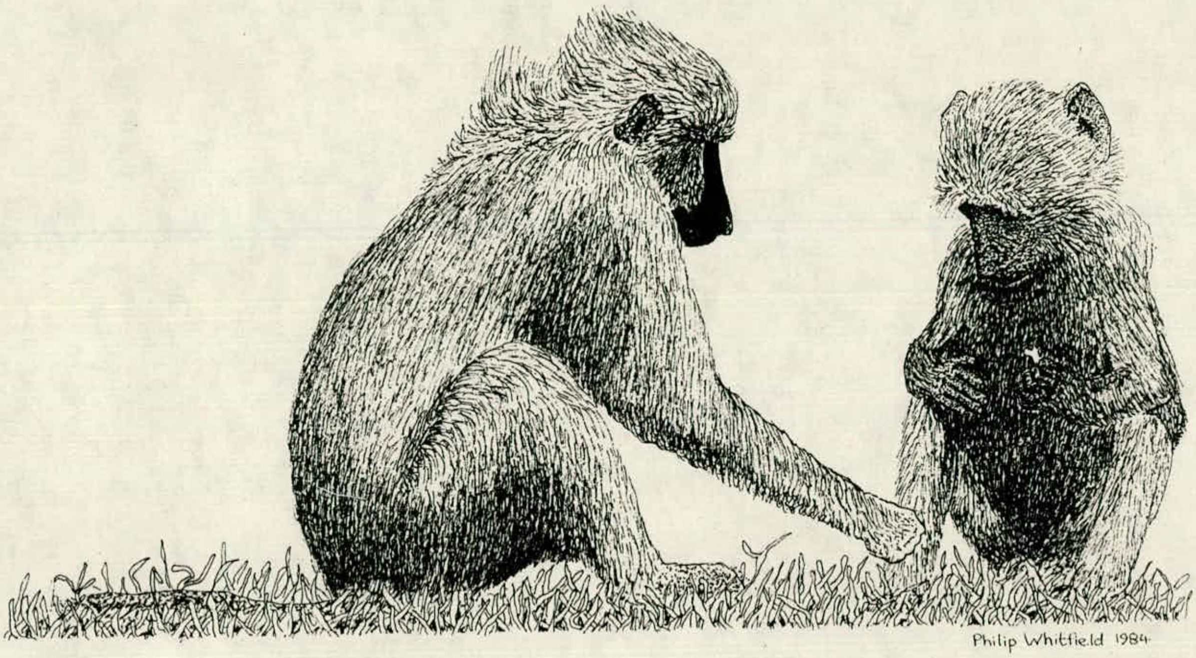

Philip Whitfield 1984

SOCIAL RELATIONSHIPS
OF JUVENILE OLIVE BABOONS

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Thesis presented for the degree of
Doctor of Philosophy
University of Edinburgh
1984

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ABSTRACT

A seventeen-month field study of the social relationships of juvenile olive baboons was carried out near Gilgil, Kenya. The troop of approximately 130 individuals contained fifty-five juveniles for most of the period of this study; of these, sixteen were observed in detail.

Six adult females died and four underwent a dramatic loss of rank just prior to this study; it was possible to assess the effects of maternal death or rank loss on the juvenile offspring. A rank order of juvenile females based on their mothers' agonistic ranks closely approximated a rank order of the juvenile females based on the direction of approach-withdraw interactions. Juvenile females aged over three years at the time of their mothers' death did not appear to lose rank; however, those females who were orphaned at less than two years of age held lower ranks than those predicted by maternal rank. If an adult female lost rank, her juvenile daughters fell in rank as well, regardless of their age.

A rank order of juvenile males based on relative size, but not maternal rank, closely approximated their agonistic rank order. Younger juvenile males were influenced by their mother's ranks, in their interactions with adult females, but, with increasing age, males were able to dominate females who out-ranked their mothers. Male rank seemed not to be affected by maternal death or rank loss.

Family members were often found in close proximity and were frequent grooming partners. Same-sex peers were frequent neighbours and this tendency increased with juvenile age. Juvenile males associated with sub-adult females during the inflating phase of the female's reproductive cycle, and grooming between these age-sex classes was reciprocal. Juvenile females maintained proximity to lactating mothers and groomed them often, although this grooming was not reciprocated. Juvenile females also groomed unrelated adult females of high rank. Grooming of unrelated individuals was not reciprocated in the formation of aggressive alliances. Particular adult male-infant relationships identified in two previous studies persisted into this study.

Juvenile females were more likely than males to lose a resource to another baboon, as were individuals of low rank. Members of each sex tended to supplant selectively members of their own sex. Finally, evidence is presented that juveniles not only differentiated between individuals ranking higher or lower than themselves, but distinguished the relative ranks of those individuals.

ACKNOWLEDGEMENTS

The study described here began in 1979. But the list of people who have made its completion possible started to grow long before that.

I thank the Sigma Xi Society, the Boise Fund, and Edna Dale for financial support.

My supervisor, Aubrey Manning, has given me valuable support and advice throughout. On his first visit to Kenya, mid-way through my field work, I was able to show him baboons in the wild behaving as they should - and his enthusiasm renewed my own.

In Kenya, I thank the Office of the President for permission to conduct research. That permission was secured through the efforts of James Else and the staff of the Institute of Primate Research.* I join many other researchers in Kenya who are grateful for their help. I also thank Jim for his friendship and hospitality at Tigoni and for the the bulging picnic hampers he always brought with him to Gilgil.

The co-directors of the Gilgil baboon study, Robert Harding and Shirley Strum, kindly gave me permission to join the project. I thank the GEMA cooperative, who own Kekopey Ranch, for tolerating both baboons and baboon researchers; and Richard Dansie, the ranch manager, and Jacquot Dansie, who were always generous with their time when researchers needed help.

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* National Museums of Kenya

My way was paved at Gilgil by Barb Smuts and Nancy Nicolson, who completed the first major studies of EC troop and kindly allowed me access to their unpublished data. With Barb's help, I learned the baboons and their (then!) range. Barb's enthusiasm and friendship was - and still is - very valuable. In the two years which followed, Debbie Snelson and then Jeff Swift shared baboon troops lost and found. They are solid field companions and close friends, and I thank them both for their company. Robin Dunbar's knowledge of field methods was of great help in organizing this study. Researchers studying PHG troop welcomed me at the Red House. I am grateful for the company of Denise Andrus, Fred Bercovitch, Deb Forthman, Debbie Manzolillo, and Bronco Quick - and especial thanks to Debbie and to Charles Nightingale for the best turkey dinner ever.

In Nairobi, Barbie Allen is well known for her kindness to stray field workers, and Andrew Hill provided hospitality and haute cuisine - the Good Life at Museum Flat One.

Back from the field with my dog-eared checksheets, I benefitted from advice on data analysis from Jeanne Altmann, Mark Beckoff, Neil Chalmers, John Colvin, and Jill Hooley. The insights of other primate field workers were always valuable and I am grateful to John Deag, Mike Harrison, Phyllis Lee, Don Lindburg, Bill McGrew, Cecilia Torres, and Richard Wrangham. Researchers into the behaviour of diverse species still face similar problems; I have benefitted from conversations with Paul Green, Joan Herrmann, Alistair Lawrence, Candace Lawrence, Cynthia

Moss, Linda Partridge, and Karen Ross. The mysteries of the computer were made more comprehensible by Martin Sharman, and by the patient staff of the Edinburgh Regional Computing Centre Advisory Service. I especially thank Julian Read for writing time-saving SIR programs. In the amateur league, Nigel and Jacquie Clark bailed me out of many SPSS messes. My thanks, too, to Peter Hetz, Jerry Jameson, Liz Rogers, and David Pilbeam. Many of these people have contributed to the completion of this thesis at many levels, both as colleagues and friends.

For support, friendship, and therapeutic frisbee sessions, particularly in this last long year, I thank the denizens of Floor One: Pat Davison, Kevin Fowler, Bob Goupillot, Geoff Harper, Peter Marsh, Jaleel Miyan, and Richard Steele. I am very grateful to Philip Whitfield, whose pen-and-ink drawings open and close this thesis.

Since introducing me to my first baboon at Gombe, Anthony Collins has greatly influenced the way I think about their social relationships. He has given advice and encouragement at every stage of this project - even from remote Tanzania - and I am deeply grateful for his help.

My heartfelt thanks go to Curt and Claranne Johnson, my parents, who have encouraged and supported me in every way.

Chapter 1

INTRODUCTION

1.1. Juveniles

The juvenile stage in an animal's life lies between infancy and reproductive maturity. A juvenile individual no longer relies solely upon its parents for food or protection; the parents' time of maximum investment in that offspring is concluded, and they will devote their energies to new infants. The juvenile has survived the period of infant vulnerability when the risk of mortality is highest, and has achieved partial or total independence.

Yet months or years may elapse before that individual joins the cohort of breeding adults. The individual grows and develops, but successful reproduction may lag behind sexual maturity. Additional growth and experience may be required before an animal is capable of acquiring and holding a territory, contesting conspecifics for a mate, or, in mammals, sustaining the energetic demands of pregnancy and lactation.

The juvenile is apparently poised between two crucial stages in its life history, and research frequently reflects this viewpoint. The question "what factors contribute to infant survival and development?" is often succeeded by "what elements ensure adult reproductive success?". But selection operates at all stages of life history, at least until reproduction is complete, and success as an adult will have been, in turn, influenced by success at the juvenile stage.

For many socially-living species, and particularly for the primates where generations overlap to a great extent, the juvenile years are occupied with more than simply "waiting" for adulthood. Maturation is slower in primates than in other mammals of comparable size. During the period of maturation, a social community provides a means for the cultural transmission of information about features of the physical environment. But, while competence in obtaining food, avoiding predators, or locating shelter will be essential to daily survival, features of the social environment and competence in that sphere will equally affect how well a primate fares as a breeding adult. It seems likely that the challenges of the social and not the physical environment have been the major selective force on primate intelligence (A. Jolly, 1966; Humphrey, 1976); the juvenile is already employing that intelligence as a member of a complex social organization.

The interaction between social organization and individual relationships and behaviour - and the impact of each on the other - is now an important area of study (see Hinde, 1976). Yet, with a few important exceptions (e.g., Cheney, 1976; Lee and Oliver, 1979) these aspects of the juvenile years of baboons have had little attention. Hrdy and Williams (1983, p. 14) recently wondered if "perhaps we are currently handicapped by a shortage of thought and data on the behavioral development of juveniles, in both our own and other species". Interestingly, the issue under discussion in that article was the shift in primatology away from a perspective which emphasized adult male behaviour to one which fully encompasses adult females as well.

In baboon research, that shift stirred interest in juvenile behaviour, because it is now appreciated that the social structure a baboon learns about and contributes to during its juvenile years has at its core the adult females of the troop.

1.2. Early field studies of savannah baboons

Members of the genus *Papio* live in a wide range of habitats throughout Sub-Saharan Africa, the Horn of Africa, and the Arabian Peninsula. The genus contains five geographically-replacing forms which taxonomists have traditionally treated as separate species (Hill, 1970): hamadryas (*P. hamadryas*); olive (*P. anubis*); yellow (*P. cynocephalus*); chacma (*P. ursinus*); and guinea (*P. papio*). Recent evidence has led some researchers to conclude that *Papio* consists of only two (Maples, 1972) or even one species (Groves, 1972). C. Jolly and Brett (1973) sensibly observed "in the present state of knowledge, carefully defined vernacular names for baboons are less ambiguous than Linnaean binomials". Because of the similarity of their social organization, the olive, the yellow, and the chacma baboons - as distinct from the hamadryas (the social structure of the guinea baboon is still unclear) - can be usefully grouped together as savannah baboons.

The early field studies described savannah baboons living in large social groups, containing both adult males and adult females, and a greater number of youngsters (Bolwig, 1959; Hall, 1963; DeVore and Hall, 1965; Rowell 1966a, 1969; Altmann and Altmann, 1970; Stoltz and Saayman, 1970; Ransom, 1971). Troops occupied over-lapping ranges, which altered with season and the availability of water.

The studies of Washburn and DeVore (1961a; 1961b; DeVore and Washburn, 1964) on the olive baboons of Nairobi Park had perhaps the greatest influence on scientific and popular literature, and thus great influence on subsequent research. Although many of their descriptions have been confirmed by other workers, some erroneous conclusions about baboon social organization seemed to have had wide popular appeal.

While Zuckerman (1932) concluded that the year-round sexuality of males and females was responsible for maintaining the structure of a baboon troop, Washburn and DeVore attempted to view the social structure in its ecological context. They regarded the troop as an adaptation to terrestrial life, a closed unit organized to ensure the protection of the troop´s most vulnerable members. The extreme sexual dimorphism and differentiation of male and female roles contributed to this end, as did the over-all primacy of the adult males. Members of a "central hierarchy" of adult males were "most active in protecting the group and policing it internally" and were "also the most effective breeders" (DeVore, 1965). The adult male dominance hierarchy was described as stable and rigidly maintained.

In contrast, female behaviour was described largely in terms of a mother's interactions with her infant (DeVore, 1963). Dominance relationships were thought to be weak and unstable, and strongly affected by a female's changing reproductive state on which her associations with adult males depended.

Washburn and DeVore's study was hampered by its short duration and largely descriptive approach. In retrospect, they overemphasized adult males and neglected the contributions of adult females to the structure of the troop. This could easily be a consequence of the fact that the males, fewer in number and twice the size of females, are much more conspicuous. It is tempting, however, to wonder whether factors besides the greater size, visibility, and recognizability of males obscured the activities of females. As physical anthropologists, Washburn and DeVore investigated baboon social organization as a model for early hominid society. Where the conclusions were erroneous, they tended to mirror the modern human society whose evolution they were meant to explain (Rowell, 1974; Haraway, 1978; Hrdy, 1981).

Subsequent studies yielded results which particularly challenged three conclusions of earlier field work: the closed nature of the baboon troop; the stability and primacy of male dominance relationships; and the instability and inconsequence of female dominance relationships.

1.3. Recent studies

Two important factors have contributed to the current understanding of baboon life. A shift to longitudinal studies in which all troop members are identified has been appropriate to the longevity of baboons and has revealed patterns of social organization a short-term study could not (Hausfater, 1975). In addition, advances in evolutionary biology have influenced the interpretation of results. In turn, theories, particularly those of sexual selection, kin selection, inclusive fitness and parental investment have shaped the design of quantitative studies.

The composition of a savannah baboon troop is affected by the emigration and immigration of its members. In common with the dispersal patterns of most mammalian species (Greenwood, 1980), the male is generally "the sex that moves" (Bateson, 1983). Around the age of sexual maturity, a young male emigrates, or "transfers" from his natal troop to another where he attempts to breed (Rowell, 1966, 1969; Altmann and Altmann, 1970; Ransom, 1971; DeVore, pers. comm. cited in Ransom, 1971; Rhine, et al., 1979; Busse and Hamilton, 1981). A similar pattern has been observed in many macaques (Japanese macaque: Yamada, 1963, 1966; Koyama, 1967; Sugiyama, 1976; rhesus macaque: Sade, 1965, 1967, 1972; Missakian, 1972; Boelkins and Wilson, 1972; Symons, 1978; toque macaque: Dittus, 1975). The male baboon may transfer again, subsequently (Packer, 1975, 1979a). There are exceptions: female transfer has been reported for olive baboons at Gombe (Ransom, 1971) and yellow baboons at Mikumi (D. Rasmussen, 1981); and two males at Amboseli (Hausfater, 1975) and one male at Gilgil (Manzolillo, cited in Moore and Ali, 1984) remained and bred in their natal troops.

