late follicular phase in the lion-tailed macaque (Lindburg *et al.*, 1985), and, in the long-tailed macaque (Zumpe and Michael, 1983) and the Japanese macaque (Enomoto *et al.*, 1979; Wolfe, 1984), levels of solicits are higher during the follicular phase than during the luteal phase. For the stump-tailed macaque, there are some indications of increases in reach-back, look-back and presents (Slob *et al.*, 1978). Also in the Celebes macaque, presents and parading in front of the male were found to be highest during the follicular and periovulatory phases of the cycle (Dixon, 1977).

In the talapoin monkey, *Niopithecus talapoin*, presents were found to be highest during the late follicular, mid-cycle phases, when the swelling of the perineum is maximum (Herbert, 1970; Dixon *et al.*, 1973). The female mangabey, *Cercocebus albigena*, also increases her solicits during maximum perineal swelling, and thus at mid-cycle (Chalmers and Rowell, 1971).

Mid-cycle presents and solicits increase also in the gorilla (Mess, 1973; Nadler, 1975; Nadler *et al.*, 1983; Fossey, 1983; Mitchell *et al.*, 1985). Similar increases in presents, solicits and approaches are also found in the chimpanzee (Yerkes, 1939; Young and Orbison, 1944; Wallis, 1982), when levels of oestradiol 17 β are highest (Nadler *et al.*, 1985).

1.2.3. Female Copulatory Behaviour in Relation to Exogenous Hormones

The relationship between follicular hormones and female behaviours is exemplified by experiments employing hormone replacement therapy.

In the thick-tailed bushbaby (Dixon, 1978; Girolami and Wielert, unpublished) and in the lesser bushbaby (Lipschitz, 1986), treatment with oestradiol 17 β induces female acceptance of the male.

Kendrick and Dixon (1985) and Dixon (1986) show that, in the common marmoset, increases in tongue flicks are induced by treatment with oestradiol 17 β , whereas testosterone is ineffective.

In the rhesus macaque, the primate most often studied in this respect, treatments with oestradiol or with testosterone have resulted in, at least, increased frequencies of presents (Trimble and Herbert, 1968; Zumpo and Michael, 1970, 1985a; Everitt and Herbert, 1971; Dixon *et al.*, 1973; Johnson and Phoenix, 1976; Baum *et al.*, 1977; Wallen and Goy, 1977; Zumpo *et al.*, 1983b). In the long-tailed macaque (Zumpo and Michael, 1985b), oestradiol and testosterone treatments have been found to induce increases in invitations and in female initiations of mounts, as well as a reduction of the time latencies for these behaviours to first occur.

Oestradiol treatment is also effective in inducing increases in presents in the talapoin monkey (Dixon *et al.*, 1973).

On the subject of hormonal influences on female primate copulatory behaviour, the following reviews may be consulted: Dixon, 1983a; Luttge, 1971; Michael and Ronsall, 1979; Baum, 1983.

1.3. FEMALE APPEARANCE

1.3.1. Visual Appearance

A discussion of morphological changes, related to ovarian hormone levels, in the genital and perineal regions of primates is given in 4.1., below.

1.3.2. Distribution of Copulations In Relation to Size of the Perineal Swelling

Peaks of copulations during maximum swelling have been found not only in the baboon (see 4.1., below) but also in all the species, studied in this respect, that show a pronounced perineal swelling. These include the Sumatran long-tailed macaque (van Noordwijk, 1985), the barbary macaque (Kunster and Paul, 1984), the pig-tailed macaque (Eaton and Resko, 1974), the Celebes macaque (Dixon, 1977), the mangabey (Chalmers and Rowell, 1971), the talapoin monkey (Herbert, 1970; Dixon *et al.*, 1973), the red colobus, *Colobus badius*, (Struhsaker and Leland, 1979) and the chimpanzee (Yerkes, 1939; Young and Orbison, 1944; Wallis, 1982).

1.3.3. Olfactory Appearance

There is plenty of evidence that olfactory communication is important in the primate order, particularly among prosimians and New World monkeys (Schilling, 1979; Eppler, 1974). However, there is little evidence to suggest what role olfactory cues play in sexual communication, this kind of evidence being mostly circumstantial (Eppler, 1976; Keverne, 1982, 1983; Goldfoot, 1982). Male ring-tailed lemurs and tamarins, *Saguinus fuscicollis*, prefer

female scent to those of males (Dugmore *et al.*, 1984; Epple, 1960). Male lemurs exhibit flehmen when investigating the scent of female genitals (Bailey, 1978). Male anosmia causes sexual impairment in rhesus macaques (Michael and Keverne, 1968; Keverne, 1982). These factors and the extensive investigation and licking of the female genitals that characterises mating in bushbabies (Doyle *et al.*, 1967; Eaton *et al.*, 1973; Lipschitz, 1988; Girolami and Bielert, unpublished), coupled with the fact that males spend more time investigating scents from oestrous females in the thick-tailed bushbaby (Clark, 1982) and in the lesser bushbaby (Girolami *et al.*, unpublished), suggest that olfactory cues serve a reproductive purpose (for more examples, see Epple, 1976; Goldfoot, 1982; Keverne, 1983). How olfactory cues do act, though, is not yet known.

Direct evidence is available for the rhesus macaque and comes from a set of experiments in which ovariectomised, untreated, females were able to elicit male copulatory behaviour following application of vaginal lavages from oestrogen-treated females (Michael and Keverne, 1968, 1970; Michael and Zumpe, 1982). The active substance was identified in a mixture of aliphatic acids (Curtis *et al.*, 1971; Michael *et al.*, 1971) which have been shown to increase around the time of ovulation in a number of species: the baboon (Bielert and Crawe, unpublished), the chimpanzee (Fox, 1982) and humans (Michael *et al.*, 1974). Some doubt may be cast on these results, however, because of the difficulty in replicating them and also because peaks of aliphatic acids have been shown to occur only after ovulation, i.e., in the luteal phase, and following progesterone treatment (Goldfoot *et al.*, 1976). The production of aliphatic acids seemed to be, then, more sensitive to progesterone than oestradiol. Goldfoot *et al.* (1976) also showed that peaks in aliphatic acids could be induced by contamination with ejaculate. Peaks in aliphatic acids during the luteal phase,

and in relation to contamination with ejaculate, were also found in the baboon (Bieleit and Crewe, unpublished). In later work, Goldfoot (1981) found that experienced males were able to discriminate by olfaction the sexual state of a female. He suggested that vaginal substances other than aliphatic acids may convey the information.

From this excursus, it is apparent that the role played by olfactory cues in reproductive communication is not yet clear and more research needs to be undertaken on this subject. Instead, what is clear is that female olfactory appearance does change across the cycle.

1.4. DISTRIBUTION OF COPULATIONS ACROSS THE CYCLE

Perioviulatory peaks of copulations, or highest levels of copulations during the follicular phase of the cycle, are common within the primate order.

In prosimians, copulation is limited to a few days of the ovarian cycle, when the female will accept the male (for the slender loris, Izard and Rasmussen, 1985; the ruffed lemur, Shideler *et al.*, 1983; the ring-tailed lemur, Jolly, 1966; Evans and Goy, 1968; the sifaka, Richard, 1974; the thick-tailed bushbaby, Eaton *et al.*, 1973; the lesser bushbaby, Doyle *et al.*, 1967). The few days of the cycle in which the female prosimian will mate may be contrasted with the few hours of the cycle in which mating occurs in the tree shrews (Conaway and Gorenson, 1966). We have already seen how, in prosimians, female acceptance of the male is related to ovulation. In prosimians, copulation also occurs only in the ovulatory phase of the cycle.

Perioviulatory or follicular increases in copulation in New World primates are also found in the marmoset (Kendrick and Dixon, 1983).

Among the macaques, such changes have been observed in the rhesus (Michael *et al.*, 1967; Czaja and Bielert, 1975; Bonsall *et al.*, 1978; Gordon, 1981; Zumba and Michael, 1983; Wallen *et al.*, 1984), the long-tailed macaque (Zumba and Michael, 1983), the lion-tailed macaque (Lindburg *et al.*, 1985), the pig-tailed macaque (Eaton and Resko, 1974), the stump-tailed macaque (Murray *et al.*, 1985; Nieuwenhuijsen *et al.*, 1986), the barbary macaque (Kuster and Paul, 1984), the Celebes macaque (Dixon, 1977), and the Japanese macaque (Enomoto *et al.*, 1979). Copulatory peaks during the late follicular phase of the cycle are found in the baboon (see 3.1, below), the talapoin monkey (Herbert, 1970; Dixon *et al.*, 1973), and the mangabey (Chalmers and Rowell, 1971). The patas monkey shows higher levels during the follicular phase than during the luteal phase (Rowell and Hartwell, 1978).

Among the great apes, mating is restricted to mid-cycle in the gorilla (Hess, 1973; Nadler, 1975; Nadler *et al.*, 1983; Fossey, 1983; Mitchell *et al.*, 1985) and in the chimpanzee (Yerkes, 1939; Young and Orbison, 1944; Wallis, 1982), whereas periovulatory increases in copulatory frequency have been observed in the orangutan (Nadler, 1977).

1.5. THE FUNCTION OF FEMALE COPULATORY BEHAVIOUR AND OF FEMALE APPEARANCE AND AIMS OF THE PRESENT STUDY

It seems evident at this point that a relationship exists between female copulatory behaviour, female appearance, and the event of copulation. The nature of such a relationship, especially between female behaviour and copulation, is not yet clear.

In 1976, Beach divided female copulatory behaviours into two types, proceptive and receptive. The former consists of appetitive behaviour and the latter of adjustments to allow copulation. The

appearance of the female, or in other words her stimulus value, was termed her "attractivity".

Female proceptivity in nocturnal prosimians is not well developed and copulation seems to be modulated by changes in female receptivity and attractiveness. This makes sense in that males are attracted to a female only when the female will allow copulation. Why then did proceptive behaviours evolve in diurnal prosimian and simian primates? Female proceptive behaviours were also described by Beach (1976) as attractive. Is it possible then that proceptive behaviours have increased at the expense of female appearance as a means of attracting the male? Lastly, how does attractiveness work? Does it signal female behavioural readiness and/or female fertility, which implies male cognition and choice, or does it act on male physiology, thus impelling the male to copulate.

Bearing these questions in mind, two species of the Cercopithecinae were selected for a study of their systems of sexual communication: the vervet monkey, *Cercopithecus aethiops pygerythrus*, a species whose females do not show changes in visual appearance and which has so far provided scanty evidence of hormone-related copulatory activity; and the chacma baboon, *Papio ursinus*, a species whose females, by contrast, show prominent changes in visual appearance and which exhibits conspicuous evidence of hormone-related copulatory activity.

¹ In this thesis, the word "attractiveness" is used in preference to Beach's term "attractivity", except where reference is made to his publication.

2. STEROID HORMONE INFLUENCES ON THE MATING BEHAVIOUR OF VERVET MONKEYS (*Cercopithecus aethiops pygerythrus*): EFFECTS ON FEMALE ATTRACTIVENESS AND PROCEPTIVITY

EXPERIMENT 1

2.1. INTRODUCTION

Steroid hormones are a very important factor in the synchronization of reproductive activity in mammals. An example of this synchronization is the phenomenon of oestrus, which consists of hormonally induced changes in sexual behaviour and physiology necessary for fertile matings (Lisk, 1978). However, the connection between reproduction and the hormonal state of the female, with the exception of prosimians (Eaton, 1973), is less clear-cut in primates.

The rhesus macaque (*Macaca mulatta*) is the species to which most attention has been devoted in terms of analytical studies on hormone-behaviour interactions. Studies have demonstrated that ovariectomy noticeably reduces male copulatory behaviours and that male interest is restored by the administration of oestradiol to the females (Michael *et al.*, 1967). Oestradiol in fact seems to have a marked effect on female attractiveness, increasing a number of male behavioural indices such as contacts, mounts, mounting rates, intromissions, and ejaculations (Trimble and Herbert, 1968; Johnson and Phoenix, 1976; Wallen and Goy, 1977). In addition, exogenous administration of another ovarian secreted steroid, testosterone, has been found to increase the display of mounts, intromissions, ejaculations, and erections (Johnson and Phoenix,

1976; Wallen and Goy, 1977). In the female, both oestradiol and testosterone have been found to increase proceptive behaviours (Trimble and Herbert, 1968; Phoenix and Michael, 1970; Johnson and Phoenix, 1976; Wallen and Goy, 1977), whereas a reduction in receptivity and attractiveness was found to be induced by higher dosages of testosterone (Trimble and Herbert, 1968; Johnson and Phoenix, 1976).

As Baum has pointed out in a recent review (1983), species differ in those sexual behaviours exhibited and in their dependence upon sex steroids. In the stump-tail macaque (*M. arctoides*), neither male nor female behaviour fluctuates predictably across the female's cycle. Ovariectomy decreased but did not eliminate male sexual behaviours (Slob et al., 1978). Additional work has shown that adrenalectomy of ovariectomized females did not affect male or female behaviour (Baum et al., 1978).

Field studies reveal that the vervet monkey (*Cercopithecus aethiops pygerythrus*) apparently exhibits mating behaviour throughout the female menstrual cycle. These studies have reported a "prolonged oestrus", during which females showed sexual behaviour on 66 consecutive days (Struhsaker, 1967a, p.31) and 56 consecutive days (Gartlan, 1969).

Although long intermenstrual cycles have been noticed in the laboratory (up to 149 days, Butler, 1966; over 50 days, Elie et al., 1986), normal cycles have been identified for the vervet monkey, as being much shorter (mean cycles of: one month, Bramblett et al., 1975; 31.4 days, Hess et al., 1979; 32.76 days, Elie et al., 1986).

The prolonged periods of female sexual behaviour appear to exceed the mean duration of a normal ovulatory cycle. In captive vervet monkeys, Rowell (1970) found cycles to have a median length of 33 days, and that females copulated each day of the cycle. She also described the females as being in a "continuous oestrus"

(Rowell, 1970, p.335). These data suggest a remarkable independence of copulations from levels of ovarian hormones. This is confirmed by the finding that females in this species can copulate before the breeding season, even though they have not resumed ovarian cyclicity (Andelman *et al.*, 1985; Andelman, 1987).

If copulatory activity, extended to the infertile phase of the cycle, may be expected in captivity, since this has been found in the Rhesus macaque during pair-tests and in restricted space (Gordon, 1981; Wallen, 1982), this same phenomenon should not occur in free-ranging animals, where the expression of an ovarian-related activity should be favoured. On the other hand, it is possible that other factors, acting directly on female behaviour, intervene, thereby creating a "prolonged oestrus".

It is now apparent that, in more limited space and in pair-test situations, if a female can control male access (Michael *et al.*, 1982), or when male access to the female is restricted (Czaja and Bielert, 1975; Pomerantz and Goy, 1983), the display of proceptive behaviour fluctuates in relation to the menstrual cycle. In fact, Baum (1983) claimed that, among female behaviours, it is the proceptive behaviours which are most likely to be influenced by ovarian hormones. This is particularly evident in the behaviour of proximity to the male partner (Czaja and Bielert, 1975; Johnson and Phoenix, 1976; 1978; Wallen and Goy, 1977; Cochran, 1979; Wallen, 1982).

Experiment 1 was designed to investigate whether the reported "prolonged/continuous oestrus" and relative copulatory activity were a true reflection of the independence of mating, and thus of attractiveness and proceptivity, from ovarian hormones, or the result of pressures posed by the social and physical environments. To this end an ovariectomised female treated with oestradiol and testosterone, one at a time, the two major ovarian hormones involved in the control of female attractiveness and proceptivity,

was pair-tested with a male. In addition, since a pair-test situation can, of itself, reduce the expression of hormonal modulation of copulatory activity, one part of the test focussed on the preceptive behaviour that, as seen before, has shown most sensitivity to hormonal changes, that is proximity to the male. The situation chosen was one in which the female was in control of her space and free from male physical influence, i.e., the male was restrained in one portion of the cage. This particular experimental situation had been employed successfully by Czaja and Bielert (1975), in a rhesus monkey study.

2.2. MATERIALS AND METHODS

2.2.1. Subjects

The subjects were wild-caught, adult vervet monkeys from the northern Transvaal near Vaalwater, South-Africa: ten females, A, B, C, D, F, G, H, J, L, P, and four males, U, V, W, Z. Nine of the females had been bilaterally ovariectomised a minimum of 4 years earlier. The tenth female was intact and unfamiliar with the others. The males had all been bilaterally vasectomised at least 5 months prior to the start of testing. Two of the males (W, Z) were familiar with the eight experimental females, having lived in the same social group for 5 years. The other two males (U, V), having recently joined the colony, were relatively unfamiliar with the subject females. No information is available on the animals before capture. Full body weight and dentition, and descent of testes were the criterion for determination of sexual maturity in males. Full body weight and dentition as well as elongation of nipples were the criterion for the determination of female sexual maturity and parity. At no time were the subjects involved in any experiment other than those described.

2.2.2. Housing

All the monkeys were housed at the Frankenwald Unit of the Central Animal Service, University of the Witwatersrand, in individual cages. Here they had been transferred 4 months before the test began. The cages measured 60x80x60 cm and were located in a large building with other monkeys and baboons. The building had no windows, but light was provided by a large wire-mesh door on one side of the building, which also constituted a source of fresh air.

The animals received a commercially prepared food pellet daily, supplemented two or three times a week with fresh fruit and vegetables. Water was available *ad libitum*. Cages were hosed down once a day and daily health checks were carried out on all of the subjects.

2.2.3. Transport, Test Room, Scoring and Habituation

For testing, the subjects were transported from their home cage to the testing room by means of a 30x30x40 cm metal sheet transport cage that they had learned to enter. The cage had punched holes, for air flow, in the two of the longer sides. The transport cage was transported on a trolley (36x54x112 cm) from home cage to the testing room. In the test room, the observer sat behind a mobile behaviour recording unit, opposite to the cage, in full view of the animals. The animals were familiar with the observer. The unit was capable of recording elapsed time as well as frequencies

of events. For the second part of the test, behaviours were recorded on a score sheet divided in five seconds intervals (see 2.2.4., below - scored categories). Time was kept by means of a stop-watch.

All the animals were made familiar with the testing routine in the 4 months before the actual test commenced. Transport cage training began 4 months before testing and preadaptation to tests began 2 weeks before testing.

2.2.4. Testing, Apparatus and Scored Categories

The test was divided into two parts. In the first part, the male was prevented from physical contact with the subject female while, in the second, the pair was free to interact. The female was transported from her home cage and placed in the testing cage, first. The wire mesh test cage (Figure 1) measured 66x72x266 cm and had guillotine doors at either end for the introduction of the animals. A sliding wire mesh partition allowed for the conversion of a portion (66x72x66 cm) of the cage into a smaller compartment. The mesh did not prevent visual, auditory, or olfactory interactions of the subjects but did prevent physical contact (Figure 1). Following the introduction of a subject female into the testing cage, the wire mesh partition was lowered and the male was collected from his home cage and prepared for his introduction into the small compartment and the start of the test. The test began with the male's entrance into the small compartment and the first part of the test continued for 10 minutes.

During this period, the frequencies of masturbation and olfactory investigation by the male were recorded as well as cumulative erection time. Walking activity and frequencies of presenting were recorded for the females. Cumulative records were also kept of the amounts of time spent in the various portions of

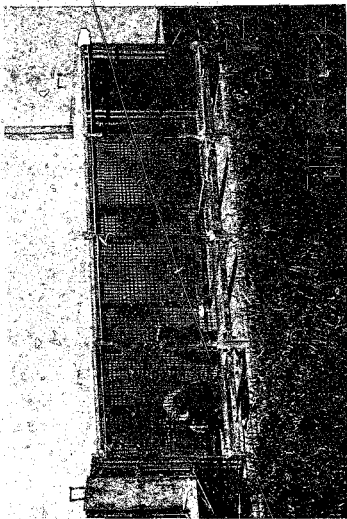


Figure 1.A. The experimental cage with the transport cages attached to the extremities. The male, in the left compartment, is separated from the female by a mesh partition for the first part of the test. The subjects can still touch and sniff each other.

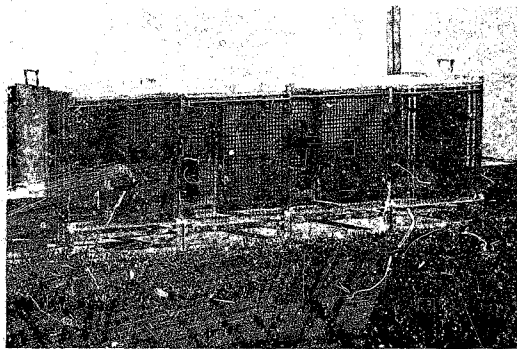


Figure 1.A. The experimental cage with the transport cages attached to the extremities. The male, in the left compartment, is separated from the female by a mesh partition for the first part of the test. The subjects can still touch and sniff each other.

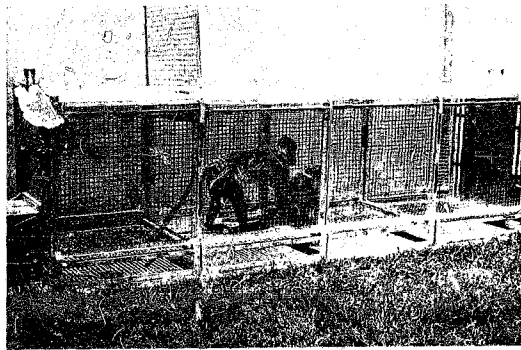


Figure 1.B. The second part of the test. The mesh partition is lifted and the male may approach the female.

the test cage. The cage area available to the female was divided into three equal portions (66x72x66 cm each), S3, S2, and S1. The portion nearest the male, S3, was further divided in two sub-sections, S3a and S3b (see Figure 2). At the end of the 10-minute test, the mesh partition was lifted and the male was allowed contact with the female.

The second portion of the test consisted of a 12-minute pair test. A number of male and female behaviours (listed and defined below) were recorded, as well as the time from the introduction of the male until ejaculation was recorded.

Each testing cycle consisted of 40 tests over a period of 2 weeks. The eight ovariectomised subject females were divided into two groups (A and B) with four individuals in each. Each subject female of the same group was paired with the four males and the two female partners (one intact and one ovariectomised) so that, at the end of the test cycle, each female had seen the male partners twice and the female partners once. Female partners were tested only in the restrained situation. During a 3x12 month testing period, a total of 320 tests were carried out.

2.2.5. Behaviours Scored

2.2.5.1. Male Behaviours

The male behaviours scored were:

Olfactory Investigation. Any clear bout of sniffing at the perineal region of a female in close proximity.

Masturbation. Any discrete period of consistent handling of the penis.

Approach. The male walks directly toward the female.

Contact. The male touches or grasps with one or both hands the hips or the waist of the female.

Mount. The male clasps female calves with his feet while holding the female's hips with his hands.

Intromission. Penile insertion into the vagina is recognized by deep and regular pelvic thrusting. The number of pelvic thrusts per intromission was recorded from the first insertive thrust.

Ejaculation. Seminal emission characterized by a short pause and body immobility after a series of long and rhythmic pelvic thrusts, followed by male dismount. It is also recognized by the presence of coagulated ejaculate visible on the vulva of the female.

2.2.5.2. Female behaviours

The female behaviours scored were:

Presenting. A direct orientation of the perineum toward the partner. This category includes all possible variations in orientation and flexion of the body and position of head and tail. It can be performed as a low crouch; sideways oriented, with tail held against the body and head either looking away or turned toward the male, or it can be a posture with fully extended legs. In this case the tail is either flexed over the back, held vertically, or left flaccid. The body can either be oriented perpendicularly toward the male or sideways and the head can be turned to the male or away from him.

Walking. Any movement requiring a minimum of two steps within or across the cage section.

Proximity. The female sits within touching distance of the male.

Yawns. A hyperextension of the mandible with slight dislocation. The lips are retracted to expose the gums and teeth.

Aggression. The female chases and hits the male with one hand while lifting the eyebrows and gaping (Struhsaker, 1967).

Negative adjustments. The female does not pay attention to the male, walks away, or else hits the male.

