SOCIAL FACTORS AFFECTING REPRODUCTIVE SUCCESS IN FEMALE GELADA BABOONS (*Theropithecus gelada*)

by

Colleen M. McCann

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Date

Executive Officer

Eric Delson

Sara Stinson

Clifford Jolly

David Abbott

Supervisory Committee

The City University of New York

ABSTRACT

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Advisor: Professor John F. Oates

A knowledge of variation in female reproductive success and of the factors responsible for such variation is essential for a full understanding of the evolution of primate life-history strategies, including social behavior. Inter-individual variation in female fertility has been observed in several primate species; and in some, evidence of a positive correlation between a female's dominance rank and her fertility has suggested that increased fertility is a corollary of the advantages accrued by dominant individuals (Harcourt, 1987; Dunbar, 1988; Abbott, 1991). In wild gelada baboons (*Theropithecus gelada*), low-ranking females raise offspring less frequently than do high-ranking females. In discussing the results of his long-term field studies, Dunbar (1989) has suggested that reproductive suppression in low-ranking females, as a consequence of social stress, is a significant factor contributing to the variation in birth rates of individual females.

In the present study, I investigated whether ovarian suppression resulting from social stress contributed to the reproductive impairment of low-ranking females. This question was investigated in semi-free-ranging groups of gelada baboons maintained at the Wildlife Conservation Society's Bronx Zoo. Observational sampling was combined with the laboratory analysis of hormones in samples of urine collected from individual females.

The main findings of this study were that a female's dominance rank can have important consequences for her relationship with other females and the unit male, and ultimately for her reproductive success. Low-ranking females experienced lower copulation frequencies and higher rates of aggression and cortisol secretion, which increased significantly during the follicular phase of the menstrual cycle. The interval between ovulations was greater for low-ranking females than it was for high-ranking females, and the increased length of the menstrual cycle was due to an elongation of the follicular phase.

The data suggest that harassment of low-ranking female gelada baboons by high-ranking females may have resulted in lengthened menstrual cycles and reduced ovulatory frequency in low-ranking females. Reduced ovulatory frequency may lead to the delay in conceptions in low-ranking females found in wild populations. High-ranking female gelada baboons may be imposing stress-induced suppression of reproduction on their female subordinates to obtain a reproductive advantage.

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CHAPTER 1. INTRODUCTION

1.1. Factors Affecting Reproductive Success in Female Primates

Natural selection is a consequence of differential survival and differential reproduction among individuals, manifested as differential reproductive success. A primary mechanism contributing to differential survival and reproduction is competition. In primates, competition between individuals for limited resources has traditionally been considered to be more pronounced in males than in females (Hrdy 1984; Wasser, 1983a; Smuts, 1987; Small, 1988). And thus, the variance in male reproductive success has likewise been considered to be greater than the variance observed in female reproductive success. Compared to males, female-female competition is notoriously inconspicuous, and can occur throughout all or any part of the reproductive process, whereas competition among males is more conspicuous and tends to be concentrated around the time of mating (Wasser and Barash, 1983). Accordingly, there have been many primate studies that focused on competition in males and the factors that affect variance in male reproductive success. An understanding of this focus on male-male competition can be found in some of the basic concepts of sociobiology: sexual selection and parental investment theory.

Darwin developed the theory of sexual selection to explain the evolution of traits that did not appear to contribute to an individual's survival (Darwin, 1871). He argued that the differences in morphology and behavior between the sexes evolved because they increased an individual's mating success. He pointed

out that this could operate through either intrasexual competition for mates or intersexual choice of mates. Intrasexual competition occurs when members of one sex compete for members of the opposite sex (mate competition), and intersexual choice occurs when members of one sex preferentially select members of the opposite sex (mate choice). The potential outcome of these processes could be exhibited as: female-female competition, male-male competition, female mate choice or male mate choice. However, Darwin noted that the outcome of these events usually involved males competing for females and females choosing among males. manifested

The patterning of male competition and female mate choice has since been delineated in terms of differential parental investment (Trivers, 1972). Trivers pointed out that there are underlying differences in the physiology of male and female gametes. For instance, the energy expenditure required to produce eggs is far greater than the energy invested to produce sperm. Females produce a limited number of large gametes that are released over long intervals, while males produce a large number of small gametes that are released at relatively short intervals. This results in an imposed limit on the number of potential offspring that can be produced by females while investing a lot of energy into each one. Males, on the other hand, while investing very little energy, can potentially produce a limitless number of offspring.

This fundamental difference in the physiology of male and female gametes produces differences in the mating strategies of males and females (Trivers, 1972). Females -- who require a greater initial energy expenditure to produce eggs -- become a limiting resource for males. In theory, if females are the limiting resource for males, males should compete with other males for access to females. Thus, males can increase their reproductive success by mating with

additional females. In contrast, since females cannot increase their reproductive success by mating with additional males, they should discriminate among possible mates by choosing males that can contribute the most genetically or behaviorally to each offspring.

Male-male competition and, to a lesser degree, female mate choice are the most illustrative forms of sexual selection (Trivers, 1972). In primates, male-male competition frequently involves aggression and often results in severe physical injuries (Lindburg, 1971; Poirier, 1974; Drickamer, 1975; Hausfater, 1975; Dittus, 1977; Smuts, 1987). The level of aggression typically intensifies around the time of mating in the presence of estrous females. Male-male competition for mates has, therefore, been viewed as a primary factor contributing to the variance in male reproductive success.

It has also been demonstrated in many primates that females exert choice over selecting mates. Females appear to choose mates either directly, by initiating or refusing solicitations to copulate, or indirectly, by influencing male group membership (Lindburg, 1971; Packer, 1979; Wolfe, 1979, 1984; Dunbar, 1984; Janson, 1985; Andelman, 1987; Smuts, 1987). The association between female mating preferences and female reproductive success is less conclusive. However, in several primate species females appear to exert mating preferences on the basis of reducing their vulnerability to male aggression, particularly infanticide (Smuts, 1987).

More recently, competition among females, and the factors that affect differential reproductive success in females, is gaining significance in sexual selection theory (Hrdy, 1981; Fedigan, 1982; Wasser, 1983a, b; Small, 1984; Dunbar, 1989; Ziegler and Bercovitch, 1990; Abbott, 1991). This recent concentration on female reproductive success is in part due to the growing body

of evidence demonstrating that females compete with other females for mates and males occasionally exhibit mate choice (Smuts, 1987; Ziegler and Bercovitch, 1990). Thus, the potential exists for males being a limiting resource for female reproductive success in addition to females being a limited resource for males (Small, 1988).

For example, females may compete for access to mates if males are in limited supply as may be the case in a monogamous or polygynous mating system. Females may also compete over access to many mates. Access to additional mates may be advantageous if having many mates results in greater protection by males from predators or from other males. And females may also compete for access to 'higher quality' mates which may result in 'higher quality' paternal investment from males, or it may result in these qualities being passed on to the offspring (Hrdy, 1984).

In addition to competition for mates, females may also compete over a variety of other resources that may affect their reproductive success, such as: access to the food resources, access to preferred food items, access to social partners, or access to coalitionary partners (Hinde, 1983; Dunbar, 1980a; Whitten, 1982, 1984; Wasser, 1983a, b; Gray, 1985; Harcourt, 1987).

All of these factors can have important consequences for individual survival and reproduction; and therefore, the possibility exists for them to be contributory factors in female reproductive success. And reproductive success, as the determining factor in fitness, is the ultimate consequence of competition. Thus, there has been a recent shift in focus from the study of male-male competition as a contributory factor in male reproductive success towards the study of female-female competition as contributing to the variance in female reproductive success.

1.1.1. Ecological Factors: Nutrition and Fertility

Variation in food intake and nutritional status can affect a female's fertility, fecundity, and virtually all other reproductive parameters. Some researchers use the terms fertility and fecundity interchangeably, and hence, the definition of these terms may differ from one source to another (e.g., Frisch, 1978; Bongaarts, 1980; Richard, 1985; Dunbar, 1988; Pianka, 1988). Broadly defined, *fertility* can be viewed as the number of offspring produced over a given period of time (reproductive performance), while *fecundity* is the physiological ability to produce offspring through the production of gametes (reproductive capacity). It is well established that ecological factors affecting the nutritional condition of individuals can be key elements in determining fertility in female mammals (Sadleir, 1969a; Hendrickx and Nelson, 1971; Smuts *et al.*, 1987; Bronson, 1989). Nutrition affects a female's ability to conceive, to carry a fetus to term, and to nourish a neonate adequately (Sadleir, 1969b). In mammals, a female's physiological condition must be maintained at a minimum nutritional threshold before ovulation can take place. Frisch and colleagues (Frisch, 1978, 1982, 1984; Frisch and McArthur, 1974) have argued that a minimum fat:body weight ratio must exist in order for ovulation, and hence a new reproductive cycle, to occur. More recently, Ellison (1990) has shown that extreme weight loss is associated with irregular or absent menstrual cycles, and that this in turn is indicative of reduced frequencies of ovulation or even complete ovulatory suppression. While the evidence provided by Ellison, Frisch and colleagues indicate that the level of fat relative to body weight strongly affects the age at first menarche and menstrual cyclicity; others (Bongaarts, 1980; Konner and Worthman, 1980; Lunn, 1985; McNeilly *et al.*, 1985; Lee, 1987) have shown that lactation and suckling behavior, and their physiological correlates also affect

reproductive functioning in that these events determine the timing of subsequent ovulations. For instance, nutritional condition can also affect a female's milk quality, infant growth and development, and interbirth intervals (French, 1983; Lee, 1987; Bronson, 1989). Thus, nutritional benefits can affect all aspects of reproduction. Despite arguments as to the mechanisms involved, however, it has been well documented that physical condition is a key element in determining fecundity in female mammals.

The results of many primate studies provide evidence correlating variation in ecological factors and variation in fertility. For example, a sudden decline in the food supply was attributed as the major cause for the drastic reduction in reproductive activity in both free-ranging chacma baboons (*Papio ursinus*: Hall, 1963) and rhesus macaques (*Macaca mulatta*: Loy, 1970). Similarly, the Koshima Island population of Japanese macaques (*Macaca fuscata*) experienced a 50% decline in birth rates during the period that artificial provisioning was withdrawn (A. Mori, 1979). Correlations between birth rate and habitat quality have also been documented in black-and-white colobus monkeys (*Colobus guereza*: Dunbar, 1987), vervet monkeys (*Cercopithecus aethiops*: Cheney *et al.*, 1988), olive baboons (*Papio anubis*: Strum and Western, 1982), Guinea baboons (*Papio papio*: Dunbar and Sharman, 1983), Japanese macaques (*Macaca fuscata*: Takahata, 1980), barbary macaques (*Macaca sylvanus*: Menard *et al.*, 1985), and long-tailed macaques (*Macaca fascicularis:* van Schaik and van Noordwijk, 1985). The implication of these observations is that a decline in habitat quality correlates with a decline in female physical condition which results in a reduction in fertility. The results of these studies provide evidence illustrating the importance of the nutritional condition of females in determining fecundity, and hence, its resultant effect on fertility.

1.1.2. Social Factors

1.1.2.a. Dominance Relationships and Competitive Ability

Competition occurs when "two or more organisms use the same resources and when those resources are in short supply" (Pianka, 1988). The term 'competition' can be qualified to distinguish whether it occurs as a result of direct or indirect interactions. For instance, when the process involves the adjustment of behaviors to that of other individuals without direct interaction, such as foraging or ranging, it is considered *exploitative*, or scramble, competition. This form of competition results in a reduction or depletion of resources. When more direct interactions are involved, such as aggression or territoriality, it is termed *interference*, or contest, competition. The outcome of this form of competition is variance in resource acquisition, survival or reproductive success (Pianka, 1988; van Schaik, 1989; Isbell, 1991).

In its most conspicuous form, competition is often assessed in terms of agonistic interactions in dominance relationships. And dominance hierarchies are often the focus of studies measuring the relative fitness of individuals. As such, dominance is defined in terms of the directionality of agonistic interactions between sets of individuals (Gartlan, 1968; Rowell, 1974; Hinde, 1978; Bernstein, 1981; Zumpe and Michael, 1986). However, dominance is not a trait, but rather a relationship between individuals. It cannot, therefore, be inherited or selected for. What can be selected for, though, are those traits that may influence one's competitive ability in agonistic interactions (Harcourt, 1987).

Alternatively, dominance *rank* is a characteristic of an individual's status among a delineated group of individuals. Therefore, an individual's dominance rank only exists relative to the other individuals in the social group. And

dominance rank is often used as a measure of an individual's relative fitness. This distinction has been viewed by some as two conceptual levels of dominance: (1) the dyadic level -- the asymmetrical relationship between two individuals, and (2) the group level -- the structure of dominance relationships within a social group (Hinde, 1978).

The study of dominance and its effect on various measures of fitness is based on the notion that priority of access to resources accrues to high-ranking individuals. And thus, a priority of access to resources could be a strong motivation to achieve high dominance status. The results of several studies provide evidence correlating dominance rank and greater access to limited resources (Gray, 1985). However, individuals that achieve high rank may only do so for a limited amount of time. And there are many studies illustrating that individual dominance ranks fluctuate over time. High rank may not, therefore, result in greater measures of fitness over an individual's lifetime. Furthermore, the costs in achieving high rank may be greater than the benefits gained, so that alternative strategies of resource acquisition may prove to be equally advantageous (Hrdy, 1984; Silk, 1987; Smuts, 1987; Dunbar, 1988; Bercovitch, 1991).

However, the fact that individuals appear to strive for dominance, and that when an opportunity to increase one's rank prevails it is actively pursued, or that across populations and species ranks within groups are continually challenged, suggest that there are at least some advantages to attaining high dominance rank (Bernstein, 1981).

Dominance status appears to play an important role in some species that have limited breeding positions, where the overwhelming majority of females that transfer out of their social group to enter another tend to be subordinate

(Chepko-Sade and Sade, 1979; Crockett, 1984; Pusey and Packer, 1987). Differences in dominance status between individuals in several primate species are stably maintained over long periods of time, as in vervet monkeys (*Cercopithecus aethiops*: Lee, 1983), Japanese macaques (*Macaca fuscata*: Kawai, 1958), rhesus macaques (*M. mulatta*: Sade, 1967) and yellow baboons (*Papio cynocephalus*: Hausfater *et al.*, 1982); or, when there is a sudden change in group composition, higher dominance status can be abruptly pursued as in long-tailed macaques (*M. fascicularis*: van Noordwijk and van Schaik, 1985, 1988), savanna baboons, (*Papio*: Bercovitch, 1986) and gelada baboons (*Theropithecus gelada*: Dunbar, 1988). Furthermore, female primates will vigorously pursue the attainment of high social rank, apparently even in the absence of immediate resources (Dunbar, 1980a; Walters, 1980; Datta, 1983).

1.1.2.b. Dominance Rank and Fertility

There is evidence that, in addition to nutritional factors, social factors also play a significant role in determining the reproductive success of individual females (reviewed in Gray, 1985; Dunbar, 1988). Dominance status is the social factor most commonly associated with fertility in primate studies, the implication being that reproductive advantage accrues to high-ranking females. While some have questioned the validity of an association (Gouzoules *et al.*, 1982; Fedigan, 1983; Fedigan *et al.*, 1986), several studies report a relationship between a female's dominance rank and her fertility (reviewed in Dewsbury, 1982; Abbott, 1987; Harcourt, 1987; Dunbar, 1988). In studies that report correlations between a female's dominance rank and her fertility, the correlations are overwhelmingly positive. That is, dominant females tend to be more fertile

than subordinate females. Dominant females reach sexual maturity and begin breeding at an earlier age (*M. mulatta*: Drickamer, 1974; Sade *et al.*, 1976; Wilson *et al.*, 1983; Meikle *et al.*, 1984; P. *cynocephalus*: Altmann *et al.*, 1988), have their first successful conception at an earlier age (*P. anubis*: Rowell, 1970; *M. mulatta*: Drickamer, 1974; Meikle *et al.*, 1984; *M. fuscata*: Sugiyama and Ohsawa, 1982; *M. sylvanus*: Paul and Thommen, 1984; *P. cynocephalus*: Altmann *et al.*, 1988), have fewer cycles to conception (*Theropithecus gelada*: Dunbar, 1980a, 1984), begin breeding and give birth earlier in the birth season (*M. mulatta*: Drickamer, 1974; *Cercopithecus aethiops*: Whitten, 1983), produce more offspring (*Saguinus fuscicollis*: Terborgh and Goldizen, 1985; *S. mystax*: Garber *et al.*, 1984; *C. aethiops*: Whitten, 1983, Fairbanks and McGuire, 1984; *M. fuscata*: Takahata, 1980, Sugiyama and Ohsawa, 1982, Gouzoules *et al.*, 1982; *M. mulatta*: Drickamer, 1974, Sade *et al.*, 1976; Wilson *et al.*, 1978; *M. sinica*: Dittus, 1979, 1986), and have offspring that experience higher survival rates than do subordinate females (*Papio ursinus*: Busse, 1982; *M. fuscata*: Sugiyama and Ohsawa, 1982; *M. mulatta*: Drickamer, 1974, Wilson *et al.*, 1978; *M. sinica*: Dittus, 1979; *M. sylvanus*: Paul and Thommen, 1984; *M. radiata*: Silk *et al.*, 1981). On the other hand, some studies that have looked for correlations between female rank and various measures of fecundity failed to find one (*Presbytis entellus*: Dolhinow *et al.*, 1979; *Erythrocebus patas*: Loy, 1981; *M. fuscata*: Wolfe, 1984; *C. aethiops*: Cheney *et al.*, 1986). Nevertheless, the phenomenon of reproductive advantages accruing to dominant individuals appears to occur on some level in a variety of New and Old World monkey species.

1.1.2.c. Dominance Rank, Fertility and Access to Food Resources

One often-cited explanation for the association between dominance and fertility is that the greater priority of access to food resources experienced by high-ranking individuals results in a higher birth rate. Some studies report that the greater fertility experienced by dominant females is indeed the result of a greater efficiency of food intake-- measured by the amount of time and energy spent in obtaining food resources and/or the amount of high quality food obtained per given amount of effort (Harcourt, 1987:476). For example, in a group of *Cebus nigrivittatus*, the alpha female foraged in the center of the group allowing her preferential access to favored fruits and insects (Robinson, 1981); similarly, dominant females in a *Cebus apella* group had a 20% higher efficiency of food intake than did subordinate females (Janson, 1985). In vervet monkeys (*C. aethiops*), dominant females spent more time feeding on favored food items than did subordinate ones (Wrangham and Waterman, 1981; Whitten, 1983), and had preferential access to watering holes in times of drought (Wrangham, 1981).

In those cases where dominant females have a greater priority of access to food resources than do subordinates, one would expect that this would also affect differences between them, or their offspring, in body weight. Riopelle *et al.* (1976) found that maternal weight at conception correlated with infant birth weight in rhesus macaques (*M. mulatta*). Similarly, where differences are found, high-ranking female Japanese macaques (*M. fuscata*) and their offspring were heavier than subordinate females and their offspring (A. Mori, 1979; Sugiyama and Ohsawa, 1982). The top ranking females in a population of vervet monkeys (*C. aethiops*) had a median weight 10% greater than the lowest ranking females (Whitten, 1983), while in a captive group of rhesus macaques, Small (1981) found that high-ranking females had higher fat indices than did

low-ranking females.

The implication of these data is that differences in fertility with respect to rank and access to food resources would more likely exist in wild populations where times of food shortage are common. For instance, during times of nutritional deprivation due to adverse ecological conditions, low-ranking individuals suffered higher mortality rates than did high-ranking ones, apparently as the result of an inability to gain access to vital resources (*M. mulatta*: Southwick, 1967; *M. sinica*: Dittus, 1979, 1986; *M. fuscata*: A. Mori, 1979; *C. aethiops*: Wrangham, 1981; Cheney *et al.*, 1981; Cheney *et al.*, 1988). However, differences in fertility with respect to rank are found as often in provisioned and captive populations as in wild populations (*C. aethiops*: Fairbanks and McGuire, 1984; *M. mulatta*: Drickamer, 1974; Wilson *et al.* 1978; Wilson *et al.*, 1983; Meikle *et al.*, 1984; *M. sylvanus*: Paul and Thommen, 1984). Of particular interest is a study by Sugiyama and Ohsawa (1982) on a provisioned group of Japanese macaques (*M. fuscata*). During the period of provisioning, dominant females, who experienced greater access to the provisioned foods, bred earlier than did subordinate females and had shorter interbirth intervals. However, when provisioning ceased, differences in birth rates between females did as well; and reproductive performance declined in all females, regardless of social rank. The data suggest to some that the distribution of food, as well as its abundance, is important in determining competitive ability between individuals (Fairbanks and McGuire, 1984; Harcourt, 1987). In other words, when resources are sufficiently clumped to allow access to them to be biased, dominant females have a greater efficiency of food intake than do subordinate females (Whitten, 1983; Janson, 1985).

1.1.2.d. Dominance, Fertility and Social Stress

While social status may be a good indicator of the relative nutritional condition of individuals, and thus indicative of relative fecundity, there is growing evidence to suggest that a decline in fertility may be driven by forces other than competition for access to food resources (Harcourt, 1987; Dunbar, 1988). Among such forces affecting individual female fertility may be the adult sex ratio, group size, competition for access to coalition partners or competition for access to mates (Dunbar, 1980b; Harcourt *et al.*, 1981; Silk *et al.*, 1981; Busse, 1982; Gouzoules *et al.*, 1982; Dunbar and Sharman, 1983; van Schaik, 1983; Wasser, 1983a; Dittus, 1986; Altmann *et al.*, 1988). A lack of coalitionary support is thought by some to be synonymous with subordinance and can be correlated with decreased fertility in low-ranking females. For example, Wasser (1983a) and Wasser and Starling (1986) report that in troops of yellow baboons (*Papio cynocephalus*) membership in a coalition is one strategy low-ranking females use to buffer the level of agonism they receive from other more dominant individuals. Similarly, having coalitionary allies is thought to reduce the amount of reproductive competition between females in gelada baboons (*Theropithecus gelada*) (Dunbar, 1984) and talapoin monkeys (*Miopithecus talapoin*) (Keverne *et al.*, 1982).

Group size has also been implicated in having an effect on female fertility. Some studies of wild primates have shown the influence of group size on various measures of competition, such as frequency of interference during feeding, frequency of agonistic interactions and distance traveled per day (Waser, 1977; van Schaik *et al.*, 1983; Watts, 1985). In a review of the primate literature, van Schaik (1983) found that in 22 out of 27 populations of New and Old World monkeys, group size was negatively correlated with fertility. In particular, he

found a negative correlation between the number of females in a group and the number of offspring produced by each female. In a sample of baboon populations, Dunbar and Sharman (1983) found a negative correlation between birth rate and the adult sex ratio, as did Silk *et al.* (1981) in a group of captive bonnet macaques: the mean birth rate decreased as the number of females per male in a group increased. Similar results have been reported for gorillas (*Gorilla gorilla beringei:* Harcourt *et al.*, 1981) and colobus monkeys (*Colobus guereza:* Dunbar, 1987).

Another factor that may have a contributory effect on female reproductive success is competition for access to mates. Wasser (1983a) and colleagues (Wasser and Barash, 1983) point out that female mammals, including primates, are in competition for 'quality' of offspring, in contrast to males, who are in competition for 'quantity' of offspring. Thus, the advantages accrued in competition for access to 'high quality' mates could include greater paternal investment from males, greater protection from males, or the passing on of 'better' alleles to offspring (Wasser, 1983a). However, conditions may also exist where females compete for many mates (Small, 1988) and males select among preferred mates (Smuts, 1987).

Some studies in female primates have demonstrated a correlation between high dominance rank and a greater priority of access to mates. For example, sexual activity is inhibited in low-ranking female rhesus macaques (*Macaca mulatta*: Wallen and Winston, 1984) and pigtail macaques (*M. nemestrina*: Goldfoot, 1971) when higher ranking females are in close proximity. In addition, Wilson (1981) showed that the duration of mount series by male rhesus macaques with high-ranking females was significantly longer when compared to the duration with lower ranking females.

In two experimental studies of dominance rank and mating preferences, the data suggest that dominant females have a greater priority of access to mates. High-ranking female rhesus macaques spent a greater number of times interacting with males and for longer durations than did subordinate females (Zumpe and Michael, 1989). However, despite the fact that males maintained a closer proximity to high-ranking females, no differences were found between high- and low-ranking females with respect to sexual activity with males. And in capuchins (*Cebus apella*), high-ranking females interacted more with males and experienced greater copulation frequencies than did low-ranking females (Linn *et al.*, 1991).

Competition among females for access to mates can also take more conspicuous forms. Females may compete for sexual access to the breeding male directly by harassing consorting pairs and interfering with copulations. Harassment of mating pairs in some species may cause lower conception rates and, thus, may be evidence of female competition for mates (Dunbar, 1988). For example, in gelada baboons dominant females, who typically associate closely with the unit male, frequently harass lower ranking females when soliciting or approaching the male during mating attempts (U. Mori, 1979a; Dunbar, 1984). In rhesus macaques, aggression by dominant females is often directed towards lower ranking ones, particularly when the consorting pair involves the alpha male (Ruiz de Elvira and Herndon, 1985). And in a captive group of capuchins, Linn *et al.* (1991) report that interruptions of sexual activity characteristically involve dominant females displaying aggressive acts towards subordinate females.

Additionally, harassment of copulating pairs by females has been observed in several other primate species: ring-tailed lemurs (*Lemur catta*) (Jolly, 1966),

squirrel monkeys (*Saimiri sciureus*) (DuMond, 1968), common marmosets (*Callithrix jacchus*) (Abbott and Hearn, 1978), saddleback tamarins (*Saguinus fuscicollis*) (Epple and Katz, 1984), howler monkeys (*Allouatta palliata*) (Young, 1981), black-and-white colobus monkeys (*Colobus guereza*) (Oates, 1977), hanuman langurs (*Presbytis entellus*) (Yoshiba, 1968; Hrdy, 1977), rhesus macaques (*M. mulatta*) (Lindburg, 1971; Ruiz de Elvira and Herndon, 1985), stump-tailed macaques (*M. arctoides*) (Gouzoules, 1974), patas monkeys (*Erythrocebus patas*) (Loy and Loy, 1977), savanna baboons (*Papio cynocephalus*) (Hall, 1962; Seyfarth, 1976; Wasser, 1983b), and chimpanzees (*Pan troglodytes*) (Nishida, 1979).

Moreover, competition among females for access to mates can also take the form of overt aggression. During the mating season, when aggression in female rhesus macaques is heightened, subordinate females in estrus are often the recipients of aggressive acts by more dominant females (Mallow, 1980; Wallen and Winston, 1984). Close associations have been found in female baboons between rates of aggression, the frequency of mating, and a female's dominance status (Seyfarth, 1976; Hall, 1962). And Rowell (1967) found that when baboon groups were biased towards females, they exhibited strict dominance hierarchies and marked degrees of aggression among females, suggesting that females may be in direct competion for mates.

There is also substantial evidence suggesting that in some species females may be in competition over limited reproductive positions. In female red howler monkeys (*Allouatta seniculus*) the competition for limited breeding positions in a troop may be so keen as to result in physical injuries in the competitors: approximately one third of the females observed had evidence of serious physical injuries (Crockett, 1984). Crockett suggests that the implications of female

aggression, coupled with the timing and patterning of female emigration, are a consequence of female-female competition for access to mates.

Aggression among females has also been observed in mountain gorillas (*Gorilla gorilla gorilla*) where females may be competing for limited breeding positions. Watts (1990) has noted that when the size of groups and the number of females per group increases, the level of aggression among females also increases. Additionally, females often transfer from their natal group to groups with fewer numbers of females, suggesting that mate competition between females may influence female transfer patterns.

Competition between females, however, can occur throughout all or any part of the reproductive process. Female mammal reproductive physiology is highly susceptible to environmental and social variables. And numerous studies on a wide variety of mammals, in addition to primates, have demonstrated that socially-dependent conditions can produce significant variations in female reproductive success. In a summary of socially-induced suppression of female fertility, Wasser and Barash (1983) review both the variety of mechanisms employed, and the timing of suppression in relation to reproductive life-history. For example, a delay in the onset of puberty has been found in subordinate house mice and prairie deer mice (Lloyd and Christian, 1969; Terman, 1973) vervet monkeys (Whitten, 1984; Fairbanks and McGuire, 1984), and in toque, rhesus, and Japanese macaques (Dittus, 1986; Drickamer, 1974; Sade *et al.*, 1977; Wilson *et al.*, 1978; Sugiyama and Ohsawa, 1982); mothers inhibit the sexual maturation of their young offspring in cactus mice and Mongolian gerbils (Skryja, 1978; Payman and Swanson, 1980), and in microtine rodents, maturation is inhibited in offspring by littermates (Batzli *et al.*, 1977). In myomorph rodents, macropod marsupials and cervid artiodactyls, nutritionally-

stressed individuals show a delay in sexual maturation (Sadleir, 1969a, b), as is the case for wildebeest and elephants living at high densities (Watson, 1969; Laws, 1969).

A delay or inhibition in sexual receptivity has been reported in subordinate house mice, dwarf mongooses, wild dogs, wolves, jackals and foxes (Lloyd and Christian, 1969; Rood, 1978, 1980; Frame *et al.*, 1979; D. Altmann, 1974; MacDonald and Moehlman, 1982). And a delay or inhibition of ovulation has been found in subordinate prairie deer mice, house mice, naked mole rats (DeLong, 1978; Bronson, 1979; Jarvis, 1981; Abbott, 1988), in several marmoset and tamarin species (Abbott and Hearn, 1978; Epple and Katz, 1984; French *et al.*, 1984; Garber *et al.*, 1984; Terborgh and Goldizen, 1985; Dietz and Kleiman, 1986; Ziegler *et al.*, 1987; Scanlon *et al.*, 1988; Stevenson and Rylands, 1988; Soini, 1988), in talapoin monkeys and baboon species (Bowman *et al.*, 1978; Rowell, 1970, Wasser and Starling, 1986; Altmann *et al.*, 1988; Dunbar, 1980a), in densely crowded Swiss mice and lesser mouse lemurs (Ryan and Schwartz, 1977; Perret, 1986), and in nutritionally and socially stressed elephants (Laws, 1969).

Failure in embryo implantation accounted for some reproductive loss in deer mice under crowded conditions and physically and psychologically stressed humans (Eleftheriou *et al.*, 1962; Peyser *et al.*, 1973). The occurrence of spontaneous abortions has been reported in marsupials under extreme environmental change (Low, 1978), in subordinate house mice and dwarf mongooses (Lloyd and Christian, 1969; Rood, 1980), in psychologically stressed rats and pigtail macaques (Herrenkohl, 1979; Sackett *et al.*, 1974), and in African mole rats living at high population densities (Jarvis, 1969). In the latest stage of reproduction, suppression can take the form of increased infant

mortality, such as has been observed in psychologically stressed rats (Herrenkohl, 1978), in genetically distant Belding's ground squirrels (Sherman, 1981), in black-tailed prairie dogs and elephant seals under high densities (Hoogland, 1981; Reiter *et al.*, 1981), in late-bearing lions (Schaller, 1972; Rudnai, 1973; Bertram, 1975), in Coke's hartebeest females who remain in the group following parturition (Goslin, 1969), in physiologically, nutritionally, or socially stressed elephants (Laws, 1969), and in subordinate rabbits, house mice, wild dogs, wolves, macaques, vervets, baboons, gorillas and chimpanzees (Mykytowyz, 1973; DeLong, 1978; Frame *et al.*, 1979; Zimen, 1976; Seal *et al.*, 1979; Drickamer, 1974; Wilson *et al.*, 1978; Dittus, 1979; Sugiyama and Ohsawa, 1982; Silk *et al.*, 1983; Whitten, 1983; Fairbanks and McGuire, 1984; Busse, 1982; Fossey, 1984; Goodall, 1977; Siebel and Taylor, 1982).

Given the frequent occurrence of socially-mediated influences on reproduction, as evidenced by the examples cited above, it seems probable that similar physiological mechanisms may have evolved in mammals as an adaptation to group living (Wasser and Barash, 1983). The disruption of ovarian functioning through behaviorally mediated means has proved to be an effective mode of influencing the reproduction of other females. It has been more recently suggested, therefore, that an observed correlation of decreased fertility and declining dominance rank is due to the physiologically disruptive effects of stress (Abbott, 1987, 1988, 1991; Dunbar, 1980a, 1984, 1985, 1988; Wasser, 1983a; Wasser and Starling, 1986, 1988). Stress was originally defined by Selye (1936) as a disruption of the body's homeostasis due to any perturbation in an animal's environment; and the stress response, later referred to as the General Adaptation Syndrome, has been defined as the set of stereotypic physiological responses of the body to diverse noxious agents. Selye (1971) noted that the

physiological adaptation to stress may proceed through several stages: (1) an initial alarm reaction occurs when the stressor is perceived and the body responds accordingly; (2) resistance occurs as a secondary response when the body restores homeostasis; and eventually under prolonged or repeated conditions of stress, (3) adaptation fails and the individual proceeds through the third stage, exhaustion.

The physiological process underlying the adaptation syndrome is described by Yen and Lein (1984) and can be briefly summarized as follows. The hormonal response to physical and psychological stress is an activation of the adrenal system and a subsequent secretion of a variety of hormones, including epinephrine (adrenaline), glucocorticoids, prolactin and endogenous opiates (enkaphalins and endorphins). The secretion of these hormones elevates metabolic and motor activity, inhibits anabolism, and dampens the pain associated with stress by causing analgesia. However, many of these hormones are also associated with reproductive functioning, and their benefits in dealing with stress have a simultaneous cost in gonadal functioning during prolonged secretion (i.e., exhaustion) (Leshner, 1978; Rose and Sachar, 1981). The release of endogenous opiates inhibits the release of luteinizing-hormone-releasing-hormone (LHRH) (Quigley and Yen, 1980; Rasmussen *et al.*, 1983; Martensz, *et al.*, 1986); subsequently, the pituitary gland is not stimulated to produce LH. Glucocorticoids and prolactin also inhibit LH secretion (Bowman *et al.*, 1978; Keverne, 1979; Yen, 1986), which causes the gonads to remain inactive. In the absence of an LH surge, ovulation will not occur (Everitt and Keverne, 1986; Hodges, 1987; Bronson, 1989). The result of prolonged or repeated secretion of these hormones can be one of:

(1) delay of the onset of puberty in juveniles;

(2) partial suppression resulting in anovulatory cycles;

or (3) total suppression of the reproductive system.

Thus, the body's physiological adaptation to various forms of stress is crucial for survival; however, overstimulation of the stress response can lead to destructive physiological alterations of bodily processes.

1.1.3. The Primate Ovarian Cycle

The primate ovarian cycle is based on the same general structural and physiological plan of placental mammals (Eutheria). The ovarian cycle of placental mammals typically comprises a sequence of events reflecting follicular growth, the ovulation of a mature oocyte and the formation of a corpus luteum, which can functionally be divided into three phases (Johnson and Everitt, 1988):

(1) A Follicular Phase -- This proliferative phase comprises the events that lead to the development of a mature pre-ovulatory follicle -- the production of oocytes. It can be further divided into the early and late follicular phase, and is considerably variable in length.

(2) An Ovulatory Phase -- This phase starts with the onset of the midcycle surge of luteinizing hormone (LH) and culminates with the follicular rupture and expulsion of a mature oocyte.

(3) A Luteal Phase -- This secretory phase immediately follows ovulation and refers to the secretion of progesterone in preparation for fertilization. It reflects the functional lifespan of the corpus luteum, and is relatively constant in length.

In primates, there is considerable variation between species in many characteristics of ovarian function, including cycle length, timing of ovulation, presence or absence of menstruation, and the influence of seasonality; however, there are basic general patterns of ovarian cyclicity evident in all primate species (Hodges, 1987). The ovarian cycle is a repetitive expression of the hypothalamic-pituitary-ovarian system (Johnson and Everitt, 1988; Yen and Lein, 1984). Throughout the cycle, ovarian function is driven by the actions of the pituitary gonadotropins --luteinizing hormone (LH) and follicle-stimulating hormone (FSH)-- the secretion of which is under the hypothalamic control of gonadotropin-releasing hormone (GnRH). Both LH and FSH are under negative feedback control by the ovarian steroids, but at mid-cycle, their pattern is reversed and expressed as a pulsatile surge in gonadotropin secretion (positive feedback). At the onset of the ovarian cycle, there is a small rise in FSH levels which appears to trigger the sequence of events leading to follicular development. The secretion of estradiol by the developing follicle consequently exerts a negative feedback effect on the pituitary gonadotropins. Subsequently, the follicle fated to ovulate shows a rapid increase in the secretion of estradiol. When the concentration and duration of oestradiol secretion reaches critical levels (the exact level varying between species), it triggers a surge in gonadotropins. This is the immediate stimulus for ovulation, which occurs some 12 - 36 h later. Once the ovum is released, the corpus luteum begins to develop and secretes progesterone during this luteal phase of the cycle. The uterine endometrium, stimulated by progesterone, prepares to receive the fertilized egg. If fertilization does not takes place, levels of progesterone decline, and in some primate species, this is followed by the sloughing of the uterine lining and menstrual discharge. Subsequently, FSH levels begin to rise again coinciding

with the onset of luteal regression, and the entire sequence of events is repeated (Yen and Lein, 1984).

All primates exhibit an ovarian cycle comprised of follicular growth, ovulation and the formation of a corpus luteum. There is considerable variation, however, in the expression of these cyclical events (Van Horn, 1980; Hodges, 1987). Therefore, there are marked differences between species in the length of the ovarian cycle and its respective phases, and the degree to which ovarian function is accompanied by menstruation or affected by the season. The length of the ovarian cycle in most Old World monkeys, apes and humans, is approximately 28 days, however, cycle length in many baboon species is typically longer, averaging 31 - 35 days (Hrdy and Whitten, 1987). The time of ovulation in these species typically occurs between day 12 and 16 of the cycle. The longest cycles are found among the strepsirhines (Izard, 1990), with lengths as long as 40 - 44 days reported for ring-tailed lemurs (*Lemur catta*: Jolly, 1966) and greater galagos (*Galago crassicaudatus*: Eaton *et al.*, 1973). In addition, under certain social conditions, cycle lengths of up to 60 days have been reported for lesser mouse lemurs (*Microcebus murinus*: Perret, 1986). Ovulation in these species can occur between days 10 and 15, or even later. The greatest variation in cycle length is exhibited by the New World monkeys. Cycle lengths range from the extremely short nine days typical of the squirrel monkey (*Saimiri sciureus*), to lengths ranging between 16 and 24 days for many New World species, including tamarins (*Saguinus oedipus*), capuchins (*Cebus apella*), woolly monkeys (*Lagothrix lagothrix*) and spider monkeys (*Ateles fusciceps*) (Hodges *et al.*, 1981), and to 28 day lengths exhibited by the common marmoset (*Callithrix jacchus*) (Abbott and Hearn, 1978). Ovulation in these species occurs between day 8 and 12 of the cycle, with the exception of the

squirrel monkey which exhibits a follicular phase of only 4 - 5 days in length.

Many primate species do not display repeated ovarian cycles throughout the year, but rather exhibit a marked influence of seasonality in ovarian function. In these species, a variety of environmental stimuli limit the full expression of ovarian function to a specific time of the year. This is the case for some species of both New World and Old World monkeys (e.g., squirrel monkeys and rhesus macaques, respectively), and appears to be the rule for strepsirhines (Van Horn, 1980). The degree to which this occurs varies greatly between species, being most pronounced in strepsirhines, and in captivity, less pronounced.

Among mammals, ovarian cycles accompanied by menstruation appear to be restricted to elephant shrews and some species of bats and primates (Spies and Chappel, 1984; Yen and Lein, 1984; Rasweiller, 1992). In primates, menstruation is generally absent in the New World species and strepsirhines, but present in most Old World monkeys, apes and humans. In those species which possess a uterine endometrium that hemorrhages, menstruation can be viewed as the external manifestation of internal hormonal changes at the close of the luteal phase. The onset of menses corresponds to the first day of the follicular phase and this is often used as a marker for the detection and monitoring of the ovarian cycle.

1.2. Studies of Reproductive Suppression in Female Primates

It is now well documented that social factors can influence reproduction in mammals in various ways (Vandenbergh, 1983; Crews, 1987; Hearn and Smith, 1988; Standen and Foley, 1989). The profound effects of the social environment on reproductive endocrinology can be seen in many rodent species, where sexual

maturation in females can be accelerated by exposure to a male (Vandenbergh, 1969; Bronson, 1989); in sheep, where female's undergo an immediate LH response when exposed to the chemical odor of the ram's wool (Martin, 1984); in goats, where the presence of a male initiates estrous cycling in females (Shelton, 1960); in male pigs, where testosterone levels surge in the presence of receptive females (Ellendorf *et al.*, 1975; Hemsworth *et al.*, 1981); and in female red deer, where the onset of ovulation may be accelerated as a result of specific male vocalizations (McComb, 1987). And in several primate species, the maturation and attainment of gonadal functioning can be dramatically altered depending on the social circumstances (Ziegler and Bercovitch, 1990).

In addition to the more direct control over female fertility, social factors have also been found to alter the ovarian cycle in more subtle ways. For instance, reproductive synchrony in several primate species appears to be due to social facilitation among females (Dunbar, 1988; Abbott, 1991). A synchronization of ovarian cycles has been observed in golden lion tamarins (French and Stribley, 1987), vervet monkeys (Whitten, 1983), patas monkeys (Rowell, 1978; Rowell and Hartwell, 1978), gelada baboons (Dunbar, 1980a), hamadryas baboons (Kummer, 1968), chimpanzees (Wallis, 1985), and humans (McClintock, 1971; Preti *et al.*, 1986). In patas monkeys and geladas, for example, females return to estrus prematurely after the takeover of their group by a new male. In addition, Rowell and Hartwell (1978) have shown that the onset of estrus cycles following lactational amenorrhea in one female triggers the onset of estrus in the other females of the same group. The monopolization of breeding males may be the cause of ovarian synchrony in golden lion tamarins and vervet monkeys, where at times when most females in a group are ovulating, the dominant females may have the best opportunity to be the first to conceive

(Abbott, 1991). And in humans, Preti and colleagues (1986) have shown that social and olfactory factors can produce a synchronization in female menstrual cycles, where cohabitating females exhibit a synchronization of their menstrual cycles (McClintock, 1971) and a decrease in cycle length when exposed to an unfamiliar male (Preti *et al.*, 1986). However, it is important to note that the significance these effects may have on female reproduction is not completely understood.

Social behavior is an integral part of the primate adaptive complex, and therefore, it is not unlikely that socially-mediated factors can influence reproductive success in a variety of ways. Traditionally, though, researchers have focused on male primates and the effects of social factors, such as dominance status, on reproduction in order to observe variations in reproductive success. However, the best documented examples of differential reproduction comes from studies of reproductive suppression in female primates (Abbott, 1991; Ziegler and Bercovitch, 1990). The consequences of differential social status on fertility are manifest more overtly in females than in males. In males, evidence of differential reproduction is primarily based on observations of the number of presumed fertile matings. On the contrary, in subordinate females reproductive suppression can be partial, such as the inhibition of ovulatory cycles, or it can be rendered complete where there are no offspring produced (Abbott, 1987; Harcourt, 1987).

1.2.1. Physiological Studies

Lemurs

Studies of lesser mouse lemurs (*Microcebus murinus*) in captivity reveal evidence of the social suppression of female fertility (for a review, see Izard, 1990). In the wild, the social structure of mouse lemurs consists of several female territories overlapped by that of a single adult male (Richard, 1987). Mouse lemurs breed seasonally in the wild and in captivity (Martin, 1973), and the suppression of female fertility may be the result of an increase in competition for resources and the maintenance of female territories. The mechanism of social suppression of fertility in female lesser mouse lemurs appears to be density-dependent.

Perret (1986) has shown that the interval between estrus bouts is significantly lengthened when the density of female lesser mouse lemurs is increased. An elongation of the luteal phase of the ovarian cycle, coupled with anovulatory cycles, has been implicated as the causative factor. Physiologically, the impairment of the ovarian cycle was due to an activation of the hypothalamo-adrenal axis that resulted in an elevation of circulating levels of cortisol.

Density-dependent reproductive suppression involves the release of pheromones or chemical signalling (McClintock, 1983), and it is well documented that mouse lemurs, as well as other prosimian primates, possess a well-developed system of olfactory communication (Schilling, 1979; Schilling *et al.*, 1984). Given the reliance on olfactory communication in these primates, it is likely that chemical signalling could mediate the social suppression of reproduction in females.

Marmosets and Tamarins

In marmoset and tamarin monkeys the social control of reproduction is so extreme as to render infertile all but the most dominant female in the group (Abbott, 1990, 1991). In social groups in the wild only one female will breed (Garber *et al.*, 1984; Terborgh and Goldizen; 1985; Kleiman *et al.*, 1988; Snowdon and Soini, 1988; Stevenson and Rylands, 1988) and in captive settings it has been determined that the dominant female in a group is the breeding female, and therefore, the only female to produce offspring (Epple, 1975; Abbott and Hearn, 1978; French *et al.*, 1984; Ziegler *et al.*, 1987; Epple and Katz, 1984.) Such an extreme control over female reproduction may be a corollary of the unique breeding system of the callitrichines. The number of offspring produced and their relatively large size create a situation where the breeding female is in need of assistance to rear the young (Sussman and Garber, 1987). This form of social structure allows for a high fertility rate in dominant females provided they receive assistance. However, for subordinate females, the best strategy may be to delay the time of their own reproduction in order to not compete with dominant females for 'helpers' and risk a greater likelihood of infant mortality. This may, therefore, explain why a breeding female will exert such extreme control over the reproduction of additional females in her group.

In studies on tamarins it has been demonstrated that the social environment and family composition directly influences the reproductive cyclicity of females. In fact, under certain social situations, normal reproductive hormonal cycles can be completely blocked. Subordinate females, both daughters and unrelated females, rarely copulate or ovulate both in saddle-back (*S. fuscicollis*) and cotton-top tamarins (*S. oedipus*) (Ziegler *et al.*, 1990). A study by Epple and Katz (1984) reported evidence of behavioral and hormonal responses to family-

induced fertility suppression in the saddle-back tamarin. They found that in families with adult offspring, subordinate females exhibited low and acyclic levels of estradiol compared to when these same females where paired with novel males. In addition, upon removing one parent from the family group, sexual activity remained absent indicating that familiarity of family members may be involved.

Similar results were reported for the cotton-top tamarin. French *et al.* (1984) found that females remaining in their natal group had low and acyclic levels of estradiol and estrone in addition to exhibiting a low frequency of anogenital scent marking and an absence of sexual behavior. As was the case with the saddle-back tamarin, when the same females were removed from their family groups they experienced significant increases in estrogen concentrations. After pairing the females with unfamiliar males, they resumed normal cycling levels of estrone and estradiol, as well as increases in anogenital scent marking and sexual activity.

Further investigations of the suppression of fertility in female cotton-top tamarins revealed low and acyclic levels of luteinizing hormone (LH) in addition to estrogen concentrations (Ziegler *et al.*, 1987). While female offspring showed occasional elevations in LH levels, they were not associated with corresponding increases in estrogen concentrations. Furthermore, these females did not exhibit normal sociosexual behavior and their scent glands were excreting low levels of sebum (Savage *et al.*, 1988). As in previous examples, following pairing of these females with novel males, they resumed normal sociosexual behaviors, increases in sebum production and scent marking, and LH and estrogen concentrations typical of normal cycling females.

In studies on common marmosets (*Callithrix jacchus*) Abbott (1984, 1986, 1987, 1988) and colleagues (Abbott *et al.*, 1981, 1988) have shown that subordinate females exhibit anovulatory cycles when in the presence of dominant females; and subsequently, the same reproductively suppressed females return to a fully fertile condition when they are removed from social groups where they maintain a subordinate social status. The physiological causative factor for socially suppressed ovulation in female common marmosets is an inhibition of pituitary gonadotropin secretion (Abbott *et al.*, 1988, 1990, 1991), resulting from the suppression of hypothalamic secretion of gonadotropin-releasing hormone (GnRH). The neuroendocrine mechanism is an increased sensitivity to the negative feedback of estradiol and endogenous opioid peptides (Abbott, 1991). To date, these studies on common marmosets provide the best example of the extent to which social factors can determine female reproduction.

Catarrhines

Data from wild and laboratory groups reveal that dominant female talapoin monkeys suppress reproduction in their subordinates (Rowell and Dixson, 1975; Bowman *et al.*, 1978; Keverne, 1979; Abbott 1987). In the wild, talapoin monkeys (*Miopithecus talapoin*) live in large multi-male groups with more than one breeding female (Rowell and Dixson, 1975). Investigations by Bowman *et al.* (1978) showed that subordinate female talapoin monkeys had marked behavioral and physiological differences compared to dominant females. Specifically, low-ranking females had lower frequencies of sexual activity, and physiologically they showed reduced LH responses when treated with an estrogen positive feedback test. The implication of these results is that subordinate females would experience higher rates of anovulatory cycles due to

their inability to produce the estrogen-induced LH surge, therefore leading to their lower reproductive output (Abbott *et al.*, 1986).

Further investigations into the mechanism of physiological suppression of ovarian function in talapoins discovered that low-ranking females had elevated plasma concentrations of prolactin and cortisol (Keverne *et al.*, 1982, 1984). Elevated levels of these particular hormones have been correlated with increased rates of agonism in subordinate female primates (Bowman *et al.*, 1978; Keverne *et al.*, 1982, 1984; Kaplan *et al.*, 1986). By treating ovariectomized subordinate females with a dopamine agonist, plasma concentrations of prolactin decreased, allowing them to subsequently respond to an estrogenic positive feedback test with an LH surge (Bowman *et al.*, 1978; Keverne, 1979). Similarly, dominant females treated with a dopamine antagonist experienced elevated levels of prolactin concentrations and were unable to produce an LH response to a positive feedback test. These results suggest the mechanism of ovarian inhibition as hyperprolactinaemia (Abbott, 1991). In sum, increased levels of agonism received by subordinate female talapoin monkeys are the causative factor resulting in their ovarian impairment (Keverne *et al.*, 1984).

A correlation between subordinate social status and reduced reproductive output has also been reported for both long-tailed (*M. fascicularis*) and rhesus macaques (*M. mulatta*). In both species subordinate females experienced an overwhelming number of anovulatory and luteal-deficient cycles (Walker *et al.*, 1983; Adams *et al.*, 1985). In addition, subordinate female long-tailed monkeys showed greater cortisol responses when treated with adrenocorticotrophic hormone (ACTH), suggesting that the effect of subordinate social status is an activation of the hypothalamo-pituitary-adrenal axis and subsequent suppression of GnRH secretion (Kaplan *et al.*, 1986). In the rhesus macaque the impairment

of ovarian function in subordinate females has been shown to be the result of an inhibition of gonadotropin secretion (Walker *et al.*, 1983). Wilson *et al.* (1978) suggest that this could explain the low reproductive success of subordinate females in captive groups of rhesus monkeys, despite no apparent difference in the frequency of sexual activity when compared to dominant females.

1.2.2. Field Studies

Marmosets and Tamarins

The most striking examples of socially-mediated influences on female fertility come from captive studies (Deag, 1977; Harcourt, 1987). In the wild, the effects appear to be less pronounced but nevertheless suggest that the same mechanisms are operating and affecting female reproduction. For instance, in marmosets and tamarins only one female in a group produces offspring, while the other females in the group remain nonreproductive (*Callithrix jacchus*: Hubrecht, 1984; Scanlon *et al.*, 1988; Stevenson and Rylands, 1988; *Cebuella pygmaeus*: Soini, 1988; *Saguinus fuscicollis*: Terborgh and Goldizen, 1985; *Saguinus mystax*: Garber *et al.*, 1984; Sussman and Garber, 1987; *Leontopithecus rosalia*: Dietz and Kleiman, 1987). This appears to be the typical pattern for the majority of callitrichine species for which there are data, with only a few known exceptions (Terborgh and Goldizen, 1985; Dietz and Kleiman, 1986). In the golden lion tamarin it has been shown that the dominant female is the breeding female and the exclusion of subordinate females from breeding groups can be so extreme at times as to cause fatal injuries (Baker, 1987).

Some researchers have suggested that such an extreme control of female fertility evolved in response to the demands of rearing offspring. For instance, MacDonald and Carr (1989) have suggested that subordinate females may benefit more by deferring reproduction while in their group than they would by the costs incurred by leaving and establishing their own feeding territory and breeding group. Additionally, subordinate females may benefit by gaining experience in rearing offspring which may prove to be valuable when rearing their own offspring. Dominant females, on the other hand, could benefit by increasing the chances of their offsprings' survival through the cooperation of female helpers, provided they are nonreproductive and do not incur any costs in feeding competition (Sussman and Garber, 1987). Thus, in the case of marmosets and tamarins, a unique system may have evolved where all individuals within groups may benefit from cooperation in infant caretaking.

Catarrhines

Unlike the callitrichine species where reproductive suppression in all but the dominant female is rendered complete, in many of the catarrhines reproductive suppression is often incomplete (Keverne, 1979; Adams *et al.*, 1985; Kaplan *et al.*, 1986; Abbott, 1987), and therefore more difficult to detect (Abbott, 1991). This may be in part due to the differences in their mating system and the consequences that ensue. It may also be due to the captive conditions themselves, which some argue may exaggerate the effects of reproductive suppression (Deag, 1977; Harcourt, 1987).

However, several studies of female catarrhine primates provide indirect evidence of reproductive suppression (Rowell, 1970, 1972; Drickamer, 1974; Sackett, 1975; Sade *et al.*, 1977; Wilson *et al.*, 1978, 1983; Wolfe, 1979;

Meikle *et al.*, 1984; Dittus, 1986; Ehardt and Bernstein, 1986; Fa, 1986; Fairbanks and McGuire, 1986; Silk, 1987; Altmann *et al.*, 1988; for a review of various mammalian species, see Wasser and Barash, 1983). In many of these primates, morphological changes (e.g., coloration and swelling of the "sexual skin") accompany the endocrine events that take place during the menstrual cycle, as do distinctive proceptive and receptive behaviors (Dixson, 1983a). As a result, studies of reproduction in these primates rely on observations of visual cues and behavioral correlates of reproductive events, such as solicitory and copulatory patterns (Dunbar and Dunbar, 1974; Struhsaker, 1975). However, studies using both behavioral and hormonal data have shown a disparity between expected and observed behaviors (e.g., French *et al.*, 1984; Andelman *et al.*, 1985; for reviews see Dixson, 1983b; Eberhart, 1988). This is in part due to the fact that physiological changes that occur during the menstrual cycle are not directly observable; and that the degree of swelling and coloration of the female's sex skin is highly variable within and among individuals (Struhsaker, 1975; Hrdy, 1977; Dixson, 1983a), as are the behavioral correlates used to assess reproductive events (Hrdy and Whitten, 1987). Therefore, evidence from field studies can provide a variety of behavioral measures indicative of reproductive suppression; however, hormonal data are ultimately needed in order to understand the physiological mechanisms inhibiting female reproductive functioning.

Baboons

Social stress is commonly implicated as the causative behavioral factor resulting in the impairment of reproduction in subordinate female primates (Keverne, 1979; Dunbar, 1984; Abbott, 1987, 1991; Harcourt, 1987), and field

studies on baboons provide the strongest evidence supporting this claim for wild groups of catarrhines. In yellow baboons (*Papio cynocephalus*), Wasser (1983b; Wasser and Starling, 1986, 1988) has illustrated the consequences of low social rank on female fertility. In this species, the formation of coalitions by females against lower ranking females is the social mechanism operating to produce reproductive suppression in subordinate females. Coalitions often involve two or three females who subsequently attack females of lower social status. Furthermore, Wasser and colleagues have shown that the timing of the attacks on subordinate females is concentrated at the most reproductively vulnerable times. For instance, the recipients of coalition attacks were most likely low-ranking females in the follicular phase of their cycle. The timing of these attacks is likely the cause of the recipients experiencing a greater number of cycles to conception and longer interbirth intervals.

Additionally, low-ranking females in the first trimester of pregnancy are also frequently the recipients of coalition attacks (Wasser and Starling, 1988). The consequences of such attacks to the recipients can be quite severe: spontaneous abortion, premature delivery or prolonged gestation. Increasing the chances of infant survival appears to be the major factor influencing this behavior in females. Infant mortality is dependent on the number of births that occur simultaneously in a birth season where competition for weaning foods and paternal investment are important factors influencing infant survival. It appears that in this species females may be suppressing the reproduction of other females in order to increase their own chances of reproductive success (Wasser and Starling, 1986, 1988).

Geladas

Studies on gelada baboons provide the best illustration of the consequences of social status on female reproductive success in wild primates (Dunbar, 1989). In discussing the results of long-term field studies, Dunbar (1980a, 1984, 1988; Dunbar and Dunbar, 1977) has suggested that reproductive suppression is a significant factor contributing to the variation in birth rates of individual females. For instance, the number of offspring of individual females within a reproductive unit is strongly correlated with her dominance rank. Dunbar (1980a) has used his field data to investigate possible causes for this rank-dependent variation in reproductive success. He found no significant difference between dominant and subordinate females in access to the male, in frequency of successful copulations, in infant mortality rates, or in access to higher quality foods. However, Dunbar (1980a) did report a significant increase in the frequency of attacks by dominant females on lower ranking females when the latter were in estrus compared to when they were anestrous. He suggested that the increased rate of harassment of lower ranking females during the estrous phase resulted in anovulatory cycles (Dunbar, 1980a, 1984, 1988). Additional evidence used to support this conclusion was the variance in interbirth intervals; subordinate females required more cycles to conceive than did dominant females. Furthermore, Dunbar (1989) has estimated that a female's birth rate will decrease by approximately 10% with each unit decline in social rank, which is clearly a significant selective differential. In conclusion, Dunbar (1984, 1988, 1989) has proposed that an observed decline in fertility with declining dominance rank within groups is due to partial reproductive suppression of lower ranking females as a consequence of social stress resulting from increased rates of harassment by dominant females. And it is the testing of this main conclusion

that is the primary goal of this study.

1.3. Research Design

1.3.1. Objectives

Field conditions make it difficult to collect the physiological data needed to test Dunbar's (1988) hypothesis. Data obtained from behavioral observations alone are rarely sufficient for a full understanding of the factors affecting birth rates. For instance, there is substantial evidence suggesting that particular aspects of social and reproductive behavior are closely linked with hormonal changes associated with social status (Sapolsky, 1987; Ziegler and Bercovitch, 1990; Abbott, 1991). Thus, data on the physiology of individual females may be necessary to understand variation in fertility. In theory, blood, urine or fecal sampling are suitable for hormone analysis so long as one does not interfere with the physiology or behavior of the individuals under study. Obtaining blood samples by darting or trapping individuals has proved to be a useful technique for males, but may be less suitable for females because of the possible disruptive effects on early stage pregnancies (Sapolsky, 1987). The collection of urine is preferable for it is a non-invasive technique and can be performed in the field provided the subjects are arboreal (Andelman, 1987; Andelman *et al.*, 1985).

However, there are obvious difficulties in obtaining these data on free-ranging female gelada baboons which are completely terrestrial: one cannot control the timing of samples or the accuracy with which they are collected. In a captive setting, samples are more easily accessible and can be collected through non-invasive techniques when animals are housed overnight.

The objectives of this study of *Theropithecus gelada* at the Wildlife Conservation Society's (WCS) Bronx Zoo were (1) to collect data on external signalling, and on the behavioral and hormonal correlates of the reproductive behavior of females, and (2) to use these data to test Dunbar's (1980a, 1984, 1988, 1989) hypothesis that behaviorally mediated reproductive suppression in low-ranking females is a significant factor contributing to the variation in birth rates. The following categories of data were collected:

1. Observations of the Visual Signs of Ovulation
   --changes in the physical appearance of the female's sex skin during the menstrual cycle.

2. Behavioral Observations
   --baseline data on gelada baboon social behavior as it relates to social status (e.g., rates of agonism received and given by females).
   --data on changes in a female's pattern of interactions with other females and with the unit male during the estrous and anestrous phase of her cycle.
   --data on patterns of reproductive behavior/activity (e.g., copulations, pregnancies and births).

3. Monitoring of Endocrine Status
   --physiological changes as they relate to social behavior (levels of stress hormones secreted) and a female's reproductive state (levels of gonadal secretion).

1.3.2. Hypotheses and Predictions

Several studies report within-population variation in female primate fertility, and in many populations this observation is associated with dominance rank (reviewed in Dewsbury, 1982; Keverne *et al.*, 1982; Wasser and Barash, 1983; Gray, 1985; Abbott, 1987; Harcourt, 1987; Dunbar, 1988). Two often-cited causes of this rank-dependent variation are (1) differential access to resources (Wrangham, 1981; Whitten, 1983; Janson, 1985), or (2) differential degrees of social stress (Dunbar, 1980a, 1984, 1988; Wasser, 1983a; Wasser and Starling, 1986, 1988). While other factors may be operating, at present these two remain the chief competing hypotheses to explain differential fertility (Harcourt, 1987; Dunbar, 1988). Variation in fertility has been reported as often in captive and provisioned populations as in the wild (Gray, 1985; Harcourt, 1987; Dunbar, 1988); and it has been observed in the Bronx Zoo population as well. Thus, the specific hypotheses and predictions tested in this study were:

Hypothesis 1: ***Variation in fertility is the result of a greater efficiency of food intake by dominant females.***

Prediction 1: Dominant females will spend more time feeding than low-ranking females, and/or more time feeding on higher quality foods.

Prediction 2: Dominant females will have a higher body weight than low-ranking females.

Prediction 3: A greater efficiency of food intake and a higher body weight will result in greater fecundity for dominant females compared to low-ranking females, as measured by gonadal (pregnanediol glucuronide -- a urinary metabolite of circulating progesterone) secretion.

While differences in time spent feeding between females were observed, in the zoo setting these effects are likely to be cancelled out by the daily provisioning of food. Nonetheless, nutritional status was investigated in order to be able to rule it out as a possible factor contributing to differences in female fertility. Following reported methods of determining nutritional condition in other studies of female primates, body weight was used as an indicator of relative nutritional status in this study (Riopelle *et al.*, 1976; A. Mori, 1979; Sugiyama and Ohsawa, 1982).

Hypothesis 2: ***Variation in fertility is the result of behaviorally mediated reproductive suppression in low-ranking females.***

Prediction 1: Social stress (as measured by high rates of harassment received by an individual) and levels of stress hormones (as measured by levels of glucocorticoids -- e.g., cortisol) will be greater in lower ranking females than in higher ranking females absolutely; and the level of stress will increase when the former are in estrus as a result of an increased rate of harassment from higher ranking females (Dunbar, 1988).

Prediction 2: High levels of stress and/or low social rank will result in suppression of gonadal activity, as measured by gonadal (pregnanediol glucuronide) secretion. Because suppression of gonadal activity results in anovulatory cycles, this is an indication of reproductive suppression (Dunbar, 1988).

In the present study, observations of *Theropithecus* at the Bronx Zoo revealed that low-ranking females do have significantly higher measures of social stress. However, in order to determine whether a high degree of social stress is sufficient to impair fertility, analysis of each female's hormonal status was conducted as well.

1.4. Outline of Thesis

A complete understanding of the evolution of primate life-history strategies is dependent on a knowledge of variation in female reproductive success and of the factors responsible for such variation. However, very few studies of wild primates have investigated proximate causes of variation in birth rates (Harcourt, 1987; Dunbar, 1988; Abbott, 1991). The present study on captive gelada baboons provided a unique opportunity to obtain both behavioral and physiological data required to investigate the relationship between social behavior and fertility.

In order to begin to understand how social behavior may influence reproduction in female gelada baboons, an understanding of the ecology, social structure and evolutionary history of the gelada is essential. This information is provided in **Chapter 2**. The methods of observational sampling of the study

group animals and the assays for the urinary hormone analysis are described in **Chapter 3.**

In this study, I investigated whether ovarian suppression contributed to the reproductive impairment of low-ranking females. This was accomplished by first describing the general patterns of the reproductive cycle in the study group females through the use of hormonal, behavioral and morphological markers. Data on the reproductive cycle and its effect on behavior were sampled on all females (N=16) over the course of 6 to 18 menstrual cycles. The general patterns of ovarian cyclicity found in the study group females are presented in **Chapter 4**, and the main findings revealed that: (1) menstrual cycles lasted a mean of 37.3 days with follicular and luteal phases lasting an average of 19.4 and 17.9 days, respectively; (2) the excretion of pregnanediol glucuronide, a progesterone conjugate, correlated with the morphological changes in the female's 'sexual skin', indicating that both are key markers of ovarian cyclicity in geladas; and (3) female estrus behavior and male copulatory behavior had the greatest frequency of occurrence during the peri-ovulatory period which correlated with the morphological and hormonal changes characteristic of the time of ovulation.