One result of male transfer will be outbreeding; avoidance of inbreeding is often cited as its function. Moore and Ali (1984), however, suggest that intrasexual competition in the natal troop is the major cause of male dispersal, and that it is unnecessary to invoke inbreeding avoidance.

The pattern of male movement, whatever the reason, has several consequences. The entry of new potential breeding males into a troop is one source of instability in the dominance relationships among adult males. Contrary to early descriptions, although adult male dominance relationships usually assume a linear, hierarchical form, these relationships are highly changeable (Hausfater, 1975; Packer, 1979b). Males holding high rank are more successful in gaining access to estrous females (Hall and DeVore, 1965; Hausfater, 1975; Packer, 1979b). Long-term alliances are not a hallmark of adult male behaviour, nor have observations supported the existence of an established "central hierarchy", with its multiple responsibilities within the troop.

Male behaviour and morphology are re-interpreted, not as adaptations which ensure troop defense, but primarily as the result of sexual selection, which "depends upon the advantage which certain individuals have over others of the same sex . . . solely in respect of reproduction" (Darwin, 1871, p. 205). In studies of primates, sexual selection has usually been understood as consisting of inter-male competition for access to females, and its complement, the discrimination by females between males ("female choice").

Due to differential investment in gametes, male reproductive success will be enhanced by a greater number of fertile matings; whereas, in general, multiple copulations will not affect female reproductive success. The attention of researchers focused on male reproductive success, which can in theory vary enormously; the female, assured of conception, appeared not to be subject to selective pressure to compete with her own sex.

Evidence emerged, however, of variation between female primates in their reproductive success, due to delays in conception (Dunbar and Dunbar, 1977; Dunbar, 1980; Wasser, 1983), the differential survival of offspring (Drickamer, 1974; Sade _et al_, 1977; Silk, _et al_., 1981a; Silk, 1983), and varying rates of maturation of daughters (Drickamer, 1974). While females may differ in inherent fertility, competition with other females also appears to contribute to the variation in reproductive success. Because of differences in the nature of the "resources" which may be crucial to successful reproduction in males and in females (Trivers, 1972;

Wrangham, 1980), it is likely that the nature of the competition differs as well. Female competition should rarely result in spectacular contests for a temporally-limited resource, analogous to intra-male competition for an oestrus female. But researchers are alert to the possible cumulative effects of more subtle competition between females which may in the longer term influence conception, pregnancy, and the welfare of living offspring. If male competition, like male reproductive success, can be simplistically viewed as an "all or none" phenomenon, more subtle processes may be involved as females compete for "more or less".

Greater understanding of the social relationships of females originated not with research on baboons, but in studies of the similarly-organized macaques. There, competition between females was found to lead to the formation of linear female hierarchies which were very stable through time (Japanese macaques: Kawai, 1965a, 1965b; Yamada, 1963; Kawamura, 1965; Koyama, 1967, 1970; Mori, 1975; rhesus macaques: Sade, 1965, 1967, 1972; Koford, 1963; Kaufmann, 1967; Missakian, 1972; crabeating macaque: Angst, 1975; bonnet macaque: Silk, <u>et</u> <u>al</u>., 1981b). It later became clear that this was quite a common Cercopithecine pattern, extending to the baboons as well. Rowell (1966b) found dominance interactions between adult females in captive olive baboons were the most consistent of any in the group, but she concluded that a linear hierarchy was the product of stress in captivity (Rowell, 1967, 1974). In comparative work on wild baboons, she detected no hierarchy.

Hausfater (1975), however, determined that adult females in a troop of yellow baboons could be arranged in a linear hierarchy, and that female dominance relationships were highly consistent throughout his study. A female's rank did not change with her reproductive state. Others have since verified these conclusions in field studies of savannah baboons at many sites (Owens, 1975; Seyfarth, 1976; Moore, 1978; Nowell and Heidrich, 1978; Collins, 1981; K. Rasmussen, 1981; Smuts, 1982).

Female ranks in baboons and macaques are not only stable over the lifetime of the individual, but across generations as well. The ranks particularly of young females, but also of young males, are strongly influenced by the mother's rank, and this is reflected in the youngsters' interactions with both peers and adults (reviewed in Cheney, 1977; Moore, 1978; Lee and Oliver, 1979). The females, who remain in their natal troop, attain ranks similar to their mothers' within the adult female hierarchy. Generally, daughters rank just below their mothers (Chapais and Schulman, 1980; but see Moore, 1978), and younger sisters at maturity out-rank elder sisters (Koyama, 1967; Missakian, 1972; Sade, 1972; Schulman and Chapais, 1980). As a result, the adult members of a female lineage, or matriline, will hold similar ranks (Hausfater, 1975; Walters, 1980). Conversely, similar ranks in adult females have been used to infer close kinship.

Where variation in female reproductive success has been documented, it has been correlated with high rank (see above, but see also Cheney <u>et al</u>, 1981). The perpetuation of rank across generations and the means by which this is achieved have consequently been of great interest. Two mechanisms, not necessarily mutually exclusive, were originally suggested by Kawai (1965a). First, through its prolonged period of close contact with the mother, an infant may by observation learn its mother's - and its own - status in the troop. Before an infant interacts independently with other troop members, it will have experienced its mother's fearful reaction at the approach of certain other individuals. Infants of high- and low-ranking mothers receive different treatment from other troop members which will shape the infant's early experience (Ransom and Rowell, 1972; Gouzoules, 1975; J. Altmann, 1978a, 1980). DeVore (1963) recognized that "it is likely that the infants of dominant females are affected by the constant attitude of pre-eminence displayed by their mothers" (p. 327), but he did not draw the now evident conclusion that this experience could have life-long consequences.

The second mechanism suggested by Kawai was the active intervention of the mother or close-ranking allies (likely to be close kin) in the agonistic interactions of the growing infant or juvenile. With this assistance, the youngster would be able to defeat individuals her mother out-ranked; in turn, she would suffer defeats in competition against individuals where her mother could be of no assistance. DeVore (1963), again, observed this in his study of baboon mothers and infants: "The dominance status of the mother thus determines the frequency of successful assertions of dominance by the juvenile". To the extent that the outcome of an agonistic interaction relied on the intervention or presence of another, older individual, Kawai identified the youngster as holding a "dependent" rank. This he distinguished from "basic" rank, which no longer depended upon another individual.

The acquisition and maintenance of rank in juveniles - in effect, the transition from dependent to basic rank - and the attributes which influence rank have been a concern of recent studies.

Hausfater (1975) concluded that "peer group dominance relationships of juveniles . . . were largely a reflection of dominance relationships among adult females," having found that the direction of agonistic bouts between pairs of the same sex and the same juvenile sub-class were consistent with their mothers' relationships. However, within a juvenile sub-class, for the three pairs concerned, he did not specify relative sizes of the partners; size has also been shown to influence immature relationships (Sade, 1967).

Cheney (1976, 1977) found for a troop of chacma baboons that the mother's rank determined the rank of both sexes of immature within a size sub-class. Maternal rank together with size accounted for the direction of over 90% of agonistic interactions between immatures; but, again, relative size within the sub-class was not specified.

High-ranking mothers aided their offspring both more effectively and more often than did low-ranking mothers; so, although infants may have learned their own status from their mother's when very young, as Kawai suggested, active intervention seems to have been important in confirming the juvenile's status. However, juveniles also attempted to form alliances with high-ranking individuals, as well as members of their families; this was more prevalent among juvenile females, who would remain in the troop, than among juvenile males, who would transfer out.

The complex interaction between the two variables, maternal rank and size, was highlighted in a study of a troop large enough that separate male and female hierarchies could be constructed. Lee and Oliver (1979) found for yellow baboons that both variables influenced juvenile rank, with striking sex differences. When juvenile males interacted with their own age-sex class, the outcome of supplant interactions was determined by size, larger males supplanting smaller ones; whereas the hierarchy among juvenile females was unaffected by size and depended upon maternal rank. Both males and females could be placed within the adult female hierarchy. The rank order of juvenile females was unchanged; they interacted with adult females in accordance with their mothers'ranks. But the importance of size in determining the male rank order was diminished when they interacted with adult females. Young males supplanted those females who their mothers out-ranked; older, larger juvenile males supplanted adult females regardless of the female´s rank.

Lee and Oliver related these findings to the adult behaviour of both sexes. The juvenile female will remain in the troop as a member of a matriline. But a male will move into another troop, away from the sphere of maternal and kin support, and his rank will depend upon competitive skills, the effectiveness of which may be enhanced by size. Lee and Oliver concluded that interventions in agonistic interactions by related animals were too infrequent to determine the transmission of rank from mother to offspring.

A young female may be able to dominate an elder in low-level agonistic exchanges, such as the supplant, although the dominance relationship between them may not yet be stable (Angst, 1975; DeWaal, 1977). Walters (1980) studied the developmental stages in the dominance relationships between adolescent females and adult female yellow baboons. He found, over time, a shift in the balance of aggressive and submissive gestures exchanged between the adolescent and adult females: from aggression by the adult and submission by the adolescent; through a mixture of aggression and submission given by one or both; to a resolution of the relationship in which the adolescent was consistently the aggressive member and the adult consistently the submissive member. The conclusion that changes in the prevalent direction of certain behaviours might precede a rank change was anticipated by Rowell (1966b).

Adult females involved in relationships in the process of this change Walters referred to as "targeted", suggesting the active though gradual challenge by the adolescent to the position of the elder female. The targeted females were generally those who ranked lower than the mothers of the adolescents. Walters concluded that maternal rank at the time of the adolescent's birth (Walter's "birth rank") alone could be sufficient for establishing dominance over adults; the intervention of others reinforced but was not necessary to rank acquisition.

Conclusions about the process of rank acquisition, its timing, and its completion will vary depending upon the method of measurement used, whether it includes all aggressive and submissive behaviours (e.g. Hausfater, 1975; Cheney, 1976), the lower-intensity supplants and avoids only (e.g. Lee and Oliver, 1979), or the occurrence of first submission by a previously dominant individual (e.g. DeWaal, 1977; Walters, 1980).

It may be instructive, however, to look at disruptions to the apparently smooth process of rank acquisition. Because the mother's rank has such an over-riding influence on the rank of her offspring, a mother's death or fall in rank could be expected to have serious consequences for their social development.

The loss of its mother through death or prolonged separation generally has fatal consequences for a young infant primate. In wild populations, a mother and her dependent infant frequently disappear simultaneously (J.

Altmann, 1978a, 1980; Hasegawa and Hiraiwa, 1980). If the infant is unweaned, it may survive its mother only briefly (Rhine, <u>et al</u>., 1980; Hasegawa and Hiraiwa, 1980), succumbing to starvation or dehydration, or sometimes exhibiting a lethargy before death which appears analogous to human depression (van Lawick-Goodall, 1971; Rhine, <u>et al</u>., 1980).

Orphans who do survive may form compensatory relationships with other group members, in particular with adult males (DeVore, 1963; Alexander, 1970; J. Altmann, 1980; Hasegawa and Hiraiwa, 1980) or older siblings (van Lawick-Goodall, 1971; Sade, 1972; J. Altmann, 1980; Hasagewa and Hiraiwa, 1980; Walters, 1981). These relationships may not only aid the orphan's survival, but also protect the orphan from possible social costs of losing its mother.

Most available evidence pertains only to female offspring. It suggests that, for baboons and macaques, an infant who is old enough to survive her mother's death has already in some sense acquired her rank; as adults, many orphans occupy the ranks in the adult female hierarchy predicted by the ranks of their mothers. Sade (1972) describes two such cases in different rhesus monkey matrilines. One is an extreme example: a nine-month old female survived her mother's death, and formed a strong relationship with her elder sister. At maturity, the orphan rose in rank over all adult females once subordinate to her mother, including her "foster mother" sister. The common pattern of the younger sister dominating the elder at maturity was repeated, despite the importance often ascribed to the mother in affecting this rank reversal.

Hasegawa and Hiraiwa (1980) describe a contrasting phenomenon in Japanese macaques. After the death of a mother, a few orphans maintained or even rose in rank (as measured by their access to food) due to their association with high-ranking adult males. But the daughters of dominant females lost rank with reference to other females. The deaths of the four highest-ranking adult females led to the subordination of their juvenile daughters to a lower-ranking but intact matriline.

The long-term baboon studies at Amboseli lend support to the idea that a female's rank is "set" at a very young age, and that females achieve ranks similar to those held by their mothers at the time of their birth. A few examples can be summarized from Amboseli studies (Hausfater, 1975; Altmann, 1980; Walters, 1980, 1981; Hausfater, et al., 1982): Adult female Fluff died when her daughter Vee was around two years old; as an adult, Vee occupied her mother's old rank relative to other adult females in the troop. A second adult female, Ring, was the lowest-ranking adult female in her troop until its fusion with another troop. Thereafter, the newcomer females ranked below her. She died the following year, leaving two daughters, aged approximately four and three years. As adults, they maintained dominant positions relative to the newcomers, despite having only one year's experience as middle-ranking animals before their mother's death. Finally, at the time of her death, adult female Alto was the highest ranking in the troop, followed by her adult daughter, Spot, who retained her high rank after Alto's death. A three-year old daughter, Dotty, formed a "compensatory" relationship with her elder sister, and retained her rank. A seventeen-month old daughter, Alice, who had been suckling occasionally before her mother's death, slept frequently with her juvenile sister and with an adult male who had been a special associate of the mother. She also maintained a rank in accordance with her mother's.

Such results, though ambiguous, suggest that an orphan - specifically, a female - does not suffer rank loss with respect to her peers or to adult females as a result of her mother's death. If this is the case and a female's rank is established by the age when she can survive independently, what happens when a mother loses rank?

Changes to adult female rank, apart from predictable changes which occur as other individuals mature or die, are rare; nevertheless, some have been observed. In some cases, the effects on offspring have been documented as well.

Hinde and Spencer-Booth (1967) mention that a reversal in the dominance relationship of two adult female rhesus in a captive colony occurred simultaneously with a parallel reversal in the relationship of their infants. The sex of the infants is not reported.

Repeated changes in the dominance relationships of rhesus mothers in a confined group were induced experimentally by Marsden (1968). Each change in a mother's status was reflected in the ranks of both daughters and sons.

Gouzoules (1980) described events leading to rank reversals in a group of Japanese macaques. A middle-ranked female, with the aid of the most dominant male, aggressively challenged the females of the highest-ranked matriline. After weeks of frequent fights, the challenger, her daughter and mother, then most other females of her matriline dominated members of the formerly highest-ranked matriline.

Nash (1973, 1974) documented female rank changes in a wild population of olive baboons at Gombe. The most dominant female, RO, fell in rank following a severe fight in which she was mauled and bitten on the head, face and hands. Her antagonists were two high-ranking females, LO and AZ, who shared a close grooming relationship and were probably sisters; and AZ's sub-adult daughter AR. RO's status changed immediately; she became submissive to all three females and kept to the periphery of the troop. The changed rank order persisted for some years (pers. obs.).