2.2.6: Hormone Administration

Females were subjected to two cycles of hormonal treatment: (1) with oestradiol benzoate (EB) and (2) with testosterone propionate (TP). Group A was injected every day for 4 weeks, with 10 µg EB suspended in 0.2 ml of arachis oil. Intramuscular injections were given once a day between 09:00 and 11:00. Treatment was initiated 2 weeks before behavioural testing and was continued during the testing period. Injections were then suspended for 30 days, after which the second cycle of hormone treatment was started. TP (1 mg), suspended in 0.2 ml of arachis oil, was administered daily, intramuscularly between 09:00 and 11:00. Treatment lasting 4 weeks was initiated 15 days before behavioural testing and continued during the test period. In group B, the procedure and steroid dosages were the same as in group A, but the order of treatments was reversed.

2.2.7. Statistical Analysis

Behaviours were recorded either as frequencies or as elapsed time. Negative adjustments to contacts, mount and intromission, as well as aggression and yawns, were transformed into binary categories (0-1) due to their very low frequencies and percentages were compared by means of a χ^2 test of association. The other frequency data were normalized using the appropriate square-root transformation and then, along with elapsed time, were subjected to an analysis of variance for unbalanced data with the general linear models procedure (SAS). Finally, a pairwise comparison of means was performed with a t -test and, for multiple means, the Duncan multiple-range test was adopted.

2.3. RESULTS

In the first part of the test, where the male was restrained, no effects of hormone treatments were found for female behaviours. Female-to-male distance, measured as the time spent by a female in each of the four sections of the cage, was not significantly affected either by EB or TP treatments. This was true also when females were tested with other females. The subject females spent the major portion of their test time in the section nearest the restrained partner (S3a) whether tested with a male or a female ($p < 0.001$). However, they spent significantly more time in S3a when a male was the partner than when tested with a female (Figure 2).

Presenting to the males was performed consistently but with marked individual variation both in the frequency (row means $\pm$ SEM ranging from 0.25 ± 1.4 to 12.75 ± 1.43) and in the posture chosen. A similar pattern was found in presenting to the females with a row mean $\pm$ SEM range of 0 to 7.5 ± 1.5 . Neither steroid treatment significantly affected frequency of presenting, but more presents were directed to male than to female partners (Figure 3, left).

The frequency of female movements within and between cage sections was consistent across the control and treatment cycles both with female and male partners. A statistically significant difference ($p < 0.0004$) was found when comparing results of tests with male and female partners, subject females being more active when exposed to males (Figure 3, right).

Certain indices of male behaviour showed significant change during hormone treatments of females. The time males spent in erection was individually specific with row means $\pm$ SEM ranging from 23.06 ± 9.73 to 58.37 ± 25.62 . Erection time was found to increase slightly with EB treatment and decreased with TP treat-

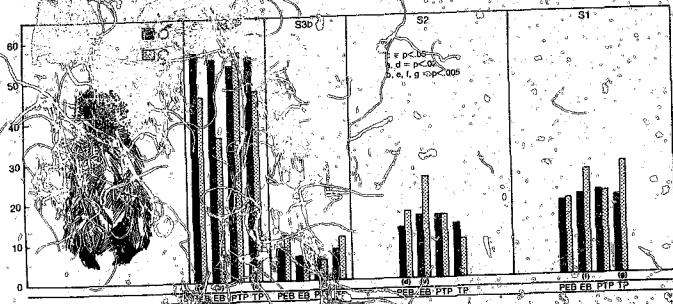


Figure 2. Schematic representation of the test situation with the restricted partner on the left of the picture. In each section of the cage, the percentage of time spent by the subject (female) with either a male (black bars) or a female partner (white bars) during the control (ES and PTP) and treatment (ES and TP) phases is illustrated.

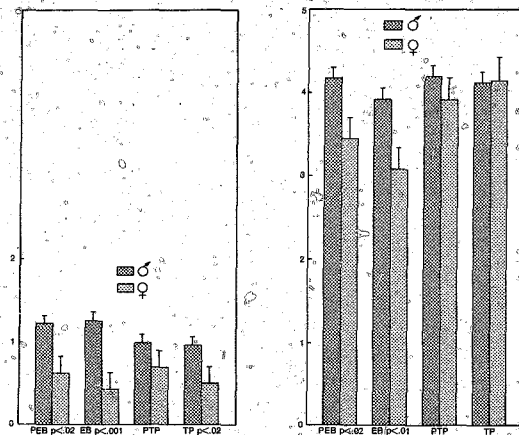


Figure 3. (left) Comparison of frequencies (means $\pm$ SEM) of presenting by the female subjects when paired with male and female partners during the control (PEB and PTP) and treatment (EB and TP) cycles. (Right) Comparison of frequencies (means $\pm$ SEM) of walking by the female subjects when paired with male and female partners during the control (PEB and PTP) and treatment (EB and TP) cycles.

ment, neither of which change was statistically significant with respect to the control periods. However, the difference between values for these hormone treatments was significant (Table 1).

Olfactory investigations were carried out through the wire mesh partition by all males and, as for erection time, a significant change in the frequency was found, only when results from EB and TP treatments were compared directly (Table 1).

No consistent effect of treatments could be found on the frequency of masturbation which instead was highly variable among the four males (row means $\pm$ SEM ranging from 0.12 ± 0.08 to 4.81 ± 0.85).

The results of the second part of the test, when the pair was free to interact, are slightly different from those just described. Female proceptive behaviours were consistently performed during the whole experimental period, as in the first part of the testing. The pattern shown for spontaneous presents (row means $\pm$ SEM ranging from 0.25 ± 0.16 to 16.00 ± 1.55) was very similar to that found in the previous part, although with significantly higher frequencies. No hormone-related fluctuations were found in proximity to the male (row means $\pm$ SEM ranging from 0.12 ± 0.12 to 3.25 ± 1.31 ; Table 2).

Negative adjustments to contact, mount, and intromission, together with aggression to the male, were very rare and were significantly absent during oestradiol treatment (see Table 2). Testosterone significantly increased yawning frequency (Table 2).

Males generally approached, contacted, and mounted the female very readily, usually as soon as the partition was lifted. No changes were observed in mounting behaviours which could be related to the treatments, but a significant decrease was found in approaching and contacting during TP administration (Table 3). Males typically ejaculated after a number of pelvic thrusts in a single mount and intromission (row means $\pm$ SEM ranging from 3.92 ± 0.35

TABLE 1

Frequencies and durations (Means $\pm$ SEM) of male behaviours during male restraint test

Male behaviour categories	Experimental periods			
	PEB	EB	PTP	TP
Olfactory investigations	0.35 $\pm$ 0.08	0.41 $\pm$ 0.08 ^a	0.34 $\pm$ 0.08	0.23 $\pm$ 0.08 ^b
Masturbations	0.83 $\pm$ 0.08	0.83 $\pm$ 0.08	0.83 $\pm$ 0.08	0.61 $\pm$ 0.08
Erection				
(in seconds)	283.40 $\pm$ 21.29	320.79 $\pm$ 21.29 ^a	298.22 $\pm$ 21.46	236.92 $\pm$ 21.46 ^b
(%)	47.23	55.46	49.7	39.48

Note. $a > b = P < 0.05$.

TABLE 2

Frequencies (Means $\pm$ SEM) and percentages of female behaviour during the pair mating test

Female behaviour categories	Experimental periods			
	PEB	EB	DTP	TP
Proximity	0.66 $\pm$ 0.08	0.70 $\pm$ 0.08	0.72 $\pm$ 0.08	0.67 $\pm$ 0.08
Presents spontaneous	1.61 $\pm$ 0.10	1.55 $\pm$ 0.10	1.17 $\pm$ 0.10	1.23 $\pm$ 0.10
Negative adjustments to contact (%)	7.81	0.00	4.69	11.11 ^a
Negative adjustments to mount (%)	10.94	0.00	1.56	9.52 ^b
Negative adjustments to intromission (%)	4.69	0.00	0.00	0.00 ^c
Aggression (%)	9.38	0.00	3.13	3.17 ^d
Yawns (%)	3.13	6.25	0.00	58.73 ^e

- ^a $\chi^2 = 7.07$, $df = 3$, $P = 0.05$.
^b $\chi^2 = 11.25$, $df = 3$, $P = 0.01$.
^c $\chi^2 = 9.06$, $df = 3$, $P = 0.02$.
^d $\chi^2 = 7.03$, $df = 3$, $P = 0.02$.
^e $\chi^2 = 105.51$, $df = 3$, $P = 0.0001$.

TABLE 3

Frequencies (Means $\pm$ SEM) of Male behaviours in the pair Mating test

Male behaviour categories	Experimental periods			
	PEB	EB	PTP	TP
Approaches	0.92 $\pm$ 0.06 ^a	0.86 $\pm$ 0.06	0.91 $\pm$ 0.06 ^a	0.68 $\pm$ 0.06 ^b
Contacts	1.26 $\pm$ 0.06	1.16 $\pm$ 0.06	1.30 $\pm$ 0.06 ^a	1.07 $\pm$ 0.06 ^b
Mounts	0.95 $\pm$ 0.05	1.03 $\pm$ 0.05	0.98 $\pm$ 0.05	0.85 $\pm$ 0.05
Intromissions	0.60 $\pm$ 0.04 ^b	0.92 $\pm$ 0.04 ^a	0.73 $\pm$ 0.04 ^b	0.64 $\pm$ 0.04 ^b
Intromissive pelvic thrusts	2.31 $\pm$ 0.34	2.30 $\pm$ 0.03	2.35 $\pm$ 0.03	2.36 $\pm$ 0.04
Ejaculations	0.59 $\pm$ 0.04 ^b	0.89 $\pm$ 0.04 ^a	0.71 $\pm$ 0.04 ^b	0.62 $\pm$ 0.04 ^b
Olfactory investigations	1.07 $\pm$ 0.08	1.24 $\pm$ 0.08	1.26 $\pm$ 0.08 ^a	0.98 $\pm$ 0.08 ^b
Time to ejaculation	44.60 $\pm$ 12.60	47.63 $\pm$ 10.29	63.58 $\pm$ 11.45	35.00 $\pm$ 12.44

Note. a>b = P<0.05.

to 7.71 ± 0.84). The time intervals before ejaculation were short (row means $\pm$ SEM ranging from 17.14 ± 2.14 seconds to 225 ± 52.32 seconds) and again, as with the number of pelvic thrusts, did not show any fluctuation according to female treatments (Table 3). Intromissions and ejaculations were significantly more frequent during the oestradiol treatment (Table 3).

Frequencies of olfactory investigations were significantly higher than in the first part of the test when the male was restrained ($p < 0.0001$) and, in addition, a decrease during TP was found with respect to the control period (Table 3). When results of olfactory investigations from the two test situations were summed, a significant treatment effect ($p < 0.01$) was found, with the highest mean frequency occurring during EB treatment (0.82 ± 0.07) and the lowest during TP (0.61 ± 0.07).

2.4. DISCUSSION

The picture that emerges from this study of sexual behaviour in vervet monkeys supports certain results of other laboratory and field studies. The active behaviour of females in terms of copulatory activity, proximity, distance from the male and taneous presents, as well as the fairly constant level copulatory performances, fits with the "prolonged/continuous oestrus" previously described (Struhsaker, 1967; Gartlan, 1969; Rowell, 1970).

Administration of EB and TP had a statistically significant influence on the sexual behaviour of the subject animals in this experimental situation. The main effect of EB treatment was accentuation of female attractiveness, as inferred from the increase in male ejaculation and intromission frequency together with less evident increases in erection time and olfactory investigation. TP treatment, on the other hand, seems to have adversely

affected attractiveness, as evidenced by increase in approaches, contacts, olfactory investigations, and erection time. It is unclear which aspects of female attractiveness were directly influenced by EB and TP since there are no visible external hormone-dependent attributes of female vervet monkeys. Furthermore, there was a general lack of effect of these hormones on female behaviours scored in this experiment. Perhaps males are aroused by oestrogen-induced chemical changes in the female perineum, a suggestion supported by the slight increase in olfactory investigation during EB treatment. It is also possible that the communication of female and male motivational states takes place at more subtle and complex behavioural levels than those considered in this study.

The only female behaviours found to change significantly were the negative or aggressive responses to the male during EB treatment and yawning during TP administration. A diminution of negative responses to advances by the male could result from oestrogen-induced changes in the vaginal secretions which facilitate intromission and pelvic thrusting. The increase in yawning, on the other hand, might be seen as the result of testosterone action directly on the central nervous system (Goy and Resko, 1972; Johnson and Phoenix, 1976).

Contrary to the findings of Czaja and Hielert (1975), Johnson and Phoenix (1976, 1978), Wallen and Goy (1977), Cochran (1979), and Wallen (1982), for the rhesus monkey, proximity to the male was found not to vary according to the hormonal state of the female, but instead changed only in relation to the sex of the partner. The same was true for spontaneous presents. The subject females not only spent more time closer to the male than to the female partner but also presented and moved more often in the presence of males. These behaviours can be seen as socially oriented in that they occur with female partners as well as males, but their

greater frequency with males also marks them as proceptive in that they may at least indirectly facilitate copulation.

Restraint of the male was used to elucidate possible hormonal influences on proceptive behaviour which otherwise might have been concealed. In fact, a test-condition-related factor was found only in the higher frequency of spontaneous presents during the pair test. Proceptive behaviour appears then not to be dependent on the hormonal state of the female nor to be obscured by physical interaction with the male.

In conclusion, results from this study indicate that hormonal treatment of ovariectomised female vervet monkeys had very little influence on sexual behaviour. The main changes were on male responses to female attractiveness, whereas female behaviours seemed to have assumed a more communicative function exhibiting, as a result, a more pronounced independence from their hormonal substrate.

3. OESTROGEN TREATMENT INFLUENCES ON FEMALE VERVET MONKEYS (*Cercopithecus aethiops pygerythrus*): PROCEPTIVITY AND ATTRACTIVENESS WHEN FEMALE AND MALE SUBJECTS HAVE A CHOICE OF PARTNER - EXPERIMENTS 2 AND 3.

3.1. INTRODUCTION

In its mating behaviour, the vervet monkey shows a marked independence from the effects of ovarian hormones. This has been shown recently in wild animals (Andelman *et al.*, 1985; Andelman, 1987) and could be inferred from other field reports (Whitten, 1984; Gartlan, 1969; Struhsaker, 1967) and observations on captive groups (Rowell, 1970, 1971, 1972),

In previous research (Experiment 1 - Chapter 2; Girolami, 1985), designed to investigate the possible dependency of sexual behaviour on ovarian steroids, a positive oestrogenic influence, seen in an increase of ejaculations, was elucidated, which suggests, at least, that, in vervet monkeys, there may well be an increase in copulatory activity at ovulation time. During oestrogen treatment, a decrease in female negative responses to male advances was found, while proceptive behaviours did not appear to increase either in the form of proximity scores or as presents. The ejaculatory frequency and minor increases in olfactory investigations and erection time suggested an oestrogenic action on female attractiveness. Attractive cues are considered by Beach (1976) to be oestrogen-induced stimuli, such as perineal elaboration and vaginal chemical compounds, both of which have been demonstrated to occur in primates (Girolami and Bielert, 1987; Curtis *et al.*, 1971), as well as solicitatory behaviours. On the

subject of perineal elaboration, Dixon (1983c) showed that, in those species that exhibit such attractive stimuli, copulations peak, or are restricted, around the ovulatory phase of the cycle when oestrogen levels are highest and when these traits are thus more pronounced. With regard to the existence of attractive cues in vervet monkeys, evidence is controversial. Vervet monkeys exhibit an orange/red sexual skin, confined to the anus and the clitoris (Henzi, 1982; Dixon, 1983c; Hrdy and Whitten, 1987). A pinkening of the sexual skin during the mating season was reported by Whitten (1984) but not by Henzi (1982), who noted, however, that, particularly during the breeding season, glances by males at the perineal region of the females were associated with erections. Wickler (1967) described a brightening of the perineal colours during oestrus although no colour fluctuations across the ovarian cycle have been reported by other authors (Struhsaker, 1967a; Rowell, 1972; Andelman *et al.*, 1985; Andelman, 1987; personal observation). With regard to olfactory cues, an increase in aliphatic acids contained in the vaginal discharge is present under oestrogen stimulation (Girolami, unpublished).

Clear increases in female soliciting behaviours, occurring regularly in relation to one portion of the ovarian cycle, have not been found in vervet monkeys (Andelman, 1987). Such increases were also not demonstrated by the previous experiment on hormonal manipulation (Experiment 1 - Chapter 2; Girolami, 1985). In this regard there is evidence, in other primates, that the occurrence of copulation and the expression of proceptive behaviours are regulated not only by ovarian hormones but also by the social environment (Goldfoot, 1971; Wallen and Winston, 1984; Zumppe and Michael, 1985a). A social environmental effect is suspected in vervet monkeys since dominant females have been observed to show sexual behaviours and give birth earlier than subordinates, in the breeding season (Whitten, 1984), and the dominant female of a caged

group was observed by Rowell (1971) to copulate more frequently at mid-cycle.

Aspects of female proceptivity, other than solicitatory behaviours, seem better to express female sexual motivation and its relation to her endocrine state, in particular when the female is in control of access to the male (Dewsbury, 1979; Beach, 1976; Feder, 1984). This is evident in the rhesus monkey and the orangutan. Female rhesus monkeys approached and spent more time with restrained or tethered males (Czaja and Bialert, 1975; Pomerantz and Goy, 1983) or performed an operant task to gain access to a male more quickly during the ovulatory phase of the cycle when levels of circulating oestrogens are highest (Bonsall et al., 1978). Female orangutans instead showed increased fertility when the door leading into the male's room permitted only the female's passage (Nadler, 1982).

In the light of these facts, two experiments were devised. The first one was intended to concentrate on female sexual motivation, and its dependence on oestrogen, as an aspect of female proceptive behaviours. An experimental situation was chosen in which the female had total control of access to her partners. This experiment investigated whether a female's choice of one of three alternatives - a male, a female or no choice at all, each partner being unaware of the female's presence - would be influenced by oestrogen treatment. The second experiment dealt with the question of attractiveness. It aimed to investigate whether the male's choice between one of two females would be affected by the oestrogen treatment of one of them. Since males have been shown to copulate regularly also with aphormonal females (see Experiment 1 above; Gifflami, 1985), a situation of direct comparison was chosen in expectation that the contrast provided by the presumed presence of the attractive attributes in the treated female, and

the lack of such attributes in the anohormonal female, would facilitate the male's choice.

3.2. GENERAL METHODS

3.2.1. Subjects

The subjects were the same four vasectomised males, and eight of the ovariectomised females (A, B, C, D, F, G, H, L), used in Experiment 1. All the subjects were familiar with each other. The females and two males, W and Z, one at a time, had lived as a group in a large cage outdoors for at least 3 years. There they established a group structure, or hierarchy, that was maintained over the years of living in single cages.

3.2.2. Housing

The monkeys were located at the Milner Park Unit of the Central Animal Service, University of the Witwatersrand, Johannesburg. They were housed indoors in individual cages which measured 60x80x60 cm. The males were in a room separate from the females. Temperature in the rooms was maintained constant at 22° C and artificial illumination was provided by fluorescent lights for twelve hours per day. The animals received a commercially prepared food pellet daily, supplemented three times a week with fresh fruit. One litre of water was provided twice a day.

3.2.3. Transport, Test-room, Scoring and Habituation

All the animals were carried to the test-room in a 30x30x41 cm metal-sheet cage, as described in Experiment 1. The test-room was adjacent to the females' room. It was illuminated by central

fluorescent lights and had the test-cage on one side. Opposite the cage, the observers sat behind a desk in full view of the animals. Behaviours were recorded on a tape recorder and then transferred, at the end of a test, onto a score-sheet. Time was kept by means of a stop-watch. The training for the task-performance for both experiments took four months.

3.2.4. Hormone Administration

The female subjects were injected once a day with 10 µg of oestradiol benzoate (EB) in 0.1 ml of arachis oil. Intramuscular injections were given between 08:00 and 09:00, three hours before the beginning of the test. Treatment was initiated 15 days before behavioural testing and continued during the test period for a total of 29 consecutive days of treatment per female. Seventeen days of rest were allowed between the last injection and the resumption of behavioural tests.

3.2.5. Statistical Analysis

Scored categories consisted of elapsed times and frequencies. Latencies to choice, elapsed times, were analysed by a two-way ANOVA with the General Linear Models Procedure (SAS). Frequencies of choice and all the scored behaviours were analysed by a Wilcoxon matched-pairs signed-rank test (Siegal, 1956). Of the scored behaviours, ejaculation was considered as a mean value over the times the female had been chosen. All the other behaviours were calculated into per-minute rates dividing the number of occurrences by the elapsed time to choice, expressed in seconds, and multiplied by sixty.

3.3: EXPERIMENT 2

3.3.1. Methods and Procedures

3.3.1.1. Apparatus

The test cage, a long wire-mesh and perspex cage (66x72x396 cm), consisted of six modules (66x72x66 cm) divided into three sections of two modules each by means of two chip-board partitions. The two partitions (96x70 cm) had swinging trap-doors (30x50 cm) which could be opened only from the central section. The doors, held closed by magnets, could easily be pushed open and were closed by gravity (Figure 4).

Mounted above each of the trap-doors at 32 cm from the cage floor was a round window (17 cm in diameter). The window was a one-way mirror that allowed vision only from the central section of the cage. The mirror, a disk of perspex, to which a self-adhesive reflective film had been applied, was mounted on the window protected by a convex metallic screen, facing the lateral compartments of the cage (Figure 4). In order to obtain the best one-way vision effect, two extra lights were mounted on each lateral compartment, whilst the central lights of the room were dimmed, thereby creating a light imbalance between the centre (darker) and the periphery (lighter) of the cage. Of the two lamps, a 200 watt globe illuminated the external module of the section, serving to increase the light level, whereas a 100 watt spotlight placed on the other module was pointed at the screened window to create a glare that served to "disguise" the window as well as to

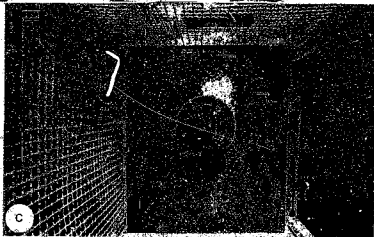
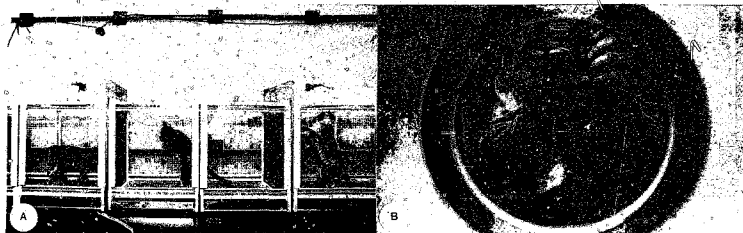


Figure 4. (A) The Female Subject (FS) in the central compartment of the cage and her two partners, female (FP) and Male. The Female Subject (FS) is looking at the Female Partner (FP) in the left compartment through the one-way mirrored window. (B) Detail of the outside of the partition. The mirrored window before and (C) after the convex screen is applied.

eliminate any mirror reflection that could distract the animals. The convexity of the screen instead served to increase the distance from the eye and the mirror, reducing any further possibility of vision from the lateral compartments (Figure 4).

3.3.1.2. Testing

The eight females were randomly divided in two groups of four referred to as the Female Subjects (FS) and the Female Partners (FP). The FS were matched to four different male-FP pairs so that thirty-two different trios were formed. All trios were tested with the FS anovulatory (PEB) as well as oestrogen treated (EB) and the roles of FS and FP were reversed at the end of the first cycle of testing so that FP could become FS and undergo their cycle of treatment. FS were always tested anovulatory first and tests were administered twice for each hormonal condition of FS for a total of 128 tests over 3 months. Only one observer was employed.