Focal, scan and ad libitum sampling were used in order to determine whether the same general patterns of social interactions were found in the study group females as in wild groups of geladas. My findings on the structure of social relationships among females in the study groups are presented in **Chapter 5** and suggest the following main conclusions: (1) females varied in the amount of time spent feeding on preferred food items, but this difference was not associated with differences in body weight; (2) a female typically interacts almost exclusively with just one other female in her unit and together they form

a 'grooming dyad; (3) 'grooming dyads' form the foundation of coalitionary alliances during agonistic encounters which can significantly affect a female's dominance rank; (4) a female's dominance rank can have important consequences for her relationship with the unit male; and (5) the unit male typically remains socially peripheral to the group, but shows a strong preference for one or two particular females in his unit.

In **Chapter 6**, I present data on the variations among females in their patterns of social behavior and reproductive functioning and investigate to what extent these two variables are related. The main findings on the relationship between social behavior and fertility found among females in my study groups are: (1) low-ranking females experienced greater intervals between ovulations than did high-ranking females, and the lengthened menstrual cycles were due to an elongation of the follicular phase, but not of the luteal phase; (2) the frequency with which males copulated with dominant females was significantly greater than was the frequency of matings with low-ranking females; (3) low-ranking females received higher rates of aggression than did dominant females and the rate of aggression increased significantly during the peri-ovulatory phase of the menstrual cycle; (4) low-ranking females exhibited greater cortisol secretion levels during the follicular phase of the menstrual cycle than did high-ranking females; and (5) high-ranking females spent more time feeding on preferred food items, however, total time spent feeding was not correlated with a female's dominance rank, body weight or any endocrinological measure of fertility. Thus, in this study, low social status in females is associated with longer menstrual cycle lengths, elongated follicular phase lengths, lower frequencies of copulations, and increased rates of harassment and cortisol secretion during estrus periods.

These findings provide some insights into the proximate mechanisms underlying the variance in fertility in female gelada baboons. Harassment of low-ranking female gelada baboons by high-ranking females may have resulted in increased cortisol secretion which, in turn, may have resulted in lengthened menstrual cycles and reduced ovulatory frequency in low-ranking females. Reduced ovulatory frequency may lead to the delay in conceptions in low-ranking females found in wild populations. High-ranking female gelada baboons may impose stress-induced suppression of reproduction on their female subordinates to obtain a reproductive advantage. The significance of these results and the implications they have for the 'Reproductive Suppression Hypothesis' (Wasser and Barash, 1983) are discussed in **Chapter 7.**

1.5. Significance of Study

The general importance of this study lies in its testing of a long-standing hypothesis on female gelada baboon reproductive strategies. In addition, the results of this study add to the growing body of data on primate socioendocrinology in the literature. Some specific points of significance in this study are as follows:

1. While Dunbar (1980a) states that the results of his study of *Theropithecus gelada* indicate that behaviorally mediated reproductive suppression is a significant factor influencing birth rates, this hypothesis has not been directly tested. The importance of the present study lies in its unique opportunity to test whether there is physiological evidence for the social suppression of reproduction in subordinate females.

2. Although many studies have reported circumstantial evidence indicative of reproductive suppression following some form of social stress (reviewed in Wasser and Barash, 1983), only a few studies, and none on *Theropithecus*, have looked directly at the effects of the social environment on reproduction. Empirical evidence obtained from this study is used to determine whether the physiological consequences of social stress are a significant factor contributing to the variation in female fertility.

3. Information of this nature is of great theoretical value to our understanding of proximate and evolutionary consequences of the reproductive strategies of this, and other primate, species. An explanation of the factors responsible for variation in female reproductive success is necessary for a comprehensive

understanding of the evolution of primate life-history strategies.

4. In addition, information from this study could be used to aid in the captive management and breeding of *Theropithecus*. *Theropithecus* is listed as threatened by the United States Endangered Species Act, rare by IUCN, under Appendix II by CITES and it is recognized as an important species in which to increase captive breeding efforts by the Old World Monkey Taxon Advisory Group of the American Zoological Association. With increasing pressure on wild primate populations, methods of enhancing reproduction in captivity of both this and other rare species are gaining in significance.

CHAPTER 2. THE GELADA BABOON AND ITS SOCIAL STRUCTURE

2.1. Phylogeny, Taxonomy and Natural History of *Theropithecus*

2.1.1. The Genus *Theropithecus* and Its Taxonomic Position in the Papionini

Taxonomically, *Theropithecus* is usually placed in the tribe Papionini of the subfamily Cercopithecinae, within the family Cercopithecidae. The Papionini also includes the genera *Papio*, *Mandrillus*, *Cercocebus* (and *Lophocebus*), *Parapapio*, *Dinopithecus*, *Gorgopithecus*, *Macaca*, *Procynocephalus*, and *Paradolichopithecus*, which are united by a series of karyological, craniodental and pedal characteristics (Jolly, 1972; Szalay and Delson, 1979; Strasser and Delson, 1987). Recognized as the most highly derived of the papionins, *Theropithecus* is distinguished from other genera by an array of derived anatomical features. Among such features in the postcranium are an elongated fore- and hindlimb, a specialized femur, a highly flexed hip, knee and ankle joint, reduced digits, and increased opposability of the hand. Many of these autapomorphic features of the postcranium are argued to be adaptations to a terrestrial habitat and unique form of feeding behavior (Jolly, 1967; Krentz, 1993).

The unique feeding adaptations of *Theropithecus* are also reflected in the skull and dentition, and in the masticatory apparatus in particular. Most notable of the derived characteristics that distinguish *Theropithecus* is a large and anteriorly placed temporalis muscle, marked post-orbital constriction, a temporo-mandibular joint set high above the occlusal plane, a deep posterior maxilla, an

upright mandibular ramus, and high-crowned bilophodont molars with columnar cusps (Jolly, 1972; Szalay and Delson, 1979; Jablonski, 1993). These characteristics together form a functional complex related to the demands of mastication and are distinct from those seen in other cercopithecines.

The numerous features of anatomical distinction displayed by *Theropithecus* traditionally had been interpreted as the result of a long independent evolutionary history of the genus, with its divergence occurring either before (Jolly, 1967) or just after the divergence of *Macaca* from the rest of the papionins (Jolly, 1972; Delson, 1975), but prior to the divergence of the common ancestor of *Papio*, *Mandrillus* and *Cercocebus*. A more recent consensus, relying on molecular evidence as well as the neontological and paleontological data, is that *Theropithecus* most recently shared an ancestor with *Papio* (for details of the various evolutionary schemes, see Eck, 1993; Leakey,1993; and Delson, 1993; Disotell, 1994). The time of divergence is somewhat problematic, but is generally agreed to have occurred between 5 and 3.5 Ma, predating the earliest known fossil remains of the *Theropithecus* lineage which have been dated at 3.5 - 4.0 Ma and 3.3 Ma.

There is also general agreement about phyletic relationships within *Theropithecus* (Jablonski, 1993). Most contend that the genus is comprised of three lineages: a lineage composed of *T. oswaldi* and *T. darti*; a lineage including *T. brumpti* and its putative forebears; and a lineage for which there is no fossil record but which leads to the sole extant species, *T. gelada* (Figure 2.1.). Given the lack of fossil evidence associated with the origin of the modern gelada lineage, the time of its divergence is best inferred by the fossil evidence relating to the other two lineages. Due to its retention of many primitive anatomical features, the gelada lineage is viewed as the most conservative of the

genus by all accounts, and it is generally accepted that it diverged close to the origin of the *T. darti-T. oswaldi* and *T. brumpti* lineages at around 3.5 Ma. The exact position of this origin is debated: some see it occurring prior to the divergence of the other two lineages (Jolly, 1972) (Figure 2.1.a.); some see its origin occurring after the divergence of the ancestor of the *T. brumpti* lineage, making *T. gelada* the sister taxon of *T. darti* (Jablonski, 1993), some see its occurrence after this divergence but recognize *T. brumpti* as the sister taxon to the *T. gelada* and *T. oswaldi* sublineages (Delson, 1993) (Figure 2.1.c.), while still others see it as unresolved by virtue of the lack of morphological evidence available to adequately assess its phyletic relationship to the other lineages (Leakey, 1993) (Figure 2.1.b.).

2.1.2. The *Theropithecus darti* -- *Theropithecus oswaldi* Lineage

The lineage comprising *Theropithecus darti* and *T. oswaldi* is considered the most successful of the *Theropithecus* lineages. Its occupation of wet, open grassland environments and exploitation of a terrestrial, grass-eating niche produced great evolutionary success in both time and space. The range in time of the *T. darti* - *T. oswaldi* lineage is well documented at approximately 3.3 to 0.4 Ma. *Theropithecus darti* is known mainly from two widely separated African sites, during the mid- to late Pliocene: Hadar in Ethiopia and Makapansgat in South Africa. In contrast, *Theropithecus oswaldi* is known from numerous Plio-Pleistocene sites throughout eastern, southern and northern Africa. In addition, there are at least two documented records of its occurrence outside Africa: a specimen from Mirzapur, India that is presently referred to as *T. oswaldi delsoni* (Delson, 1993), and a specimen from Cueva Victoria, Spain (Gibert *et al.*, 1995).

The *T. darti* - T. *oswaldi* lineage is distinguished from other lineages of *Theropithecus* by its extreme terrestriality and its exploitation of a nearly exclusively graminivorous diet in lowland grassland habitats. This adaptation is reflected in the morphological specializations of the lineage (Jolly, 1972). Compared to *Theropithecus oswaldi*, *T. darti* appears to exhibit features thought to be primitive for the genus, with regards to aspects of the muzzle dorsum, piriform aperture, zygomatic arches, post-glenoid process, body size, and the relative size of the incisors and canines. This has led some to consider *T. darti* as a small, primitive species directly ancestral to *T. oswaldi* (Jolly, 1972; Eck, 1993), while others consider it one of 3 or 4 subspecies of T. oswaldi (Leakey, 1993; Jablonski, 1993; Delson, pers. comm.). The weight of the fossil evidence strongly suggests that *Theropithecus oswaldi* evolved from *T. darti* at approximately 2.8 - 2.4 Ma, with the former occupying a 'grazing' niche with great success for over 2 million years in the grasslands of the African Plio-Pleistocene. This adaptation to harvesting large amounts of grasses involved anatomical and morphological changes, most noteworthy being the enormous increases in body size (estimated between 35 and 65 kg) and the specialization of the masticatory apparatus (Leakey, 1993; Jablonski, 1993).

2.1.3. The *Theropithecus brumpti* Lineage

The *Theropithecus brumpti* lineage was far more restricted in time and space than the *T. darti* - *T. oswaldi* lineage. Fossil evidence suggests *T. brumpti* was restricted geographically to the Turkana basin and temporally to approximately 2.8 to 2.0 Ma (Leakey, 1993). Morphologically, *T. brumpti* is viewed as the most autapomorphic species of the genus. Its unique suite of characters-- a long muzzle and muzzle dorsum, strongly developed maxillary and

mental ridges, broad zygomatic arches, an increased flexibility of the shoulder joint and stability of the elbow-- reflect a specialized masticatory apparatus and changes in the post-cranium to accommodate a partly arboreal locomotor mode. *T. brumpti* is thought to have inhabited riverine forests and to have had an expanded diet that included shoots, tubers, and fruits. *T. brumpti* is recognized by a unique suite of characters that shows the greatest departure from the general *Theropithecus* morphology and reflects its unique feeding and locomotor adaptations to a forest dwelling habitat (Jablonski, 1993).

While there is no argument surrounding the unique adaptations of *T. brumpti*, there is considerable disagreement as to the phyletic relationships of other species that may belong to the *T. brumpti* lineage. It has been argued by some that the fossil material originally referred to as *Papio baringensis* and *P. quadratirostris* (ca. 3.2 - 2.9 Ma) is preferably placed in *Theropithecus* due to the presence of derived characteristics shared with *T. brumpti*-- indicative of a close, if not ancestral, relationship (Jablonski, 1993). This view is accepted by Leakey (1993) on the basis of recently discovered fossil evidence from West Turkana that suggests an *in situ* transition in the *T. brumpti* lineage, with specimens referred to *T. baringensis* ancestral to *T. brumpti*, and *T. quadratirostris* as a possible intermediate between the former two species. This evolutionary scheme differs from that proposed by Delson and Dean (1993), who tentatively accept ?*T. baringensis* as primitive and ancestral to *T. brumpti* on the basis of the morphology of the facial skeleton, dentition and neurocranium; however, they argue that *P. quadratirostris* is most accurately placed within *Dinopithecus* (which they include in *Papio*) and not *Theropithecus*, due to its 'non-gelada-like dentition' and cranial morphology. While there may be a general consensus that *T. baringensis* was the predecessor of *T. brumpti* with

their relationship described by either specific or subspecific designations, at present, there is not sufficient paleontological evidence on *P. quadratirostris* to produce a consensus on its phyletic position and taxonomic affinity (see also Jablonski, 1994). The *T. brumpti* lineage is assigned a subgenus designation of *T.* (*Omopithecus*) (Delson, 1993).

2.1.4. The *Theropithecus gelada* Lineage

Theropithecus gelada is one of the most terrestrial of the Old World monkeys, frequently climbing cliff-faced gorges but rarely climbing trees. The gelada diet is also unique, and many of its postcranial features are associated with their unique grazing behavior. Geladas feed on grasses, seeds and rhizomes which they obtain primarily by using their thumb and index finger in a pincer-like grip. Their postural feeding behavior typically involves sitting upright and moving between feeding sites by displaying a 'shuffle gait' in which they move forward bipedally with hips, knees and ankles in full flexion. In addition to these traits, *T. gelada* exhibits several primitive features for the genus, as evidenced by its reduced incisors, high-crowned molars, and small body size. A narrow piriform aperture and a concave facial profile are two autapomorphic characters of *T. gelada* that have been argued to be respiratory specializations that aid in the reduction of heat loss through the nasal mucosa in the dry, cold air of the Ethiopian Plateau (Jolly, 1972; Dean, 1988). The combination of primitive and uniquely derived characters has led to the recognition of *T. gelada* as morphologically conservative with a long history of adaptations to the Ethiopian highlands and isolated from the other *Theropithecus* forms that inhabited the lowlands of the surrounding areas (Jolly, 1972; Szalay and Delson, 1979).

2.1.5. The Extinction of the Theropiths of the Plio-Pleistocene

In sum, the weight of fossil evidence available to date suggests that *Theropithecus* was well established by 3.5 Ma. The results of more recent morphological and molecular analyses suggest that among the Papionini, *Theropithecus* is most closely related to *Papio*; and it is generally agreed that the two most probably share an ancestor with an estimated divergence time of between 5.0 and 4.0 Ma. The three known lineages of *Theropithecus* appear to have diverged from one another within a relatively short span of time prior to 3.5 Ma, but the exact phyletic relationships of the three remain unresolved. The *T. darti* - *T. oswaldi* lineage spread widely throughout the lowland grasslands of Africa evolving its largely terrestrial graminivorous niche, while in contrast, the more uniquely specialized and less expansive *T. brumpti* lineage displayed an interesting combination of features that differed from its congeners by its greater commitment to arboreality and broadened diet. The *T. gelada* lineage, with no known fossil record, and represented by the only extant species, is limited in its distribution to the cold highlands of central Ethiopia. The modern gelada is an exclusively terrestrial, relatively small-bodied, montane grass-eater. It is postulated that the lineage leading to the extant gelada became isolated in the Ethiopian highlands, equipped with the specific characteristics of the neurocranium and postcranium that allowed it to succeed as a 'primate grazer', and separated from its larger-bodied lowland congeners (Jablonski, 1993). Taking into account the paleontological and neontological evidence of all the known *Theropithecus* specimens suggests that a terrestrial adaptation and feeding mode involving 'manual grazing' were established early on in the evolutionary history of the genus.

Despite the relatively limited range of the extant *T. gelada*, *Theropithecus* fossils have been reported from a variety of sites in northern, eastern and southern Africa, from strata ranging in age from 4 Ma to the present day, in addition to its occurrence in Indian and Spanish Pleistocene deposits. The distribution of extinct *Theropithecus* species at the two latitudinal extremes of Africa represents the most expansive range of any extant African primate genus, rivaled only by that of *Macaca* (Pickford, 1993). The addition of fossils from Spain and India far exceeds the range of any primate, except *Homo*, and the large majority of mammals. However, the present range of *T. gelada* is smaller than many other cercopithecoids, especially *Papio* species. Among the factors argued to have influenced the reduction of such a widespread taxon to its present day range are: competition for resources by other herbivores, interactions with predators (including humans), and changing climatic conditions.

The fossil record reveals that *Theropithecus* and *Homo* lived contemporaneously in Africa during much of the Pleistocene. In an evaluation of the relationship between these two genera, Pickford (1993) suggests that for most of its history, the distribution of *Theropithecus* was relatively unaffected by the presence of hominid activity; this claim is substantiated by the fact that *T. oswaldi* experienced its greatest expanse in distribution during the Acheulean when pressures from hominid hunting practices presumably accelerated. However, the effect of hominid activity on the distribution of *Theropithecus* increased over time and became more prominent during recent history, with significant advances in tool technology and hunting techniques, and increasing human populations and habitat alterations. Such advances presumably influenced the reduction in geographic range of the theropiths.

Competition for resources from other herbivores appears to have more strongly affected the distribution of the now extinct theropiths. The genus *Papio* currently has one of the largest distributions among African primates (Wolfheim, 1983). While fossil specimens of *Papio* are less abundant than are those of *Theropithecus*, there is some evidence to suggest that the radiation of *Papio* in sub-Saharan Africa in the Pleistocene led to increased competition for food resources and sleeping sites with *Theropithecus*. In addition, the high-altitude grasslands where the extant gelada is present today are one of the few habitats that *Papio* species are unable to successfully occupy.

Among the non-primate herbivores, the African warthog, *Phacochoerus*, is reported to have had an equally expansive distribution pattern, and to have been a likely competitor for food resources with *Theropithecus* (Pickford, 1993). With a similar distribution pattern in time and space as *Papio*, it is possible that the competition from both of these herbivores contributed to the shrinkage in distribution of *Theropithecus* ranges in all lower altitude habitats by the close of the Middle Pleistocene.

In addition to interactions with *Homo* and competition for resources with *Papio* and *Phacochoerus*, regional and global climatic changes appear to have had the most significant effect on the pattern of distribution of the theropiths. Pickford (1993) and Foley (1993) have each examined the effect of climatic changes on the reduction in distribution of *Theropithecus* throughout the Pleistocene to present day. Pickford (1993) suggests that latitudinal shifts in the distribution of *Theropithecus* are correlated with the shifts in boundaries between the Ethiopian and Palaearctic biogeographic realms resulting from global-scale climatic changes. For instance, the relatively short periods of time when *Theropithecus* occurs at extreme latitudes may have coincided with interglacial

periods, while its absence from these areas coinciding with glacial periods. In other areas of its range, such as in equatorial Africa, species diversity and ranging patterns appear to be related to regional-scale climatic changes brought about by the rise of the 'Roof of Africa' during the Plio-Pleistocene.

Foley (1993), on the other hand, looks at evolutionary patterns during the Plio-Pleistocene by comparing the radiations of the Hominidae, *Theropithecus*, and various other baboon species (what he has termed the 'African Terrestrial Primates'). In contrast to the above biogeographical analysis, Foley (1993) suggests that the primary factor responsible for species diversity and distribution patterns of *Theropithecus,* and other African Terrestrial Primates, is the frequency of climatic oscillations. By examination of a number of climatic parameters, Foley concludes that the African Terrestrial Primates appeared to be most strongly affected by climatic instability, with hominids being the least sensitive and *Theropithecus* being the most. Furthermore, *Theropithecus* may have been more closely affected by these stochastic changes, because of its dietary dependence on grasses whose distribution and abundance would have presumably fluctuated markedly. While both authors have focused on different aspects of the relationship between climatic change and the evolutionary patterns exhibited by the African primates, nevertheless, they both strongly implicate climatic factors as having the most direct influence over the course of theropith evolution.

Despite a relatively successful period during the Pliocene and Early Pleistocene, in the later Middle and Late Pleistocene the once widespread and abundant *Theropithecus* was reduced to the small relict population of their present day representatives. What factors may have contributed to the extinction of the theropiths has been discussed by many and continues to receive

considerable attention. Predation by early hominids and competitive pressures from other baboon species have both been thought to contribute to the demise of this taxon; however, changing climatic conditions has been implicated as having the most significant effect on the extinction of the large theropiths. While most investigators still view the changing climate as the most important contributory factor, more recently, the emphasis has been placed on the consequences these changes had on behavior. In particular, Lee and Foley (1993) apply a model of energetic requirements and a variety of other life-history parameters to explore the causes of extinction of the *T. oswaldi* lineage. In doing so, they illustrate that their demise was the result of limited nutritional intake and the constraints this would have placed on reproduction. They suggest that the animals were limited by the amount of time needed to exploit a low quality food resource and this, in turn, would have reduced their reproductive rate. Given these conditions, they would have been particularly vulnerable to localized environmental perturbations, and hence to extinction.

Also making use of a systems model, but with a slightly different perspective, is the socioecological model put forth by Dunbar (1993b). In this approach, Dunbar investigates the effect of varying climatic conditions on group size for populations of extinct theropiths. Based on size-specific life-history parameters, Dunbar shows that the theropiths of the Plio-Pleistocene were not large enough to exploit poorer quality food resources at lower altitudes; thus, their distribution was more restricted than present day populations. Furthermore, he suggests that the later Pleistocene theropiths were even more narrowly adapted by being restricted to areas with either cooler ambient temperatures or greater quality grasses than the current conditions of the extant gelada. Such specific localities would most probably have occurred near a

permanent water source, and thus, would have made them highly vulnerable to extinction.

In explaining how climatic changes are mediated through behavior, Dunbar (1993b) uses his socioecological model to show that the giant theropiths of the Middle Pleistocene could not have maintained the basic nutritional and social demands needed to survive. He suggests that the increasing amounts of time needed to meet energetic requirements would have adversely affected the time invested in socializing by disrupting the cohesion of social groups. Thus, changes in climate are shown to have triggered a series of behavioral changes that ultimately led to a reduced reproductive rate as a consequence of size-specific life-history parameters. The important consequences of environmental change, coupled with hominid predation and competitive pressure from other species, most likely contibuted to the demise of this once successful taxon.

2.2. General Aspects of Gelada Ecology and Social Organization

2.2.1. History of Field Studies

Although there are a few accounts of this species (referred to as the 'sphinx monkey') throughout the Roman and Medieval periods, it was not until the 1830s that the gelada baboon (*Theropithecus gelada*) was collected and formally described by the naturalist Ernst Rüppell (Jolly and Ucko, 1969; Dunbar, 1993a). The first landmark field study on the gelada by J.H. Crook and colleagues during the mid 1960's (Crook, 1966; Crook and Aldrich-Blake, 1968) launched what was to be a period of intensive examination of this unique species of the Ethiopian highlands. This pioneer study provided a basic description of the unusual ecological and social adaptations of the gelada. R.I.M. Dunbar and

P. Dunbar followed this study in the next decade with two field sessions in which they focused on the adaptive significance of the gelada social system. During this period M. Kawai and colleagues also conducted observations on gelada populations and made a systematic analysis of inter-individual relationships within units and inter-unit relationships of herd dynamics (Kawai, 1979). This was shortly followed by an ecological study by R.W. Wrangham (1976) that specifically focused on the species' peculiar feeding strategy. Thus, through field studies which spanned one and a half decades and made detailed observations of its basic socio-ecological features, our present knowledge of the gelada baboon is one of the most complete among the primates.

2.2.2. The Ecology of the Gelada

Theropithecus gelada is distributed along the gorges and escarpments of the Amhara highlands of Ethiopia, and there is a recently discovered population in the Arussi region to the southeast (Mori and Belay, 1990) (Figure 2.2.). In the mid-seventies, total population size was estimated at about 500,000 (Dunbar, 1993a). Despite relatively large numbers, the gelada faces some risk of extinction due to its ecological specialization and restricted geographical distribution. Gelada habitats range in altitude from 1500 to 5000 m a.s.l. with most populations found at approximately 2000 to 3000 m (Iwamoto, 1993). Compared to the neighboring lowland *Papio* species, the climate of this habitat is wet and cool with annual rainfall averaging 1200 mm, distributed from June to September, and average temperatures being as low as 15°C in the Amhara and 5°C in the Simien plateau (Iwamoto and Dunbar, 1983).

The vegetation of the plateau ridges and gorge surfaces consists of a variety of thicket plant species, while the more expansive plateau grassland areas contain grass species adapted to the high altitudes. Gelada populations are restricted to the areas adjacent to the cliff faces along the escarpment and the geladas use the cliffs as sleeping sites. The gelada ranging pattern is equally restricted. Groups typically move only 1 to 2 km per day and range significantly beyond the cliff edges only when they congregate in large herds. This observation has led some to view the formation of congregations as an adaptation to increased predation pressure when they expand their exploitation of the habitat (Dunbar and Dunbar, 1975). The population density of geladas in these areas is very high compared to other sympatric primate and ungulate species, ranging from 63 to 77 animals per km^2 and reaching an estimated biomass of 459 kg/km^2 (Bole Valley) (Dunbar, 1978). Such high densities have been attributed to the feeding behavior of the gelada, which is using the most abundant plant resources.

The gelada shows little niche overlap with its two sympatric primate species, *Papio anubis* and *Cercopithecus aethiops*, but does exhibit overlap in diet with other mammals that inhabit this region (e.g., Walia ibex, klipspringer, bushbuck, bush duiker, horse and cattle). Geladas are graminivorous, preferring grass blades, rhizomes, flower and seeds which make up approximately 90% of their diet (Dunbar and Dunbar, 1975). In the dry season, when grasses decrease in abundance, the gelada rely more on the herbaceous plant *Trifolium* which has a high protein content. How the digestive system of the gelada processes these large volumes of vegetation is somewhat unclear. Iwamoto (1993) suggests that the gelada may possess some hindgut fermentation abilities and copes with its highly folivorous diet in additional ways. One way is by grinding tough plant

foods with specialized molar morphology (e.g., greater surface relief; Jolly, 1972). Second, the gelada increases its food intake rate during the dry season by prolonging the time spent feeding, and shifting from eating grasses to herbs. The quality of food, however, does not decrease in the dry season because of the high nutritional content of *Trifolium*. The greater energy intake might be explained as the result of increased need for thermo-regulation during this colder period. The amount of time the gelada spends feeding is comparatively high for a herbivorous primate ranging between 35.7 % (Bole Valley) to 67 % (Simien) and averaging 50 - 85 % of time spent in foraging behavior (moving and feeding) (Iwamoto, 1993).

2.2.3. The Social Structure of the Gelada

The social system of the gelada baboon is comprised of an hierarchical arrangement of increasingly inclusive social groupings. This multi-level system is analogous to that exhibited by the hamadryas baboon (*Papio hamadryas*) and together the two have been argued to be unique among the primates in their degree of organizational complexity (Stammbach, 1987). The two main components of the system are the individual reproductive units and the clustering of these units, along with all-male groupings of bachelor males, into higher-level groupings termed 'bands' (Dunbar, 1984). The units of the band frequently associate with one another and share common ranging patterns. The one-male units are considered the basic social grouping where all social behavior and reproductive activities take place, whereas the bands are considered the basic ecological unit (Kawai *et. al.* 1983).

The band can be viewed as the ecological equivalent of the *Papio* and *Macaca* multi-male troop. The band is also considered to be the basic genetic unit of the gelada in that members of a given band tend to be more closely-related than members of different bands; gene flow between neighboring bands is estimated to be as low as 5% (Shotake, 1980). Bands typically consist of 2-27 reproductive units and 1-3 all-male bachelor groups, totaling on average 100 individuals. Occasionally, some units of a band may associate more closely with each other than with other units, termed a 'team', which is viewed as intermediate between the reproductive units and the band (Kawai *et al.*, 1983). This differs from the gelada 'herd' which is used to define temporary aggregations of a variable number of units (between 2 and 60), usually from the same band but sometimes including units from other bands, which at any given time may be dispersed throughout a common ranging area. The herd is unstable in composition and highly variable in duration, and thus, unstructured in association patterns.

A further level of grouping that has been recognized by some is the 'community' (Kawai *et al.*, 1983), which consists of 1-4 bands whose ranging areas extensively overlap and whose constituent reproductive units form 'mixed-band herds'. The exact significance of this level of organization is not completely understood (Dunbar, 1984). The composition of these various groupings changes gradually over time as a result of births and deaths, with significant changes in size occurring more erratically as the result of group fissioning, or emigrations of reproductive units to new ranging areas as a consequence of group fissioning (Ohsawa and Dunbar, 1894).

2.2.4. Structure of Reproductive Units

The basic social grouping of the gelada, the one-male reproductive unit, typically consists of a single breeding male and four or five reproductive females and their dependent offspring (Dunbar, 1984). Units are highly variable in size (there may be up to 12 females) and composition. A notable proportion (approximately 25%) of units contain additional adult males, called 'followers', of two types. Some followers are former harem holders who despite being displaced by younger rivals remain with the group. The other class of followers are typically younger males who join the group and develop grooming alliances, and occasionally mate, with one or a few of the more peripheral females of the unit.

Gelada reproductive units are highly structured, closed social units. Analysis of the structure of these units revealed small clusters of females who spend most of their available time interacting with one another (Dunbar and Dunbar, 1975). This network of female relationships typically includes two to three post-pubertal females, that form dyads, whose members mutually groom one another to the exclusion of others and provide support for each other during intra- and inter-group agonistic encounters. Demographic analyses of these coalitions strongly suggest that they are comprised of close female relatives, usually mothers and daughters or sisters, and this inference was further confirmed by observations made on individuals of known relationship in a captive population (Dunbar, 1982).

The social relationships between females in a dyad are primarily serviced by grooming and the strength of these dyadic relationships has been shown to have profound consequences for females in many aspects of their social life. Females who lack close female relatives spend little time interacting with other

females in their unit, remain socially peripheral to the group, and substitute adult female grooming partners with the unit male or immature individuals in the group. In contrast, females who are members of a grooming dyad are significantly less likely to be attacked by other members of the group, and both younger and older female members of a group that are in dyads occupy higher dominance ranks within a group than do those who do not belong to dyads. A female is significantly more likely to give coalitionary support to a female with whom she forms a grooming relationship than to one she rarely grooms. Females who are members of such alliances experience a significantly higher birth rate than females of the same age and rank who do not form such alliances (Dunbar, 1980a, 1988).

Dominance relationships among females tend to be non-transitive and their stability is a function of the size of the unit: smaller units exhibit more stable hierarchies than larger units (Dunbar, 1984). A female's rank in a hierarchy is determined by three different criteria: (1) a young adult female occupies a rank that is dependent solely on her aggressive abilities relative to other females of similar age; (2) females of other age-classes occupy ranks that are immediately below that of her highest ranking female relative; and (3) females of other age-classes who do not have mature female relatives in their unit will occupy a rank at the bottom of the hierarchy based on their own intrinsic aggressiveness in relation to other females who have no relatives. Within matrilines, rank is dependent upon an individual's aggressiveness, while between matrilines rank is dependent solely on the aggressiveness of their highest ranking member, irrespective of matriline size. In addition, a female's dominance rank and aggressiveness have been shown to be unaffected by the degree of interaction with the unit male. In general, females low in the

hierarchy experience increasing amounts of harassment and aggression from other females in their group of higher dominance rank. This accumulation of aggression increases as a female's rank decreases.

The existence of coalitionary alliances has been shown to buffer these agonistic encounters and significantly affect their outcome (Dunbar, 1984). A female with limited intrinsic abilities to achieve high status can increase her relative dominance rank by forming an alliance with a higher-ranking female. In a detailed analysis of the relationship between female rank and birth rate, Dunbar (1980a) concluded that lower-ranking females produced fewer offspring and experience a reduced conception rate. Dunbar (1980a) attributed this to a disruption of reproductive physiology caused by the stressful effects of the accumulation of aggression over time. Because coalitionary alliances can minimize the frequency with which a female is harassed, such alliances may reduce the stress to which a low-ranking female might otherwise be exposed.

Dunbar (1984) describes the integrity of the reproductive unit as being maintained by the stability of female coalitionary relationships, with the unit male being socially peripheral to the core of the unit. The unit male has little or no effect on a female's dominance status, and therefore is not a preferred candidate for an ally. However, females that lack female grooming partners or allies will choose the male as a social partner, treating him as a substitute female. This relationship closely resembles the relationship between female coalitionary partners, with grooming being reciprocated somewhat equally. It differs, however, from the relationship other 'non-partner' females have with the unit male which is best described as 'perfunctory' (Dunbar, 1984:46). Non-partner females are less likely to reciprocate grooming bouts with the male, less likely to initiate social interactions with him, and more likely to abandon him.

The male is viewed as a less valuable social partner, in part due to his relatively short tenure in any given reproductive unit. As a result, a female will benefit the most from forming strong alliances with other females who remain in the group throughout their lives than by forming an alliance with a male, who most likely will not be present as an ally in later years, when her own intrinsic physical abilities are likely to be declining.

The dominant female of the reproductive unit has priority of access to the male and exercises her prerogative to do so on occasion. In addition, she consistently maintains control over access to the male and actively positions herself between him and other females, including the male's grooming partner, interfering in their interactions. This pattern of behavior can potentially have significant consequences in reproductive behavior. An interesting departure from this general pattern of interaction between the unit male and females is that exhibited by the lowest ranking females of the group. These females show the greatest interest in new harem males (following a take-over of the reproductive unit), and in young follower males who remain on the periphery of the unit. In both instances, particularly with followers, the low-ranking female may have the opportunity to increase her rank as an outcome of a change in group composition (Dunbar, 1984).

2.2.5. Female Socio-Reproductive Strategies

Within the gelada social structure, females can be viewed as having three main strategies in order to increase their reproductive fitness. As discussed above, her first option involves the formation of an alliance with another female, preferably a close relative, in order to increase her dominance rank. By forming

a coalition with a more dominant and more aggressive partner, a female will gain an advantage by maintaining a higher rank than that which would normally accrue to her as a result of her intrinsic abilities. In addition, a female can derive an advantage through the gains in fitness of her relatives as a result of coalitionary behavior.

A second strategy for a female is to become the male's main grooming partner, and to use him as a substitute for a female ally. The grooming relationship with the male can also be used as a way to reduce the amount of interference from more dominant females with regard to gaining sexual access to him. However, a particular female may only resort to this option under certain conditions. Although the male is invariably dominant to all of his females, he does not influence the rank order of females. The male also tends not to provide more support to a grooming partner female in altercations than he does to non-partner females. Nonetheless, for a female who lacks female relatives, becoming a partner with the unit male may accrue some short-term advantages. One such advantage is that partner females experience a slight but significant increase in copulation rates compared to non-partner females; and in some instances, partner females are harassed less frequently than non-partner females of equivalent age and rank (Dunbar, 1984). At the very least, a female allying with the male may gain a small advantage by offsetting the disadvantages normally incurred by the absence of a close female ally.

One further option a female can explore is that of desertion. If a female remains continually in a low-ranking position, she may benefit by deserting the present male for another. It is rare for a gelada female to desert her entire natal group and join a group of unfamiliar individuals, but a female may still attach herself to a young follower male, or form a close relationship with a male

attempting to take over the unit. Either situation involves a decrease in the number of competing females, and thus the likelihood of increasing her relative rank and the benefits accrued thereof.

2.2.6. Male Socio-Reproductive Strategies

Typically, gelada males will leave their natal groups upon reaching puberty to join an all-male group, which is likely to contain some relatives. Residency in an all-male group usually lasts between 2 and 4 years, after which a male will attempt the arduous task of acquiring his own females (Dunbar, 1984). A male's ability to mate and produce offspring is based solely on whether or not he can monopolize a group of females and thereby maintain mating access to them to the exclusion of other males. A male can accomplish this by employing one of two different strategies. One option is for a male to take over an intact unit by ousting the resident male; the other is to become a follower.

The take-over strategy can incur a high risk of injury, and as a result, more commonly involves older males. Although males in all-male groups are considered adults (averaging 6 years of age), they are on average significantly smaller than males who are residents of reproductive units (averaging 10 years of age). Take-over attempts involve very aggressive fighting and often result in serious injuries to one, or both, of the males. The challenger male's behavior during the time of the take-over includes attempts to approach, solicit and groom the females, while the incumbent male's behavior alternates between actively chasing the intruder male away and maintaining social contact with his females, often by frantic bouts of grooming and mating. However, once an outside male

begins to challenge an incumbent male for possession of the unit, his success is strongly influenced by the willingness of the females to desert the incumbent in favor of the new challenger. Furthermore, the behavior of females will have more influence on the final outcome of a take-over as does the physical prowess of the young challenger (Dunbar, 1984).

In great contrast is the route taken by the follower male. While the follower is initially met with aggression by the resident male, his response is often a submission rather than challenge; and in a relatively short amount of time this usually leads to the acceptance of the young male into the unit. Once in the unit, he begins by interacting with the juveniles, followed by a small number of low-ranking or peripheral adult females. Over a period of 1 to 3 years he develops relationships with a small nucleus of females within the unit, at which point the nucleus fissions and becomes an independent unit (Dunbar and Dunbar, 1975).

By beginning with a small number of females and gradually nurturing relationships with them, the follower male seldom achieves a unit size that makes him susceptible to a take-over and he is therefore able to maintain tenure for relatively long periods. In contrast, the main factor that allows a challenger male the opportunity to acquire a reproductive unit is the same factor that makes him equally susceptible to the fate of being ousted, namely large unit size. Compared to smaller reproductive units, larger units contain a greater number of low-ranking females who lack coalitionary alliances and therefore tend to be more willing to accept and support a new male entering the unit. Through the analysis of relevant demographic parameters, Dunbar (1984) has shown that the two alternative strategies are equally advantageous over an individual's lifetime. The initial advantage incurred by a challenger in acquiring a large number of

females through a take-over is offset by the fact that a male only experiences the reproductive advantages accrued as unit leader for a short period compared to the male who opts for the follower strategy. In summary, males that opt for a take-over strategy can be characterized as (1) significantly older than males who choose the strategy of a follower, (2) they acquire more females initially by taking over entire, intact units, (3) they experience a high failure rate and a high level of aggression in doing so, and (4) they experience a significantly shorter tenure length as the unit leader.

2.2.7. Evolution of the Gelada Social System

In characterizing the gelada social system, two main features form the basis of its structure, namely, (1) females live in small cohesive matrilineal groups and (2) these small groups combine together to form large unstable herds. All other aspects of the gelada social system have been shown to be consequences of these two key features (Dunbar, 1984). In an analysis of primate grouping patterns, it has been suggested that the number of males in a group is dependent on the number of females in the group and the extent to which their reproductive cycles are synchronized (Dunbar, 1988). Thus, whether a group has a one male or multimale grouping pattern depends on its size. And the formation of reproductive units into bands can be seen as a consequence of the fact that geladas show a preference for foraging in large aggregations, or herds. A corollary of the coalescing of units into herds is the fact that some units tend to remain in closer proximity to each other than others. Since units are composed of close female relatives, it follows that closely related

units tend to remain in the same area, creating a band-like structure with kin ties being the main factor determining the membership of units in particular bands.

Living in large aggregations, such as that exhibited by the gelada, is unique among the primates (Smuts *et al.*, 1987). An analysis of variation in herd size in relation to a number of ecological variables suggested that predation pressure is the main force influencing this grouping pattern (Dunbar, 1988). In areas where predation risk is high, herds reach their maximum size. Compared to other habitats, predators in the Ethiopian highlands at present are relatively scarce, although native dogs appear to be the most serious threat commonly causing the geladas to flee to the safety of the cliff edges when they are nearby (Dunbar, 1986).

Paradoxically, the gelada strategy for exploiting its food resources is what places them at greatest risk of predation, while their strategy to avoid predators decreases their efficiency of food intake. The cliff faces provide protection from predators, but they offer relatively little in terms of food resources. In contrast, the flat plateau tops provide a rich supply of grasses, but leave the geladas completely exposed to predators. Hence, in order to be able to exploit the rich supply of grasses on the plateau tops while avoiding the risk of predation, the one-male units coalesce into herds to provide mutual protection from predators while foraging (Dunbar, 1986). However, the abundance of grasses on the cliff faces are not sufficient to support an entire herd of geladas, and herds often disperse when foraging on the cliff faces. The gelada social system can, therefore, be interpreted as a series of social solutions to two important, yet conflicting, ecological problems: exploitation of resources and predator avoidance, and the consequences that ensue as a result of these two strategies.

Despite the advantages incurred from avoiding predators, living in large herds inevitably has its costs to the individual. The stresses caused by group living, presumably increased in larger groups, can lead to a disruption in reproduction (Dunbar, 1988); and females have evolved ways in which to minimize these tensions without decreasing the benefits that accrue from the formation of herds. Females form coalitions, and Dunbar (1984, 1988, 1993) has argued that the one-male reproductive units are essentially female coalitions created to reduce the stresses imposed on individuals from living in large herds.

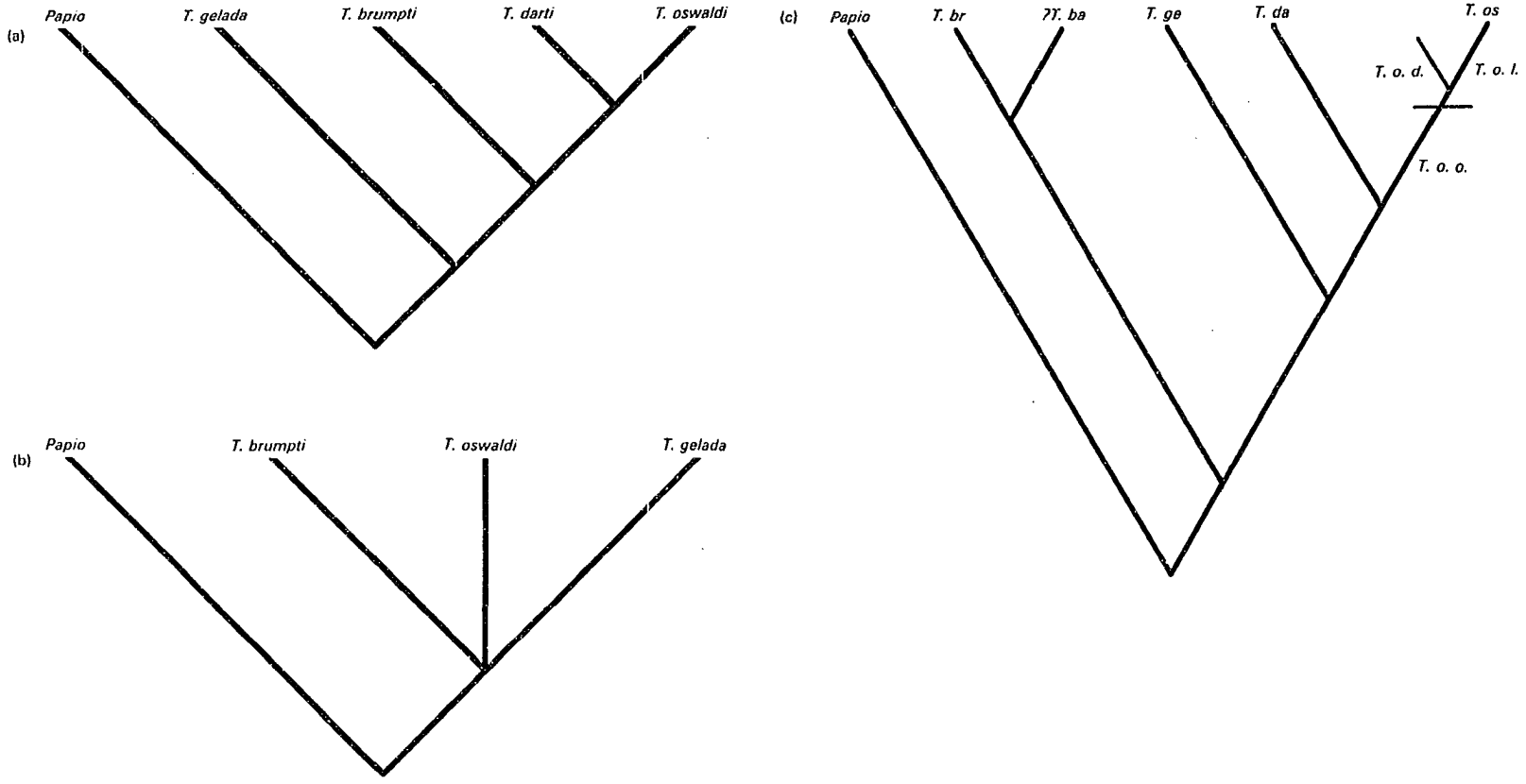
In sum, the gelada social system is based on a set of strategies designed to most efficiently exploit food resources while minimizing predation. The gelada is unique among the baboons taxonomically, ecologically and to some degree, socially. Faced with a changing environment, the ancestral theropiths moved out onto the open grasslands and exploited a grazing niche, but here were subsequently faced with an increase in predation pressure and a reduction in the number of trees to use for refuge (Jolly, 1972). Confronted with these new circumstances, forming larger groups would be an obvious solution. The ancestral theropiths shifted their diet to the more abundant and evenly distributed grasses, whose exploitation would allow the maintenance of large groups.

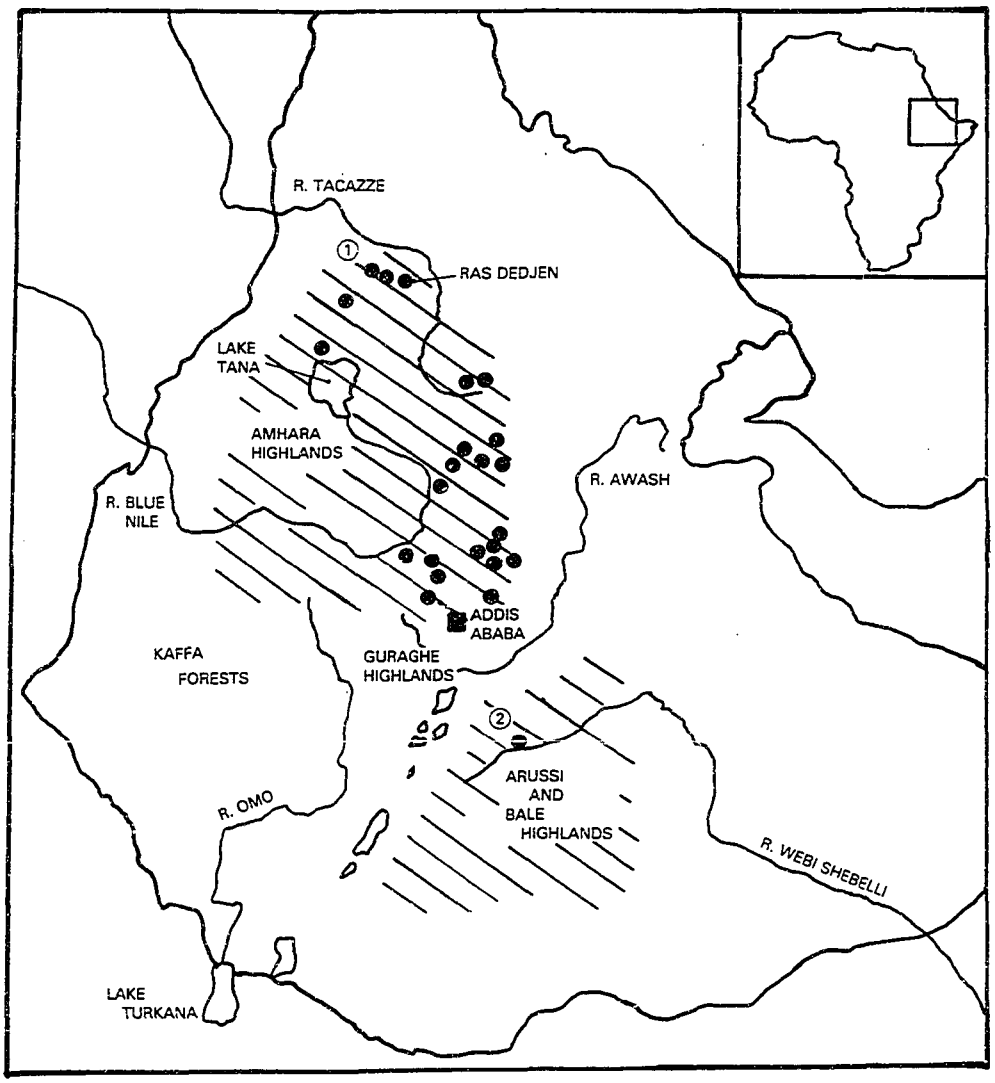
Presumably evolving from a *Papio* social system with matrilineal groupings, the gelada one-male reproductive units and the female coalitions within them, result in large but highly structured groups. Early on in the history of the genus, the ancestral theropiths moved from the open grasslands and invaded the highland plateau region (Jolly, 1972; Szalay and Delson, 1979), and were faced with the two distinct ecological aspects of this habitat. The formation of herds on the open plateau would disband when on the cliff edges. It seems highly probable then that the small female matrilines that together made up the

larger groupings would be the splitting level of groupings that resulted when the pressures of predation were minimal on the cliff edges (Dunbar, 1986).

In conclusion, an examination of the gelada social system provides a key to the understanding of a species' adaptation to a new ecological niche and the consequences that follow. As Dunbar (1988: 303) suggests, the gelada occupied an open grassland niche -- perhaps in response to decreasing forest habitats during the late Miocene -- which created the new problem of increased predation risk, which was solved by forming larger groups, which in turn resulted in increased stress socially and reproductively, which was mediated by the formation of female coalitions.

FIGURE 2.1. Phylogenetic Hypotheses for *Theropithecus*
(from Jablonski, 1993)





Map of Ethiopia showing known localities of where gelada occur (1. Simien Mountains; 2. Arussi highlands) from Dunbar, 1993c)

CHAPTER 3. METHODS

3.1. Design of Enclosures

The "Baboon Reserve" at the Bronx Zoo (Figure 3.1) is a 1.5 hectare exhibit occupied by Nubian ibex (*Capra ibex*), rock hyrax (*Procavia capensis*), Abyssinian blue-winged geese (*Cyanochen cyanopterus*), cape teal (*Anas capensis*), in addition to the groups of gelada baboons. The spacious expanse of the exhibit is its most significant feature, as it is the largest primate exhibit in any U.S. zoo (Doherty, 1991). The exhibit is designed to simulate the Afro-alpine zone of the Ethiopian highlands, complete with high rock outcrops. The majority of the exhibit is surrounded by a moat, which ensures the captivity of the animals as well as providing water for drinking and a home to the waterfowl. Also in the exhibit is a matrix of hardy plants and grasses (Table 3.1) which allows the ibex, hyrax and geladas to graze throughout the day. Another added feature of the exhibit is the inclusion of automatic seed dispensers. There are four such feeders in the exhibit hidden within artificial rocks. With timers attached, the feeders periodically dispense a variety of seeds (commercially bought bird feed mixture) at programmed times (1130 and 1330 hr). By providing grasses and seeds throughout the exhibit, natural foraging behaviors are simulated.

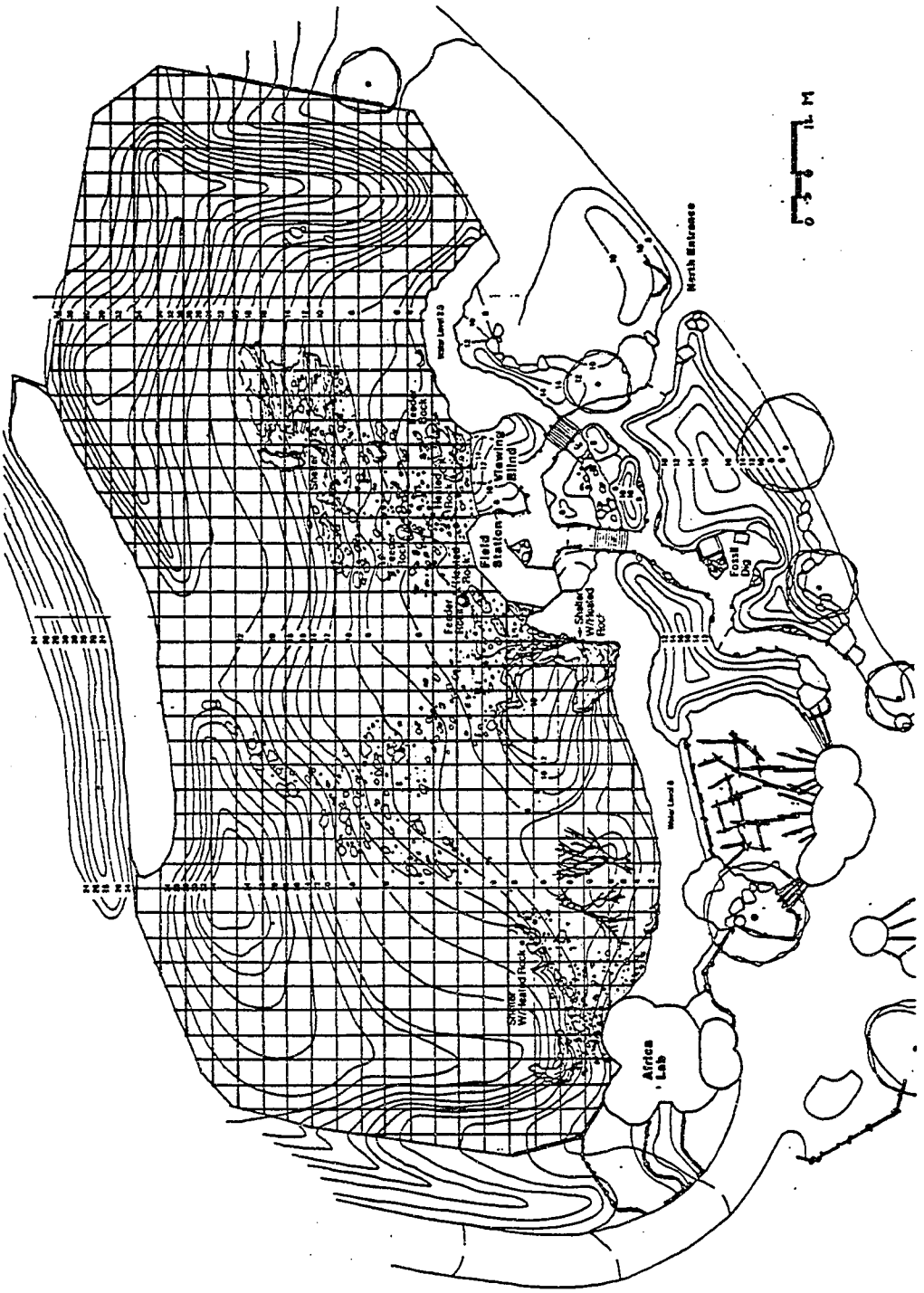


FIGURE 3.1 WCS/BRONX ZOO "BABOON RESERVE"

TABLE 3.1. PLANT COMPOSITION OF "BABOON RESERVE"

SCIENTIFIC NAME	COMMON NAME	SCIENTIFIC NAME	COMMON NAME
Actium minus	burdock	*Eragrostis curvula*	Canada blue grass
Ailanthus altissima	tree of heaven	*Festuca sp.*	non-blue grass
Alopecurus sp.	foxtail	*Kniphofia uvarin*	red hot poker
Amaranthus sp.	pigweed	*Lactuca scariola*	wild lettuce
Ambrosia sp.	ragweed	*Lepidium virginicm*	pepper grass
Anthemis cotula	mayweed	*Miscanthus sp.*	white clover
Chenopodium albm	lambs quarter	*Oenothera biennis*	evening primrose
Crocosmia sp.	Af. red gladiolus	*Onopordon sp.*	African thistle
Cyperus sp.	nut grass	*Paspalum sp.*	paspalum
Dactylis glomerata	orchard grass	*Plantago rugelii*	plantain
Daucus carota	wild carrot	*Polygonum sp.*	smartweed
Deschampsia sp.	tufted hair grass	*Setaria sp.*	foxtail grass
Digitaria sp.	crabgrass	*Solanum sp.*	nightshade
Echinochloa crus	barnyard grass	*Verbena urticifolia*	white vervain
Eragrostis curvuia	weeping love grass	*Yucca sp.*	yucca

A high rock bluff complete with fissures and cavities, some leading to heated night quarters within the rock, provide a kopje-like habitat for the rock hyrax in addition to providing shaded cliff overhangs for the geladas. Two additional rock shelters are present in the north and south ends of the exhibit. While the shelters provide shade during the hotter times of the year, strategically placed heating pads hidden within the rock work also provide some relief from the colder temperatures during the winter months.

The holding building (10 x 20m) is situated behind the north hill out of public view and includes an indoor (6.6 x 3.5 x 4m) and an outdoor (5.3 x 8.6 x 3m) area, with two separate cages for each group of geladas, plus additional cages for isolated or surplus animals. The indoor cages have direct access to their respective outdoor pen areas through a Plexiglas guillotine door. While the indoor cages are used primarily as sleeping quarters, the outside pen areas provide a staging area where animals are placed immediately prior to entering the exhibit. The outside pen area was the most important design feature of the exhibit for this particular study, for it provided a means to consistently collect urine samples from individuals without any disruption to the animals or their daily routine.

3.2. *Theropithecus* Study Population

3.2.1. The Value of the WCS/Bronx Zoo Population

The gelada baboons at the Wildlife Conservation Society's (WCS) Bronx Zoo provide a unique opportunity to gain information not easily accessible under natural conditions on key reproductive parameters affecting female fertility in this species. The benefits of a study of this population include:

1. Group Size -- The group size of *Theropithecus* maintained at the Bronx Zoo is within the range found under natural conditions (Dunbar and Dunbar, 1975; Kawai, 1979). In addition, the total number of individuals, the inclusion of more than one group within the exhibit, and the relatively large size of the exhibit allow for significant behavioral observations to be made (Dunbar, 1982). The fact that this is a semi-free-ranging group and that individuals are never separated from their social group or handled by humans (unless medical attention is needed) is another valuable feature of this population for a behavioral study.

2. Physiological Data -- The close monitoring of endocrine events requires daily or frequent sampling from each individual. In the wild, sampling regimes are too often compromised due to the nature of the site conditions. In captive settings, important hormonal data are more easily and efficiently obtained through the non-invasive method of urine sampling. Although the geladas at the Bronx Zoo are free-ranging within an enclosed outdoor exhibit during most of the day, they return to a holding area overnight for management purposes. Urine samples are obtained at the beginning of each day when individuals are on artificial substrates in their outdoor holding cages.

In sum, the benefits of this particular zoo setting for a study of this nature are two-fold: while having the control necessary to conduct daily urine sampling afforded by captivity, social dynamics are not compromised because individuals remain in their social group at all times.

3. Stable Food Supply -- Due to the distribution of resources exploited by *Theropithecus* in the wild, Dunbar (1977, 1980a) reports that resource competition is not a significant factor determining intra-group variation in birth rates among females. In the zoo setting the nutritional effects of resource competition, if observed, are controlled for by the constant availability of an abundant food supply. The daily provisioning of a nutritionally balanced diet is designed to properly ensure the nutritional health of all individuals. Therefore, it can be assumed that resource competition is not a contributory factor affecting reproduction. Nevertheless, in order to rule out any effects of resource competition, data were collected to test whether differences in nutritional status correlated with differences in reproductive condition (Small, 1981).

3.2.2. Composition of Study Groups

At the time of the study (January 1991 - December 1992), the population of gelada baboons at the Bronx Zoo included 26 individuals, 9 males and 17 females (Table 3.2.). All animals were captive born, with the exception of three individuals (#'s 64, 65 and 94) with unknown origins. One male (#10) and two females (#'s 11 and 13) were previously part of the Bronx Zoo collection, while all other geladas were brought to the Bronx from other zoos on a breeding loan. Eighteen animals were housed in two social groups, nine in group CN and nine in group LH, and were maintained as exhibit groups. One subadult male, one subadult female and one young adult female were received at a later date from the Los Angeles Zoo. They were housed separately from the exhibit group for a short period; subsequently, all three individuals were integrated into the CN group. Five adult males were surplus to the exhibit groups and were housed

TABLE 3.2. STUDY POPULATION OF *Theropithecus gelada*

FEMALES			MALES		
ID #	Age-Class	Body Weight (kg)	ID #	Age-Class	Body Weight (kg)
11	Ad 2	17.1	10	Ad 2	34.1
13	Ad 2	16.6	60	Ad 2	26.8
15	Ad 2	16.3	61	Ad 1	30.4
16	Ad 3	15.9	86	Subad	27.9
12	Ad 2	17.9			
14	Ad 2	15.6		N = 4	
17	Ad 3	18.4			
18	Ad 3	18.8			
62	Ad 2	18.0			
63	Ad 3	17.2			
64	Old Ad	11.4			
65	Ad 2	17.4			
66	Old Ad	14.7			
67	Ad 3	12.6			
68	Juv	x			
87	Ad 1	13.1			
88	Subad	12.3			
	N = 17				

Female Age-Classes (years)	Male Age-Classes (years)
Juvenile = < 2	**Subadult = < 5**
Subadult = 3 - 4	**Adult 1 = 6 - 8**
Adult 1 = 5 - 7	**Adult 2 = 8 - 12**
Adult 2 = 8 - 10	
Adult 3 = 10 - 12	
Old Adult = >14	

TABLE 3.3. GELADA BABOON GROUP COMPOSITION

Group Composition (Phase I):

Group CN	Group LH	Group LA*
1 Adult Male (#60)	1 Adult Male(#10)**	1 Subadult Male (#86)
6 Adult Females (#62-67)	8 Adult Females (#11-18)	1 Young Adult Female (#87)
1 Young Adult Male (#61)		1 Subadult Female (#88)
1 Juvenile Female (#68)		

Group Composition (Phase II):

Group JR	Group JD
1 Young Adult Male (#61)	1 Subadult Male (#86)
4 Adult Females (#11, 13, 15, 16)***	4 Adult Females (#12, 14, 17, 18)***
1 Subadult Female (#88)****	1 Young Adult Female (#87)****

Group CN

1 Adult Male (#60)

4 Adult Females (#63, 64, 65, 67)

1 Juvenile Female (#68)

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*Not part of exhibit group during Phase I.
**Adult male from LH group ousted by subadult male (#61) from CN group.
***Four LH females (#'s 12, 14, 17 and 18) join LA subadult male (#86) to form a new group (JD); remaining LH females and male #61 form group JR.
****LA juvenile and subadult females transfer out of CN group and into groups JR and JD, respectively.

separately and maintained in the Bronx Zoo collection until transferred to other zoos on breeding loan.

Group LH consisted of 1 adult male and 8 adult females. Six adult females from various zoo collections were added to the adult male and two females already part of the Bronx collection. In order to enhance familiarity and the formation of a group, these individuals went through a series of introductions in indoor enclosures for a period of 2-3 months. The CN group consisted of 1 adult male, 6 adult females and 1 juvenile female and 1 young adult male. The entire CN group was an intact one-male group transferred from the Cincinnati Zoo collection to the Bronx Zoo collection. However, within six months after behavioral observations began, two adult females had died (#'s 62 and 66) and the subadult male (#61) had transferred out of the CN group and replaced the resident breeding male of the LH group. At this time, the three Los Angeles Zoo (LA) individuals (#'s 86, 87 and 88) were integrated into the CN group.

During the duration of the study, the group composition of the geladas went through several changes (Table 3.3.). While the death of certain individuals accounted for some of the changes in group composition, the major change in group dynamics occurred as a result of the behavior of the two subadult males. The first change occurred when the subadult male (#61) from the CN group began challenging the adult male (#10) from the LH group. After a period of approximately 6 months, the younger male won the support of the females and ousted the then resident male, who was subsequently removed from the exhibit group and eventually transferred to another zoo on breeding loan.

The second major change in group composition occurred approximately five months later when the LA subadult male (#86) began pursuing four of the LH females, who were peripheral to the core of the group. They soon fissioned

from the LH group and joined the young male and formed their own group (JD), thus, making a total of three exhibit groups. Subsequent to this change, the two LA females transferred out of the CN group and attempted to enter into the other two groups, JR and JD.

3.2.3. Management of Study Groups

In order to reduce potential aggression resulting from the introduction of the two one-male groups into the outdoor exhibit, the exhibit was at first temporarily divided into north and south sections. Initially, the females in the LH group were admitted to the south end of the exhibit on one day and the next day the females in the CN group were admitted to the north end. After approximately one week, the males of each group were admitted to the outdoor exhibit with the females. The purpose of this procedure was to allow each group to get familiar with one area of the exhibit. After a short habituation period, both groups were admitted simultaneously to the exhibit on their respective sides. After another brief habituation period, approximately one month later, the barrier was removed, and the two groups were admitted simultaneously to the exhibit with access to all areas.