The circumstances of rank changes at Amboseli are not reported, although the effects on offspring - females, once again - may be summarized. Adult female Oval gradually dropped in rank until she was subordinate to five females she had previously dominated (J. Altmann, 1980). Her daughter Fanny was three years old by that time. Walters (1980), however, reports Fanny targeting and eventually dominating adult females in accordance with her mother's former, higher rank.

By contrast, adult female Judy lost nine places in rank when her daughter Janet was only one year old. The daughter dropped from the top (J. Altmann, 1980) to the bottom (Walters, 1980) of the juvenile female hierarchy. Later, she targeted and dominated some, but not all, of the adult females who were by then dominant to her mother, but who all held ranks lower than her mother's former rank. These two examples imply that the daughter's age at the time of her mother's rank loss is critical (Hausfater, _et_ _al_., 1982).

A dramatic loss of rank among olive baboon females occurred in EC troop at Gilgil, prior to the beginning of this study. In a cohort of forty adult females, the four who had been highest-ranking (DD, ZD, TH, PH) fell in rank to the bottom of the adult female hierarchy (Smuts, 1980; in prep). This followed the death of female HH, who had ranked fifth in the adult female hierarchy; her death may somehow have precipitated the change. Although the events leading up to the change in rank were not observed, circumstantial evidence indicates many parallels with the rank-change at Gombe described by Nash (1973). The pattern of injuries suggested a number of severe fights had occurred, involving the four females who lost rank (hereafter called the Fallen females) and the next highest-ranking females in the troop. The nature of the wounds also resembled those inflicted in the fight at Gombe: wounds to the hands and facial lacerations were of a sort rarely inflicted by males. Subsequently, a fifth female (LE) fell eight places in rank, and female ranks stabilized once again. Smuts concluded that nothing in their behaviour distinguished the fallen females from other low-ranking females, except a greater tendency to be spatially peripheral to the troop - another similarity to the Gombe account. An observer, seeing EC troop for the first time, would have no reason to suspect that there had been changes in the adult female hierarchy. This implies that changes in adult female ranks, although rare, may occur more often than previously believed and go undetected.

1.4. Aims of the present study

This study of the juvenile baboons in EC troop commenced shortly after the events described above. My original intention was to examine the social relationships formed by young males and females in the context of a very large troop.

But an additional opportunity arose. The upset in the adult female hierarchy of EC troop involved five females and their twelve juvenile and infant offspring of both sexes. In addition, the troop contained nine orphaned juveniles, both males and females. This "natural experiment" allowed me to compare the social relationships of normal juveniles with those who had lost their mothers at different ages, as well as those whose mothers held radically different ranks during this study from the ranks they had occupied at the time of the offspring's birth.

The broad questions concerning juveniles were these: Did relationships differ for females, who would remain in the troop, and males, who would someday transfer to another troop? If so, did the differences foreshadow the adult behaviour of the two sexes? A very large troop, such as EC, offered a wide "choice" of social partners. Did this allow an earlier expression of sex differences in social relationships? Did a mother's rank influence her son's as well as her daughter's rank, and how pervasive was this influence?

A juvenile grows up in a troop in which the social continuity is provided by the stable female membership. If overall mortality is low, the juvenile will have numerous close relations among the adult females of the troop; there is ample opportunity for beneficial kin-directed behaviour within a matriline. In contrast, except under circumstances where immigrant adult males are brothers, the juvenile will only be closely related to one adult male. Is there any evidence that the "special relationships" which sometimes exist between adult males and particular infants persist into the juvenile period?

Finally, evidence from Amboseli suggests that "the rank position 'targeted' by a maturing female is the same as that of her mother in the first year of the daughter's life rather than the mother's rank at some later stage in the daughter's social development" (Hausfater, et al., 1982). For a large group of juveniles in EC troop, the death of a mother, or her loss in rank provided me with an opportunity to examine the timing and confirmation of a juvenile's independent status in the troop.

Chapter 2

THE STUDY SITE, THE ANIMALS, AND STUDY METHODS

2.1. The study site

2.1.1. Kekopey Ranch

The baboons who were the subjects of this study live mainly on Kekopey Ranch, a cattle ranch in the Rift Valley of Kenya near the village of Gilgil and 115 kilometres northwest of Nairobi. The ranch covers 182 km^2 of open grassland with patches of mixed scrub, largely leleshwa (*Tarchonanthus camphoratus*) and stands of *Acacia xanthophloea*. Block faults associated with the major rift have divided the land into parallel plains which descend like steps to the valley floor. On their western side, these plains rise gently then drop away in steep cliffs up to 90 metres in height where baboon troops sleep (See Harding 1973, 1976 for a more complete description). The Eburru Cliffs, one favoured sleeping site, give their name to the troop I studied: Eburru Cliffs Troop, or EC Troop.

The ranch was first settled in 1903. Lake Elmentaita, a soda lake and undrinkable for most species, was the only naturally occurring standing water at that time. Water troughs, fed by a natural hot spring on the ranch, were constructed. This permanent source of water supports the three- to four-thousand head of cattle, as well as many wild species. It is not clear how many species were only able to colonize the ranch once water was provided; however, ungulates have increased in number since the 1950's (Blankenship and Qvortrup, 1974). In the baboons, significant inter-troop genetic variation suggests very rapid population growth (Byles and Sanders, 1981).

An estimated dozen troops of baboons live in the area, and a few groups of vervet monkeys in patches of woodland. Thompson's and Grant's gazelle, warthog, eland and zebra are abundant. Other indigenous ungulates include cape buffalo, waterbuck, bushbuck, duiker, mountain and bohor reedbuck, klipspringer, and dikdik. Among the predators, bat-eared fox and three species of jackal are fairly common, but predators which endanger people or cattle have largely been shot. Hyaena live in the more remote areas; I saw them only once within the baboons' range. Cheetah have been seen on several occasions; on one, I watched while six baboons - three adult males, one pregnant female, and two lactating females - threatened three cheetah away from the rest of EC troop. Leopard, probably the major predator on baboons elsewhere, are rare, though their tracks and droppings were seen. People posed a greater danger to the baboons than any predators: wire snares, set by poachers to catch antelope, gravely injured baboons instead; poachers' dogs killed a female baboon in 1977; and thirteen baboons drowned in water storage tanks during one period. (Although researchers did not generally interfere with the baboons, when injury was human-caused, intervention was justified; animals were helped out of snares or water able to colonize the ranch once water was provided; however, ungulates have increased in number since the 1950's (Blankenship and Qvortrup, 1974). In the baboons, significant inter-troop genetic variation suggests very rapid population growth (Byles and Sanders, 1981).

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Part of the ranch was divided into one-acre plots and sold for farming prior to this study. Farmers threw stones and chased those baboons tempted to raid crops; EC Troop seems to have responded by shifting their range away from inhabited lands. However, while human influence - the construction of water troughs, the gathering of firewood which is gradually modifying the rangelands, and the establishment of farm plots - was substantial, actual interaction between EC troop and humans was minimal during my study.

2.1.2. Rainfall.

Conventionally, it is said that rain in the Kenyan Rift Valley occurs in two seasons: the long rains from April through June, and the short rains around November. Some rain fell, however, in nearly every month of my study, and Harding (1976) points out that during forty-three years of rainfall measurements, every month has at some time been the wettest in its calendar year.

Researchers studying Pumphouse troop recorded rainfall daily. I have grouped the rain records into half-monthly totals (which vary, of course, from fourteen to sixteen days in length). Monthly rain totals would have obscured the sudden onset of heavy rains which occurred, for example, in March of 1981; whereas weekly totals create spurious "dry" spells in the middle of rainy periods when vegetation was tanks.)

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Half-months in which more than the mean amount of rain fell (more than 24.06 mm), I designated "wet". Using the mean in this way is common for rainfall data, though not strictly correct; the median would be appropriate for this non-normal distribution. Use of the much lower median as a cut-off, however, would add only three "wet" half-months and result in the absurdly low criterion of 14 mm of rain in half a month to define a wet spell.

With the exception of three isolated half-months, the wet blocks correspond with the traditional short and long rains (Fig 2-1), and I shall refer to the "wet season" and the "dry season" throughout this thesis.

2.2. The Study Troop

2.2.1. Previous studies

In 1970, Robert Harding began a study of baboon behaviour and ecology at Kekopey Ranch, focusing on a troop he named the Pumphouse Gang (PHG). Eburru Cliffs Troop (EC) was one of several troops on the ranch Harding identified at the time. Studies of PHG have continued almost without interruption since then, but research on EC was more sporadic at first. Linda Muckenfuss observed EC for a short time in 1973. In 1976, Shirley Strum studied adult males who transferred from PHG, her focal troop, into EC troop and she eventually identified all adult and sub-adult males.

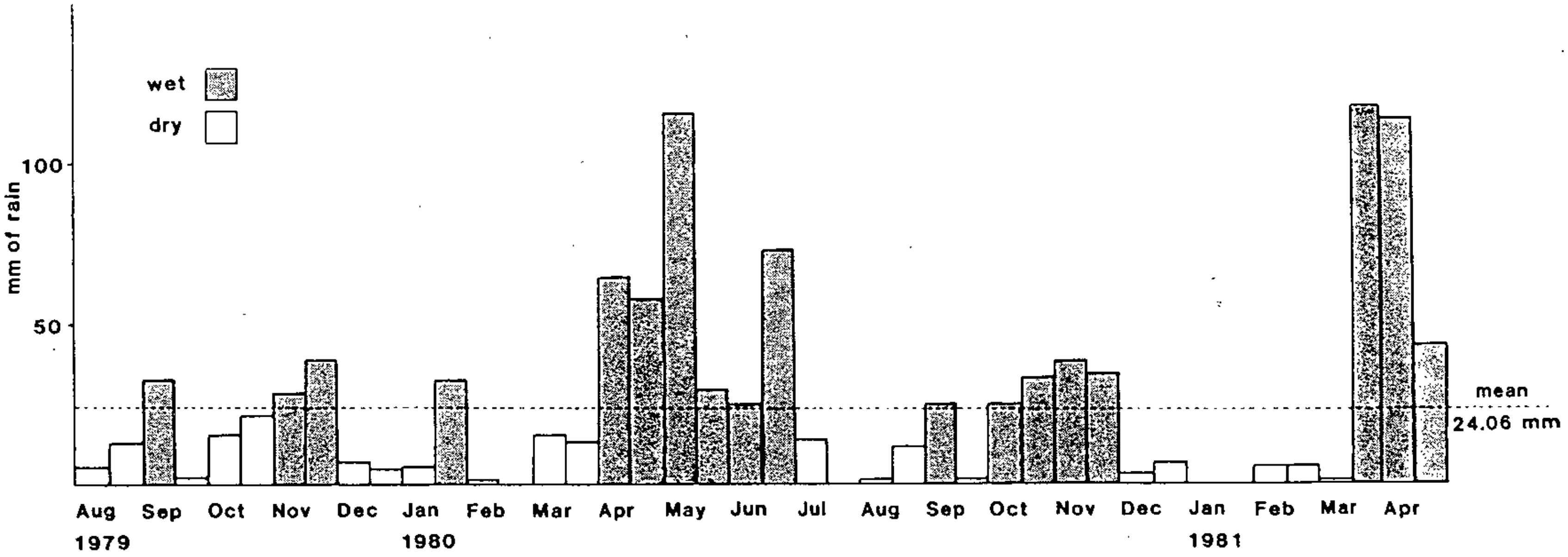


Figure 2-1. Rainfall during the study.

However, it is the studies of Nancy Nicolson (1982) and Barbara Smuts (1982), begun in 1977, which form the background to this study. Nicolson and Smuts identified all the troop members and accustomed the troop to human observers working on foot. They identified the mothers of young infants, and assigned putative kinship relationships to young baboons already independent of their mothers (see Kinship Assignment, Section 2.3.3.).

In her study of weaning, Nicolson focused on infants who later became the juvenile subjects of my study. Smuts worked on special relationships between adult females and males, but also documented the relationships between adult females. From their agonistic interactions she constructed a linear dominance hierarchy, to which I refer in this study. One unusual event concerning the hierarchy held particular interest: early in 1979, a dramatic change occurred when the females ranking first through fourth fell in rank to the bottom of the adult female hierarchy (Smuts, 1980, in prep.). The death around this time of the female who had ranked number five may have precipitated this change. The fate of the juvenile daughters and sons of these 'fallen females' and their dead peer became an important aspect of my study.

Between December, 1978, and March, 1979, over 90% of the then-members of Eburru Cliffs troop were captured for biomedical sampling by a team from the Institute of Primate Research, led by Dr. James Else. Baboons were darted or trapped, examined, then released the same day. Samples of blood, saliva, and milk from lactating females were collected. Dental eruption and wear were examined, and physical characters measured (Byles and Sanders, 1980). Pertinent to this study, a numbered tag was attached to each baboon's ear. This was a useful means of verifying identification early in my study, though no substitute for individual recognition which was possible later.

The relative weights of juveniles, according to the data collected in the biomedical study, could not be assumed to be still valid by late 1979 when I began collecting data, and I evaluated relative sizes as described in Chapter 3.

2.2.2. Demography

The number of baboons in EC Troop varied between 105 and 128 individuals during this study, with a total of 137 individuals who were members at some point. The troop was censused as completely as possible each study day. Births, immigration and emigration ('transfers in or out') and deaths were recorded. The age-class composition of the troop also altered as animals matured (see Table 2-1). These changes through the study are summarized in Table 2-2 (Troop composition) and Table 2-3 (Demographic changes).

Of twenty-nine births during my study, fourteen were females and fifteen were males. J. Altmann (1980), in a long-term field study of yellow baboons at Amboseli, and Simpson and Simpson (1982), studying captive rhesus monkeys, have both found a significant tendency for high-ranking

	Female	Male
Infant	0 - 2 years. Black natal coat persists for the first six months.	
Juvenile	2 years and over	
Subadult	Menarche (around four years*) to first birth.	Testes descend. Same size or larger than adult female.*
Adult	First birth (around six years*)	Full growth and canine development*

Table 2-1. Age-sex class categories used at Gilgil. These categories match those used by Nicolson (1982) and Smuts (1982), and are consistent with the long-term demographic records on PHG troop.

* The criteria used to assign females to a new age-class (menarche, first birth) are much more exact than those applied to males.

Age Class	Female	Male	Sub-total by Age Class
Adult			
mean	29.0 (25.2%)	7.9 (6.9%)	36.9 (32.1%)
range	28 - 32	7 - 9	35 - 39
Subadult			
mean	10.8 (9.4%)	7.7 (6.7%)	18.5 (16.1%)
range	5 - 13	7 - 10	13 - 23
Juvenile			
mean	22.1 (19.2%)	17.5 (15.2%)	39.6 (34.4%)
range	19 - 24	16 - 20	35 - 43
Infant			
mean	11.0 (9.6%)	9.1 (7.9%)	20.1 (17.5%)
range	8 - 15	4 - 16	12 - 31
Sub-total by sex			Troop total
mean	72.9 (63.3%)	42.2 (36.7%)	115.1 (100%)
range	67 - 79	38 - 49	105 - 128

Table 2-2. Membership of Eburru Cliffs Troop. The mean numbers of individuals in each age-sex class and the range during this study.