The test consisted in placing a male and a FP, one each, in one of the two lateral sections of the cage, on successive trials on a random basis, and FS, the experimental subject, in the middle section. The male and FP were let in first and the FS was brought to the test-room in a covered transport cage. The test was initiated when the FS was introduced to the central section and ended 5 minutes after she had made a choice. If no choice was made after 5 minutes, the test was ended and no interaction was allowed. Latencies of choice and number of peeps and attempts (see below) by FS were scored. When males were chosen by FS, the number of ejaculations was scored.

3.3.1.3. Categories Scored

Choice: Female entrance into one of the two lateral compartments (all four limbs inside the compartment), or the holding wide open of one of the doors for more than five seconds (Figure 5).

Latency of choice: Time elapsed from the start of the test to the choice.

Peep: Any discrete instance of looking through the window (Figure 5).

Attempt: Any touching, with a hand, of the partition, either slightly or strongly enough to push open the partition without actually holding it open (Figure 5).

Ejaculation: As in Experiment 1.

3.3.2. Results

Female subjects constantly preferred male partners, choosing them 73.44% of the time. Only one female, female B, regularly chose female partners, contributing 60% to the total of those tests in which females were chosen as partners. In a remaining 7% no choice was made (Figure 6 and Table 4). Oestrogen did not significantly affect female choice (Table 4).

The females chose rather quickly, with latencies ranging from 7.86 seconds (X) for female D during EB to 143.60 seconds (X) for female C during PEB (see Figure 7). Female latencies of choice were found to be significantly shorter during EB treatment (Figure 7).

None of the female behaviours scored showed any dependence on the hormonal treatment when a per-minute rate was considered (Table 5). However, the subjects devoted more peeps to the male partners than to the FP's under both hormonal conditions (Table 5).

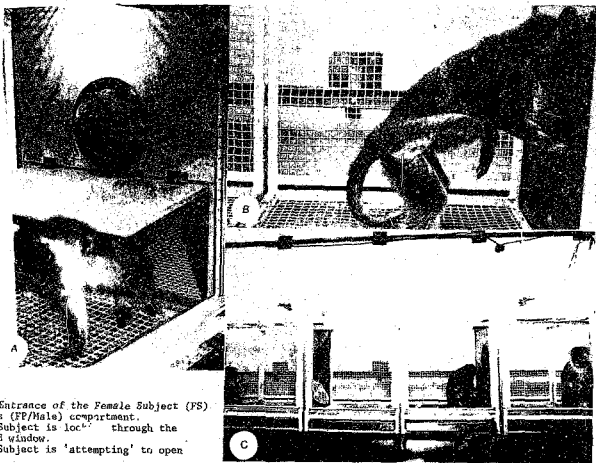


Figure 5. (A) Entrance of the Female Subject (FS) into a partner's (FF/Male) compartment.
 (B) The Female Subject is 'looking' through the one-way mirrored window.
 (C) The Female Subject is 'attempting' to open the door.

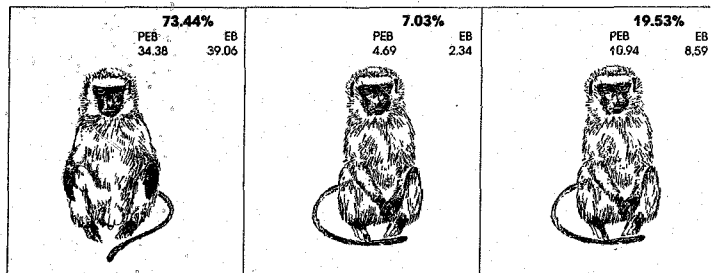


Figure 6. Schematic representation of the test situation of Experiment 2, with the Male in the left, the Female Subject (FS) in the middle, and the Female Partner (FP) in the right section of the cage. The percentages represent, respectively from the left, female choice of Males, female no choice, and female choice of Female Partners. The percentages are further divided into those occurring before (PEB) and during (EB) Female Subject treatment.

TABLE 4

Frequencies of choice by Female Subjects of Male, no choice or Female Partners (FP) before (PFB) and during (ED) oestrogen treatment.

Female Subjects	PFB			ED		
	Male	No choice	FP	Male	No choice	FP
A	8	0	0	8	0	0
B	1	0	7	0	0	8
C	2	3	3	5	2	1
D	6	0	2	6	0	2
F	5	2	1	7	1	0
G	6	1	1	8	0	0
H	8	0	0	8	0	0
L	8	0	0	8	0	0
TOT	44	6	14	50	3	11
	68.75%	9.37%	11.87%	78.15%	4.68%	17.18%

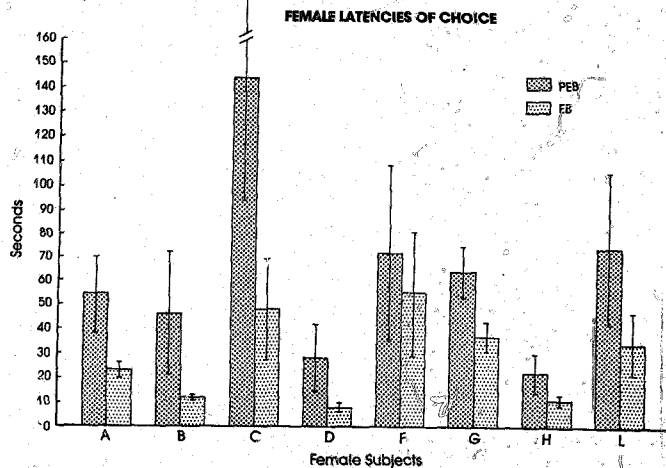


Figure 7. Comparison of latencies (mean $\pm$ SEM) of choice by each Female Subject (FS) before (PEB) and during (EB) oestrogen treatment.

TABLE 5

Frequencies/rates or means of female subjects' behaviors towards male and female partners as well as stimulations received before (PDB) and during (DB) oestrogen treatment.

Female subjects	Attempt				Penp				Stimulation received	
	Male		Female partners		Male		Female partners		FSR	ED
	FSR	ED	FSR	ED	FSR*	ED*	FSR*	ED*		
A Rates (Freq.)	1.39 (50)	2.60 (8)	0.55 (4)	1.63 (5)	2.09 (51)	1.63 (5)	1.67 (14)	2.28 (7)	1.00	1.00
B Rates (Freq.)	0 (0)	0 (0)	1.67 (4)	0.73 (2)	4.39 (10)	2.96 (5)	4.19 (10)	5.13 (6)	1.00	-
C Rates (Freq.)	1.11 (30)	0.80 (18)	0.99 (27)	0.87 (13)	4.66 (130)	3.36 (50)	4.21 (114)	2.55 (18)	1.00	1.00
D Rates (Freq.)	0 (0)	0.95 (1)	0.26 (1)	1.90 ^b (2)	1.57 (6)	5.71 (6)	0.78 (3)	2.85 (3)	1.00	1.33
E Rates (Freq.)	2.08 (36)	2.70 (31)	1.39 (24)	1.13 (13)	2.36 (39)	3.75 (43)	0.99 (17)	1.39 (16)	0.60	0.85
F Rates (Freq.)	0.63 (8)	0.60 (5)	0.57 (1)	0 (0)	1.59 (20)	3.44 (37)	0.37 (1)	1.82 (9)	1.00	1.25
G Rates (Freq.)	2.71 (8)	1.30 (2)	0 (0)	0 (0)	5.42 (16)	6.52 (10)	2.71 (4)	0.65 (1)	1.25	1.12
H Rates (Freq.)	0.60 (0)	1.50 (33)	0.20 ^b (2)	0 (0)	2.83 (38)	7.25 ^b (3)	0.22 (0)	1.50 (9)	1.37	1.12

*Wilcoxon matched-pairs signed-rank test $\alpha=0.05$; NS; $p=0.005$ for one-tailed test.

^bWilcoxon matched-pairs signed-rank test $\alpha=0.05$; NS; $p=0.02$ for one-tailed test.

When the chosen partner was a male, males copulated readily with the female subjects in both hormonal conditions and ejaculatory frequency was not significantly different between PEB and EB (Table 5).

3.4. EXPERIMENT 3

3.4.1. Methods and Procedures

3.4.1.1. Apparatus

The same cage, divided into three sections as in Experiment 2, was used, but in a slightly modified form. The trap-door partitions in this experiment were made of clear perspex so that vision was possible from both sides of the partition, and no extra lights were used.

3.4.1.2. Testing

Because female attractiveness seems to be related to hierarchical status (Goldfoot, 1971; Keverne *et al.*, 1982; Seyfarth, 1977; Zumpfe and Michael, 1981; Harcourt, 1987), four pairs of females of similar rank were formed and were rotated so that each of the four males could be combined with them, thus forming sixteen different trios. In order to allow all the females to be treated, the females were divided into two groups - the Female Subjects, those to undergo oestrogen-treatment (FS), and the Female Partners, those to remain anhormonal (FP). The trios were tested in two conditions - with both females (FS and FP) anhormonal and one female treated with oestrogen. After the first cycle of tests in which FS and FP were anhormonal (PEB), and then FS were treated and FP left anhormonal (EB) the roles were reversed so that female

partners became female subjects and vice-versa and a new cycle of tests could be started. FS were always tested anohormonal first. Tests were administered only once per pair under each hormonal condition of FS, for a total of sixty-four tests over two months. Two observers were employed - one following the action on the left half of the cage, the other on the right half.

Two females, one FS and one FP, were placed, one each, in one of two randomly selected lateral sections of the cage. A male, the experimental subject, was put into the middle section. The test consisted in presenting the male with a choice of either of the two females, or no choice at all. The females were let into the two lateral sections first. The partitions/doors were covered with cardboard sheets to prevent uncontrolled visual interaction, as was the transport cage containing the male (Figure 8). The test was initiated when the male was introduced to the central section and the cardboard sheets were removed. It ended 5 minutes after the male had made his choice, the whole test lasting a maximum of 10 minutes as in Experiment 2. If no choice was made after the first 5 minutes, the test was ended and no interaction was allowed. The time elapsed between the beginning of the test and male choice, as well as the frequencies with which the male looked, approached, head flagged and attempted to open the door, for each female, were scored. The behaviours considered for the two females were presents, looks and approaches to the male. After male choice the number of ejaculations were scored.

3.4.1.3. Categories Scored

Choice: The male's entrance into one of the lateral compartments (all four limbs inside the compartment) (Figure 8).

Latency of choice: The time elapsed from the start of the test to male choice.

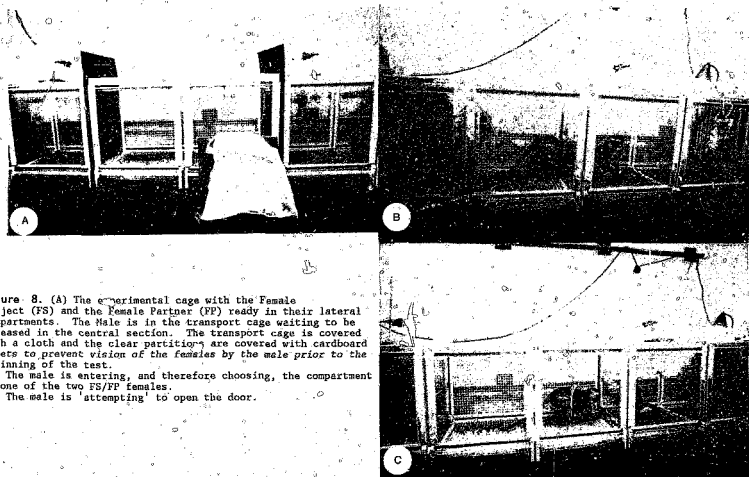


Figure 8. (A) The experimental cage with the Female Subject (FS) and the Female Partner (FP) ready in their lateral compartments. The Male is in the transport cage waiting to be released in the central section. The transport cage is covered with a cloth and the clear partitions are covered with cardboard sheets to prevent vision of the females by the male prior to the beginning of the test.
 (B) The male is entering, and therefore choosing, the compartment of one of the two FS/FP females.
 (C) The male is attempting to open the door.

Look: Any glance or peer at the animal in the adjacent section of the cage, including those delivered by the females while presenting.

Approach: Any walk towards the partition ending at or within touching distance of the partition.

Attempt: As in Experiment 2 (Figure 8).

Headflag: A lateral jerking of the head which might involve the shoulders, with the eyes kept on the partners, accompanied, at times, by genital display.

Present: An orientation of the perineum towards the partner often performed as a low crouch with the body oriented sideways (see Girolami, 1985).

Ejaculation: As in Experiment 1.

3.4.2. Results

Males made a choice in every test. Female subjects were chosen 31 times in 56 tests, 45% of which were during PEB and 55% during EB (see Figure 9). This slight increase applies only in four of the seven (FS-FP) female pairs (the eighth pair, F-L had to be dropped from this experiment due to an injury to female F) and does not reach the required level of significance (see Table 6).

As with the females in Experiment 2, male choice was made rather quickly, the latencies ranging from 3.28 seconds (X) for male Z during EB to 59.57 seconds (X) for male V during EB (Figure 10). Latency of choice was found to decrease during EB treatment in three of the four males (Figure 10) though no statistical difference was found between PEB and EB.

Males ejaculated, at least once, for each choice they made and no increase in ejaculatory scores was found when the female subjects had been treated, whether the female subjects themselves or the female partners had been chosen (Tables 7 and 8).

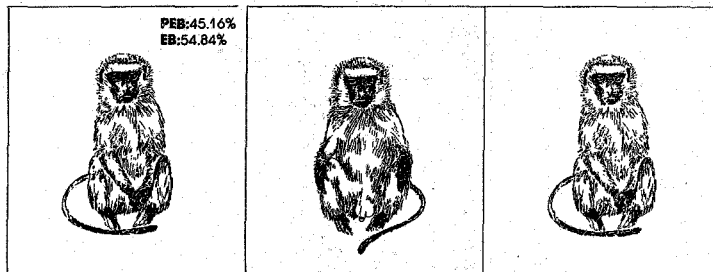


Figure 9. Schematic representation of the test situation of Experiment 3 with the Female Subject (FS) in the left, the Male in the middle, and the Female Partner (FP) in the right sections of the cage. The percentages represent male choice of the Female Subject before (PEB) and during (EB) the hormonal treatment.

TABLE 6

Frequencies of choice by Males of Female Subjects (FS) or Female Partners (FP) of seven FS-FP pairs before (PB) and during (DB) oestrogen treatment of FS.

Female Subject	Female Partners	PB		DB	
		FS	FP	FS	FP
A	G	3	1	4	0
B	C	1	3	1	3
C	B	3	1	4	0
D	H	0	4	1	3
G	A	1	3	2	2
H	D	3	1	3	1
L	F	3	1	2	2
TOT		14	14	17	11
		25%	25%	30.36%	19.64%

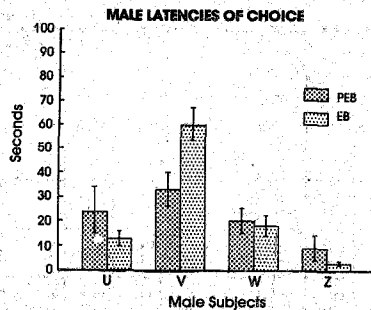


Figure 10. Comparison of latencies (mean $\pm$ SEM) of choice by each male before (PEB) and during (EB) oestrogen treatment of the Female Subject (FS).

TABLE 7

Frequencies, rates or means of Male behaviours towards Female Subjects before (PEB) and during (EB) oestrogen treatment of FS.

Male Subjects	Head Flag		Approach		Glance		Attempt		Ejaculation	
	PEB	EB	PEB	EB	PEB	EB	PEB	EB	PEB	EB
U Rates (Freq.)	0 (0)	0.64 (1)	1.76 (5)	1.29 (2)	4.94 (14)	7.74 (12)	1.42 (4)	0.64 (1)	1.50	1.33
V Rates (Freq.)	3.36 (14)	2.87 (20)	2.86 (11)	2.87 (20)	8.31 (32)	6.18 (43)	0.51 (2)	1.15 (8)	1.00	1.00
W Rates (Freq.)	0.43 (1)	0.46 (1)	0.43 (1)	2.86 (6)	5.56 (13)	7.96 (17)	0.43 (1)	1.87 (4)	1.00	1.50
Z Rates (Freq.)	0 (0)	0 (0)	2.72 (3)	0 (0)	9.09 (10)	2.62 (1)	0 (0)	0 (0)	1.00	1.33

TABLE 8

Frequencies, rates or means of Male behaviours towards Female Partners before (PEB) and during (EB) Oestrogen treatment of Female Subjects

Male Subjects	Head Flag		Approach		Glance		Attempt		Ejaculation	
	PEB	EB	PEB	EB	PEB	EB	PEB	EB	PEB	EB
U Rates (Freq.)	2.47 (7)	0 (0)	2.82 (9)	2.58 (4)	6.70 (19)	8.38 (13)	0.35 (1)	3.22 (5)	2.00	1.75
V Rates (Freq.)	1.03 (4)	1.58 (11)	2.07 (8)	2.44 (17)	6.75 (26)	5.17 (36)	0.77 (3)	1.15 (8)	1.00	1.00
W Rates (Freq.)	0 (0)	0 (0)	1.73 (4)	1.87 (4)	5.21 (12)	7.50 (16)	0.43 (2)	0.46 (1)	1.00	1.00
Z Rates (Freq.)	0 (0)	0 (0)	2.72 (13)	5.21 (12)	1.54 (5)	5.21 (2)	0.90 (1)	2.60 (1)	1.00	1.33

Treatment effect is found only as an increase in attempts towards FP. When attempts towards FP and M are summed, a significant increase during EB is also found (Tables 7 and 8).

Of the female behaviours considered, only presents show a constant pattern in relation to the hormonal treatment. Frequencies and per-minute rates increase in six of the seven female subjects during the EB treatment, though the results become statistically significant only when female B is excluded from the analysis (Table 9). Very interesting, instead, is the significant increase found in all seven of the female partners in their frequency and per-minute rate of presents during the female subjects' EB treatment (Table 10). However, when FS and FP presents during EB treatment are compared, no difference is found between the two categories. A tendency to decrease during EB is found in FS and FP approaches and FS glances in five FS-FP pairs out of seven.

3.5. DISCUSSION

Results from the two experiments taken together indicate that sexual behaviour in the vervet monkey is sensitive to ovarian hormones. They also indicate that the hormonal changes influence female behaviours rather than male responses. The first experiment of this chapter (Experiment 2) was designed to elucidate hormonal effects on female sexual motivation. The main parameter chosen to represent female sexual motivation was the choice between a female and a male partner. Males turn out largely to be the favourite partner for females in anohormonal conditions, as well since they were chosen more often and received a larger amount of visual attention (peep) than females. Furthermore males were repeatedly chosen even by females in which the long-standing anohormonal condition caused them to bleed and, presumably, to be in pain following copulatory attempts by the males, as in the case

TABLE 9

Frequencies and rates of female subjects behaviors before (PEB) and during (ED) oestrogen treatment.

Subjects	Present		Approach		Glance	
	PEB	ED	PEB	ED	PEB	ED
A Rates (Freq.)	0 (0)	2.53 (2)	3.15 (7)	3.84 (5)	5.41 (12)	5.38 (7)
B Rates (Freq.)	2.30 (2)	0 (0)	0.07 (7)	5.71 (6)	0.07 (7)	4.76 (5)
C Rates (Freq.)	3.18 (6)	3.30 (7)	4.24 (8)	3.30 (7)	4.77 (9)	6.61 (14)
D Rates (Freq.)	1.51 (2)	1.78 (3)	2.27 (3)	1.78 (3)	9.11 (32)	4.15 (7)
E Rates (Freq.)	0 (0)	0.58 (1)	4.89 (4)	2.35 (4)	11.25 (9)	5.29 (9)
F Rates (Freq.)	2.95 (3)	3.12 (5)	2.95 (3)	1.87 (3)	9.85 (9)	4.37 (7)
G Rates (Freq.)	0.50 (1)	1.27 (2)	1.51 (3)	2.35 (4)	5.54 (21)	9.29 (13)

* Wilcoxon matched-pairs signed-rank test $z=0$; N6 (excluding female B); $P < 0.02$ for one-tailed test.

TABLE 10

Frequencies and rates of Female Partners behaviours before (PEB) and during (SB) oestrogen treatment of Female Subjects.

Female Partner	Present		Approach		Glance ^c	
	PEB ^a	Ep ^a	PEB	EB	PEB	SB
A Rates (Freq.)	0 (0)	2.30 (3)	1.80 (4)	5.15 (8)	2.70 (6)	11.53 (15)
B Rates (Freq.)	0 (0)	0.95 (1)	6.92 (6)	8.57 (9)	8.07 (7)	7.61 (8)
C Rates (Freq.)	1.59 (3)	1.88 (4)	1.59 (3)	2.36 (5)	4.77 (9)	6.61 (14)
D Rates (Freq.)	0 (0)	1.18 (2)	3.03 (4)	1.78 (3)	3.79 (5)	4.15 (7)
F Rates (Freq.)	0.50 (1)	2.55 (4)	3.52 (7)	3.19 (5)	5.54 (11)	7.02 (11)
G Rates (Freq.)	0 (0)	0.58 (1)	2.49 (2)	2.35 (4)	9.9 (8)	4.72 (8)
H Rates (Freq.)	4.91 (5)	4.99 (8)	5.90 (6)	4.37 (7)	9.83 (10)	6.87 (11)

^a Wilcoxon matched-pairs signed-rank test $T=0$, $N=7$, $P<0.01$ for one-tailed test.

of females F and D. A preference for male over female partners, regardless of the hormonal conditions of the female, was also found in previous research (Experiment 1; Girolami, 1985). The preference for male partners thus suggests that females are attracted to males and are motivated to copulate even when an hormonal. Therefore, as reflected by the choice of males, female motivation shows only slight sensitivity to oestrogen treatment. The choice of male partners should be reflective of an interest in the male rather than of an act of submission to the stronger partner since the Female Subjects were in control of access to either companion and the males were not aware of the identity of the animal next door, i.e., the Female Subject. In this regard it is suggested that control of access over a male partner, either partial (Experiment 1; Girolami, 1985) or total, does not have a facilitatory effect on the performance of female proceptive behaviours in this species, as indicated for others. It is possible, however, that the manifestation of female sexual interest in relation to the ovarian cycle is facilitated by female control of male access mainly in those species in which the male is dominant over the female and forced matings can occur (Nadler, 1977; Nadler and Miller, 1982). In the rhesus monkey, males are not dominant as a rule over the females, possibly due to a reduction in canines and body size dimorphism (Hill, 1966; Lancaster, 1971; Rowell, 1971; Whitten, 1984).

In Experiment 2, speed of choice by FS, rather than any other parameter considered, showed sensitivity to oestrogen. This result is in agreement with a shorter latency of choice at the late follicular phase found in female Rhesus monkeys in similar experimental conditions (Bonsall *et al.*, 1978).

Experiment 3 was geared to show if oestrogen affected female attractiveness. If female attractiveness and its relation to oestrogen is judged from the results of mate choice and ejaculatory

frequency according to criteria elucidated by Beech (1976) and reviewed in Primates by Dixon (1980) and Hrdy and Whitten (1987), it would appear that the ability to attract an estrous male is not oestrogen-dependent in female vervets. A bias towards oestrogen-treated females was found in male choice but the other parameter of male arousal - ejaculatory frequency - was the same for the treated and untreated females for the two experiments. These findings are in agreement with previous work (Experiment 1, Girolami, 1985) in which not all measures of male arousal were affected by EB treatment. Since no change was observed in their sexual-skin, it is unlikely that the female perineum acted as an attractive stimulus, more so in the light of the fact that, in those species which show an oestrogen-sensitive perineal elaboration, this is a powerful stimulus (Girolami and Dieler, 1979). A possible involvement of olfactory cues should instead be discussed. Male vervet monkeys frequently examine female genitalia (Booth, 1962; Struhsaker, 1967a; 1971; Hrdy, 1982; Whitten, 1984; Girolami, 1985) but, in this experiment, they never attempted to sniff female genitalia prior to taking a choice. Even though the perspex partition, which could be lifted, might have interrupted direct sniffing, this itself was made of open mesh wire and thus did not prevent olfactory communication. If olfactory cues were significant for male arousal, as they are in rodents (Dessi-Fulgheri *et al.*, 1980), the pattern of choice should have favoured more strongly the EB-treated females. The presence of odoriferous substances, such as oestrogen-dependent increases in aliphatic acids, which occur in human females (Michael *et al.*, 1974), does not necessarily imply that they are used in sexual communication. On the other hand, the isolation of olfactory cues as a necessary stimulus for male arousal does not eliminate the possibility that these are a source of information for the male about the reproductive disposition of the female. In conclusion

it seems that female vervets do not rely on oestrogen-dependent attractive stimuli to arouse their males; they are highly attractive *per se*. Like human females it could be said that they "conceal" their ovulation (Andelman, 1987).