The gelada baboon exhibit is managed to simulate the geladas' natural multilevel social organization. As in the wild, the simplest structural unit is the one-male unit, containing one breeding male and 4-10 adult females and their dependent offspring. Out in the exhibit, the one male groups spend the day moving about, interacting and feeding on the variety of grasses grown in the exhibit. At the end of the day, the groups return to the holding building where they are housed overnight in separate sleeping quarters for each group.

The animals remain in their indoor holding areas from approximately 1700 hours to 0800 hours. At 0800 hours each group is admitted to an outdoor holding area and remain there until 1000 hours. At this time they are admitted to the outdoor exhibit, where they spend the majority of the day. At approximately 1700 hours they return to the holding building where they are fed their daily diet. In addition to the variety of grasses and seeds available for grazing in the outdoor exhibit, indoors they are given additional food items to ensure that all individuals are provided with basic daily nutritional requirements (Table 3.4.).

Upon entering the Bronx Zoo collection, all of the geladas were placed under quarantine, at which time they received a complete physical examination. However, beyond this initial exam, the animals are not routinely examined unless serious medical attention is needed. The general policy of the Mammal Department is to avoid any interference with social dynamics unless an individual's physical well-being is being greatly compromised.

TABLE 3.4 WCS/BRONX ZOO DIET (*Theropithecus gelada*)

Bronx Zoo Diet Form

Gelada Baboon (*Theropithecus gelada*)

Sex: Female (Adult)	**Weight:** 15 kg	**Kcal Requirement:** 900
Sex: Male (Adult)	**Weight:** 28 kg	**Kcal Requirement:** 1400

Daily Diet

Adult Female (1100 kcal)		**Adult Male (1500 kcal)**	
Primate Diet	200 g	Primate Diet	200 g
Hi-Fiber Chow	200 g	Hi-Fiber Chow	300 g
Greens	200 g	Greens	200 g
Yam or Carrot	100 g	Yam or Carrot	100 g
Orange	75 g	Orange	75 g
Banana	25 g	Banana	25 g

*NOTE: 2 drops (.1 ml) vitamin E on fruit; mixed hay with scattered seed in exhibit and fresh browse whenever possible.

3.3. Behavioral Sampling Techniques

Behavioral observations on several aspects of individual female behavior and group dynamics were made from the best possible vantage points. There are four exhibit viewing areas available for observations. Each viewing area allows optimal visibility when the animals are in different areas of the exhibit; however, due to the size of the exhibit and the maximum distance possible between the subject under observation and the observer, binoculars were used to ensure accurate animal identifications. During preliminary observations it was discovered that individuals could be accurately recognized through the identification of distinguishing physical characteristics. The main focus of the study was centered on individual female behavior as it relates to reproduction: the pattern of social behavior between females and their relationship with the unit male, and its effect on reproduction. The assessment of social relationships among females was made by focal animal, scan and ad libitum sampling (Altmann, 1974; Martin and Bateson, 1986). This closely follows the approach employed by Dunbar (1978, 1980a, 1983, 1984; and Dunbar, 1975) and proved to be the most appropriate method of sampling during preliminary observations of *Theropithecus*. All behavioral events were scored based on the ethogram from Dunbar and Dunbar (1975) but modified to the behavioral repertoire of the gelada baboons at the Bronx Zoo (Table 3.5).

TABLE 3.5. *Theropithecus gelada* ETHOGRAM
(after Dunbar and Dunbar, 1975, Appendix A and B)

NON-SOCIAL ACTIVITY

01. Rest/Sit
02. Lay down
03. Sleep
04. Move
05. Explore/Investigate
06. Eat (grasses)
07. Eat (seeds/feeder)
08. Drink
09. Urinate
10. Defecate

SOCIAL ACTIVITY

Affiliative

11. Approach
12. Avoid
13. Lipsmack
14. Present chest
15. Present rear
16. Present genitals (either by cocking up nearside leg or by standing bipedally)
17. Sniff/Nuzzle
18. Touch/Hug (a momentary event lasting < 10 seconds)
19. Embrace/Cuddle (a prolonged event lasting > 10 seconds)
20. Follow
21. Autogroom
22. Allogroom
23. Inspect vesicles (smell, touch or taste vesicles)
24. Mounting attempt (male lipflutters to female while grabbing hold of fur at the hip)
25. Copulatory stance (female adopts crouching posture and holds leg of male during mount)
26. Copulation (incomplete-- < 7 thrusts w/ no sign of ejaculate)
27. Copulation (complete-- 11-15 thrusts with ejaculate visible)

Play

28. Grin (play face)
29. Box/Jump at
30. Mouth wrestle
31. Play chase (with frequent role reversals)

Maternal/Weaning

32. Hold/Cuddle
33. Carry (ventral or dorsal)
34. Restrain
35. Grab/Pull towards
36. Push away
37. Suckling
38. Prevent suckling

Uncertainty/Crisis

39. Scratch
40. Rub muzzle or eyes
41. Shake cape (males)
42. Yawn
43. Lip-flip (eversion of upper lip)
44. Bipedal rocking (standing bipedally and performing side to side rocking)

Aggressive

45. Displace
46. Tail vertical (or arched over back)
47. Stare (directly with lowered head)
48. Alternate stare (alternates looking at aggressor and nearest neighbor(s)
49. Raised eyebrows (revealing light area above eyelids)
50. Open-mouth gape
51. Paw/Slap ground
52. Throw objects (backwards and underarm and/or with mouth)
53. Bounce off substrate
54. Lunge

55. Charge
56. Chase
57. Hit (at)
58. Bite

Fear/Submissive

59. Teethchatter
60. Look away (avoid direct eye contact)
61. Avoid (move away, often while looking over shoulder)
62. Snarl face/grimace (bared teeth)
63. Cringe (body flattened to ground)

Vocalizations

64. Grunt (contact call)--low-pitched grunt emitted in phrases of 1-6.
65. Moan (contact call)--quavering call of variable duration, pitch and intensity, given singly or in long phrases.
66. Interrupted grunt boat (contact call)--prolonged moan broken up into staccato units, often ending with single reverberant inhalation.
67. Vocalized yawn (uncertain)--single reverberant inhalation ending in a yawn.
68. Lipsmacking sound (friendly, greeting)--caused by lip and tongue movements during lip-smacking.
69. Pre-copulation call (sexual invitation)--rapid staccato series of exhalations with mouth slightly open; quiet 'ha-ha-ha'.
70. Post-copulation call (female)--rapid exhalation series with lips together and pouted, rising in intensity and pitch.
71. Post-copulation call (male)--low-pitched rapid exhalation-inhalation series, with open mouth, rising in intensity, often terminated by #67.
72. Cheek pumping (threat)--popping sound made by inflating and deflating cheeks rapidly during fights.
73. 'How Bark' (aggression)--single-phase, high-pitched, dog-like bark.
74. Snarl (fear, mild threat)--force exhalation at low-medium pitch, with mouth open and teeth exposed; harsh sound.
75. Scream (intense fear)--similar to #74, but emitted at higher pitch and intensity, and very loud.
76. Yelp (display)--series of loud 2-tone calls rising in pitch and intensity, given in bouts of 3-6, 'Ee-yow'.

3.3.1. Focal Sampling

Continuous focal animal sampling was employed in order to best assess the social relationships between females and between each female and the unit male. This method most accurately yielded the rates of aggression received and given by individual females, and the rates of affiliative and coalitionary interactions by females with other group members (Altmann, 1974; Dunbar, 1978, 1980a). Samples were randomized so that they were equally distributed across time and across individuals. I began each sample day with a different individual and rotated among individuals at 30 minute intervals. Sample days were grouped into 18-day sampling periods (N=20), which allowed each female (N=15) and male (N=3) to be sampled at all times of the day. An attempt was made to obtain an equal number of samples during each stage of the menstrual cycle for all females (Dunbar, 1978).

During focal sampling all behavioral events were recorded using a Tandy 101 laptop computer (Radio Shack) and an observational sampling program written in computer BASIC language. At the start of each sample period, the focal animal's location, nearest neighbor (and distance), proximity to the unit male, and her reproductive state (vesicular score) were recorded. During each 30-minute sample, all behaviors were recorded continuously. If the activity observed was social, I recorded with whom the female was interacting with, whether the interaction was agonistic or affiliative, the direction of the behavior (actor or receiver) and any coalitionary support received from, or given to, other individuals. When the first behavior is keyed into the computer, the start time automatically is recorded. As each succeeding behavior was recorded, the time of the occurrence of the new behavior was recorded concurrently. This program, therefore, provided both durations and frequencies of behaviors

resulting from each focal sample period conducted. In addition, at the end of each sample day, all the files recorded on the laptop were immediately transferred to a personal computer where they were stored in a database. This system provided the advantage of permitting large amounts of detailed information to be recorded efficiently, as well as allowing the immediate transference of files from the laptop to files on the hard drive of a computer, avoiding the error involved in re-entering data from checksheets.

3.3.2. Scan Sampling

Scan sampling was used to collect data on dyadic associations of females, intra-group spatial relationships (proximity of females to the unit male) and inter-group spatial relationships (Crook, 1966, 1972; Dunbar, 1978, 1980a, 1984; and Dunbar, 1975; Kawai, 1979). Scan samples of all individuals were made before and after each focal sampling interval. A prepared checksheet was used to record the following data: the location of each individual (XY coordinates based on 3 x 3 m quadrant map of exhibit, see Figure 3.1), nearest neighbor, distance from nearest neighbor and the behavior observed.

3.3.3. Ad Libitum Sampling

Ad libitum sampling ("all-occurrence") was also used to record significant behaviors and rare events of interactions observed among other individuals during focal female samples. Such behaviors included conspicuous sexual behaviors (e.g., attempted mounts and copulations), overt agonistic behaviors involving females (e.g., lipflips, lunges, charges, chases and attacks) and all

intergroup interactions (e.g., supplants and agonistic encounters). A SONY (Model #L296) tape recorder was used to document these behaviors. This was the most efficient means to collect these data, which often involved detailed complex interactions, typically occurring in a rapid time span.

3.4. Reproductive Monitoring

In order to assess variation in the behavior of females during the different phases of the menstrual cycle, close monitoring of the cyclic changes in coloration and swelling of the sexual skin of females was necessary. The sexual skin of the gelada baboon is striking in appearance and unique among the catarrhine primates. For instance, the areas undergoing periodic changes are the bare skin areas of the throat, chest, pubic and perineal regions as well as the subcutaneous vesicles bordering them, which may contain pheromonal secretions (Crook, 1972). However, there has been some question as to whether the changes in intensity of coloration of the chest patch show cyclic variations associated with estrus, as first reported by Mathews (1956) and later by Smith and Credland (1977). Studies since then (Alvarez, 1973) have shown that in addition to changes associated with estrus, the intensity of red color in these areas is also affected by the social context, particularly agonistic encounters, in which the color of red intensifies, and by sickness and physical injury, where the color can fade dramatically. The data do indicate that the feature that shows the most marked cyclic changes correlating with the menstrual cycle is the appearance of the fluid filled vesicles surrounding the chest patch and pubic areas (Mathews, 1956; Alvarez, 1973; Dunbar and Dunbar, 1975; Moos-Heilen and Sossinka, 1990). Both the color and degree of development of the vesicles

increase midway throughout the menstrual cycle, around the time of ovulation, and decrease in size and lessen in color as menstruation approaches.

In the present study, I monitored both the changes in coloration of the bare skin areas and the changes in appearance of the vesicles. At the start of every sample day the condition of the chest patch and vesicles was recorded on prepared monthly charts, based on the methods reported in Alvarez (1973) and Dunbar (1978). The color of the bare skin areas and the vesicles were given a score of 0, 1 or 2: 0 = pink bare skin areas and opaque colored vesicles, 1 = red bare skin areas and light pink vesicles, and 2 = bright red bare skin areas and intensely pink vesicles. Likewise, the morphology of the vesicles was also recorded and given a score of 0-2 based on the degree of tumescence: 0 = wrinkled or deflated vesicles as low as the bare skin surrounding them, 1 = vesicles showing some degree of swelling, 2 = vesicles in full tumescence.

It should be noted that while all females displayed cyclic changes in the appearance of the sex skin, there is considerable variation among individuals with regards to the number of vesicles, the maximum intensity of coloration of the sexual skin and the maximum vesicular tumescence. In order to better quantify these data, photographs of each female during the different phases of the cycle were obtained. This allowed a comparison of the varying attributes between individuals, as well as an overall picture of the characteristic pattern of cyclic changes that take place during the menstrual cycle.

In addition to monitoring each individual's sexual skin changes, I also monitored the synchrony or asynchrony of cycles among the females within each reproductive unit in order to assess the social and reproductive strategies among females (U. Mori, 1979a; Dunbar, 1980b, 1984).

3.5. Physiological Sampling Techniques

The hormonal data were obtained from the analysis of urine samples from individual females. The results of the hormonal analysis and behavioral observations allow correlations of social behavior and reproductive physiology to be made.

3.5.1. Procedures for the Collection of Urine Samples

Urine samples were obtained in the morning (0800 - 1000 h) when individuals had access to perches, with collection trays attached, in their outdoor holding areas. During preliminary observations, it was discovered that the animals regularly used particular perches and that early morning voids could be obtained readily at this time. Consequently, several different collection trays were designed in order to determine the one that would accurately yield uncontaminated samples. After a trial basis, the most efficient design was chosen and trays were then built for the remaining perches. Immediately after, I began practicing the method of collecting samples in order to establish the routine involved and the amount of time this daily procedure would entail.

Urine samples were collected six days a week from all females. Urine samples from the males (N=4) were also collected, but are not included in this study and will be assayed at a later date. Since some females were more difficult than others to obtain samples from, urine collection had to be conducted on a frequent basis. On average, I obtained samples from each female every 1-3 days. At 0800 hours the animals were put into the outside holding areas with urine collection trays attached. At 1000 hours they are then let out into the exhibit area, at which time I would enter the holding area to collect the urine from the urine trays. Most females voided urine within the first hour they were

in the holding area, in which case they would be let out into the exhibit soon afterwards in order to expedite the collection process. The total time elapsed from when the urine was voided to when the sample was put in the freezer was not less than 1 and not greater than 2 hours.

Following collection, urine samples were spun on a tabletop centrifuge at 1000 rpm for three minutes to eliminate any obvious contaminants, such as, dust dirt and food. Each sample was then separated into duplicate aliquots of 3-5 ml in polypropylene vials and stored at -25°C until assayed.

3.5.2. Procedures for the Steroid Hormone Assays

Urinary hormone values were determined by enzyme-linked immunoassays and expressed as per creatinine concentration. Hormone concentration levels for individual females were used to:

(1) accurately assess each female's reproductive condition;

(2) determine relative levels of stress hormones (cortisol) between females; and

(3) correlate these data with observations on social behavior.

To investigate whether ovarian suppression contributed to the reproductive impairment of low-ranking gelada baboon females, I monitored ovarian activity across the menstrual cycles of 16 females by measuring excreted urinary pregnanediol glucuronide. Pregnanediol glucuronide is a prevalent urinary metabolite of progesterone excreted in Old World primates, including the gelada baboon (Spies and Chappel, 1984; Yen and Lein, 1984). The measurement of excreted levels of pregnanediol glucuronide in samples of urine is a reliable method for detecting hormone concentration provided the sample is corrected for variable fluid intake and output. Unlike circulating levels of hormones in samples of blood, which yield direct measurements, the use of urine

sampling provides excreted levels. Consequently, determination of the hormone level in urine samples from individuals can be influenced by the amount of fluid present in the excreted sample. The concentration of a sample can be determined by obtaining a creatinine value for each sample being measured (Klopper, 1976). Once a creatinine value is derived, it is factored into the pregnanediol glucuronide value, which yields a more accurate measurement of the hormone in question.

In order to determine whether low-ranking females that received high rates of social stress (i.e., harassment) experienced physiological stress as well, cortisol levels were measured in each female for every urine sample obtained. Cortisol, a glucocorticoid, is commonly secreted during times of stress and is known to have an adverse effect on gonadal functioning. And in studies on mouse lemurs (*Microcebus murinus*: Perret, 1986), talapoin monkeys (*Miopithecus talapoin*: Keverne *et al.*, 1982, 1984), and long-tailed macaques (*Macaca fascicularis*: Kaplan *et al.*, 1986) increased cortisol levels have been implicated as the causative factor impairing ovarian function.

Pregnanediol glucuronide (PdG) and cortisol (F) levels in samples of gelada baboon urine were measured by using enzyme-linked immunoassays (ELISA) validated for use in the gelada baboon at the Wisconsin Regional Primate Research Center. The ELISA is a widely used technique for the determination of the level of biological substances in unknown samples. In this method, a steroid hormone to which an enzyme has been linked competes with the steroid hormone to be measured for the sites of an antibody coated to a solid surface. After separating the free steroid hormone by washing the solid surface, a substrate is used to measure the bound enzyme conjugate and thus the amount of steroid hormone.

3.5.2.a. Creatinine Assay

To control for variable fluid intake and output, hormone concentrations in the urine were indexed by the creatinine concentration of each sample (Klopper, 1976). The creatinine concentration was measured in duplicate by an assay validated for the cotton-top tamarin (French, 1983) and modified for use in the gelada baboon. Urine (6.3 μl) was diluted in 500 μl H_2O in micro tubes to make a 1:80 dilution. Equal parts of picric acid (.04 M) and sodium hydroxide (.75 M) were mixed and 100 μl of the Picric Acid:NaOH solution was added to 200 μl diluted urine sample in microtiter plates. The optical density at 500 nm was read 15 minutes later on a Dynatech MR-5000 microtiter plate reader with a Mac SE/30 as the communication and capture device. A creatinine standard curve (Sigma, St. Louis, MO) with 8 points (0 - 1.5 mg/ml) was assayed in triplicate with each microtiter plate of unknown duplicate samples (N=32 (samples per plate)). Intra-assay variability was measured by repeated assays of a gelada baboon urine pool at two concentrations. The coefficient of variation was 3.21% for the low concentration pool and 3.02% for the high concentration pool (N=36). Inter-assay variability was measured by the repeated assay of two gelada baboon pools in successive assays. The coefficient of variation was 4.21% for the low concentration pool and 4.44% for the high concentration pool (N=36 assays).

3.5.2.b. Pregnanediol Glucuronide Assay and Validation

Pregnanediol Glucuronide Assay

Ovarian cyclicity in female gelada baboons was determined by the measurement of excreted levels of pregnanediol glucuronide, a common urinary metabolite of progesterone in Old World primates (Spies and Chappel, 1984; Hodges, 1987; Johnson and Everitt, 1988). Excreted levels of PdG were determined by an ELISA modified for use in the gelada baboon at the Wisconsin Regional Primate Research Center, from that described from Munro and Stabenfeldt (1984). Samples of urine (10.42 μl) were mixed with EIA-Buffer (250 μl) to make a 1:25 dilution. Then, 400 μl enzyme label, pregnanediol glucuronide:horseradish peroxidase (PdG:HRP) conjugate (provided by G. Stabenfeld, University of California, Davis) diluted 1:240,000 in EIA-Buffer was added to 100 μl of the diluted urine. 96-well flat bottom microtiter plates (Nunc-Immuno Plate, Maxisorb, F96 certified, VWR Scientific, Chicago, IL) coated with 200 μl antibody (G. Stabenfeld) diluted 1:40,000 in 50 mM bicarbonate buffer, pH 9.6 for 6 hours at room temperature and for 2 days at 4°C before storing at -20°C with EIA-Buffer were brought to room temperature and 200μl of the PdG:HRP-sample mixture was added to duplicate wells. A PdG standard curve (Sigma) (range:10 to 3162 pg, N=6), prepared in 150 μl phosphate buffered saline (0.1 M, pH 7.0) with 0.1% bovine serum albumin (PBS:BSA), together with two gelada baboon urine pools to serve as quality controls were included in duplicate on each plate. After a 2 hour incubation in a humidity chamber at room temperature, the plates were washed five times with 0.15 M NaCl, containing 0.05% Tween 20 to remove the unbound sample/conjugate using an automated plate washer (UltraWash II, Dynatech). The plates were then rapped dry to rid of excess wash solution and 200 μl

freshly prepared ABTS substrate solution [25 ml 0.05 M Citrate Buffer (pH 4.0), 80 μl 0.5 M H_2O_2 and 250 μl 40 mM 2,2'-azino-bis (3-ethylbenzthiazoline-6-sulfonic acid)] was added to each well. The plates were placed in the humidity chamber again for a 20-30 minute incubation period, at which time 50 μl of a Stop solution (15 ml 0.15 hydrofluoric acid containing 6.0 mM NaOH and 30 μl EDTA) was aliquoted to each well to stop the reaction. The optical density readings at 410 nm were then determined by the Dynatech MR5000 plate reader with MAC data uptake.

Assay Validation

The biological validity of the pregnanediol glucuronide assay was assessed by tests of parallelism and accuracy. The test of parallelism used a linear regression-parallel-line biological assay (after Brownlee, 1960) and was done by measuring, in triplicate, serial dilutions of a gelada baboon urine pool (1:8 to 1:256, N=6) from a female in the follicular and luteal phase of the ovarian cycle and comparing the slope of the resulting binding inhibition curve with the slope of the standard curve. Slope tests revealed that neither of the slopes for serial dilutions of urine were significantly different from the slope of the standard curve (t for difference in slopes = 1.59 for 41 df; $p>0.05$) (Figure 3.2). To test for accuracy, a gelada baboon urine pool was added to a second standard curve, in quadruplicate, including the $B_{\emptyset}$s as controls. The resulting assay values compared to the expected values yielded a 104.4 $\pm$ 1.85% (s.e.) recovery (Table 3.6).

The antibody (R1126) was raised in rabbit against pregnanediol glucuronide:bovine serum albuin. The sensitivity of the assay at 90% binding is 20.6 pg and the cross-reaction of other steroids with this antibody is given in

Table 3.7. As is seen in Table 3.7, there is a high cross-reactivity of the antisera with hydroxy-progesterone. Whether the pregnanediol glucuronide levels measured by the EIA used in this study reflect measurements of hydroxy-progesterone as well awaits confirmation by high pressure liquid chromatography (HPLC) analysis.

Intra-assay variability (Rodbard, 1974) was measured by repeated assays of a gelada baboon urine pool at two concentrations (65% and 29% binding). The coefficient of variation was 4.31% for the low concentration pool and 3.38% for the high concentration pool (N=44). Inter-assay variability was measured by the repeated assay of two gelada baboon pools in successive assays. The coefficient of variation was 8.69% for the low concentration pool and 6.41% for the high concentration pool (N=44 assays).

FIGURE 3.2 DISPLACEMENT OF PREGNANEDIOL GLUCURONIDE IN GELADA BABOON URINE

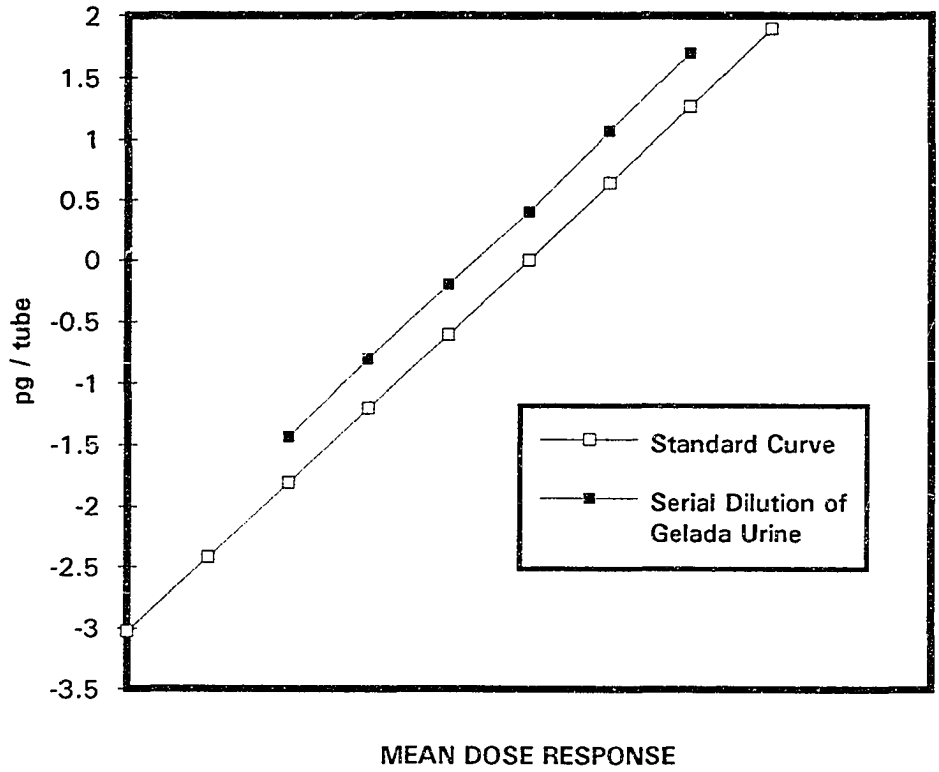


TABLE 3.6. Recovery of Pregnanediol Glucuronide (PdG) in Gelada Baboon Urine

GELADA URINE: CONTROL	PLUS PdG STANDARD	EXPECTED VALUES	PdG ASSAY VALUES	PERCENT OF EXPECTED	AVERAGE PERCENT
136.9	18.9	158.1	163.7	103.5	
144.4	18.9	158.1	153.2	96.9	
143.4	18.9	158.1	169.7	107.3	
132.4	18.9	158.1	167.5	105.9	103.4
136.9	43.1	182.4	174.3	95.6	
144.4	43.1	182.4	182.5	100.1	
143.4	43.1	182.4	183.7	100.7	
132.4	43.1	182.4	191.8	105.2	100.4
136.9	80.6	219.9	223.3	101.6	
144.4	80.6	219.9	219.6	99.9	
143.4	80.6	219.9	223.3	101.6	
132.4	80.6	219.9	228.6	104.0	101.7
136.9	153.5	292.8	319.4	109.1	
144.4	153.5	292.8	306.2	104.6	
143.4	153.5	292.8	302.0	103.2	
132.4	153.5	292.8	320.5	109.5	106.6
136.9	306.8	446.1	481.0	107.8	
144.4	306.8	446.1	467.8	104.9	
143.4	306.8	446.1	449.9	100.9	
132.4	306.8	446.1	466.0	104.5	104.5
136.9	619.3	758.6	798.9	105.3	
144.4	619.3	758.6	775.6	102.2	
143.4	619.3	758.6	791.0	104.3	
132.4	619.3	758.6	783.2	103.2	103.8
136.9	1194.4	1333.7	1494.2	112.0	
144.4	1194.4	1333.7	1505.0	112.8	
143.4	1194.4	1333.7	1473.0	110.4	
132.4	1194.4	1333.7	1452.0	108.9	111.1
136.9	2554.1	2693.4	2963.2	110.0	
144.4	2554.1	2693.4	2895.6	107.5	
143.4	2554.1	2693.4	2768.2	102.8	
132.4	2554.1	2693.4	2737.9	101.7	105.5
136.9	5627.3	5766.5	6153.4	106.7	
144.4	5627.3	5766.5	6282.6	108.9	
143.4	5627.3	5766.5	5573.3	96.6	
132.4	5627.3	5766.5	5681.2	98.5	102.7
MEAN = 139.3				MEAN =	104.4
				S.E. =	1.04

TABLE 3.7. Specificity of Pregnanediol Glucuronide Antibody (R1126)

STEROID	% CROSS REACTION*
Cortisol	000.001
Estradiol-3-glucuronide	000.006
Estrone-3-glucuronide	000.007
Pregnenalone	000.070
11a Hydroxy-progesterone	000.126
17a Hydroxy-progesterone	000.302
Androstinedione	000.531
Testosterone	000.626
Estrone-3-sulfate	000.800
5B Pregnanetriol	000.811
Progesterone	003.104
5B Pregnanedione	004.210
20B Hydroxy-progesterone	013.542
5B Pregnanediol	027.460
20a Hydroxy-progesterone	157.500

* 50% inhibition point of dose-response curve

3.5.2.c. Cortisol Assay and Validation

Cortisol Assay

Direct measurements of gelada baboon urinary cortisol concentrations were made, without extraction, using a heterologous enzyme immunoassay modified from that described by Munro and Stabenfeldt (1984). Briefly, 96-well, flat-bottom polystyrene microtiter plates (Nunc-Immuno Plate Maxisorb F96 certified, VWR Scientific, Chicago, IL) were coated with 100 μl cortisol antibody (provided by G. Stabenfeldt, University of California, Davis) diluted 1:22,000 with coating buffer (50 mM bicarbonate buffer, pH 9.6). The antibody coating of plate wells continued for 6 hours at room temperature and for 2 days at 4°C. The excess antibody was decanted off, and 150 μl phosphate buffered saline (0.1 M, pH 7.0) with 0.1% bovine serum albumin (PBS-BSA) was added to each well prior to storage at -15°C for up to 3 months. Before application of the samples, the plates were brought to room temperature in a humidified chamber for a minimum of 2 hours. Samples were prepared by adding 10.1 μl gelada baboon urine to 1000 μl PBS-BSA resulting in a 1:100 urine dilution. A cortisol standard curve (range: 2.5 to 500 pg, N=8) prepared in PBS-BSA was included on each plate. Diluted sample and standards (50 μl) were added to 250 μl enzyme label, cortisol-horseradish peroxidase conjugate (provided by G. Stabenfeldt) diluted 1:62,500 with PBS-BSA. This sample-conjugate mixture was prepared in 1.2 ml banded micro-tubes, allowing samples to be transferred to the microtiter plate using a 12-channel pipette. The plate was emptied of PBS-BSA, and 100 μl of the sample:conjugate mixture was added to duplicate wells. The plate was then returned to the humidified chamber for 2 h and subsequently washed five times with 0.15 M NaCl, containing 0.05% Tween 20, to remove the unbound sample:conjugate using an automated plate washer.

Immediately after washing, 100 μl freshly prepared ABTS substrate [250 μl 40 mM 2,2'-azino-bis (3-ethylbenzthiazoline-6-sulfonic acid) and 80 μl 0.5M H_2O_2 added to 24.67 ml 0.05 M citrate (pH 4.0)] was added to each well. The plate was incubated in the humidified chamber for 1 hour before the reaction was stopped with 100 μl/well stopping reagent (25 ml 0.15 hydrofluoric acid containing 6.0 mM NaOH and 50 μl 1.0 M EDTA). Absorbence was measured at 410 nm on a Dynatec MR 5000 microelisa plate reader.

Assay Validation

The biological validity of the cortisol assay was assessed by tests of parallelism and accuracy. The test of parallelism used a linear regression-parallel-line biological assay (after Brownlee, 1960). Serial dilutions of a gelada baboon urine pool (1:100 to 1:64,000, N=7) with PBS:BSA, in triplicate, gave a displacement curve parallel to that obtained with cortisol standards (Sigma, St.. Louis, MO). Slope tests revealed that neither of the slopes for serial dilutions of urine were significantly different from the slope of the standard curve (t for difference in slopes = -1.32 for 28 df; $p>0.05$) (Figure 3.3). In the test for accuracy, the mean ± s.e. recovery of cortisol standards, including the $B_{ø}$s as controls, added to 5 μl gelada baboon urine pool with low concentration was 106 ± 1.6% recovery (Table 3.8).

The antibody (R4866) was raised in rabbit against cortisol:BSA and the cross-reactivity of other steroids with this antibody is given in Table 3.9. Whether the cortisol levels measured by the EIA used in this study reflect measurements of cortisone as well awaits confirmation by high pressure liquid chromatography (HPLC) analysis.

The sensitivity of the assay at 90% binding is 4.3 pg. The intra- and inter-assay coefficients of variation (Rodbard, 1974) of a gelada baboon urine pool (52% binding) assayed in duplicate on each plate were 6.65% and 11.71% (N=50), respectively, and for a second pool (24% binding) were 6.92% and 10.66%, respectively (N=48).

FIGURE 3.3 DISPLACEMENT OF CORTISOL (F) IN GELADA BABOON URINE

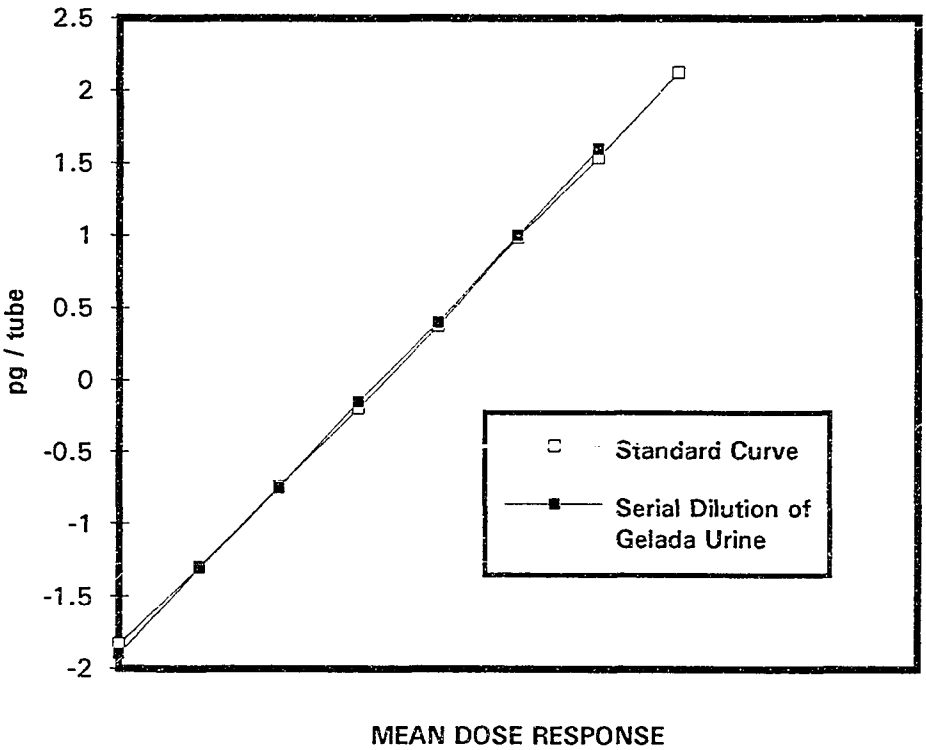


TABLE 3.8. Recovery of Cortisol (F) in Gelada Baboon Urine

GELADA URINE: CONTROL	PLUS F STANDARD	EXPECTED VALUES	F ASSAY VALUES	PERCENT OF EXPECTED	AVERAGE PERCENT
36.01	3.90625	44.30	50.19	113.29	
36.01	3.90625	44.30	46.84	105.73	109.51
42.78	7.81250	48.21	51.54	106.91	
40.12	7.81250	48.21	50.16	104.05	105.48
42.56	15.62500	56.02	62.40	111.39	
44.89	15.62500	56.02	61.74	110.21	110.80
	31.25000	71.65	73.29	102.30	
	31.25000	71.65	67.97	94.87	98.58
	62.50000	102.90	105.05	102.09	
	62.50000	102.90	113.24	110.05	106.07
	125.00000	165.40	184.32	111.44	
	125.00000	165.40	175.85	106.32	108.88
	250.00000	290.40	285.45	98.30	
	250.00000	290.40	310.33	106.86	102.58
MEAN = 40.40				MEAN =	105.99
				S.E. =	1.62

TABLE 3.9. Specificity of Cortisol Antibody (R4866)

STEROID	% CROSS REACTION*
Cholesterol	00.000
Estradiol	00.000
Dihydroandrosterone	00.000
20a Hydroxy-progesterone	00.000
17a Hydroxy-pregnenolone	00.001
11a Hydroxy-progesterone	00.006
Testosterone	00.013
20B Hydroxy-progesterone	00.014
Progesterone	00.050
Aldosterone	00.090
11B Hydroxy-progesterone	00.200
17a Hydroxy-progesterone	00.263
Deoxycorticosterone	00.800
Corticosterone	02.500
Cortisone	60.001
Prednisone	66.001
Prednisolone	96.001

* 50% inhibition point of donse-response curve

3.6. Statistical Analyses

The statistical program "SYSTAT" was used to perform Student t-tests and calculate t values based on the degrees of freedom for any pair of values. All t-tests for both independent and dependent samples were two-tailed, unless otherwise noted. A significance level of 0.05 was adopted throughout the analyses. It is important to note that with a critical level of significance set at 0.05, the probability of rejecting the null hypothesis (H_0) when it is in fact true is less than one in twenty. Scoring a 'false positive' by incorrectly rejecting a true null hypothesis is referred to as a Type I, or Alpha, error. However, reducing the acceptance level of significance increases the likelihood of scoring a 'false negative' by accepting a false null hypothesis, called a Type II, or Beta, error (Sokal and Rohlf, 1981). The likelihood of committing a Type I error in the present study, where numerous t-tests were applied for data analysis, is proportional to the number of tests performed.

Analysis of variance (ANOVA) were also conducted to determine differences between means and computed by the "SYSTAT" program and based on the degrees of freedom provided by this program. Significant associations between two variables were determined by employing the Spearman Rank Correlation Coefficient (r_S).

CHAPTER 4. FEMALE REPRODUCTIVE CYCLES IN THE STUDY POPULATION

4.1. The Female Primate Reproductive Cycle and Estrus Behavior

Studies of primate behavior and reproductive biology have shown that many catarrhines are unique in not exhibiting the traditional mammalian pattern of strictly circumscribed periods of estrus (Hrdy and Whitten, 1987). In these catarrhines, the reproductive cycle is distinct in that it includes menstruation, the periodic sloughing of the uterine lining, and an extended period of estrus with considerable flexibility in the timing of receptivity. While all female primates show a tendency to increase mating activity at midcycle, in several catarrhine species sexual receptivity throughout all or much of the cycle is not uncommon. For these reasons many primatologists have broadened the use of the term *'estrus'* to not only imply the specific physiological events associated with ovulation, but also employ the term in a behavioral sense measured by female proceptive and receptive behaviors which may indeed occur beyond the specific time of ovulation (Keverne, 1981; Loy, 1987; Nadler, 1994).

Interest in the reproductive endocrinology of Old World monkeys has increased in recent years. In numerous field studies, data obtained from observations of estrus behaviors have been used to define the reproductive cycle and assess reproductive strategies among both males and females. However, such observational data are insufficient on their own to provide a complete understanding of the factors influencing the reproductive physiology of a species.

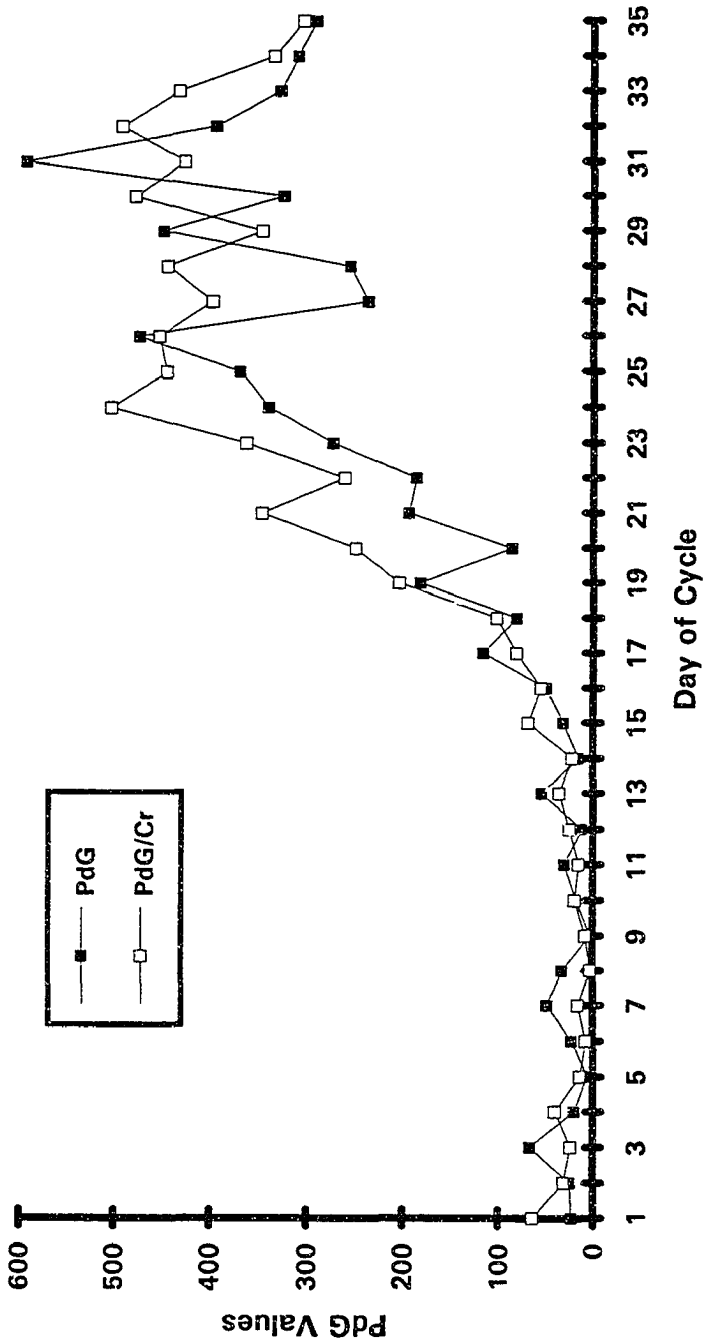
Such an understanding requires other kinds of data, such as the endocrinological data collected in this study.

4.2. The Menstrual Cycle

Ovulation occurs when the egg erupts from the mature follicle, marking the transition from the follicular to the luteal phase of the menstrual cycle. Upon its release, the ovarian follicle is transformed into a solid body, the corpus luteum. The formation of a corpus luteum spurs a sudden and rapid increase in the release of progesterone which prepares the uterus for fertilization. Therefore, a dramatic rise in the concentration of progesterone in the luteal phase of the cycle is indicative of an ovulatory cycle.

Ovarian cyclicity in the study group females was determined by reference to sustained elevations in pregnanediol glucuronide (PdG), an elevation being defined as the sudden rapid rise and subsequent maintenance of PdG concentrations corresponding to the luteal phase of the cycle, followed by a gradual decline in PdG levels falling to basal levels at the onset of menses. Figure 4.1 presents pregnanediol glucuronide concentrations in a study group female before and after adjusting for variable fluid intake and output. The data illustrate that elevations in pregnanediol glucuronide concentrations are primarily due to increases in excreted PdG rather than due to changes in creatinine metabolism and excretion. Levels of creatinine excretion are similar for both elevated and nadir samples, but there is a 10 fold increase in levels of pregnanediol glucuronide excretion on elevated days over nadir day samples (paired t-test: $t = 4.091$, $df = 15$, $p < 0.001$). In addition, while creatinine concentrations between females tended to vary, concentrations for each

FIGURE 4.1. A Comparison of Pregnanediol Glucuronide Values Before and After Applying Creatinine Values



individual remained relatively consistent throughout each cycle.

Table 4.1 illustrates the variability in excreted pregnanediol glucuronide levels across females, with mean peak values for individuals ranging from 330.8 to 407.5 ng/mg Cr with a mean ($\pm$ s.e.) of 369.3 $\pm$ 2.4, and nadir values ranging from 14.6 to 24.8 ng/mg Cr (mean = 19.3 $\pm$ 0.3). Representative cycles from 3 females (during Phase I of study) of similar age are presented in Figure 4.2. for a comparison of the pattern of pregnanediol glucuronide excretion between females.

The menstrual cycle was defined as the first day of menses (Me1) until the day before the next onset of menses. Menses was visually identified in the samples of urine or in some cases in small traces on the perineum. Menstrual cycles ranged from 27 to 83 days with a mean ($\pm$ s.e.) of 37.3 $\pm$ 6.1 days (Table 4.2). The excretion of pregnanediol glucuronide during the menstrual cycle is characterized by a nadir of 14.4 days beginning with the onslaught of menses and ending just prior to the first rapid increase in pregnanediol glucuronide levels. The rise in pregnanediol glucuronide occurs on average between day 15 and 23 of the cycle. After the initial increase beyond basal values, PdG concentrations continue to rise rapidly and plateau at levels ranging from 217.7 to 369.3 ng/mg Cr where they are maintained for the duration of the cycle. Figure 4.3 represents the characteristic pattern of pregnanediol glucuronide excretion based on a composite of mean values of 44 cycles from 10 females.

TABLE 4.1. Mean (± s.e.) Nadir and Peak Urinary Pregnanediol Glucuronide Concentrations in Study Group Females

Female ID #	Nadir PdG (ng/mg Cr) Values	Peak PdG (ng/mg Cr) Values	No. of Cycles Measured
11	16.8 ± 1.7	366.1 ± 12.8	12
12	21.2 ± 2.1	351.0 ± 9.3	15
13	18.9 ± 2.2	370.9 ± 11.9	15
14	24.8 ± 1.8	406.7 ± 13.6	15
15	18.1 ± 1.0	396.9 ± 10.4	15
16	22.2 ± 1.3	351.4 ± 7.7	13
17	20.4 ± .6	345.8 ± 9.5	15
18	19.7 ± 1.6	398.5 ± 12.4	13
62	17.5 ± 1.9	389.4 ± 10.9	6
63	18.3 ± 2.3	377.6 ± 7.6	14
64	24.8 ± 2.7	327.2 ± 14.3	14
65	14.6 ± .9	407.5 ± 8.9	15
66	21.9 ± 2.8	330.1 ± 11.4	6
67	16.7 ± 1.4	343.8 ± 9.7	15
87	17.4 ± 1.7	359.1 ± 6.2	12
88	14.7 ± 2.5	384.3 ± 8.8	12
N = 16	Total Mean ± s.e. 19.3 ± .3	Total Mean ± s.e. 369.3 ± 2.4	Mean ± s.d. 12.9 ± 2.9

Nadir and Peak Values are based on PdG values over the menstrual cycle excluding the "peri-ovulatory" period (4 days prior to and after Pdg values rise above 60 ng/mg Cr).

Nadir Values = Values from the first day of menses until 4 days prior to rise in PdG levels above 60 ng/mg Cr.

Peak Values = Values from 4 days after rise in PdG levels above 60 ng/mg Cr to the day before the first day of menses.

FIGURE 4.2. Representative Pregnanediol Glucuronide Cycles in Three Adult Females

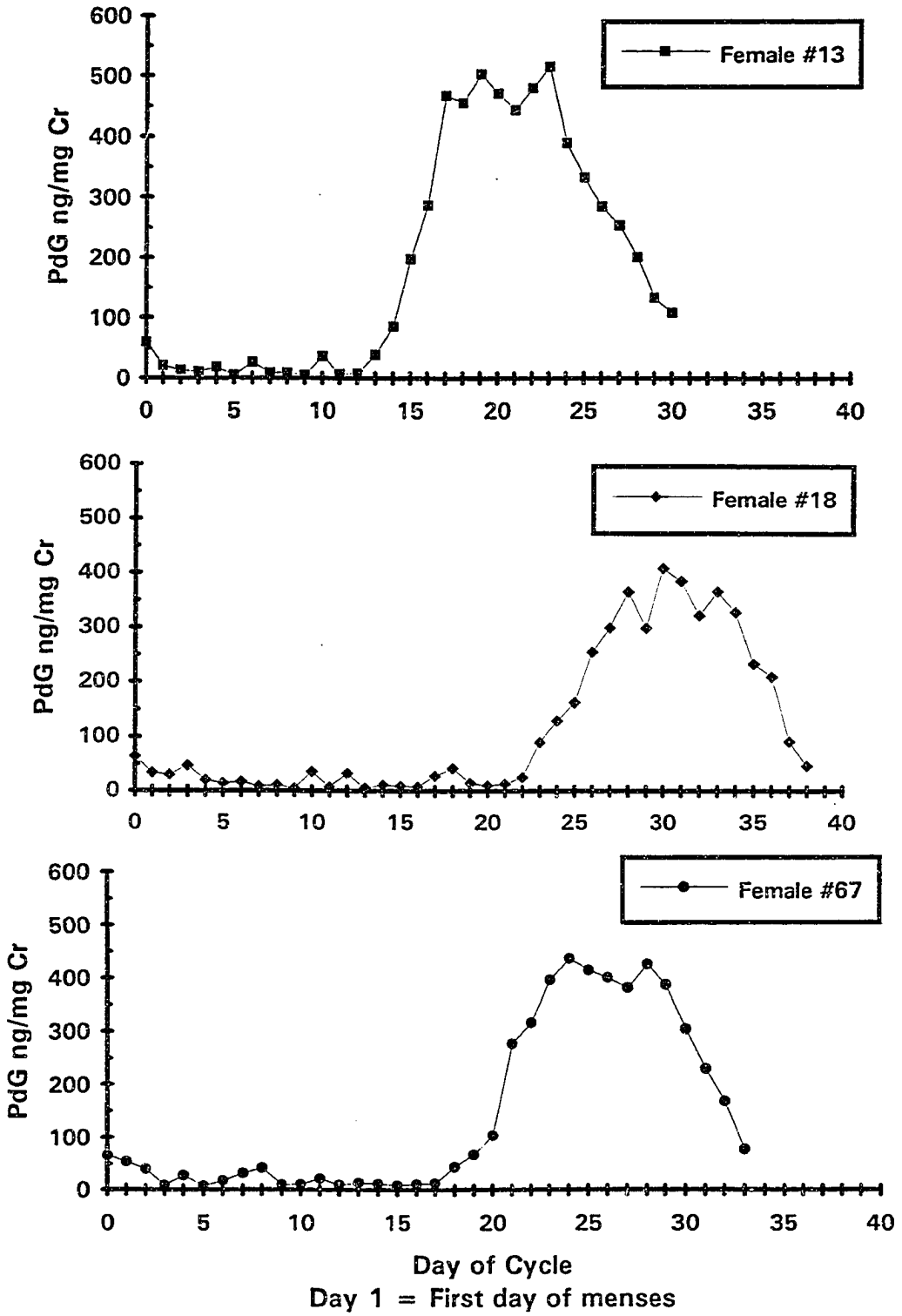
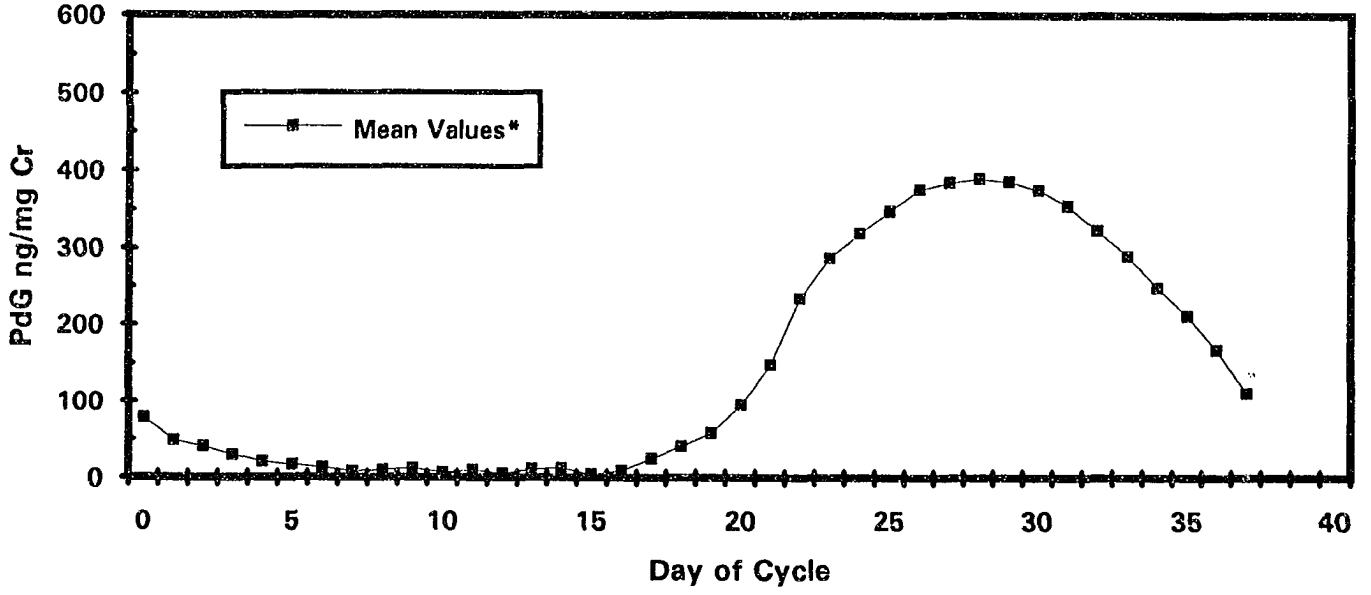


TABLE 4.2. Menstrual Cycle Length of Study Group Females via Urinary Pregnanediol Glucuronide (PdG) Measurements

Female ID #	Menstrual Cycle Range (Days)	Menstrual Cycle Length (Mean ± s.e.)	No. of Cycles Measured
11	29 - 34	31.2 ± 1.5	12
12	33 - 59	42.7 ± 9.3	15
13	27 - 32	29.4 ± 1.9	15
14	29 - 44	35.6 ± 0.9	15
15	35 - 63	39.6 ± 4.1	15
16	34 - 71	41.3 ± 6.2	13
17	30 - 57	34.3 ± 2.1	15
18	34 - 56	42.1 ± 7.3	13
62	29 - 33	32.1 ± 1.4	6
63	33 - 61	36.2 ± 3.7	14
64	39 - 67	45.3 ± 5.9	14
65	36 - 83	38.9 ± 7.4	15
66	37 - 68	44.5 ± 9.1	6
67	27 - 31	28.9 ± 1.6	15
87	33 - 77	39.6 ± 8.7	12
88	31 - 45	38.5 ± 5.1	12
N = 16	Total Range 27 - 83	Total Mean ± s.e. 37.3 ± 6.1	Mean ± s.d. 12.9 ± 2.9

FIGURE 4.3. The Mean Pattern of Progestagen Cyclicity in Study Group Females



Day 1 = First day of menses
*Values are based on 44 cycles from 10 females

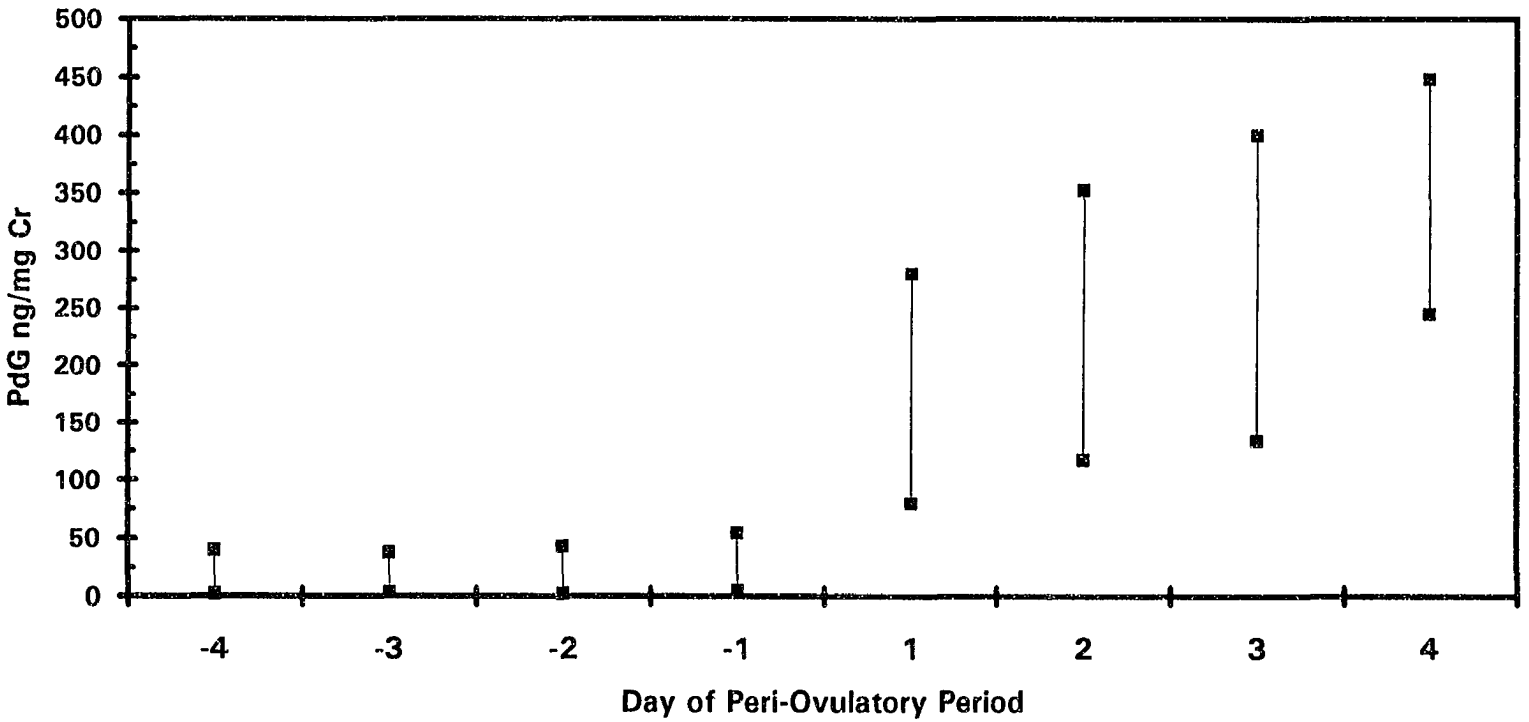
4.2.1. The Peri-Ovulatory Period

In order to accurately determine when ovulation had occurred in my study animals, a peri-ovulatory period had to be defined. It was defined as the period 4 days prior to and 4 days after the first sudden rise in PdG levels (Figure 4.4). This period of the cycle was calculated for every cycle of each female. Subsequently, the PdG levels during this period were analyzed to determine what levels of PdG distinguish the follicular phase, which includes ovulation, from the luteal phase, which begins immediately following ovulation. The maximum PdG values for the 4 days prior and the minimum PdG values for the 4 days after were analyzed in each cycle for every female in order to determine a PdG value that was mutually exclusive of the two sample periods. This analysis resulted in a mean PdG threshold value of 60 ng/mg Cr marking the onset of the luteal phase. The reliability measure for the figure 60 ng/mg Cr was 97.3%. This figure was then used as a baseline to calibrate cycles as a whole. Table 4.3 summarizes data on the PdG levels showing the drastic change in PdG values across the peri-ovulatory period (paired t-test: $t = 4.146$, $df = 15$, $p < 0.001$).

4.2.2. The Follicular Phase

The follicular phase was defined as the first day of menses (Me1) to the day before PdG values rose above 60 ng/mg Creatinine (i.e., the time of ovulation). During the follicular phase mean PdG values were 23.1 ($\pm$ 0.3) ng/mg Cr and nadir values for individual females ranged from 1.9 to 76.1 ng/ mg Cr (Table 4.4) (Note: PdG values exceeding 60 ng/mg Cr were occasionally found at the start of the follicular phase at the onset of menses, which accounts for the PdG values >60 listed in Table 4.4). Follicular phase length averaged 19.4 $\pm$ 0.9 days for individual females and ranged from 12 to 64 days.

FIGURE 4.4. High and Low Pregnanediol Glucuronide Values* Across the Peri-Ovulatory Period of the Menstrual Cycle in Study Group Females



*Data are based on mean PdG values of 207 cycles from 16 females

TABLE 4.3. Mean (± s.e.) Pregnanediol Glucuronide Values Across the Peri-Ovulatory Period of the Menstrual Cycle in Study Group Females

Female ID #	Mean (± s.e.) PdG Values 4 Days Prior 60 ng/mg Cr	Mean (± s.e.) PdG Values 4 Days After 60 ng/mg Cr	No. of Cycles Measured
11	12.0 ± .7	205.9 ± 13.6	12
12	12.4 ± 1.9	164.1 ± 9.7	15
13	11.1 ± 1.3	231.5 ± 12.2	15
14	15.4 ± 1.1	215.8 ± 13.4	15
15	14.1 ± 1.2	244.0 ± 15.9	15
16	13.3 ± 1.4	171.9 ± 10.6	13
17	8.6 ± .6	188.4 ± 13.8	15
18	22.6 ± 1.7	235.3 ± 12.7	13
62	21.1 ± 2.8	179.2 ± 15.2	6
63	15.7 ± 1.0	197.3 ± 13.4	14
64	26.8 ± 1.7	200.9 ± 13.9	14
65	17.2 ± 1.3	223.7 ± 12.5	15
66	19.9 ± 3.2	218.4 ± 16.7	6
67	14.5 ± 1.2	202.6 ± 14.0	15
87	10.3 ± 3.3	190.8 ± 22.2	12
88	23.4 ± 1.5	239.5 ± 24.5	12
N = 16	Total Mean ± s.e. 16.2 ± .8	Total Mean ± s.e. 204.7 ± 3.4	Mean ± s.d. 12.9 ± 2.9

TABLE 4.4. The Follicular Phase of the Menstrual Cycle
Mean Duration, Range, and Pregnanediol Glucuronide Values

Female ID #	No. of Cycles Measured	Minimum PdG (ng/mg Cr) Value	Maximum PdG (ng/mg Cr) Value	Mean (± s.e.) PdG (ng/mg Cr) Value	Follicular Phase Range (Days)	Mean (± s.e.) Duration (Days)
11	12	3.5	55.6	22.5 ± 1.8	14 - 17	15.1 ± 0.5
12	15	1.9	69.2	26.2 ± 2.0	16 - 41	24.3 ± 2.6
13	15	2.6	71.7	20.7 ± 1.7	12 - 16	14.4 ± 0.4
14	15	5.4	58.5	24.3 ± 0.7	17 - 24	18.5 ± 0.8
15	15	7.9	39.3	28.4 ± 1.8	18 - 45	21.2 ± 3.0
16	13	4.1	47.3	25.5 ± 1.6	16 - 53	23.6 ± 2.0
17	15	6.3	45.5	17.2 ± 2.3	14 - 19	17.1 ± 0.7
18	13	3.9	50.4	21.6 ± 1.1	17 - 38	22.8 ± 3.5
62	6	8.5	44.2	22.5 ± 1.4	13 - 16	14.9 ± 0.2
63	14	2.1	32.7	21.5 ± 1.5	14 - 43	19.4 ± 0.9
64	14	4.3	49.2	18.9 ± 2.0	18 - 39	23.6 ± 1.0
65	15	3.7	59.5	19.3 ± 0.9	16 - 64	21.7 ± 4.8
66	6	2.2	40.6	27.7 ± 2.3	17 - 50	24.9 ± 1.3
67	15	5.9	76.1	27.1 ± 1.6	13 - 16	15.1 ± 0.5
87	12	6.8	67.9	25.8 ± 1.8	14 - 59	20.1 ± 0.9
88	12	5.0	53.3	19.6 ± 1.3	15 - 27	19.7 ± 0.6
N = 16	Mean ± s.d. 12.9 ± 2.9	Mean ± s.e. 4.6 ± .2	Mean ± s.e. 53.8 ± 1.1	Total Mean 23.1 ± .3	Total Range 12 - 64	Total Mean ± s.e. 19.4 ± .9

Follicular Phase = The first day of menses to the day before PdG levels rise above 60 ng/mg Cr.

4.2.3. The Luteal Phase

The luteal phase was defined as the day after PdG values rose above 60 ng/mg creatinine (Cr) to the day before the next menses (Mel). At the onset of the luteal phase, PdG levels increased rapidly and substantially. The average level across the phase was 317.8 (± 3.3) ng/mg Cr and ranged from 68.3 to 585.4 ng/mg Cr (Table 4.5). Peak values were maintained for the duration of the phase; there was an equally rapid decrease at the cessation of the luteal phase. Luteal phase length averaged 17.9 (± 0.4) for individual females and ranged between 14 and 26 days.