Table 2-3. Demographic Changes in EC Troop

Date	Event	Animal
1979		
October	Death	J Fem (LY) disappears
	Death	J Fem (CP) - hernia
	Death	Ad Fem (AT) disappears - old
	Birth	i Male (PP) born to PO
November	Emigration?	Ad Male (AC) disappears
	Emigration?	Ad Male (HD) disappears
	Death	Ad Fem (JO) after miscarriage
	Death	i Fem (LG) disappears
	Death	i Fem (ME) disappears
	Death	i Fem (OC) disappears
December	Birth	i Fem (ET) born to EU
	Class Change	J Fem (JN) becomes sub-adult
	Class Change	J Fem (MA) becomes sub-adult
	Class Change	J Fem (SP) becomes sub-adult
1980		
February	Immigration	Ad Male (ZM) enters troop
	Class Change	i Fem (ER) becomes juvenile
	Class Change	i Fem (PR) becomes juvenile
	Class Change	i Male (XU) becomes juvenile
	Class Change	J Fem (EP) becomes sub-adult
March	Death	i Male (DS) disappears
	Birth	i Fem (CS) born to CC
	Class Change	i Fem (RD) becomes juvenile
	Class Change	i Male (MD) becomes juvenile
	Class Change	J Fem (VT) becomes sub-adult
April	Immigration	Ad Male (LN) enters troop
	Class Change	J Fem (NY) becomes sub-adult
May	Birth	i Fem (II) born to IO
	Class Change	i Fem (PA) becomes juvenile
	Class Change	i Fem (DE) becomes juvenile
	Immigration	J Male (DK) enters troop
June	Birth	i Male (CU) born to CG
	Class Change	J Fem (CD) becomes sub-adult
	Class Change	J Fem (SX) becomes sub-adult
July	Birth	i Male (LA) born to LU
	Birth	i Fem (PI) born to PY
	Birth	i Fem (AX) born to AN
	Birth	i Fem (TS) born to TH
	Class Change	J Male (IC) becomes sub-adult
	Class Change	J Male (OV) becomes sub-adult
	Class Change	i Fem (ZA) becomes juvenile
August	Emigration?	J Male (CR) disappears
	Emigration?	Sub-Ad Male (VS) disappears
	Birth	i Fem (UR) born to AU
	Birth	i Male (RS) born to RH

Date	Event	Animal
August (cont)	Death	i Fem (CS) disappears
	Class Change	i Fem (DN) becomes juvenile
	Class Change	i Fem (CA) becomes juvenile
September	Birth	i Fem (CY) born to CB
	Birth	i Male (DI) born to DL
October	Birth	i Fem (PX) born to PS
	Birth	i Male (LC) born to LI
	Birth	i Fem (MY) born to ML
	Emigration?	J Male (MR) disappears
	Emigration?	Sub-Ad Male (HS) disappears
November	Death	J Fem (CE) disappears
	Class Change	J Fem (MT) becomes sub-adult
	Birth	i Male (EX) born to EK
	Birth	i Male (DR) born to DP
	Birth	i Male (MK) born to MM
	Birth	i Male (OZ) born to OL
December	Birth	i Male (ZB) born to ZD
	Birth	i Fem (ZO) born to ZN
	Birth	i Male (LB) born to LE
	Birth	i Male (MO) born to MN
	Emigration?	Ad Male (TN) disappears
	Class Change	i Male (ZK) becomes juvenile
1981		
February	Birth	i Male (IA) born to IP
	Class Change	Sub-Ad Fem (IP) becomes adult
	Birth	i Male (JK) born to JU
	Class Change	i Male (HA) becomes juvenile
March	Birth	i Fem (NE) born to NM
	Class Change	Sub-Ad Fem (NM) becomes adult
	Class Change	J Fem (IT) becomes sub-adult
	Class Change	J Fem (LL) becomes sub-adult
	Class Change	J Male (DT) becomes sub-adult
April	Death	i Male (OZ) disappears
	Birth	i Male (DO) born to DD
	Birth	i Fem (HI) born to HN
	Class Change	J Fem (TC) becomes sub-adult
	Class Change	J Male (TB) becomes sub-adult

In this table, it is assumed that an infant ('i') or young juvenile ('J') who disappears has died. Female baboons very rarely transfer troops; a female who disappears is presumed dead. Males, however, transfer to other troops; those who disappear from EC and are not seen again are listed as 'emigrated?'. These males were all young and in good health; we have no evidence that they might have died rather than transferred.

Appendix 1 contains a key to the names of the baboons and the two-letter abbreviations used here.

mothers to give birth to females, and low-ranking females to give birth to males. In a study of captive bonnet macaques, low-ranking females gave birth to over twice as many sons as daughters, although birth sex-ratios to high-ranking mothers were not affected (Silk <u>et</u>. <u>al</u>., 1981). Nicolson was not able to demonstrate this tendency in EC troop. Although I found a trend, it was not significant: the ratio of male to female births was 6:9 in the higher-ranking half of the females, and 8:6 in the lower-ranking half.

Annual mortality rates were calculated on the basis of the number of immatures who died, compared to the number who survived that entire year of age during my study; immatures who were observed for one full year of age and only part of a second during my study were excluded from the second year's figures. Annual rates are shown below in Table 2-4.

Age in years	Number of immatures	Number of deaths	Mortality
0 - 1	10	3	.30
1 - 2	15	4	.27
2 - 3	16	2	.13
3 - 4	11	0	.00
4 - 5	19	0 or 2	.00 or .11

Table 2-4. Mortality rates among immatures during this study.

Between four and five years of age, the mortality rate was either zero or .11; two juvenile males disappeared at this time. Since a male of roughly that age (DK) transferred into EC troop in 1980, it is possible that the two natal males successfully transferred to a neighbouring troop. These mortality figures show a similar trend to those reported for this troop by Nicolson (1982), and by J. Altmann (1977, 1980) for the Amboseli baboons; that is, baboons are at highest risk during their first and second year, also the period of maximum maternal investment. Thereafter, during the years covered by this study, the risk of death drops almost to zero.

Mortality rates were higher for females than for males in their first, second, and third years, though not in the fourth and fifth; none of these differences were statistically significant (Fisher exact probability test).

2.2.3. Troop ranging

The range of EC troop during Smuts' study (1982) was approximately 30 km^2, limited to the central area of Kekopey ranch. During Nicolson's study (1982) the range increased by about 8 km^2, due, she states, to human settlement on Kekopey. The new range reached into Marula Estate, an adjacent cattle ranch to the south. This may have represented a real increase in range, or it may be that EC has always used portions of Marula. Though broadly similar in habitat to Kekopey, Marula is more hilly and both the lack of good access roads and the thicker vegetation may have prevented the troop from being observed.

EC shifted to Marula for long periods during my study, and it seemed that the troop's range was indeed expanding. The troop utilized areas in the first year of my study in which they had not been seen previously, either by researchers or people living or working in those areas. Expansion continued in the second year; my subjective impression was that the troop was more nervous and prone to alarm as it travelled south on what I took to be its initial forays into new areas.

Periods of weeks or months spent in Marula alternated with periods back at Kekopey, so the move was of an episodic, rather than permanent nature. Nicolson suggests that increased human settlement initiated this shift south, though this does not explain the continued expansion of the range. Nicolson's and Smuts' studies occurred during an unusually wet period, when the mean monthly rainfall was 68.4 mm, compared with 24.06 mm during this study. Perhaps the return to drier conditions encouraged the range expansion which human interference initiated. It frequently happened that moves south occurred during a dry period, and returns to Kekopey after a period of rain, but this was not always the case. The ranches' boundaries did not coincide with important ecological boundaries. However, certain foods - Opuntia vulgaris (prickly pear) and Euphorbia candalabrum - were available in Marula but nowhere else in the troop's range.

EC's total range size during this study was approximately 69 km^2, this estimate based upon counting on a map all kilometre squares in which the troop was seen. Though this is a crude measure, the result is nearly double the previously recorded range sizes. This dramatic increase may have affected the baboons' behaviour. Compared with ranges reported for other baboon field sites (compiled by Lee, [illegible] 1983), EC's range is large, and more typical of the sizes recorded for yellow baboons living in more arid habitats.

This range was shared by at least six other baboon troops which were encountered occasionally. At least seven different sleeping cliffs were used, most presumably used by other troops, as well. Ironically, Eburru Cliffs, itself, was never used during my study by its namesake troop.

2.3. This study

I began systematic data collection in December of 1979. By that time, I knew the baboons by sight, and they me; I could approach them on foot to a distance of two metres without causing any obvious disturbance. I tried, however, to approach only as close as the most nervous animals would tolerate, so that my presence would not prevent those animals from interacting with others who were better habituated.

2.3.1. Choice of subjects

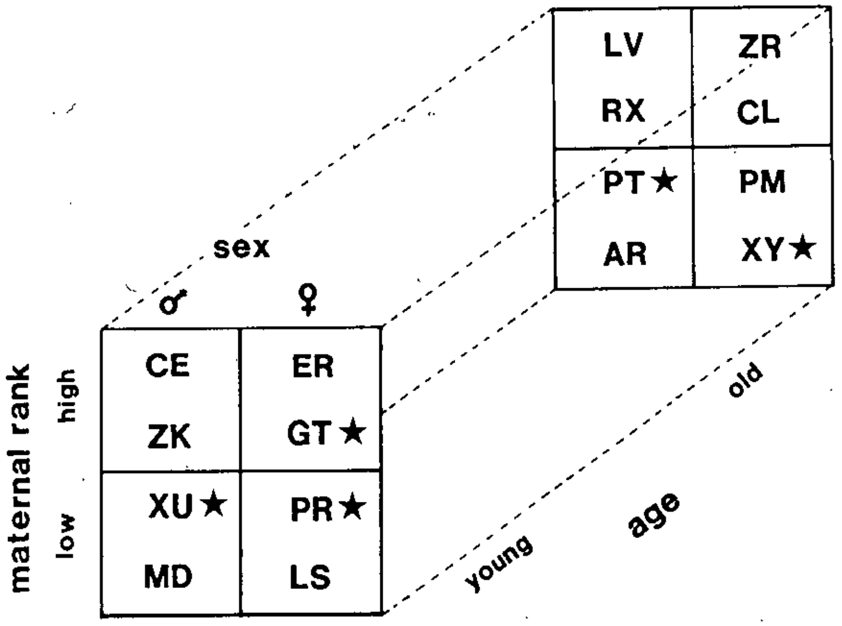
Initially, I selected thirty-one juveniles as subjects for my study. Eventually, sixteen Main subjects were chosen, though the fifteen Secondary subjects were still sampled occasionally; in the event of the death of a main subject -

which, thankfully, never happened - a replacement subject would have been available.

The sixteen main subjects included eight females and eight males, and they were balanced as nearly as possible for high or low maternal rank, and age within the juvenile group. This produced eight pairs of animals who were the same sex, similar maternal rank, and similar age (Figure 2-2). Five out of the sixteen subjects were orphans, but at most one in each pair; the importance of this will be discussed later. It was not possible to take family size into consideration.

2.3.2. Sampling procedures

Each of the sixteen juveniles selected was the subject of forty half-hour focal-animal samples during the study; the secondary subjects were sampled less often. The focal-animal sampling method (J. Altmann, 1974) takes a single individual as its target, and all actions of a specified kind are recorded over a known length of time. My focal-animal samples included information gathered by both instantaneous and continuous sampling methods. On the minute, each minute, the activity of the focal animal and some additional information was recorded on a checksheet (see Table 2-5). Three times during the sample, at fifteen-minute intervals, I noted the individual who was the nearest neighbour to my subject, and all baboons within two, five, and ten metres. Throughout the half-hour, I



Main Subjects

orphans ★

Figure 2-2. Choice of main focal animals. The names are represented by two-letter abbreviations as follows:

Archimedes	AR	Plutarch	PT
Caesar	CE	Pomona	PM
Cicily	CL	Pyrrha	PR
Euphoria	ER	Rex	RX
Galatea	GT	Xuthus	XU
Lisa	LS	Xylia	XY
Livy	LV	Zeke	ZK
Midas	MD	Zora	ZR

Appendix 1 contains a key to the names and initials of the entire troop.

On-the-minute activity	Definition, other information recorded
Feeding	Gathering, manipulating or chewing food while standing or seated. Type of food and position also recorded.
Travel-feeding	Gathering or chewing food while walking or running.
Travelling	Includes all forms of locomotion, except when the baboon is also feeding or interacting.
Resting	The baboon is standing, sitting or lying down; not interacting, feeding, or grooming.
Social interaction	Exchanging gestures with another baboon, excluding grooming. Identity of interaction partner also recorded. Includes play.
Social grooming	Picking through hair and skin of another animal with hands and teeth. Identity of grooming partner and direction of grooming recorded.
Self grooming	

Table 2-5. Categories of behaviour sampled on-the-minute, definitions, and other information recorded.

recorded any social interactions involving the subject. An interaction commenced whenever one animal moved within one metre of another ('approach'), whether gestures were exchanged or not. It ended when one baboon moved once again outside the one metre limit ('leave'). 'Mutual approach' and 'mutual leave' were, of course, also possible. In addition, when animals gestured to one another without approaching, this was also recorded as an interaction, although I was less likely to notice gestures directed towards my subject by others over a distance.

For the purpose of the focal samples, the day was divided into three time blocks: 0700 to 1000; 1000 to 1600; and 1600 to 1900. On the assumption that the morning and evening, when the troop is in the vicinity of their sleeping cliffs, is qualitatively different from the middle of the day, mid-day forms one time block, the length of the morning and evening blocks together. For practical reasons, most of the samples occurred during the longer middle block. Samples for all sixteen main subjects were distributed similarly over the three time blocks (see Table 2-6). The distribution of samples between the two seasons differed somewhat from animal to animal, and possible effects of this are examined in Chapter 4 (Activity Budgets).

At first, I sampled my focal animals in a pre-selected manner each day, but I found searching for the next subject could take longer than the sample itself. Eventually, I chose each new subject in the following manner, to preserve independence of samples, yet not waste time:

Juvenile	Time Block			Season	
	I	II	III	Dry	Wet
Archimedes	7	29	4	14	26
Caesar	7	29	4	16	24
Cicily	9	27	4	12	28
Euphoria	8	29	3	18	22
Galatea	10	26	4	17	23
Lisa	10	25	5	15	25
Livy	7	30	3	15	25
Midas	12	25	3	11	29
Plutarch	6	30	4	15	25
Pomona	7	29	4	16	24
Pyrrha	11	25	4	18	22
Rex	8	28	4	12	28
Xuthus	8	27	5	16	24
Xylia	8	28	4	17	23
Zeke	7	28	5	13	27
Zora	10	26	4	14	26

Table 2-6. Distribution of samples in the three blocks and two seasons.

1) No baboon was sampled more than once in a day.

2) After concluding a sample, I walked through the troop before choosing a new subject. (This was also a good opportunity for <u>ad libitum</u> observations.)

3) I avoided those baboons who had been interaction partners in the previous sample.

4) I tried not to select an animal on the basis of its activity.

Firm decisions had to be made, also, on the treatment of interrupted samples. Although observation conditions were generally excellent, in certain thick areas of Kekopey and Marula, it was easy to lose a baboon in the brush. To discard interrupted samples would bias my results further towards open-terrain samples. I also wanted to avoid the statistical problems of samples of varying lengths. After losing an animal, I gave myself a strict amount of time - five or ten minutes precisely - to find the subject. If I was successful, I resumed the sample on the minute at the pre-selected time; if not, I discarded the sample.