Experiment 3 revealed an oestrogenic effect on female behaviour in terms of female presents. The same effect was not revealed by the previous work on hormonal manipulation (Girolami, 1985). An effect of oestrogens on presents and, in general, on proceptivity in primates has been established although this particular aspect of female sexuality is subject to other influences that might well mask the effects of endocrine changes (Beach, 1976; Bawa, 1983; Dixon, 1983a). Pair-tests and minimal space conditions tend to obscure the hormonal effect on proceptive behaviour whereas a group situation or larger space enhances it (Wallen, 1982; Wallen and Winston, 1984). In this experiment as well the increase in presents found suggests that the dependency of this behaviour on oestrogen is facilitated in this species by a social situation, just as it is concealed by pair-tests.

In Experiment 5, concomitant to the increased frequencies of presents found in treated females (FS), increases in presents were also evident in their an-hormonal Female Partners. The social environment is a very powerful variable which can interfere with hormonal effects on proceptive behaviours. Proceptive behaviours are suppressed in some females even when they are in the "appropriate" hormonal condition, i.e., either in the late follicular phase or when oestrogen treated, and enhanced in others which are not in the "appropriate" hormonal condition (Eweritt and Herbert, 1969; Goldfoot, 1971; Zumpo and Michael, 1985). In a small group situation, this may result in monopolization of sexual behaviour by one female (Herbert, 1968; Eweritt and Herbert, 1969), later found to be the highest ranking female (Goldfoot, 1971; Boyman *et al.*, 1978; Keverne *et al.*, 1982; Zumpo and Michael, 1985; Abbot

et al., 1986). In a small group situation, often containing only one male, it is logical to attribute this phenomenon to female competition as Zumba and Michael (1985) have done. Female primates are known to establish a hierarchy of dominance through which they regulate access to resources. Female vervet monkeys have been found to establish a hierarchy and to compete for a number of resources, with high-ranking females obtaining privileged access to food, water, grooming partners and males (Lancaster 1971; Rowell, 1971; Seyfarth, 1980; Wrangham and Waterman, 1981; Angham, 1981; Whitten, 1984). Also they prefer to copulate with alpha-males, as in the talapoin monkey, and dominant females have been shown to be more successful than subordinates in interacting with alpha-males (Keverne *et al.*, 1982; Keddy, 1986; Andelman, 1987). Increases in interactions with the male have been reported for dominant females at mid-cycle and dominant females have been observed to copulate and to give birth earlier in the season (Rowell, 1971; Whitten, 1984). At this point, it is interesting to note that, in Experiment 2, of the four females that chose other females, three were the most dominant (B, C and D in ranking order) with the alpha-female choosing other females almost exclusively. Female B also never entered the other female's compartment first but kept the door lifted and then circled around the other female or paced to and fro holding the tail raised in the red-white-blue display as Struhsaker (1967a) described for dominant males.

The behavioural mechanism through which sexual monopolization is achieved is unclear (Abbott, 1987). Only a few episodes of overt aggression or supplants by the dominant females have been recorded (Keverne *et al.*, 1982; Abbott, 1987; Harcourt, 1987). The subordinates have been described as if they "...ensured their own celibacy" (Abbott *et al.*, 1986, p.336), by avoiding males. In vervet monkeys, subordinate females, avoiding higher ranking females, have been observed to allow them to monopolize spatially

restricted food resources (Whitten, 1984), and subordinate females at mid-cycle avoided the most dominant females (Rowell, 1971). Also a striking lack of aggression was reported by Struhsaker (1967b) in vervets competing for restricted vital resources. In fact when threats and attacks or supplants over male have been reported, they occurred either when groups were formed and hierarchies had to be established or when subordinate females were (physiologically) more likely to interact with the males, as a result of hormonal manipulation or at mid-cycle (Herbert, 1968; Everitt and Herbert, 1969; Goldfoot, 1971; Wallen and Winston, 1974; Floody, 1983; Zumpe and Michael, 1985; Abbott, 1984, 1986; Harcourt, 1987). Usually the dominant female shows high levels of presents and affiliative behaviours when these decrease in the subordinates (Herbert, 1968; Everitt and Herbert, 1969; Goldfoot, 1971; Zumpe and Michael, 1985). It seems, at this point, that the enhancement of proceptivity displayed by the dominant female is due to suppression of proceptive behaviours in the subordinates caused mainly by avoidance of the dominant and her possible aggression and also as an active agonism, by the dominant female, in proceptive behaviour. In certain cases, not only is female behaviour suppressed but also female reproductive physiology and ultimately fertility, through hypothalamic inhibition of the gonadotropin releasing hormone (GnRH) output, suppression of the luteinizing hormone (LH) surge and thus of ovulation. This phenomenon is predominant in New World monkeys (Bowman *et al.*, 1978; Keverne *et al.*, 1982; Abbott, 1984, 1986, 1987; Harcourt, 1987; French *et al.*, 1984). The increase in proceptive behaviours found in the anovulatory females during Experiment 3 is similar in a way to that found in the phenomenon, mentioned above, of monopolization of sexual behaviour. In this case, the increase in presents in the Female Partners seems to be triggered by the oestrogen-induced increase in proceptive behaviours of the Female Subjects. A pos-

sible explanation is that, in this case, females were of similar rank so that dominant-subordinate engendered inhibition was not present leaving the two females free to outbehave each other. It is suggested that the main behavioural mechanism through which mate competition is carried out, as well as behavioural or physiological suppression, resulting in infertility, is a contest of performance of preceptive behaviours.

In order to monopolize sex, females need the collaboration of males. Males seem to be very attracted to dominant females and devote most of their sexual attention to them even where, in those species which present oestrogen-induced arousing stimuli, these are absent and males cannot ejaculate (Herbert, 1968; Everitt and Herbert, 1969; Goldfoot, 1971; Keverne *et al.*, 1982; Zumpo and Michael, 1985; Harcourt, 1987). In the vervet monkey, dominant females have been reported to receive the most mounts, approaches, and genital investigations and the least withdrawals by males (Whitten, 1984; Keddy, 1986). It is possible that dominant females are more attractive because of the elevated levels of preceptive behaviours that they show.

Goldfoot (1981, 1982) has demonstrated that EB increases the probability of a female rhesus initiating copulatory interaction, and that males are not very successful in copulating unless the female initiates the interaction. Andelman (1987) reported only a 0.4 probability of male success for a male-attempted copulation in vervet monkeys. Female vervet monkeys are also known to attack male solicitors (Struhsaker, 1967a; Rowell, 1971; Girolami, 1985; Keddy, 1986; Andelman, 1987; Smuts, 1985). If that is the case, males should be ready to gauge when to respond to the female. The increased frequency of presents of FP and FS means that they presented more rapidly per unit time. This increased rapidity is in agreement with the faster choice they made in Experiment 2 and suggests that males also needed a shorter time to make a choice

which, in three cases out of four, they did. The fourth male, V, was probably the least experienced and showed longest copulatory latencies in other experiments as well (Experiment 1; Girolami, 1985, unpublished). Confronted by two highly solicitous females, he might have had difficulty in choosing. In fact, his latency during EB was even longer. The increase during EB of attempts shown by all the males also suggests an increased difficulty in making a choice. It is suggested then that females were chosen on the basis of their proceptive behaviour, more specifically, the promptness with which they solicited, as indicated by the increased presents and by the latencies of male choice.

In conclusion, female behaviours show a sensitivity to ovarian hormones and proceptive behaviours are increased by oestrogen, although they are also subjected to social modulation. Males, in order to copulate, appear to rely on female behaviour, probably assisted by oestrogen-induced olfactory cues in their judgement. Together with evidence from previous research (Girolami, 1985), it would seem then that, although the occurrence of copulation is not dependent on female ovarian hormones, the presence of oestrogen does increase the likelihood of its occurrence. Ultimately, however, copulation is controlled by social factors.

4. THE CHACMA BABOON (*Papio ursinus*) FEMALE PERINEAL SWELLING AND ITS EFFECTS ON MALE SEXUAL AROUSAL - EXPERIMENT 4

4.1. INTRODUCTION

The female reproductive tract is a prominent target for female hormones. At a cellular level, nuclear and cytosomal oestrogen and progesterone receptors have been identified in various sites of the urogenital tract and in particular the uterus, oviducts and sexual skin of a number of primate species (Chrousos *et al.*, 1984; West and Brenner, 1983; Kato *et al.*, 1980; Onouchi and Kato, 1983; Ozesu and Gould, 1982; McClellan *et al.*, 1984, 1986; Weaker *et al.*, 1983; Potgieter *et al.*, 1985). Specific site hormonal binding is the cause of a number of phenomena that occur in the mammalian female reproductive tract.

We know already of the proliferative effects that oestrogens, in particular oestradiol 17 β , have on the endometrium (Blum, 1985) and how the same oestrogens induce quantitative and qualitative changes in the vaginal and cervical epithelial cells and mucosa, so much so that these latter changes are often considered in the detection of oestrus and impending ovulation (D'Souza, 1978; Birnberg *et al.*, 1963).

A more dramatic phenomenon related to ovarian activity is the periodical perforation and closure of the vagina occurring in myomorph, sciurormorph and histricomorph rodents (Rowlands and Weir, 1984) and, among primates, in prosimians (Hrdy and Whitten, 1987). Closure of the vagina is obtained by the formation of a membrane produced by epithelial hyperplasia and fusion. In *Galago*

crassicaudatus and *G. senegalensis*, closure followed permanent ovariectomy and was also induced by progesterone administration (Girolami and Bielert, unpublished; Lipschitz, 1988), whereas perforation and cornification of the vaginal epithelium were obtained by subsequent oestradiol benzoate treatment (Girolami and Bielert, unpublished; Dixon, 1978; Lipschitz, 1988).

Similar to the phenomena mentioned above, in that it involves the external genitalia, is the tumescence that in various degrees of areas involved, inflation and erythema, is found in many mammalian females at oestrus. The most spectacular ones are found in some mustelids and across the primate order (Rowlands and Weir, 1984). In primates this phenomenon has been studied in detail and Dixon (1983c) reviewed all the information available on the distribution of sex-skin swellings in the order, the morphology, the anatomy and physiology of the sexual skin and presented an hypothesis on its evolution. In brief, the females of some catarrhines have evolved a specialized perineal skin which is sensitive to the female reproductive status. It responds to circulating oestrogens with oedema and/or erythema, whereas progesterone antagonizes these effects.

If a vulvar tumescence is acceptable to our minds as a preparation of the genital tract for coitus, analogous and probably homologous to the mechanism of vaginal perforation, it is more difficult to accept and understand the development of much larger and more elaborate structures which exist in the colobus, mangabey, baboon, chimpanzee and pygmy chimpanzee (Dixon, 1983c; Dahl, 1985) unless a communicative function is invoked.

Already in 1876, Darwin postulated that the sex-skin evolved as a sexual attractant. Pocock (1906) recognized an aphrodisiac function of the baboon swelling and in general this concept has been widely accepted and further extended to supposed sexual releasing stimuli in the human female (Goodhart, 1964; Wickler, 1967;

Eibl-Eibesfeldt, 1975). Desmond Morris (1967), in "The Naked Ape", hypothesized that human breasts and buttocks evolved as sexual signals analogous to the swollen perineum. Acceptance of this hypothesis, however, is based only on "A wealth of circumstantial evidence..." as Dixon mentioned in his review (1983c, p.70).

The chacma baboon (*Papio ursinus*) shows the largest sex-skin swelling among primates (Rowell, 1972) and therefore could be considered the best subject for investigation of the communicative function of this structure.

A positive association between swollen females and sexual behaviour has been noted in many of the species which present this phenomenon (Dixon, 1983c; Rdy and Whitten, 1987; Rowell, 1972). In wild and laboratory-tested chacma baboons copulations were found to be more frequent with increasing size of the swelling (Bielert, 1986; Saayman, 1970; Hall and DeVore, 1965; Hall, 1962). In *P. cynocephalus*, male masturbatory activity increased in proportion to the number of swollen females present in the troop (Hausfater, 1975), which indicates that males were in a heightened state of arousal. Recently Bielert and his co-workers have demonstrated clearly that male arousal, which is reflected in increased copulations, masturbation and testosterone levels, is positively correlated with female perineal turgescence in chacma baboons (Bielert, 1982; Bielert *et al.*, 1980; Bielert and van der Walt, 1982; Bielert and Girolami, 1986). In contrast, when subject females were hidden behind screens but still in auditory and olfactory contact, no alteration of male arousal state was found. This suggested that male arousal was mediated by a visual cue only (Bielert, 1982).

In many mammals, oestrogen is responsible for dramatic changes in female proceptive and receptive behaviours. Such behavioural changes have often been considered as important factors which

elicit male response (Beach, 1976). In the case of female primates, behavioural changes at ovulation are shown in various degrees (Baus, 1983), mainly as an increased frequency of so called "solicits" normally shown in the behavioural repertoire (see Hrdy and Whitten, 1987, for a broad overview). In the baboon, changes in female behaviour across the menstrual cycle have been reported in *P. cynocephalus* (Hausfater, 1975; Hausfater and Skoblick, 1985), *P. anubis* (Rowell, 1967; Rowell, 1969) and *P. ursinus* (Saayman, 1970; Bielert *et al.*, 1986; Bielert and Girolami, 1986). In *P. anubis* and *P. ursinus*, both in captive or free ranging conditions, presents were found to be most frequent for swollen females (Rowell, 1967; Saayman, 1970; Bielert, 1986). Presents and lipsmacks were found to increase in the chacma baboon also in our testing situation, from the early follicular to the ovulatory phases of the cycle (Bielert and Girolami, 1986). Therefore, the practical difficulty in isolating visual cues, provided by the swollen sex-skin, from those of oestrogen-induced behaviours has so far prevented an accurate assessment of the communicative importance of the perineal elaboration. This experiment aimed at testing the effectiveness of the perineal elaboration on male arousal in the absence of hormonal modulation of female behaviours.

4.2. MATERIALS AND METHODS

4.2.1. Subjects

Six ovariectomised female chacma baboons, A-3, A-4, B-1, Jaz, Jp-1456, VP-4, and nine males, A, B, C, E, F, G, H, BKA 278, and BKA 160, were employed in this experiment. The females were parous and had been ovariectomised a number of years previously. Three of the males, A, B, C, were vasectomised. All the subjects were wild-caught as adults, in the Northern Transvaal near Vaalwater,

and had been in captivity for a number of years. Full body weight, dentition and descent of testis were the criterion for determination of sexual maturity in the males whereas regular perineal/menstrual cycles and elongation of nipples as well as full body weight and dentition were the criterion for determination of sexual maturity and parity in the females. No information is available on the animals before capture but it is assumed that they all received species-typical socialization. At no time were the animals involved in any experiment other than the one described.

4.2.2. Housing

All animals were housed at the Frankenwald Unit of the Central Animal Service, University of the Witwatersrand. For the duration of the experiment, the subjects were in individual cages (91x91x190 cm), each provided with a sitting shelf, and located in a room with windows and fibreglass roof panels that allowed exposure to natural light cycles. An underfloor heating system maintained a minimum temperature of 18° C.

4.2.3. Testing and Apparatus

The nine males were arranged around the three sides of the room and faced a cage which contained one of the six females who was in full view of all the males (for further details see Bialert, 1982). The female was left with the males for a total of eight days. For each female, behaviour was observed for 30 minutes a day for the eight days of testing. For the first four days, the females were observed with unswollen perinea (PRESWELL). On the fourth day, after the behavioural observation, the females were sedated with ketamine hydrochloride (7.5mg/kg, IM) and fitted with

a moulded plastic model perineum (Fig. 1) which reproduced in detail a fully swollen sex-sk'n. The plastic model was obtained by anaesthetising (see above) a fully swollen female and taking a plaster of Paris impression of her perineum which was then used to mould the artificial swelling with thermoplastic splinting material.¹ Finally, it was painted with a combination of red and white oil paint to mimic the natural colouration. The model was held in position by an adjustable belt and two straps made of grey nylon belt webbing padded with foam. The model perineum was well tolerated by the females who showed no signs of distress. Observations of female behaviours were resumed the following day and carried on for a further period of four days (SWELL).

The level of sexual arousal of each male was recorded for the eight days of testing. Male response to each female was measured by scoring the daily occurrence of coagulated seminal emissions resulting from masturbation, the same system adopted previously by Bielert *et al.* (1980) to assess male arousal in similar experimental conditions. It does not take into account the actual frequency of masturbation but only the daily presence or absence of seminal emissions as evidence of masturbation. Due to inter-individual variability in masturbatory frequency, this was considered to be a more accurate assessment of a "psychophysiological" state such as sexual arousal. When a group of individually caged males is housed together in the absence of a female, these seminal emissions are a very rare phenomenon across the year (Bielert *et al.*, 1980). With the introduction of a cycling female, males show significant increases in seminal emissions only at the time of maximal turgescence of the female perineum (Bielert and van der

¹ San Splint XR, Smith & Nephew Inc., 2100 52 Avenue, Lachine, Quebec, Canada H8T 2Y5.



Figure 11. (A) One of the experimental subjects wearing the perineal model.
 (B) The perineal model and harness.
 (C) The model as it came out of the mold.

Walt, 1982; Bielert and Sirolami, 1986). Observations were made in a total of 48 tests over a period of 3 months.

4.2.4. Scoring

Due to the excitability of the males, when they are exposed to a fully swollen female, and to the relative unfamiliarity of the observer with the subjects, the observer sat behind a screen containing a one-way mirror providing a good view of the experimental subject. Female behaviours were recorded on a score sheet divided in five minute intervals. Time was kept by means of a stop-watch.

4.2.5. Measures Scored

Presents: A quadrupedal posture in which the female orients her perineum towards another animal, with a swinging motion of the hind quarters. A present might be accompanied by a stare "Eye contact" with the female turning her head at the individual to whom the present is addressed. A present is also often accompanied by "Lip-smacks".

Lip-smacks: Smacking of the lips while looking at another individual. Smacking of the lips is most often audible, but might also be silent. It is usually accompanied by brow and ear retraction and "Eye contact".

Seminal emissions: Solidified ejaculate, visible on the floor underneath the cage, resulting from masturbation, the presence of which was scored daily for each male before the cleaning of the room floors. This system (following Bielert *et al.*, 1980) has proven to be a reliable measure of male sexual arousal under these experimental conditions.

4.2.6. Habituation

The female subjects, already familiar with the males and the experimental situation, were moved into the experimental room approximately one week before the commencement of the tests.

4.2.7. Statistical Analysis

Due to the low frequency of presents, presents and lip-smacks were combined into a new category called "Solicits". Mean frequencies of solicits and mean occurrences of seminal emissions were analysed by a Wilcoxon matched-pairs signed-rank test and correlations were tested with the Spearman's correlation coefficient (Siegel, 1956).

4.3. RESULTS

Female behaviour was not significantly affected by the swelling (Table 11). In fact, from a mean per female, per half-hour, of 10.83 during PRESWELL, it decreased slightly to 9.12 during the SWELL period. Nor was the frequency of presents alone found to be significantly different between the two test periods (mean number of presents per female per half-hour of 0.20 during PRESWELL and 0.25 during SWELL).

On the other hand, the behaviour of the males changed dramatically when the females wore the artificial swelling (Table 12 and Figure 12). In the first part of the tests, when the females were not wearing the prosthesis, 22% of the males produced seminal emissions; in the second part of the tests when the females wore the artificial swelling, 89% of the males did.

TABLE II

Frequencies and mean values of female behaviour (presents in brackets), male responses and percentages of male responders per female preceding (PRESWELL) and during (SWELL) the application of the perineal model.

Female Identification	PRESWELL					SWELL				
	Female Behaviour *	Male Response	Male Responders			Female Behaviour *	Male Response	Male Responders		
	(Freq)	($\bar{x} \pm SD$)	(Freq)	($\bar{x}$)	(%)	(Freq)	($\bar{x} \pm SD$)	(Freq)	($\bar{x}$)	(%)
A-3	86	21.50 $\pm$ 7.18	1	0.02	11.11	62	25.50 $\pm$ 3.10	3	0.06	22.22
A-4	(2) 41	10.25 $\pm$ 8.73	1	0.02	11.11	(5) 71	17.75 $\pm$ 7.27	8	0.22	44.44
B-1	45	11.25 $\pm$ 3.30	2	0.05	11.11	19	4.75 $\pm$ 2.51	4	0.11	11.11
JEZ	1	0.25 $\pm$ 0.50	0	0	0	5	1.25 $\pm$ 1.25	10	0.27	44.44
JP-1456	43	10.75 $\pm$ 3.86	0	0	0	(1) 17	4.25 $\pm$ 2.06	7	0.19	55.55
VP-4	(3) 44	11.00 $\pm$ 2.16	0	0	0	45	11.25 $\pm$ 3.30	13	0.36	66.66
Total	260	10.83 $\pm$ 6.72	4	0.01	-	219	9.12 $\pm$ 6.70	45	0.20	-

* Wilcoxon matched-pairs signed-rank test $T = 8.5$; $N = 6$; $H.S.$

TABLE 11

Frequencies and mean values of female behaviour (presents in brackets), male responses and percentages of male responders per female preceding (FRESHWELL) and during (SWELL) the application of the perineal model.

Female Identification	FRESHWELL					SWELL				
	Female Behaviour *		Male Response		Male Responders	Female Behaviour *		Male Response		Male Responders
	(Freq)	($\bar{x} \pm SD$)	(freq)	($\bar{x}$)	(%)	(freq)	($\bar{x} \pm SD$)	(freq)	($\bar{x}$)	(%)
A-3	86	21.50 $\pm$ 7.18	1	0.02	11.21	62	15.50 $\pm$ 3.10	3	0.08	22.22
A-4	(2) 41	10.25 $\pm$ 8.73	1	0.02	11.11	(5) 71	17.75 $\pm$ 7.27	8	0.22	44.44
B-1	45	11.25 $\pm$ 3.30	2	0.05	11.11	19	4.75 $\pm$ 2.51	4	0.11	11.11
JEE	1	0.25 $\pm$ 0.50	0	0	0	5	1.25 $\pm$ 1.25	10	0.27	44.44
JP-1456	43	10.75 $\pm$ 3.86	0	0	0	(1) 17	4.25 $\pm$ 2.06	7	0.19	55.55
VP-4	(3) 44	11.00 $\pm$ 2.16	0	0	0	45	11.25 $\pm$ 3.30	13	0.36	66.66
Total	260	10.83 $\pm$ 6.72	4	0.01	-	219	9.12 $\pm$ 6.70	45	0.20	-

* Wilcoxon matched-pairs signed-rank test $T = 8.5$; $N = 6$; N.S.

TABLE 12

Occurrences and mean values of male response and percentage of females eliciting male response preceding (PARKSWELL) and during (SWELL) the application of the perineal model.

Male Identification	PARKSWELL			SWELL		
	Male response *		Females eliciting male response (%)	Male response *		Females eliciting male response (%)
	(Freq)	(%)		(Freq)	(%)	
A	0	0	0	0	0	0
B	3	0.12	33.33	16	0.66	100.00
C	0	0	0	14	0.53	83.33
E	1	0.04	16.66	2	0.08	33.33
F	0	0	0	3	0.12	33.33
G	0	0	0	3	0.12	33.33
H	0	0	0	5	0.20	50.00
NKA 278	0	0	0	1	0.04	16.66
NKA 160	0	0	0	1	0.04	16.66
Total	4	0.01	-	45	0.19	-

* Wilcoxon matched-pairs signed-rank test $T = 0$, $N = 8$; $p < 0.009$ for one-tailed test.