4.3. Variation in Patterns of Cyclicity Across Age-Classes

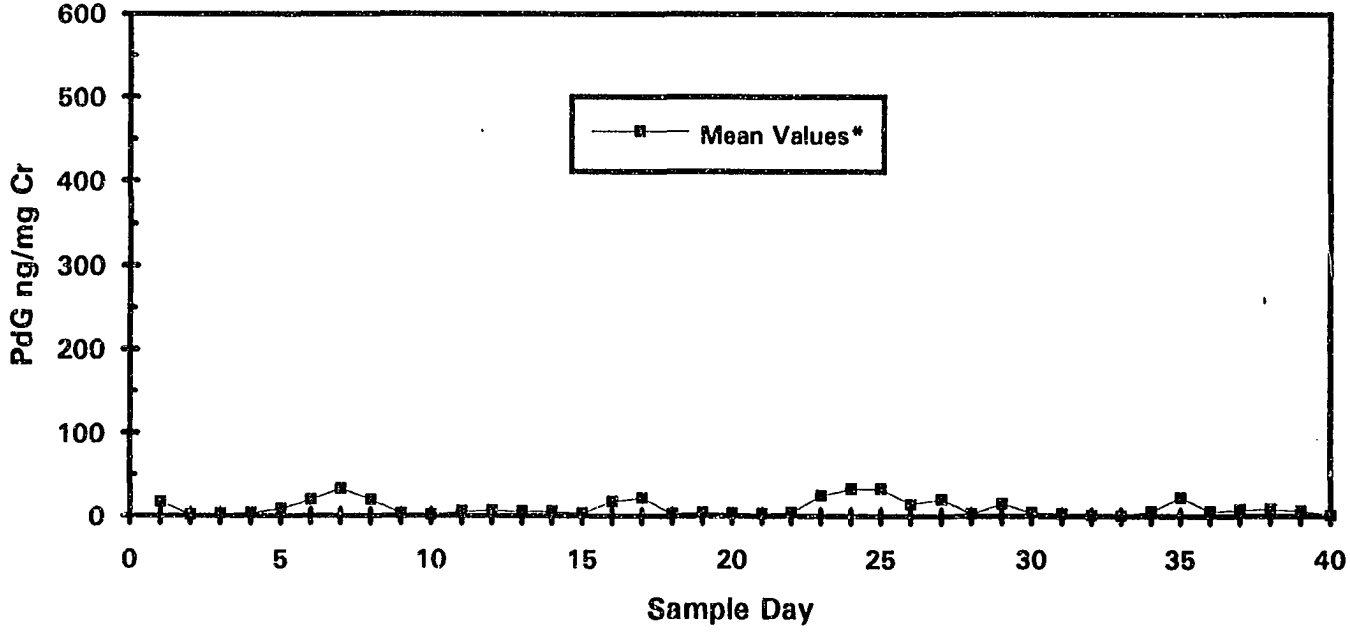
In addition to nutrition, age is a significant factor influencing female reproductive performance. This is evident when comparing the cycles of females from different age-classes: juvenile females, adult females, and old adult females. As in other mammals, the pattern of pregnanediol glucuronide excretion in geladas varies significantly with female age and reproductive condition. For instance, juvenile females do not show a cyclic pattern of hormonal secretion until they reach puberty. Prior to sexual maturation, the pattern of progestagen excretion remains at basal levels and in some cases is barely detectable. Figure 4.5 illustrates the pre-pubertal pattern exhibited in a juvenile female (2 years old) from the present study. There was no cyclic pattern of pregnanediol glucuronide excretion exhibited by this female during this sampling period; a pattern comparable to that of the adult females became apparent when this particular female was approximately 3 years of age.

TABLE 4.5. The Luteal Phase of the Menstrual Cycle
Mean Duration, Range, and Pregnanediol Glucuronide Values

Female ID #	No. of Cycles Measured	Minimum PdG (ng/mg Cr) Value	Maximum PdG (ng/mg Cr) Value	Mean (± s.e.) PdG (ng/mg Cr) Value	Luteal Phase Range (Days)	Mean (± s.e.) Duration (Days)
11	12	86.4	540.9	349.7 ± 13.1	15 - 19	16.1 ± 0.3
12	15	92.6	585.4	332.9 ± 13.3	16 - 21	18.4 ± 1.3
13	15	80.9	408.5	337.3 ± 8.8	14 - 18	16.2 ± 0.9
14	15	76.1	486.6	296.2 ± 11.6	16 - 20	17.1 ± 1.0
15	15	101.9	522.5	379.8 ± 14.6	15 - 26	18.4 ± 0.3
16	13	105.4	502.2	323.2 ± 13.2	14 - 24	17.7 ± 0.5
17	15	70.6	494.4	294.2 ± 12.8	16 - 19	17.2 ± 0.7
18	13	83.8	489.6	316.2 ± 11.7	15 - 22	19.3 ± 0.8
62	6	79.8	492.3	374.3 ± 8.4	14 - 19	17.2 ± 0.6
63	14	69.2	423.2	306.3 ± 10.9	15 - 18	16.8 ± 1.1
64	14	68.3	371.9	203.6 ± 8.8	15 - 21	19.7 ± 1.3
65	15	102.7	418.7	325.4 ± 14.7	15 - 20	18.2 ± 0.6
66	6	97.2	431.1	217.7 ± 7.9	14 - 19	19.6 ± 0.7
67	15	94.1	442.4	314.7 ± 9.4	15 - 19	14.4 ± 0.9
87	12	88.5	392.8	322.1 ± 8.3	14 - 18	19.5 ± 0.5
88	12	116.6	515.5	356.6 ± 12.9	16 - 23	18.8 ± 0.4
N = 16	Mean ± s.d. 12.9 ± 2.9	Mean ± s.e. 88.4 ± 2.3	Mean ± s.e. 469.8 ± 5.4	Total Mean 317.8 ± 3.3	Total Range 14 - 26	Total Mean ± s.e. 17.9 ± .4

Luteal Phase = The day after PdG levels rise above 60 ng/mg Cr to the day before the next menses.

FIGURE 4.5. Pattern of Progestagen Cyclicity in a Juvenile Female (ID #68)



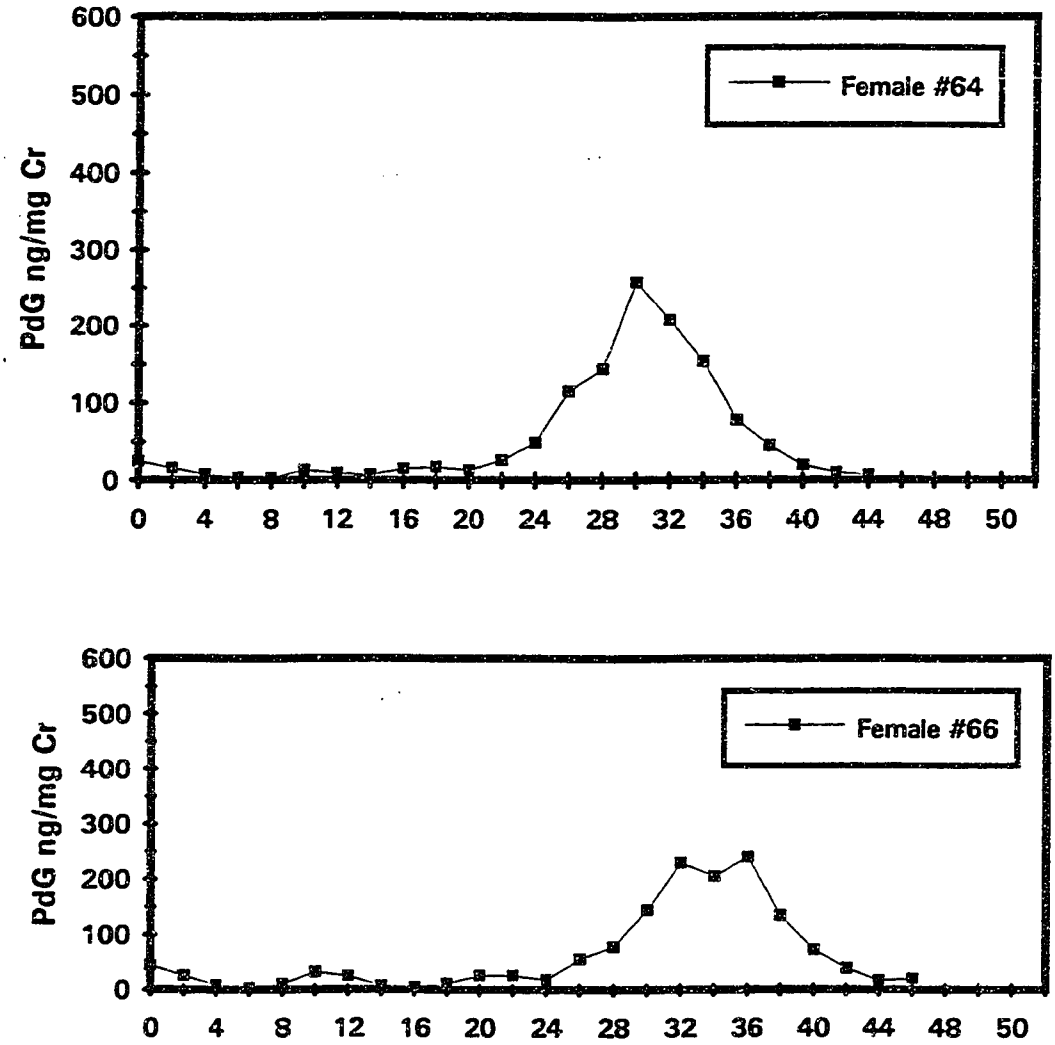
*Values are based on 2 successive sample periods of 40 day duration

In old adult females (> 14 years, N = 2) the menstrual cycle characteristically exhibits an irregularity in the cyclicity of pregnanediol glucuronide excretion. Figure 4.6 illustrates the pattern typically seen in older females in this study population. When these particular females displayed a cyclic pattern in pregnanediol glucuronide, the mean excretion levels during the luteal phase tended to be lower than that of other females (210.6 $\pm$ 8.2) and the duration of their cycles were longer (45.9 $\pm$ 7.6 days compared to 36.8 $\pm$ 4.6 days) ($t = 12.816$, $p<0.05$). Furthermore, these particular females also exhibited a greater number of times in which they did not cycle (24.3 % anovulatory cycles). Anovulation was determined on the basis of a deficient rise and subsequent maintenance of pregnanediol glucuronide levels (<60 ng/mg Cr and less than 2 standard deviations of the mean cycle length for the study group).

4.4. Variation in Patterns of Cyclicity Across Reproductive States

During pregnancy, there is a surge of pregnanediol glucuronide to levels approximately 5 times greater than mean values exhibited during the luteal phase of the menstrual cycle in cycling females (paired t-test: $t = 16.724$, $df = 2$, $p<0.01$) (Table 4.6). Figure 4.7 illustrates the pattern of pregnanediol glucuronide excretion during pregnancy in a sample of females from this study. The data presented are based on pregnancy cycles from 3 individual females. Gestation length in these females ranged from 179 to 184 days, and had a mean ($\pm$ s.e.) of 181.8 $\pm$ 0.4 days (N = 3). The mean was derived from both hormonal monitoring of individual pregnancy cycles and concurrent observations on times of mating. An additional pregnancy that occurred subsequent to the study period revealed a gestation length of approximately 182 days. Gestation in this population, therefore, had an average duration of 6 months.

FIGURE 4.6. Pattern of Pregnanediol Glucuronide Excretion* in Old Adult Females



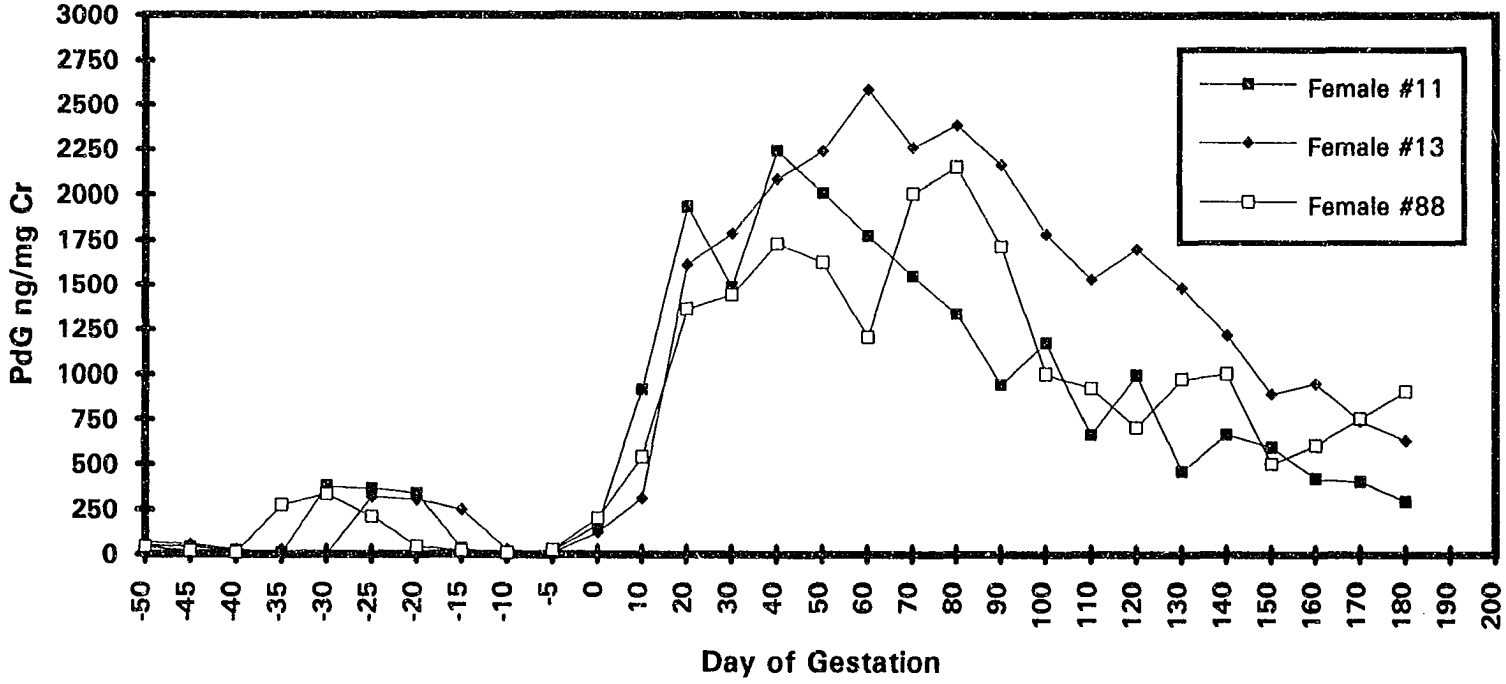
Day 1 = First day of menses

*Mean PdG values over 4 menstrual cycles

TABLE 4.6. A Comparison of Pregnanediol Glucuronide Concentrations in Cycling and Non-Cycling (Pregnant) Females

Female ID #	Reproductive Status	Range PdG (ng/mg Cr) Values	Mean (± s.e.) PdG (ng/mg Cr) Values
11	Cycling	3.5 - 585.4	219.5 ± 56.7
	Pregnant	197.2 - 2317.9	857.1 ± 48.2
13	Cycling	2.6 - 540.9	232.7 ± 60.1
	Pregnant	256.1 - 2893.7	1058.2 ± 61.9
88	Cycling	5.0 - 515.5	267.4 ± 43.2
	Pregnant	212.3 - 2549.6	1176.3 ± 668
		Total Range	Total Mean (± s.e.)
	Cycling	2.6 - 585.4	226.1 ± 9.4
N = 3	Pregnant	197.2 - 2893.7	957.6 ± 36.7

FIGURE 4.7. Pattern of Pregnanediol Glucuronide Excretion During Pregnancy (N = 3)



Day 1 = First day of gestation
Values between Day -50 and -1 represent last menstrual cycles prior to gestation

In addition to the changes in pregnanediol glucuronide excretion, pregnancy is accompanied by noticeable visual changes in the bare skin area of the throat and chest. Displayed in Figure 4.8. are photographs taken of a female two days prior to parturition. The first noticeable change that occurs during gestation is a slight wrinkling in the bare skin of the throat, which becomes apparent in the second month of gestation. In addition, the color of the entire chest patch area is bright red in appearance. These morphological changes occur in the early stages of gestation, prior to any apparent changes in the overall size and shape of the abdominal area of a female. The wrinkling of the throat area and intensity of color of the chest patch both increase progressively throughout the remaining four months of gestation, and by the third month, the increased size of the abdomen is detectable.

FIGURE 4.8. Changes in the Appearance of the Chest Patch During Pregnancy

(a)

(b)

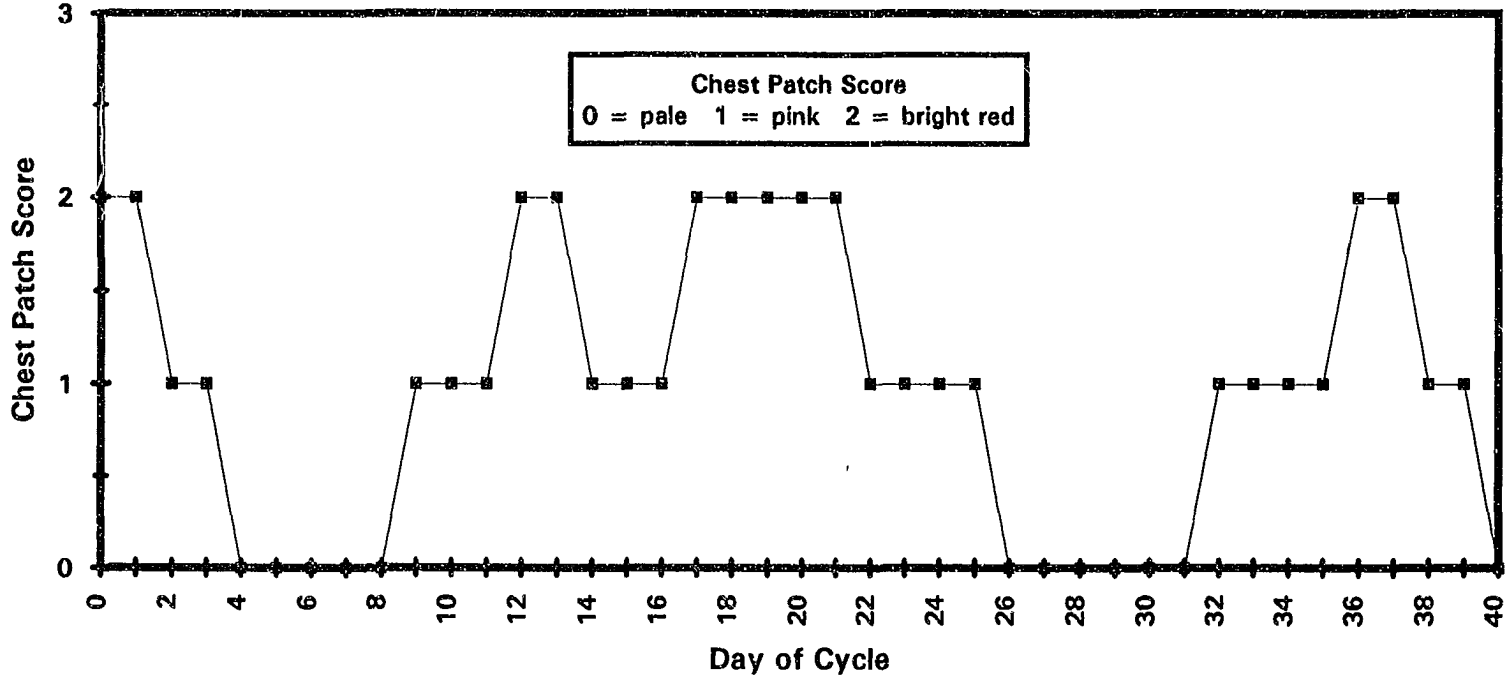
4.5. Behavioral Correlates of the Reproductive Cycle

Behavioral correlates of the reproductive cycle can include olfactory, auditory, behavioral and visual signals. Nonhuman female primates indicate their readiness to mate by combining many of these signalling tactics (reviewed in Hrdy and Whitten, 1987). Like other mammals, male primates use a variety of external cues to monitor the reproductive state of females. Pheromonal secretions, which respond to mid-cycle increases in estrogen, increase a female's attractivity to her mate; vocalizations, such as solicitation calls, increase in frequency during estrus; and distinctive postures, gestures, and presentations of the hindquarters are indications of readiness to mate. Perhaps most dramatic is the external manifestation in female morphology ('sexual skin') in many catarrhine species that occurs in response to hormonal changes that take place during the menstrual cycle. All of these signalling tactics appear to act as external advertisements of a female's internal hormonal condition.

4.5.1. Visual Changes in the Sexual Skin

Among the catarrhines, *Theropithecus* is unique in that an area of skin responding to hormonal changes in the ovarian cycle is located on the chest and throat rather than on the perineal regions. Characteristically, a bare patch of skin on the throat and chest is surrounded by fluid-filled vesicles. In this study, I monitored the changes in coloration of the bare skin areas and the changes in appearance of the vesicles. The aspect of this feature that showed the most marked cyclic changes correlating with the menstrual cycle was not the color of the bare skin but the appearance of the fluid filled vesicles (Figure 4.9). While the chest patch area tended to be bright red in color around the time of ovulation and paler in color around the time of menstruation in some females, in other

FIGURE 4.9. Changes in the Appearance of the Chest Patch Area During the Menstrual Cycle*



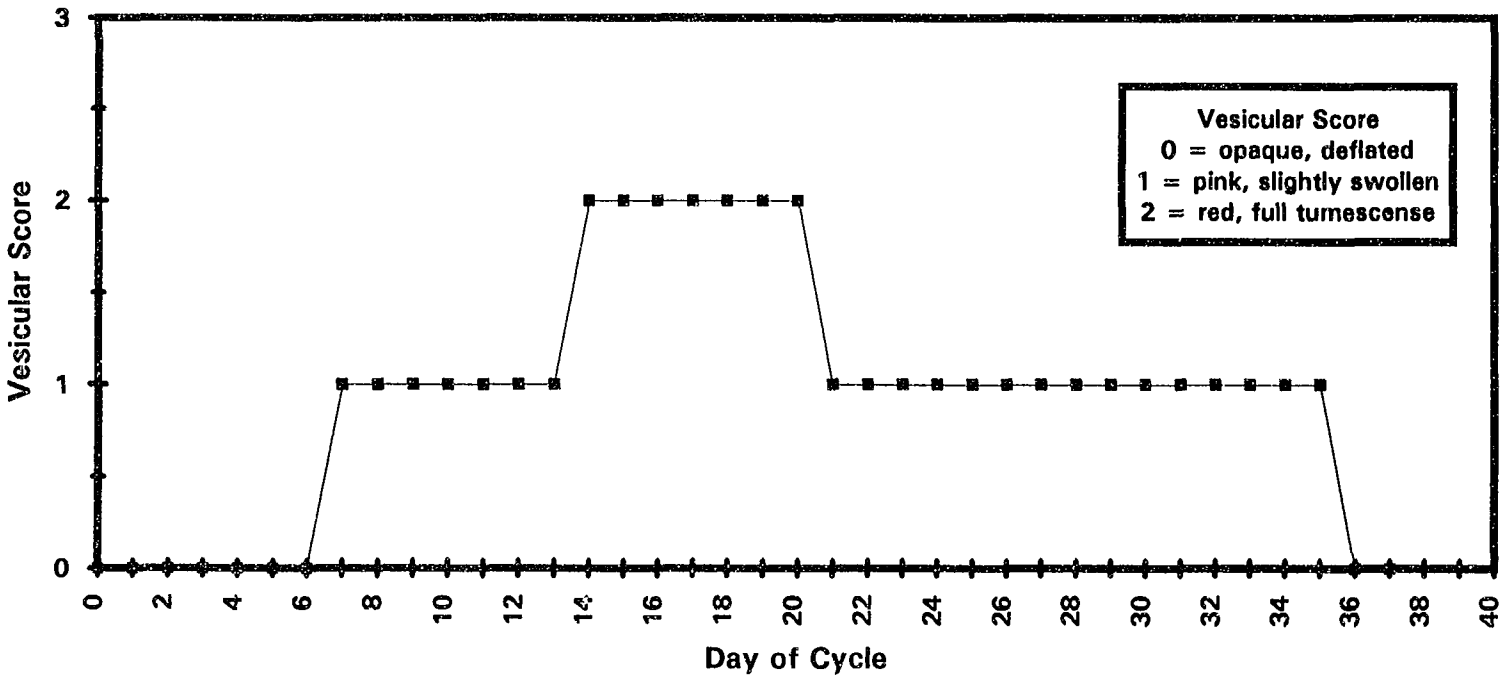
Day 1 = First day of menses

*Data represent mean scores of 207 menstrual cycles from 16 females

females a bright red coloration was also observed just prior to the onset of menstruation. More importantly, chest patch coloration proved to be very sensitive to both the social circumstances and an individual's physical condition. For example, during all agonistic encounters -- beyond low-intensity threat gestures -- chest patch color would invariably intensify greatly to a deep bright red hue. On the contrary, in many cases when an individual experienced physical injury (typically a bite wound), the chest patch color would subsequently fade, turning almost white in color, regardless of the phase of the cycle (87%, N = 39 records). Based on these data, it was decided that the variability in this feature would impede its use as a reliable marker for the monitoring of the menstrual cycle.

The vesicles that border the chest patch proved to be a more reliable marker. Both the color and degree of development of the vesicles increased midway through the menstrual cycle, around the time of ovulation, and decreased in size and lessen in color as menstruation approached (Figure 4.10). Figures 11 and 12 display photographs taken of two of the study group females (a. female ID #18, b. female ID #87) during the different stages of the cycle which illustrate the changes in vesicular morphology. At the start of the follicular phase, when there are visual signs of menstruation, the vesicles surrounding the sexual skin are deflated and opaque in color (Figure 11). Six to ten days later, the vesicles begin to slightly swell and appear pink in color. At the time of ovulation, approximately 14 - 20 days after menstruation, the vesicles intensify in color to a bright red and increase in size to full tumescence (Figure 12). Vesicular changes during the luteal phase begin with the first breakdown of full tumescense and progressively decrease in size and intensity of color until menses commences. Figure 4.13 shows the changes in vesicular morphology

FIGURE 4.10. Changes in Vesicular Morphology During the Menstrual Cycle*



Day 1 = First day of menses

*Data represent mean scores of 207 menstrual cycles from 16 females

FIGURE 4.11. Visual Changes in Vesicular Morphology During the Non-Ovulatory Phase of the Menstrual Cycle

(a) Female ID #18

FIGURE 4.11. continued

(b) Female ID #87

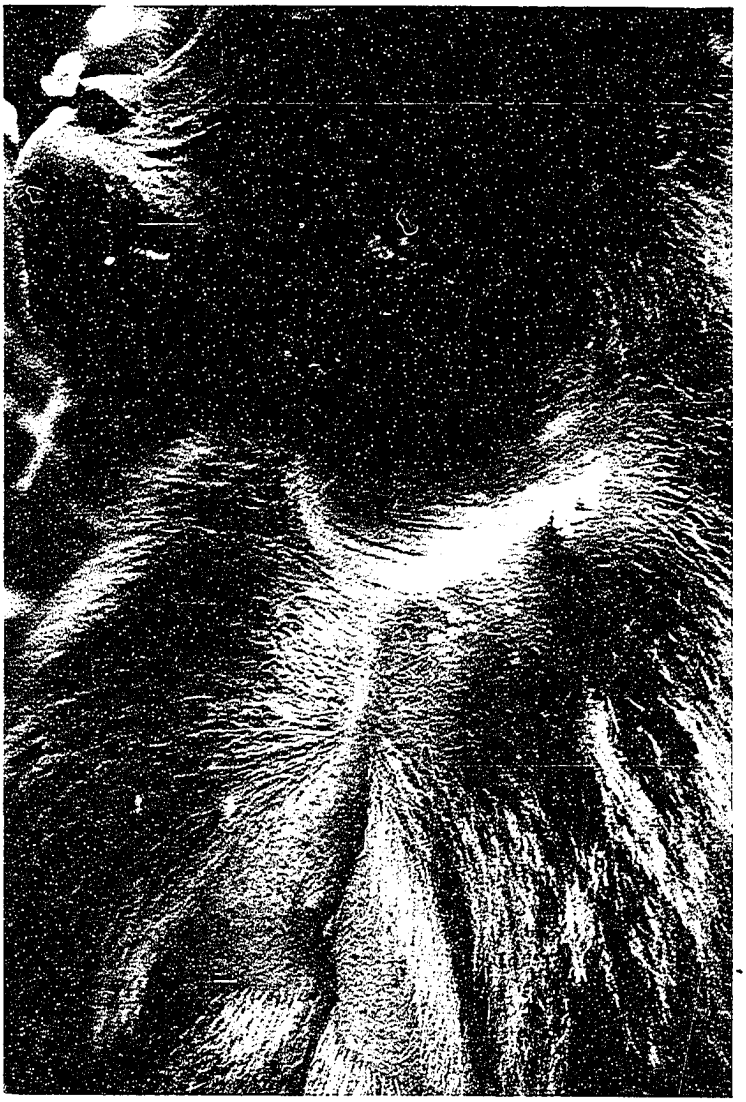


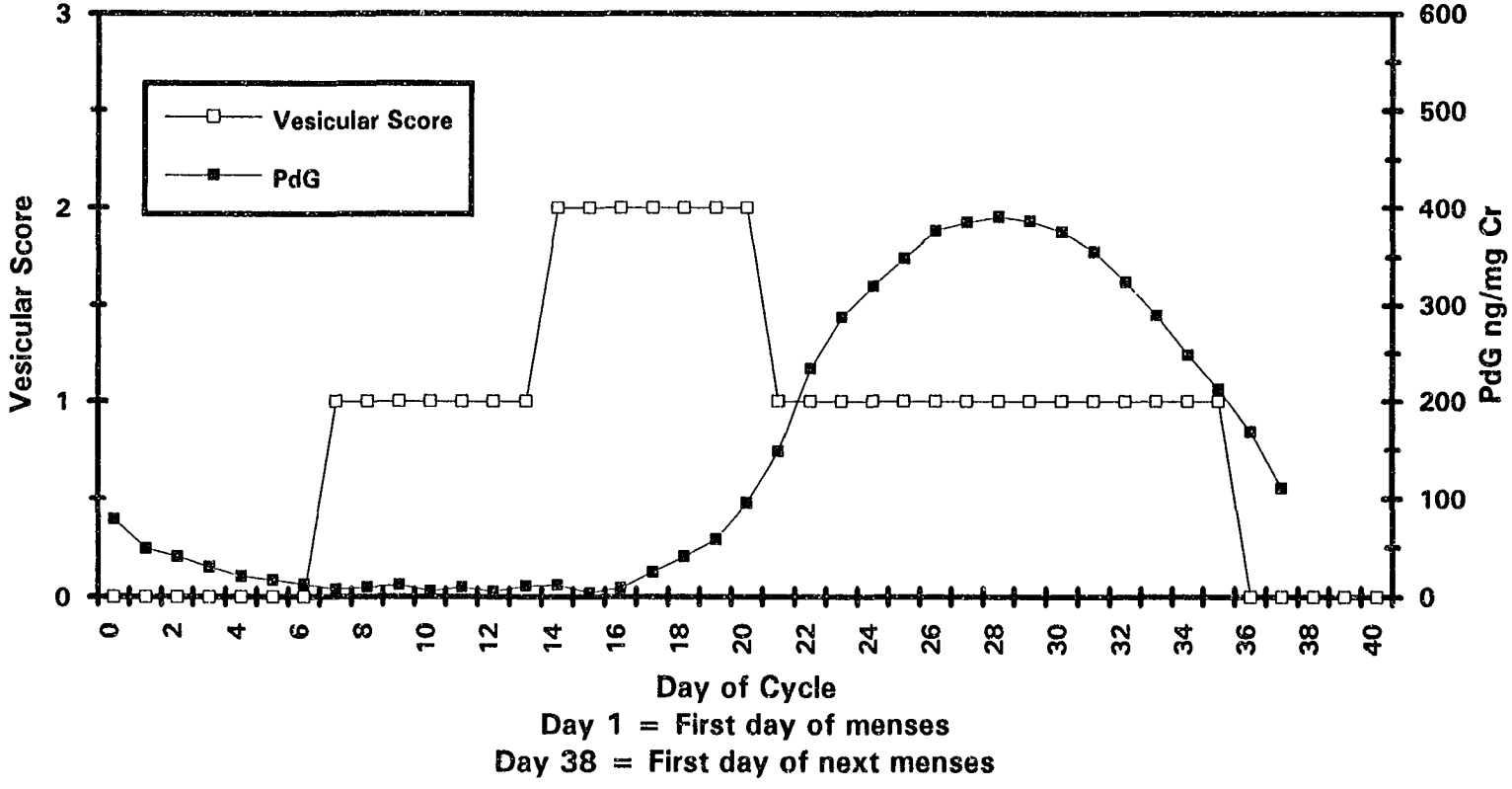
FIGURE 4.12. Visual Changes in Vesicular Morphology During the Peri-Ovulatory Phase of the Menstrual Cycle

(a) Female ID #18

FIGURE 4.12. continued

(b) Female ID #87

FIGURE 4.13. Changes in Vesicular Morphology and Pregnanediol Glucuronide Excretion Levels During the Menstrual Cycle



with the excretion of pregnanediol glucuronide during the menstrual cycle indicating that their cyclicity is correlated.

4.5.2. Estrus Behavior

Traditionally, the term estrus refers to the discrete period around the time of ovulation that is accompanied by related changes in behavior: attractivity, proceptivity and receptivity (Hrdy and Whitten, 1987). Attractivity is measured in terms of the male's behavior toward a female as a mate (e.g., mounting attempts by the male); proceptivity refers to affiliative behaviors (e.g., approaching and maintaining close proximity to the male) and behaviors that act to solicit sexual contact with the male (e.g., presenting the hindquarters to the male); and receptivity refers to behaviors that act to facilitate copulation (e.g., adopting the appropriate copulatory stance). Defined here, estrus behavior refers to an increase in proceptive and receptive behaviors exhibited by females. In the present study, when females approached the peri-ovulatory phase of their cycle, they exhibited a number of proceptive and receptive behaviors. These behaviors included presenting the genitalia for inspection, presenting the chest patch for inspection of vesicles and grooming, approaching the male, keeping close proximity with the male (within 3m) and eliciting solicitation calls. Although these behaviors also occurred during different times of the menstrual cycle, their frequency of occurrence increased significantly when females approached the time of ovulation. Table 4.7 compares the frequency of proceptive and receptive behaviors between the peri-ovulatory and non-ovulatory periods.

TABLE 4.7. The Frequency of Estrus Behaviors During the Peri-Ovulatory and Non-Ovulatory Phase of the Menstrual Cycle

Estrus Behavior	Frequency (%) During Non-Ovulatory Phase*	Frequency (%) During Peri-Ovulatory Phase*	P Value**
Groom	12.9	20.5	<.05
Present	22.5	61.3	<.001
Approach	13.4	21.2	NS
Solicit Call	26.5	44.3	<.01
Proximity to Male	10.1	46.6	<.001

Data are based on 4,680 scan samples taken over 207 menstrual cycles in 16 females

*Percentages are proportions of total behaviors elicited by females that were estrus behaviors.

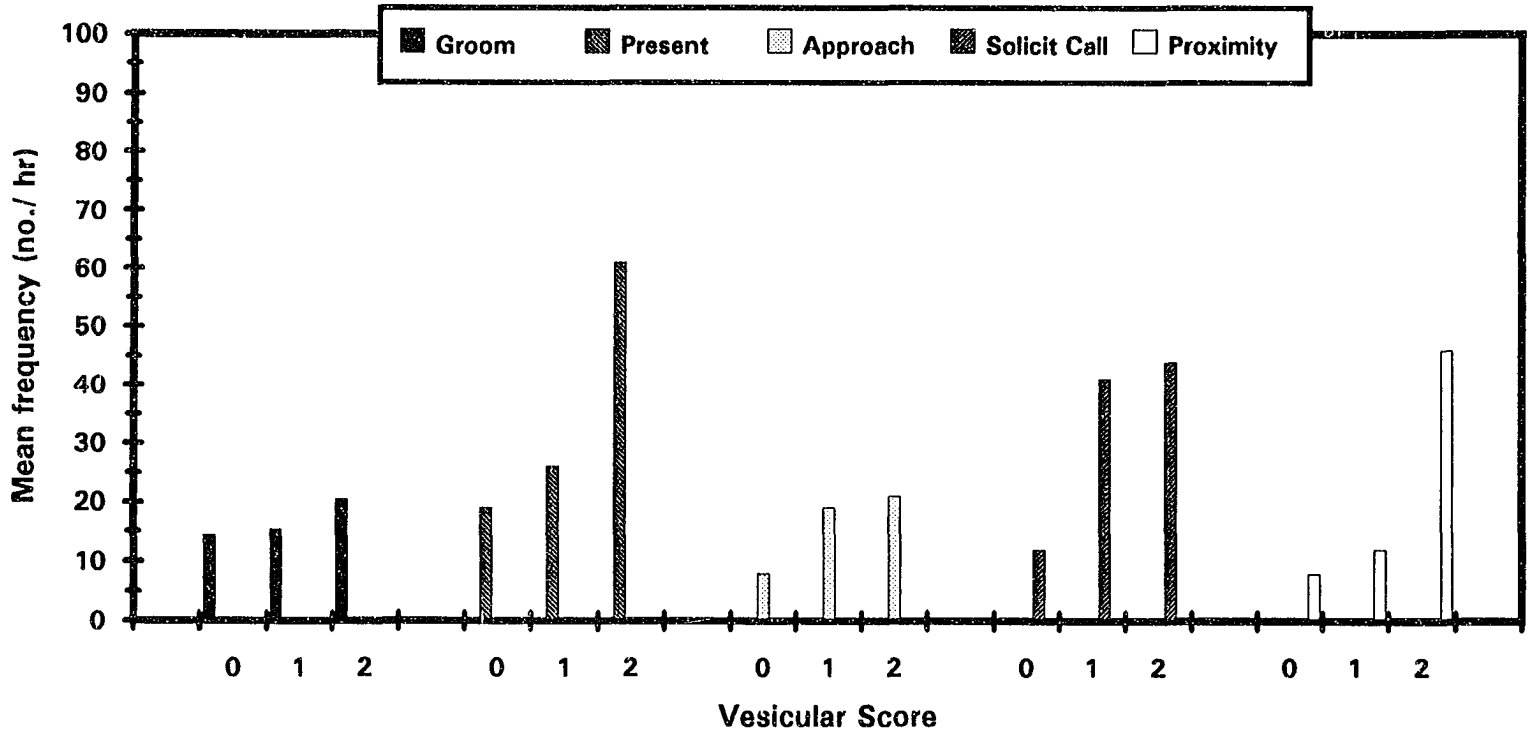
**Student's t-test, two-tailed.

When comparing the data on the frequency of estrus behavior and vesicular morphology, it is evident that the proceptive and receptive behaviors are correlated with the time the vesicles come into full tumescense (Figure 4.14). It was also apparent that estrus behavior is most frequent between days 13 and 26 of the menstrual cycle around the time when pregnanediol glucuronide levels begin to surge (Figure 4.15).

4.5.3. Copulatory Behavior

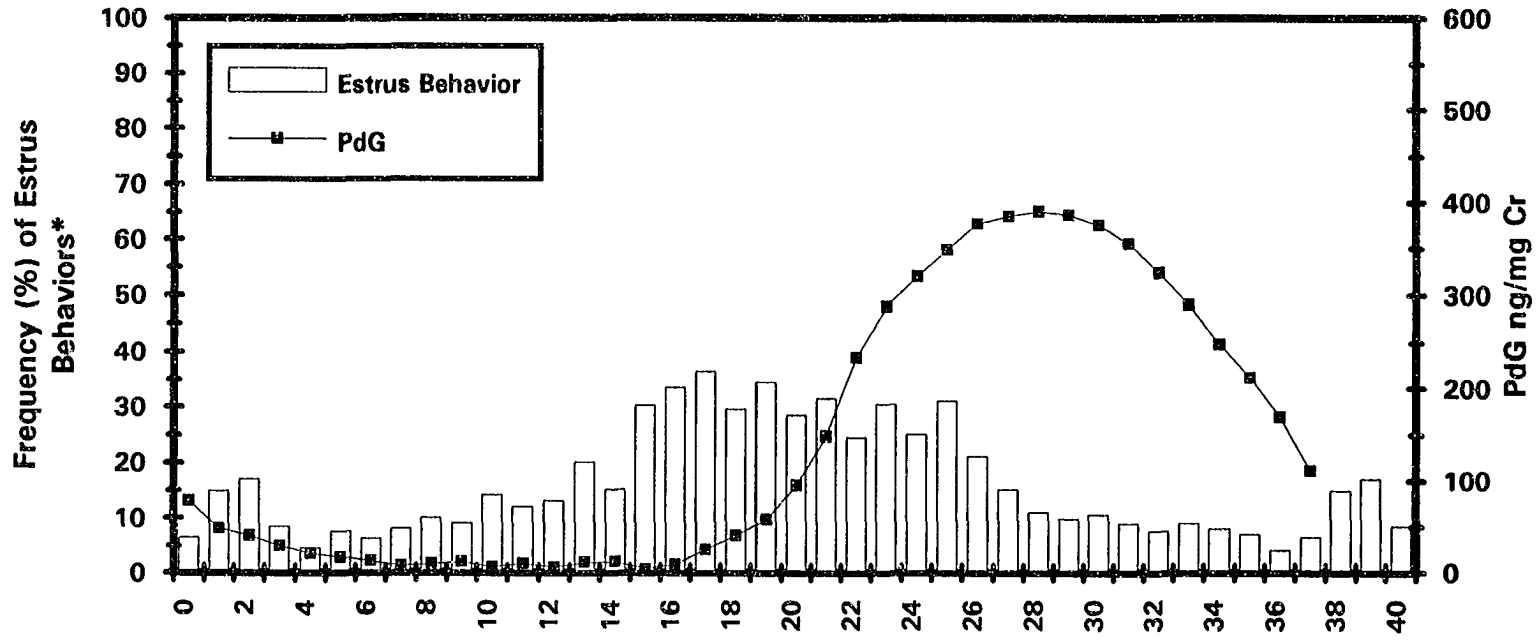
As in many other cercopithecoid monkeys (Hrdy and Whitten, 1987), copulations can occur at all times during the menstrual cycle. Figure 4.16 gives the distribution of copulations throughout the menstrual cycle in this study population. However, also like other cercopithecoids, copulations were more frequent during the peri-ovulatory period (paired t-test:$t = 6.036$, $df = 3$, $p<0.01$) (Figure 4.17). In regard to the changes in vesicular morphology, copulations tended to reach peak frequencies when the vesicles on the sexual skin attained their maximum color and size, as is illustrated in Figure 4.18. The distribution of copulations in relation to the cyclic changes in the excretion of pregnanediol glucuronide is displayed in Figure 4.19. These data illustrate that while copulations do occur in all phases of the cycle, there is a noticeable increase in frequency on the days just prior to the initial surge in pregnanediol glucuronide (between Days 15 and 23).

FIGURE 4.14. Frequency of Estrus Behaviors in Relation to Changes in Vesicular Morphology During the Menstrual Cycle



Data are based on 2,688 focal female samples (N = 16 females)

FIGURE 4.15. Frequency of Estrus Behaviors in Relation to Changes in Pregnanediol Glucuronide Excretion Levels During the Menstrual Cycle



Data are based on 2,688 focal female samples over 207 menstrual cycles
*Values represent the percentage of total behaviors elicited by females that were estrus behaviors (N = 16)

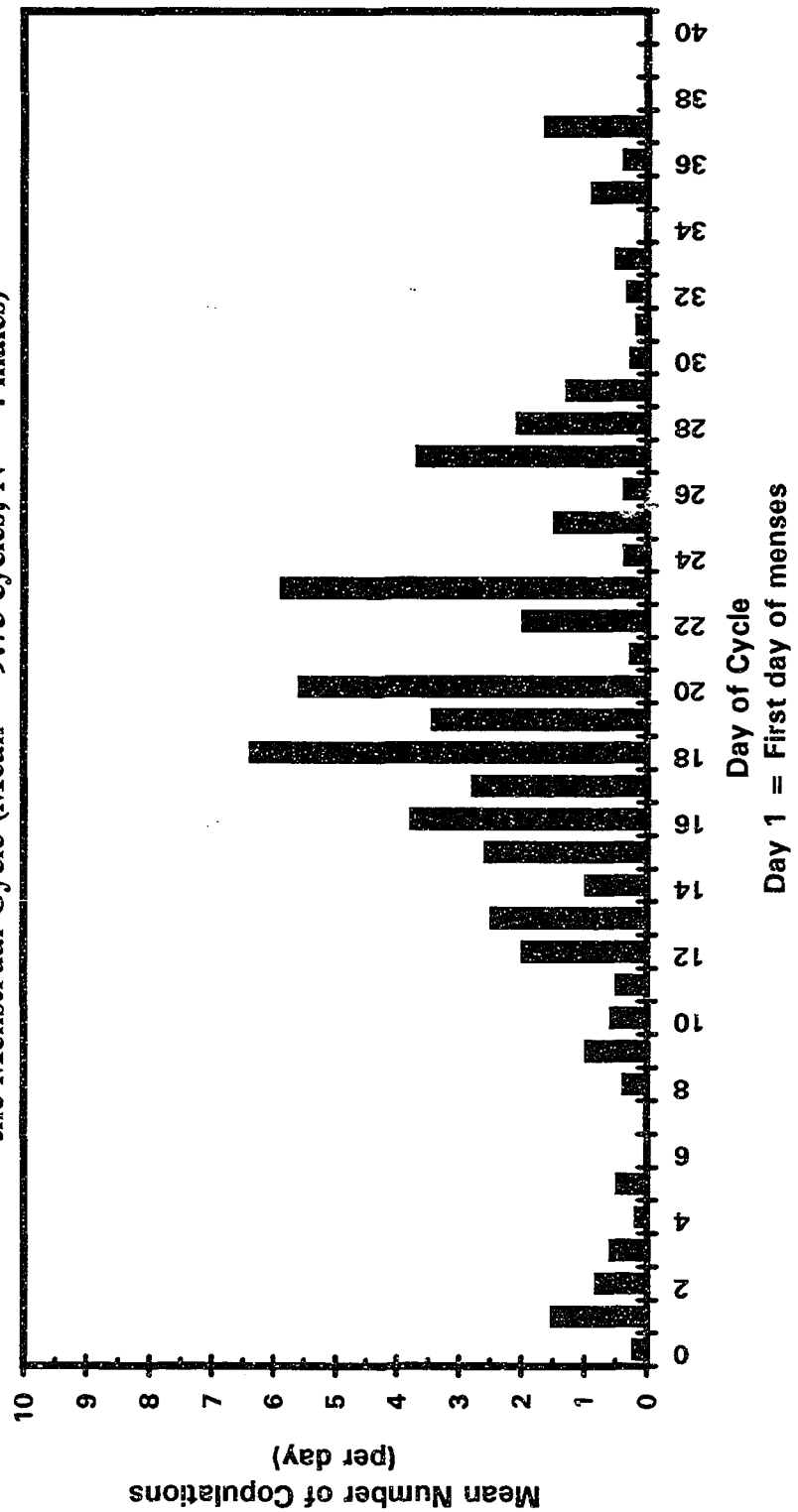
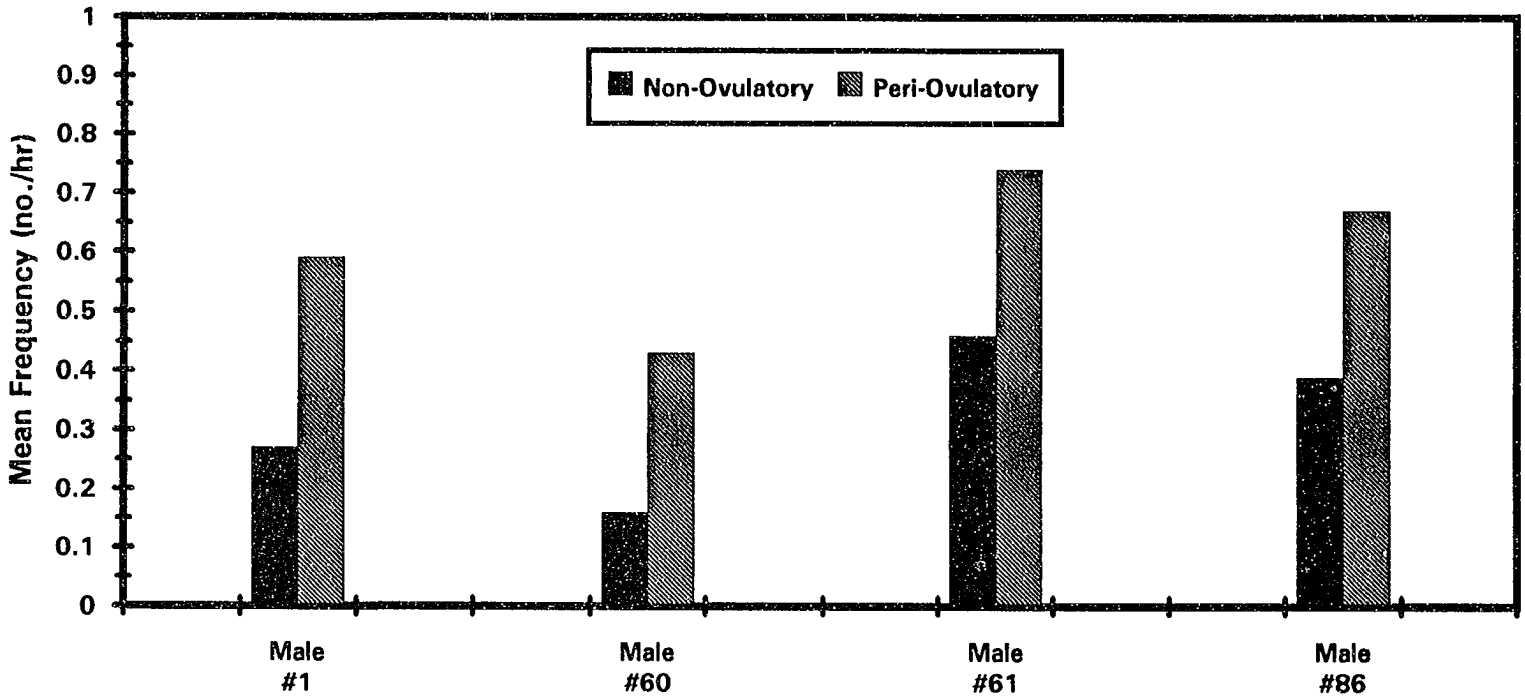


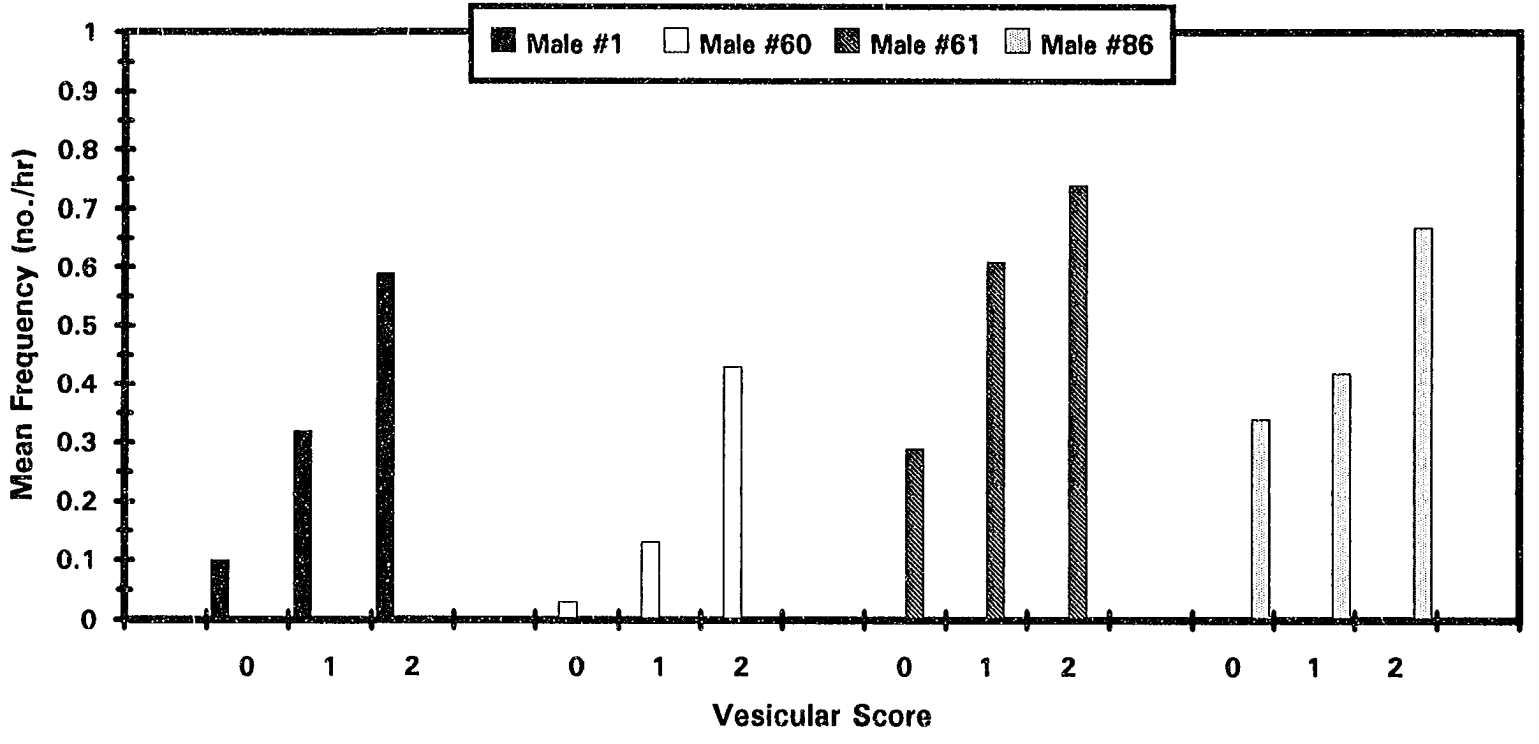
FIGURE 4.16. The Distribution of Copulation Frequencies Throughout the Menstrual Cycle (Mean = 9.75 cycles, N = 4 males)

FIGURE 4.17. The Frequency of Copulations During the Menstrual Cycle



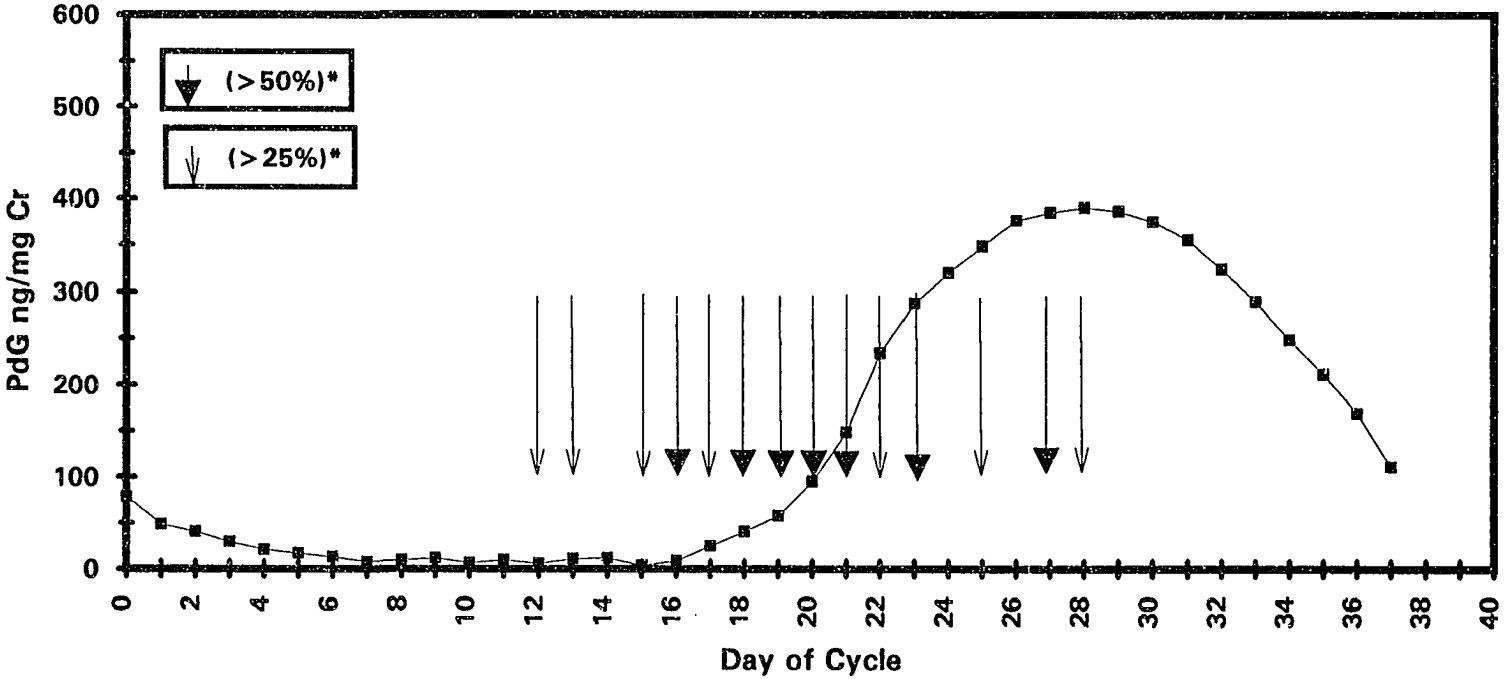
Data are based on 864 ad libitum samples over 38 menstrual cycles

FIGURE 4.18. Frequency of Copulations in Relation to Changes in Vesicular Morphology During the Menstrual Cycle



N = 864 ad libitum samples over 38 menstrual cycles

FIGURE 4.19. Days of Highest Mean Copulation Frequencies in Relation to the Excretion of Pregnanediol Glucuronide During the Menstrual Cycle



Day 1 = First day of menses

*Percentages represent the proportion of total number of copulations observed per day of the menstrual cycle

4.6. Summary of Results

My results demonstrate that the excretion of urinary pregnanediol glucuronide in adult females is cyclic, thus providing an accurate index to the reproductive cycle in gelada baboons. The findings on the ovarian cycle in females in my study groups suggest the following main conclusions:
(1) Menstrual cycles lasted a mean of 37.3 (± 6.1 s.e.) days and ranged from 27 to 83 days; (2) there is a dramatic increase in pregnanediol levels across the peri-ovulatory period marking the transition from the follicular to the luteal phase; (3) the follicular phase lasted a mean of 19.4 ± 0.9 days and pregnanediol glucuronide values averaged 23.1 (± 0.3) ng/mg creatinine; (4) the mean luteal phase length was 17.9 ± 0.4 days and pregnanediol glucuronide values averaged 317.8 (± 3.3) ng/mg creatinine; (5) the pattern of pregnanediol glucuronide excretion and cyclicity in females varies with age and reproductive condition; (6) the visual changes in vesicular morphology are correlated with the changes in pregnanediol glucuronide excretion indicating that the former is a key marker of ovarian cyclicity in geladas; (7) estrus behaviors have the greatest frequency of occurrence during the time the vesicles reach full tumescense and just prior to the time when pregnanediol glucuronide levels show a rapid rise in concentration; and (8) copulations reach peak frequencies when the vesicles are in full tumescense and just prior to the initial surge in pregnanediol glucuronide levels.

CHAPTER 5. FEMALE SOCIAL RELATIONSHIPS IN STUDY GROUPS

5.1. Social Structure in Wild Gelada Baboons

The pattern of social relationships among wild female gelada baboons described by Dunbar and Dunbar (1975) is that:

(1) females tend to form relatively small, stable grooming clusters, often of only two mature females;

(2) it is highly probable that these clusters consist of closely related individuals, usually mothers and their reproductively mature daughters;

(3) these grooming clusters are functionally important as a basis for coalition formation; and

(4) the evolutionary significance of these coalitions lies in their effect on an individual female's reproductive output.

Dunbar and Dunbar (1975) defined grooming dyads as females who spend more than 10% of their available social time interacting with each other, and such females are referred to as grooming partners. In these dyadic interactions, grooming takes precedence over other behaviors. Analysis of the composition of grooming dyads in wild populations of geladas suggests that they typically contain close relatives (mother/daughter or sisters) (Dunbar, 1979).

5.2. Data Analysis

As stated in chapter 3, at the start of the sampling period the study population consisted of two groups, LH and CN (referred to as Phase I). Shortly after the unit male (#10) of group LH was replaced by the young male (#61) in Group CN, three additional individuals were added to the population, and subsequently, group LH fissioned into groups JR and JD (Phase II). In order to eliminate any bias in the analysis, the data on individuals are presented separately for both Phase I and II. This allows the individual and group means to be viewed based on group composition, as well as providing the basis for values derived for the total population.

The data on inter-individual interactions within groups (sociograms) were derived from an analysis of the frequency of interactions and mean proximity between individuals, based on S.A. Altmann's (1968) model of social networks (Lehner, 1979). The association patterns among the members of each unit were further analyzed using a single-link cluster analysis which used nearest neighbor frequencies to determine the relative level of association among individuals producing a dendrogram of the groupings that result (Lehner, 1979).

5.3. The Structure of Reproductive Units

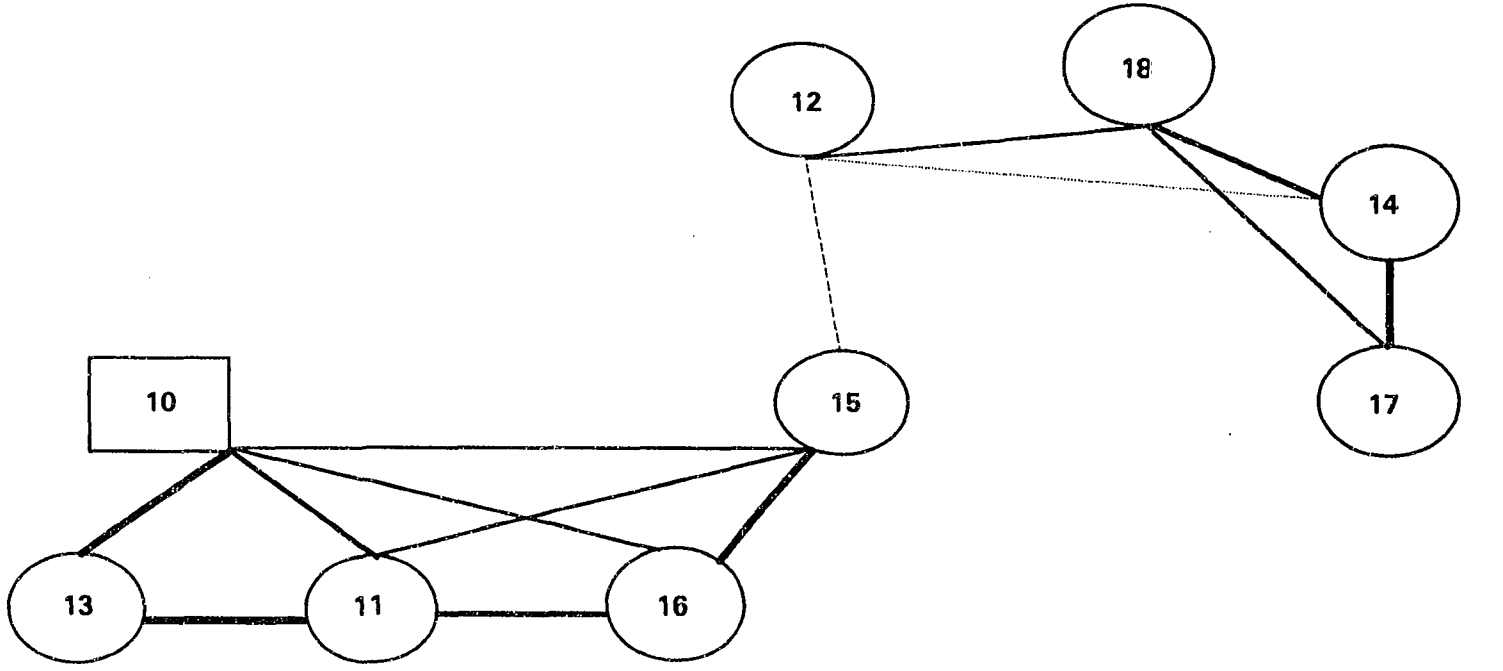
As in wild geladas, the study groups each consisted of one breeding male, 4 to 8 adult females, and a varying number of immature individuals. Also, as in wild geladas, the study groups were composed of small subsets of two, or occasionally three, adult females who interacted with each other almost to the exclusion of other individuals. The harem male spent less time socializing than did females, but when socializing, time was spent among the adult females of his unit. In addition, he did not interact equally with all females, but rather showed a preference for particular females. A sociogram of each group is presented in Figure 5.1 which clearly illustrates the pattern of inter-individual interactions, and a cluster-analysis of association patterns both among and between the members of each unit is given in Figure 5.2. Both figures illustrate the tendencies for distinct dyads to form within the unit.

5.4. Activity Time Budgets

Wild geladas spend nearly two-thirds of their available daylight time foraging (Dunbar, 1984). Given the ready availability of food in captivity, an obvious difference one would expect to find in the activity budgets of captive groups would be in the amount of time devoted to feeding. Of interest, then, is how the additional time gained from a reduction in foraging is redistributed among other categories of activity.