A second checksheet was used in addition to the focal sheets. On a single daily sheet, I recorded <u>ad libitum</u> interactions in which I was interested in direction, but not frequency, e.g. supplants. On the daily sheet was also recorded the morning and evening sleeping cliffs, demographic events, the identity of consort pairs, illness or injury, predation by the baboons, as complete a troop census as possible, and the reproductive state of adult and sub-adult females. This last was recorded as follows:

<u>Pregnant</u>. After the first month, pregnancy is easily detected by the reddening of the paracallosal skin (S.

Altmann, 1970). For analysis, early pregnancy was assigned retrospectively.

Lactating. After giving birth, a female is classified as lactating only until resumption of sexual cycles, despite the fact that she may continue suckling her infant. This category cannot apply to sub-adult females who, by definition, are nulliparous.

Cycling. Sexual cycles were differentiated by the condition of the perineal skin (Hendrikx and Kraemer, 1969) as follows:

> Inflating. After menstruation, the perineal skin begins to swell.
>
> Full. Ovulation occurs during this maximum tumescence of the perineal skin, generally around three days before detumescence.
>
> Deflating. Following ovulation, the perineal skin detumesces.
>
> Flat. The perineal skin is smooth and flat until the onset of the next swelling.

2.3.3. Kinship assignment

Kin relationships between baboons were identified wherever possible during the two studies which preceded mine (Nicolson, 1982; Smuts, 1982). Infants and juveniles could be assigned to their mothers with confidence; kinship involving older animals was inferred from social interactions and proximity (as in Cheney 1977, 1978a, 1978b; Lee and Oliver, 1979).

Walters (1981), in a study of six female juvenile baboons, found that a juvenile's mother could be easily identified from behavioural data if she was living. However, orphans formed compensatory relationships with other adult females which resembled the mother-offspring relationship, and could lead to the misidentification of kin. In the case of this study, EC troop had been observed for sufficient time that the identities of all the mothers and many of the siblings were definitely known. However, the misidentification of older siblings was still a risk. Where appropriate, putative and known siblings will be distinguished.

2.3.4. Sources of bias

The observation conditions were generally excellent, but my data are biased towards open conditions. This would be of greatest consequence in, say, a study of feeding, where animals enter areas of low visibility to exploit particular foods. There is no evidence that the same applies to social interactions, my main concern here. Nevertheless, in conditions where an observer is better able to see the baboons, the baboons are better able to see one another, and there may be unknown consequences in both the frequency and quality of interactions. Visual contact over a greater distance would allow baboons to better monitor each other's activities. One might expect, for example, that the rates of supplanting others from feeding sites would be higher in areas where it is easier to see what they are eating. Likewise, visual signals are important in soliciting aid from others during agonistic interactions. Therefore, polyadic aggression may be more frequent in open areas. Studies to demonstrate this have not been done.

It would have been preferable had each time block during the day been equally represented in the focal-animal samples. For practical reasons this was not possible. The difficulties in finding the troop in their large range often meant I did not begin sampling until late in the morning. The afternoon block is also under-represented; afternoon samples could only be carried out if I located the troop early and could stay with them all day.

The distribution of samples across the three time blocks roughly represents the length of the blocks (the proportions being 21:69:10, compared to 25:50:25). But the difference is great enough that I have not analyzed data for time-of-day effects. Comparisons between individuals, however, are valid, since the samples are distributed in the same way.

Finally, no focal animal samples were taken in the rain, due to transportation difficulties in the mud.

2.3.5. Data analysis

Focal-animal and *ad libitum* data on certain categories of behaviour were entered on the Edinburgh Regional Computing Centre system. SPSS (Statistical Package for the Social Sciences, Nie *et al*, 1975) was used mainly in searching for and sorting interactions. SIR (Scientific Information Retrieval, Robinson *et al*, 1980) was used for more complex, hierarchical searches. Most of the actual statistical analysis was done by hand or on a hand calculator.

Non-parametric statistics have been used throughout (Siegel, 1956, in particular), because of the small number of subjects and the non-normal distribution of scores. If a result is described as 'significant', I have given the level of probability. In figures and tables, levels of significance are represented by stars: $p < .05$ by one star, $p < .01$ by two, and $p < .001$ by three.

Certain statistical tests occur repeatedly. Before comparing juvenile behaviour across several conditions (e.g. median amount of time devoted to different activities, median number of interactions with different age-sex classes of partner), it is necessary first to demonstrate that the juveniles are behaving in a broadly similar manner which makes the medians meaningful. The Kendal coefficient of concordance is used, and the value of W given.

The Friedman two-way analysis is used to compare the behaviour of subjects across several conditions (e.g. were there significant differences in the time devoted to different activities?). The statistic computed is X_r^2, and the value is given in the text or figures.

When the behaviour of the same animals in two different conditions (e.g. amount of time spent feeding in two seasons) is examined, a Wilcoxon matched-pairs signed-ranks test is used. The value of T is given in the text or figures.

When juveniles are ranked according to their scores on two measures and those rank orders compared to look for a correlation (for example, between size and dominance rank), the Spearman rank correlation, r_s, is given.

The fourth commonly used test, the Mann-Whitney U, tests for differences between two groups of animals (e.g. males and females) for their scores under one condition. The value of U is given.

One method of calculating expected scores deserves mention here. The demographic composition of the troop and, particularly, the reproductive-state of its mature females changed day by day. These changes had implications for the analysis of behavioural data. The sixteen juvenile subjects were not sampled on the same days; in a sense, each was observed in a troop with a slightly different composition. From the daily census records, a computer file was created on SIR which contained for every baboon the dates of any changes in its age classification and reproductive state, and its presence or absence from the troop. It was then possible to extract information on the composition of the troop for the forty particular days on which any given juvenile was observed. The mean number of animals in each class per day was calculated, giving a mean troop composition for that individual juvenile. The proportion of the juvenile's behaviour given to a particular class can then be compared to that class's representation in the troop. The availability of interaction partners of a particular class is taken into account by use of this individual mean troop composition.

Chapter 3

ASSESSING RANK

3.1. Introduction

The dominance relationships of primates have been regarded by many as fundamental to social structure, but definitions of dominance, appropriate methods of measuring it, and the utility of the entire concept of dominance have been debated. One animal's capacity to prevail over another has been assessed in the laboratory and in the field with respect to a wide variety of behaviours, including priority of access to food, mates, or water; the direction of supplants, threats, or aggressive interactions; grooming; and even the avoidance of electric shock (reviews by Bernstein, 1970; Richards, 1974; Deag, 1977).

The issue has been further complicated by ascribing to the dominant animal additional social qualities which benefit the group, extending beyond the observed ability to defeat other individuals (however measured). Thus Hall (1965) suggested that, in addition to priority of access to preferred foods and females should be added other "functions of such a dominant animal . . . far more important to the group", including preventing fights within the group, protecting mothers and infants from other group members, protecting the group from outside dangers and alien con-specifics, and leading the group.

Considering the wide range of definitions and measures applied, it is hardly surprising that different measures of dominance did not necessarily correlate with one another; conclusions based on one measure, one age-sex-class, or one species often could not be generalized to other situations.

This led some critics to question the usefulness of the concept of domininance. Gartlan (1964) doubted the existence of hierarchies, except as an artefact of stress in captivity. Rowell (1966b, 1974), in broad agreement, credited the maintenance of hierarchies in captivity to the decisive role of the subordinate animal, which "cautiously observed and maintained the hierarchy". She proposed a hierarchy of subordinance, not dominance. Observations of primates in the wild, however, demonstrated the existence of dominance relationships, dependent upon the contributions to the relationship of both the dominant and subordinate individuals, and the existence of hierarchies (Hausfater, 1975; Deag, 1977).

It is still debated how pervasive dominance can be in influencing a wide range of social behaviours, both agonistic and affiliative (Bernstein, 1981). A dominance relationship is inferred from the agonistic interactions between two animals. Yet, their social interactions - hence, their social relationship - probably include many exchanges which are not agonistic. It may be inappropriate to characterize an entire relationship by its competitive elements, although correlations between dominance and some affiliative behaviours, such as grooming, have been found (Cheney, 1978a; Seyfarth, 1977, 1980).

To the extent that dominance can be invoked to predict the direction or frequency of behaviour, it can be treated as an independent variable. Dominance may also be viewed as a dependent variable if it is closely associated with one or several independent variables, such as age, size, or kinship. Hinde (1978; Hinde and Datta, 1981) resolved this confusion by suggesting that dominance is most usefully regarded as an intervening variable.

As used in this study, dominance is not an attribute individuals possess to varying degrees, but an observer's description of one property of a dyadic relationship, in which asymmetric interactions occur in a consistent direction. The term dominance hierarchy implies that the dyadic relationships in a group exhibit an overall consistency and stability, such that the individuals may be conveniently arranged in a linear order: A > B > C . . . X > Y > Z, in which A is the dominant member of the dyad in all its relationships, and Z in none. These individuals are referred to by the ranks they hold relative to others in the hierarchy. The highest-ranking individual (A), by convention, holds rank number One. A sub-group of animals (A, B, C) may also be referred to as "high-ranking" with respect to the rest of the hierarchy, and others (X, Y, Z) as "low-ranking". Nothing is implied about the frequency, only the direction of interactions.

In this chapter, rank orders based on two independent variables are compared with those based upon the direction of one selected behaviour. Do the same independent variables influence the the outcome of agonistic interactions of both males and females? Do the independent variables which are important in one set of relationships influence agonistic interactions in all relationships? Finally, do orphans and the offspring of the fallen differ from other juveniles and, if so, do they differ from one another?

3.2. Methods

In many of the analyses which follow, ranks assigned to individuals are compared with rank orders based on the direction or frequency of interactions. It is conventional to rank individuals according to the direction (occasionally frequency) of a single or several types of agonistic behaviour (eg., supplants, threats, fights).

However, because of the large size of EC troop, many pairs of juveniles were never seen to interact, so there were insufficient data to rank juveniles on interactions alone. Several studies, though, have found non-behavioural attributes which are reliable predictors of rank within an age-sex class: in particular, the agonistic rank of a juvenile's mother, and the size of a juvenile relative to its peers (Owens, 1976; Cheney, 1976, 1977; Lee and Oliver, 1979). I decided to use these two non-behavioural measures to assign rank, then test for each sex which of these rankings most closely approximated a rank order based on available behavioural data.

The agonistic behaviour I chose for this test was the approach-withdraw interaction. Approach-withdraw interactions will be defined in full and analyzed in Chapter 7. Briefly, these involve one animal moving towards another, who then moves away without any aggressive gestures; the first animal is judged the "winner".

I selected the approach-withdraw interaction in preference to other agonistic behaviours for two reasons: first, as conflict escalates, there is an increasing likelihood of reversals (Rowell, 1966b; Lindburg, 1971; Simpson, 1973; Owens, 1975; Packer, 1979b). Second, baboons tend to form alliances in aggressive interactions (Kummer, 1967; Stoltz and Saayman, 1970; Packer, 1977; Seyfarth, 1980; Walters, 1980); whether or not this actually occurs, "the outcome of an aggressive interaction could be altered by the probability of the aggression becoming polyadic" (Seyfarth, 1980; also Struhsaker, 1967). Since approach-withdraw interactions by definition contained no threats, vocalizations, or aggressive gestures, it seemed the type of interaction least likely to elicit the support of other troop members who might influence the outcome of the interaction.

The interactions were drawn from all sources: focal-animal samples and <u>ad libitum</u> observations both during and outside focal-animal samples.

In constructing a rank order based on the interactions, the direction - but not the frequency - of the interaction was examined. The winner of each interaction was determined, and the animals ranked in an order which minimized the number of reversals. The number of interactions observed was far fewer than the possible combinations of same-sex animals. I assumed, therefore, that the rank order was transitive; that is, if individual A defeated B, and B defeated C, A would be able to defeat C. Thus, it was the identity and not the number of opponents that an animal was seen to defeat which determined its position in the rank order.

The behavioural and non-behavioural methods of assigning rank to the juvenile male and female baboons must be weighed for their benefits and disadvantages. If not all pairs of animals were observed interacting, I was unlikely to have definitive data for all pairs which would allow me to place each individual correctly in the rank order. For example, in a rank order based only on threats, an animal may be judged to out-rank only those animals it is actually observed to threaten. The result could be an inaccurate rank order, with rarely-observed animals incorrectly placed and a consequent risk of spurious rank "reversals" occurring when that order is used to examine other behaviours. On the other hand, my method, using non-behavioural measures, runs the risk of ranking females incorrectly if their mothers′ ranks are incorrect, or of establishing a rank order which, though highly correlated with observed behaviour, is not entirely accurate for each individual.

3.3. Results

3.3.1. Ranking juvenile females.

Early in 1979, the adult females of EC troop underwent an unusual upheaval in their dominance order (see Introduction). To assign all the juveniles a maternal rank, it was first necessary to examine whether the adult female hierarchy had remained stable during my study.

Figure 3-1 shows the adult female hierarchy at the beginning of this study, based on agonistic interactions of all types (Smuts pers comm). Plotted in the matrix are all agonistic interactions I observed between pairs of females during the subsequent months of my own study. Only 2.2% of the interactions contradict Smuts' final rank ordering; during her study when the adult female hierarchy was stable, 0.85% of the interactions did not follow the expected direction (Smuts, 1982). I concluded that the adult female dominance hierarchy did not change during my study.

