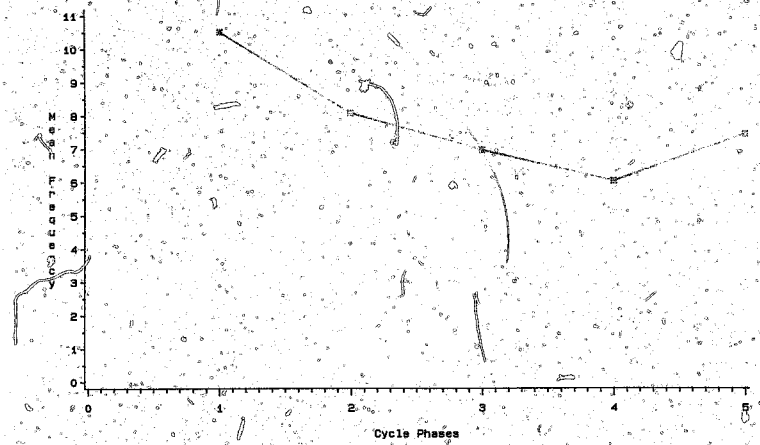
Figure 34. Female Solicits For All Menstruel Cycles Combined



Yellow represents Frequency of Solicits

Skoblick (1975), behaviour shows normal levels perimenstrually and is suppressed around ovulation.

A uniform decrease in presents was found across the menstrual cycle, in the PANTS cycle. This might be another indication of the susceptibility of this behaviour, among female proceptive behaviours, to environmental influences and thus of its unreliability as an indicator of the ovarian activity of the female.

As the results show quite clearly, male response is dependent only on the presence of a visible swelling. In fact, male response follows closely the swelling pattern, step by step, as shown in previous studies (Bielert *et al.*, 1980; Bielert, 1982; Bielert and Anderson, 1985; Bielert *et al.*, 1986; Bielert and Girolami, 1986; Girolami and Bielert, 1987) and in Chapter 4. When the swelling is visible, male response is not related to female solicits (Figure 33). This lack of correlation has already been pointed out (see Chapter 4; Bielert and Girolami, 1986; Girolami and Bielert, 1987). When the swelling is concealed, male response follows female behaviour during phase 1 very closely. The similarity in the two curves, however, is not maintained in the other phases (Figure 32). Because female solicits are usually high, in combination with a flat perineum, during phase 1 (Figure 33 and Chapter 5, Figure 18), males showing, instead, very low response rate, the high level of male response registered here should not be seen as dependent on female behaviour but rather as a reaction to the novelty constituted by the changed appearance of the female perineum. This explanation would account also for the maintenance of low levels of male response throughout the rest of the cycle after the initial phase. In brief, males do not respond to female soliciting behaviours: i.e., they are not aroused by, nor do they respond to, female behaviour - rather, they respond to and are aroused by the sight of a full swelling.

It is appropriate to remark upon the levels of male response found in this experiment during exposure to a flat or a concealed perineum. With the smaller group of males, male response approximated zero. This has been the norm for this group size in past experiments and is corroborated by results from field studies. This leads one to believe that males are not normally aroused by a flat perineum. At one stage in this experiment, males were added to the group to increase the sample size. Unfortunately, this caused an increased state of activation in the males, possibly causing a lowered threshold of arousal so that the males showed levels of response to flat or concealed perinea slightly greater than zero. Thus, this should not be interpreted to be male arousal caused by flat or concealed perinea but only as a shift in the baseline.

The experimental procedure resulted in clear effects on female behaviour. It seems that the application of pants affected female behaviour more at the beginning of the cycle, during phases 1 and 2. Furthermore, presents and lip-smacks were affected differentially. The reduction registered in the first two phases of the cycle might be seen as a phase of adjustment to the new situation. It should be remembered that the follicular phase is the phase of the cycle most susceptible to environmental changes (see Chapter 5 - Discussion). In this regard, females could be reacting to two different factors. First, they could be adapting to discomfort or hindrance to mobility caused by the garment. Second, they could be adjusting to a reaction by the males to the altered appearance of the female. Either hypothesis could be correct and perhaps both factors may have contributed to the changed levels of behaviour shown by the females. However, there was no evidence of any abnormality in the movement of the females when wearing the pants. They continued to climb up and down the shelf as before. For this reason, the second hypothesis seems more

appropriate. The even reduction in presents across the cycle could also be explained by the difficulty females may have experienced in their movements, or it might be explained by the fact that presents lost their communicative value, since the female now had no visible perineum to display. Not receiving appropriate feedback from the males, the females did not present as often. This interpretation is supported by the small increase in female presents and lip-smacks during phase 3 of the PANTS cycles. This increase seems to be caused by an all-male environment (as shown in the previous experiment, Chapter 5) and it also seems plausible that the reason for this is that females know that, during full swelling, they have better chances of initiating interaction with the males (see 5.3. above). Perhaps the females tried again, during a period more favourable, to elicit a response in the males. If presents do not stimulate the appropriate response, lip-smacks might do so since only the "rear end" appearance has changed. This might explain then the increase in lip-smacks during phases 4 and 5 of the PANTS cycles compared with the same phases of NOPANTS. It is plausible then that females learned to use the behaviour most appropriate to the circumstances. The increase in yawns during PANTS could also be interpreted as a sign of discomfort and/or possibly as indicating conflict regarding the most appropriate behaviour.