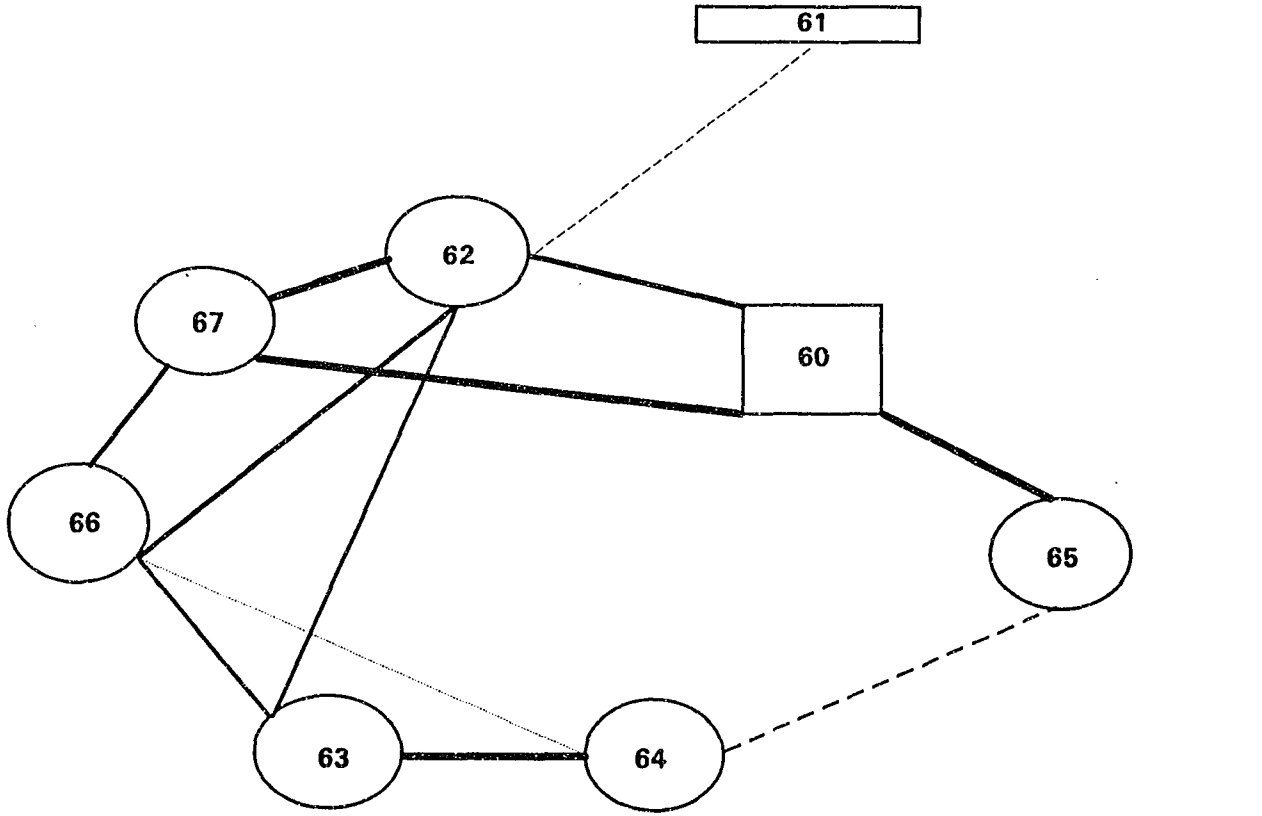
Samples of activity in the Bronx Zoo animals revealed that on average the members of each group spent the majority of their available time in social interaction (Figure 5.3.). When compared to activity budgets of wild geladas, it can be seen that the zoo animals spent less time moving and feeding, and much

FIGURE 5.1.a. Sociogram of Group LH Based on the Rate of Interaction Between Individuals



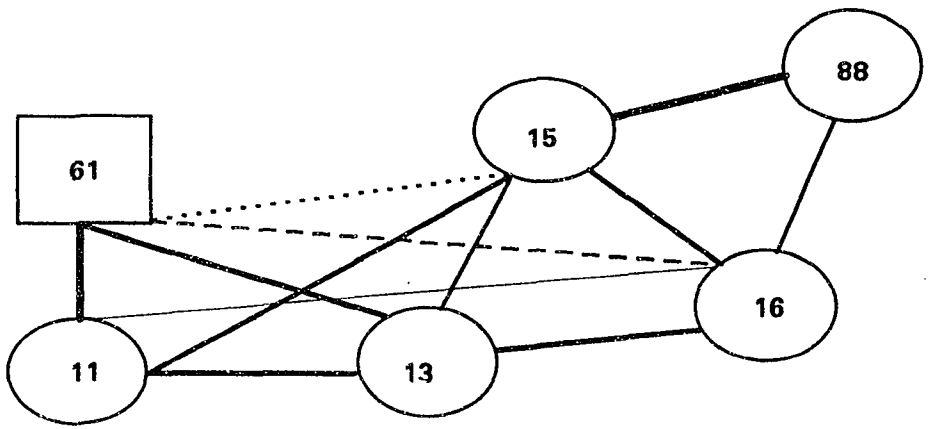
Squares = Unit Male; Ovals = Adult Females; Numbers = ID#
Width of the lines are proportionate to the frequency of interaction based on scan sampling (N = 1,872)

FIGURE 5.1.b. Sociogram of Group CN Based on the Rate of Interaction Between Individuals (Phase I)



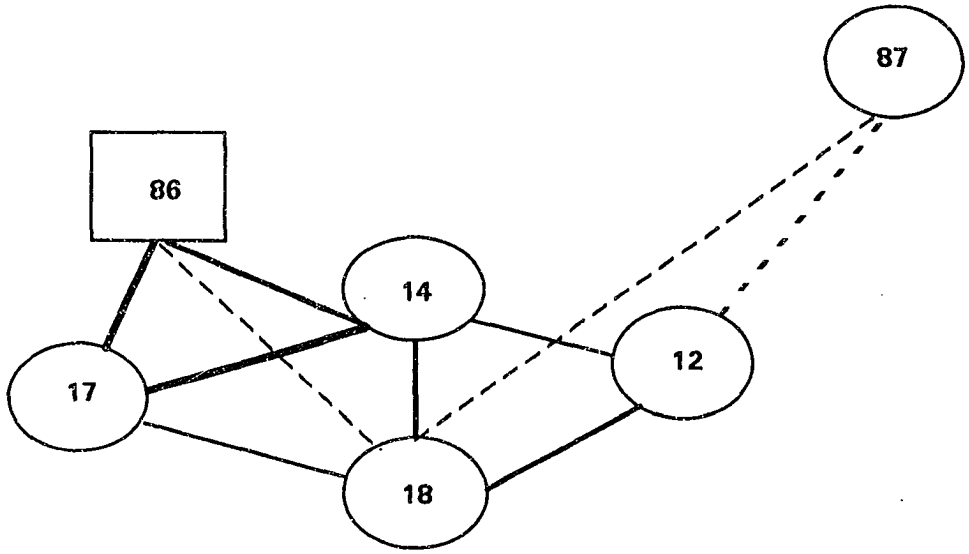
Squares = Unit Male; Rectangles = Subadult Male; Ovals = Adult Females; Numbers = ID#
Width of the lines are proportionate to the frequency of interaction based on scan sampling (N = 1,872)

FIGURE 5.1.c. Sociogram of Group JR Based on the Rate of Interaction Between Individuals



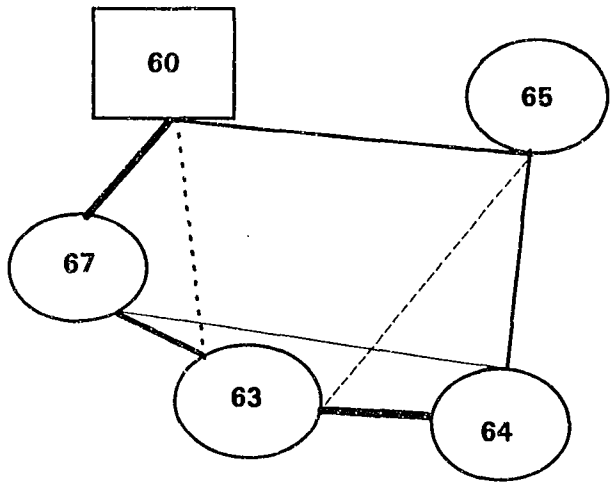
Squares = Unit Male; Ovals = Adult Females; Numbers = ID#
Width of the lines are proportionate to the frequency of interaction based on scan sampling (N = 3,122)

FIGURE 5.1.d. Sociogram of Group JD Based on the Rate of Interaction Between Individuals



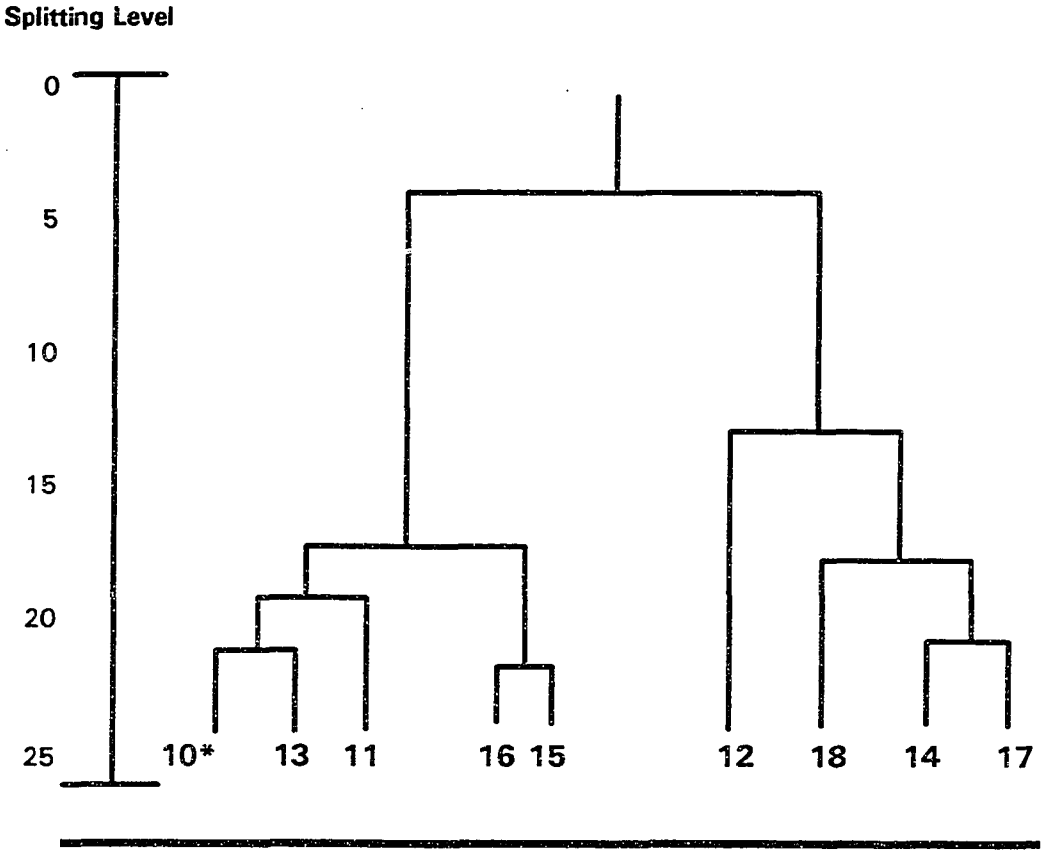
Squares = Unit Male; Ovals = Adult Females; Numbers = ID#
Width of the lines are proportionate to the frequency of interaction based on scan sampling (N = 3,122)

FIGURE 5.1.e. Sociogram of Group CN Based on the Rate of Interaction Between Individuals (Phase II)



Squares = Unit Male; Ovals = Adult Females; Numbers = ID#
Width of the lines are proportionate to the frequency of interaction based on scan sampling (N = 3,122)

FIGURE 5.2.a. Single-Link Cluster Analysis of Association Frequencies Among Individuals of Study Group LH

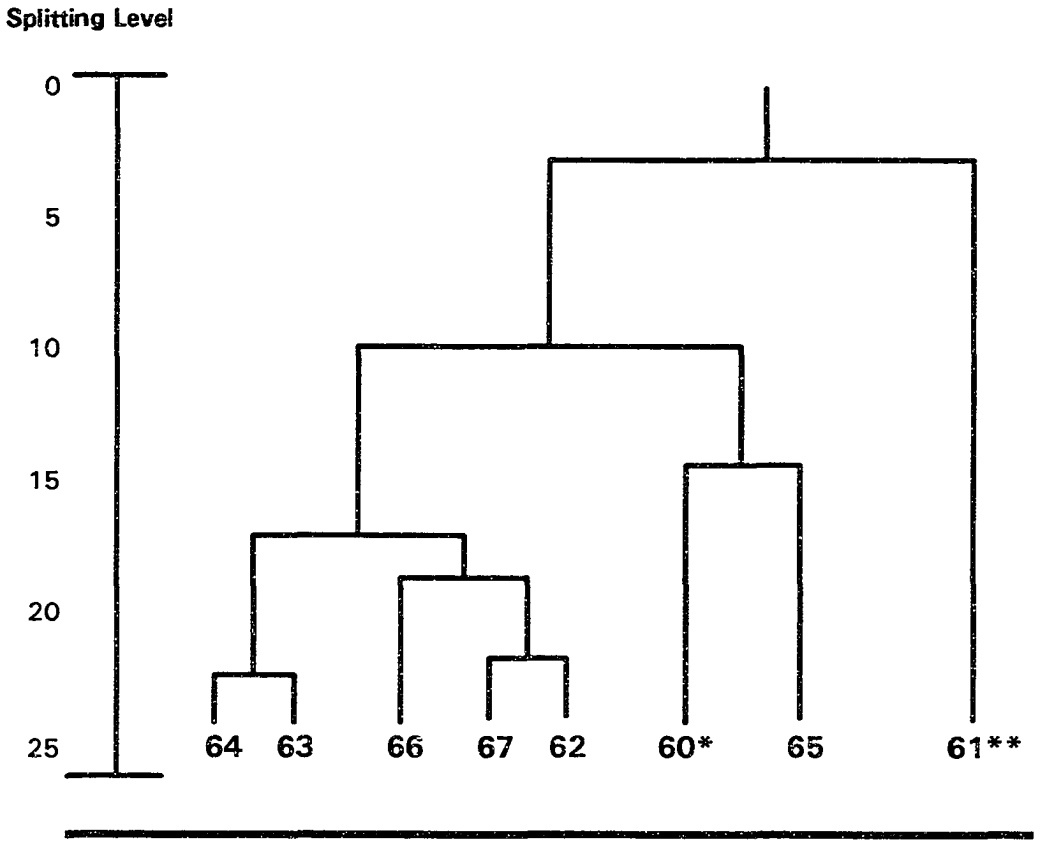


* Adult Male

X-axis shows the ID# of the individuals in Group LH

Y-axis shows the splitting level of association patterns based on nearest neighbor frequencies

FIGURE 5.2.b. Single-Link Cluster Analysis of Association Frequencies Among Individuals of Study Group CN (Phase I)

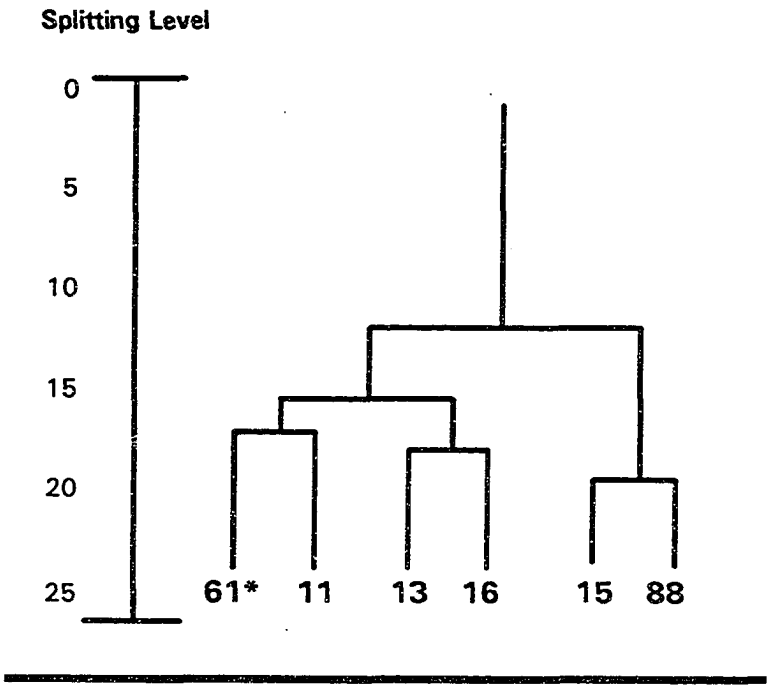


* Adult Male ** Subadult Male

X-axis shows the ID# of the individuals in Group CN

Y-axis shows the splitting level of association patterns based on nearest neighbor frequencies

FIGURE 5.2.c. Single-Link Cluster Analysis of Association Frequencies Among Individuals of Study Group JR

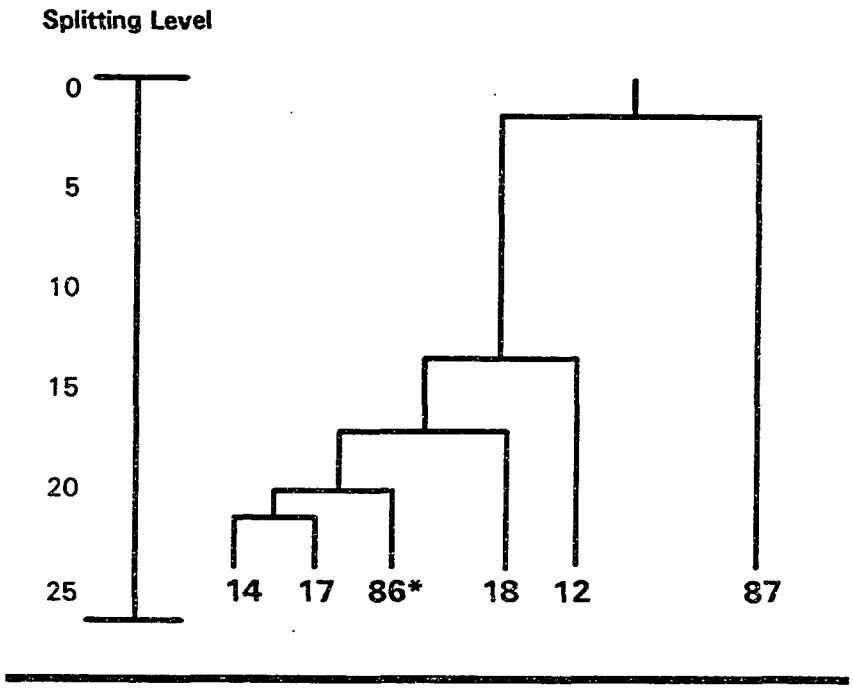


* Subadult Male

X-axis shows the ID# of the individuals in Group JR

Y-axis shows the splitting level of association patterns based on nearest neighbor frequencies

FIGURE 5.2.d. Single-Link Cluster Analysis of Association Frequencies Among Individuals of Study Group JD

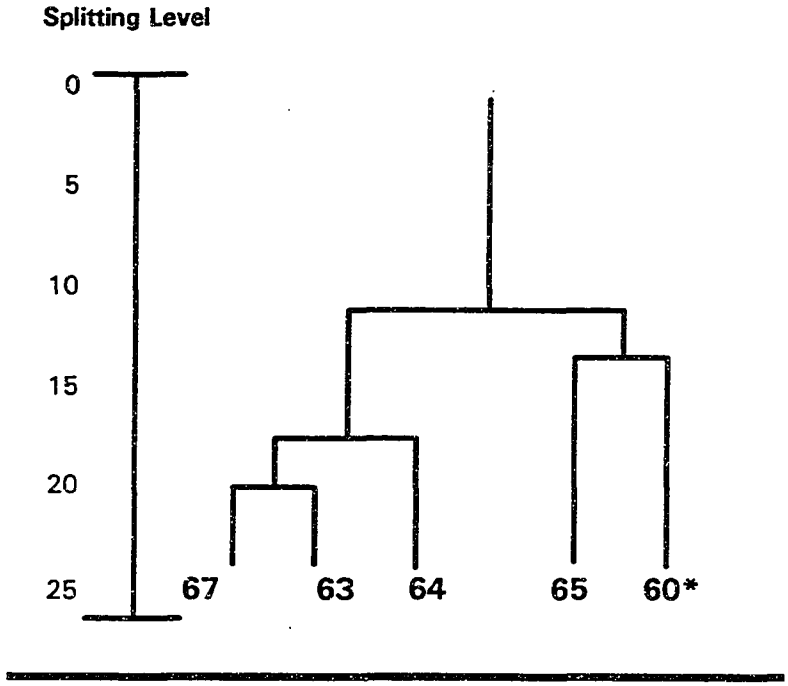


* Subadult Male

X-axis shows the ID# of the individuals in Group JD

Y-axis shows the splitting level of association patterns based on nearest neighbor frequencies

FIGURE 5.2.e. Single-Link Cluster Analysis of Association Frequencies Among Individuals of Study Group CN (Phase II)



* Adult Male

X-axis shows the ID# of the individuals in Group CN

Y-axis shows the splitting level of association patterns based on nearest neighbor frequencies

more time socializing (Figure 5.4.). These differences are statistically significant (t-test: moving $p<0.01$; feeding $p<0.02$; socializing $p<0.001$). Time spent resting, however, remained relatively unchanged ($p>0.05$).

While differences in activity budgets between the study groups were small, there were considerable differences between individuals within each reproductive unit (Table 5.1). The greatest difference in activity levels occurred between males and females, with males spending more of their time feeding while females spent more time socializing ($t = 2.992$, $p<0.01$). Among females, there was some difference in the amount of time spent socializing ($F = 2.835$, $df = 3,60$, $p<0.05$), and they also varied in the percentage of time spent feeding ($F = 3.684$, $df = 3,60$, $p<0.02$). This difference in feeding, however, was only found with regard to certain preferred food items as is shown in Table 5.2.

In the captive setting, a commercially prepared diet (canned primate diet and monkey biscuit) is provided daily to the animals which supplies them with a full complement of necessary nutrients and vitamins, in addition to a selection of fresh fruits and vegetables (see Table 3.3 for details of diet). However, when the animals are in their outdoor enclosure, they feed on a variety of grasses distributed throughout the exhibit and a mixture of seeds that are dispersed routinely by automated dispensers. Table 5.2 presents data on individual percentages of time spent feeding on diet items in both locations. On exhibit, each group spent a significantly greater amount of time feeding on grasses than they did on seeds ($t = 8.737$, $p<0.001$). However, within group variations were found with respect to males, who spent more time feeding on seeds than did the females ($t = 2.316$, $p <0.02$), and among females, who also exhibited

FIGURE 5.3.a. Activity Budgets of Study Groups of Gelada Baboons Based on Scan Samples Taken During Phase I (N = 1,872)

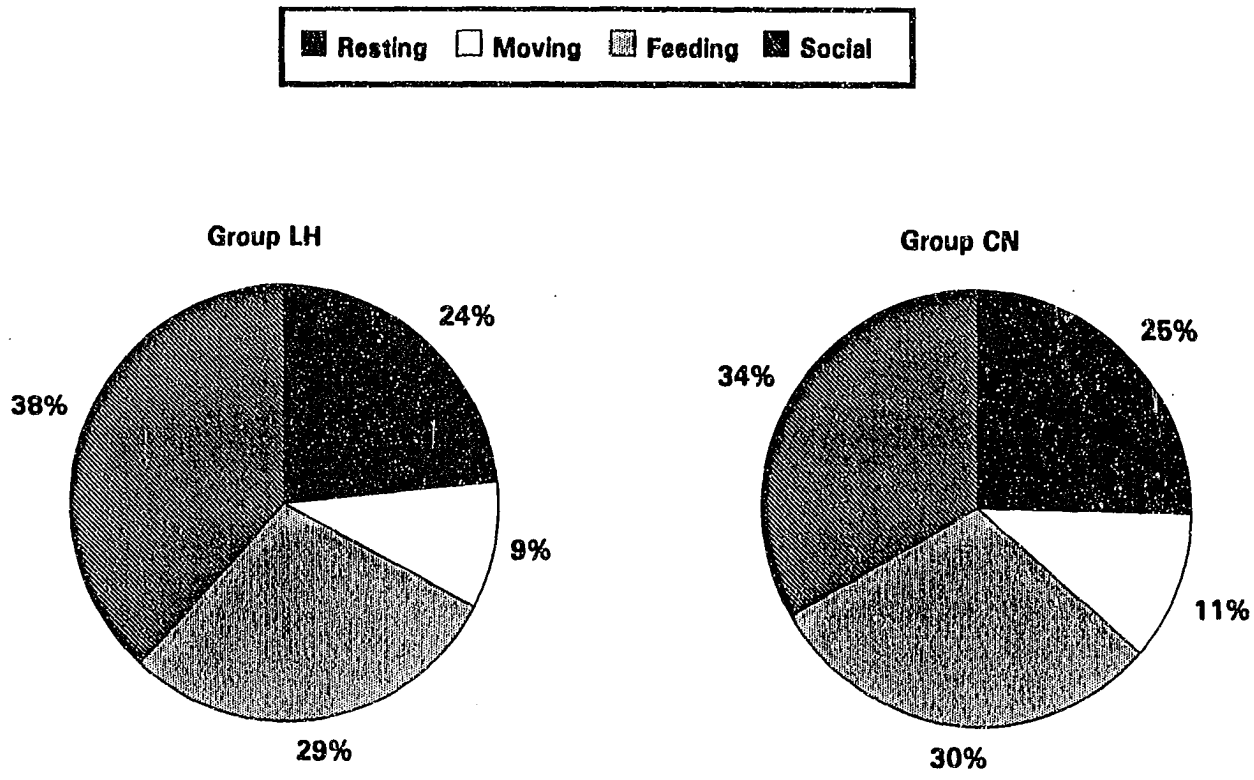


FIGURE 5.3.b. Activity Budgets of Study Groups of Gelada Baboons
Based on Scan Samples Taken During Phase II (N = 3,122)

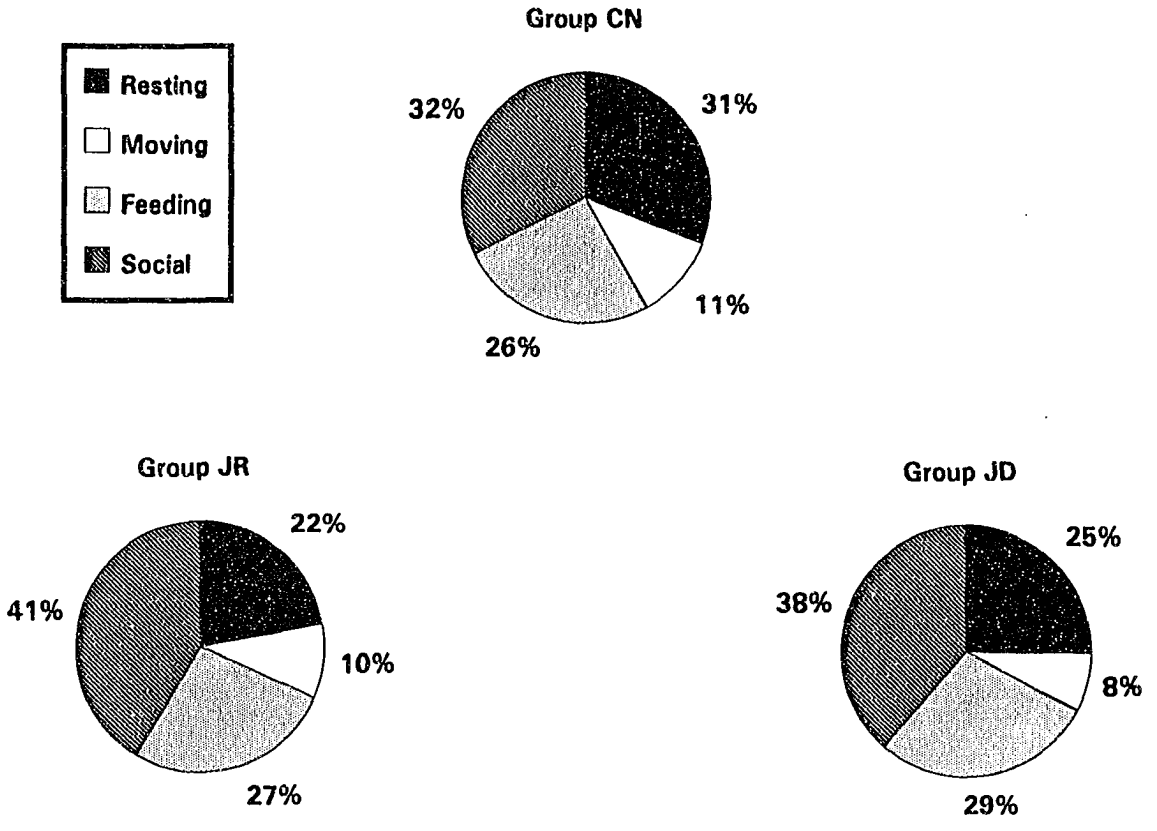
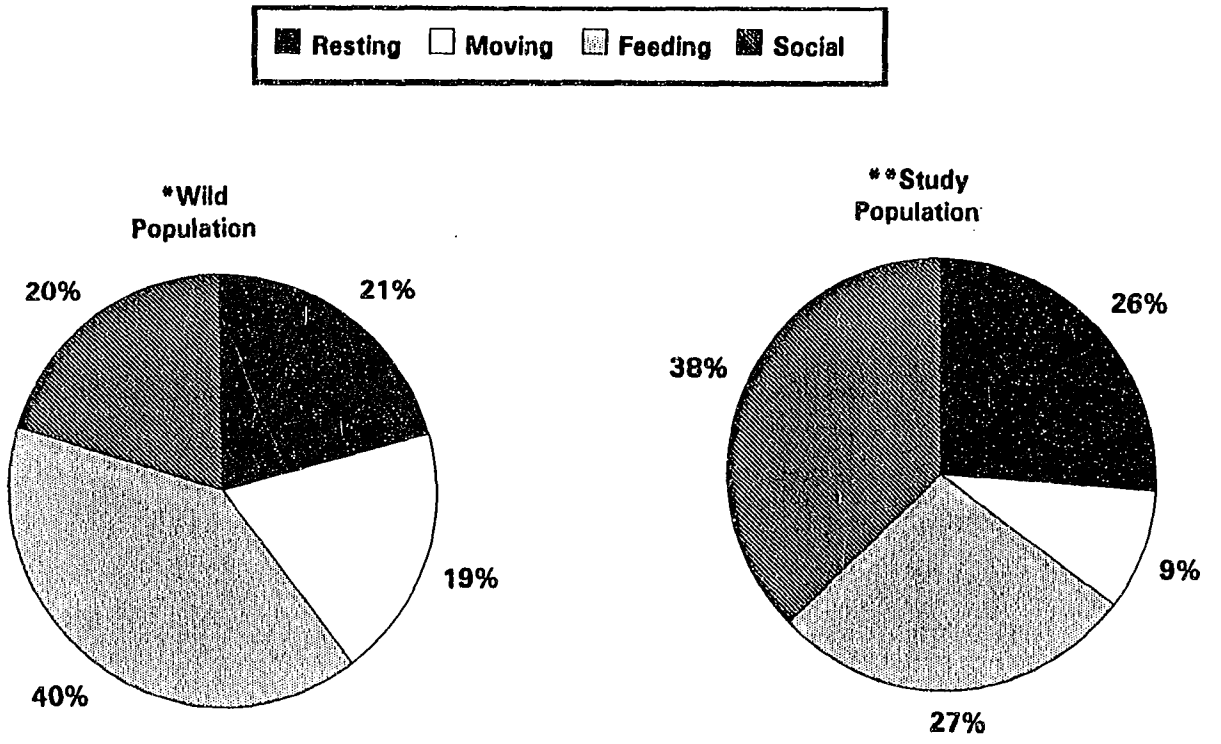


FIGURE 5.4. A Comparison of Activity Budgets (in percent of time allotted to different activities) of Wild Gelada Baboons and the Study Population of Gelada Baboons



Source of Data: *Mean % of Sankaber and Bole gelada populations (Dunbar,1984) **Mean % of study groups

TABLE 5.1.a. Activity Budgets of Individual Geladas During Phase I (N = 1,872 scan samples)

		Activity (%)			
Animal ID#	Sex	Resting	Moving	Feeding	Social
Group LH					
10	M	29.1	6.9	34.8	29.2
11	F	22.5	9.2	24.5	43.8
12	F	21.7	11.7	37.2	29.4
13	F	24.1	7.3	28.5	40.1
14	F	22.3	9.1	25.9	42.7
15	F	25.2	11.4	26.1	37.3
16	F	22.4	10.1	28.8	38.7
17	F	21.4	10.3	24.7	43.6
18	F	23.6	8.9	32.2	35.3
N = 9	1.8	Mean (± s.e.) 23.6 ± .8	Mean (± s.e.) 9.4 ± .5	Mean (± s.e.) 29.2 ± 1.5	Mean (± s.e.) 37.8 ± 1.9
Group CN					
60	M	30.1	7.2	38.4	24.3
61	M	15.7	13.2	33.2	37.9
62	F	26.5	8.6	28.3	36.6
63	F	27.4	10.0	26.7	35.9
64	F	28.2	12.2	29.1	30.5
65	F	22.3	17.2	30.7	29.8
66	F	25.1	10.8	27.5	36.6
67	F	27.4	9.6	28.6	34.4
N = 8	2.6	Mean (± s.e.) 25.3 ± 1.7	Mean (± s.e.) 11.1 ± 1.1	Mean (± s.e.) 30.3 ± 1.4	Mean (± s.e.) 33.3 ± 1.6

TABLE 5.1.b. Activity Budgets of Individual Geladas During Phase II (N = 3,122 scan samples)

Animal ID#	Sex	Activity (%)			
		Resting	Moving	Feeding	Social
Group JR					
61	M	26.6	6.6	34.3	32.5
11	F	20.5	7.2	29.2	43.1
13	F	21.4	7.1	31.2	40.3
15	F	23.8	9.8	20.1	46.3
16	F	22.3	11.3	21.7	44.7
88	F	19.3	15.1	26.5	39.1
N = 6	1.5	Mean (± s.e.) 22.6 ± 1.0	Mean (± s.e.) 8.6 ± .8	Mean (± s.e.) 27.2 ± 2.3	Mean (± s.e.) 41.4 ± 2.0
Group JD					
86	M	19.3	5.2	30.2	45.3
17	F	27.2	6.1	25.1	41.6
14	F	24.7	5.6	26.9	42.8
18	F	26.8	6.6	27.7	38.9
12	F	28.7	8.1	30.8	32.4
87	F	25.2	13.5	32.6	28.7
N = 6	1.5	Mean (± s.e.) 25.3 ± 1.3	Mean (± s.e.) 7.5 ± 1.3	Mean (± s.e.) 28.9 ± 1.1	Mean (± s.e.) 38.3 ± 2.6
Group CN					
60	M	34.6	9.7	27.4	28.3
63	F	30.6	10.3	24.2	34.9
64	F	31.7	13.2	23.6	31.5
65	F	27.8	12.7	29.7	29.8
67	F	29.8	9.1	25.2	35.9
N = 20	1.4	Mean (± s.e.) 30.2 ± 1.7	Mean (± s.e.) 10.7 ± .5	Mean (± s.e.) 27.2 ± 1.4	Mean (± s.e.) 31.9 ± 2.1

TABLE 5.2.a. Percentage of Time Individuals Spent Feeding on Various Diet Items (Phase I)

		On Exhibit*		Off Exhibit**	
Animal ID#	Sex	Grasses	Seeds	Fruits and Vegetables	Commercial Diet
Group LH					
10	M	42.2	57.8	61.5	38.5
11	F	62.6	37.4	40.7	59.3
12	F	88.1	11.9	25.6	74.4
13	F	59.6	40.4	46.8	53.2
14	F	81.2	18.8	34.9	65.1
15	F	76.9	23.1	40.9	59.1
16	F	74.4	25.6	41.7	58.3
17	F	80.9	19.1	37.8	62.2
18	F	85.5	14.5	33.5	66.5
N = 9	1.8	Mean (± s.e.) 72.4 ± 4.9	Mean (± s.e.) 27.6 ± 4.6	Mean (± s.e.) 40.4 ± 3.7	Mean (± s.e.) 59.6 ± 3.3
Group CN					
60	M	69.6	30.4	68.7	31.3
61	M	60.3	39.7	73.6	26.4
62	F	75.3	24.7	59.4	40.6
63	F	89.2	10.8	36.3	63.7
64	F	94.6	5.4	32.2	67.8
65	F	88.8	11.2	30.7	69.3
66	F	83.7	16.3	45.2	54.8
67	F	71.9	28.1	61.8	38.2
N = 8	2.6	Mean (± s.e.) 79.2 ± 4.2	Mean (± s.e.) 20.8 ± 3.8	Mean (± s.e.) 51.1 ± 5.7	Mean (± s.e.) 48.9 ± 4.9

*On Exhibit (N = 1,872 scan samples)

**Off Exhibit (N = 1,256 scan samples)

TABLE 5.2.b. Percentage of Time Individuals Spent Feeding on Various Diet Items (Phase II)

Animal ID#	Sex	On Exhibit*		Off Exhibit**	
		Grasses	Seeds	Fruits and Vegetables	Commercial Diet
Group JR					
61	M	47.6	52.4	66.6	33.4
11	F	57.6	42.4	55.3	44.7
13	F	68.6	31.4	42.2	57.8
15	F	71.9	28.1	39.2	60.8
16	F	79.4	20.6	36.7	63.3
88	F	82.7	17.3	40.8	59.2
N = 6	1.5	Mean (± s.e.) 67.9 ± 5.4	Mean (± s.e.) 32.1 ± 5.1	Mean (± s.e.) 46.8 ± 4.8	Mean (± s.e.) 53.2 ± 4.6
Group JD					
86	M	63.5	36.5	66.3	33.7
17	F	67.9	32.1	44.2	55.6
14	F	71.2	28.8	40.9	59.1
18	F	77.5	22.5	35.5	64.5
12	F	80.1	19.9	30.6	69.4
87	F	89.3	10.7	22.9	77.1
N = 6	1.5	Mean (± s.e.) 74.9 ± 3.8	Mean (± s.e.) 25.1 ± 4.1	Mean (± s.e.) 40.1 ± 6.1	Mean (± s.e.) 59.9 ± 5.7
Group CN					
60	M	69.6	30.4	68.7	31.3
63	F	79.2	20.8	41.9	58.1
64	F	90.6	9.4	32.2	67.8
65	F	89.8	10.2	36.4	63.6
67	F	71.9	28.1	60.8	39.2
N = 5	1.4	Mean (± s.e.) 80.2 ± 4.4	Mean (± s.e.) 19.8 ± 4.6	Mean (± s.e.) 48.9 ± 6.6	Mean (± s.e.) 51.1 ± 7.1

*On Exhibit (N = 3,122)

**Off Exhibit (N = 1,356)

differences in relation to feeding on seeds ($F = 7.891$, $df = 1,30$, $p<0.01$). Given that the seeds are a preferred food item that are dispersed in small, clumped locations in contrast to the evenly distributed grasses, it is not surprising that variations were found in this regard. The dominant individuals in each group were able to displace the lower ranking individuals from these feeding sites at all times.

Off exhibit, where animals were fed the prepared diet, each group spent roughly equal proportions of time feeding on both the commercial foods and the fruits and vegetables. The study animals showed a strong preference for the fruits, and to a lesser extent vegetables, over the commercially prepared foods, so much so that individuals would seek to monopolize them. Males in particular would exert physical control over these items, by threatening and chasing most individuals who attempted to obtain a portion. Males spent a greater amount of time feeding on the fruits/vegetables, while females fed more on the commercial foods ($t = 3.254$, $p<0.02$); and comparisons between females revealed that some individuals fed more on fruits/vegetables than did others ($F = 4.863$, $df = 1,30$, $p<0.05$). Males did show some tolerance for the most dominant female in the unit, but these dominant females were very intolerant of other females attempting to feed on these preferred items.

5.5. Diet and Body Weight

The food items most preferred are the least nutritionally valuable. Therefore, although certain individuals spent less time feeding on these preferred items, this would not necessarily result in lowered nutritional intakes for these females. More importantly, despite differences in time spent feeding, all individuals received sufficient amounts of food to fulfill basic nutritional

requirements. This is reflected in the data on body weights for this population which ranged from 11.4 - 18.8 kg (mean $\pm$ s.e. = 15.9 $\pm$ 3.1) for females and 26.8 - 34.1 kg (mean $\pm$ s.e. = 29.4 $\pm$ 2.6) for males. Body weight was not correlated with time spent feeding (Spearman rank correlation coefficient, males: (N=4) $r_S = 0.03$, $p>0.10$, n.s.; females: (N=16) $r_S = 0.08$, $p>0.10$, n.s., two-tailed).

5.6. Female Affiliative Relationships

The one, or occasionally two, other female(s) with whom a female interacts were either a close relative when available, or more commonly another female with whom an established relationship existed prior to the formation of the present study group. These small subsets of females are here referred to as grooming dyads and the individuals as grooming partners. Dyads were determined by the percentage of time (>10% of total social time) females spent socializing with one another (Dunbar and Dunbar, 1975). Table 5.3 shows how each female distributed her social interactions among the members of her unit; as in wild groups of geladas, females do not socialize with all individuals equally. In the interactions between these subsets of individuals, grooming predominated over other affiliative behaviors (e.g., lipsmacking, presenting, nuzzling, touching, embracing) (Figure 5.5). Partners within a grooming dyad were most often each other's nearest neighbor and tended to remain in close proximity to one another while remaining more distant from other individuals in their unit (Phase I: $t = 4.581$, $df = 13$, $p < 0.001$; Phase II: $t = 4.226$, $df = 13$, $p<0.001$) (Table 5.4).

TABLE 5.3.a. Distribution of Time Spent in Affiliative Social Interactions Among Females in Reproductive Units Based on Focal Female Sampling (N = 1,008) During Phase I

Focal Female ID#	% Time with Female Grooming Dyad Partner	% Time with Other Female Group Members	% Time With Unit Male
Group LH			
11	49.6	23.5	26.9
12	*	97.4	2.6
13	56.5	3.3	40.2
14	75.3	20.1	4.6
15	67.2	18.4	14.4
16	60.1	29.0	10.9
17	81.1	13.2	5.7
18	38.5	59.7	1.8
N = 8	Mean (± s.e.) 61.2 ± 5.2	Mean (± s.e.) 33.1 ± 10.9	Mean (± s.e.) 13.4 ± 4.8
Group CN			
62	49.6	22.1	28.3
63	72.2	20.0	7.8
64	78.8	16.9	4.3
65	**	29.4	70.6
66	49.3	34.2	16.5
67	40.4	23.1	36.5
N = 6	Mean (± s.e.) 58.1 ± 6.7	Mean (± s.e.) 24.3 ± 2.6	Mean (± s.e.) 27.3 ± 9.9

*Focal Female is not in a "Grooming Dyad"

**Focal Female is in a "Grooming Dyad" with Unit Male

TABLE 5.3.b. Distribution of Time Spent in Affiliative Social Interactions Among Females in Reproductive Units Based on Focal Female Sampling (N = 1,680) During Phase II

Focal Female ID#	% Time with Female Grooming Dyad Partner	% Time with Other Female Group Members	% Time With Unit Male
Group JR			
11	**	49.3	50.7
13	44.9	30.2	24.9
15	51.5	25.7	22.8
16	49.0	32.3	18.7
88	42.8	36.6	20.6
N = 5	Mean (± s.e.) 47.1 ± 1.8	Mean (± s.e.) 34.8 ± 4.0	Mean (± s.e.) 27.5 ± 5.9
Group JD			
12	55.3	17.4	27.3
14	41.8	15.3	42.9
17	43.4	11.5	45.1
18	42.7	20.5	36.8
87	*	90.8	9.2
N = 5	Mean (± s.e.) 45.8 ± 2.8	Mean (± s.e.) 31.1 ± 14.1	Mean (± s.e.) 32.3 ± 6.5
Group CN			
63	56.9	26.3	16.8
64	66.4	26.9	6.7
65	**	58.1	41.9
67	46.9	32.4	20.7
N = 4	Mean (± s.e.) 56.7 ± 4.9	Mean (± s.e.) 35.9 ± 7.6	Mean (± s.e.) 21.5 ± 7.4

*Focal Female is not in a "Grooming Dyad"
**Focal Female is in "Grooming Dyad" with Unit Male

FIGURE 5.5. Frequencies of Grooming Behavior Compared to Frequencies of Other Affiliative Behaviors by Study Group Females (N = 2,688 Focal Female Samples)

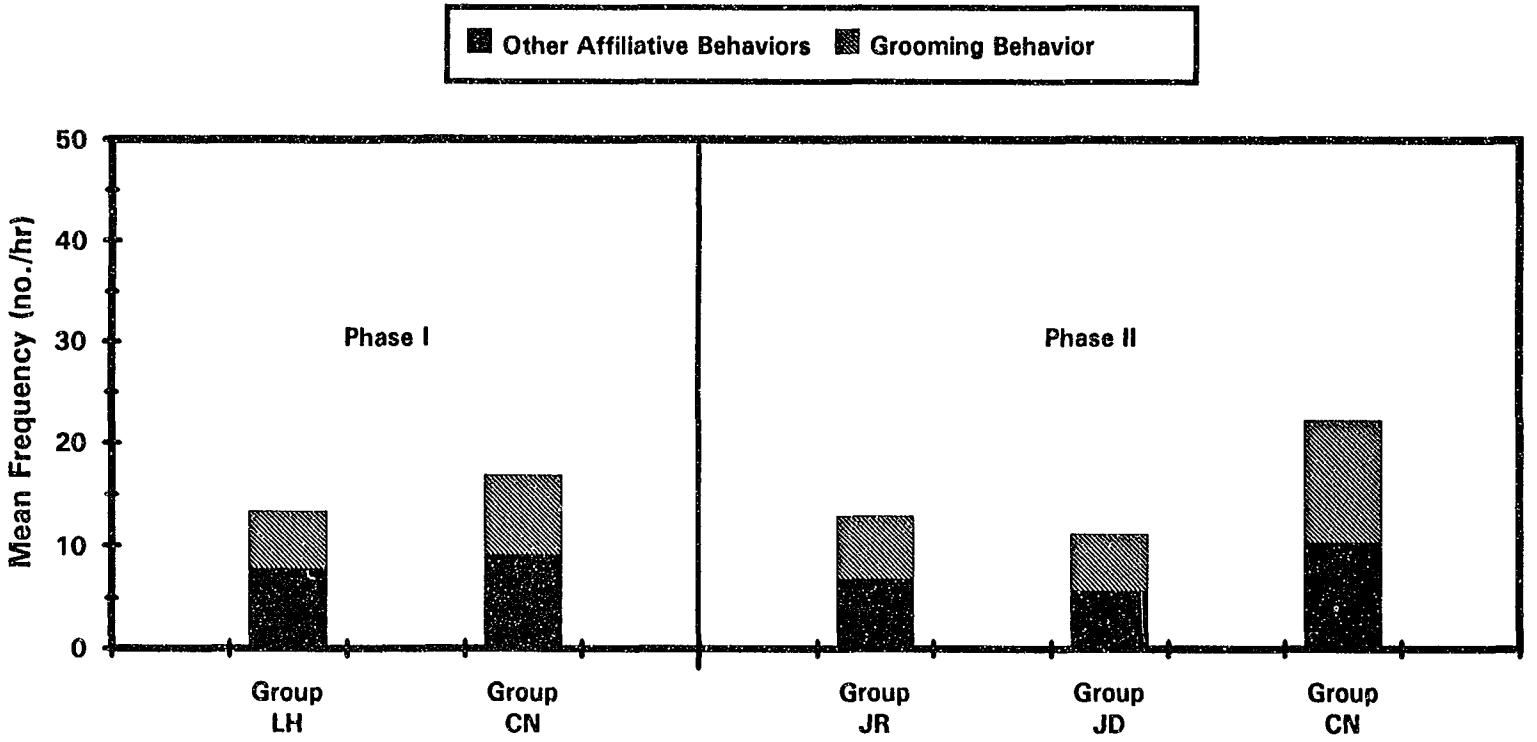


TABLE 5.4.a. Mean Distance and Identification of Focal Female Nearest Neighbors Based on Instantaneous Scan Sampling (N = 1,872) During Phase I

Focal Female ID#	ID# of NN	Mean Distance (m) of NN from Focal Female	ID# of 2nd NN	Mean Distance (m) of 2nd NN from Focal Female
Group LH				
11	13*	0.6	10~	1.3
12	18	1.6	14	2.4
13	10~	0.3	11*	1.0
14	17*	0.5	18	0.8
15	16*	0.5	11	1.0
16	15*	0.4	11	0.9
17	14*	0.6	18	1.4
18	14*	0.9	12	1.5
N = 8		Mean (± s.e.) 0.7 ± .1		Mean (± s.e.) 1.3 ± .2
Group CN				
62	67*	0.4	60~	0.8
63	64*	0.5	66	0.6
64	63*	0.4	65	1.5
65	60*~	1.6	64	2.1
66	67*	0.5	62	1.0
67	62*	0.4	66	0.7
N = 6		Mean (± s.e.) 0.6 ± .2		Mean (± s.e.) 1.1 ± .2

*NN is Focal Female's Grooming Partner
~NN is Unit Male

TABLE 5.4.b. Mean Distance and Identification of Focal Female Nearest Neighbors based on Instantaneous Scan Sampling (N = 3,122) During Phase II

Focal Female ID#	ID# of NN	Mean Distance (m) of NN from Focal Female	ID# of 2nd NN	Mean Distance (m) of 2nd NN from Focal Female
Group JR				
11	61*~	0.7	13	0.8
13	11	0.6	16*	1.1
15	88*	0.7	16	0.6
16	13*	0.8	15	1.7
88	15*	0.9	16	1.7
N = 5		Mean (± s.e.) 0.7 ± .1		Mean (± s.e.) 1.2 ± .2
Group JD				
12	18*	1.9	86~	2.8
14	17*	0.3	86~	2.3
17	14*	0.4	86~	1.4
18	17	0.6	12*	1.6
87	12	2.4	86~	3.5
N = 5		Mean (± s.e.) 1.1 ± .4		Mean (± s.e.) 2.3 ± .3
Group CN				
63	67*	0.4	60~	1.1
64	63*	0.5	67	0.8
65	60*~	0.8	64	0.7
67	63*	0.5	60~	0.9
N = 4		Mean (± s.e.) 0.6 ± .1		Mean (± s.e.) .9 ± .2

*NN is Focal Female's grooming partner
~NN is Unit Male

The maintenance by females of strong affiliative relationships with a small number of other females has an important effect on the outcomes of interactions with other group members and other reproductive units. Membership in a grooming dyad forms the basis of coalitionary support. Table 5.5 shows that a female in a grooming dyad is more likely to support her partner in agonistic encounters than to support non-partner females (Phase I: $t = 3.821$, $df = 13$, $p<0.01$; Phase II: $t = 4.072$, $df = 13$, $p<0.01$). This pattern of interaction by females becomes overtly apparent during observations of agonistic encounters. Often, the individuals involved erratically alternate between stares and approaches directed to both the aggressor and the grooming partner. Given the high probability that grooming partners will provide coalitionary support to one another, it is not surprising that females spend a proportionately high amount of time maintaining close bonds with these individuals.

5.7. Female Dominance Relationships

Female relationships result from interactions that are both affiliative and agonistic. Agonistic interactions demonstrate dominance relationships. In the wild, dominance relationships among females have been shown to depend both on the degree of support from an individual's coalitionary partner and on her aggressiveness; female geladas do not inherit rank positions (Dunbar, 1980a). These same factors proved to be the determining variables of dominance relations in this captive study as well.

Approach-retreat interactions (supplantations) were used to determine the rank of the females in each unit. All approach-retreat encounters between females of the same group were recorded and placed into a win-loss matrix, and

TABLE 5.5.a. Probability of Coalitionary Support by Grooming Dyad Partners and Non-Partner Females During Intra-Group Encounters (Phase I)

Focal Female ID# (ID# of Grooming Dyad Partner)	Number of Times (%) Focal Female is Supported by Grooming Dyad Partner	Number of Times (%) Focal Female is Supported by Other Female Group Members
Group LH		
11 (13)	64.2	32.6
12*	*	6.8
13 (11)	80.4	22.9
14 (17)	69.6	40.4
15 (16)	76.5	35.8
16 (15)	88.1	37.7
17 (14)	91.1	31.3
18 (14)	53.7	19.8
N = 8	Mean (± s.e.) 74.8 ± 4.7	Mean (± s.e.) 28.4 ± 3.9
Group CN		
62 (67)	85.2	59.7
63 (64)	84.3	23.1
64 (63)	81.4	19.6
65 (60)**	30.5	8.3
66 (67)	63.6	37.8
67 (62)	70.6	48.6
N = 6	Mean (± s.e.) 69.3 ± 8.5	Mean (± s.e.) 32.9 ± 7.9

*Focal Female is not in a "Grooming Dyad"

**Focal Female is in a "Grooming Dyad" with Unit Male

TABLE 5.5.b. Probability of Coalitionary Support by Grooming Dyad Partners and Non-Partner Females During Intra-Group Encounters (Phase II)

Focal Female ID# (ID# of Grooming Dyad Partner)	Number of Times (%) Focal Female is Supported by Grooming Dyad Partner	Number of Times (%) Focal Female is Supported by Other Female Group Members
Group JR		
11 (61)**	39.1	20.7
13 (16)	83.3	17.4
15 (88)	70.6	30.5
16 (13)	67.9	22.8
88 (15)	35.4	8.2
N = 5	Mean (± s.e.) 59.3 ± 9.3	Mean (± s.e.) 19.9 ± 3.6
Group JD		
12 (18)	37.9	19.5
14 (17)	71.3	46.8
17 (14)	93.6	53.1
18 (12)	87.4	29.2
87*	*	5.3
N = 5	Mean (± s.e.) 72.6 ± 11.2	Mean (± s.e.) 30.8 ± 8.9
Group CN		
63 (67)	66.1	33.4
64 (63)	74.7	24.6
65 (60)**	28.3	7.6
67 (63)	89.6	44.2
N = 4	Mean (± s.e.) 64.7 ± 13.1	Mean (± s.e.) 27.5 ± 7.7

*Focal Female is not in a "Grooming Dyad"
**Focal Female is in "Grooming Dyad" with Unit Male

the rank order of the females within the group determined by calculating who consistently supplanted whom in these interactions (Lehner, 1979). The dominance matrices that resulted are provided in Table 5.6. Linearity was calculated using Landau's Index of Linearity ($h = 12 / n^3 - n (V_a - 1/2 (n-1))^2$) (Lehner, 1979; Martin and Bateson, 1986) where n = the number of individuals in the group and V_a= the number of individuals that have retreated from A. The indices for each group are given in Table 5.7. The index is 1.0 in each case indicating completely transitive, linear relationships (i.e., A is dominant to B, and A and B are dominant to C). Spearman correlations showed that the total number of times an individual retreated from another was negatively correlated with rank (i.e., 'A' retreated from others the least number of times and 'E' retreated from others the most number of times) while the total number of times an individual was retreated from was positively correlated with rank (i.e., 'A' was retreated from by others the most number of times and others retreated from "E' the least number of times) (see Table 5.7 for rank orders).

In the next chapter, correlations between these social relationships and ovulatory function will be explored.

5.8. Male-Female Relationships

On average, a harem male spends over 50% of his social time interacting with adult females and relatively little time with other members of his unit (Dunbar, 1984). Although the composition of the groups in the present study did not allow this distinction to be made, the harem male's time spent socializing was unequally distributed across the females in his unit (Figure 5.6). Males spent the majority of their social time in grooming interactions with one or two

particular females but a much lower frequency with other females in their unit (Phase I: Group LH, $F = 29.696$, $df = 1,7$, $p<0.001$; Group CN, $F = 17.543$, $df = 1,5$, $p<0.01$; Phase II: Group JR, JD, , $F = 9.623$, 11.044, $df = 1,4$, $p<0.05$, respectively, and Group CN, $F = 10.752$, $df = 1,3$, $p<0.05$). During Phase I, the main grooming partner of the male in one of the study groups (CN) was a female who lacked a female grooming partner, and this was the case for two out of the three groups (Groups JR and CN) during Phase II. It appeared to be that these females were using the male as a substitute female, as reported in wild populations (Dunbar, 1984). In addition, in all study groups the individuals that maintained a close grooming relationship with the unit male also maintained a close spatial relationship to the male (Spearman rank correlation coefficient: Phase I ($N = 14$) $r_s = 0.916$, $p<0.01$; Phase II ($N = 14$) $r_s = 0.751$, $p<0.05$) (Figure 5.7).

Differences in the relationship between a female and her unit male occurred as a result of whether a female was in the ovulatory or non-ovulatory phase of her cycle. Most notably, during the ovulatory phase of the menstrual cycle females exhibited a greater frequency of proceptive and receptive behaviors, while males displayed a significantly greater proportion of affiliative behaviors towards females. However, females that maintain a relatively low rank in a group received a significantly greater amount of agonistic threats and interference from more dominant females as a consequence of these interactions with the unit male. Variations in male-female relationships throughout the ovulatory cycle are described in the next chapter.

TABLE 5.6.a. The Number of Occasions When Individuals are Supplanted During Approach-Retreat Interactions Observed During Focal Female Sampling (N = 576)

Phase I: Group LH

	Supplantee								
ID#	13	11	16	15	17	14	18	12	TOTALS
13	--	26	15	19	8	11	7	4	90
11	0	--	12	7	6	10	3	2	40
16	0	0	--	14	13	9	12	5	53
15	0	0	0	--	20	6	17	16	59
17	0	0	2*	5*	--	16	22	18	63
14	0	0	0	1*	0	--	27	10	38
18	0	0	0	0	0	0	--	23	23
12	0	0	0	0	0	0	0	--	0
TOTALS	0	26	29	46	47	52	88	78	366

*These interactions are not considered reversals in dominance but rather occasions where additional animals in close proximity may have influenced the outcome of the interaction of the two initial individuals.