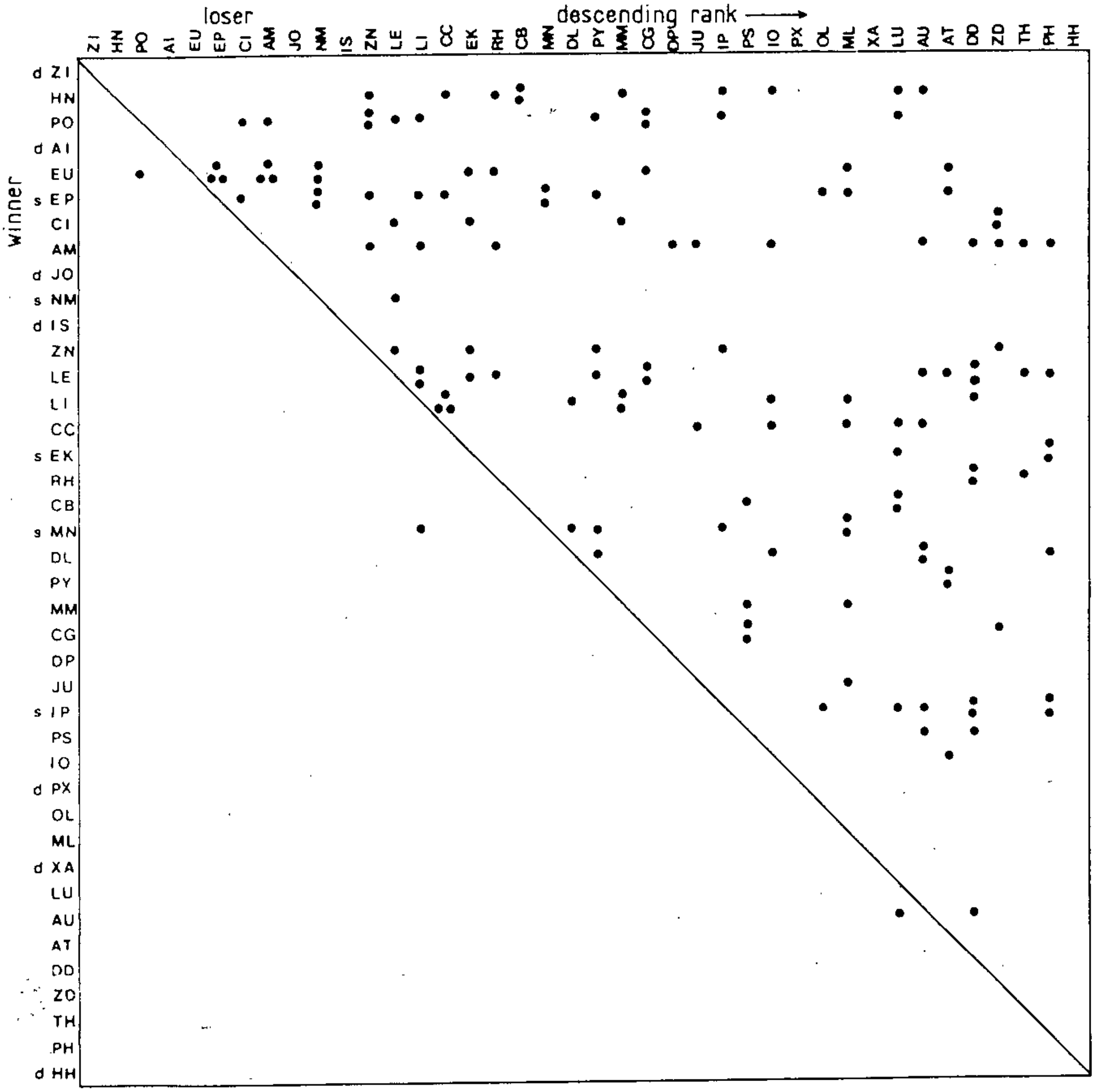
The thirty juvenile females in the troop were then assigned ranks one to twenty-four, based on their mothers' position in the adult female hierarchy. Juvenile sisters were assigned tied ranks; where the younger sister surpasses the elder in rank, this generally does not occur until adolescence (as in rhesus: Missakian, 1972; Sade, 1972; Schulman and Chapais, 1980; **but see Moore, 1978, and Hausfater *et al.*, 1982, concerning baboons).**

The resulting rank order is shown in Figure 3-2. I also ranked the females according to the direction of all

Figure 3-1. Adult female dominance hierarchy and distribution of agonistic interactions. All dyadic agonistic interactions recorded during this study are plotted in the matrix, only 2.2% of these being reversals. The order of the females is based on Smuts´ 1979 rank order.Where I have included new adult females into Smuts´ original ranking they were assigned a position under their mothers, but above older sisters.

Seven females who died before or at the beginning of this study are included in the ranking if they left known offspring, since their daughters´ and sons´ maternal ranks are derived from the mother´s position. They are indicated by a "d"

Females who lost rank are shown in their new, lower position. HH, the lowest ranking female shown here, occupied position five in the hierarchy during her life. Her death immediately preceded the loss of rank by DD, ZD, TH, and PH, formerly the highest-ranking, but here the lowest-ranking four among adult females. Although HH never occupied this lowest position while she lived, she is shown here since her surviving daughter seems to have lost rank together with the Fallen Females. See text.



Adult Females' Agonistic Interactions (n=136)

s=subadult
d=died

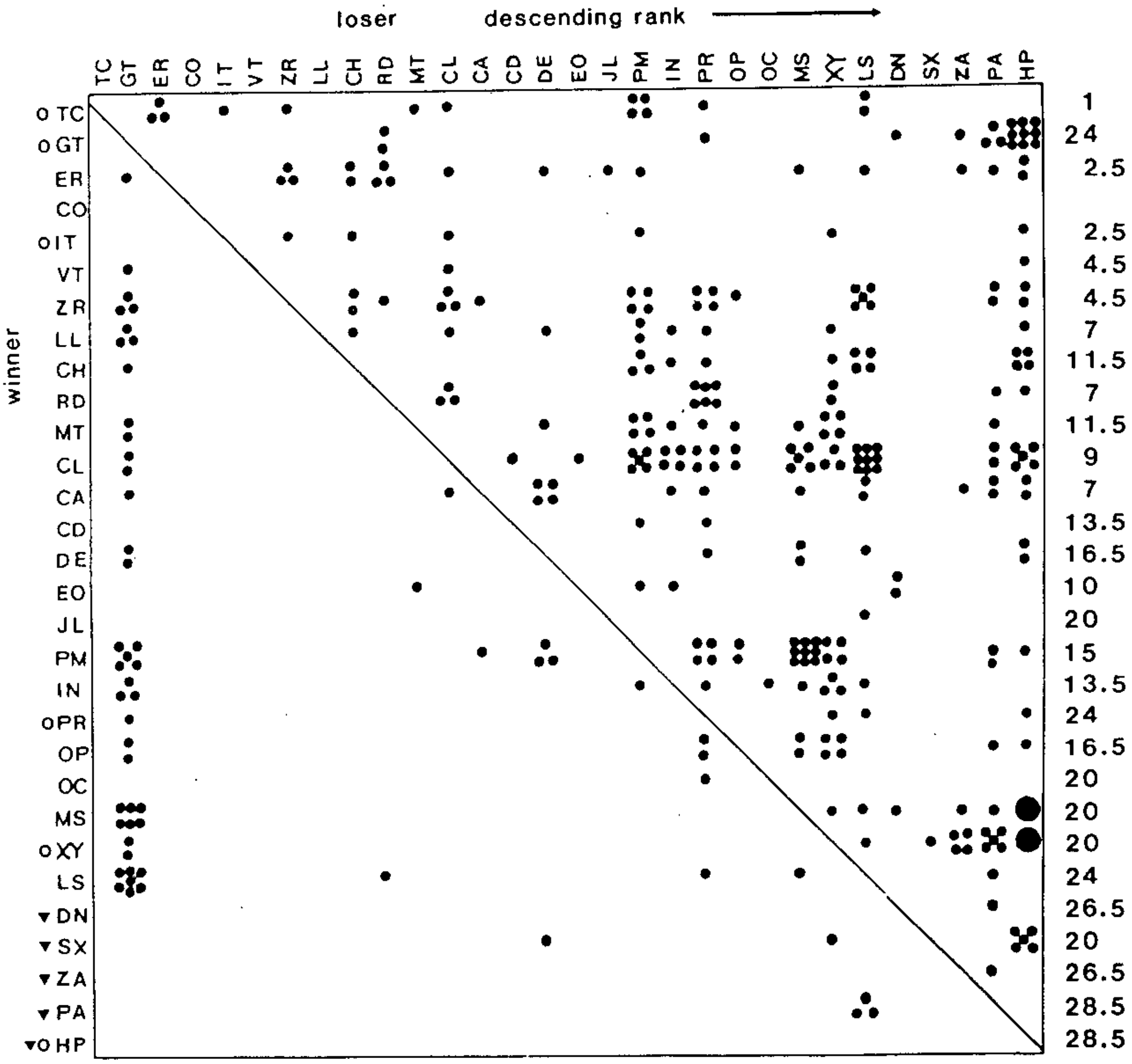


Figure 3-2. Juvenile female ranks, based on maternal rank, and distribution of approach-withdraw interactions. Each small dot in the matrix represents one interaction; large dots represent ten or more (n = 344). A second rank order, based on these interactions, is shown on the right. Females were arranged in an order which minimized reversals; where there were insufficient data, individuals were assigned tied ranks.

Orphans are indicated by an "o"; an arrow indicates the daughters of the females who lost rank.

The mother of one of the older juvenile females (NY) was unknown; she is excluded from the figure. A second (CO) was never observed in an approach- withdraw interaction, but is nevertheless positioned here according to her mother's rank. A third (OC) was never sized accurately and died early in the study. These animals are omitted from relevant correlation calculations described in the text.

approach-withdraw interactions. The correlation between the two rank orders - the approach-withdraw order and the ranking based on maternal rank - is high ($r_s = .83$, $p < .01$ $n=29$), although 17.4% of the observed interactions are reversals. When the six orphans (indicated in the figure by an 'o') are removed from the calculations, the correlation is higher ($r_s = .93$, $p < .01$ $n=23$), and only 4% of the interactions are reversals.

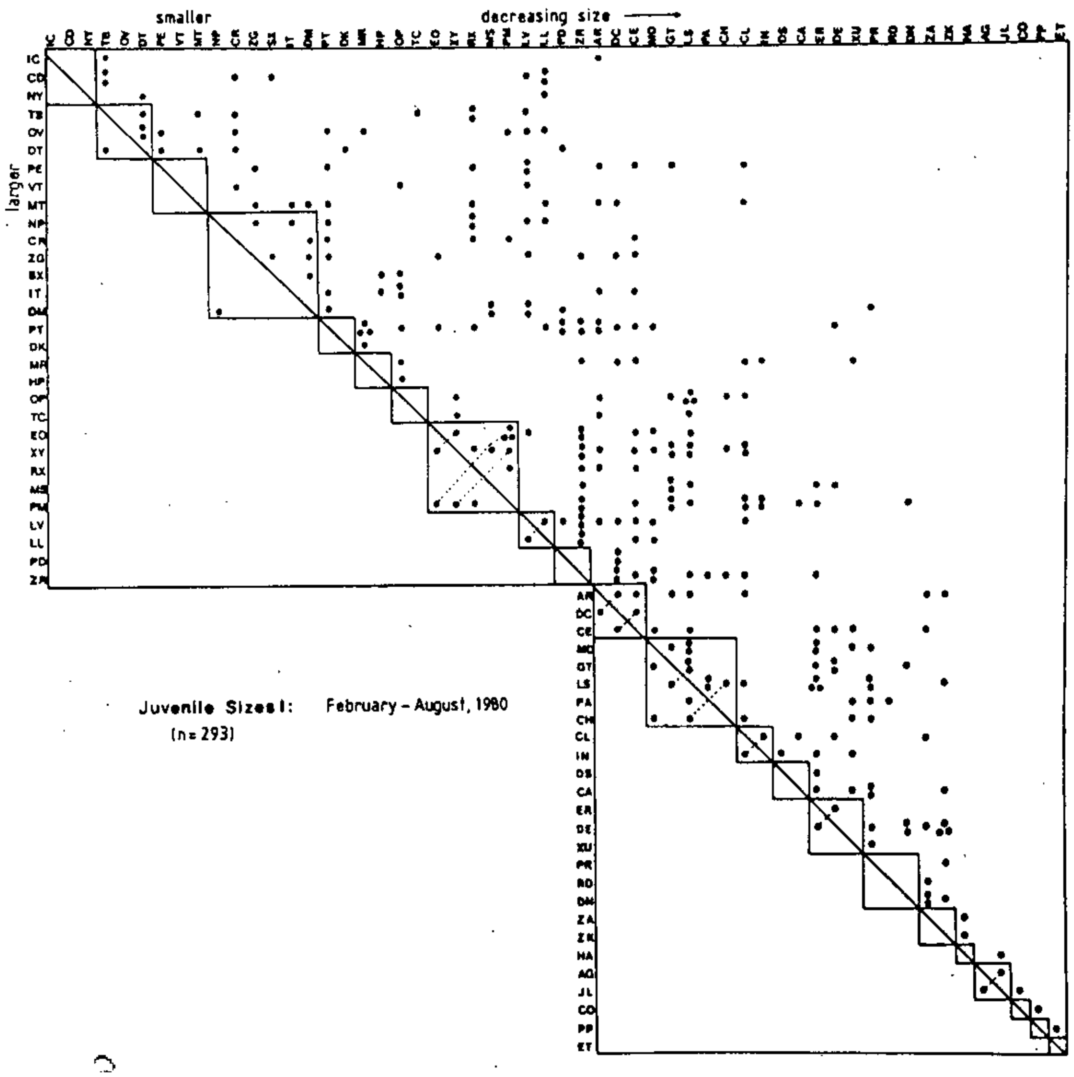
In contrast to these results on maternal rank, the correlation between size, the variable used below to calculate male ranks, and the rank order based on the direction of approach-withdraw interactions was not significant (rs = .227).

3.3.2. Ranking juvenile males.

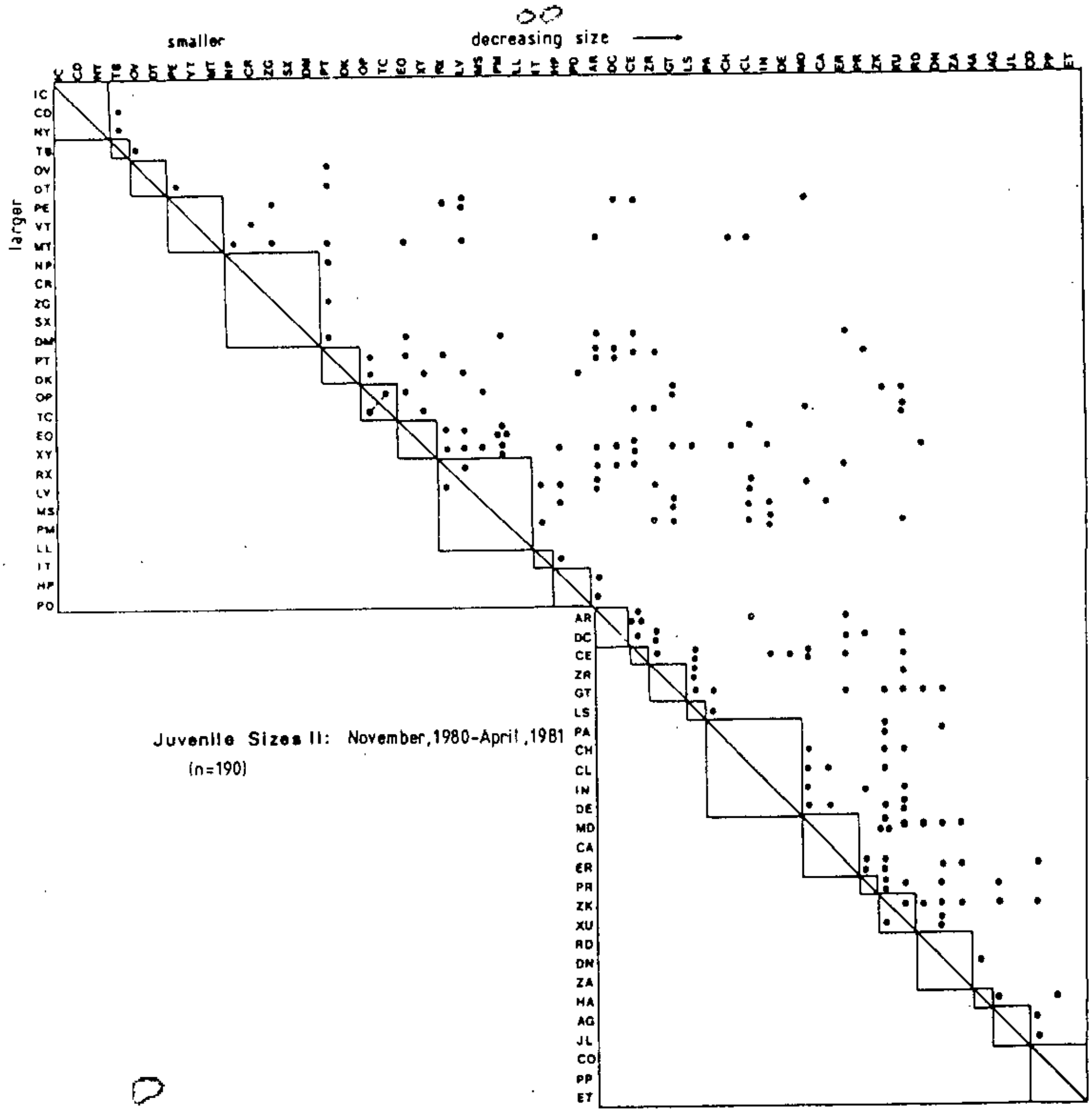
Six months before this study began, nearly all the baboons in EC troop were trapped for biomedical sampling. Although relative sizes for the juvenile group were then known, it seemed likely they would have changed by the time this study began or in subsequent months (see section 2.2.1.).