The small increase in presents found during phase 3 of NOPANTS is repeated in the same phase during the PANTS cycle. Furthermore, lip-smacks during phase 3 of PANTS were even more frequent than in the same phase of NOPANTS. These results suggest that the female subjects, and possibly female baboons in general, are not aware of their changes in attractiveness and of the fact that their increased success-rate might be due to their increased attractiveness (see 5.3.). Instead they might associate their success with their perception or proprioception of their changed physiological con-

dition during the phase of full swelling. If the experimental females had been aware of their attractiveness, or in particular of their lack of attractiveness, during phase 3 of the PANTS cycles, they should not have increased their solicits but should, rather, have adapted their behaviour to that of the males by a reduction in solicits. For the same reason, in Experiment 4, the female subjects should have increased their solicits when wearing the artificial swelling.

In summary, this experiment showed that concealment of the perineal swelling abolishes completely male response, or drastically reduces it relative to the levels shown when the swelling is visible. This confirms that male arousal is dependent on the visual stimulus of a swollen perineum and is not related to female soliciting behaviour. The wearing of pants had a complex effect on female soliciting behaviour which could be explained either by the physical discomfort caused by the garment or by changes in male-female visual interaction due to the concealement of the perineum. The latter interpretation seems more plausible. In addition, it appears that female soliciting behaviour is used by the baboon as a signal rather than as an arousing stimulus.

7. GENERAL DISCUSSION AND CONCLUSIONS

The results obtained suggest that females of the two species under discussion modulate copulatory behaviour in two ways. Vervet monkeys use mainly proceptive behaviours, whereas the baboons use their perineal swelling. In both species female proceptive behaviours tend to increase the likelihood of copulation but they do not have an arousing effect on the males. The perineal swellings of female baboons also increase the likelihood of copulations, but, unlike proceptive behaviours, they do arouse the males. In Beach's description (1976) of three aspects of female sexuality in mammals, i.e., receptivity, proceptivity and attractivity, proceptivity and receptivity were comprised of behaviours only, whereas attractivity included physical traits as well as behaviours. According to his classification, the perineal swelling should be considered as attractive, whereas the soliciting behaviours are both proceptive and attractive. However, since behaviours *per se* were shown not to be arousing, they should not be considered attractive. Beach's classification, with respect to primates, could well be reconsidered so that only those traits that induce and regulate male arousal in a quantitative way, as a sign stimulus would do, are defined as attractive. The existence of behavioural or vocal displays, that could have such effect on males, is still under discussion (Hrdy and Whitten, 1987).

The oestrogen sensitivity of female behaviours and perineal elaboration suggest that female behaviour and perineal swelling have a function of increasing the likelihood of copulations during the period of maximum fertility, since oestrogens are highest at the time of ovulation. It appears, at this point, that vervet

monkeys and the baboons have adopted two different systems to serve the same purpose, the former based on proceptivity, the latter on attractiveness.

In tree shrews and prosimians hormone-induced behavioural changes seem to be associated with changes in attractiveness (Conaway and Sorenson, 1966; Eaton *et al.*, 1973; Doyle *et al.*, 1967; Dixson, 1978). This is, in fact, what happens in the majority of female mammals and has been defined as oestrus (Lisk, 1978). The extent to which proceptive behaviour is used in tree shrews and prosimians varies but, generally, proceptive behaviours are not well developed and the main behavioural changes brought about by ovarian steroids are in receptivity. Attractiveness instead is constituted by chemical cues (Hrdy and Whitten, 1987). A shift from chemical to visual attractiveness is understandable, as suggested also by Dixson (1983c), considering the increasing importance that the visual system has acquired in primates at the expense of the olfactory system (Ankel-Simons, 1983).

Female vervet monkeys, in the research under discussion, showed a sensitivity to oestrogens in their receptive behaviours. Female baboons, also, showed a sensitivity of proceptive behaviours to oestrogens but, in this case, with the possible exception of a small portion of presents, the hormonal effect was negative. It seems possible that the communication systems adopted by the vervet monkeys and the baboons originated from the oestrus system shown by other mammals. Each of the two systems seems to have emphasised or reduced one, or more, of the three components, i.e., receptivity, proceptivity and attractiveness.

With the exception of prosimians, hormonal-induced changes in receptivity are minimal in primates (Baum, 1983). It is possible that a shift from receptivity to proceptivity was imposed by the requirements of a social life. Results from the experiments on baboons have shown that interactive behaviours decrease in corre-

spondence with increases in circulating oestrogens. It would seem that, in this species, proceptivity is not only reduced but even reversed in correspondence with high levels of circulating oestrogens. It seems possible that, in a species in which females can be seriously injured by males (Smuts, 1985, 1987), assertive behaviours at the time of fertility, and thus of maximum attractiveness, were selected against. In addition, the lack of changes in female receptivity (Bielert, 1986) with the restricted use of proceptivity suggest that, in this species, receptivity had already undergone reduction in importance and had been already substituted by proceptivity. The reduced proceptivity noted should therefore be seen as a subsequent adaptation, due possibly to the development of the visual attractiveness. A system based on attractiveness is, in fact, more powerful in terms of restricting the copulations around ovulation time, than a system based on behavioural changes (proceptivity). This might be due to the fact that, in the attractiveness system, it is the males that regulate the copulatory activity whereas, in a proceptivity system, it is the females. In the case of vervet monkeys, it seems that it is attractiveness that has undergone reduction. This is suggested also by Dixson (1983c). Vervet monkeys, like all Cercopithecoidea, must have acquired a visual attractiveness, i.e., some form of perineal elaboration, at one stage of their evolution, when they adapted to a terrestrial way of life. That visual attractiveness is an adaptation to terrestrial life is shown by the fact that New World monkeys, that have always been arboreal, have conserved a chemical attractiveness. Why vervet monkeys have adopted a proceptivity system, reducing their attractiveness, and baboons have developed an attractiveness system, reducing their proceptivity, is difficult to say at this stage.

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