TABLE 5.6.b. The Number of Occasions When Individuals are Supplanted During Approach-Retreat Interactions Observed During Focal Female Sampling (N = 432)

Phase I: Group CN

	Supplantee						
ID#	**62**	**67**	**66**	**63**	**64**	**65**	**TOTALS**
62	--	17	9	18	10	20	74
67	0	--	7	8	13	16	44
66	0	0	--	14	4	6	24
63	0	0	0	--	6	11	17
64	0	0	0	0	--	8	8
65	0	0	0	0	0	--	0
TOTALS	0	17	16	40	33	61	**167**

TABLE 5.6.c. The Number of Occasions When Individuals are Supplanted During Approach-Retreat Interactions Observed During Focal Female Sampling (N =630)

Phase II: Group JR

	Supplantee					
ID#	11	13	15	16	88	TOTALS
11	--	36	18	10	27	91
13	0	--	15	21	17	53
15	0	0	--	28	8	36
16	0	0	0	--	11	11
88	0	0	0	0	--	0
TOTALS	0	36	33	59	63	191

TABLE 5.6.d. The Number of Occasions When Individuals are Supplanted During Approach-Retreat Interactions Observed During Focal Female Sampling (N = 570)

Phase II: Group JD

	Supplantee					
ID#	17	14	18	12	87	TOTALS
17	--	28	14	9	21	72
14	0	--	11	17	13	41
18	0	0	--	5	14	19
12	0	0	0	--	7	7
87	0	0	0	0	--	0
TOTALS	0	28	25	31	55	139

TABLE 5.6.e. The Number of Occasions When Individuals are Supplanted During Approach-Retreat Interactions Observed During Focal Female Sampling (N = 480)

Phase II: Group CN

	Supplantee				
ID#	67	63	64	65	TOTALS
67	--	19	8	23	50
63	0	--	12	16	28
64	0	0	--	5	5
65	0	0	0	--	0
TOTALS	0	19	20	44	83

TABLE 5.7. Landau's Index of Linearity and Spearman Rank Correlation Coefficients for Females Based on Pairwise Approach-Retreat Interactions During Focal Animal Observations (N = 2,688)

Phase I

Group ID	Number of Hours of Focal Female Sampling	Landau's Index of Linearity (h)	Spearman Rank Correlation Coefficient	
			Supplanter	Supplantee
LH	576	1.0	-0.96	0.97
CN	432	1.0	-1.0	1.0

Phase II

JR	615	1.0	-0.97	1.0
JD	585	1.0	-0.99	0.98
CN	480	1.0	-1.0	1.0

FIGURE 5.6.a. Distribution of the Unit Male's Social Interaction Time Across Individuals in His Unit During Phase I (N = 216 Focal Male Samples)

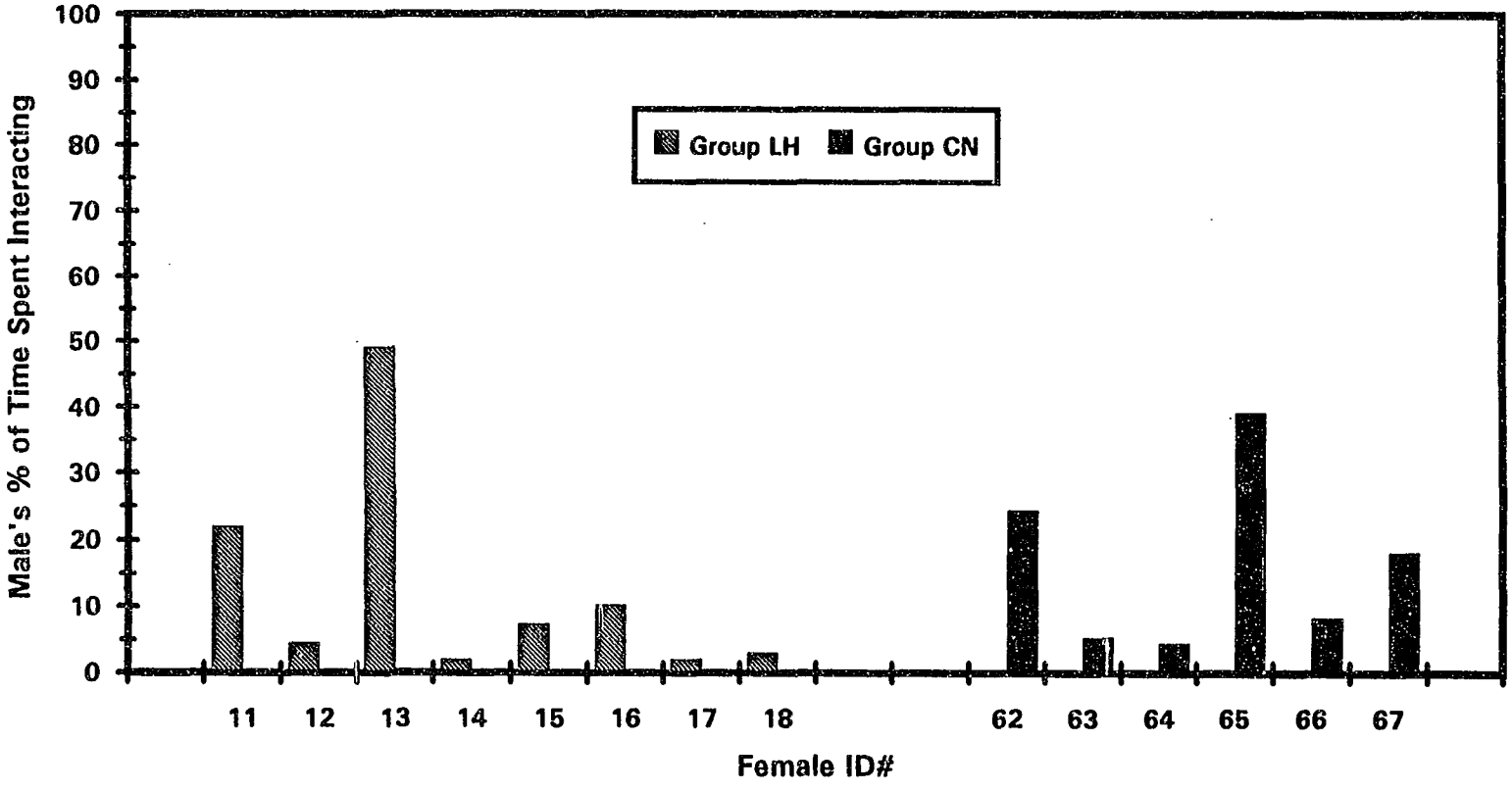


FIGURE 5.6.b. Distribution of the Unit Male's Social Interaction Time Across Individuals in His Unit During Phase II (N = 360 Focal Male Samples)

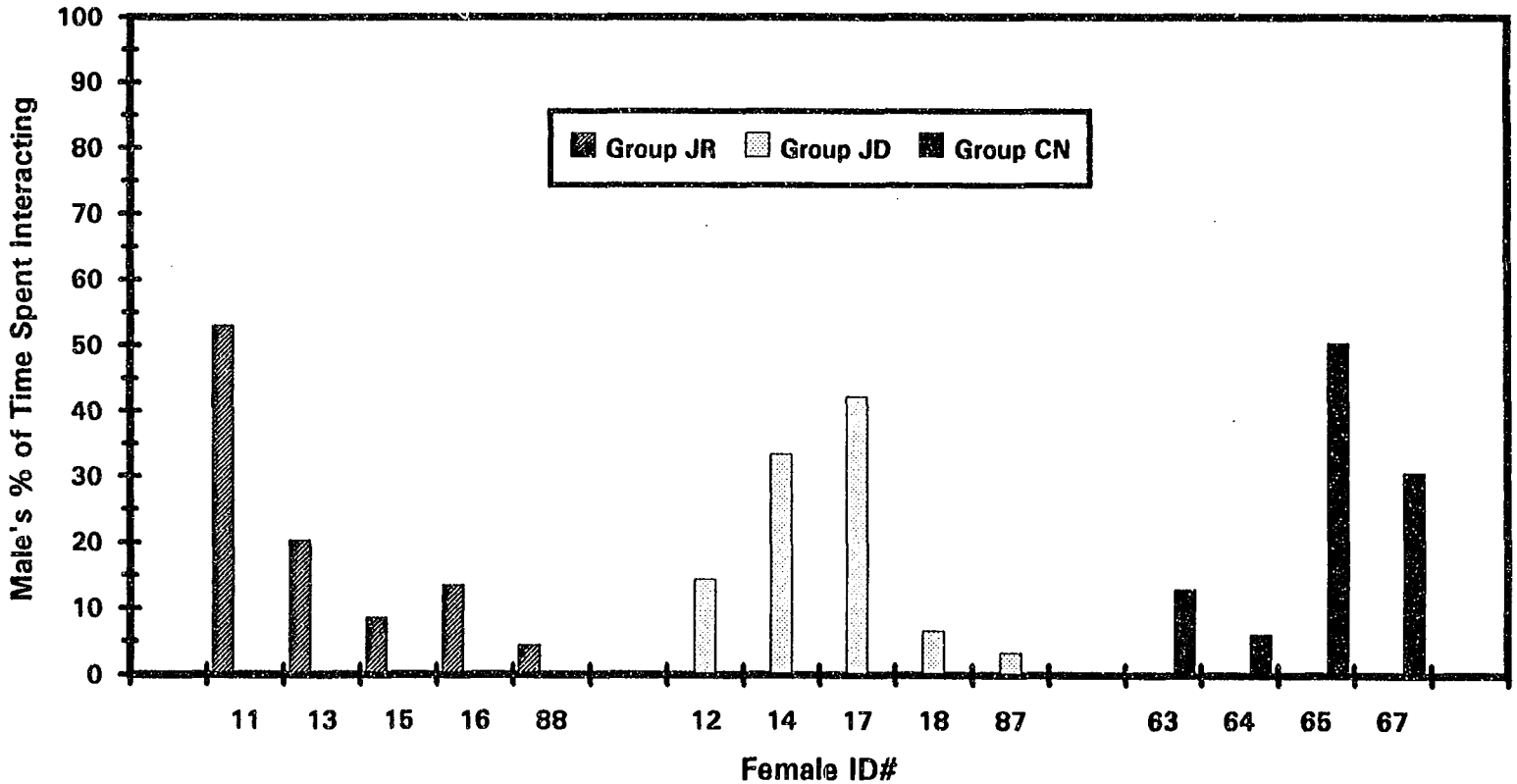


FIGURE 5.7.a. The Number of Occasions (%) When the Unit Male is the Female's Nearest Neighbor Phase I (N = 1,872 Scan Samples)

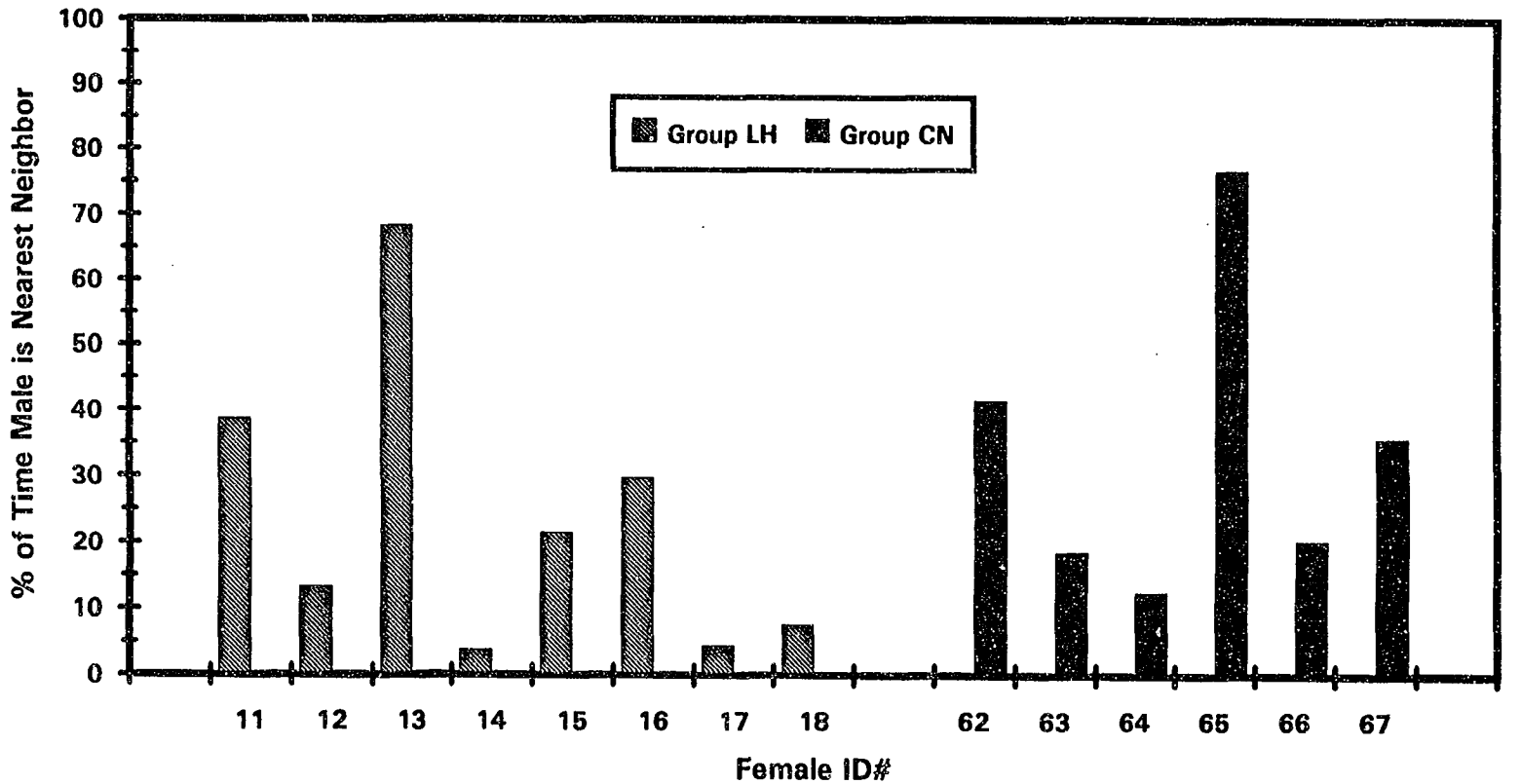
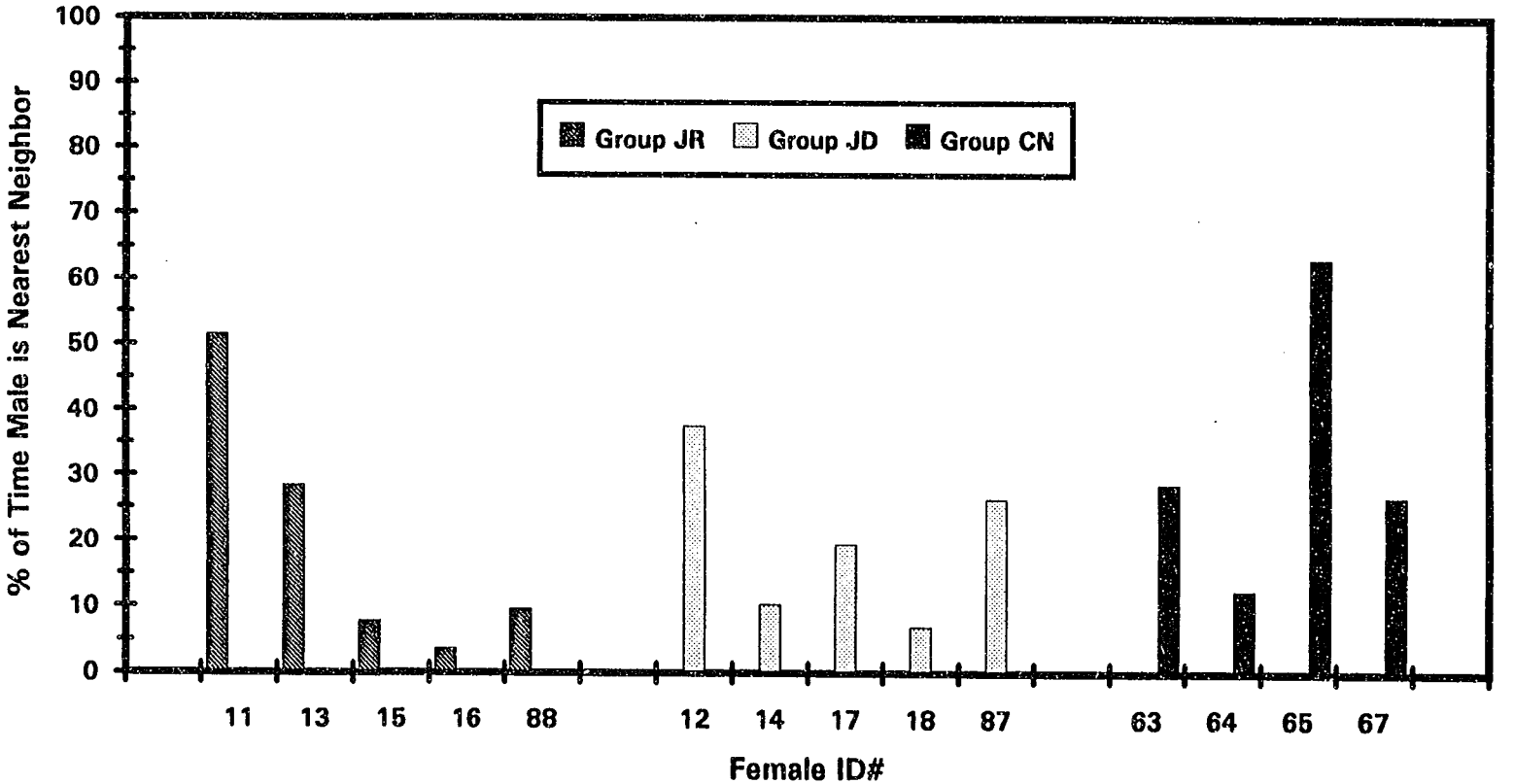


FIGURE 5.7.b. The Number of Occasions (%) When the Unit Male is the Female's Nearest Neighbor Phase II (N = 3,122 Scan Samples)



5.9. Summary of Results

In captive female geladas, the same general patterns of interaction were found as in groups of wild geladas. My findings on the structure of social relationships among females in my study groups suggest the following main conclusions. First, among females there was a difference in time spent feeding on certain preferred food items, however, this difference was not correlated with a female's body weight. Second, each female has most of her interactions with only a small number of other individuals; this network may extend to two or three individuals, but a female will typically interact almost exclusively with just one other female in her unit. Third, the most common social interaction is mutual grooming, where the respective participants form a grooming dyad. As group composition changed-- through the fissioning of groups and the death of certain individuals-- dyad partners changed as well. Fourth, partners in such grooming dyads are more likely to support one another in agonistic encounters with other members of their unit or between reproductive units. Fifth, these grooming dyads form the foundation of coalitionary alliances which can significantly affect a female's dominance rank. Sixth, when a close relative or ally is not available, a female will use the unit male as a grooming partner; otherwise, the male remains relatively peripheral to the group. And sixth, the male does not interact equally with his females; he shows a preference for one or two particular females in his unit.

CHAPTER 6. SOCIAL CORRELATES OF VARIATION IN OVARIAN FUNCTION IN STUDY GROUP FEMALE GELADA BABOONS

6.1. Introduction

In this chapter the relationships between social behavior and reproduction are explored, in particular, the issue of how social interactions between females might affect their fertility. This analysis is based on data drawn from the previous two chapters. In chapter 4, the reproductive cycle of gelada baboons was defined and the pattern of ovarian functioning described along with its hormonal, morphological and behavioral correlates. In chapter 5, the patterns of social relationships among females in the study groups were described and compared to those found in wild populations of geladas.

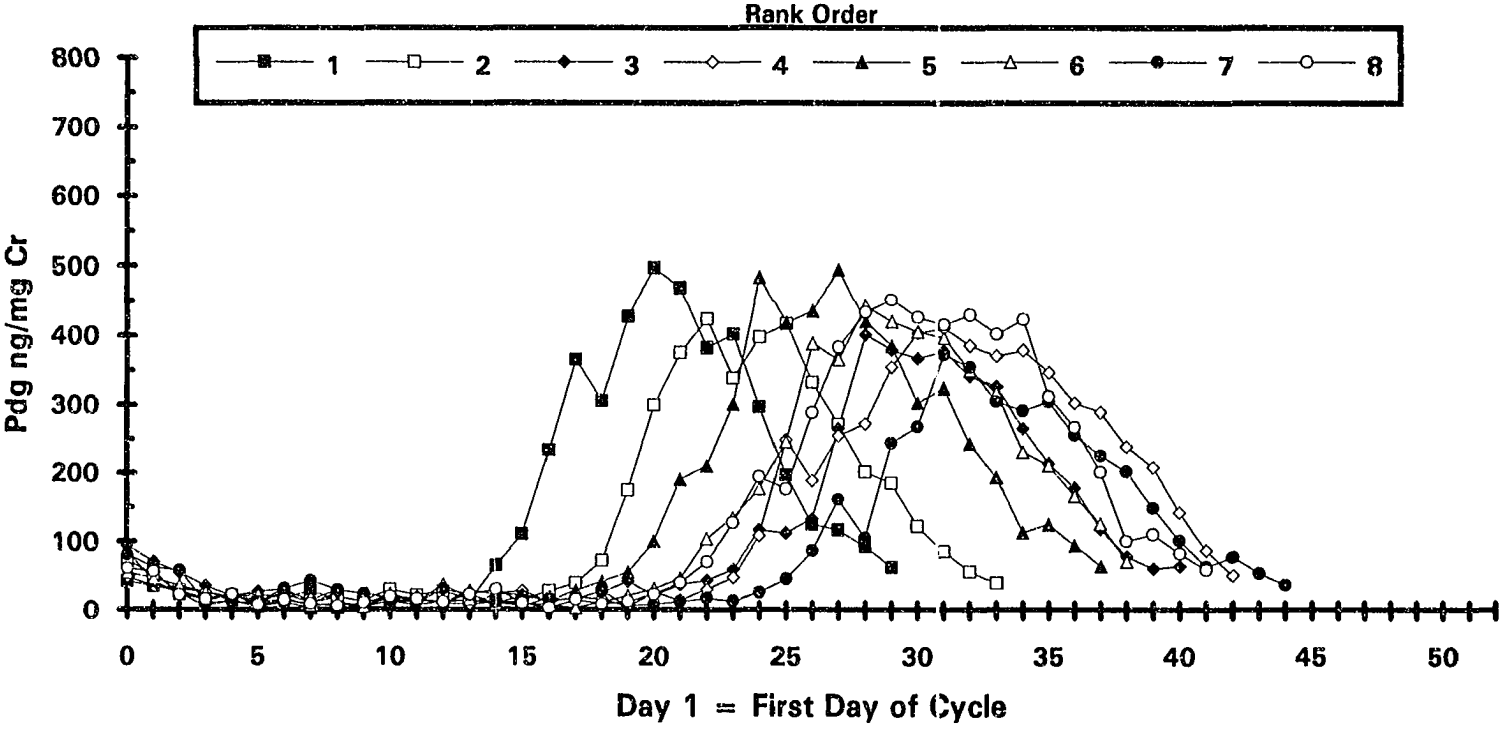
The nature of the relationships among female geladas involves a complex series of affiliative and agonistic interactions, and their outcome produces a hierarchical arrangement of individuals. Here, rather than focusing on general patterns, I discuss variations among females in their social behavior and reproduction, and explore to what degree the two are related. That is, are variations in the patterns of behavior and reproductive functioning related to a female's social position in the group?

6.2. Variation in the Patterns of Ovarian Cyclicity

In Figure 6.1. the mean patterns of ovarian cyclicity for each of the females in all the study groups is presented. When the mean cycling pattern for each female is compared to her social position in the group, adistinct pattern emerges. Low-ranking females (Ranks 3 - 8 [Phase I: N = 10; Phase II: N = 8]) experienced longer cycles than did high-ranking females (Ranks 1 and 2 [Phase I: N = 4; Phase II: N = 6]), based on both hormonal data and the observations on the cyclic changes in vesicular morphology (Table 6.1.). The menstrual cycles of high-ranking females ranged from 27 to 40 days (Figure 6.2.). However, in low-ranking females, 65% of menstrual cycle lengths exceeded the mean for high-ranking females by at least 2 standard deviations. The range in cycle length for low-ranking females was significantly greater, from 31 to 83 days (Figure 6.3). The menstrual cycles for high-ranking females lasted a mean ($\pm$ s.d.) of 31.9 $\pm$ 2.2 days (Phase I: 31.3 $\pm$ 2.1; Phase II: 32.2 $\pm$ 2.3), while for low-ranking females they lasted an average of 41.1 $\pm$ 5.9 days (Phase I: 41.3 $\pm$ 3.1; Phase II: 40.9 $\pm$ 3.6) (Phase I: $t = 2.108$, Phase II: $t = 1.943$, $p<0.10$, n.s.) (Figure 6.4).

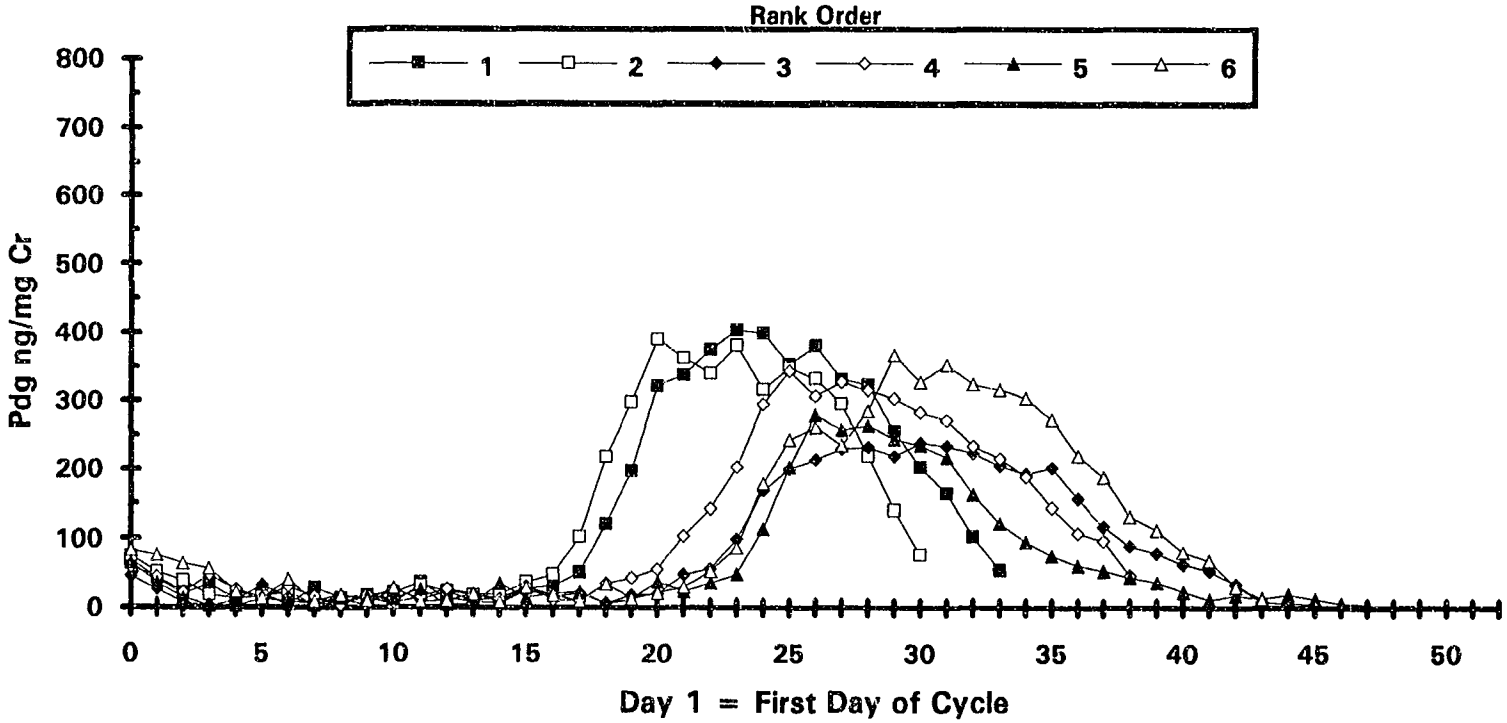
Further analyses revealed that the elongated menstrual cycles in low-ranking females were due to a significant increase in follicular phase length (Table 6.2). Follicular phase lengths averaged 14.5 ($\pm$ 0.5 s.d.) days (Phase I: 14.6 $\pm$ 0.9, Phase II: 15.2 $\pm$ 1.3) for high-ranking females; while for low-ranking females the average was significantly longer at 23.0 $\pm$ 4.3 days (Phase I: 23.2 $\pm$ 2.1, Phase II: 23.9 $\pm$ 2.5) (Phase I: $t = 3.162$, Phase II: $t = 3.345$, $p<0.01$) (Figure 6.5.). Luteal phase length, however, was 16.4 $\pm$ 0.4 days (Phase I: 16.6 $\pm$ 1.2, Phase II: 16.8 $\pm$ 0.9) for high-ranking females, while for low-ranking females it averaged 17.8 days $\pm$ 0.6 (Phase I: 18.1 $\pm$ 1.3, Phase

FIGURE 6.1.a. Mean Menstrual Cycle Patterns*
of Study Group Females of Different Social Rank (Group LH)



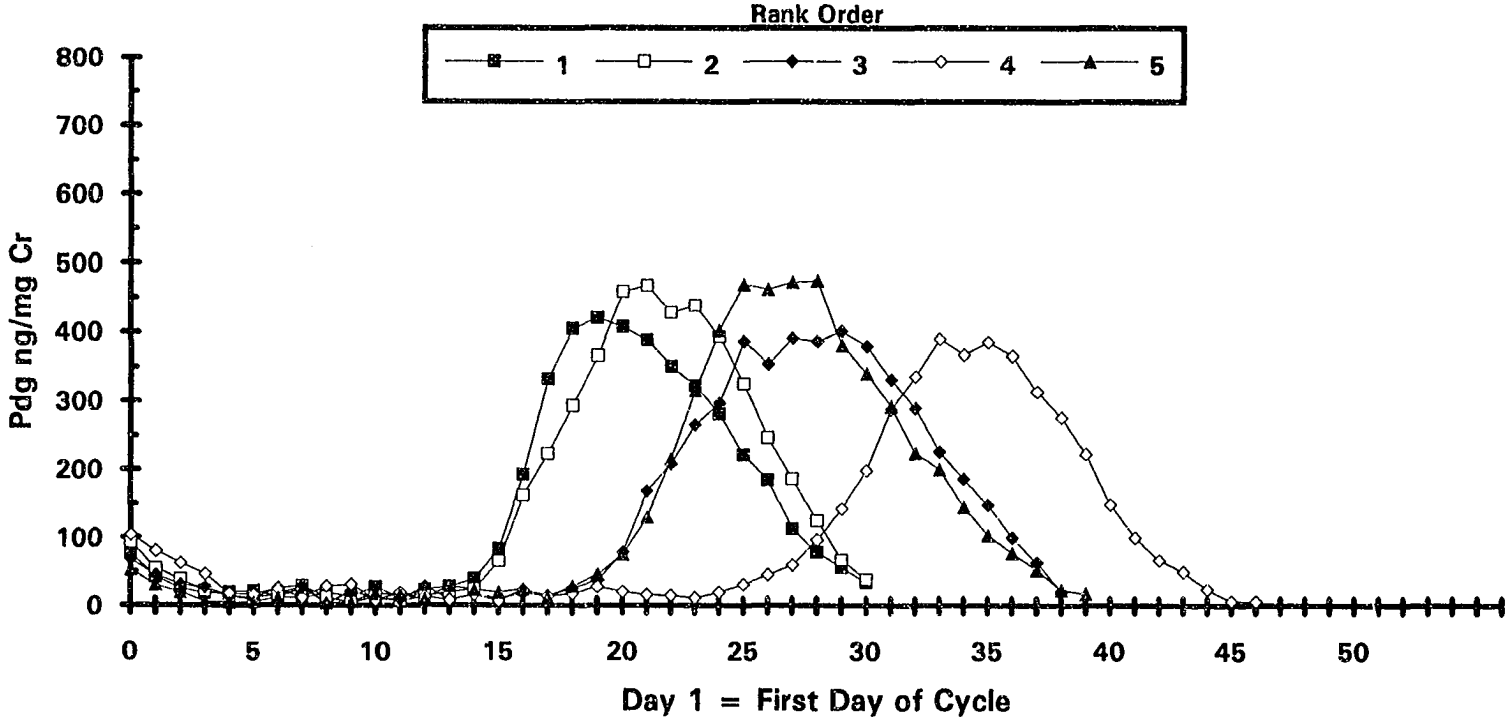
*Patterns are derived from mean lengths for follicular, luteal and menstrual cycles and mean PdG excretion levels during each phase.

FIGURE 6.1.b. Mean Menstrual Cycle Patterns*
of Study Group Females of Different Social Rank (Group CN)



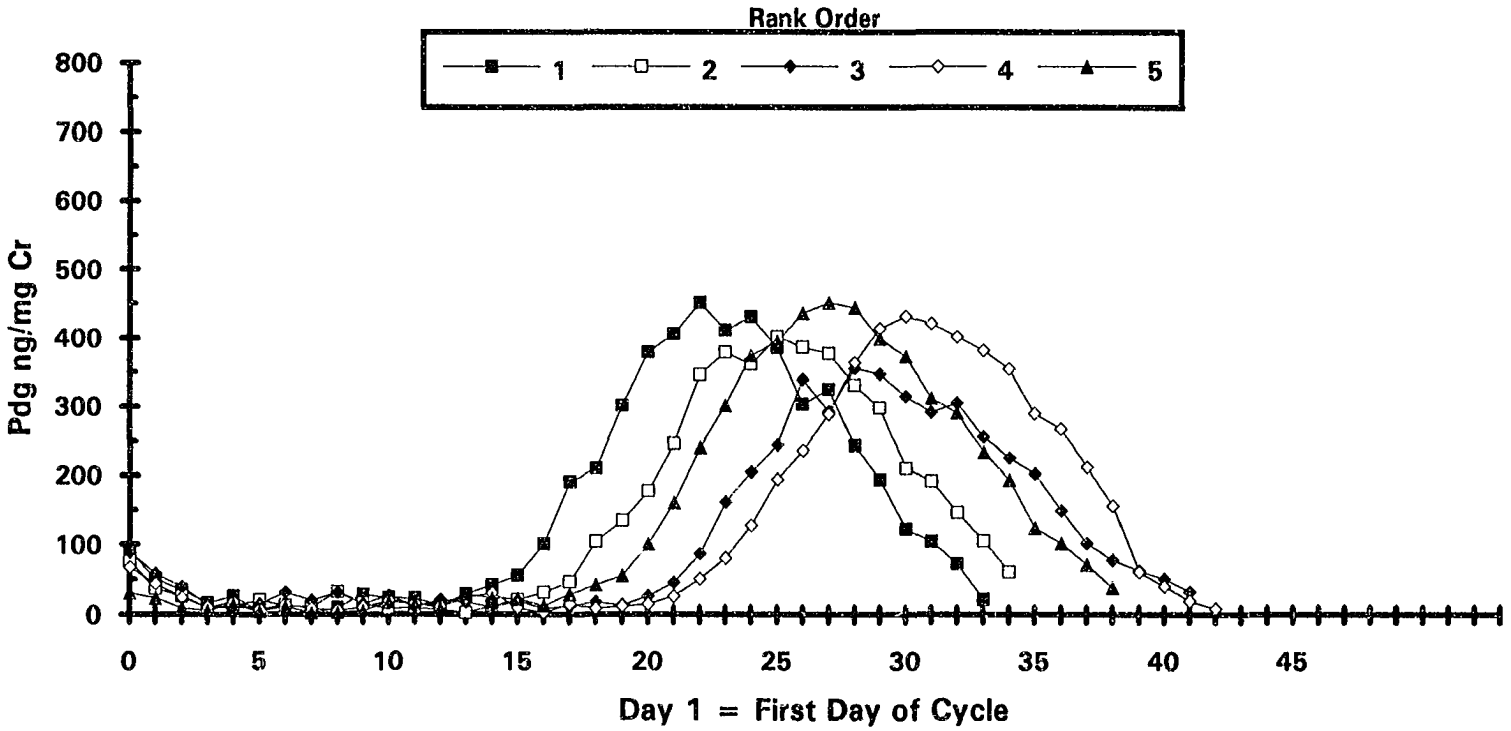
*Patterns are derived from mean lengths for follicular, luteal and menstrual cycles and mean PdG excretion levels during each phase.

FIGURE 6.1.c. Mean Menstrual Cycle Patterns*
of Study Group Females of Different Social Rank (Group JR)



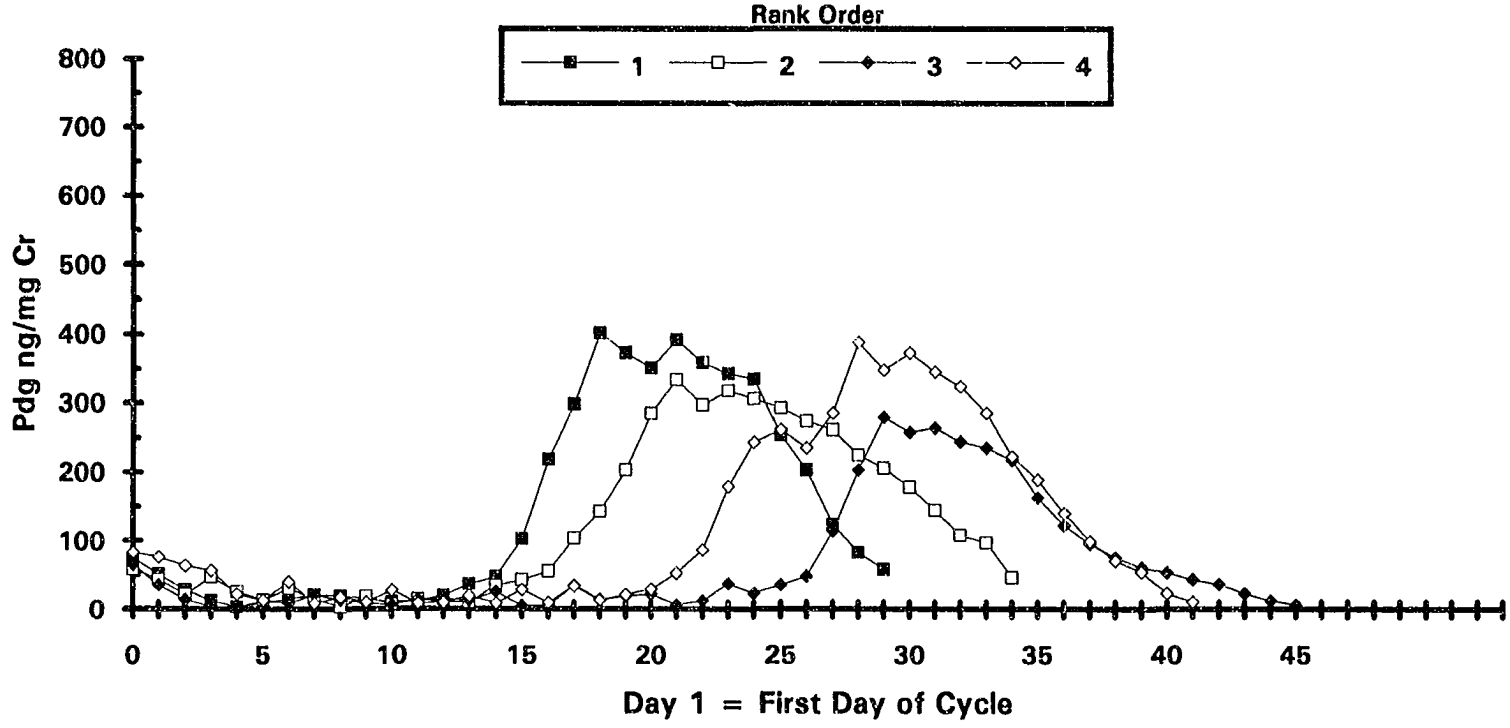
*Patterns are derived from mean lengths for follicular, luteal and menstrual cycles and mean PdG excretion levels during each phase.

FIGURE 6.1.d. Mean Menstrual Cycle Patterns*
Across Social Rank in Study Group JD Females



*Patterns are derived from mean lengths for follicular, luteal and menstrual cycles and mean PdG excretion levels during each phase.

FIGURE 6.1.e. Mean Menstrual Cycle Patterns*
Across Social Rank in Study Group CN Females (Phase II)



*Patterns are derived from mean lengths for follicular, luteal and menstrual cycles and mean PdG excretion levels during each phase.

TABLE 6.1. A Comparison of Menstrual Cycle Length Among Females of Different Social Rank

Phase I

Group ID: Female ID#	Social Rank	Cycle Length Range (Days)	Cycle Length Mean ± s.e. (Days)	% (N) Anovulatory Cycles
LH: 13	1	27 - 30	28.8 ± 1.9	16.6 (1)
11	2	30 - 34	33.3 ± 1.4	0
16	3	34 - 49	40.1 ± 5.9	0
15	4	37 - 63	42.4 ± 4.1	20.0 (1)
17	5	33 - 44	37.2 ± 2.4	0
14	6	35 - 49	37.6 ± 1.1	0
18	7	34 - 57	43.7 ± 7.3	16.6 (1)
12	8	33 - 59	40.9 ± 8.6	33.3 (2)
CN: 62	1	29 - 33	32.7 ± 1.4	0
67	2	27 - 31	30.2 ± 1.7	0
66	3	37 - 68	44.5 ± 7.8	16.6 (1)
63	4	36 - 48	38.1 ± 5.7	0
64	5	39 - 62	46.4 ± 3.9	33.3 (2)
65	6	38 - 83	41.7 ± 9.4	20.0 (1)

Phase II

JR: 11	1	29 - 33	30.4 ± 1.3	0
13	2	29 - 32	30.7 ± 1.8	0
15	3	35 - 54	38.2 ± 4.0	0
16	4	38 - 71	45.6 ± 6.2	28.5 (2)
88	5	31 - 45	38.5 ± 5.1	0
JD: 17	1	30 - 34	33.4 ± 2.1	0
14	2	29 - 38	34.3 ± .9	0
18	3	34 - 56	40.5 ± 6.9	0
12	4	33 - 47	42.1 ± 9.8	11.0 (1)
87	5	33 - 77	39.6 ± 8.7	22.2 (2)
CN: 67	1	27 - 30	28.9 ± 1.6	0
63	2	33 - 40	34.4 ± 5.1	0
64	3	42 - 67	45.1 ± 3.7	12.5 (1)
65	4	36 - 72	38.2 ± 6.3	22.5 (2)

FIGURE 6.2. The Range in Menstrual Cycle Length in High-Ranking Females (Ranks 1 and 2)

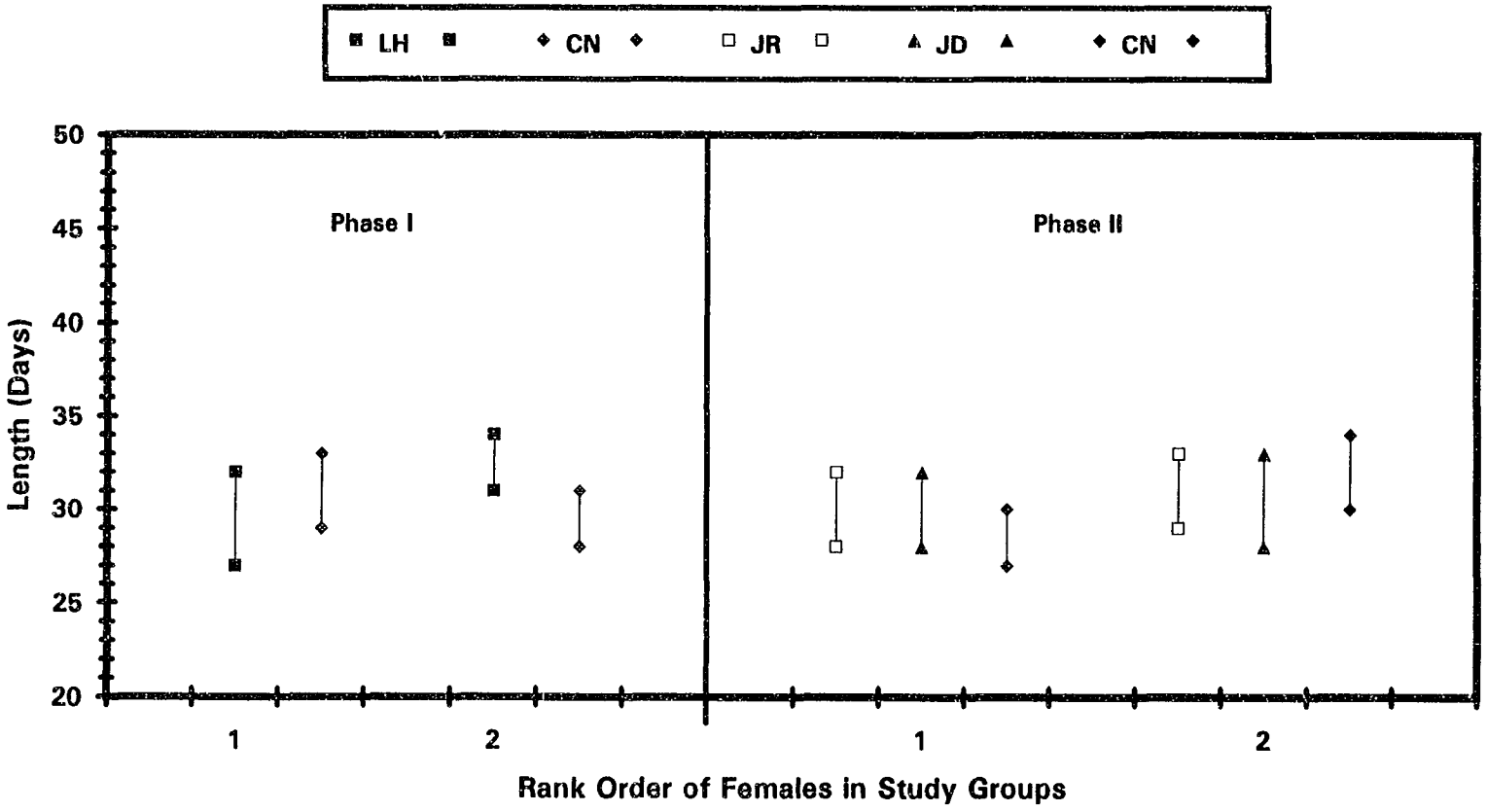


FIGURE 6.3. The Range in Menstrual Cycle Length in Low-Ranking Females (Ranks 3 - 8)

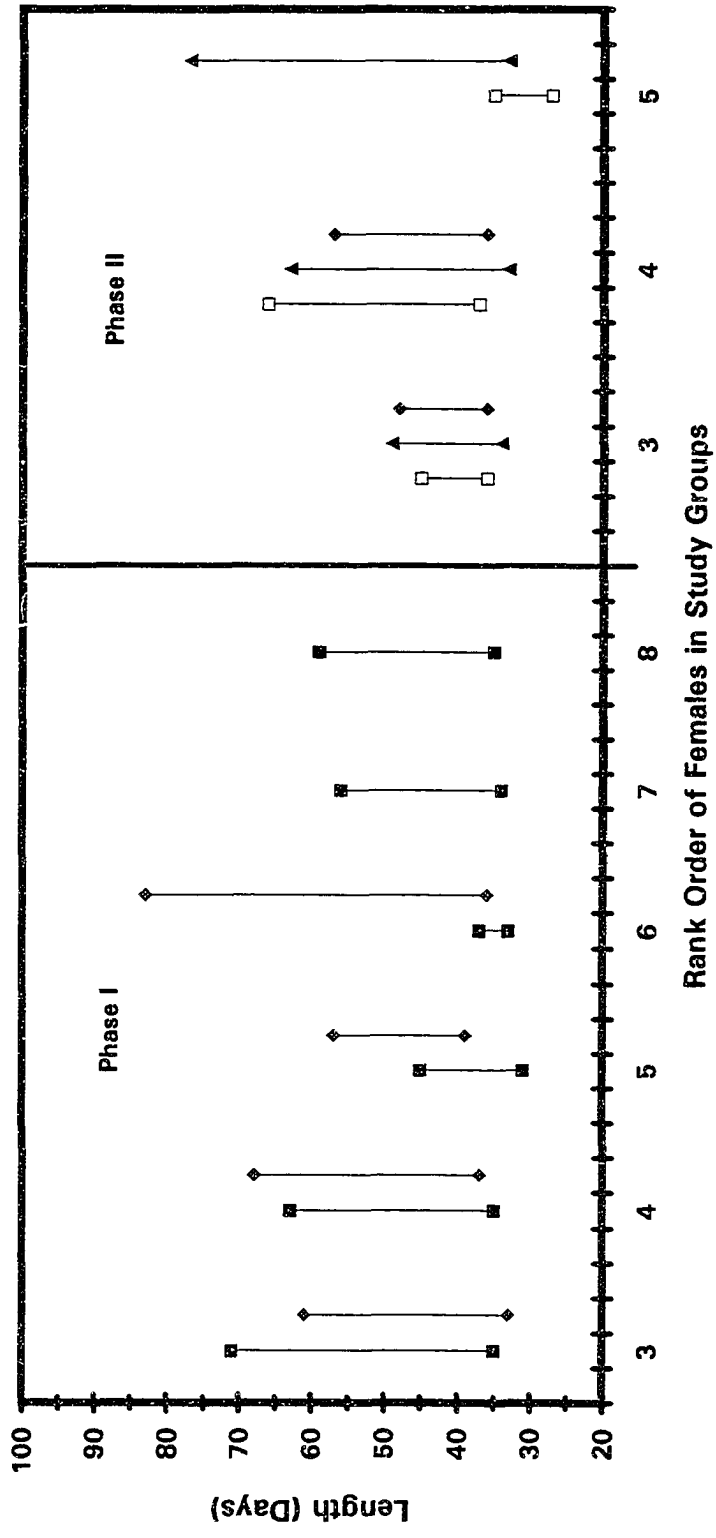


FIGURE 6.4.a. Mean Duration of Menstrual Cycle Length in Study Group Females

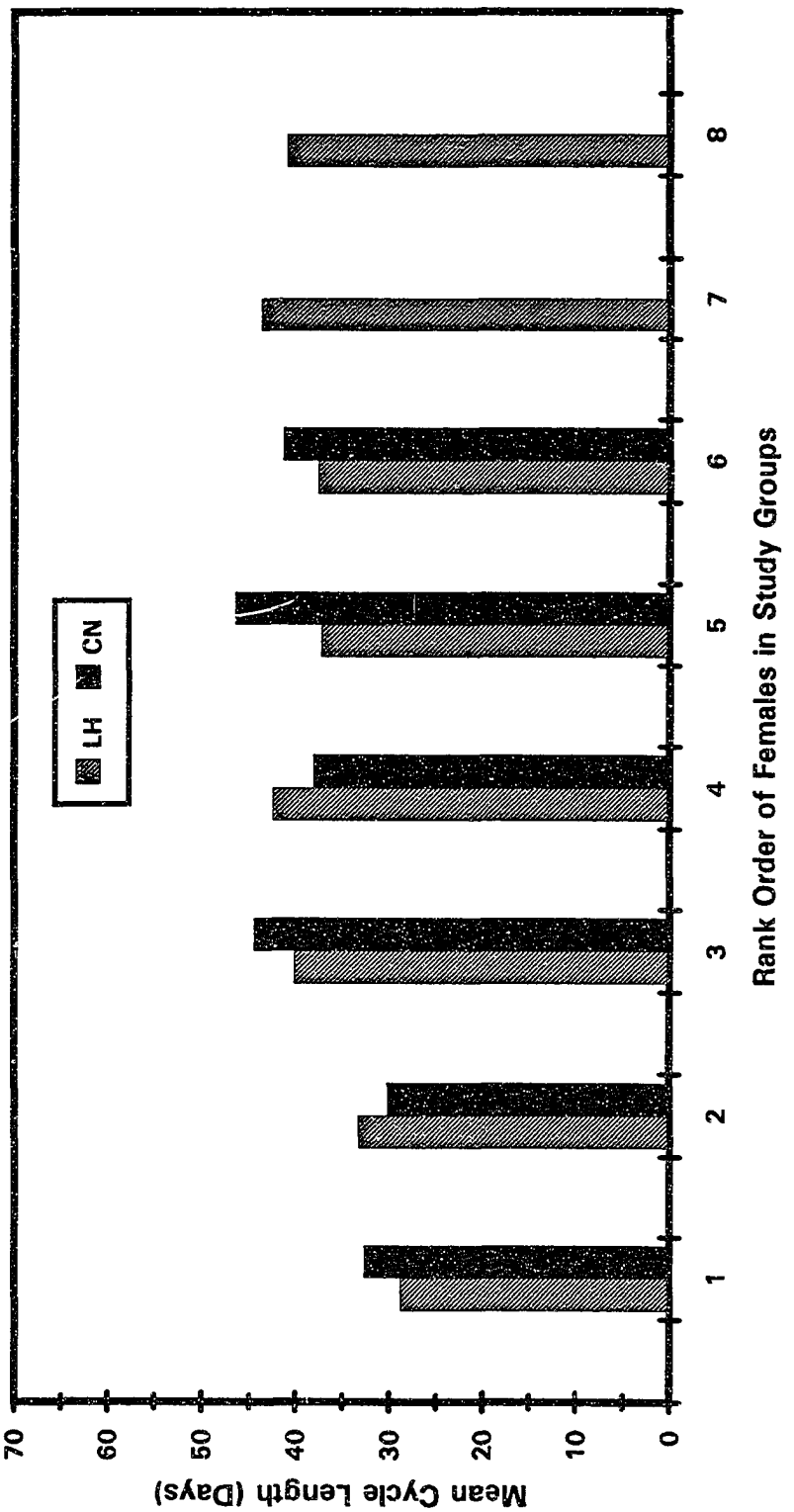


FIGURE 6.4.b. Mean Duration of Menstrual Cycle Length in Study Group Females

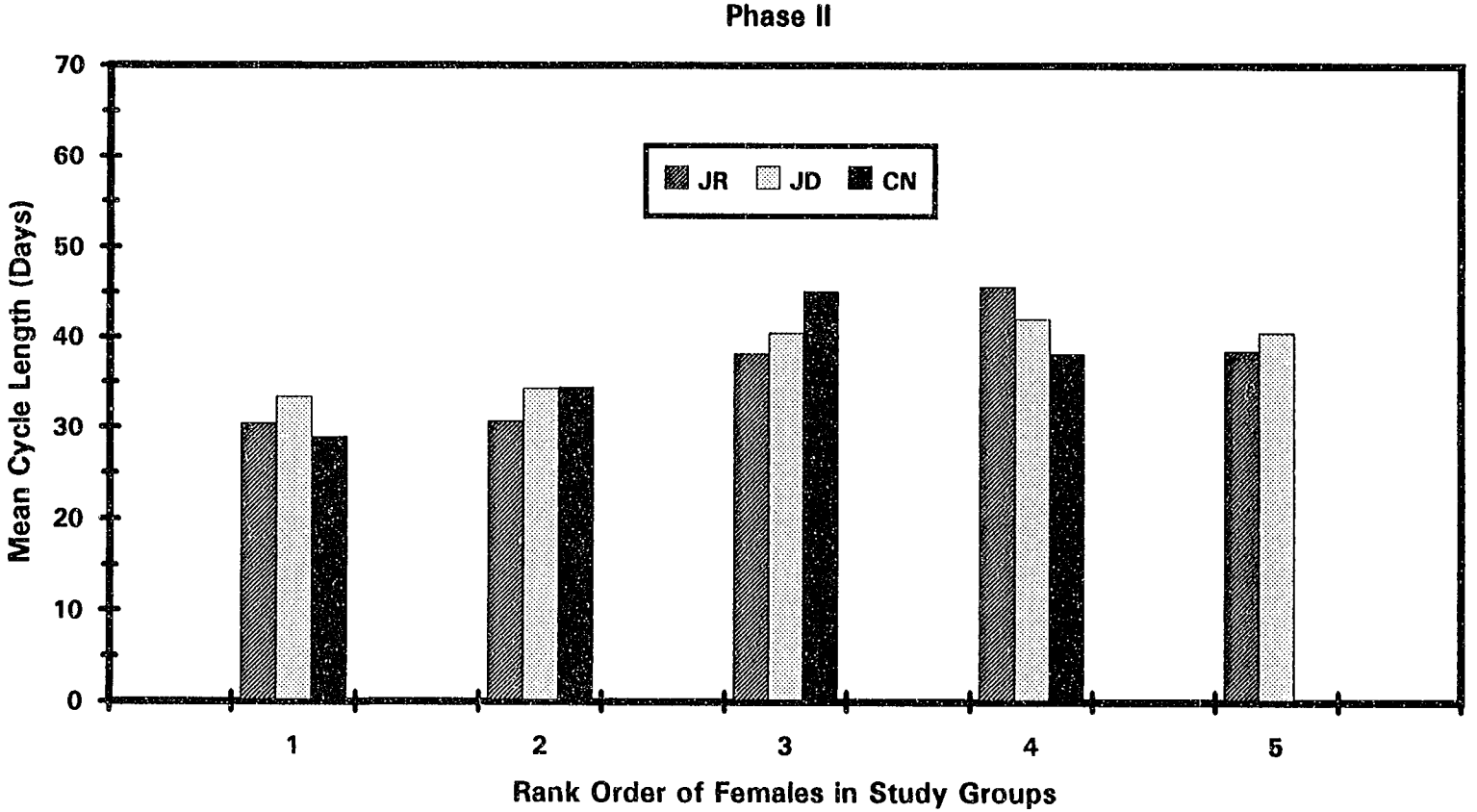


TABLE 6.2. A Comparison of Follicular and Luteal Phase Length Across Social Rank in Study Group Females

Phase I

Group ID: Female ID#	Social Rank	Follicular Phase Range (Days)	Luteal Phase Range (Days)
LH: 13	1	12 -15	14 - 17
11	2	14 - 17	16 - 19
16	3	16 - 43	15 - 20
15	4	21 - 45	18 - 26
17	5	16 - 19	17 - 19
14	6	17 - 24	16 - 20
18	7	19 - 38	17 - 21
12	8	16 - 39	16 - 21
CN: 62	1	13 - 16	14 - 17
67	2	12 - 16	16 - 18
66	3	17 - 50	16 - 22
63	4	15 - 43	16 - 18
64	5	18 - 39	17 - 21
65	6	19 - 64	16 - 19

Phase II

JR: 11	1	12 - 16	15 - 18
13	2	13 - 16	14 - 18
15	3	18 - 36	16 - 21
16	4	20 - 53	17 - 24
88	5	15 - 27	16 - 23
JD: 17	1	14 - 17	16 - 19
14	2	18 - 20	17 - 20
18	3	17 - 24	15 - 19
12	4	18 - 41	16 - 20
87	5	14 - 59	17 - 21
CN: 67	1	13 - 16	15 - 19
63	2	14 - 21	15 - 17
64	3	19 - 33	15 - 20
65	4	16 - 48	14 - 18

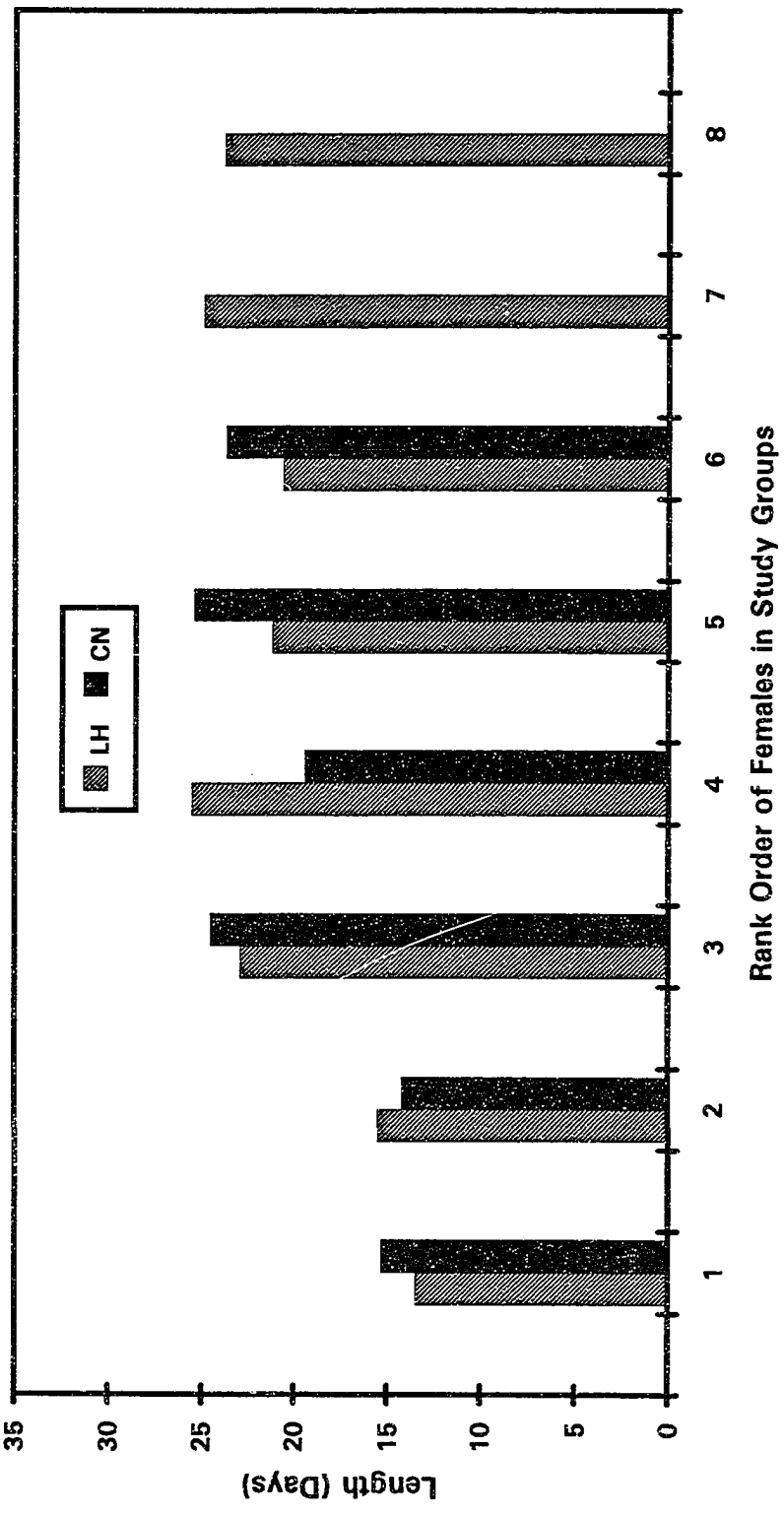


FIGURE 6.5.a. Mean Follicular Phase Length in Study Group Females

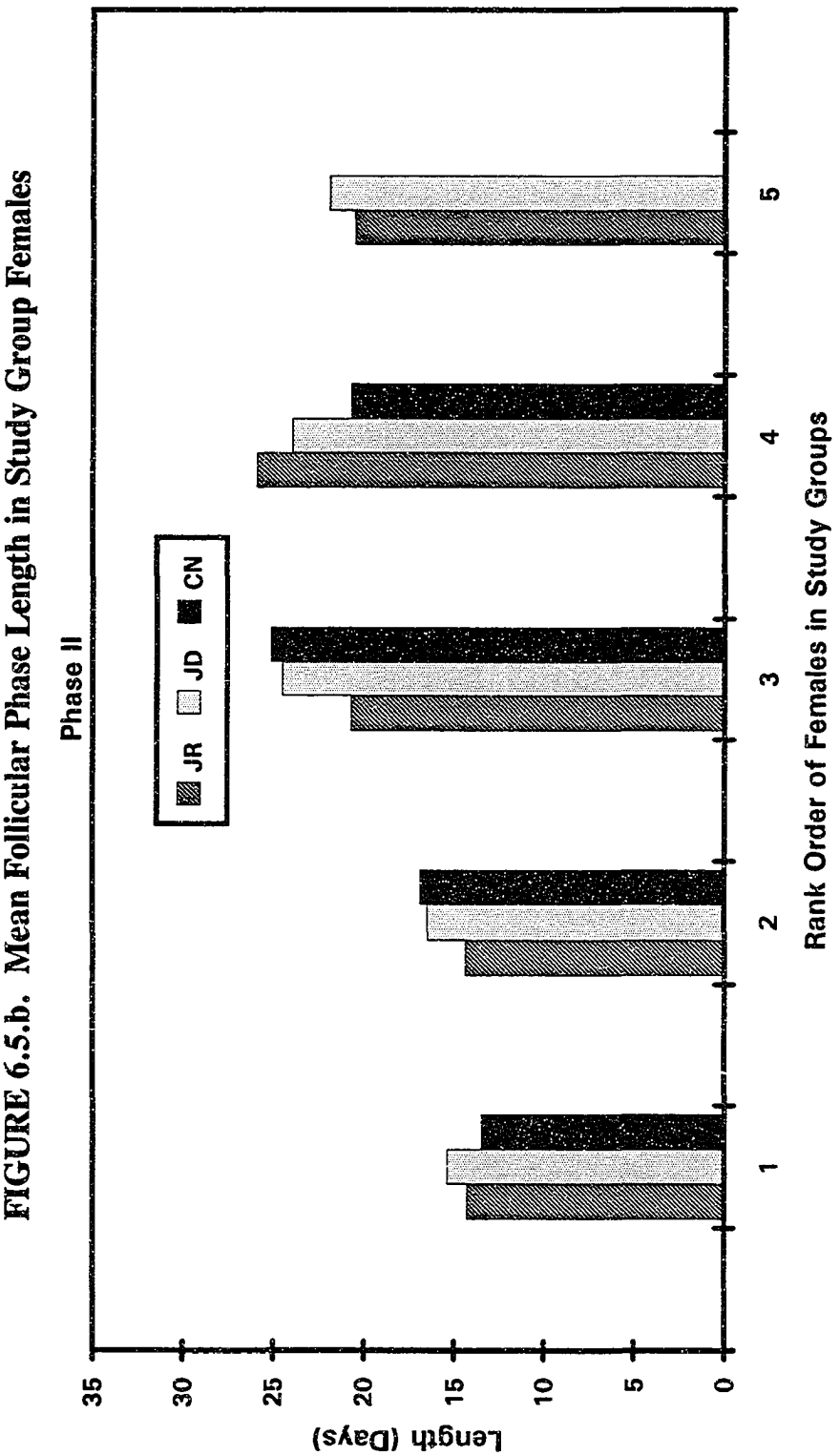


FIGURE 6.5.b. Mean Follicular Phase Length in Study Group Females

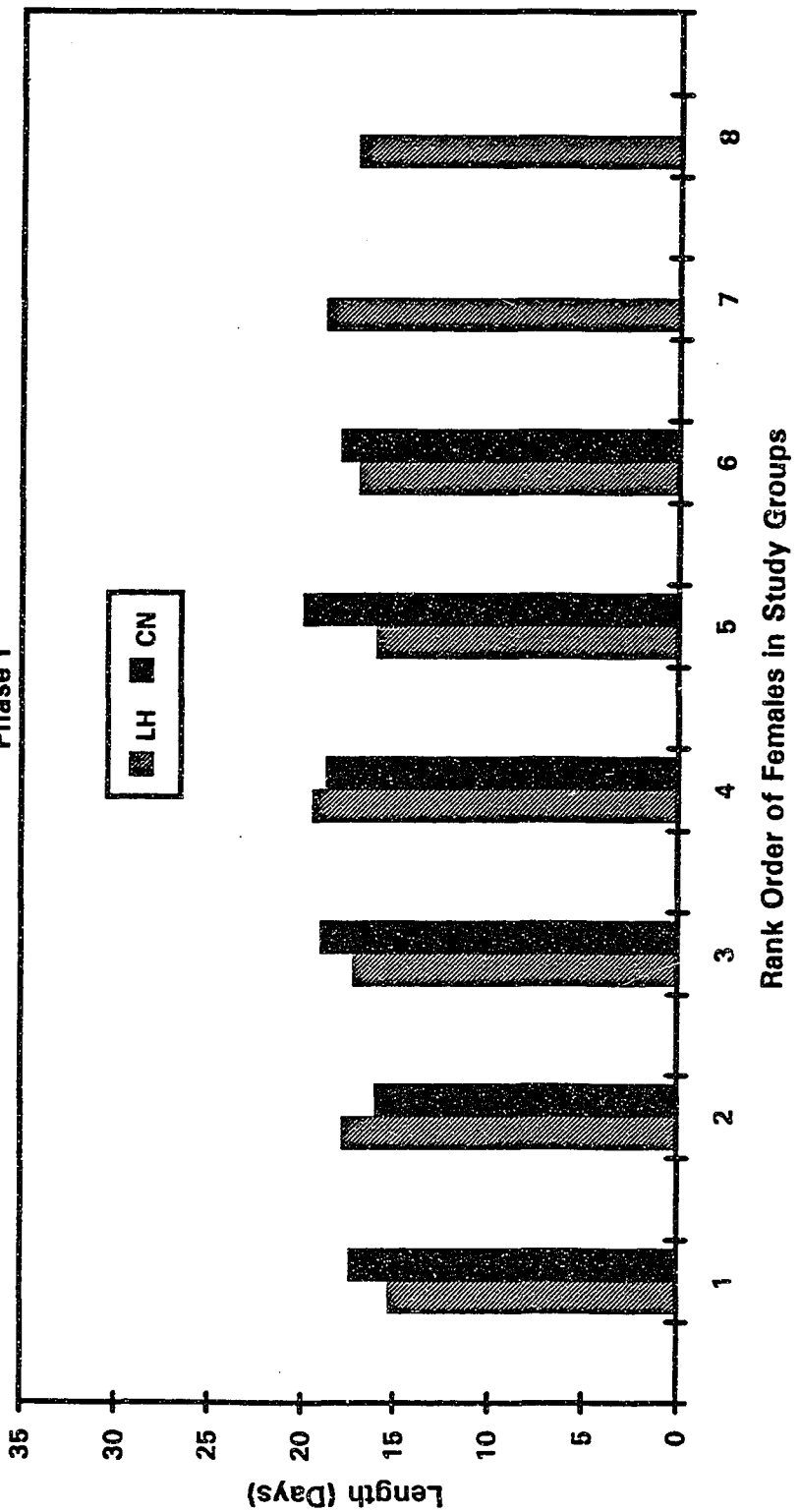


FIGURE 6.6.a. Mean Luteal Phase Length in Study Group Females

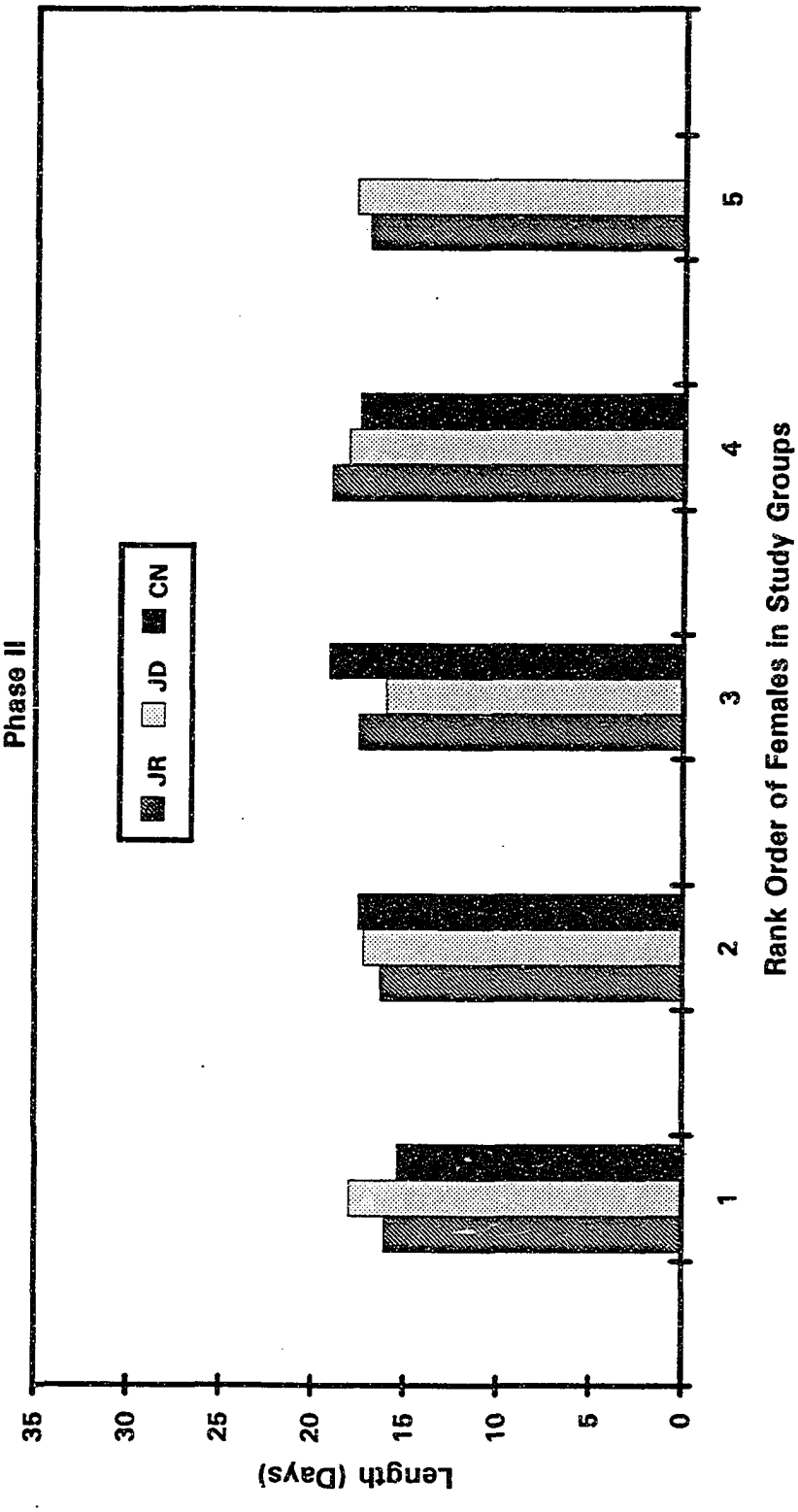


FIGURE 6.6.b. Mean Luteal Phase Length in Study Group Females

FIGURE 6.7. A Comparison of Mean Follicular and Luteal Phase Lengths in High-Ranking and Low-Ranking Females