% OF FEMALES ELICITING MALE RESPONSE

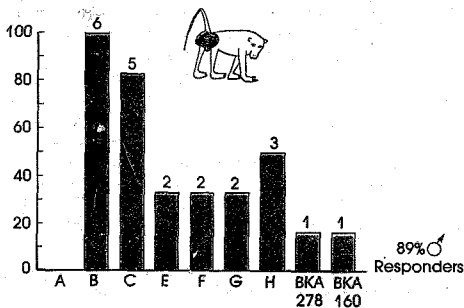
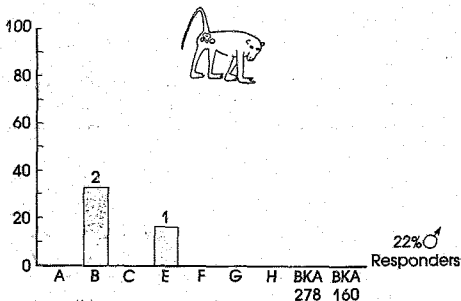


Figure 12. Percentage of females eliciting response in each of the male subjects during PRESWELL and SWELL.

Furthermore, seminal emissions increased, from a mean per male per day of 0.01 to a mean of 0.19, as did the number of females to which the males responded. Only three females (50%) elicited male response during PRESWELL whereas 6 (100%) did so during SWELL.

Male response was not correlated with any of the female behaviours (Table 11 and Figure 13). Neither the female performing the highest number of solicits (A-3), nor the one with the highest frequency of presents alone (A-4), elicited the greatest male response.

4.4. DISCUSSION

Female behaviour frequency was in the range of that shown by ovariectomised females in similar experimental conditions (Bielert and Girolami, 1986) and was not affected by the artificial swelling. Also male response showed comparable levels and patterns of individual variation to those obtained under similar experimental conditions (Bielert and van der Walt, 1982; Bielert, 1982; and for discussion on individual variation, Bielert and Girolami, 1986). When the females were wearing the prosthesis, males responded as if exposed to fully swollen females (Bielert and Girolami, 1986; Bielert and Anderson, 1985; Bielert, 1982; Bielert and van der Walt, 1982; Bielert *et al.*, 1980). They showed higher levels of masturbation and the number of responders increased. In fact the shift in percentage of responders is very similar to that found in another group of eleven males tested under similar experimental conditions with two ovariectomised females before (18% of responders) and during (94%) oestrogen treatment (Bielert *et al.*, 1980).

The artificial swelling made the females more attractive. Not only did the levels of male response increase in a larger number of males, but also all the females become effective in eliciting

FREQUENCIES OF ♀ BEHAVIOUR AND ♂ RESPONSE

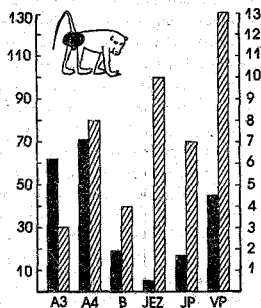
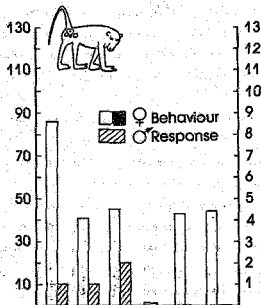


Figure 13. Frequencies of female soliciting behaviour in relation to occurrence of male response during PRESWELL and SWELL.

male response when wearing the prosthesis. This change in female attractiveness can be attributed solely to the application of the artificial swelling. Hormonally induced odour changes, as found in rhesus monkeys (Michael and Keverne, 1968), could be excluded as a factor since the females were ovariectomised. Furthermore, olfactory and acoustic cues had been ruled out previously as critical arousing stimuli effective in this experimental situation (Bielert, 1982).

Finally no correlation was found between female behaviour and male response.

The results from this experiment confirm a previous conclusion that the perineal swelling is the stimulus that sexually arouses the males (Bielert and Girolami, 1986). The fact that no direct causative link had previously been found between female swelling and male copulation or genital investigations (Rowell, 1967) is probably because the swelling as a stimulus has a priming action on male arousal. It is, therefore, concluded that, in the chacma baboon, and possibly in the other species which present the same phenomenon, the perineal swelling has a definite function in sexual communication - it is the main element of female attractiveness.

The fact that the male baboons responded to a female wearing a model in the same way that they responded to a swollen female allows for some speculation on the stimulus itself and the type of communication involved. Males clearly respond to the size of the swelling. When males are in the presence of females, either in a pair-test situation or when allowed only to watch, their response, in terms of copulatory or masturbatory ejaculations, increases with increases in the size of the perineal swelling (Bielert, 1986; Bielert and Girolami, 1986; Bielert *et al.*, 1982). In fact, there appears to be a threshold constituted by a minimum size to which males will start responding (Bielert, 1982; Bielert and van der Walt, 1982; Bielert *et al.*, 1986), and males show an

exaggerated response to females that have developed exceptionally large swellings (Bielert and Anderson, 1985). Male testosterone levels rise together with seminal emissions at the mere exposure to swollen females and appear to be positively related to the degree of swelling (Bielert *et al.*, 1980; Bielert and van der Walt, 1982). The colour of the swelling is also an important determinant in the inducement of male arousal. Alterations of male response can be obtained by the manipulation of colours of artificial swellings worn by females, and adequate response is achieved only by the colour red (Bielert *et al.*, in press). Additionally, in the absence of females, male levels of seminal emissions show seasonal changes which correspond to an increase in swelling females in feral animals living in the same region (Bielert *et al.*, 1980).

All characteristics shown by male response could indicate a type of communication implicating a releaser. The female perineal swelling would be a releasing stimulus eliciting (under natural conditions) male copulation through the inducement of male arousal. Current interpretations of the concept of releaser do not restrict the response elicited by a releaser to "innate" behaviour and do not consider this aspect as qualifying for the stimulus (McFarland, 1981; Heymer, 1977; McFarland, 1985; for a list of releasers, see Eibl-Eibesfeldt, 1975). Like Curio's descriptive definition of a sign stimulus, a definition of a releaser "*leaves open the question of the developmental history of the response in the individual animal*" (Curio; cited by McFarland, 1981, p. 507). Attempting to establish whether the reaction to the swelling on the part of the males is innate, acquired, or both is beyond the scope of this experiment. A proper assessment of experiential or inborn aspects of male response would in fact require additional work, since none of the males in this study was known to be sexually inexperienced.

The perineal swelling shares certain characteristics with other releasing stimuli. It is a conspicuous, very well-differentiated anatomical structure that develops and subsides in a rhythmic way. It is rendered conspicuous by its size and by the behaviour of the female. It conveys information important to conspecifics - the reproductive state of the female. It is a visual stimulus that can be perceived easily by conspecifics at a distance, since vision is highly developed in higher primates. Finally it has a specific effect (Bernstein and Gordon, 1979) in "...that the colour and inflammation appeal to the aesthetic sense and sexual emotions of the males and act as an aphrodisiac impelling them to pair with females in which the characters are pronounced rather than with those in which they are poorly developed or absent" (Pocock, 1906).

5. FEMALE CHACMA BABOON CHANGES ACROSS THE MENSTRUAL CYCLE, IN VISUAL INTERACTIVE BEHAVIOURS. A COMPARISON BETWEEN MENSTRUAL CYCLES IN FEMALE VERSUS MALE SOCIAL ENVIRONMENTS - EXPERIMENT 5.

5.1. INTRODUCTION

Soliciting behaviour is directed not only toward adult males but to other classes of individuals as well and is not used exclusively in a sexual context (Rowell, 1967; Hausfater and Takacs, 1967). The hypothesis to be tested here, therefore, is whether soliciting behaviour would show a difference, either in terms of frequency or in terms of distribution across the cycle, according to the sex of the recipient. To this purpose female solicits to females and to males, across a menstrual cycle, will be compared in an experimental situation that does not involve physical contact, in the expectation that the female subject will express her preferences more freely, in the absence of threats of physical attack.

5.2. MATERIALS AND METHODS

5.2.1. Subjects

This experiment employed nine female and fourteen male chacma baboons. Three of the females were the experimental subjects: 1081, 1087 and 1135. The other six formed the "female social environment": Mh-1, Mh-2, DB-9, BO-10, TH-1, and 83. The fourteen

males were divided into two groups which alternately formed the "male social environment". The first group included males A, B, C, E, F, G and H, while the second group included males NST-110, NST-111, NST-112, NST-113, NST-114, K-17 and EKA-54. For the criteria for the selection of the subjects, see 4.2.1. above.

5.2.2. Housing

For the two male groups - As in 4.2.2.

The six females were housed in individual cages in a large outdoor enclosure sheltered by a roof, and parts of two walls, of corrugated iron. The remaining walls of the enclosure were of wire mesh. The premises were as in 4.2.2.

5.2.3. Testing

Seven males or six females were arranged, as in 4.2.3. above, in their individual cages around the three sides of their housing room/enclosure. They faced a cage which contained one of the three experimental subject females. For each of the three females, behaviour was observed for 36 minutes per day, as in 4.2.4. above, each day for one full menstrual cycle in the presence of seven males (FM) and for a full menstrual cycle in the presence of the six females (FF). The experimental subjects were tested with the same group of six females. Females 1081 and 1135 were tested with the first group of seven males while female 1087 was tested with the second group. Each experimental subject female saw one group of males and one group of females. Tests with males preceded tests with females for Females 1087 and 1081 whereas the opposite was true for Female 1135. Cycles were not consecutive but, for each female, only one cycle intervened between the experimental cycles.

In order to determine the stages of the menstrual cycle of the experimental subject, the three females were checked visually daily for the occurrence of menses and for the degree of swelling of the perineum. The latter is directly related to the hormonal conditions of the female and constitutes an external indicator of ovarian activity (Gillman and Gilbert, 1946). For this reason systems based on the degree of swelling or on the state of the perineum have been adopted for obvious reasons of practicality in a number of field and laboratory studies. The cycles are usually divided in two parts, the phase of turgescence and the phase of deturgescence, which are further subdivided according to the degree or the state of the swelling. Scales of 1-5 points or of 1-3 points, as in this study, have been adopted to define the degree of swelling. The swelling has also been described as flat, inflating, fully swollen, and deflating. The phase of turgescence begins at the onset of bleeding, ending through full turgescence, up to the point of sudden deturgescence. The phase of deturgescence follows sequentially and is terminated by the onset of bleeding. The landmark between the two parts is the first day of deturgescence, called by some authors 'D' for detumescence or, as in this study, 'BD' for breakdown (Rowell, 1967, 1969; Saayman, 1970; Hausfater, 1975; Seyfarth, 1978a, 1978b; Ransom, 1981; Scott, 1984; Smuts, 1985; Rasmussen, 1985). This subdivision, and the perineal rating scales used to individuate the cycle stages, have been possible as a consequence of the pioneering work of Gillman (1937) and Gillman and Gilbert (1946). The particular system employed in this study (see Perineal Swelling Rate in 5.2.4.) is that adopted previously by Bielert (Bielert and Howard-Tripp, 1983; Bielert and Busse, 1983; Bielert and Girolami, 1986; Bielert, 1986).

Scoring was the same as in 4.2.4. above. A total of 77 observations were carried out over 6 months.

5.2.4. Measures Scored

Perineal Swelling Rate (Swell Rate): A three-point scale was used to describe the degree and state of perineal swelling. The perineum was considered a '1' if flat, a '2' if inflating or deflating and a '3' if fully swollen. The day of a "just detectable" decrease in the full turgescence was designated as the day of sex-skin "breakdown" or 'BD'. Assessments of swell rate were visually.

Presents: As in 4.2.5.

Lip-smacks: As in 4.2.5.

Yawns: Hyperextension and slight dislocation of the mandible. The lips are retracted and the gums and teeth exposed.

5.2.5. Habituation

As in 4.2.5. The groups of males and females had been together for at least one month before the beginning of the tests.

5.2.6. Cycle Phases and Statistical Analysis

Each menstrual cycle was divided into five sequential phases. Phase 1 begins with the day of onset of menses and consists of the days in which the perineum is flat (Swell Rate 1). Phase 2 consists of those days in which the perineum starts and continues to inflate (Swell Rate 2). Phase 3 consists of the days in which the perineum is fully swollen (Swell Rate 3). Phase 4 consists of the days in which the perineum starts and keeps deflating (Swell Rate 2). Phase 5, which consists of the days in which the perineum is again

flat (Swell Rate 1), ends the day before the ensuing menstrual bleeding.

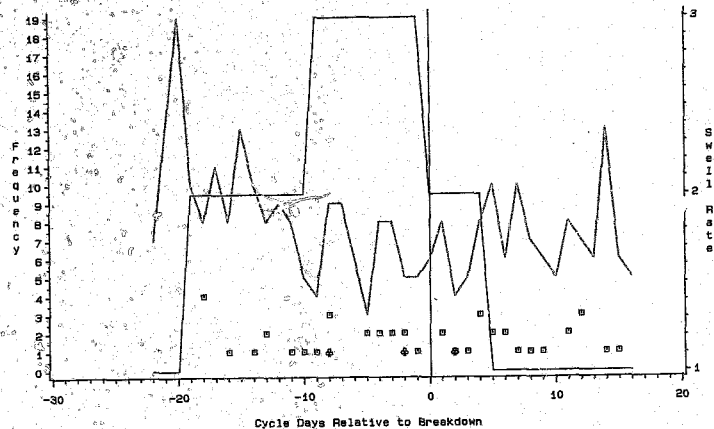
Frequencies of female behaviour were compared in different phases within individual cycles and in cycles of the three subject females combined (during FF, during FM, and with FF plus FM) by an analysis of variance for unbalanced data with the General Linear Models Procedure (SAS). The Duncan multiple range test was adopted to reveal significant differences between the means.

5.3. RESULTS

Menstrual cycles of the female subjects ranged in length from 34 to 39 days with a mean of 36.33 ± 1.86 days (Figures 14, 15, 16). Cycles of the females when exposed to males were slightly longer ($\bar{X} \pm SD$; 36.66 ± 1.15 vs 36.00 ± 2.64) than those when with female companions. Menstrual bleeding ranged from 2 to 5 days and it lasted ($\bar{X} \pm SD$) 2 ± 0.0 days for female 1087, 2.5 ± 0.70 for female 1081, and 4 ± 1.41 for female 1135. For female 1087, the time, from the onset of menstrual bleeding to breakdown day, was 22 days for the FF cycle and 23 for the FM cycle. Her perineum was fully swollen for 9 days during FF and 14 during FM (Figure 14). Female 1081 took 23 days to reach breakdown during FF and 26 during FM. She was fully swollen for 14 days during FF and for 15 during FM (Figure 15). Female 1135 reached breakdown after 19 days during FF and after 21 days during FM. She was fully swollen for 10 days with female partners and for 11 days with male partners (Figure 16).

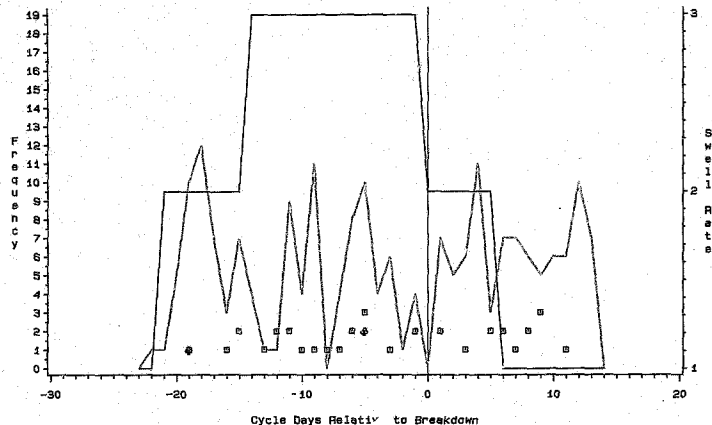
Female behaviours were given at very different rates. Presents were a rather rare occurrence (Total N=21; range 0-3), yawns were performed at low frequencies (Total N=18; range 0-7) and lip-smacks were the most frequent behaviour. Lip-smacks and presents were combined and considered statistically as "Solicits" (Figures

Figure 14a. Female 1087 vs Females



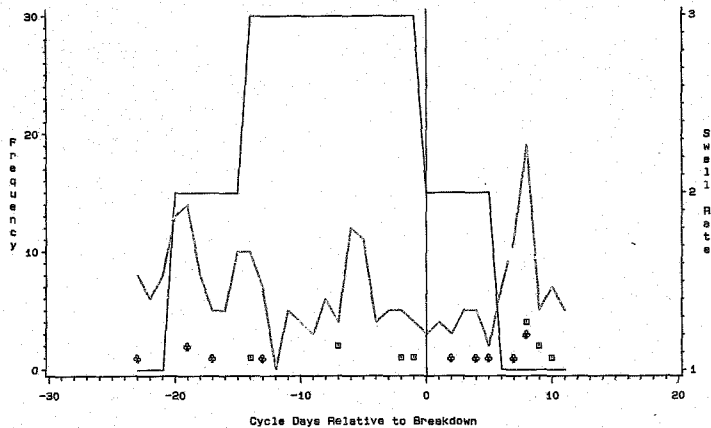
Yellow represents Frequency of Solicits Red represents Frequency of Yawns
Green represents Frequency of Presents Blue represents Swell Rate

Figure 14b. Female 1087 vs Males



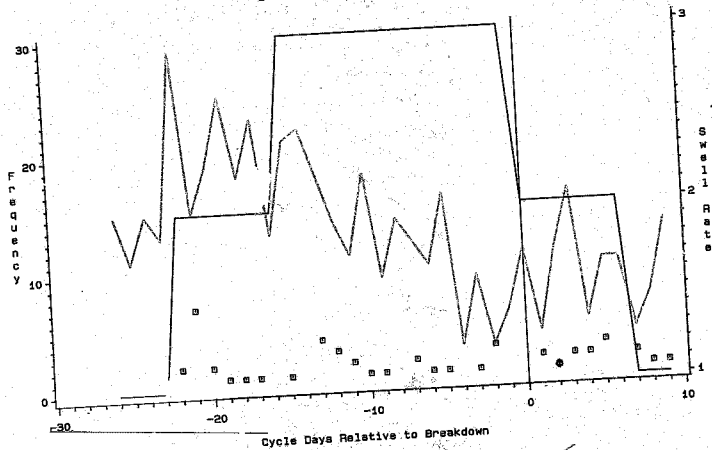
Yellow represents Frequency of Solicits Red represents Frequency of Yawns
Green represents Frequency of Presents Blue represents Swell Rate

Figure 15a. Female 1081 vs Females



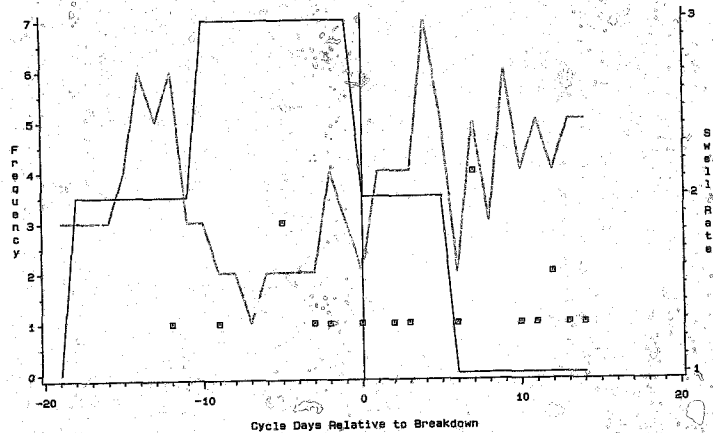
Yellow represents Frequency of Solicits Red represents Frequency of Yawns
Green represents Frequency of Presents Blue represents Swell Rate

Figure 15b. Female 1081 vs Males



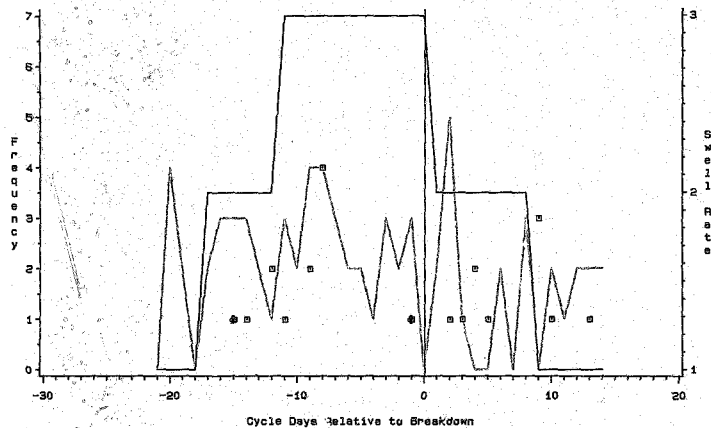
Yellow represents Frequency of Solicits
Green represents Frequency of Presents
Red represents Frequency of Yawns
Blue represents Swell Rate

Figure 16a. Female 1185 vs Females



Yellow represents Frequency of Solicits
Green represents Frequency of Presents
Red represents Frequency of Yawns
Blue represents Swell Rate

Figure 16b. Female 1135 vs Males



Yellow represents Frequency of Solicits Red represents Frequency of Yawns
Green represents Frequency of Presents Blue represents Swell Rate

14, 15, 16), as in 4.2.6. above, and in Bielert and Girolami (1986). The majority of presents were eye-contact presents. In fact, for two of the females and Female 1081 during FM, they were 100% eye-contact. For female 1081, only 75% of the presents given to females were the eye-contact type.

An analysis of variance elucidated significant differences between solicits given to either males or females. Females 1087 and 1135 gave more solicits to females; in contrast, female 1081 gave more solicits to males (Table 13). Yawns tended to be more frequent during FM although only in Female 1081 was the increase statistically significant (Table 14). Considering presents alone, female 1087 gave the same number of presents (N=3) to males and females, whereas female 1081 presented more to females (N=12) than to males (N=1), and female 1135 presented twice to males and never to females (Figures 14, 15, 16).

Female 1087 (Figure 14) shows a reduction in her solicits to females from day BD-10 to BD+3 whereas with males a clear reduction is not visible, even though a few days with very low values could be seen between days BD-13 and BD. Phase 3, which includes the days just mentioned, shows a much greater variability during the FM as contrasted to the FF condition. This is reflected in the larger standard deviation (Table 13). The solicits of female 1081 to other females (Figure 15) are consistently lower from day BD-8 to BD+5 although a sudden transient increase, seen on the graph as a spike, can be seen on days BD-6 and BD-5. In contrast, solicits to males show a gradual decline from day BD-16 to day BD+2, although the minimum values are reached between days BD-4 and BD+1, and a higher variability during phase 3 (Table 13). Female 1135 shows a clear reduction in solicits to females, visible as a trough from day BD-11 to day BD-3. The same feature is not visible in solicits to males whereas the variability for the same period, which corresponds to phase 3, is higher here.

TABLE 13

Frequencies (Means $\pm$ SD) of female solicits across menstrual cycles, when the subject is in a female social environment (FF) and in a male social environment (FM).