Therefore, I assessed relative size whenever two juveniles stood close together. The resulting rank order is shown in Figure 3-3. The observations were divided into two blocks, of eleven months and six months in length, representing the shortest time period for which it was possible to rank all the juveniles. In the following chapters,

Figure 3-3. Relative juvenile sizes for two blocks of the study. Dots indicate occasions when a particular pair of juveniles was seen together and relative size could be assessed. The squares along the diagonal enclose pairs of animals I judged to be the same size, or for whom there were not sufficient data to rank by size. **Within the squares, dotted lines join conflicting observations on the same pair of juveniles.**



Juvenile Sizes I: February – August, 1980
(n = 293)



Juvenile Sizes II: November, 1980-April, 1981
(n=190)

the ranking from the appropriate time block is used when behaviour is analyzed with respect to size.

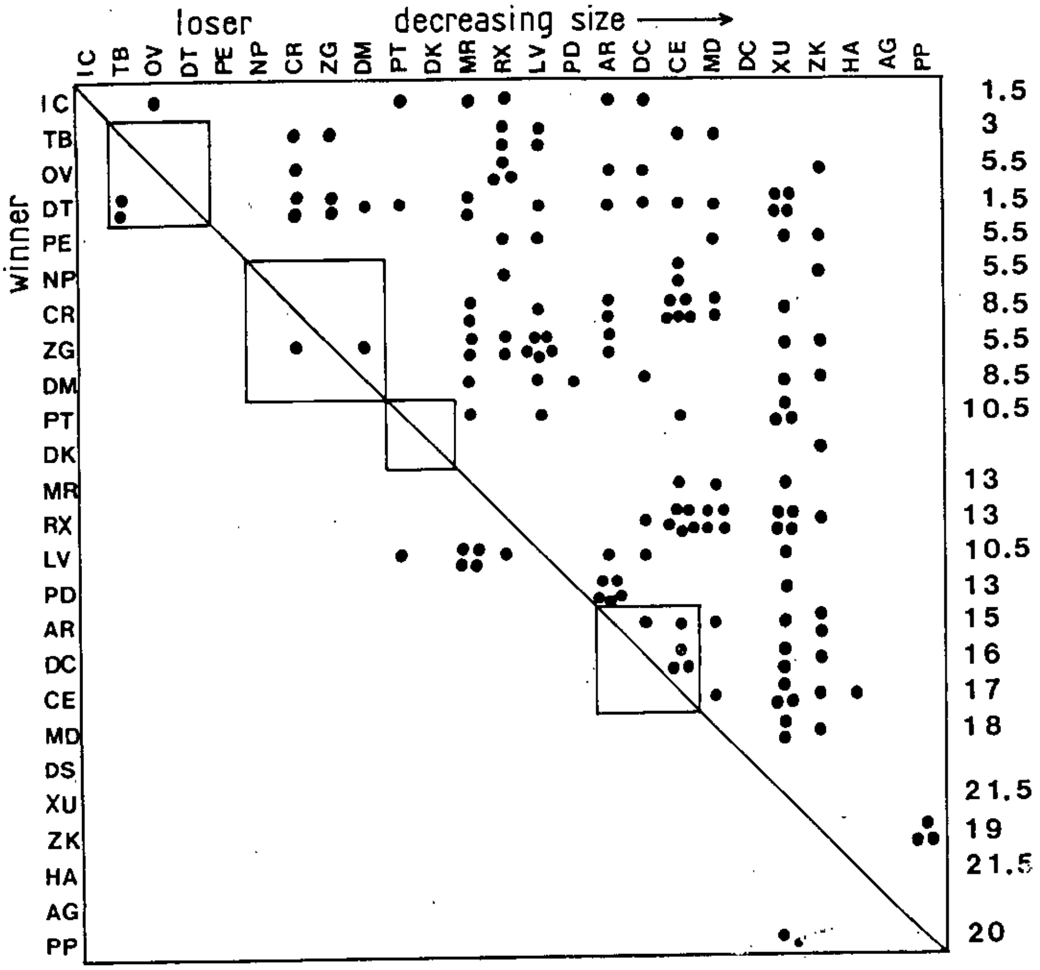
Once again, a separate rank order was constructed, assuming transitiveness, based on the direction of approach-withdraw interactions between juvenile males, and compared with the ranks derived from the independent variable, size. Figure 3-4 shows all approach-withdraw interactions between juvenile males in the two parts of the study: size correlates highly with the approach- withdraw rank order (Part I: $r_s = .974$; Part II: $r_s = .979$; $p < .01$ n = 22). Only two individuals, LV and PP, defeated partners whom I judged to be larger; they were responsible for the 3.5% of observed interactions which were reversals. These reversals lie close to the diagonal; that is, the opponents were fairly close in size. In addition, both these males were sons of high-ranking mothers, higher in rank than the mothers of the males they were seen to defeat, so some effect of maternal rank cannot be discounted. In general, though, the correlation between approach-withdraw rank and maternal rank is not significant (Part I: $r_s = -.231$; Part II: $r_s = -.173$). Also in contrast to results on juvenile females, omitting orphans from the correlation makes no difference (Part I: $r_s = .976$, Part II: $r_s = .977$).

3.3.3. Adult female interactions with juvenile females

Juvenile ranks with respect to same-sex peers were correlated with two different independent variables: the

Figure 3-4. Juvenile male ranks, based on relative size, and the distribution of approach-withdraw interactions in the two time blocks of the study. Each dot in the matrices represents one interaction (top: n = 148; bottom: n = 82). A second rank order, based on the 148 interactions in Part I of the study, is shown to the right of each matrix; there were no reversals. Where there were insufficient data, individuals were assigned tied ranks. The same order was used in Part II of the study; the 82 interactions alone were insufficient to rank the males. However, no interactions went contrary to the earlier rank order.

Among the twenty-five juvenile males, six (DS, HA, AG, CR, PD, PP) were not observed in approach-withdraw interactions during at least one part of the study, and the mothers of three were unknown (OV, PD, TB). One male (DK) transferred into the troop at an unusually young age; as a newcomer to a troop, DK was atypical among his peers in having no known members of his family and no long-term relationships. These males are omitted from the relevant calculations described in the text.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ZK
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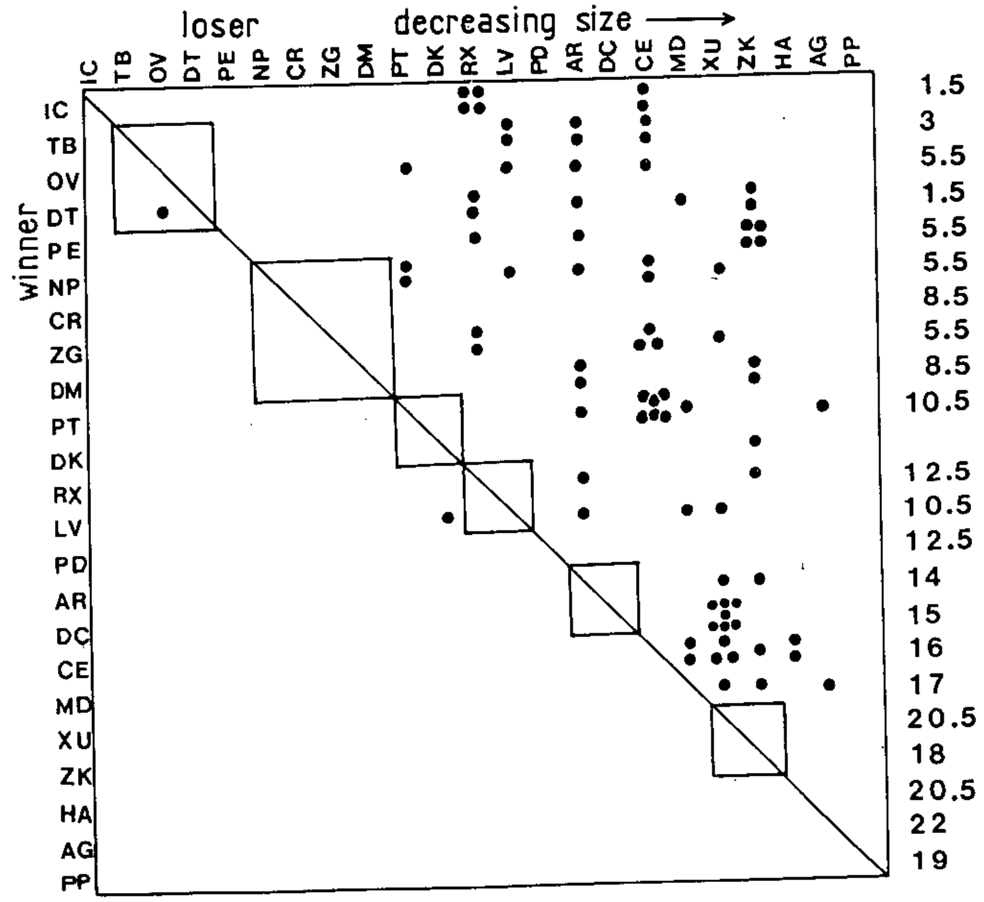
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relative size of males and the maternal rank of females. Did these same variables influence the direction of approach-withdraw interactions with adult females?

Figure 3-5 shows all approach-withdraw interactions between juvenile females and adult females. Data are drawn from all sources. The shaded portion of the diagram covers all dyads in which the juvenile female's mother out-ranked the adult female and where, if maternal rank is of overriding importance, the juvenile is expected to be the winner. The pattern of wins and losses suggests that juvenile females did hold positions within the adult hierarchy dependent upon their mothers' agonistic rank.

However, juveniles are under-represented as winners. In 56.07% of the potential juvenile female-adult female dyads (545 out of 972) the adult female out-ranked the juvenile (that is, she held a rank higher than the juvenile's mother). Yet these dyads accounted for 68.86% of the interactions (146 out of 212), and all interactions were in the predicted direction. The remaining dyads, in which the juvenile outranked the adult female, comprised 43.93% of the total, but accounted for only 31.13% of the interactions, with seventeen of the dyads being reversals. It is possible that I was more likely to observe those interactions in which a larger animal defeated a smaller than vice versa. However, these data include interactions in which the loser avoided the winner, as well as those in which the winner supplanted the loser (described in full in Chapter 7).

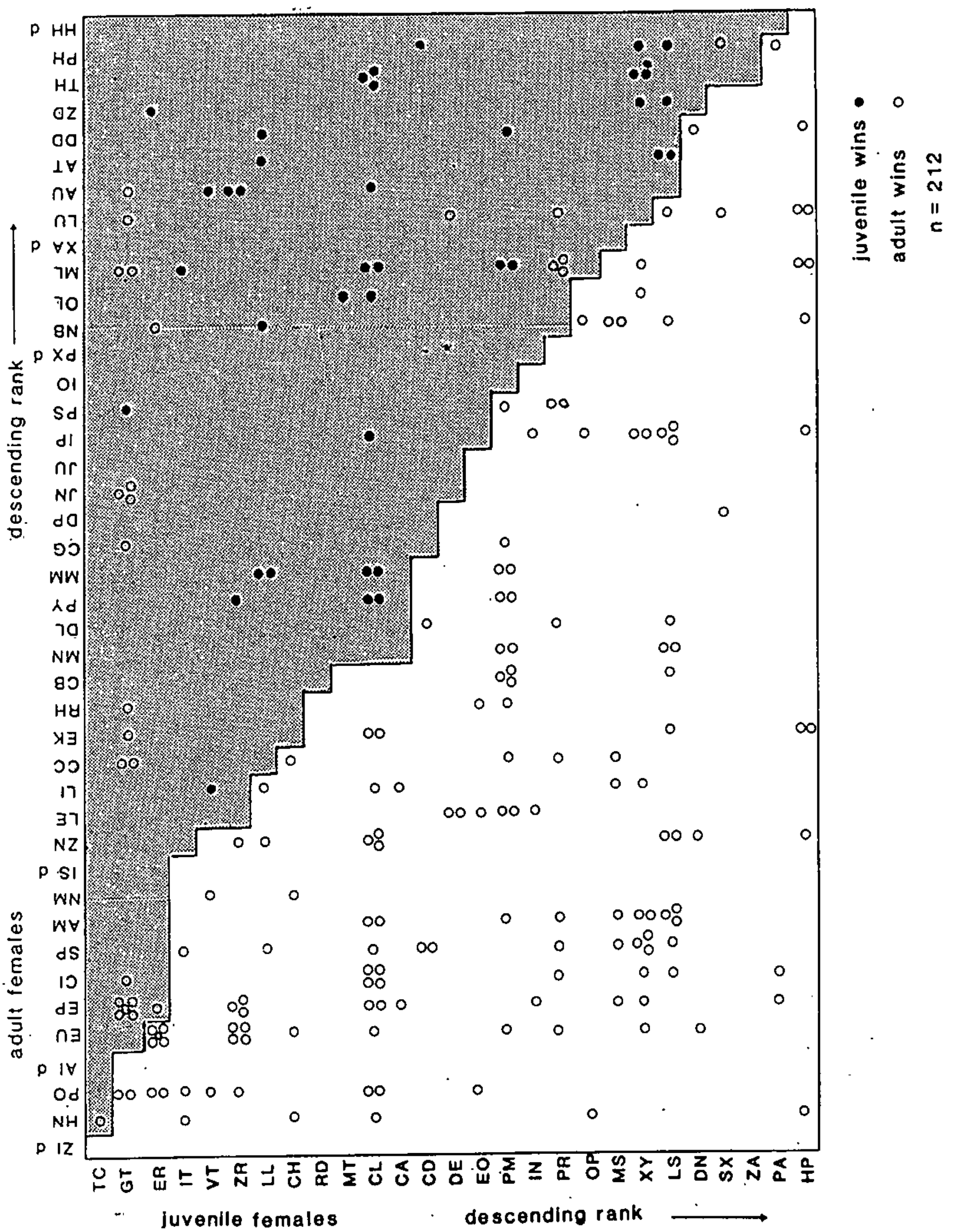


Figure 3-5. All approach-withdraw interactions between adult females and juvenile females. Adult females are arranged in descending order of agonistic rank. Juvenile females are arranged in descending order of maternal rank. The shaded portion of the diagram covers all dyads in which the juvenile's mother held a higher rank than the adult female. Each interaction is represented by a dot: juvenile wins by a closed dot and adult wins by an open dot.