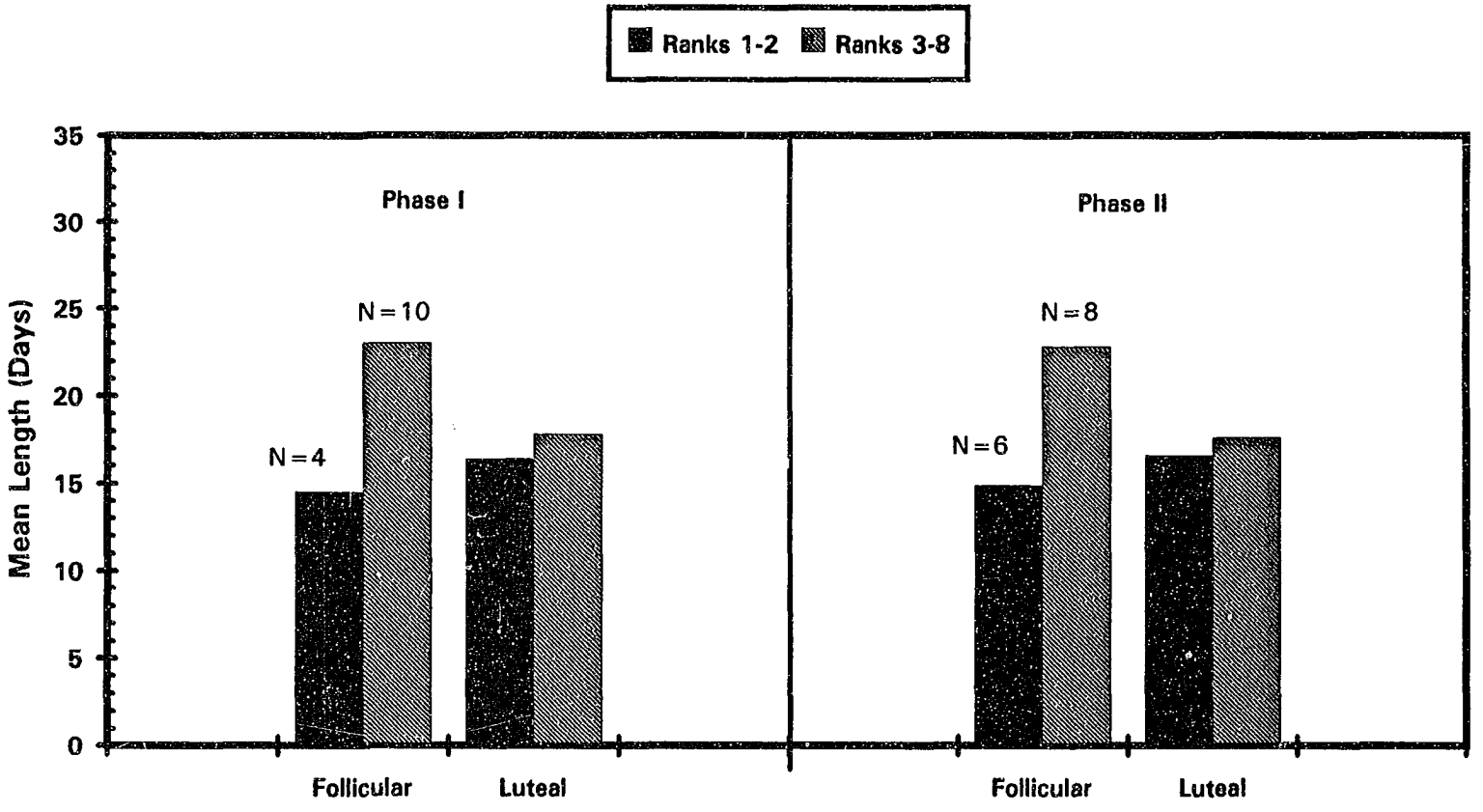
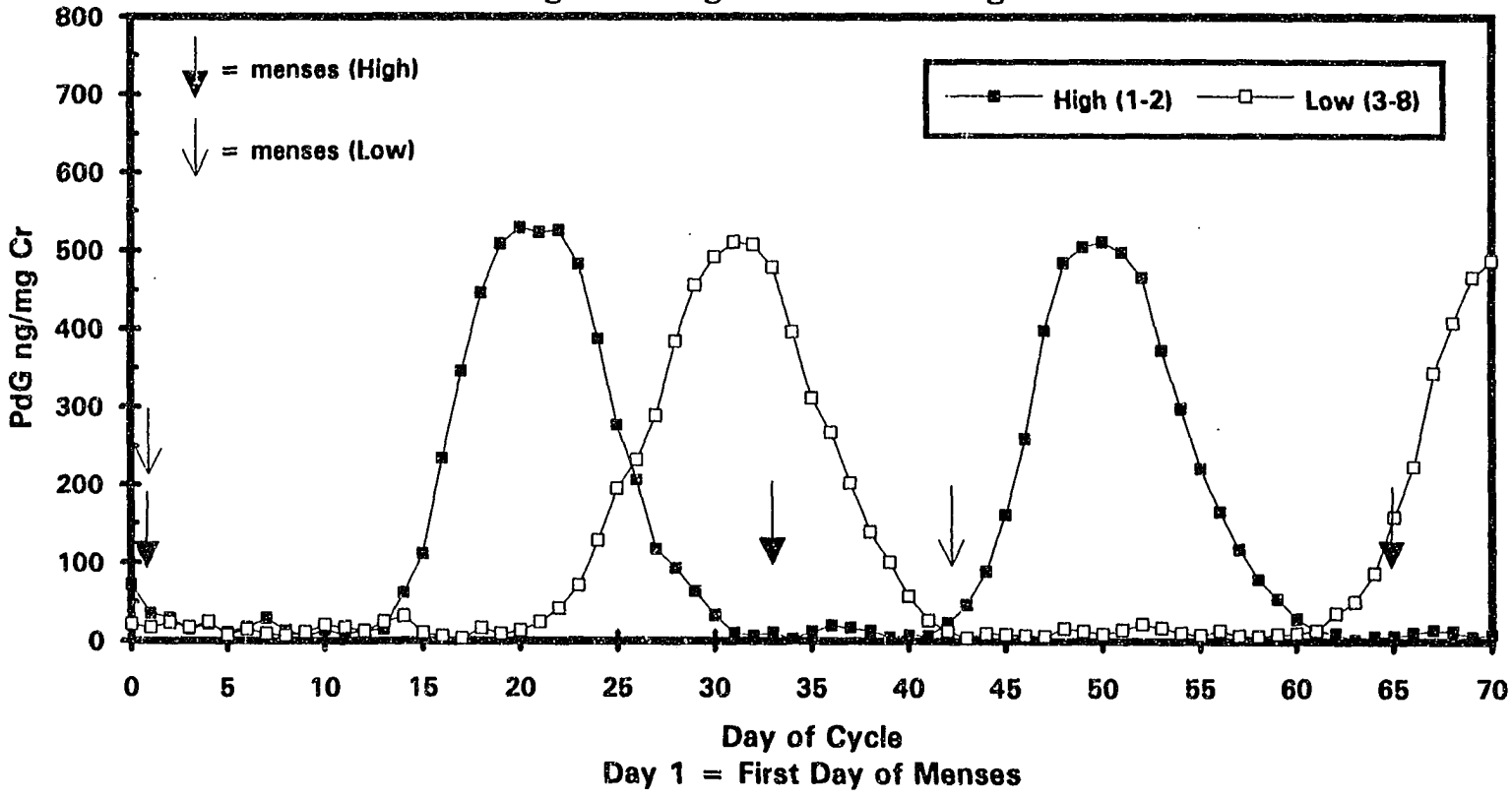


FIGURE 6.8. A Comparison of Mean Menstrual Cycle Lengths in High-Ranking and Low-Ranking Females



II: 17.7 ± 1.0) (Figure 6.6.), which is not a significant difference in length (Phase I: $t = 1.416$, Phase II: $t = 1.394$, $p > 0.10$, n.s.) (Figure 6.7). To illustrate the variance found in menstrual cyclicity, a comparison of mean cycle lengths in high-ranking and low-ranking females is presented in Figure 6.8. The data represent composites based on 18 cycles from 6 females and 22 cycles from 7 females, respectively.

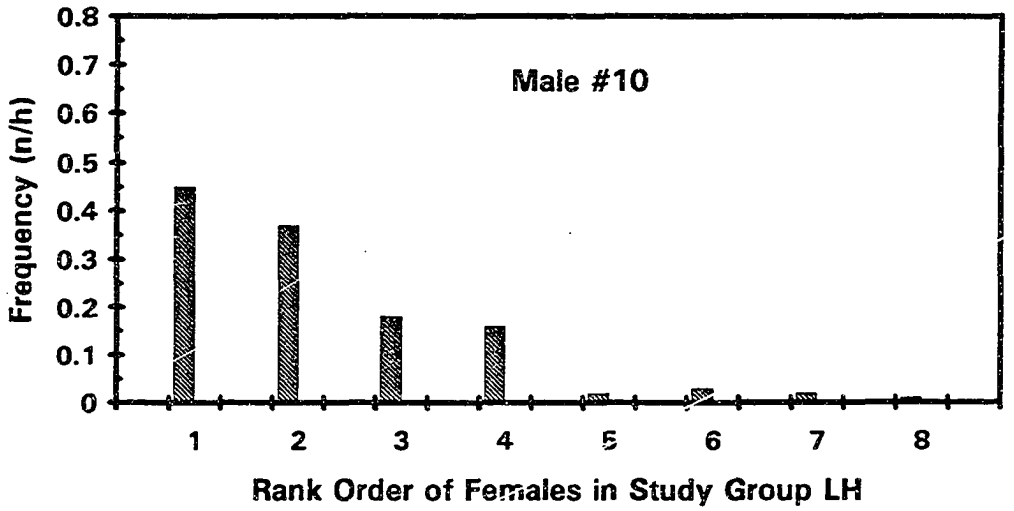
6.3. Variation in Male Copulatory Behavior

Mating occurs throughout the female's menstrual cycle, though its frequency increases markedly during the peri-ovulatory period. Copulations occur on average about once every 90 minutes around the time of ovulation, with greater than 80% of these being initiated and actively solicited by the female. While there exists a consistent pattern of sexual behavior exhibited by both the male and his females, variations in individual behavior occur between males, and between the male and his females. Figure 6.9 illustrates the difference in the frequency of copulations exhibited by the males in the study groups ($N = 4$). The most notable difference occurred with regard to the status of the male. Males that were the established residents (#10 and #60) copulated less frequently than did males who were in the process of, or had recently acquired, females (#61 and #86) ($t = 3.589$, $df = 3$, $p < 0.05$). In the case of the newly established harem males, copulations occurred at relatively high frequencies during the non-ovulatory periods as well. Furthermore, other affiliative behaviors also occurred at higher frequencies during the time when a new male emerged as harem holder as is shown in Figure 6.10. This difference reflects the importance to new harem males of devoting a significant amount of their

time to establishing bonds with their newly acquired females. Once bonds are established, as is the case in resident males, there is a decline in the amount of time the male allots to maintaining these relationships.

In addition to individual differences between males, variations were also found with regard to the male's behavior towards each of his females. While males copulated with their females more frequently around the time of ovulation, the frequency with which they copulated with a particular female varied significantly (Phase I: Group LH, df = (1,7) $F = 14.01$ $p<0.01$, GroupCN, df = (1,5) $F = 8.21$, $p<0.05$; respectively; Phase II: Group JR, JD, df = (1,4) $F = 7.79, 9.26$, $p<0.05$, respectively, and Group CN, df = (1,3) $F = 10.33$, $p<0.05$). Table 6.3 gives the frequency with which each male copulated with the females in his unit according to the females' social rank. Males tend to mate more frequently with particular females, and that these females are the more dominant females in their group. While the number of copulations with dominant females was greater than that with lower-ranking females, the number of unsuccessful copulations varied as well. Figure 6.11 presents data on the variance between females in the percentage of successful and unsuccessful copulations which shows that there is a significant difference among females in this respect (Phase I: Group LH, df = (1,7) $F = 30.07$, $p<0.001$, Group CN, df = (1,5) $F = 19.26$, $p<0.01$; Phase II: Group JR, df = (1,4) $F = 23.15$, $p<0.01$, Goup JD, df = (1,4) $F = 9.76$, $p<0.05$, Group CN, df = (1,3) $F = 11.12$, $p<0.05$).

FIGURE 6.9.a. The Frequency of Copulations by Males with Females of Varying Dominance Rank



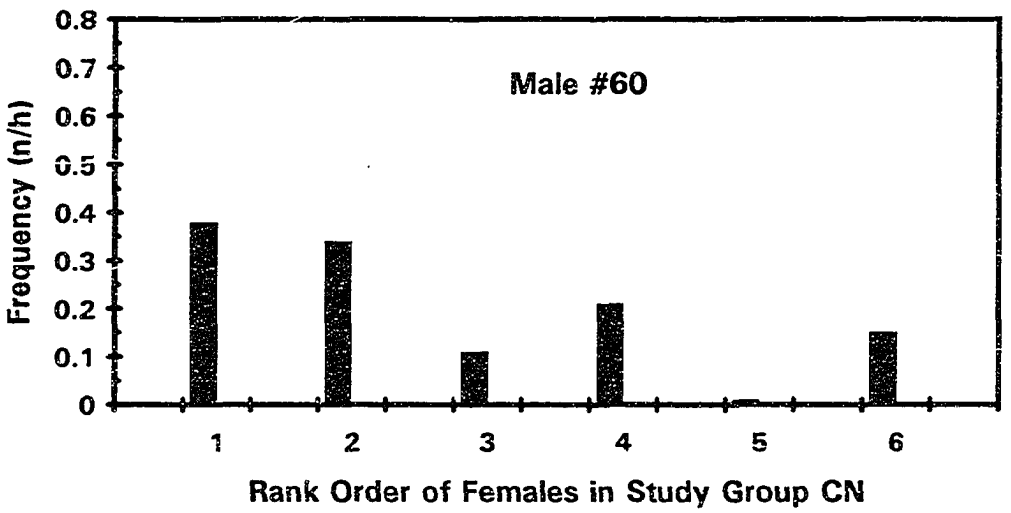
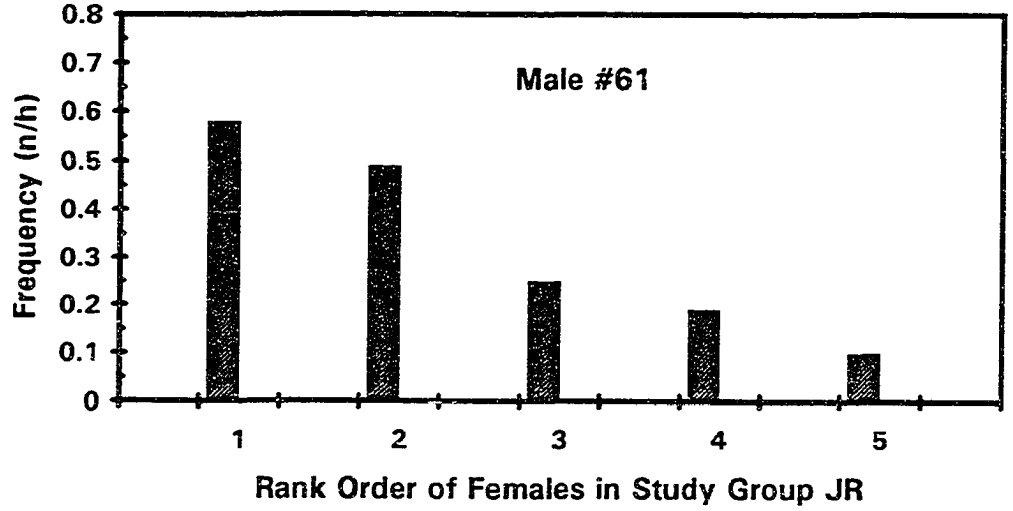
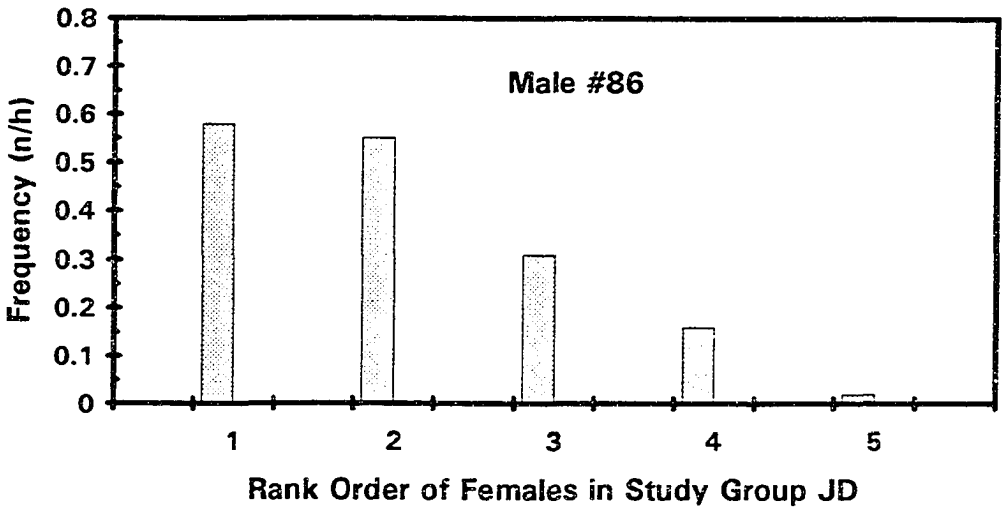


FIGURE 6.9.b. The Frequency of Copulations by Males with Females of Varying Dominance Rank





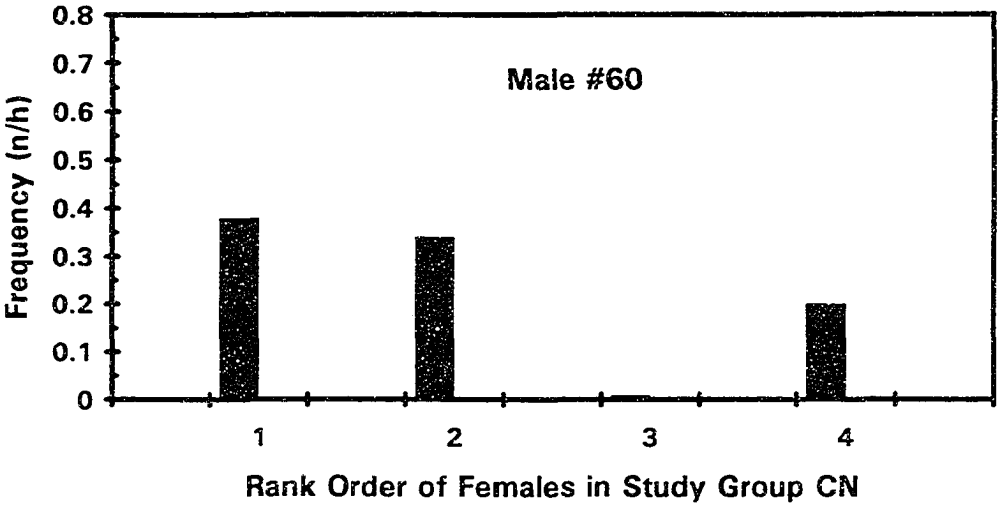
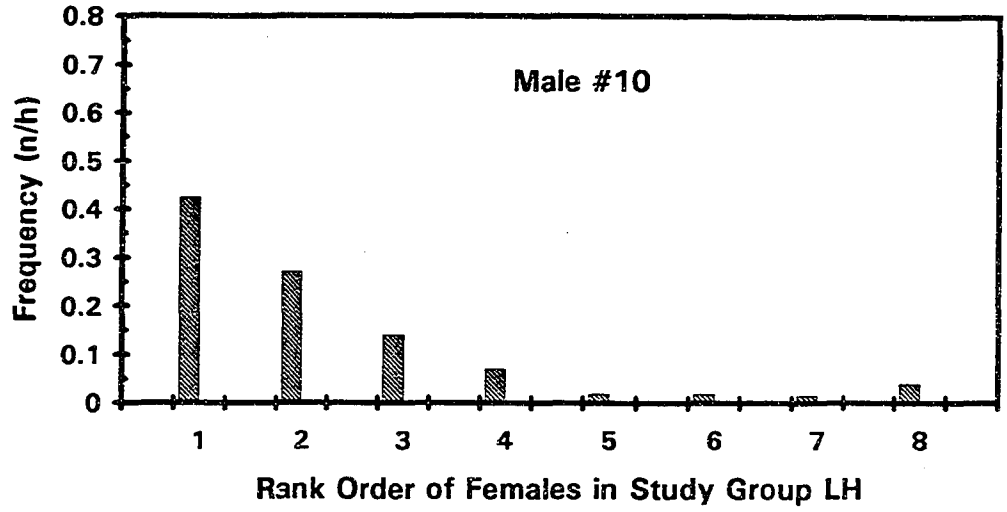


FIGURE 6.10.a. The Distribution of Male Affiliative Behavior Across Females of Varying Dominance Rank



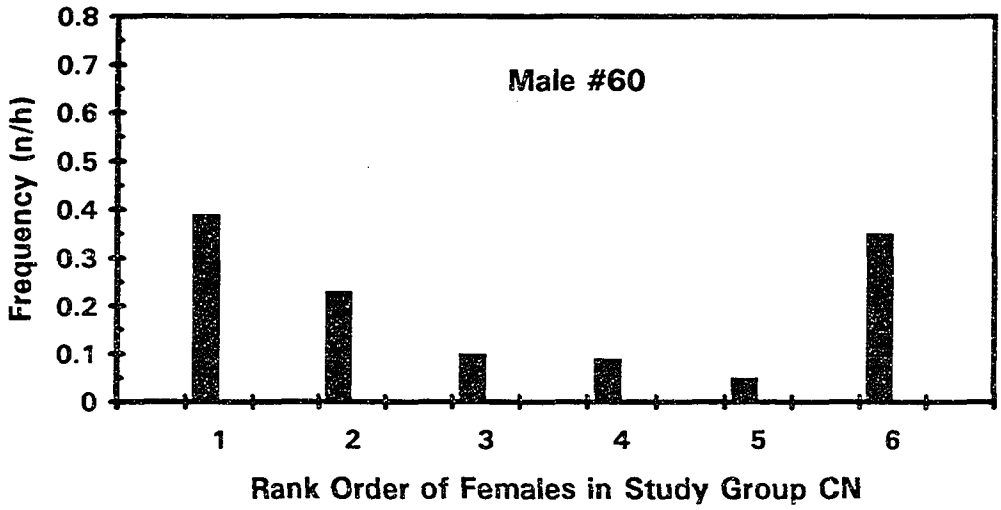
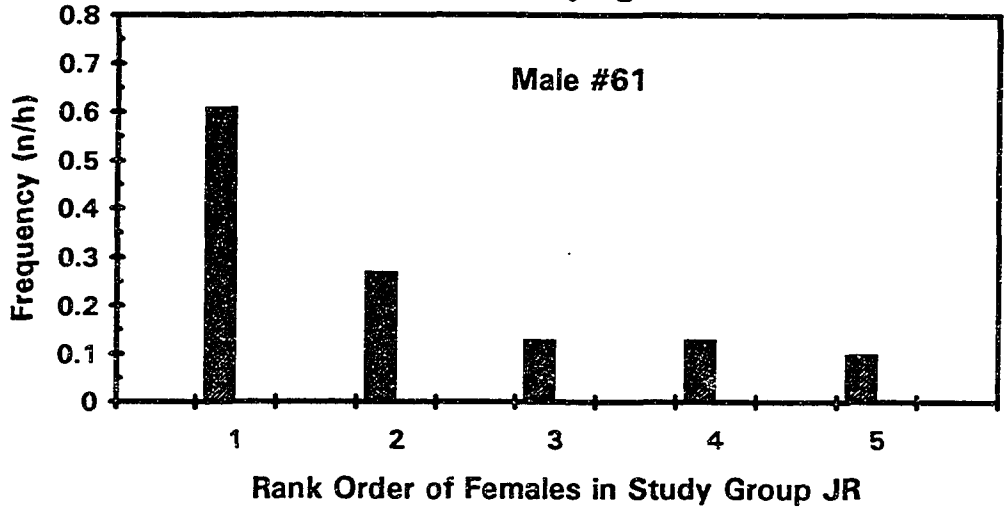
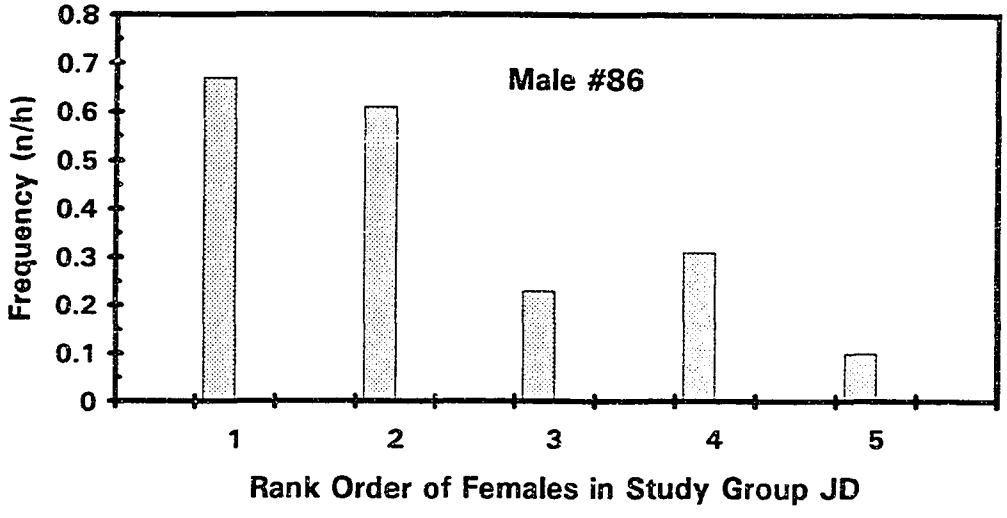


FIGURE 6.10.b. The Distribution of Male Affiliative Behavior Across Females of Varying Dominance Rank





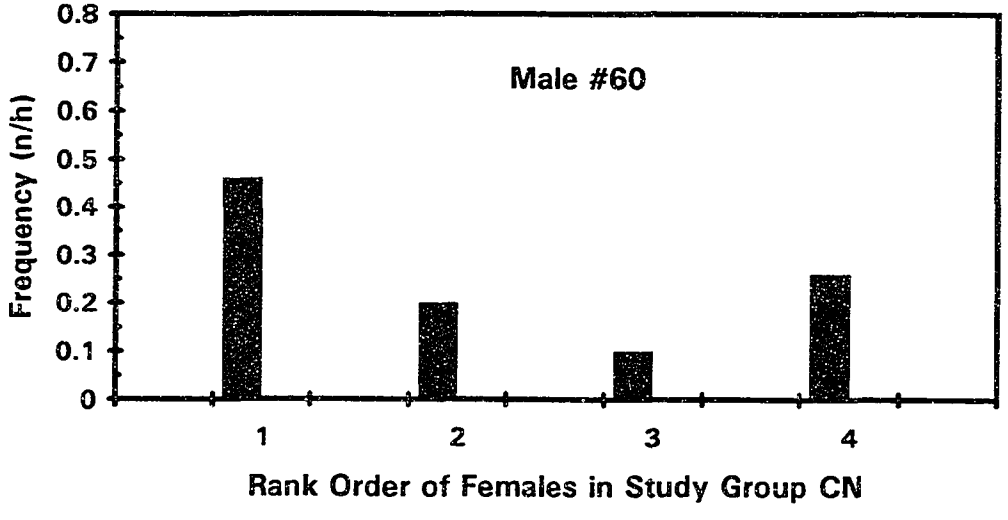


TABLE 6.3. A Comparison of the Frequency of Copulations by Males with Females of Different Social Rank

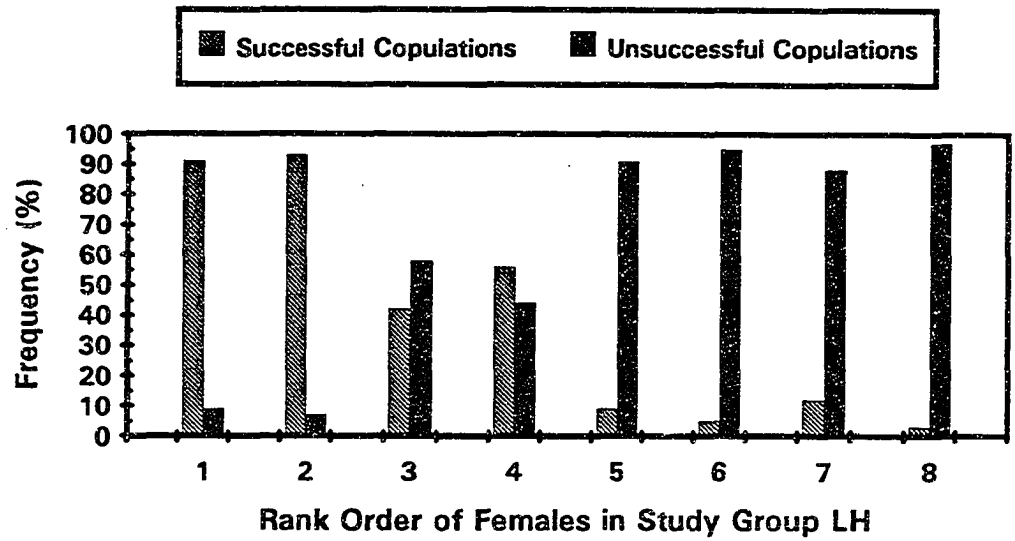
Phase I

Group ID: Female ID#	Social Rank	No. Copulations (Mean/hour)	Male ID#
LH: 13	1	0.45	10
11	2	0.37	10
16	3	0.18	10
15	4	0.16	10
17	5	0.02	10
14	6	0.03	10
18	7	0.02	10
12	8	0.01	10
CN: 62	1	0.38	60
67	2	0.34	60
66	3	0.15	60
63	4	0.27	60
64	5	0.01	60
65	6	0.11	60

Phase II

JR: 11	1	0.58	61
13	2	0.49	61
15	3	0.36	61
16	4	0.23	61
88	5	0.18	61
JD: 17	1	0.58	86
14	2	0.55	86
18	3	0.41	86
12	4	0.32	86
87	5	0.02	86
CN: 67	1	0.38	60
63	2	0.34	60
64	3	0.01	60
65	4	0.17	60

FIGURE 6.11.a. The Variance in the Number of Successful and Unsuccessful Copulations (Phase I)



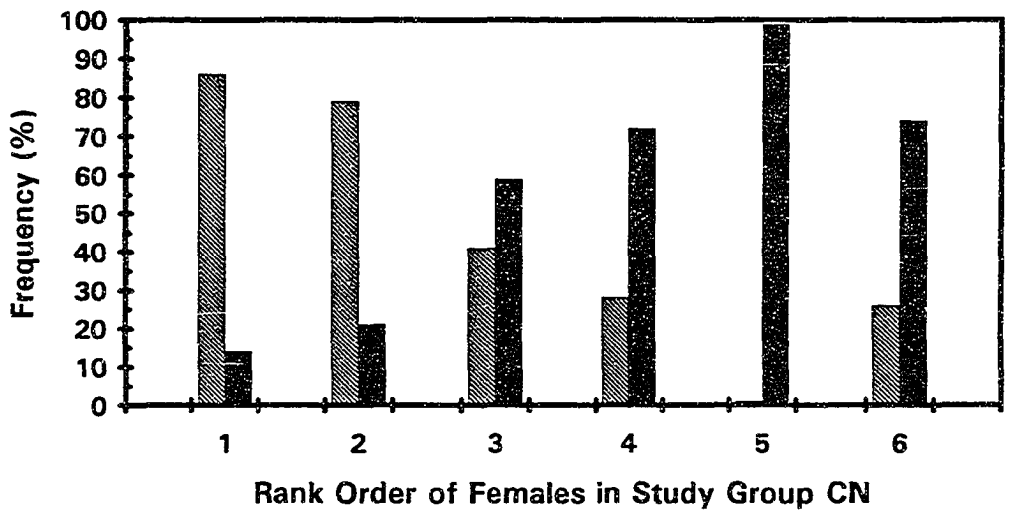
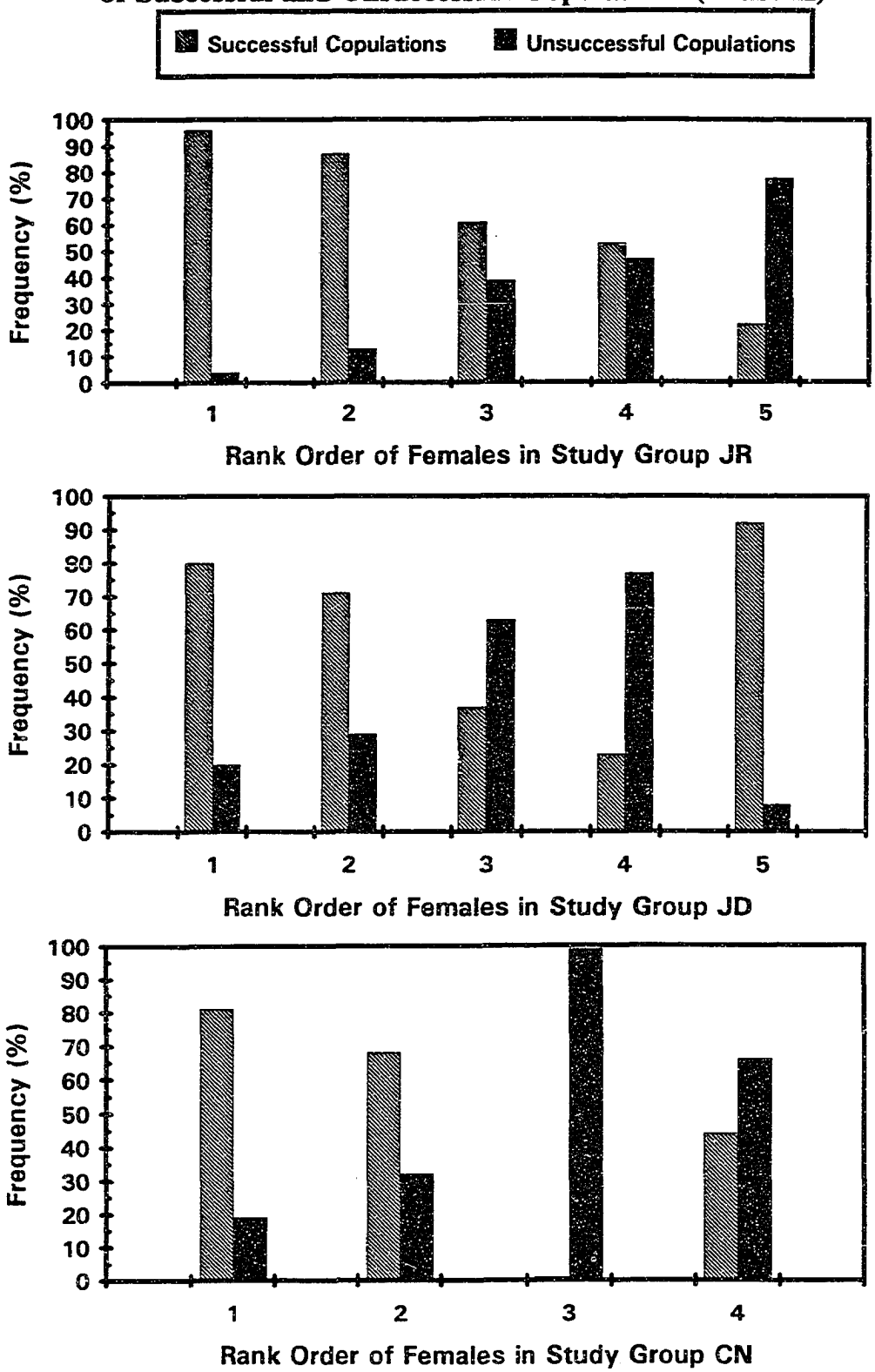


FIGURE 6.11.b. The Variance in the Number of Successful and Unsuccessful Copulations (Phase II)



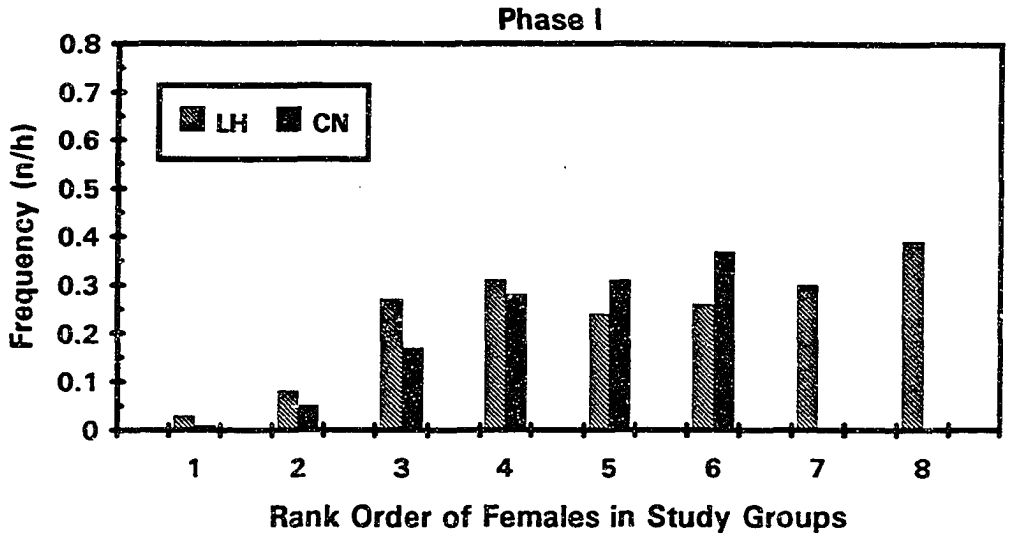
6.4. Variation in the Rate of Agonism Between Females

Female gelada relationships involve a complex series of affiliative and agonistic interactions, the outcome of which results in a hierarchical arrangement of individuals. Among the females in the study groups there was a marked difference in the direction of aggressive behavior received by individuals with regard to their social position in the group. Analyses of all agonistic encounters recorded during focal female (N = 2, 688) and ad libitum (N = 1, 644) sampling revealed that females of low rank received higher rates of aggression directed towards them than did higher-ranking females (Phase I: $t = 2.357$, Phase II: $t = 2.120$, $p<0.05$) (Figure 6.12.). In addition, the rate of aggression increased significantly for low-ranking females during the follicular phase compared to the rate during the luteal phase (Phase I: $t = 3.369$, $p<0.01$; Phase II: $t = 3.011$, $p<0.02$) (Figure 6.13.). The mean ($\pm$ s.d.) rate of aggression during the follicular phase was 0.46 ($\pm$ 0.23) (Phase I: 0.48 $\pm$ 0.24; Phase II: 0.44 $\pm$ 0.21) compared to a rate of 0.22 ($\pm$ 0.14) (Phase I: 0.24 $\pm$ 0.13, Phase II: 0.21 $\pm$ 0.11) during the luteal phase of the cycle (Figure 6.14).

Females compete with one another for access to the harem male, and this becomes most evident when a female enters the ovulatory phase of her cycle. Table 6.4 shows the number of copulations that were interrupted (the overwhelming majority of which resulted in unsuccessful copulations) as a result of harassment by other members of the unit. The data illustrate the significant difference in the frequency of aggression during mating among females of different social ranks (Phase I: $F = 8.96$; Phase II: $F = 7.81$ $df = (1, 26)$ $p<0.01$). In addition, the increase in aggressive behavior during the time of estrus was apparent both within and between females of different grooming

FIGURE 6.12. Rates of Aggression Among Females

Frequency (per hour) of Harassment Received by Females From Other Females in Their Group



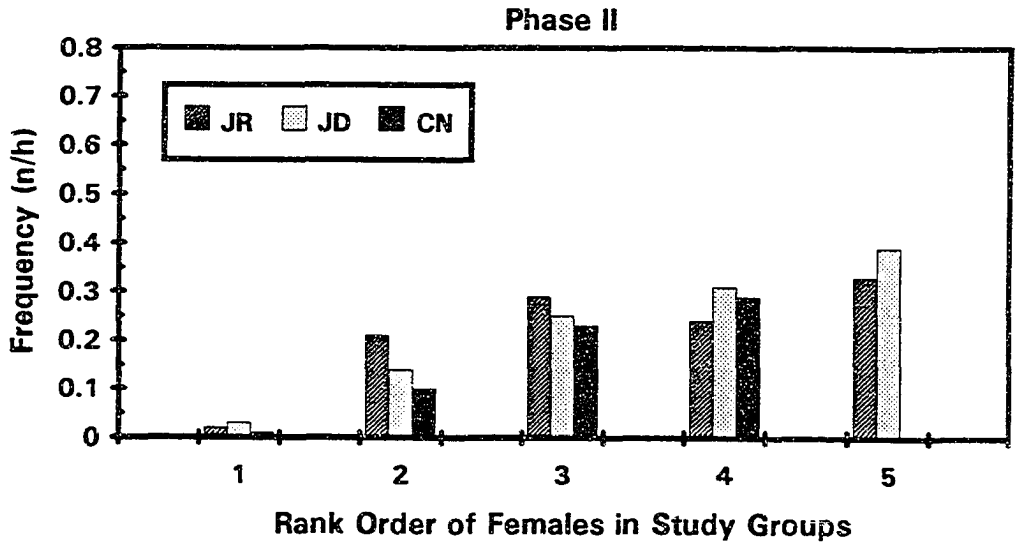
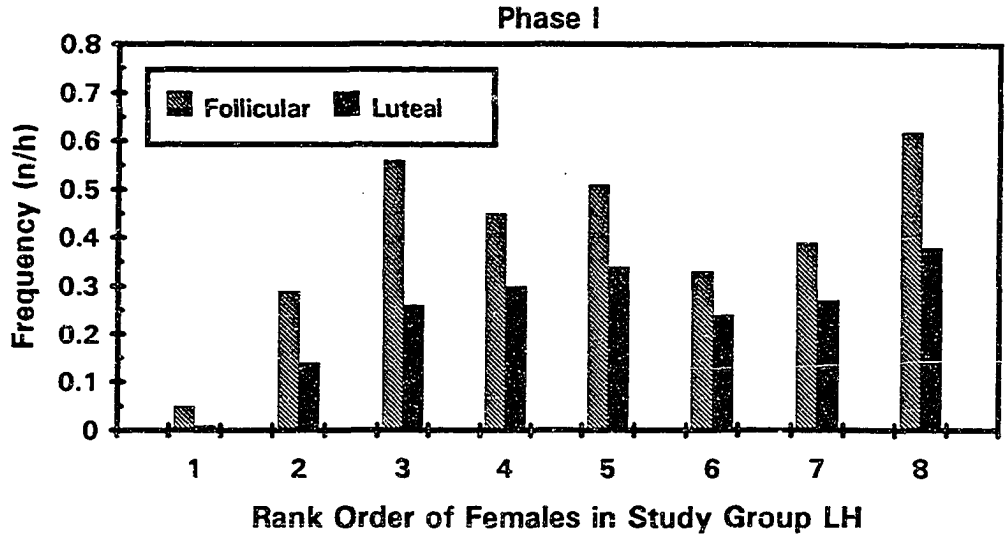


FIGURE 6.13.a. Rates of Aggression Among Females
Frequency (per hour) of Harassment Received During the Follicular and Luteal Phase of the Menstrual Cycle



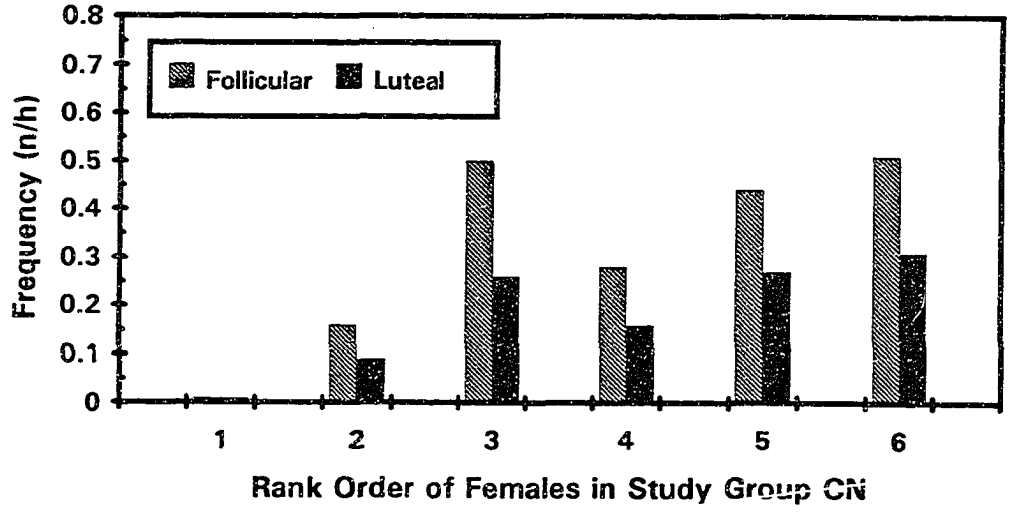
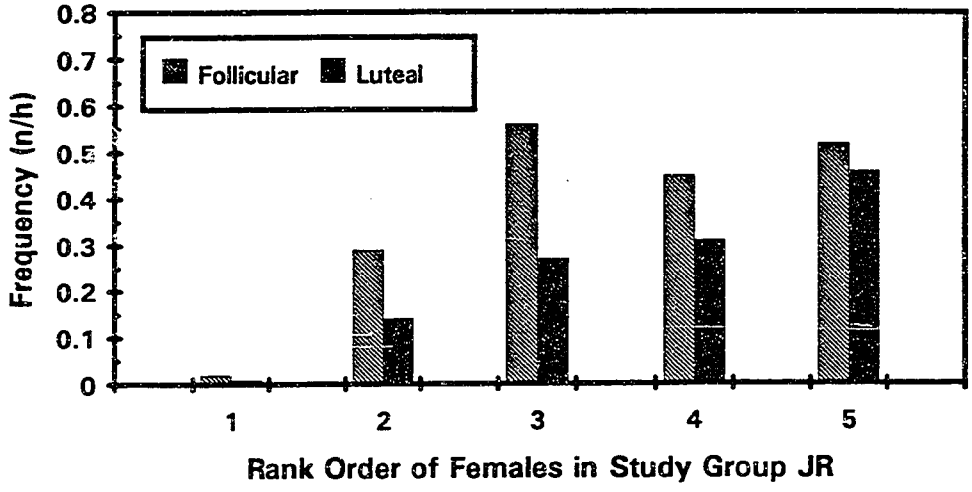
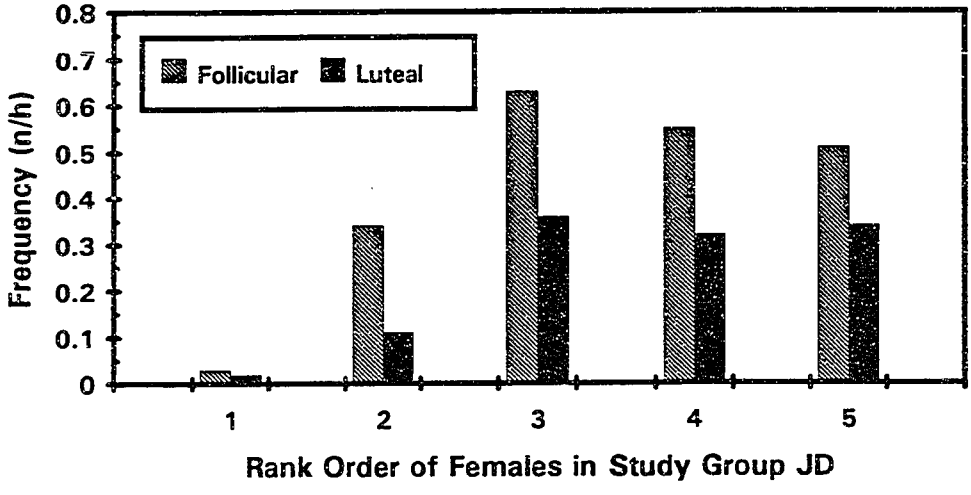


FIGURE 6.13.b. Rates of Aggression Among Females
Frequency (per hour) of Harassment Received During the Follicular and Luteal Phase of the Menstrual Cycle
Phase II





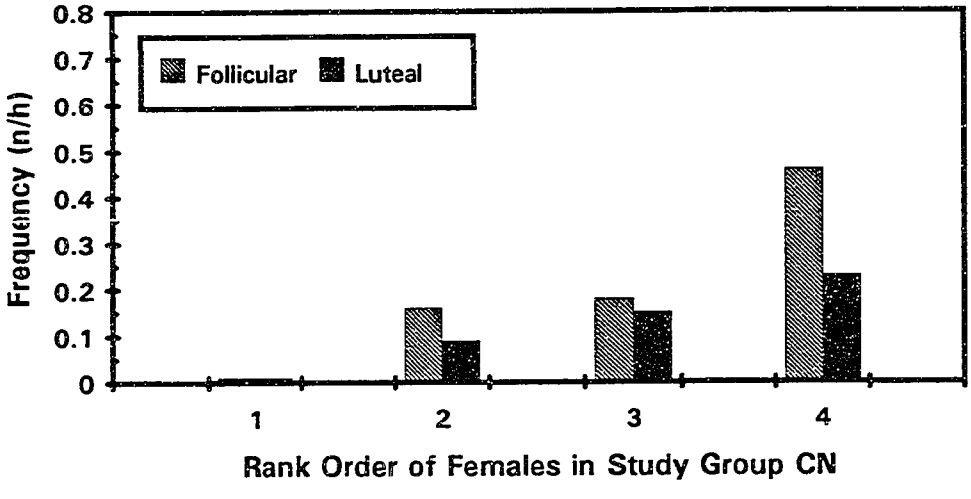


FIGURE 6.14. A Comparison of Mean Rates of Aggression Among High-Ranking and Low-Ranking Females

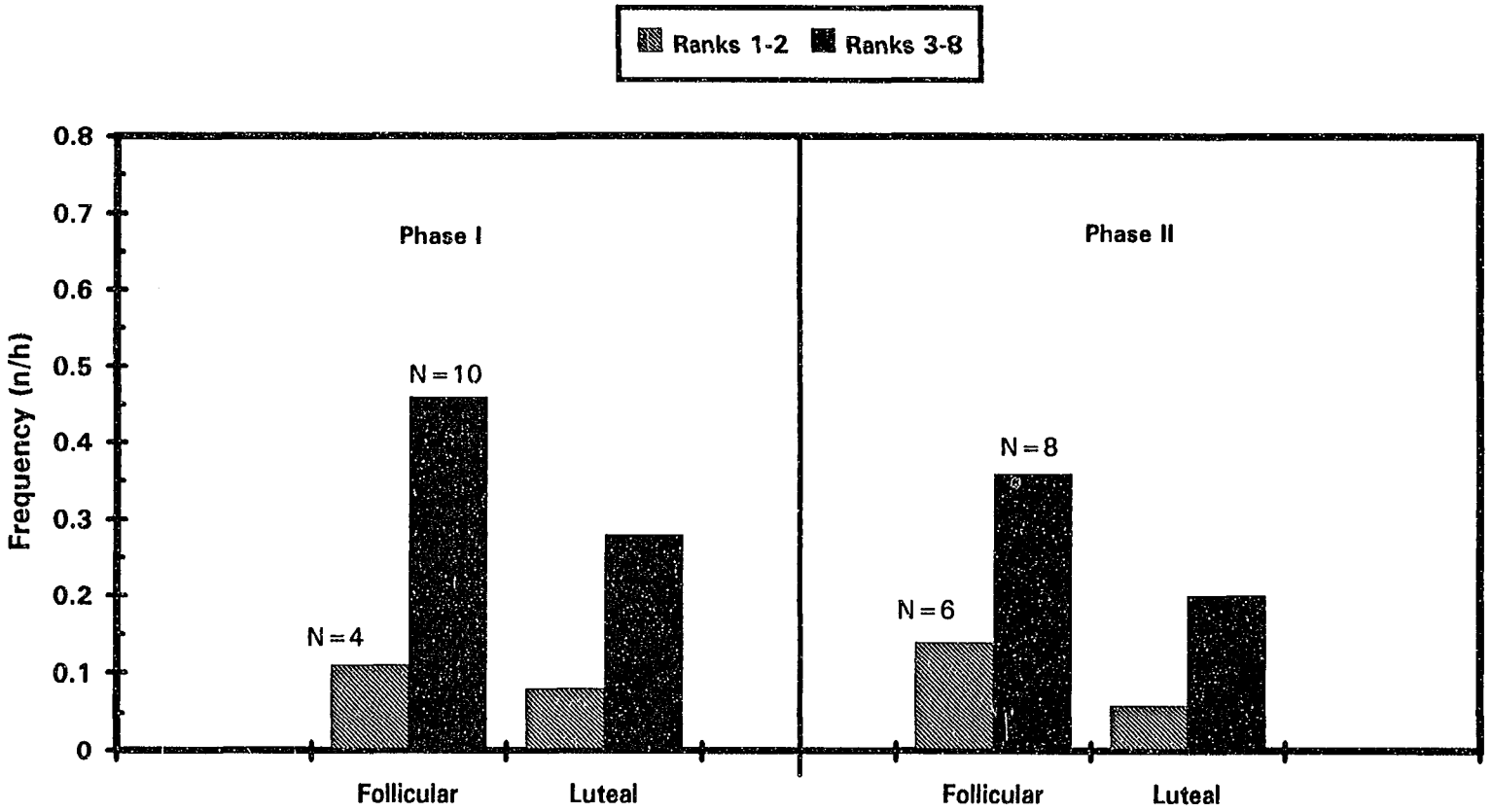


TABLE 6.4. A Comparison of the Frequency of Aggression Received During Copulations Among Females of Different Social Rank

Phase I

Group ID: Female ID#	Social Rank	Rate of Aggression Received (n/h)	Rate of Aggression Received During Mating (n/h)
LH: 13	1	0.01	0.05
11	2	0.08	0.13
16	3	0.27	0.33
15	4	0.31	0.38
17	5	0.24	0.49
14	6	0.26	0.43
18	7	0.33	0.57
12	8	0.39	0.66
CN: 62	1	0.01	0.01
67	2	0.05	0.07
66	3	0.17	0.21
63	4	0.28	0.39
64	5	0.31	0.44
65	6	0.37	0.77

Phase II

JR: 11	1	0.01	0.01
13	2	0.21	0.41
15	3	0.29	0.38
16	4	0.24	0.46
88	5	0.33	0.59
JD: 17	1	0.02	0.03
14	2	0.14	0.27
18	3	0.25	0.42
12	4	0.31	0.71
87	5	0.39	0.84
CN: 67	1	0.001	0.01
63	2	0.1	0.19
64	3	0.23	0.33
65	4	0.28	0.52

dyads. In other words, females who were grooming partners showed the same pattern of agonistic behavior with each other during the time of estrus as they did toward non-partner females. Thus, a female's relationship with the unit male is strongly influenced by her interactions with other females in the group.

6.5. Variation in Patterns of Urinary Cortisol Excretion

The amounts of agonism received show that subordinate female geladas are harassed frequently by dominant females in their group. This social stress may be compared to physiological measures of stress, to explore the possible reproductive consequences of harassment from other group members. Cortisol levels in females were measured and used to: (1) determine the general pattern of excretion exhibited across the menstrual cycle; and (2) examine quantitative differences between females. These data were then compared to the data obtained on the behavioral and reproductive differences found among females.

6.5.1. Patterns of Cortisol Excretion Across the Menstrual Cycle

Cortisol, a glucocorticoid, is one of the variety of hormones secreted in times of stress (Sapolsky, 1982; Johnson and Everitt, 1988; Bronson, 1989). In addition to being released in response to a specific stressor, cyclic fluctuations in cortisol excretion may also occur (Spies and Chappel, 1984; Yen and Lein, 1984). Therefore, the pattern of excretion throughout the menstrual cycle was first examined in order to determine if there existed a general tendency for hormone values to increase or decrease during specific phases of the cycle. Once the general pattern of excretion in female geladas was determined, individual differences were examined.

The urinary cortisol excretion values among study group females ranged from .01 to 6.56 ng/mg Creatinine (Cr) and displayed a mean (± s.e.) of 0.47 ng/ mg Cr (± 0.05) (Table 6.5). There was no significant difference between the study groups in the range and mean of cortisol excretion levels ($t = 2.539$, $df = 4$, $p < 0.10$). Figure 6.15 displays the mean pattern of cortisol excretion throughout the menstrual cycle exhibited by the study group females in relation to the changes in pregnanediol glucuronide. An examination of the changes in excretion levels throughout the cycle revealed a small increase in cortisol values during the follicular phase of the cycle compared to the luteal phase, as is exhibited in Table 6.6. Mean (± s.e.) cortisol values during the follicular phase were 0.57 ng/mg Cr (± 0.08) (Phase I: 0.58 ± 0.08, Phase II: 0.56 ± 0.07) compared to 0.40 ng/mg Cr (± 0.06) (Phase I: 0.42 ± 0.06, Phase II: 0.37 ± 0.04) during the luteal phase (Phase I: $t = 2.151$, Phase II: $t = 2.148$, $df = 13$, $p > 0.05$). In each study group in total, and in every individual female, cortisol excretion levels were greater in the follicular phase of the menstrual cycle. The general excretion pattern exhibited by the study animals corresponds to the midcycle increase in cortisol-- associated with the rise in circulating levels of estradiol-- reported by Yen and Lein (1984).