Female Subjects and Experimental Cycles	Cycle Phases					ALL
	1	2	3	4	5	
1087 FF	13.00 $\pm$ 6.00 ^a	9.00 $\pm$ 2.15 ^b	6.33 $\pm$ 2.23 ^b	6.20 $\pm$ 1.76 ^b	7.41 $\pm$ 2.42 ^b	7.84 $\pm$ 3.08 ^a
1087 FM	6.50 $\pm$ 0.70	5.42 $\pm$ 1.82	4.78 $\pm$ 1.55	5.33 $\pm$ 1.72	6.00 $\pm$ 2.64	5.23 $\pm$ 1.45 ^a
1081 FF	7.33 $\pm$ 1.15	9.16 $\pm$ 3.06 ^a	5.71 $\pm$ 3.29	3.66 $\pm$ 1.21 ^b	9.00 $\pm$ 5.36	6.05 $\pm$ 3.86 ^a
1081 FM	13.50 $\pm$ 1.91 ^b	20.28 $\pm$ 5.67 ^a	12.40 $\pm$ 5.94 ^b	9.57 $\pm$ 4.03 ^b	8.00 $\pm$ 4.58 ^b	13.33 $\pm$ 6.26 ^a
1135 FF	3.00	4.12 $\pm$ 1.35	2.33	4.33 $\pm$ 1.63	4.33 $\pm$ 1.22	3.69 $\pm$ 1.46 ^a
1135 FM	1.50 $\pm$ 1.91	2.33 $\pm$ 0.81	2.63 $\pm$ 0.92	1.44 $\pm$ 1.74	1.50 $\pm$ 0.83	1.97 $\pm$ 1.31 ^a
FF	9.14 $\pm$ 5.27 ^a	7.41 $\pm$ 3.36	4.93 $\pm$ 2.97 ^b	4.64 $\pm$ 1.89 ^b	6.74 $\pm$ 3.44 ^b	6.17 $\pm$ 3.44
FM	6.10 $\pm$ 6.57	10.05 $\pm$ 8.78	7.05 $\pm$ 5.95	5.09 $\pm$ 4.53	4.83 $\pm$ 3.51	6.75 $\pm$ 6.24
ALL	7.35 $\pm$ 6.00 ^b	8.61 $\pm$ 6.47 ^a	6.11 $\pm$ 4.94 ^b	4.89 $\pm$ 3.60 ^b	5.97 $\pm$ 3.56 ^b	6.47 $\pm$ 5.05

Note. a > b; * p < 0.05

TABLE 14

Frequencies (Means $\pm$ SD) of female teens across menstrual cycles, when the subject is in a female social environment (FF) and in a male social environment (FM).

Female Subjects and Experimental Cycles	Cycle Phases					ALL
	1	2	3	4	5	
1041 FF	0.00	1.00 $\pm$ 1.00	1.00 $\pm$ 1.00	1.40 $\pm$ 1.34	1.56 $\pm$ 0.93	1.12 $\pm$ 1.05
1087 FM	0.00	0.57 $\pm$ 0.78	1.14 $\pm$ 0.95	0.92 $\pm$ 0.98	1.00 $\pm$ 1.11	0.92 $\pm$ 0.94
1041 FF	0.00	0.00	0.35 $\pm$ 0.43	0.00	1.16 $\pm$ 1.60	0.34 $\pm$ 0.83 ^a
1081 FM	0.00	2.00 $\pm$ 2.10	1.33 $\pm$ 1.23	1.82 $\pm$ 1.13	2.33 $\pm$ 0.97	1.33 $\pm$ 1.43 ^a
1135 FF	0.00	0.17 $\pm$ 0.35	0.55 $\pm$ 1.01	0.50 $\pm$ 0.54	1.22 $\pm$ 1.20	0.60 $\pm$ 0.93
1135 FM	0.00	0.66 $\pm$ 0.81	0.72 $\pm$ 1.07	0.55 $\pm$ 0.76	0.71 $\pm$ 1.11	0.61 $\pm$ 0.96
FF	0.00 ^b	0.55 $\pm$ 0.93	0.71 $\pm$ 0.94	0.58 $\pm$ 0.87	1.19 $\pm$ 1.14 ^a	0.71 $\pm$ 1.00
FM	0.00	1.10 $\pm$ 1.58	1.12 $\pm$ 1.17	0.90 $\pm$ 0.97	1.00 $\pm$ 1.02	0.96 $\pm$ 1.18
ALL	0.00 ^b	0.78 $\pm$ 1.29 ^a	0.94 $\pm$ 1.07 ^a	0.76 $\pm$ 0.93 ^a	1.11 $\pm$ 1.09 ^a	0.83 $\pm$ 1.08

Note. a > b; * p < 0.05

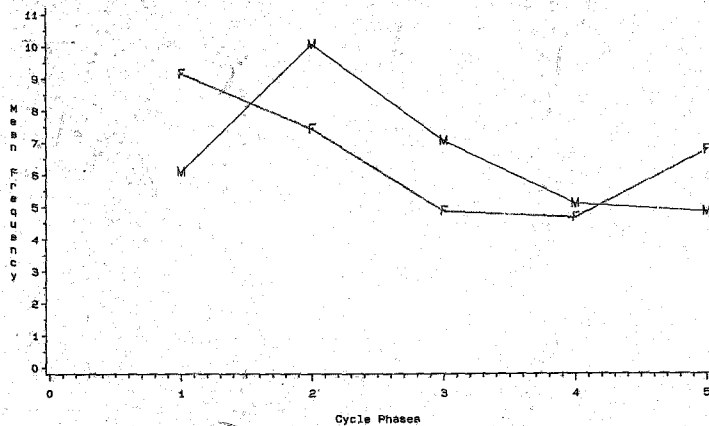
Considering the individual cycles, it appears that, in the three females tested with other females (FF), mean solicits from phase 3 appear among the two lowest scores across the five phases, whereas this is not so when the females are tested with males (Table 13). Among the highest scores are solicits in phase 2 and among the lowest, solicits during phase 4 (Table 13). If the three FF cycles are combined, phases 1 and 2 show the higher frequencies of solicits, and phases 3 and 4 the low, whereas, for the three combined FM cycles, solicits are higher in phases 2 and 3 and lower in phases 4 and 5 (Table 13). Comparing each phase directly for the combined FF and FM, it appears that solicits with male partners (FM) are lower than with female partners (FF) during phases 1 and 5, whereas they are higher during phases 2, 3 and 4 (Table 13 and Figure 17). If phases 1 and 2 are lumped together and considered as one, the early follicular phase, and phases 4 and 5 as the luteal phase, the resulting averages show very little difference between experimental conditions. They emphasize instead the difference between FF and FM during phase 3 (Figure 18).

In general, females were significantly more active during phases 1 and 2 and significantly less active during phase 4 (Table 13). A similar trend is visible in yawns (Table 14).

5.4. DISCUSSION

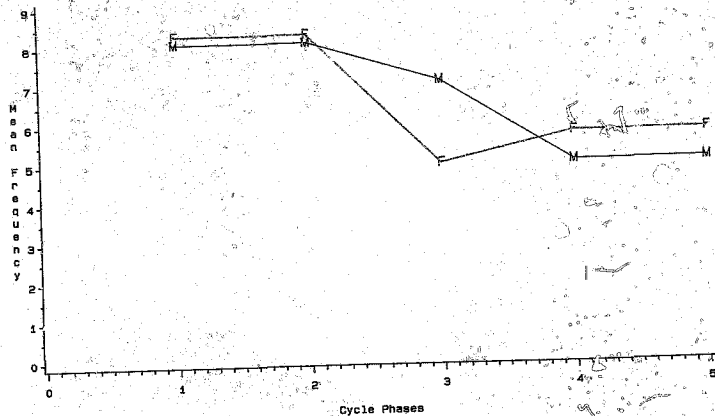
The cycle lengths obtained are well within the range of 20 to 42 days reported by Gillman and Gilbert (1946), for normal cycles of the chacma baboon. Also within normal ranges seem to be the duration of bleeding and the lengths of the phases of perineal turgescence, deturgescence and rest. The same authors report: for the bleeding, a mode of 4 days; for turgescence, a mean of 19.45 days and a range of 10 to 32 days; for deturgescence, a mean of 16.07 days and a range of 6 to 25 days; and for the period of perineal rest, occurring before turgescence and after

Figure 17. Female Solicits: To Females vs To Males



Yellow represents Frequency of Solicits to Females
 Orange represents Frequency of Solicits to Males

Figure 18. Female Solicits To Females vs To Males with Phases 1,2 and 4,5 Averaged



Yellow represents Frequency of Solicits to Females
 Orange represents Frequency of Solicits to Males

deturgescence, a range of 2 to 16 days. Gillman's results were reported previously by Gillman (1937), and correspond to results obtained by Bielert (1986), for the ch. baboon, and by Hendrickx (1967), for other species of baboon. Since no abnormalities could be found in any of their components, the cycles may be considered to be normal and ovulatory.

Of interest is the slight difference in the cycle length between the two experimental conditions. FM cycles are longer mainly in the follicular phase, which is also the phase, in contrast to the luteal phase, that shows more variation in length in the baboon (Gillman and Gilbert, 1946) and in primates in general (Hodges, 1987). The longer follicular phase, during the cycles in which the females were exposed to males, could be an indication of the action of the social environment on the reproductive physiology of the females. An alteration of the follicular phase, in relation to differences in the social environment, has been described in the chacma baboon (Howard-Tribe and Bie, 1978). They found that the follicular phases of females, that had physical contact with males, were shorter than those of females denied physical contact. The only experimental variable in their study was physical contact with males. A direct comparison of the results is not possible, nonetheless both results suggest ovarian sensitivity to social environmental factors.

Neither social sequences of yawns nor of solicits appear to reflect the nature of the social environment. It may be that both reflect individual characteristics of the female subjects.

Clear differences are present in the distribution of behaviour across the cycle phases, within and between experimental conditions. The profiles of solicits from each female give the impression that, during FF and around the time of full swelling, the females decreased solicits substantially. The only exceptions are isolated 2-day increases in Female 1135, on days BD-2 and BD-1.

and in Female 1081, on days BD-6 and BD-5. By contrast, a comparable decrease in solicits around the same stage of the cycle is not clearly detectable in FM cycles. Those valleys, which represent graphically the day during FF cycles in which low values were reported, are seen to be filled in during FM. Days of high frequencies alternate with days of low frequencies to produce a profile which resembles a saw instead of a valley (Figures 14, 15 and 16). The interpretation suggested is that, in both experimental conditions, solicits decrease during the central portion of the cycle, as shown by phases 3 and 4 (Figure 17), but during phase 3 of FM, the tendency of solicits to decrease is reduced by a counterbalancing force. This force must be rather powerful since phase 3 during FF shows, along with phase 4, significantly lower values, whereas the decrease of solicits during phase 3 of FM does not reach statistical significance (Figure 17 and Table 13).

Numerous authors have reported that levels of behaviours, such as agonistic and affiliative behaviours, activity and feeding, are high during the early stages of the menstrual cycle and then decrease to lower levels during full turgescence and deturgescence. Hausfater and Skoblick (1985) reported that, in the wild yellow baboon (*P. cynocephalus*), agonistic interactions, that involve menstruating females, were four times higher than those which involved oestrous females. Wasser and Starling (1986) found, in the same species, that menstruating females attacked other females significantly more than expected. In a captive group of *P. cynocephalus* and *P. anubis*, Noll et al. (1982) found that threats and attacks were given significantly less during the swollen phase. Self-biting, possibly a form of redirected aggression, was shown to occur only at the beginning of the cycle in a female chacma baboon kept in a single cage (Sielert and Howard-Tripp, 1983). In olive baboons (*P. anubis*), Rowell (1967, 1969) found that flat females avoided other females less than when they were in oestrus.

phases of their cycle. Friendly interactions, such as grooming, presenting and lip-smacking to each other, decreased gradually from the early stages of the cycle to reach a minimum during full swelling (and, in one female, during deturgescence). Saayman (1970) reported that wild female chacma baboons are more mobile and groom more males while inflating, i.e., during phases 1 and 2 of the cycle. According to Seyfarth (1978a), females groom and follow males less during consortship or, in other terms, while fully swollen. Feeding behaviour is reduced during full swelling in captive and wild chacma baboons (Bielert and Busse, 1983; Gilbert and Gillman, 1956), and in high-ranking yellow baboon females who are consorting (Rasmussen, 1985). In the yellow baboon, feeding behaviour reaches its highest levels perimenstrually (Hausfater and Skoblick, 1985).

Presents and solicits show a more complex pattern across the menstrual cycle and need to be discussed in more detail. Seyfarth (1978a) reported that presents decrease from higher levels from the beginning of the cycle through full swelling and consortship and keep decreasing during the phases of deturgescence and perineal rest. Saayman (1970) found the total number of presents to be high in the inflating phase, slightly lower during the phase of full swelling, lowest during the deflating phase and high again during the flat phase. So far, both findings are in total agreement with the results of the present study. What is interesting is that the percentage of presents given within each of the cycle phases varied with the class of males to which presents were directed. For example, presents given to subadults showed the same distribution across the cycle, whereas presents to adult males were highest during full swelling (Saayman, 1970). A similar phenomenon was reported by Rowell (1967). Presents to a subadult male were at the same level during the inflating and full swelling phases and decreased during the deflating and flat phases. Presents to adult

males on the other hand were highest during maximum turgescence and decreased during deturgescence and perineal rest.

An additional factor that contributes to a differential distribution of presents across the cycle phases is the type of present. It is now apparent that there exist various types of presents, which are differentiated by posture and by the context in which they occur, and that they show a different distribution across the cycle. In the study of Hausfater and Takacs (1987), "submissive" presents followed the pattern shown here. They were highest during the inflating phase, lower during full swelling and deturgescence, and increased again during the flat phase. By contrast, "sexual" presents were highest during the inflating phase, only slightly lower during full swelling, and decreased more dramatically during the deflating and flat phases. Thus far it seems that presents follow the pattern shown also by other behaviours. Only "sexual" presents given to adult males differ, in that they show considerable increases during full swelling.

Results on female presents and soliciting behaviour from the laboratory are presented not per cycle phase but per day, each day representing a mean of the frequencies obtained for the same day of the cycle from all the cycles considered. The cycles are aligned according to BD day and the days are numbered from it. This system unfortunately renders comparisons difficult and also can not represent faithfully perimenstrual changes in that those days of longer cycles, that are not in common with the other cycles, are cut off (for a further discussion, see also Hausfater and Skoblick, 1985). On the other hand, this system can provide insight on those changes that occur around BD and therefore ovulation, since the cycles are aligned on BD day.

Spontaneous presents during pair-tests (Bielert, 1986) showed some degree of fluctuation at the beginning of the cycle, though values were fairly high, and decreased appreciably from BD-8 to

BD-2, approximately the phase of full swelling. They re-increased around BD day, decreased further and increased again at the end of the cycle. The curve plotted from those data is also very similar to the results reported here. Eye-contact presents instead showed a different pattern. They started low and peaked during the phase of maximum tumescence even though reduction between BD-6 and BD-3 was still visible. After BD, this ~~view~~ declined progressively and then increased towards the end of the cycle (Bielert, 1986). In an experimental situation very similar to the one adopted in this work (Bielert *et al.*, 1986), presents given by adolescent females showed higher levels for most of the follicular phase and then dropped to lower levels which were maintained for the rest of the cycle from BD-6, in other words during the phase of full swelling. Once again the picture that emerges is very similar to the one presently discussed. Presents from adult females showed instead a different picture. They exhibited, in general, low levels that were slightly higher at the beginning of the cycle, more elevated from day BD-6 to BD-2 and dropped to remain lower for the rest of the cycle. Lip-smacks given by the same females showed a low start, an increase during the inflating phase and again a decrease during the swollen phase, to increase again and stabilize during the luteal phase on the levels shown at the beginning of the cycle. The drop in behaviour during the phase of full swelling was greatly advanced (from day BD-6) in the adolescent females compared with the adult females (from day BD-2) (Bielert *et al.*, 1986).

To recapitulate, a general decrease during the phases of full swelling and detumescence, in contrast to higher periaestrous levels, is found in social, non-social and sexual behaviours in a variety of social environments. In addition, if some of the above-listed decreases in female behaviours were and could be considered as a direct consequence of the phenomenon of

consortship, i.e., when a fully swollen female associates preferentially with one male, this has been shown not to be true for at least feeding behaviour (Bielert and Busse, 1983) and for grooming and presenting (Seyfarth, 1978a). It seems likely, therefore, that the fluctuations in female behaviour registered are instead under the control of ovarian hormones.

Studies which have focussed upon the association between circulating hormones and female behaviour in the baboon unfortunately are lacking. Therefore, indirect evidence must be considered. A nest reduction in feeding behaviour is shown by female chacma baboons in association with oestradiol benzoate treatment (OB) (Bielert and Busse, 1983). One of two females in an experimental situation, similar to the one presently under discussion, showed a progressive suppression of soliciting behaviours in response to increasing dosages of oestradiol (Bielert and Girolami, 1986). Oestradiol-treated wild female chacma baboons showed more presents and mobility when their perineum was only partially swollen, i.e., with lower levels of circulating oestradiol, than females who had obtained full swelling in response to the treatment (Saayman, 1973).

Additional information can be gained through the analysis of behavioural changes around the day of perineal breakdown. It is, in fact, known that ovulation occurs a few days before deturgescence (Gillman and Gilbert, 1946). According to Shaikh *et al.* (1982), ovulation occurs a mean of 2.07 days before BD (range 0 to 5 days). Oestrogens peak a mean of 41.4 hours before ovulation, and thus approximately four days before deturgescence (Shaikh *et al.*, 1982). Three to four days before deturgescence is also the time when peaks of urinary oestrogens occur (Stevens *et al.*, 1970). Feeding behaviour reaches its lowest point on BD-3 and returns to initial levels on day BD-2 (Bielert and Busse, 1983). Rowell (1967) reported a reduction in female behaviours

and in interaction with males on day BD-1. Females also appear to be less active in following males on days BD-3 and BD-2 (Seyfarth, 1978a). Female presents drop on BD-1, then increase again on days BD and BD+1, only to decrease again (Hausfater, 1975). According to Bielert (1986), presents decrease from day BD-7 to day BD-3, increase again briefly around BD day, and then decrease again. A dip in female solicits is found on day BD-2 and BD-3 (Bielert and Girolami, 1986). Grooming dips significantly on BD-3 (Hausfater, 1975). Smaller peaks are also found from BD-5 to BD-2 (Bielert, 1986) and, in the data presented here, on days BD-6 and BD-5 of FF (Figure 15) and on days BD-2 and BD-1 of FF (Figure 16). In contrast, consort activity seems to be highest on day BD-3 (Hausfater, 1975; Scott, 1984; Smuts, 1985). Male following and herding also are highest around days BD-3 and BD-2 (Hausfater, 1975; Seyfarth, 1978a). It is suggested that these periovulatory fluctuations are a clear indication of a hormonal dependency of female behaviour. It is rather difficult, however, to establish the responsible hormones or hormonal mechanisms without the appropriate analyses of circulating hormones. It could be that female behaviour in the follicular phase, i.e., phases 1 and 2 and part of phase 3, is negatively correlated with oestrogen levels; a gradual increase in oestrogens corresponds to a decrease in behaviour. By the same token, dips in female behaviour could correspond to oestrogen peaks. This suggestion is supported by the peak in male "possessive" behaviour that occurs at the same time, since oestrogens are positively correlated with female attractiveness (Bielert *et al.*, 1980; Bielert, 1984; Bielert and Girolami, 1986). Peaks in female behaviour on BD day appear to reflect the decline in oestrogen level occurring right after the ovulatory peak (Stevens *et al.*, 1970).

The foregoing explanation does not account for the further decrease in scored behaviours, or at least the lack of increase,

found during phase 4 when an increase should be expected corresponding to lowered oestrogen levels. At this point another phenomenon seems to take place. Progesterone in the chacma baboon (Du Toit, 1956) and progestins (Stevens *et al.*, 1970) show low and steady levels during the follicular phase. These levels start to increase 5 days after ovulation (Du Toit, 1956) or the second day after the oestrogen peak (Stevens *et al.*, 1970) reaching a maximum 11 days after ovulation (Du Toit, 1956) or on day ED+8 (Stevens *et al.*, 1970). They then decline and reach follicular levels around the sixteenth day after the oestrogen peak (Stevens *et al.*, 1970) and drop on the day of bleeding (Du Toit, 1956).

Administration of Provera (17 α -hydroxy-6 α -methylprogesterone acetate) to oestrogen-treated ovariectomised females caused a marked reduction in presents and female mobility (Ssayman, 1975). It seems that progesterone has a suppressive effect on female behaviour. This suggestion is strengthened by the evidence that pregnant females, in which progesterone levels are highest, tend to be less frequently involved in both friendly and agonistic interactions, either given or received (Rowell, 1967; 1969). They also tend to present less and to be less in proximity of males (Rowell, 1967; Seyfarth, 1978b; Hausfater and Takacs, 1987).

Despite similarities in the FF and FM curves, due to the same hormonal modulators, differences are also noticeable (Figure 17). It is possible that the discrepancies in the two cycles are just a product of the system of subdivision of the cycles into phases, in particular for phases 1 and 2. Phase 1 in fact is a very short phase that is considered by many authors together with phase 2 as the "inflating" phase. It may consist only of one day, a fact that would make it more susceptible to chance events. Therefore, it may be less reliable as a representation of the changes that occur at the beginning of the cycle. If the two phases are combined for each cycle and then averaged, there is no longer much difference

between FF and FM (Figure 18). Also, combining phases 4 and 5 for each cycle would eliminate the difference between the FF and FM cycles with regard to those phases (Figure 18). In this way the original difference could be explained by the difficulty in discriminating between the two phases and actually between the two perineal conditions. Certainly Figure 18 emphasizes the different frequencies of behaviour between FF and FM during phase 3. Resmussen (1985) found that the reduction in feeding behaviour during consortship was directly proportional to the female's rank, so that high-ranking females suppressed their behaviour whereas low-ranking females increased it. Since presents and solicits are among the proceptive behaviours that show a looser correlation with the female cycle (Goldfoot, 1971; Seyfarth, 1978a; Baum, 1983; Dixon, 1983a), and since differences in their relation to the cycle could be attributed to the type of context in which presents are given, as discussed above, it would seem that the differences in the two cycles could be explained by differential pressure from the social environment. As a form of suppression of reproduction, female baboons attack lactating females, recruiting for help mainly menstruating and inflating females (Wasser and Starling, 1986). Swollen females are more likely to ignore threats from other females (Seyfarth, 1978a) and a marked reduction in involvement in agonistic interactions is found around days BD-3 and BD-2 (Hausfater, 1975). Lactating and deflating females seem to be attacked more often than others (Rowell, 1969; Wasser and Starling, 1986). This could explain the high level of lip-smacks shown at the beginning of the cycle as part of the establishment of bonds which may lead to a coalition. The low levels of lip-smacks during phases 3 and 4 may be seen as avoidance of interactions and of potential attacks.

In the case of solicits to males, we have already seen that those presents and lip-smacks that could be considered sexual

i.e., those given to adult males as opposed to juveniles (Rowell, 1967; Saayman, 1970), those reported in a sexual context (Hansfater and Takacs, 1987), eye-contact presents (Bialert, 1986), and those given by adult females rather than by adolescents (Bialert et al., 1986), instead of decreasing, increase during phases 2 and 3 and are low for the rest of the cycle. The higher level of solicits given to males than to females during the phase of inflation and full turgescence could, therefore, be due to an increase in sexual solicits. That such an increase is not as evident as in the reported examples is probably due to the artificiality of the experimental conditions selected.

At this point, it would be interesting to know the reason why the female increases sexual solicits during full swelling and at the same time reduces social presents and other behaviours. One explanation could be that sexual solicits are directly influenced by oestrogens unlike the other behaviours. Support for this explanation is provided by another experiment conducted by Bialert (1984) in which pair-tested ovariectomised oestrogen-treated females increased their level of presents. The negative results obtained by Saayman (1973) instead can be explained by the fact that treated females interacted only with juveniles. Another explanation, however, would seem more feasible. Among baboons, female initiation of copulation has been widely reported to occur much less often than male initiation (11%, Ransom, 1981; 10.14%, Rowell, 1967; 2.8%, Hansfater and Takacs, 1987; 4.25%, Seyfarth, 1978a; 17.02%, Saayman, 1970; 8%, Scott, 1984). It seems though that males respond more to solicits when the female shows some degree of turgescence, particularly when she is fully swollen, and are also keener to mount (Bialert, 1986; Saayman, 1970; Seyfarth, 1978a; Rowell, 1967; Ransom, 1981). Although females seem to compete for access to males throughout their cycle, they appear to have few opportunities to assert their preferences for males

(Smuts, 1985). In fact, if persistent in their solicits, they might be attacked by the male recipient (Ransom, 1981). It seems then that females would express their preferences by addressing presents to the chosen male. It is possible then that, in order to select a partner, females increase their solicits when they know that they have a better chance of being successful, i.e., when they are inflating and fully swollen.