6.5.2. Patterns of Cortisol Excretion Among Females of Different Social Status

In addition to examining the general patterns in cortisol excretion levels in the study group females, a further analysis was made of the variance in means between females of different social ranks. A comparison between high-ranking and low-ranking females of the range in cortisol excretion levels revealed no

TABLE 6.5. A Comparison of Cortisol Excretion Levels Across Social Rank in Study Group Females

Phase I

Group ID: Female ID#	Social Rank	Cortisol (ng/mg Cr) Value Range	Mean ± s.e. Cortisol (ng/mg Cr) Value
LH: 13	1	.04 - 3.88	0.33 ± .08
11	2	.02 - 2.44	0.24 ± .05
16	3	.06 - 1.41	0.51 ± .09
15	4	.05 - 2.76	0.41 ± .13
17	5	.07 - .84	0.40 ± .04
14	6	.08 - 4.84	0.48 ± .17
18	7	.06 - 1.88	0.39 ± .12
12	8	.16 - 4.36	0.66 ± .15
N = 8		Total Range .00 - 4.84	Total Mean ± s.e. .43 ± .04
CN: 62	1	.01 - 1.56	0.14 ± .02
67	2	.01 - 3.29	0.11 ± .06
66	3	.04 - 2.67	0.29 ± .10
63	4	.05 - 3.48	0.96 ± .16
64	5	.23 - 1.96	0.75 ± .09
65	6	.08 - 3.69	1.04 ± .28
N = 6		Total Range .01 - 3.69	Total Mean ± s.e. .55 ± .17

Phase II

JR: 11	1	.04 - 4.14	0.27 ± .04
13	2	.07 - 3.24	0.36 ± .06
15	3	.02 - 5.26	0.71 ± .11
16	4	.12 - 2.17	0.64 ± .08
88	5	.03 - 3.02	0.40 ± .05
N = 5		Total Range .02 - 5.26	Total Mean ± s.e. .48 ± .08
JD: 17	1	.04 - 4.61	0.25 ± .03
14	2	.02 - 1.99	0.37 ± .14
18	3	.03 - 3.74	0.59 ± .10
12	4	.04 - 2.31	0.43 ± .12
87	5	.07 - 4.93	0.78 ± .15
N = 5		Total Range .02 - 4.93	Total Mean ± s.e. .46 ± .09
CN: 67	1	.04 - 2.34	0.29 ± .05
63	2	.11 - 4.59	0.38 ± .11
64	3	.09 - 1.06	0.44 ± .07
65	4	.03 - 6.56	0.88 ± .24
N = 4		Total Range .03 - 6.56	Total Mean ± s.e. .51 ± .13

FIGURE 6.15. Mean Cortisol and Pregnanediol Glucuronide Excretion Levels During the Menstrual Cycle

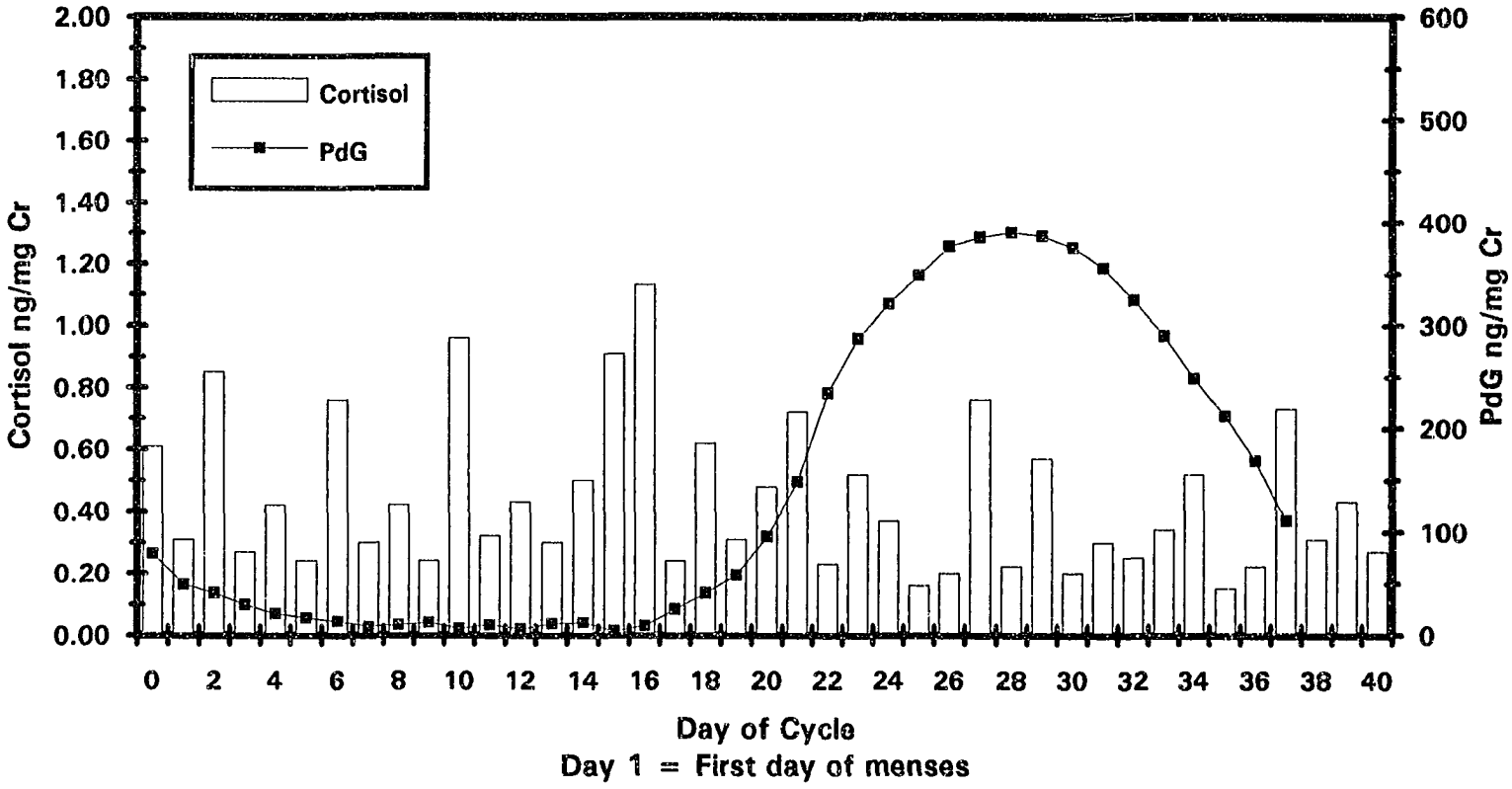


TABLE 6.6. A Comparison of Mean Cortisol Excretion Levels Among Females During the Follicular and Luteal Phase of the Menstrual Cycle

Phase I

Group ID: Female ID#	Social Rank	Follicular Phase Mean ± s.e. Cortisol (ng/mg Cr) Value	Luteal Phase Mean ± s.e. Cortisol (ng/mg Cr) Value
LH: 13	1	.35 ± .03	.31 ± .02
11	2	.28 ± .03	.20 ± .01
16	3	.54 ± .04	.47 ± .03
15	4	.49 ± .06	.32 ± .04
17	5	.43 ± .05	.36 ± .03
14	6	.58 ± .04	.37 ± .05
18	7	.41 ± .03	.36 ± .04
12	8	.87 ± .08	.45 ± .06
N = 8		Total Mean ± s.e. .49 ± .06	Total Mean ± s.e. .39 ± .03
CN: 62	1	.15 ± .02	.13 ± .01
67	2	.13 ± .02	.09 ± .01
66	3	.33 ± .05	.24 ± .03
63	4	1.08 ± .13	.83 ± .10
64	5	.79 ± .04	.70 ± .03
65	6	1.06 ± .11	.81 ± .09
N = 6		Total Mean ± s.e. .61 ± .14	Total Mean ± s.e. .45 ± .11

Phase II

JR: 11	1	.30 ± .02	.24 ± .02
13	2	.43 ± .03	.29 ± .01
15	3	.92 ± .15	.49 ± .06
16	4	.75 ± .07	.53 ± .04
88	5	.47 ± .05	.32 ± .03
N = 5		Total Mean ± s.e. .68 ± .12	Total Mean ± s.e. .43 ± .06
JD: 17	1	.27 ± .03	.23 ± .01
14	2	.40 ± .03	.33 ± .02
18	3	.67 ± .06	.51 ± .04
12	4	.48 ± .04	.37 ± .02
87	5	.92 ± .09	.64 ± .05
N = 5		Total Mean ± s.e. .57 ± .07	Total Mean ± s.e. .40 ± .04
CN: 67	1	.33 ± .03	.24 ± .01
63	2	.54 ± .04	.21 ± .02
64	3	.47 ± .03	.41 ± .03
65	4	1.13 ± .09	.62 ± .07
N = 4		Total Mean ± s.e. .55 ± .06	Total Mean ± s.e. .36 ± .05

notable differences, as shown in Figure 6.16 and Figure 6.17. However, mean cortisol excretion values among females displayed marked differences. The mean (± s.e.) for high-ranking females (Ranks 1 - 2) was 0.29 (± 0.07) ng/mg Cr (Phase I: 0.32 ± 0.08; Phase II: 0.28 ± 0.07) whereas the mean for low-ranking females (Ranks 3 - 8) was 0.61 (± 0.11) ng/mg Cr (Phase I: 0.67 ± 0.13; Phase II: 0.55 ± 0.10) (Phase I: $t = 12.766$, $p = 0.049$; Phase II: $t = 12.417$, $p = 0.053$) (Figure 6.18).

Further analyses comparing these differences found significant differences between females in the rate of cortisol excretion during both the follicular and luteal phase of the menstrual cycle (Figure 6.19). During the luteal phase, low-ranking females excreted higher levels of cortisol (0.57 ± 0.14 ng/mg Cr) (Phase I: 0.65 ± 0.15; Phase II: 0.49 ± 0.12) than did high-ranking females (0.22 ± 0.06 ng/mg Cr) (Phase I: 0.18 ± 0.05; Phase II: 0.26 ± 0.04) (Phase I: $t = 13.204$; Phase II: $t = 12.823$, $p<0.05$), however, the greatest difference between females was during the follicular phase, 0.76 ± 0.23 in low-ranking females (Phase I: 0.80 ± 0.30; Phase II: 0.73 ± 0.24) compared to 0.31 ± 0.07 ng/mg Cr in high-ranking females (Phase I: 0.23 ± 1.1; Phase II: 0.38 ± 1.3) (Phase I: $t = 73.407$, $p<0.01$; Phase II: $t = 62.889$, $p<0.02$). These data are represented in Figure 6.20 and illustrate the marked differences between females with respect to social rank and cortisol excretion levels.

FIGURE 6.16. The Range in Cortisol Excretion Levels in High-Ranking Females (Ranks 1 and 2)

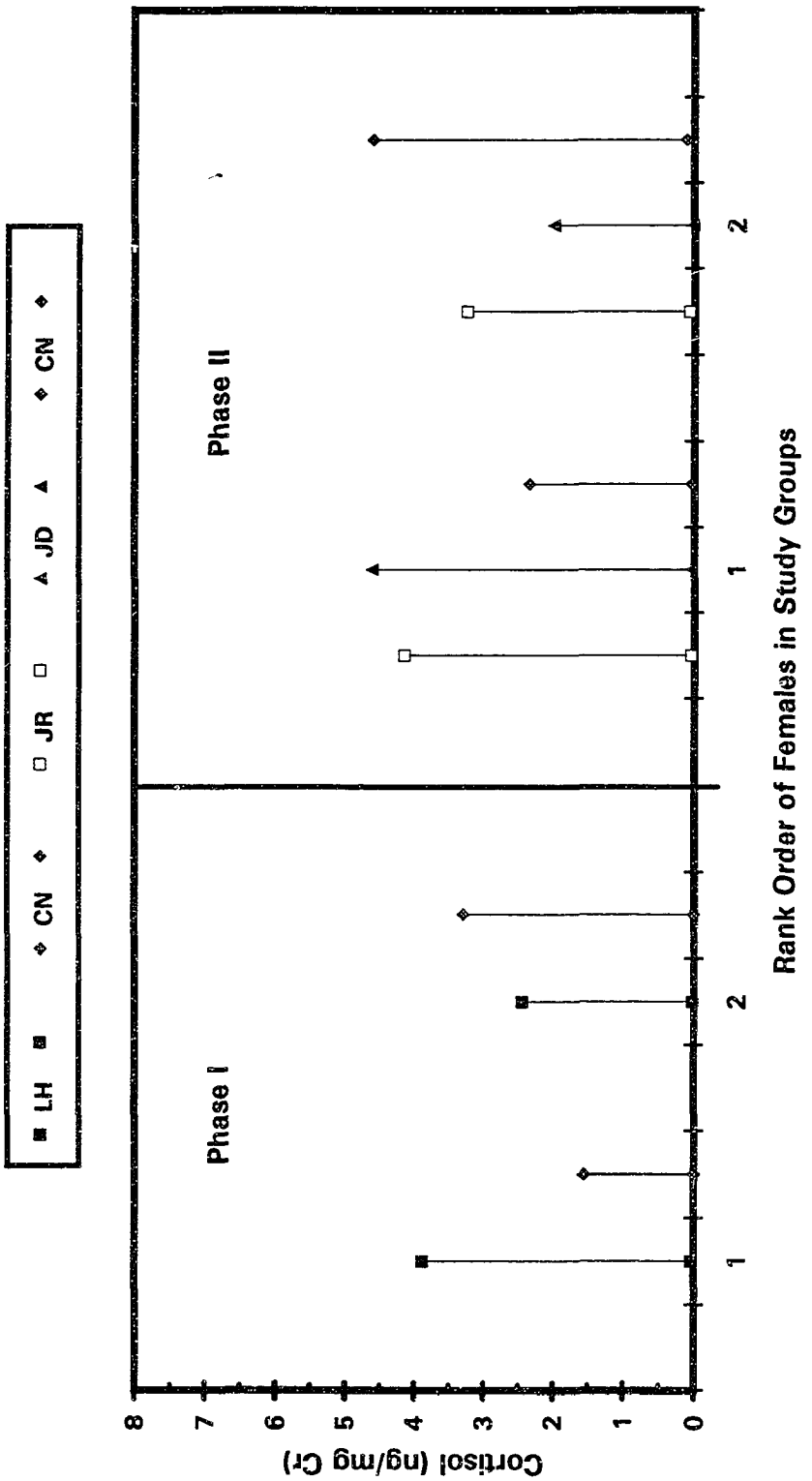


FIGURE 6.17. The Range in Cortisol Excretion Levels in Low-Ranking Females (Ranks 3 - 8)

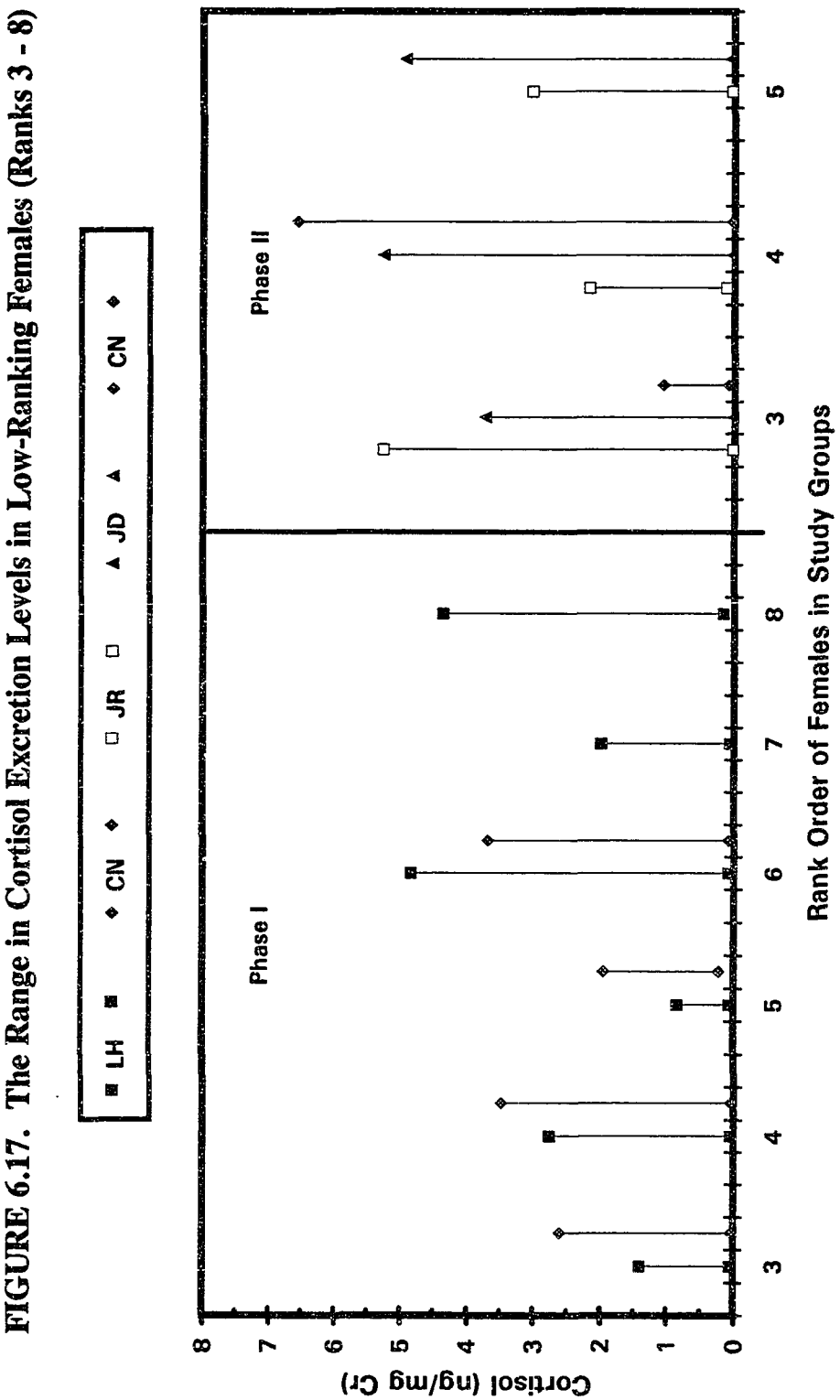
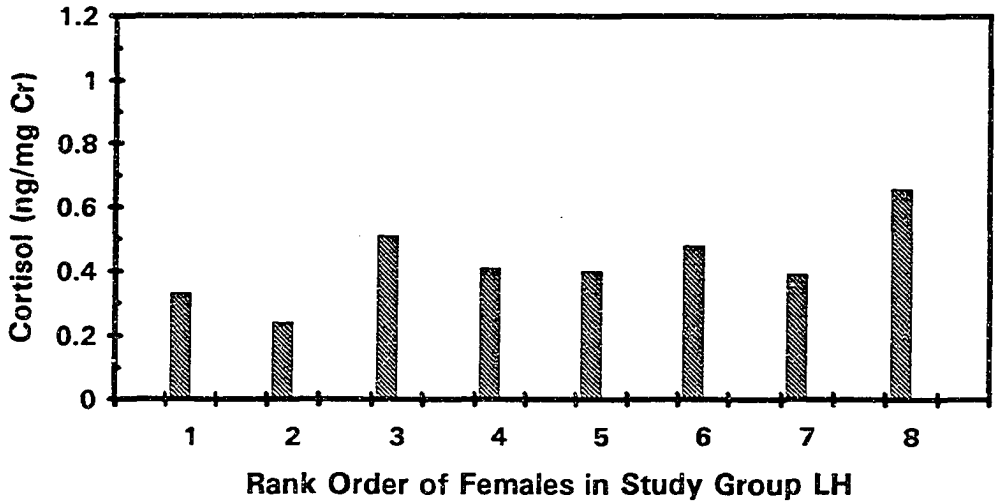


FIGURE 6.18.a. The Variation in Mean Cortisol Excretion Levels Across Social Rank in Study Group Females



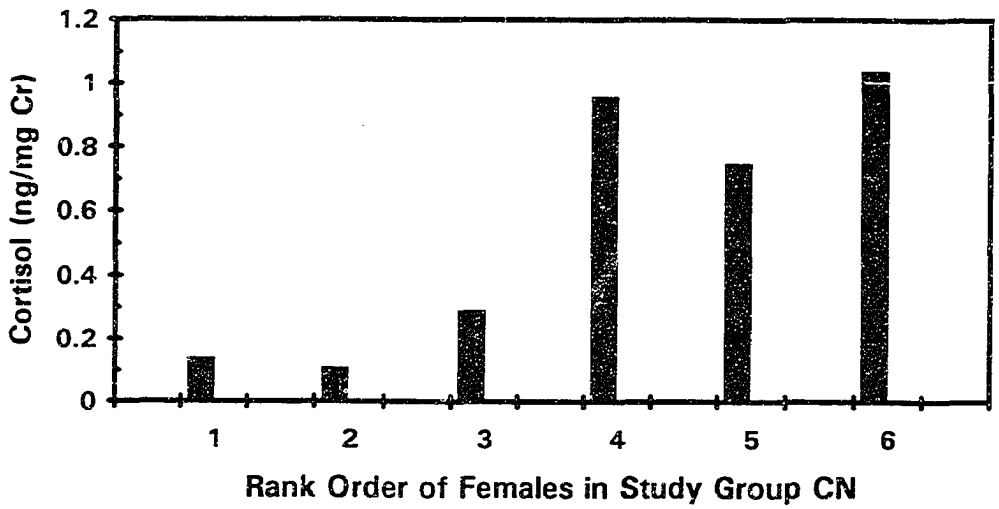
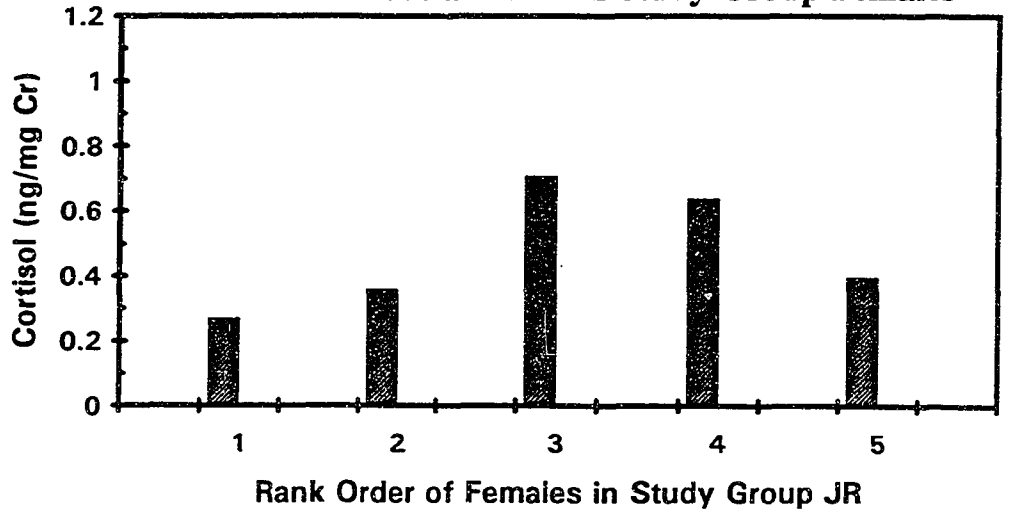
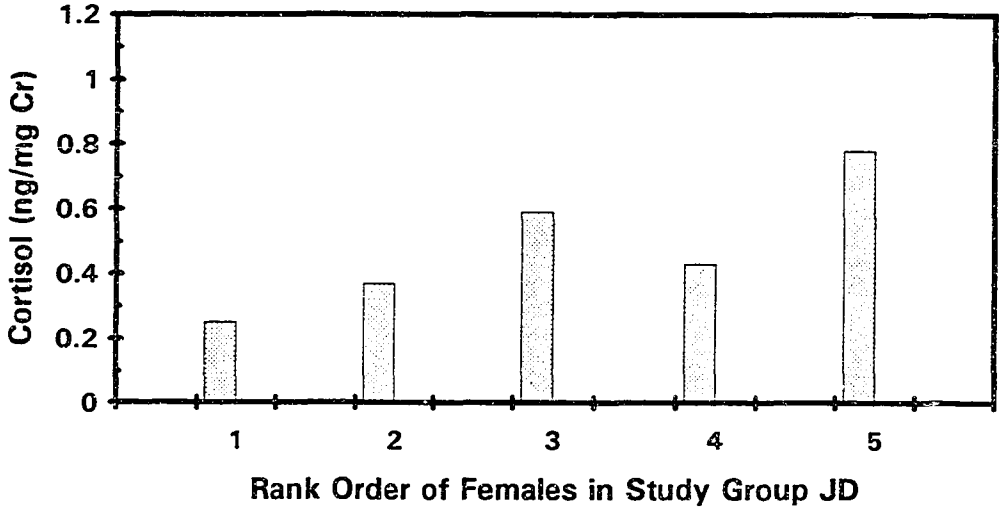


FIGURE 6.18.b. The Variation in Mean Cortisol Excretion Levels Across Social Rank in Study Group Females





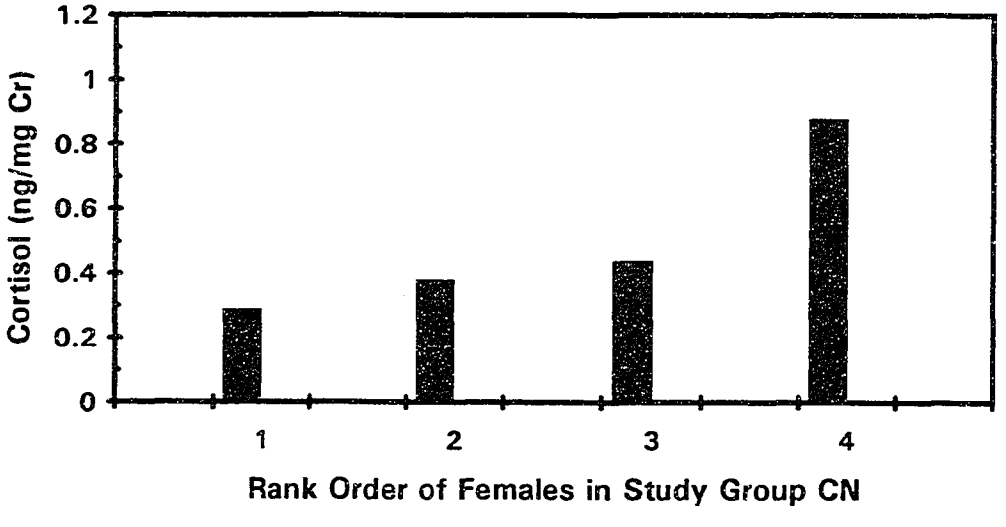
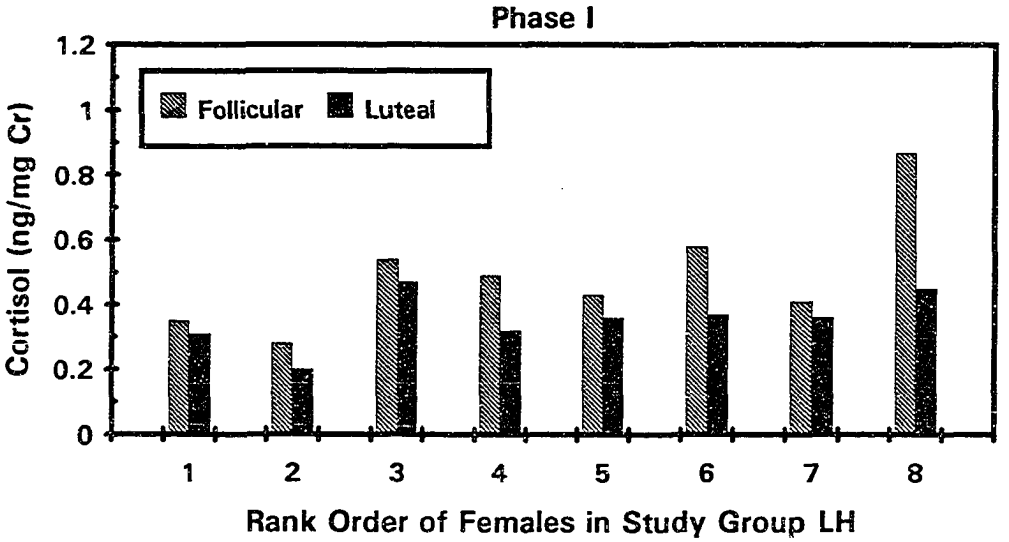


FIGURE 6.19.a. The Variation in Cortisol Excretion Levels During the Follicular and Luteal Phase of the Menstrual Cycle



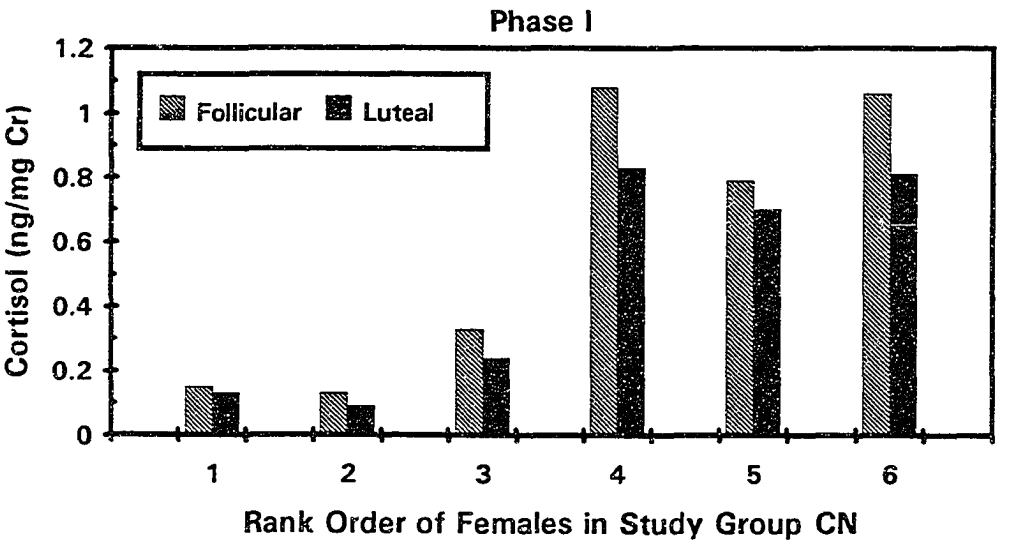


FIGURE 6.19.b. The Variation in Cortisol Excretion Levels During the Follicular and Luteal Phase of the Menstrual Cycle

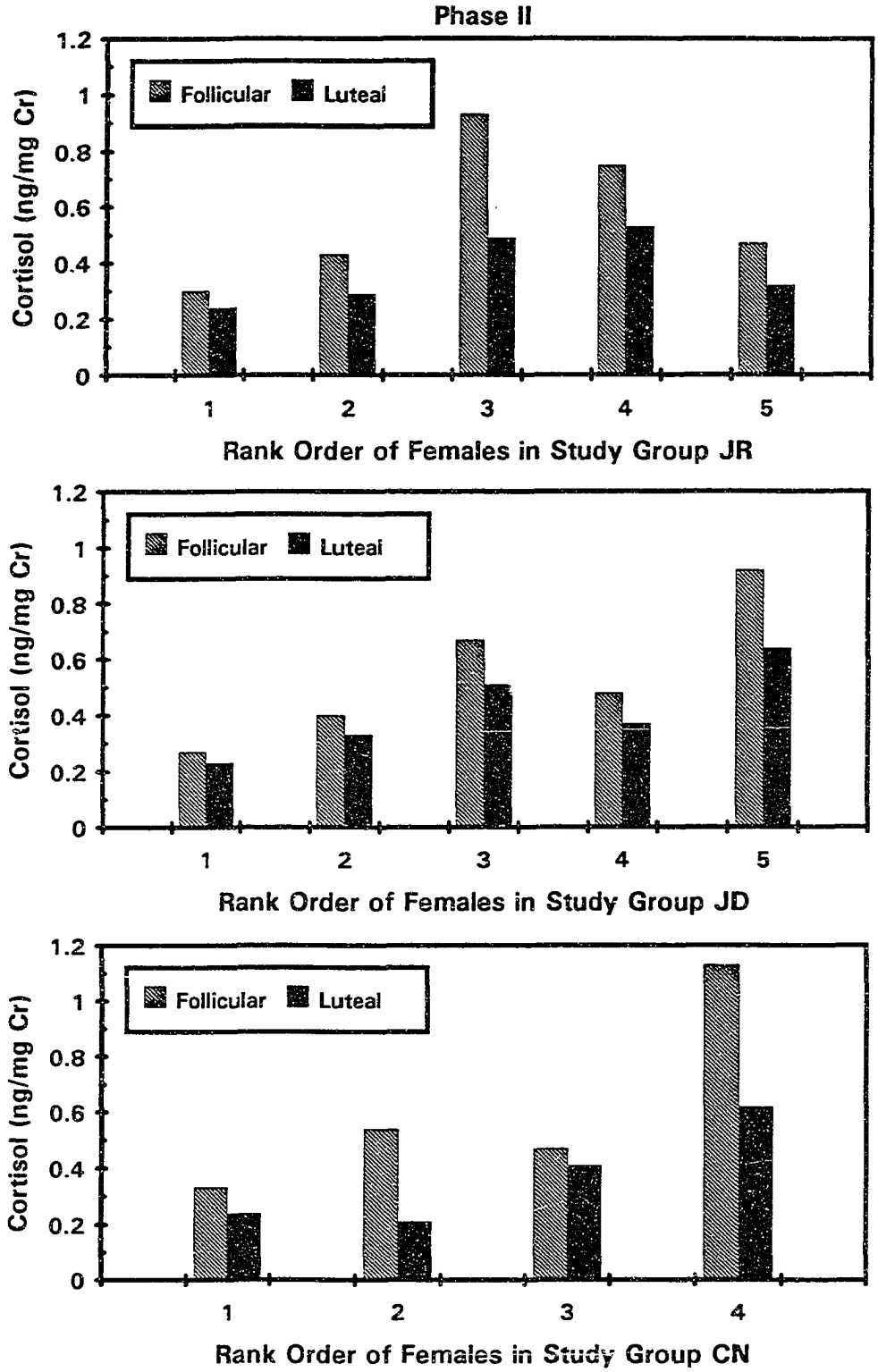
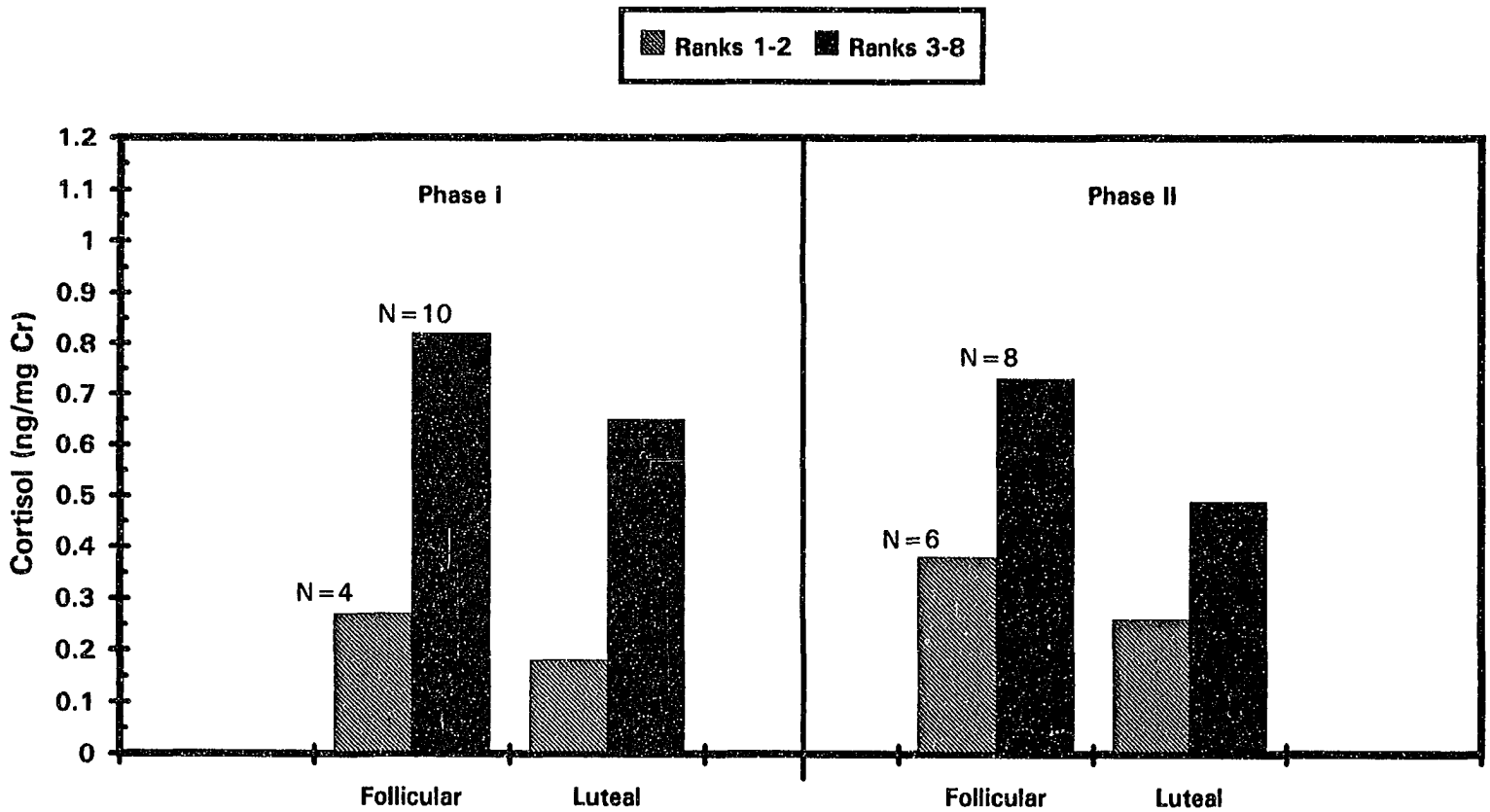


FIGURE 6.20. A Comparison of Mean Cortisol Excretion Levels Among High-Ranking and Low-Ranking Females



6.6. The Relationship Between Variations in Behavior, Physiology and Reproduction Among Female Geladas

Correlations between social, nutritional, reproductive and endocrine variables were explored to look for significant associations. Spearman rank correlation coefficients showed no apparent association between a female's: dominance rank and her mean body weight ([N = 14] Phase I: $r_S = 0.585$; Phase II: $r_S = 0.446$, $p>0.05$, n.s.); dominance rank and her age (Phase I: $r_S = 0.652$; Phase II: $r_S = 0.567$, $p>0.05$, n.s.); age and her mean menstrual cycle length (Phase I: $r_S = 0.488$; Phase II: $r_S = 0.536$, $p>0.05$, n.s.); or age and her mean body weight (Phase I: $r_S = 0.619$; Phase II: $r_S = 0.581$, $p>0.05$, n.s.). In addition, while the amount of time spent feeding was not correlated with a female's dominance rank (Phase I: $r_S = 0.693$; Phase II: $r_S = 0.621$, $p>0.05$, n.s.), there was a positive correlation between social rank and the amount of time spent feeding on seeds and fruits (Phase I: $r_S = 0.822$, Phase II: $r_S = 0.926$, $p<0.01$).

An analysis of the data on cortisol levels along with the behavioral and hormonal data presented above revealed some marked associations. Spearman rank correlation coefficients showed that the differences among females in cortisol excretion were positively correlated with differences in rates of aggression. As social rank declined, rates of aggression increased along with cortisol levels (Phase I: $r_S = 0.731$, Phase II: $r_S = 0.717$, $p<0.05$). This was also the case for menstrual cycle length and follicular phase lengths between high- and low-ranking females. As social rank declined, menstrual cycle length and follicular phase length increased (Phase I: $r_S = 0.794$, Phase II: $r_S = 0.788$,

$p<0.05$). The data on male copulatory behavior showed a similar relationship: the number of copulations decreased with declining social rank in females (Phase I: $r_S = -0.813$, Phase II: $r_S = -0.838$, $p<0.01$), while the frequency of interrupted copulations increased with declining rank (Phase I: $r_S = 0.926$, Phase II: $r_S = 0.941$, $p<0.001$). The significance of these associations between behavior, physiology and reproduction will be explored in the next chapter.

6.7. Summary of Results

The main findings on the relationship between social behavior and fertility found among females in my study groups can be summarized as follows: (1) low-ranking females experienced greater intervals between ovulations than did high-ranking females; (2) the increased length of the menstrual cycle was due to an elongation of the follicular phase, but not of the luteal phase; (3) the frequency with which males copulated with females increased around the peri-ovulatory period; however, there was a significant difference between females in the number of matings with the unit male; (4) low-ranking females received higher rates of aggression than did dominant females; (5) the rate of aggression received by low-ranking females increased significantly further during the peri-ovulatory phase of the menstrual cycle; (6) low-ranking females exhibited greater cortisol excretion levels than did high-ranking females; (7) the pattern of cortisol excretion rates among all females revealed a slight increase during the follicular phase of the menstrual cycle; however, this increase proved to be significantly greater in low-ranking females when compared to females of high rank; and (8) high-ranking females spent more time feeding on preferred food items, however, total time spent feeding was not correlated with a female's dominance rank, body weight or any endocrinological measure of fertility. Thus, in this study, a low social rank in females is associated with:

--longer menstrual cycle lengths;

--elongated follicular phase lengths;

--lower frequencies of copulations;

--increased rates of harassment during estrus periods; and

--increased rates of cortisol secretion during the estrus periods.

CHAPTER 7. DISCUSSION

7.1. Patterns of Reproductive Suppression in the Study Population

> "... at least two key factors affect the birth rates of individual females as a consequence of their dominance rank, namely access to food and stress. Which of these two emerges as the more important, if either, will depend on the particular ecological and demographic contexts in which the animals happen to live...One of the challenges of the future clearly lies in sorting out exactly what is happening here at the proximate level" (Dunbar, 1988:69).

The main objective of the present study was to investigate what proximate factors might be operating to produce differential fertility in a group of captive female gelada baboons. In particular, analyses of both behavioral and physiological factors were conducted in order to determine whether social factors contributed to reproductive impairment in subordinate females. In wild populations of geladas, Dunbar (1980a, 1984) has suggested that differences in birth rates among females resulted from behaviorally mediated reproductive suppression in subordinate females. He proposed that differential degrees of agonism received by females resulted in increased rates of social stress experienced by low-ranking females. The physiological effects of stress in turn produced an adverse effect on the reproductive functioning of those females. Several of the findings of this study suggest that social factors can have a profound effect on many aspects of reproduction. The analyses conducted revealed the following findings:

(1) High-ranking females spent more time feeding on certain preferred (but less nutritionally-valuable) foods than did low-ranking females; however, there was no significant difference found among females in the total amount of time spent feeding. In addition, while body weights among females varied slightly, there was no association found with regard to a female's dominance rank, age or any endocrinological measure of fertility;

(2) Low-ranking females received higher rates of aggression than did dominant females, and the rate of aggression received by low-ranking females increased significantly during the peri-ovulatory phase of the menstrual cycle;

(3) Low-ranking females experienced significantly lower copulation frequencies and a proportionally greater amount of interference during mating;

(4) Females were able to buffer the amount of harassment received by forming a coalitionary alliance with another female. Females within grooming dyads received coalitionary support significantly more often than did females who were not part of a grooming dyad with another female;

(5) Cortisol levels in low-ranking females were higher than those in more dominant females and the increased rate of cortisol excretion was most notable in the follicular phase of the menstrual cycle; and

(6) Low-ranking females experienced greater intervals between ovulations than did high-ranking females, and the increased length of the menstrual cycle was due to an elongation of the follicular phase, but not of the luteal phase.

To what extent do these findings tend to support or refute the two hypotheses that this study set out to test? The two hypotheses are:

1. ***Variation in fertility is the result of a greater efficiency of food intake by dominant females.***

2. ***Variation in fertility is the result of behaviorally mediated reproductive suppression in low-ranking females.***

7.2. The Effect of Food Intake on Fertility

Many of the findings on food intake and measures of nutritional fitness in this study did not support the hypothesis that a greater fertility, as evidenced by a greater fecundity, in dominant females was the result of a greater efficiency of food intake. The results on food intake showed that dominant females did not spend more time feeding than did low-ranking females. There was, however, competition among females for certain preferred foods (e.g., seeds -- dispersed on exhibit, and fruits -- dispersed off exhibit). These particular foods, though, were not the most nutritionally valuable foods in their diet. Therefore, dominant females who spent more time feeding on these foods did not necessarily gain a nutritional benefit from doing so. With respect to the higher quality foods (e.g., the commercially prepared foods), there was no difference found among females in time spent feeding.

The results on body weight also revealed no significant difference among females in this respect. The mean body weight for the study group females was greater than that reported for wild groups (15.9 kg compared to 13.6 kg,

respectively; $t = 39.017$, $p < 0.02$). In addition, when comparing a female's dominance rank with her mean body weight, no association was found. A greater fecundity in dominant females, therefore, was unlikely to be due to the nutritional effects of a higher body weight. The results illustrate the point that despite the fact that competition for certain foods existed among females, this did not result in lower body weights for low-ranking females. Thus, any differences found among females in reproductive functioning could not be the result of differences in food intake and its ensuing advantages; Hypothesis 1 is therefore rejected.

These findings are similar to those reported by Small (1981) and Riopelle *et al.* (1976) on captive rhesus macaques where differences between females were found with respect to the amount of food intake. However, while high-ranking females had higher body weights, the body weights of low-ranking females were not reduced to a degree to suggest that they experienced deficiencies in overall nutritional condition. It can be assumed then that both high-ranking and low-ranking females were able to obtain their minimum nutritional requirements, and any differences among females observed can be viewed as probably unrelated to their basic nutritional condition.

7.3. The Effect of Social Behavior on Fertility

Several of the findings of this study support the hypothesis that differences among females in fecundity are the result of behaviorally mediated reproductive suppression in low-ranking females, and results, therefore, in differential fertility. One particular finding, the rate of aggression received by females, demonstrates how differences in the amount of harassment a female

receives are proportional to her social rank. As reported in wild geladas, the higher rates of aggression that lower-ranking females experienced became particularly evident when females entered the estrous phase of the cycle. In addition, this pattern of interaction occurred as often between grooming partner females as it did between non-partner females. Not only did the frequency of agonistic behavior increase at the time around ovulation, the level of intensity of the behaviors themselves heightened as well. When females approached the ovulatory phase of their cycle, they began displaying proceptive behaviors towards the male; at this time the female's behavior shifted from being almost exclusively directed towards other females to being directed towards the male. Typically, these displays of solicitation by subordinate females led to aggressive responses by more dominant females. More subtle threats, such as the flashing of eyelids and baring of teeth, were replaced with the more assertive lunges, charges and high-intensity chases.

The predictability of these patterns of interaction among females provides an explanation of the cautionary behavior taken by low-ranking females during mating attempts. The high frequency of interrupted mating attempts experienced by low-ranking females was striking. When copulations took place in close proximity to more dominant females, the latter responded with overt aggressiveness directed towards the mating pair, which ultimately resulted in an incomplete copulation. Initiations of copulations by low-ranking females were less likely to occur, therefore, when more dominant females were in close proximity (<5 m), and copulations were more likely to be uninterrupted if the mating pair was considerably distant from the rest of the group. The high rates of harassment during mating attempts resulted, therefore, in lowered frequencies of successful copulations in subordinate

females. And this is further evidenced by the relatively small number of births recorded in this study. Of the four pregnancies observed, three occurred in high-ranking females (Rank #1 females = two pregnancies, Rank #2 = one pregnancy, and Rank #5 = one pregnancy). It appears as though the low copulation frequencies, and high rates of harassment during mating attempts, coupled with the partial suppression of ovulatory function has effectively rendered low-ranking females infertile. Indeed, in each of the study groups observed, it appeared that the female's social and reproductive relationship with the unit male was strongly influenced, and to some degree directly controlled, by her relationships with the females in her unit. Such severe behavioral constraints on the reproductive behavior of subordinate females undoubtedly must have adverse effects on their reproductive success.

Harassment during copulations has been reported in some wild populations of geladas (U. Mori, 1979a). However, Dunbar (1980a) did not observe disruptions during copulations in his study population and he found no differences in copulation frequencies between dominant and subordinate females. In this respect, my study groups differed markedly from those reported by Dunbar, but displayed a pattern of harassment during mating similar to that reported by Mori. Furthermore, Dunbar (1984) has shown that the interactions between females are largely influenced by their relative degree of relatedness. The patterns of agonistic behavior observed in this study were similar to patterns observed in the wild, and closely paralleled those reported by Kummer (1975) in a study of dyad formation in captive geladas. In both this study and Kummer's the composition of the study groups primarily consisted of adult females, with varying degrees of relatedness. In the absence of closely related kin, the patterns of interactions were largely influenced by

their dominance relationships. Thus, while the structure of the social groups was broadly similar to groups in the wild, the pattern of dominance relationships among these females was notably more overt. Furthermore, detailed analyses of wild groups suggest that females within units that lacked close relatives to form a strong grooming relationship would, secondarily, assort themselves on the basis of dominance ranks (Dunbar, 1983a, b). Thus, the patterns of interactions among females in wild and captive groups are influenced by both kin and dominance relations, and these in turn can evidently influence female reproduction. The data resulting from this study suggest that dominant females can limit reproduction in subordinate females by behavioral mechanisms.

7.3.1. The Importance of Coalitions

Another factor that has been shown to be important in influencing the outcome of interactions between females is the formation of coalitions. As Dunbar (1984) reports for wild geladas, females of low dominance rank can to some degree buffer the amount of agonism they receive by forming coalitionary alliances with other females. By establishing alliances with others, a female can maintain and increase her dominance rank. In addition, having an alliance with a close relative could give a female an additional benefit in terms of inclusive fitness. In the present study coalitionary support proved to be an important component of the social dynamics among females as well. This became most apparent when comparing grooming partner and non-partner females during agonistic encounters. Females in grooming dyads, who were coalitionary allies, were significantly more likely to support one another during

agonistic encounters than they were to support other females. On the contrary, females that were not part of a grooming dyad, and lacked a close female ally, received support by other females only a relatively small percentage of the time, usually on occasions involving inter-group encounters. For these particular females, the consequences of low social dominance appeared to be extreme. However, non-dyad females used alternative strategies to alleviate the amount of harassment incurred from more dominant females by forming a grooming dyad with the unit male. The male is a less preferred grooming partner than a female because males typically do not actively support females in encounters with other females. But a male's presence alone may be enough to even slightly reduce the number of times a female is threatened. Coalition formation has also been found to be an integral part of the social mechanism operating to produce lowered fertility rates in yellow baboons (Wasser and Starling, 1986). Frequent coalitionary attacks on females of low social status have been implicated as the causal factor producing reduced fertility in these females.

7.3.2. The Endocrine Evidence

These results suggest that harassment of low-ranking females, through higher rates of agonism, has a significant physiological effect, as is evidenced in the increased rates of cortisol excretion. The results on cortisol excretion derived from this study lend credence to the hypothesis that a female's social position in her group, and the consequences that ensue, influences her reproduction. The hormones cortisol and prolactin have been implicated in mediating the suppression of hypothalamic GnRH and pituitary LH release,

both of which are known causes of ovarian impairment (Yen, 1986). Elevations of both hormones have been associated with suppressed reproductive function in subordinate female talapoin monkeys (Bowman *et al.*, 1978; Keverne, 1979) and long-tailed macaques (Kaplan *et al.*, 1986). In this study, the general pattern of urinary cortisol excretion by females was of a slight mid-cycle increase, resulting in higher levels being secreted during the follicular phase compared to the luteal phase of the menstrual cycle. However, there were significant differences among females in this general pattern of cortisol excretion. Cortisol levels in low-ranking females were notably higher than those in more dominant females and the rate of excretion in low-ranking females increased substantially more in the follicular phase of the menstrual cycle. Furthermore, the rate of cortisol excretion was strongly correlated with the rate of agonism, and both of these variables increased as social rank declined. This finding demonstrates the physiological consequences of female social behaviors. In earlier studies on wild populations of geladas it had been suggested that increased rates of harassment of low-ranking females ultimately lead to adverse physiological consequences (Dunbar, 1980a, 1984, 1988). However, until this study, the physiological evidence needed to test this hypothesis was lacking.

7.3.3. Effects on the Menstrual Cycle and Ovulation

Perhaps the most significant findings of this study are those on the menstrual cycle itself. Harassment of low-ranking female gelada baboons by high-ranking females resulted in greater degrees of stress, as is evident in the higher levels of cortisol excretion by low-ranking females. This in turn

appeared to produce lengthened menstrual cycles and reduced ovulatory frequency in low-ranking females. Menstrual cycles in the study group females lasted a mean of 37.3 (± 6.1 s.e.) days, similar to the mean length of 35 days reported in wild populations of geladas (Dunbar, 1978a). In this study, however, the mean menstrual cycle length for low-ranking females was significantly greater than the mean for dominant females, as measured by behavioral, morphological and hormonal indices. In addition, 65% of their menstrual cycles exceeded the mean of high-ranking females by at least 2 standard deviations. This difference in menstrual cycle length points to lowered fertility in low-ranking females. In an analysis of variance in birth rates between females, Dunbar (1980a) suggested that a lower birth rate in low-ranking females was in part due to high rates of anovulatory cycles producing longer intervals between conceptions. While low-ranking females in this study exhibited slightly more anovulatory cycles than did high-ranking females, the data show that subordinate females did regularly experience ovulatory menstrual cycles. A cycle is determined as anovulatory when there is no apparent cyclicity in ovarian hormones and ovulation remains undetectable based on hormonal markers. Therefore, the primary factor responsible for differences in fertility between the females in this study was not chronic anovulation, but rather the relative frequency with which females ovulated. The difference between a lengthening of the menstrual cycle and an anovulatory cycle is in the relative interval between ovulations, and therefore, a matter of the degree of suppression. Although the increased rates of harassment and elevated cortisol levels displayed by the subordinate females in this study resulted in reproductive impairment, reproductive suppression was not complete. The lengthening in the relative duration of the menstrual cycle does,

however, indicate that low-ranking females experienced greater intervals between ovulations than did high-ranking females and thus, over time, low-ranking females would have decreased chances for conception. Consequently, subordinate females in this study experienced partial reproductive suppression.

Further analyses conducted in this study revealed that the increased length of the menstrual cycle was due to an elongation of the follicular phase, but not of the luteal phase. An extension in follicular phase length was positively correlated with increased rates of agonism and higher levels of cortisol secretion in low-ranking females. This strongly suggests that increased rates of harassment by more dominant females directed towards lower-ranking females in estrus leads to increased cortisol secretion by the latter, which in turn is responsible for the delay in the onset of ovulation, as evidenced by increases in the duration of the follicular phase in these females. Elevated levels of cortisol secretion have been associated with the suppression of hypothalamic GnRH release and pituitary LH response in some cercopithecine species (Walker *et al.*, 1983; Adams *et al.*, 1985; Kaplan *et al.*, 1986). Cortisol can also act directly on the ovary impairing follicular function, conception, implantation or early pregnancy (Yen and Lein, 1984). A possible physiological mechanism causing a delay in the onset of ovulation in the females in this study may be an activation of the hypothalamic-pituitary-adrenal axis.

7.4. The Adaptive Significance of Reproductive Suppression in Female Gelada Baboons

Both behavioral and physiological mechanisms appear to be operating in limiting reproduction in subordinate female gelada baboons. High-ranking females may impose stress-induced suppression of reproduction on their female subordinates to obtain a reproductive advantage. Reduced ovulatory frequency may lead to the delay in conceptions in low-ranking females found in wild populations. In wild geladas, and in the captive population observed in this study, the social suppression of female reproduction appears to be partial, in contrast to the total suppression of reproduction that has been observed in several callitrichine species. Unlike marmosets, female geladas do not need helpers to aid in rearing offspring. However, in the wild, low-ranking females produce fewer offspring than do high-ranking females (Dunbar, 1989).

Socially-induced suppression of reproduction in subordinate females appears to be due to an impairment of ovarian function caused by high rates of aggression. The fitness benefits gained by dominant females who harass subordinate females during estrus seem to lie in the suppression of the latter's fertility, resulting in an increase in the harasser's relative reproductive success. It has been suggested that this behavior constitutes an example of evolutionary spite (Dunbar, 1980a). In the gelada, and in talapoin monkeys as well, females do not appear to be competing for any specific resource, or at least not a resource that can be significantly affected by the harassment of the members of a female's unit. It might be argued, then, that the cost of harassing other females is relatively low compared to the benefits to be gained. In theory, once a hierarchy is established, the hierarchy can be maintained with modest efforts: the use of low-intensity threats, such as facial gestures and passive supplants,

with only occasional heightened aggressive exchanges. Furthermore, the perception of subordinate status alone may be sufficient to maintain the hierarchy, and the stress induced by this perception may likewise be sufficient to cause reproductive impairment (Rowell, 1966).

7.5. The Significance of Reproductive Suppression in Female Mammals

A female's lifetime reproductive output is largely determined by the life-history parameters and demographic structure that exist in her population. The particular demographic structure of a population is constrained, in part, by species-specific characteristics that prescribe its basic grouping patterns and reproductive capacities. This in turn, will have significant implications for the behavior and reproductive strategies of females. Within this framework, however, demographic processes can vary under the influence of a number of environmental and social variables that directly affect such fundamental life-history processes, as the rate at which individuals give birth and die.

Variations in fertility can occur throughout a female's lifetime, as well as between females in a population and between populations of a species (Ziegler and Bercovitch, 1990). Fluctuations in female fertility can arise in a number of ways. Clearly, environmental factors play an important role in differential fertility because they can directly affect a female's physical condition, and hence her fecundity. Additionally, social factors may operate to produce differences in nutritional status which then can lead to differences in fertility. In many cases, however, differential fertility may occur independent of nutritional resources, and alternatively, be driven purely by social factors. Such socially-mediated factors can include the adult sex ratio, group size,

access to social partners, access to mates, access to preferred spatial positions in a group, resource competition, aggression, and stress (Wasser and Barash, 1983; Gray, 1985; Harcourt, 1987; Dunbar, 1988). They are considered socially-mediated factors because they are the direct result of being part of a social group and the consequences that ensue.

Indeed, the most often cited socially-mediated factor affecting a female's fertility is her social status. Where correlations between a female's dominance rank and her fertility have existed, the subordinate female is at a disadvantage (Wasser and Barash, 1983; Gray, 1985; Harcourt, 1987; Dunbar, 1988; Ziegler and Bercovitch, 1990; Abbott, 1991). The negative effect social subordination can have on reproduction takes many forms and is found in a wide variety of mammalian species. The vast array of socially facilitated reproductive impairment exhibited across numerous taxa demands an understanding of the mechanisms operating to produce disparities in female reproductive success. One such evolutionary explanation is the 'Reproductive Suppression Theory' (Wasser and Barash, 1983). In an overview of reproductive impairment in mammals, Wasser and Barash (1983) review the various causes and outcomes of reproductive failure evident in a wide variety of species. In doing so, they present a model of reproductive suppression which expands on existing evolutionary models that seek to explain the suppression of reproduction as a proximate mechanism to increase lifetime reproductive success. The model is based on the relationship of present to future reproductive conditions, as determined by the temporal patterns of an individual's biological, psychological, and environmental conditions. It makes the assumption that not all conditions are equally favorable for reproduction. Thus, under environmental adversity -- physical or social -- a female can

optimize her lifetime reproductive success by suppressing her own reproduction until better future conditions provide improved prospects for the survival of her offspring. Additionally, females may be able to improve the current conditions for their own reproduction by suppressing the reproduction of other females.

The 'Reproductive Suppression Model' also has some implications for sexual selection theory, and in particular, female-female competition. As Trivers (1972) suggested in his theory of parental investment and sexual selection, the greater the parental investment contributed to a reproductive event, the more unlikely it is to replace failed conceptions. This in turn has led to selection for mechanisms which lead to the avoidance of wasted investment in conceptions that are not likely to succeed. Typically, female mammals invest great amounts of energy in parenting, and therefore mechanisms that aid in the avoidance of wasteful conceptions are thought to be particularly important for female mammals. The primary mechanism usually invoked in sexual selection theory as being most important to female mammals is the choice of high quality mates. However, the Reproductive Suppression Model provides two additional mechanisms for the avoidance of unsuccessful conceptions in female mammals: (1) the deferral of one own's reproduction until more optimal conditions for infant survival exist, and (2) the suppression of other females' reproduction in order to improve the conditions for one's own net reproductive success.

Given these assumptions, the Reproductive Suppression Model predicts that variations in the suitability of conditions for reproduction should have led to the evolution of reproductive patterns among females that cause them to suppress reproduction whenever the long-term cost of deferring reproduction is less than the cost of the deferment itself. Females who exhibit such

reproductive patterns will be at a reproductive advantage; hence, if the behaviors producing these patterns are to some degree heritable, such patterns should have evolved. Under these conditions, females are expected to delay or prevent reproduction whenever available cues (e.g., the individual's physical or psychological condition, the physical or genetic status of the fetus, the availability of resources, and the social or environmental conditions at the time of birth) suggest that the conditions of 'inequality' exist.

Furthermore, whenever socially dependent conditions affect reproductive success, females may improve their current probability of reproductive success by influencing the timing and frequency of births among other females in their social group. Socially facilitated suppression occurs whenever reproduction is "inhibited by one's interactions with, and the reproductions of, other individuals" (Wasser and Barash, 1983:522). Accordingly, individuals most likely to be suppressed tend to be those who are least likely to defend themselves in competitive interactions (i.e., females of low social status). The stage at which reproductive suppression is imposed, however, is dependent on the degree to which current and future conditions for reproduction are predictable. That is, when future conditions are highly predictable, reproductive suppression should be imposed in the early stages of reproduction, whereas an uncertainty of future conditions should lead to suppression at progressively later stages.

Behaviorally mediated reproductive suppression is known to occur in a wide variety of mammalian taxa (see Chapter 1, section 1.1.2.d, for a review of studies on reproductive suppression). The data derived from these studies show that socially-dependent conditions can produce significant variations in female reproductive success through a variety of mechanisms, and in various

times during a female's reproductive life-history (Wasser and Barash, 1983). For instance, the suppression of reproduction can be manifested through a delay or inhibition in the onset of puberty, sexual maturation, sexual receptivity, or ovulation. Furthermore, suppression may be imposed in progressively later stages of reproduction, as in embryo implantation, early gestation (spontaneous abortions) or during neonatal development (infant mortality).

The data on variance in female reproductive success in mammals suggest that the predictions of the Reproductive Suppression Model are in large part supported. When environmental conditions remain poorly predictable, as reported in many of these studies, reproductive suppression occurs in progressively later stages of the reproductive event (e.g., implantation, gestation or post-partum) . This was apparent in those species where competitive conditions often occurred at the time of birth (e.g., house mice, rabbits, prairie dogs, lions and elephant seals). In these species, the conditions at the time of birth (e.g., the availability of food resources for infant survival) often cannot be predicted prior to the time of the birth itself. Thus, the suppression of reproduction in some females may result in high rates of neonatal mortality.

In contrast, in those species where environmental conditions were more predictable, suppression occurred early on in the reproductive process (e.g., the onset of puberty, maturation, or ovulation), particularly when there was a scarcity in socially dependent resources. This was evident in many highly social species, such as dwarf mongooses, wolves, elephants and primates. In many of these species, when breeding resources (e.g., food, mates, helpers, territories, etc.) were in limited supply, subordinate females often exhibited a

deferral or delay in reproductive output until prospects for increasing their relative social status and breeding success improved.

The findings on female gelada baboons, both from this study and from studies conducted on wild populations, also support the predictions of the Reproductive Suppression Model. In wild geladas, dominant females give birth to offspring more often than do the subordinate females in their group. And in this study, dominant females experienced ovulatory events more frequently than did females of lower social status. The variance in female fertility evident in both populations appeared to be the result of increased rates of harassment on subordinate females. The evidence suggests that the high rates of agonism directed towards subordinate females may be an attempt by dominant females to manipulate the reproduction of the recipients of the aggression in relation to their own reproduction. The endocrinological data resulting from this study strongly suggest that this may indeed be the case. The harassment, and the physiological stress it produces as a result, apparently serves to inhibit ovulation in the recipients. Thus, the females harassed most were predicted to be those most vulnerable to suppression, as well as being in reproductive states that are most physiologically vulnerable. This would have the effect of decreasing the harassed female's reproductive output while increasing the probability of the harassing female's reproductive success.

The Reproductive Suppression Model predicts that suppression will be most frequent in those females least likely to succeed in competitive situations. And physiologically, it will be more advantageous to impose suppression early in the reproductive process. Thus, females approaching ovulation are more susceptible to stress-induced ovulatory inhibition than are females in later stages of the cycle. Under these assumptions, one would predict that (1)

subordinate female geladas are more susceptible to stress-induced reproductive suppression than are dominant females, and (2) subordinate females will be harassed more frequently as they approach ovulation. The data from this study on the direction of agonistic threats and the timing of such interactions support these predictions: subordinate females are harassed more frequently by dominant females, and increasingly so during the follicular phase of the menstrual cycle compared to the luteal phase. Thus, it appears that dominant females may be suppressing the reproduction of more subordinate females in order to improve the current conditions for their own net reproductive gain.

Considering the consequences for female fitness of these mechanisms, it can be seen that females of high social status could increase their own relative reproductive success by harassing less dominant females, thereby suppressing reproduction in these females. Alternatively, when females are faced with low social status they could defer reproduction and employ alternative strategies in order to overcome the consequences of low rank and increase their own reproductive output. If we make the assumption that a female will pass through all social ranks during her lifetime, we might expect a pattern to emerge where her social rank would rise as she grows older, reach its maximum at her prime, and decline as she grew older. Given this assumption -- and in the absence of competiton for food resources -- all females would be expected to have a similar reproductive output. Thus, if a female altered her behavior to increase her fitness at any one stage of her life, it could potentially increase her lifetime reproductive success relative to others. Indeed, it has been shown that a female has a variety of options available to her in order to do just that:

(1) to form an alliance with another female in order to increase her own dominance rank. Forming coalitions with close female relatives, such as mothers and daughters or sisters, is preferable for it allows a female to maintain her dominance status as she declines in age, as well as providing additional reproductive gains in her inclusive fitness.

(2) to become the male's main grooming partner, either in order to use him as a substitute female ally or to minimize the amount of social and physiological stress incurred as a result of agonistic interactions with more dominant females. While the male is a less desirable ally, a female's chances of gaining sexual access to the male or avoiding harassment from dominant females are increased. Thus, for females lacking female allies, acquiring the male as an ally may provide some short-term gains.

(3) to desert the male in favor of another male who has fewer females or who is currently establishing relationships with his females in order to increase her dominance rank. A female can either form a close relationship with a new male attempting to take over a unit or join a follower male when her unit undergoes fission. In either case, a low-ranking female would have greater chances of increasing her dominance rank than she would by remaining in her current social situation, given the vagaries of the demographic process.

Whether or not females faced with different options available to them would yield equivalent lifetime reproductive outputs in the long run is difficult to test without knowledge of the genetic relatedness of individuals and complete life-histories. However, the data currently available suggest that dominant

females may be able to increase their reproductive success relative to others by imposing behaviorally-mediated reproductive suppression in lower-ranking females.

In conclusion, the inhibition of reproduction in female primates demonstrates the profound effects social factors can have on fertility. While the salient role social factors play in the reproductive success of male primates has been discussed since the first field studies on primates began, there has been a growing appreciation of the diverse ways in which social conditions can influence many aspects of reproduction in female primates. Dominance status is the most common social factor implicated as either directly or indirectly affecting fertility in these studies. Intrasexual competition among females is increasingly being viewed as a means of enhancing the survivorship and reproductive success of offspring. Compared to males, however, female-female competition is notoriously inconspicuous, and can occur throughout all or any part of the reproductive process. While the relative degree of the suppression of reproductive events varies with each species and the prevailing social environment, the evidence overwhelmingly suggests that the effects of a female's social relationships with other females do influence her reproductive output. Given the degree to which social behavior is an integral part of the evolution and adaptation of the primate order, it should not be extraordinary, then, that changes in a female primate's social environment can have important consequences for her reproduction.

In the evolution of mammalian reproductive strategies, the disruption of ovarian functioning must have played an important role in mediating the social suppression of reproduction in females. Only further investigations into the physiological mechanisms producing inhibitions in reproductive functioning will demonstrate whether there are common neuroendocrine mechanisms operating in different species of primates and in other group-living mammals.

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