In conclusion, differences related to male and female environments were found in the length of the menstrual cycles and in the distribution of solicits across the cycle. Menstrual cycles were shorter when the subject females were in a "female social environment" than when they were with males. In general, it seems that solicits, as other behaviours reviewed, are under hormonal modulation and thus show their highest levels perimenstrually. Solicits to females showed higher levels perimenstrually than those to males and were lower during the central portion of the cycle than solicits to males. This difference is considered to be due to the different purpose for which the solicits are employed with either male or female conspecifics.

6. FEMALE CHACMA BABOON CHANGES ACROSS THE MENSTRUAL CYCLE IN VISUAL INTERACTIVE BEHAVIOURS. A COMPARISON, IN AN ALL-MALE SOCIAL ENVIRONMENT, BETWEEN NORMAL MENSTRUAL CYCLES AND CYCLES IN WHICH THE ATTRACTIVE STIMULUS IS CONCEALED - EXPERIMENT 6.

6.1. INTRODUCTION

Female solicits to either males or females have been found to differ in their distribution across the menstrual cycle. This suggests that solicits fulfill a different purpose with regard to the sex of the recipient, and in particular that solicits to males could be involved in sexual communication (Chapter 5). This experiment, therefore, was designed to explore the stimulus value of soliciting behaviour on male arousal. For this purpose, the perineal swelling, which constitutes the main modulator of male sexual arousal (see Chapter 4), was concealed. Male responses and female behaviours were then recorded across the female menstrual cycle.

6.2. MATERIALS AND METHODS

6.2.1. Subjects

Three intact female chacma baboons, Q-436, DB-9, 83, the experimental subjects, and thirteen males, A, B, C, E, F, G, H, M-1, M-2, M-3, M-4, M-5, M-9, were employed in this experiment. For the criteria used in selection of the subjects, see 4.2.1.

6.2.2. Housing

As in 4.2.2.

6.2.3. Testing and Apparatus

The animals were arranged in the room and the observations were carried out as in 4.2.3. Female 83 was exposed to seven males, the first seven of those listed above, whereas Female Q-436 and DB-9 were exposed to all thirteen males. Each female was left in the room with the males and observed for two full menstrual cycles. For one of the two cycles, the females were tested wearing a pair of pants which concealed the perineal swelling. The pants (Figure 19), made out of dark brown woven material, measured 60 cm at the waist and were 50 cm long. They were tailored to allow space for the swelling to develop, free leg movement and easy elimination of faeces. To prevent chafing, foam padding was used at the waist where a nylon webbing belt was inserted to secure the pants on the female. The belt was buckled on the dorsum of the female right above the root of the tail. The tail projected out of the pants through a 7 cm slit from the waist downwards. Tightening of the belt at the waist produced pleats necessary to accommodate and yet conceal the swelling (Figure 19). Females 83 and Q-436 were tested wearing the pants for their first cycle whereas Female DB-9 was tested wearing the pants for her second cycle. In order to put on or remove the pants, the females were sedated with 7.5 mg/kg body weight, IM injection of ketamine hydrochloride. Cycles were planned to be consecutive which was the case for Females 83 and DB-9. Unfortunately for Female Q-436, bleeding could not be detected, observations were stopped on the forty-first day of her



Figure 19. (A) The pants. The buckle goes on the dorsum of the female. Below the buckle is the slit that allows space for the tail.
(B) and (C) One of the experimental subjects wearing the pants. It can be seen that mobility of the hind limbs is not hindered by the garment.

cycle, and the pants taken off on her sixty-third day. Five days later, she was bleeding and the second cycle of observations was started.

Female weight fluctuations were monitored daily throughout the two menstrual cycles. When the perineal swelling was concealed by the pants, it was impossible to use the Swell Rate system based on the change in size of the perineal swelling (see Chapter 5) to follow the phases of the menstrual cycle. Bielert and Busse (1983) demonstrated a clear correlation between female body weight and perineal swelling, in that the weight increases gradually as the swelling becomes larger and drops on the day of breakdown. They also showed that the increase in weight reflects the weight of the swelling itself since female food intake decreases during full turgescence. Further, it is also known that hormonally induced perineal changes are associated with water metabolism (Gillman and Gilbert, 1946), rather than selective food intake (Gilbert and Gillman, 1956), and it is known that the perineal swelling is an edema with large accumulation of water in the interstitial tissue (Krohn and Zuckerman, 1937). Therefore, the pattern of increase and decrease of female body weight was adopted as the means of following the phases of the menstrual cycle.

On each of the days of the two female menstrual cycles, the occurrence of coagulated seminal emissions from male masturbation was scored (see 4.2.3.).

Scoring was as in 4.2.4. above. A total of 260 observations were carried out over a period of 6 months.

6.2.4. Measures Scored

Female body weight: Females, in an iron-grid transport cage (60x50x60 cm), were weighed on a scale (see Bielert and Busse, 1983, for further details). By subtraction of the weight of the

cage (18.2 kg), the female's weight was obtained and recorded on a calendar sheet. Weights were taken daily at approximately 08:00 before the females had been fed.

Presents: As in 4.2.5.

Lip-smacks: As in 4.2.5.

Yawns: As in 5.2.4.

Seminal emissions: As in 4.2.5.

6.2.5. Habitation

As in 4.2.5. The males were together in the same room for at least one month before the beginning of the tests.

6.2.6. Cycle Phases and Statistical Analysis

Each female cycle was divided into five phases according to the body weight changes across the menstrual cycle. Phase 1 was considered as beginning on the day menstrual bleeding started onset and comprised those days in which the weight fluctuated around the baseline, i.e., the weight registered on the first day of the cycle. Phase 2 began on the day in which a steady increase in weight was noticed and continued for those days in which weight kept increasing. Phase 3 began on the day in which 95% of the weight increase had been reached and weight stabilized. Phase 4 began on the day in which an appreciable decrease in weight, or the beginning of a steady decline in weight that was maintained over several days, was noticed. This phase comprised the days in which weight decreased. The first day of weight decrease was considered to be BD day. Phase 5 began when weight started stabilizing around the baseline and no further decline was perceived.

Cycles were compared in their phases for frequencies of female behaviour and male response by an analysis of variance for unbal-

anced data with the General Linear Models Procedure (SAS); the Duncan multiple range test was adopted to reveal significant differences between the means.

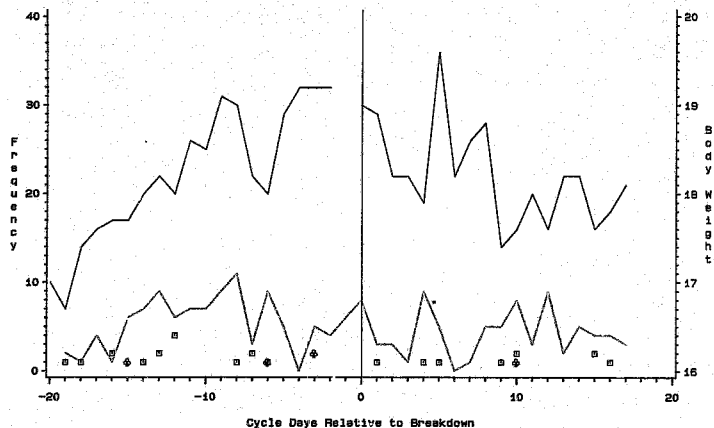
6.3. RESULTS

The lengths of menstrual cycles ranged from 31 to 45 days with a mean of 38.20 ± 4.72 days (Figures 20, 21, 22). This mean length, however, excludes the PANTS cycle of Female Q-436. The end of this cycle could not be assessed because menstrual bleeding was not detected. The cycle length, however, was estimated to be 29 days as inferred from the body weight curve (Figure 23).

Bleeding was considered only for the NOPANTS cycles and ranged from 3 days for Female 83 to 5 days for the other two females.

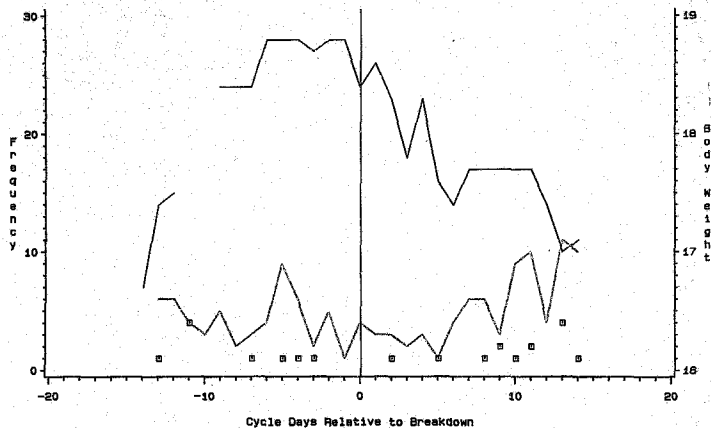
For the three females, body weight increased by a mean increment of 1.95 ± 0.36 kg over the mean weight scored on the first day of the cycle (14.53 ± 1.85 kg). The weight of Female Q-436 ranged, during the PANTS cycle, from 16.7 to 18.8 kg, an increase of 2.1 kg. Her body weight increase during the NOPANTS cycle was 2.2 kg, from 17.0 to 19.2 kg. The first extra kilogram was gained within 5 days during PANTS and within 7 days during NOPANTS. The second extra kilogram was gained within 9 and 12 days of the PANTS and NOPANTS cycles respectively. During PANTS, the maximum weight was reached by day 9 (BD-6) and was maintained for 6 days and, during NOPANTS, was reached by day 12 (BD-9) and was maintained for 9 days. During the PANTS cycle, it took the female 14 days before a drop in her body weight occurred. The equivalent time for the NOPANTS cycle was 20 days (Figure 20). The weight of Female 83 during the PANTS cycle ranged from 13.7 to 15.8 kg, an increase of 2.1 kg. During the NOPANTS cycle, her weight increased from 14.0 to 16.3 kg. In the PANTS cycle, the first extra kilogram was gained by day 4 (BD-11), the second extra kilogram by day 11 (BD-4),

Figure 20.A. Female Q-436 - NOPANTS



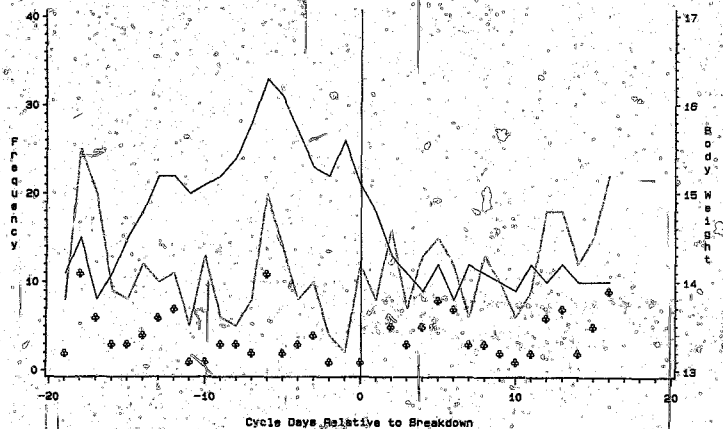
Yellow represents Frequency of Solicits Red represents Frequency of Yawns
Green represents Frequency of Presents Blue represents Body Weight

Figure 20.B. Female Q-436 - PANTS



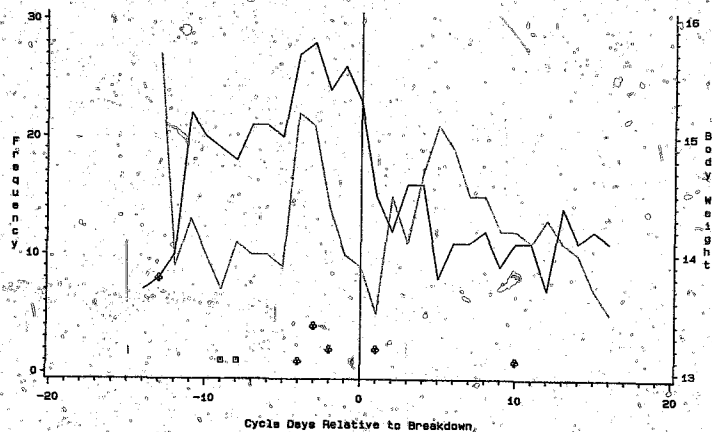
Yellow represents Frequency of Solicits
 Green represents Frequency of Presents
 Red represents Frequency of Yawns
 Blue represents Body Weight

Figure 21.A. Female 83 - NOPANTS



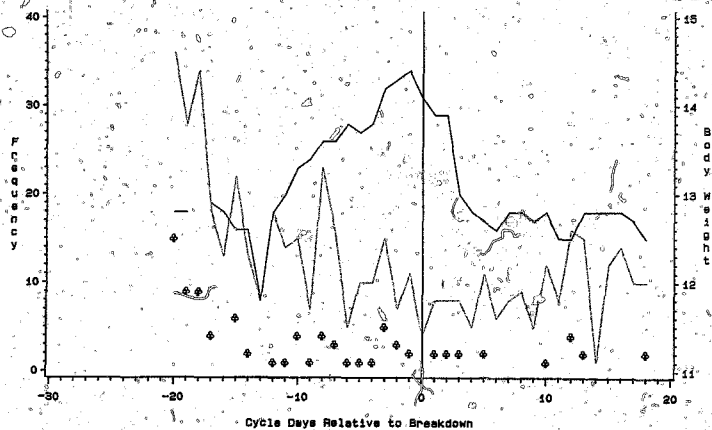
Yellow represents Frequency of Solicits
 Red represents Frequency of Yawns
 Blue represents Body Weight

Figure 21.B. Female 83 - PANTS



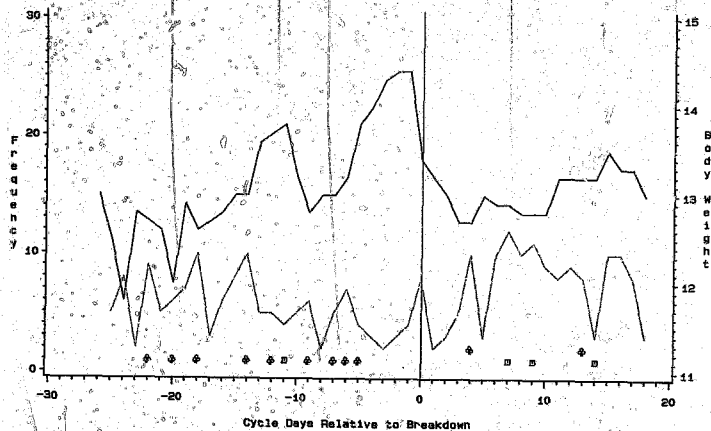
Yellow represents Frequency of Solicits Red represents Frequency of Yawns
 Green represents Frequency of Presents Blue represents Body Weight

Figure 22.A. Female DB-9 - NOPANTS



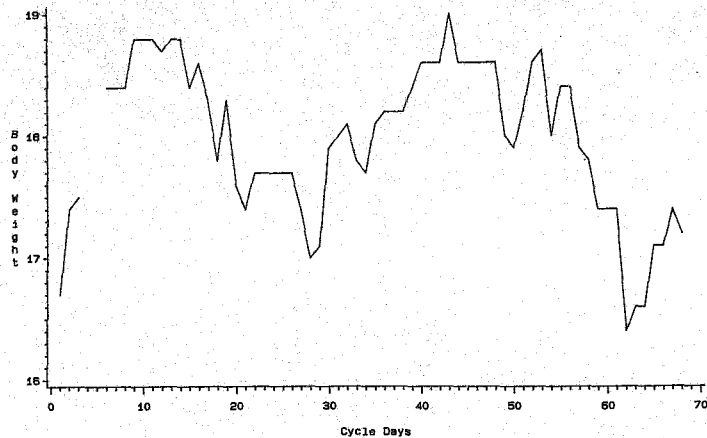
Yellow represents Frequency of Solicits
 Green represents Frequency of Presents
 Red represents Frequency of Yawns
 Blue represents Body Weight

Figure 22.3. Female DB-9 - PANTS



Yellow represents Frequency of Solicits
 Green represents Frequency of Presents
 Red represents Frequency of Yawns
 Blue represents Body Weight

Figure 23. Female Q-436 - Body Weight Across Two Menstrual Cycles



Blue represents Female Body Weight

and the full weight was maintained for four days. During the NOPANTS cycle, weight was gained more slowly: a 1 kg increase was reached by the eighth day and the maximum weight was attained on the fourteenth day (BD-7) and then maintained for 7 days. It took this female 14 and 20 days before weight started to drop during the PANTS and NOPANTS cycles respectively (Figure 21). The initial weight of Female DB-9 during the PANTS cycle was 13.0 kg and increased to a maximum of 14.4 kg on day 25 (BD-2). Her weight fluctuated around the baseline for 13 days and then began to increase so that the first extra kilogram was reached by the twenty-third day (BD-4). Full weight was maintained for 4 days. A similar pattern was shown by the weight increase during the NOPANTS cycle. The female started with a weight of 12.8 kg (actually the weight registered on the second day of this cycle, the one from the first day being missing). After fluctuating around the baseline for 10 days, her weight started to increase and 1 kg (95% of the increase) had been gained by day 16 (BD-6). Her full weight of 14.4 kg was maintained for 6 days. The sudden drop in body weight occurred after 26 days of PANTS cycle and 21 days of the NOPANTS cycle (Figure 22).

Female behaviours occurred at different frequencies. Yawning was rare (Total N=52, range 0-4): its mean performance per observation ranged from 0.00 for Females 83 and DB-9 during the NOPANTS cycle to 0.78 for Female Q-436 during the PANTS cycle (Table 15). Female presents were performed by all the females, with the exception of Female Q-436 during the PANTS cycle. The highest mean performance was 3.94 shown by Female 83 during the NOPANTS cycle (Table 16). Eye-contact presents always constituted the majority (91%) of given presents. They constituted respectively 100% of presents of Female Q-436-NOPANTS cycle, 84.26% and 92.30% of Female DB-9-NOPANTS and PANTS cycles, and 83.68% and 94.44% of Female 83-NOPANTS and PANTS cycles. The two types of

TABLE 15

Frequencies (Means $\pm$ SD) of female Yama across menstrual cycles, when the female subjects are wearing pants (PANTS) and when they're not wearing pants (NO PANTS).

Female Subjects and Experimental Cycles	Cycle Phases					
	1	2	3	4	5	ALL
DE-9 NO PANTS	0.00	0.00	0.00	0.00	0.00	0.00
DE-9 PANTS	0.00	0.10 $\pm$ 0.31	0.00	0.00	0.20 $\pm$ 0.41	0.09 $\pm$ 0.29
Q-436 NO PANTS	1.00	1.11 $\pm$ 1.36	0.44 $\pm$ 0.72	0.40 $\pm$ 0.54	0.53 $\pm$ 0.77	0.64 $\pm$ 0.91
Q-436 PANTS	1.00	0.63 $\pm$ 1.60	0.50 $\pm$ 0.54	0.28 $\pm$ 0.48	1.33 $\pm$ 1.30	0.78 $\pm$ 1.10
S3 NO PANTS	0.00	0.00	0.00	0.00	0.00	0.00
S3 PANTS	0.00	0.25 $\pm$ 0.46	0.00	0.00	0.00	0.06 $\pm$ 0.25
NO PANTS	0.01 $\pm$ 0.27	0.37 $\pm$ 0.93	0.23 $\pm$ 0.54	0.11 $\pm$ 0.33	0.18 $\pm$ 0.51	0.21 $\pm$ 0.60
PANTS	0.07 $\pm$ 0.26	0.33 $\pm$ 0.86	0.23 $\pm$ 0.43	0.11 $\pm$ 0.33	0.41 $\pm$ 0.85	0.27 $\pm$ 0.69
ALL	0.07 $\pm$ 0.26	0.25 $\pm$ 0.89	0.22 $\pm$ 0.49	0.13 $\pm$ 0.32	0.29 $\pm$ 0.70	0.24 $\pm$ 0.64

Note. a > b: *p < 0.05.

TABLE 16

Frequencies (Means $\pm$ SD) of Female Presents across menstrual cycles, when the female subjects are wearing pants (PANTS) and when they are not wearing pants (NO PANTS).

Female Subjects and Experimental Cycles	Cycle Phases					
	1	2	3	4	5	ALL
DB-9 NO PANTS	5.11 $\pm$ 5.10 ^a	2.00 $\pm$ 1.41	3.33 $\pm$ 1.52	1.14 $\pm$ 1.06 ^b	0.75 $\pm$ 1.25 ^b	2.28 $\pm$ 3.10 ^a
DB-9 PANTS	0.33 $\pm$ 0.49	0.50 $\pm$ 0.52	0.00	0.00	0.26 $\pm$ 0.70	0.29 $\pm$ 0.55 ^a
Q-436 NO PANTS	0.00	0.11 $\pm$ 0.33	0.33 $\pm$ 0.70	0.00	0.07 $\pm$ 0.22	0.13 $\pm$ 0.41
Q-436 PANTS	0.00	0.00	0.00	0.00	0.00	0.00
63 NO PANTS	6.33 $\pm$ 4.50	3.30 $\pm$ 1.94	3.50 $\pm$ 3.23	2.80 $\pm$ 2.28	4.58 $\pm$ 2.74	3.94 $\pm$ 2.97 ^a
63 PANTS	8.00 ^a	0.00 ^b	1.75 $\pm$ 1.70 ^b	0.33 $\pm$ 0.81 ^b	0.09 $\pm$ 0.30 ^b	0.60 $\pm$ 1.85 ^a
NO PANTS	5.00 $\pm$ 4.83	1.85 $\pm$ 1.93	1.88 $\pm$ 2.78	1.29 $\pm$ 1.72	1.77 $\pm$ 2.61	2.10 $\pm$ 2.88
PANTS	0.85 $\pm$ 2.10 ^a	0.20 $\pm$ 0.41	0.53 $\pm$ 1.19 ^a	0.31 $\pm$ 0.48 ^b	0.14 $\pm$ 0.50 ^b	0.30 $\pm$ 0.98
ALL	2.65 $\pm$ 4.17 ^a	1.07 $\pm$ 1.64 ^b	1.32 $\pm$ 2.31 ^b	0.70 $\pm$ 1.38 ^b	0.90 $\pm$ 2.07 ^b	1.24 $\pm$ 2.37

Note. a>b; *^a : P<0.05.

presents (eye-contact and non-eye-contact), therefore, were considered together for purposes of statistical analysis. Lip-smacking was the most frequent behaviour observed, ranging from a mean per observation of 4.72, for Female Q-436 during NOPANTS, to a mean per observation of 12.10, for Female 83 during the PANTS cycle (Table 17).

Mean male response ranged from 0.03 for Female 83-PANTS cycle, to a maximum of 5.11 for Female DB-9-PANTS cycle (Table 18).

When the behaviour of each female was considered in relation to the two experimental conditions, consistent differences between NOPANTS and PANTS cycles were found in the frequency of female presents. They decreased in all the females during the NOPANTS cycle, the differences being significant in Females DB-9 and 83 (Table 16 and Figures 20, 21, 22). Instead yawns increased in all the females during the PANTS cycle, although, probably due to the small numbers involved, the increases were not statistically significant (Table 15 and Figures 20, 21, 22). No distinctive trends could be found in lip-smacks: they increased significantly in Female 83 during the PANTS cycle, decreased significantly for Female DB-9 in the same cycle, and remained virtually unaltered in Female Q-436 (Table 17). Solicits, the combined lip-smacks and presents, follow the lip-smacks trend (Figures 20, 21, 22).

In general, females were significantly more active during phase 1 of the cycle, when they showed the highest frequencies of presents and lip-smacks (Tables 16 and 17).

When one considers the cycles of the three females together in each of the experimental conditions and compares the behaviour frequencies for each phase, it is apparent that presents are reduced in all phases from the NOPANTS to the PANTS cycles although the difference is more marked in phases 1 and 2 and less marked in phase 3 (Table 16 and Figure 24). Lip-smacks instead are greatly reduced only in phases 1 and 2 and increase slightly during phase

TABLE 17

Frequencies (Means $\pm$ SD) of female lip-movements across menstrual cycles, when the female subjects are wearing pants (PANTS) and when they are not wearing pants (NO PANTS).

Female Subjects and Experimental Cycles	Cycle Phases ^a					ALL
	1	2	3	4	5	
DB-9 NO PANTS	16.00 $\pm$ 5.22 ^a	15.50 $\pm$ 4.65 ^b	7.46 $\pm$ 3.21 ^b	6.00 $\pm$ 1.52 ^b	9.25 $\pm$ 3.64 ^b	10.25 $\pm$ 5.14 ^a
DB-9 PANTS	6.25 $\pm$ 2.30	4.10 $\pm$ 1.10 ^b	3.00 $\pm$ 1.00 ^b	4.50 $\pm$ 2.64 ^b	6.00 $\pm$ 2.95 ^b	5.97 $\pm$ 2.84 ^a
Q-436 NO PANTS	2.00	5.22 $\pm$ 2.77	5.44 $\pm$ 3.43	4.85 $\pm$ 5.49	4.07 $\pm$ 2.39	4.72 $\pm$ 2.65
Q-436 PANTS	6.00	3.83 $\pm$ 3.47 ^b	4.50 $\pm$ 2.83	2.85 $\pm$ 3.04 ^b	7.27 $\pm$ 3.62 ^b	4.82 $\pm$ 2.78
83 NO PANTS	11.33 $\pm$ 4.61 ^a	5.40 $\pm$ 2.87 ^b	6.16 $\pm$ 1.70 ^b	8.40 $\pm$ 2.88	8.41 $\pm$ 3.08	7.44 $\pm$ 3.54 ^a
83 PANTS	19.00	9.87 $\pm$ 1.73	15.00 $\pm$ 4.96	12.66 $\pm$ 6.37	11.72 $\pm$ 3.94	12.16 $\pm$ 5.36 ^a
NO PANTS ^c	11.84 $\pm$ 6.20	6.85 $\pm$ 4.11	6.05 $\pm$ 3.40	6.35 $\pm$ 2.94 ^a	7.16 $\pm$ 3.78	7.56 $\pm$ 4.59
PANTS	7.14 $\pm$ 4.01	5.95 $\pm$ 3.15 ^b	7.38 $\pm$ 6.17	6.70 $\pm$ 5.35 ^b	9.05 $\pm$ 3.70 ^a	7.46 $\pm$ 4.52
ALL	10.37 $\pm$ 6.12 ^a	6.43 $\pm$ 3.64 ^b	6.61 $\pm$ 4.71 ^b	6.52 $\pm$ 4.60 ^b	8.07 $\pm$ 3.83 ^b	7.50 $\pm$ 4.54

NOTE: a > b; *p < 0.05.

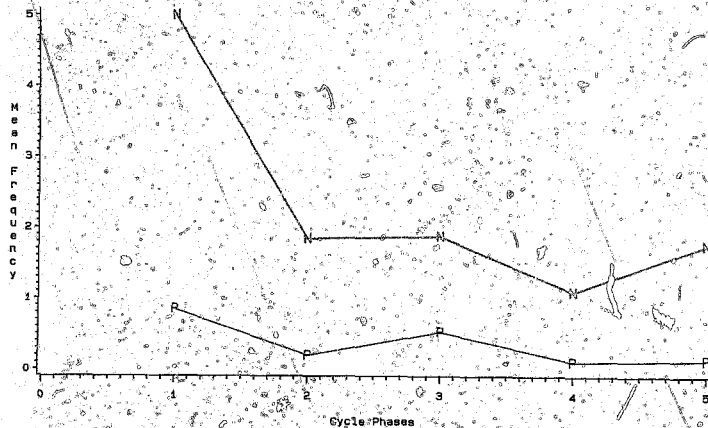
TABLE 16

OVERWEIGHTS (MEANS $\pm$ SD) of Male Response across the menstrual cycles of the female subjects, and the female subjects are wearing pants (PANTS) and when they are not wearing pants (NO PANTS).

Female Subjects and Experimental Cycles	Cycle Phases					
	1	2	3	4	5	ALL
00-9 NO PANTS	3.22 $\pm$ 0.80 ^a	2.75 $\pm$ 4.38 ^a	5.65 $\pm$ 0.57 ^a	4.28 $\pm$ 2.05	1.25 $\pm$ 1.20 ^b	4.02 $\pm$ 3.65 ^a
00-9 PANTS	6.58 $\pm$ 2.35 ^a	5.30 $\pm$ 1.89	2.66 $\pm$ 2.08 ^b	5.25 $\pm$ 0.89	4.36 $\pm$ 2.48 ^b	5.11 $\pm$ 2.03 ^a
Q-436 NO PANTS	1.00	3.22 $\pm$ 2.26	4.89 $\pm$ 4.72 ^a	1.60 $\pm$ 1.14 ^b	1.45 $\pm$ 0.67 ^b	2.72 $\pm$ 2.81
Q-436 PANTS	4.80	3.80 $\pm$ 2.00	4.86 $\pm$ 0.01	3.42 $\pm$ 2.14	3.37 $\pm$ 1.50 ^b	3.60 $\pm$ 1.68
R3 NO PANTS	0.00	2.30 $\pm$ 1.25	1.00 $\pm$ 1.26	0.00 ^b	1.46 $\pm$ 0.38	1.12 $\pm$ 1.50 ^a
R3 PANTS	1.00 ^a	0.00 ^b	0.00 ^b	0.00 ^b	0.00 ^b	0.03 $\pm$ 0.18 ^a
NO PANTS	-2.30 $\pm$ 3.83 ^b	3.92 $\pm$ 3.12 ^a	5.05 $\pm$ 4.03 ^a	2.23 $\pm$ 2.33 ^b	0.97 $\pm$ 1.05 ^b	2.68 $\pm$ 3.04
PANTS	6.00 $\pm$ 2.66 ^a	2.55 $\pm$ 1.67 ^b	2.70 $\pm$ 2.31 ^b	2.64 $\pm$ 2.54 ^b	2.67 $\pm$ 2.35 ^b	3.13 $\pm$ 2.67 ^a
ALL	4.02 $\pm$ 3.25 ^a	3.47 $\pm$ 2.96 ^a	4.09 $\pm$ 3.56 ^a	2.44 $\pm$ 2.41 ^b	1.78 $\pm$ 1.92 ^b	3.93 $\pm$ 2.87

Note. a > b, p < 0.05.

Figure 24. Female Presents During PANTS Cycles vs During NOPANTS Cycles



Yellow represents Frequency of Presents during NO PANTS
 Orange represents Frequency of Presents during PANTS

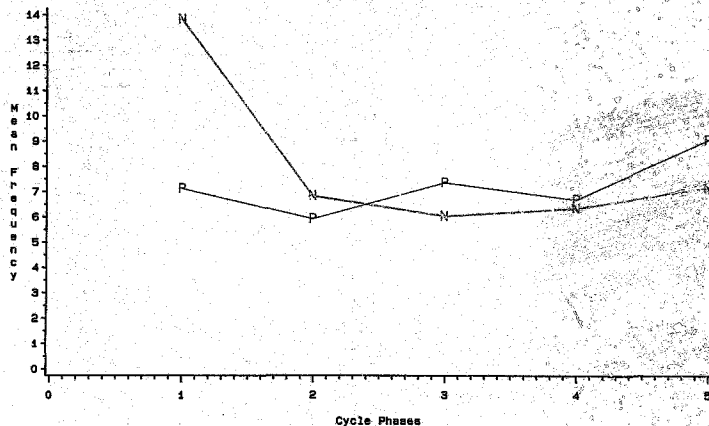
3 (Table 17 and Figure 25). If presents are combined with lip-smacks as solicits, the curves obtained show more clearly a great reduction of female behaviour during phases 1 and 2, during the PANTS experimental conditions, whereas the behaviour shows a remarkably similar pattern for the other three phases (phases 3, 4 and 5) of the cycle (Figure 26). The difference in the first two phases, between the two experimental conditions, is more clearly visible when the two phases are averaged, i.e., when they are summed and the average values obtained are plotted (Figure 27).

Mean male response per experimental cycle for the two females, that were exposed to the same number of males (Females DB-9 and Q-436), increases during the PANTS cycle whereas it decreases for Female 83 in the same cycle (Table 18). Male response instead shows great differences between the two experimental conditions in the shape of its distribution (see Figures 28, 29, 30; and for a direct comparison of the distributions, see Figure 31). When the phases of the NOPANTS cycles are compared with each other, significant differences are found with phases 2 and 3 showing the highest frequencies. By contrast, no significant differences are found among the five phases during the PANTS cycle, although a high level of response is noted during phase 1 (Table 18). Male response did not seem to be correlated with female behaviour but rather with the increase in female body weight, hence with the perineal swelling, during the NOPANTS cycles (Figures 28, 29, 30). This is even more clear when male response is plotted against female solicits for the three PANTS (Figure 32) and NOPANTS (Figure 33) cycles.

6.4. DISCUSSION

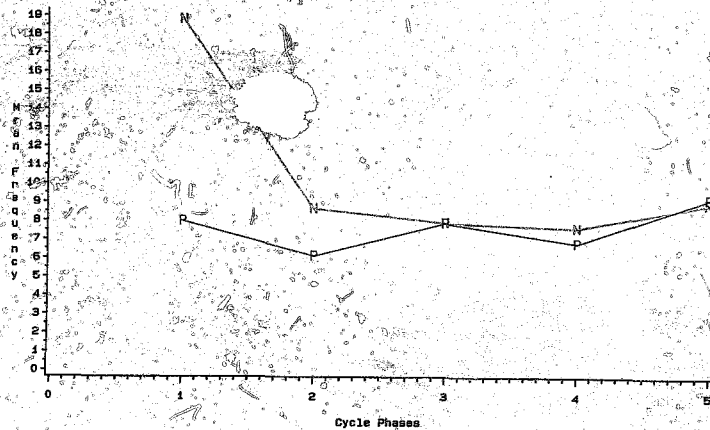
All the menstrual cycles were within the range described by Gillman and Gilbert (1946). The body weight profiles obtained in

Figure 25. Female Lip-Smacks During PANTS Cycles vs During NOPANTS Cycles



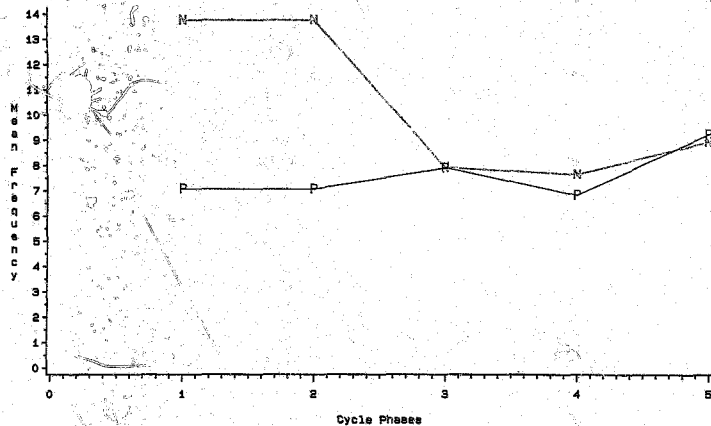
Yellow represents Frequency of Lip-Smacks during NO PANTS
 Orange represents Frequency of Lip-Smacks during PANTS

Figure 28. Female Solicits During PANTS Cycles vs During NOPANTS Cycles



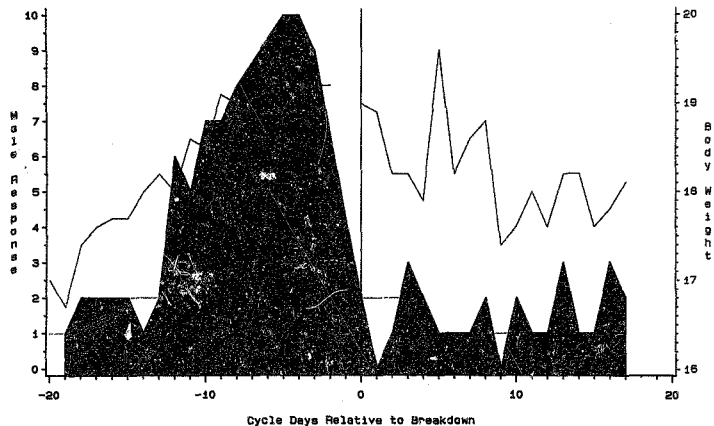
Yellow represents Frequency of Solicits during NO PANTS
Orange represents Frequency of Solicits during PANTS

Figure 27. Female Solicits During PANTS and NOPANTS Cycles with Phases 1 and 2 Averaged



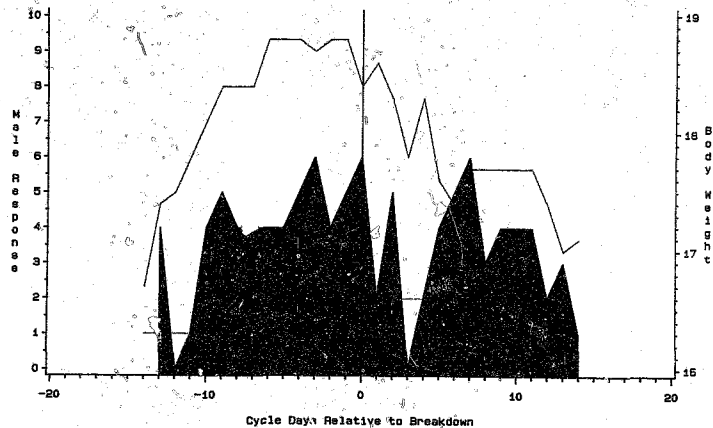
Yellow represents Frequency of Solicits during NO PANTS
 Orange represents Frequency of Solicits during PANTS

Figure 28.A. Female Q-436 - NOPANTS



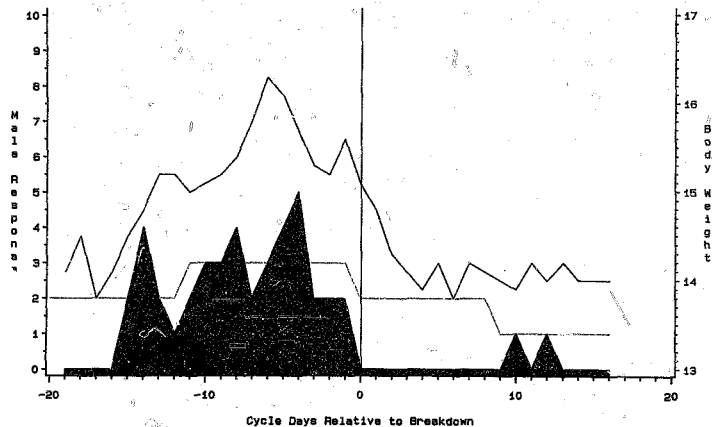
Green represents Occurrence of Male Response Blue represents Female Body Weight
Yellow represents Swell Rsts

Figure 28.B. Female Q-436 - PANTS



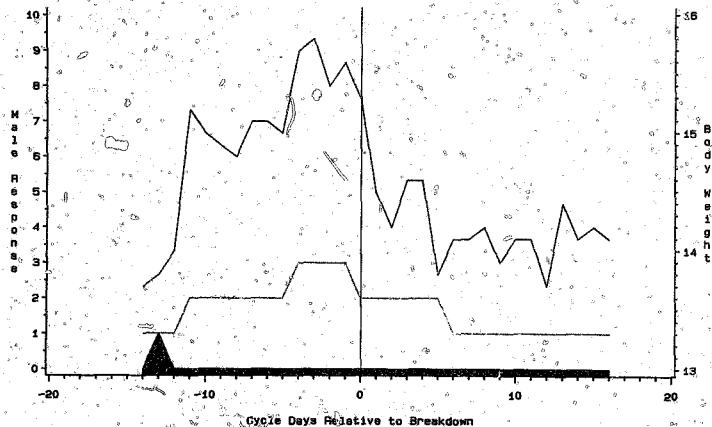
Green represents Occurrence of Male Response. Blue represents Female Body Weight. Yellow represents Inferred Swell Rate.

Figure 29.A. Female 83 - NOPANTS



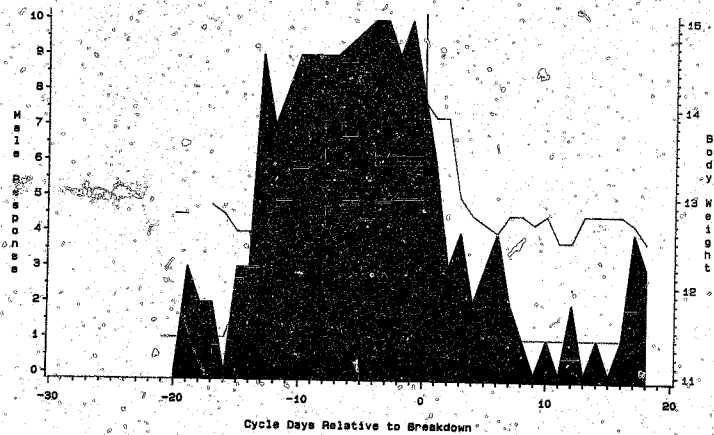
Green represents Occurrence of Male Response Blue represents Female Body Weight
Yellow represents Shell Rate

Figure 29.B, Female 83 - PANTS



Green represents Occurrence of Male Response Blue represents Female Body Weight
Yellow represents Inferred Swell Rate

Figure 30.A. Female DB-9 - NOPANTS



Green represents Occurrence of Male Response
 Blue represents Female Body Weight
 Yellow represents Swell Rate

Figurs 30.B. Female EB-9 - PANTS

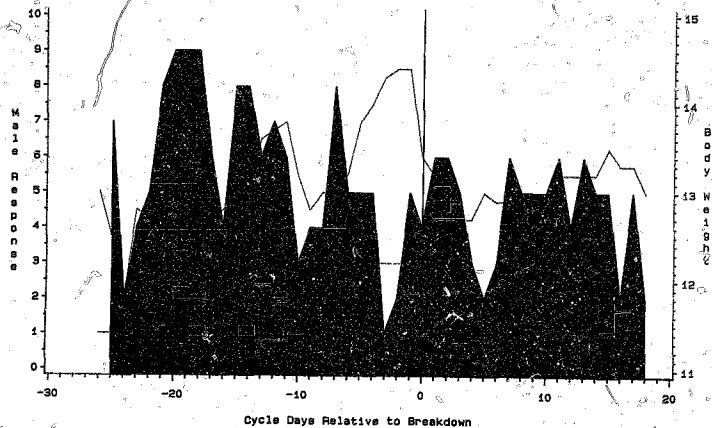
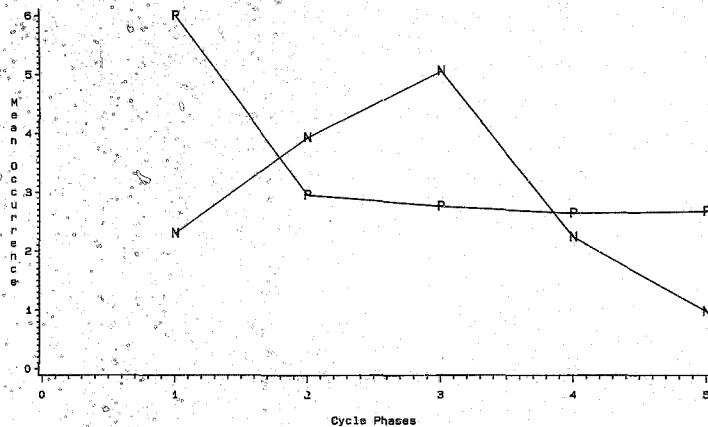
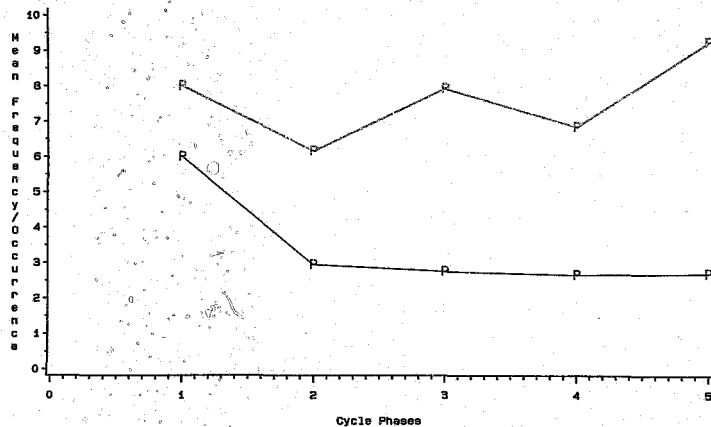


Figure 31. Male Response During PANTS Cycles vs During NOPANTS Cycles



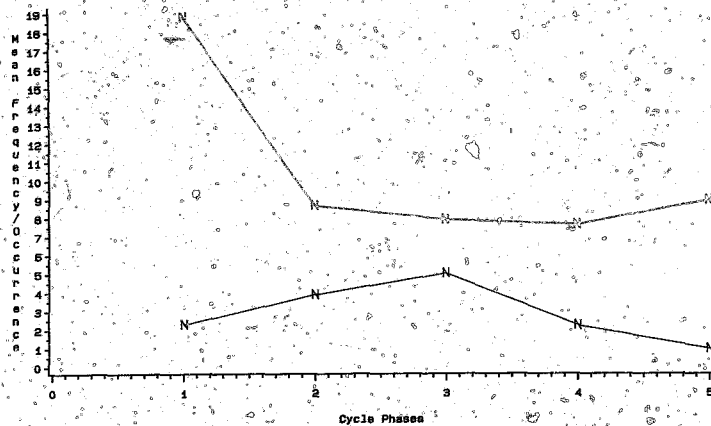
Green represents Occurrence of Male Response during NO PANTS
 Blue Represents Occurrence of Male Response during PANTS

Figure 32. Female Solicits vs Male Response During PANTS Cycles



Yellow represents Frequency of Solicits
Blue represents Occurrence of Male Response

Figure 33. Female Solicits vs Male Response During NOPANTS Cycles



Yellow represents Frequency of Solicits
Green represents Occurrence of Male Response

this study matched those described by Bialert and Busse (1983) for the chacma baboon. They reported the following: an average weight of 17 ± 2.8 kg with a range of 13.7 to 25.1 kg; an average increase in body weight over the menstrual cycle of 2.4 ± 0.9 kg; an average interval between the attainment of maximum body weight and BD day of 2.4 days with the former occurring at any time between BD-8 and BD-1. All the cycles, including the problematic PANTS cycle of Female Q-436, could therefore be considered normal and ovulatory.

The profiles obtained for female soliciting behaviour across the cycle phases for the two experimental conditions are very similar to the curves found in the preceding experiment (Chapter 5), in particular the curve obtained from the FF cycles. Frequencies of soliciting behaviour are highest during phase 1, decrease during phases 2, 3 and 4, and then increase again during phase 5. The similarity of the curves obtained in the two experiments, in particular with the FF cycles, strengthens an interpretation that the discrepancy found in the previous experiment between phases 1 of the FF and FM curves is an artifact which is caused by the small sample size used. It also suggests that the subdivision of the menstrual cycle into phases by means of body weight fluctuations is as appropriate, perhaps even more accurate, than subdivision according to the degree of sexual swelling.

When all the cycles from the two experiments, namely Experiment 5 and Experiment 6, are combined, a curve is obtained in which the highest values are postmenstrual, i.e., in phase 1 (Figure 34). They decline gradually towards the periovulatory phase to reach a nadir during phase 4, the early luteal phase, and start to increase again during the late luteal or premenstrual phase, phase 5. Although the hormonal mechanism involved is not known and can only be inferred (refer to Chapter 5 for a discussion on the matter), it appears clear that female soliciting behaviour is under hormonal control and that, in reply to the question posed by Hausfater and

Author Girolami Letizia

Name of thesis The Female's Role In Primate Socio-sexual Communication: A Study Of The Vervet Monkey (*cercopithecus Aethiops Pygerythrus*) And The Chacma Baboon (*papio Ursinus*). 1989

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