When both age and maternal rank favoured the same member of the dyad - the female was both older and held a rank superior to the juvenile's mother - interactions were frequent and completely consistent in direction. When, however, those two variables exerted opposing influences, the interactions appeared to occur at lower frequencies, and those which did occur were inconsistent in direction.

The reversals are of interest. The orphan GT was defeated in eighteen interactions with females of lower rank than her late mother, and the orphan PR was defeated in four similar interactions. Two reversals concerned younger juveniles (ER and DE). The remaining reversals were between juvenile females and their putative sisters (TC and HN; ER and EP); in as much as sisters share maternal ranks, these are not "reversals". Although younger sisters may assume adult ranks higher than their elder sisters (as in rhesus: Missakian, 1972; Sade, 1972; Schulman and Chapais, 1980), there is no evidence that this had occurred by the late juvenile period.

3.3.4. Adult female interactions with juvenile males

Although juvenile males held ranks among their peers according to relative size, were their interactions affected by the matrilineal organization of the troop? Figure 3-6 shows all approach-withdraw interactions between juvenile males and adult females, drawn, again, from all data sources. The shaded portion of the diagram covers all dyads in which

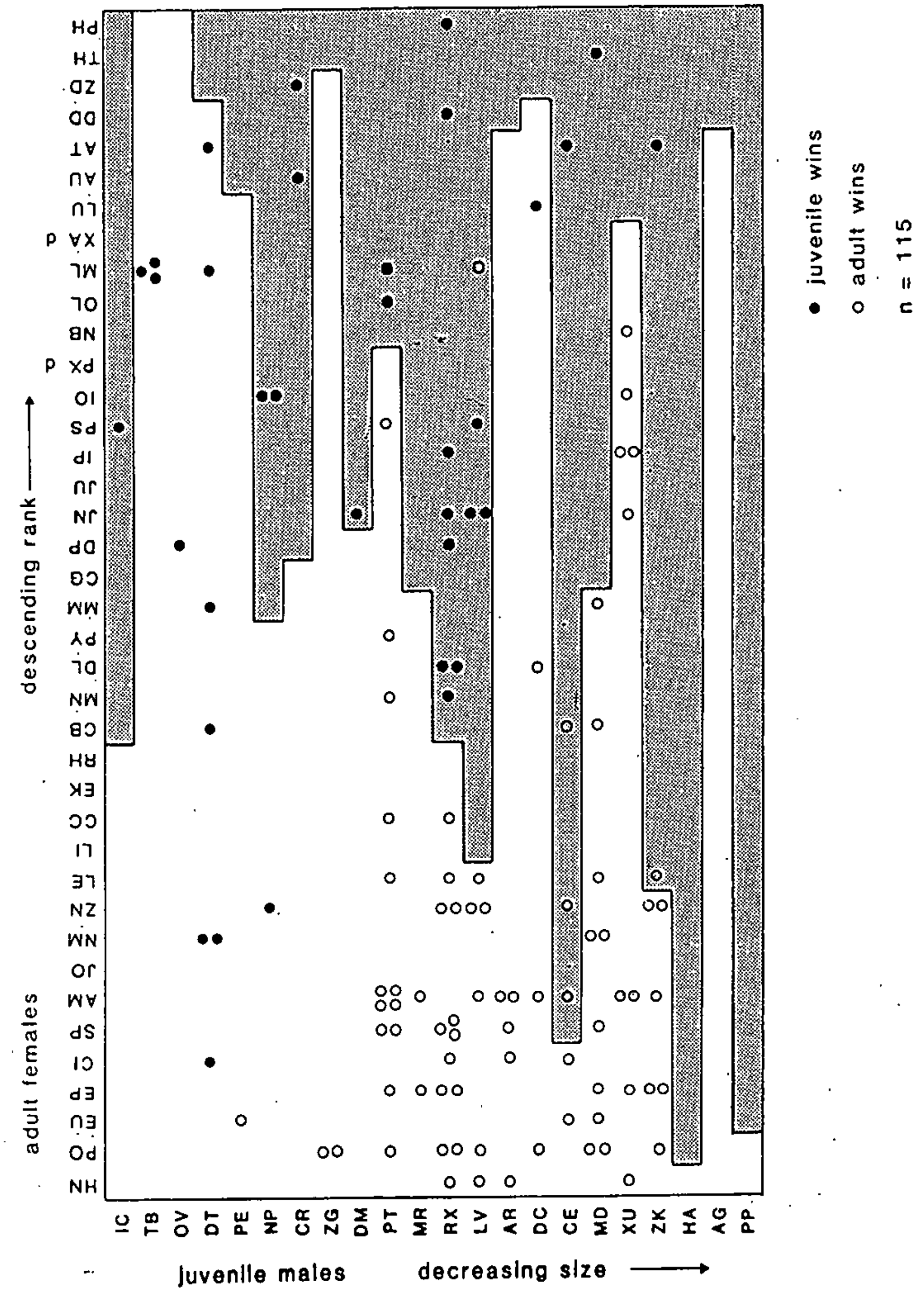


Figure 3-6. All approach-withdraw interactions between adult females and juvenile males. Adult females are arranged in descending order of agonistic rank. Juvenile males are arranged in order of decreasing size. The shaded portion of the diagram covers all dyads in which the juvenile's mother held a higher rank than the adult female. Each interaction is represented by a dot: juvenile wins by a closed dot, adult wins by an open dot.

the juvenile's mother out-ranked the adult female, the dyads in which, if maternal rank influenced the outcome of approach-withdraw interactions, the juvenile should win.

As with the juvenile females, the majority of interactions occurred in the direction predicted by maternal rank, although the juveniles appear once again to have been under-represented as winners. Of 740 potential juvenile male-adult female dyads (excluding OV and TB, whose mothers were unknown), in 56.35% (417), the adult female out-ranks the male's mother; these dyads account for 78.37% of the interactions. The remaining 43.65% of the dyads in which the male out-ranked the adult female accounted for 21.62% of the interactions.

The majority of interactions appear to be concentrated between the more dominant adult females and the younger juvenile males. Young males were defeated by adult females, but did defeat some females lower-ranking than their mothers. With increasing age, they defeated adult females in all interactions.

3.3.5. Interactions between males and females

The pattern of wins and losses between adult females and juvenile males reflects a young male's ability to defeat larger females, first in accordance with his mother's rank, then all adult females, regardless of their ranks with respect to his mother. It might be expected that juvenile males were already capable of defeating juvenile females their same size. Figure 3-7 indicates this was the case.

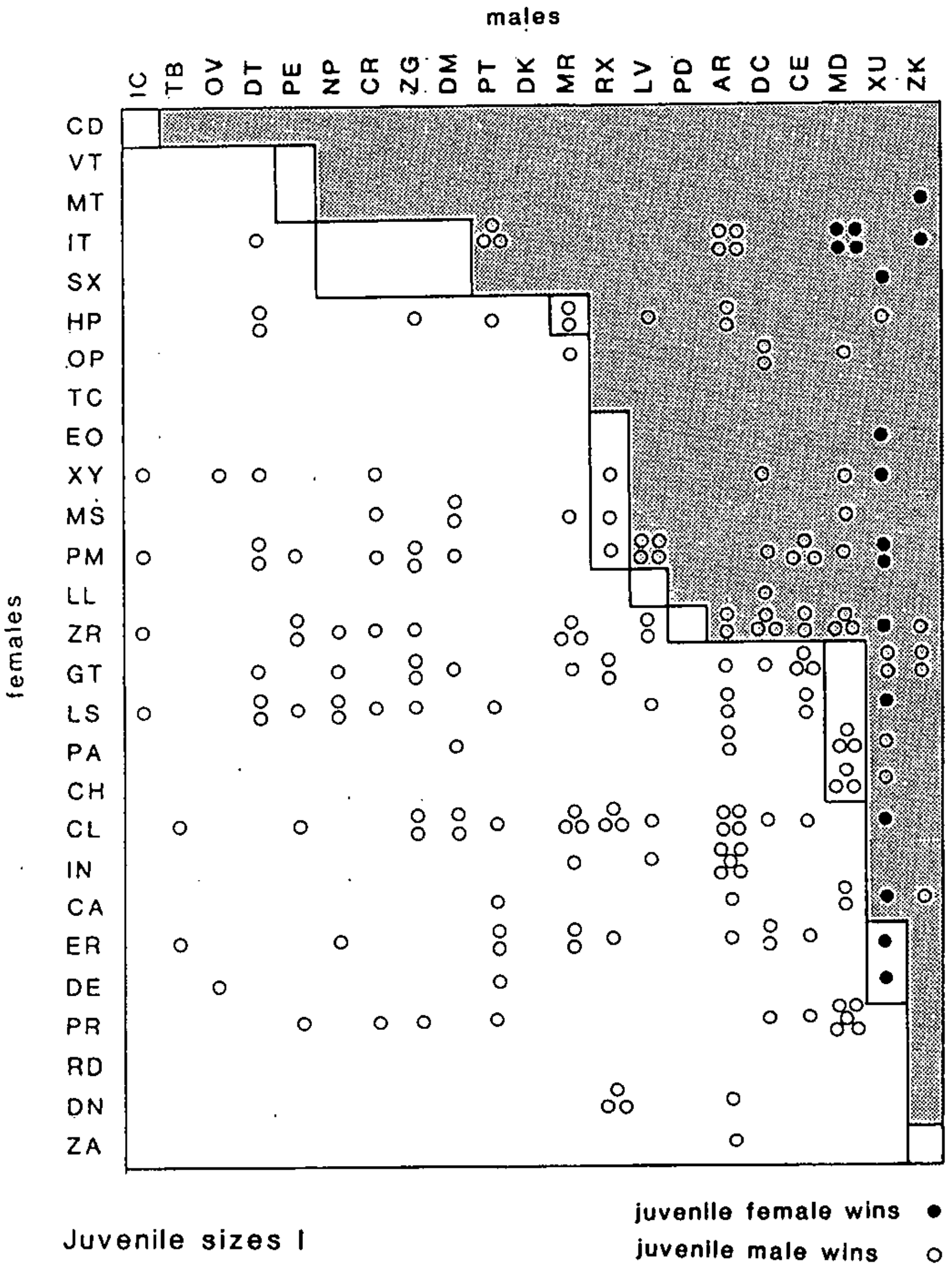
Both males and females are arranged according to size, for the two size blocks of the study. In the shaded portion of the diagram, the female is the larger partner. In the majority of dyadic interactions, the male was the winner, regardless of size. In interactions in which a female was the winner, she was both larger, and of higher maternal rank. The only exception involved the youngest male orphan, XU. He was defeated by a larger juvenile female (LS), who held a lower maternal rank. XU was also the only juvenile male to be defeated by his sister.

3.4. Discussion

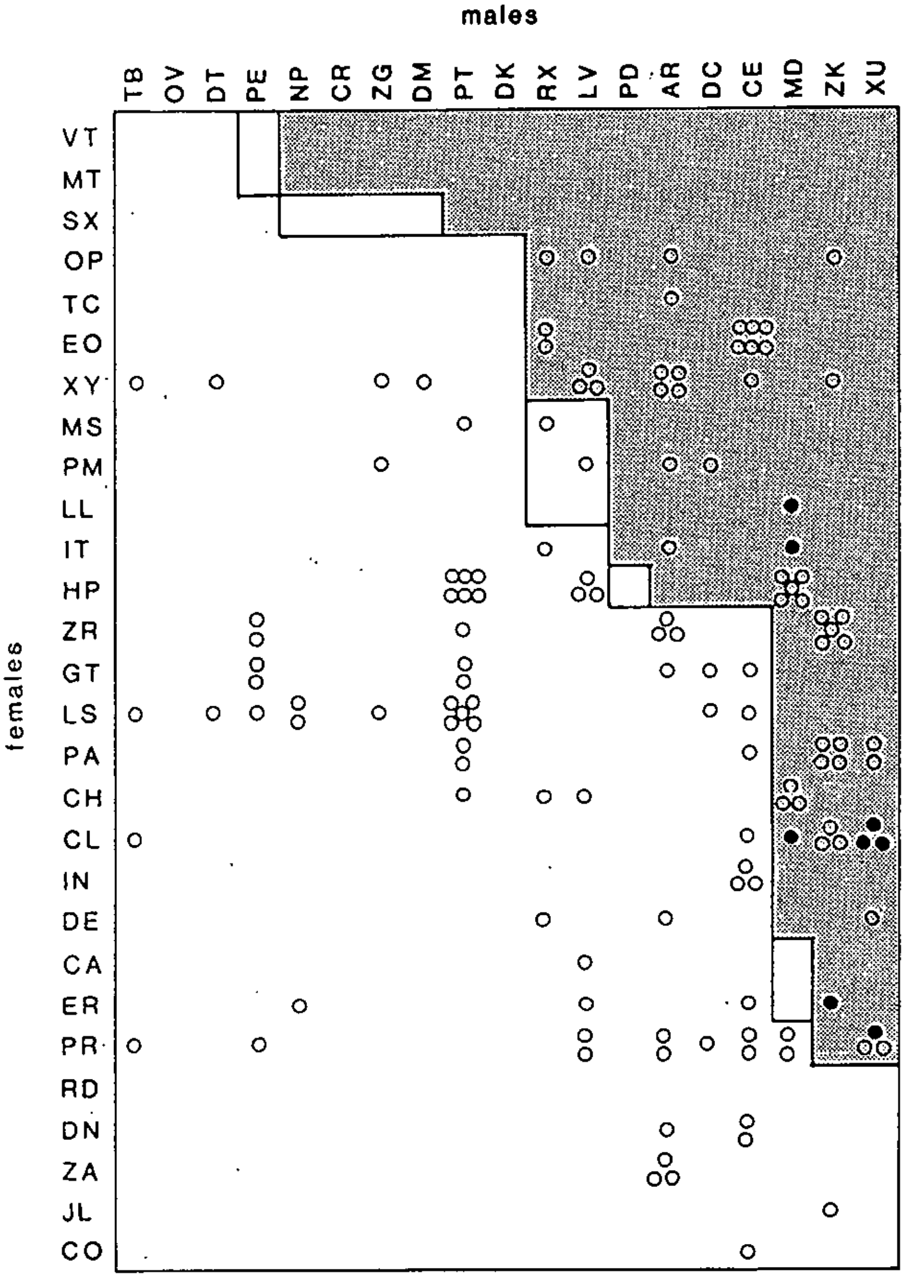
Juvenile rank appeared to be influenced by two major factors: the agonistic rank of the mother, and juvenile size; and to be vulnerable to disruption by a third factor: the death of a mother or her loss of rank. Males and females were affected differently, and the relative importance of the factors varied, depending upon the age-sex class of the interaction partner. Thus, the direction of most, but not all, juvenile female interactions could be accounted for by maternal rank; and the direction of most, but not all, juvenile male interactions depended upon male size.

The exceptional interactions make more sense if the process of rank acquisition can be viewed from a theoretical adult endpoint. As an adult, a female will achieve a rank among other females which reflects her

Figure 3-7. All approach-withdraw interactions between juvenile females and juvenile males in the two time blocks of the study. Both sexes are arranged in descending order of size. The shaded portion of the diagram covers dyads in which the female was larger than the male. Boxes enclose dyad in which both partners were of the same size. Each interaction is represented by a dot: female wins by closed dots, male wins by open dots.



Juvenile sizes I



Juvenile sizes II

mother's rank. A male will transfer to a new troop in which he is individually dominant to all females. His rank relative to other males will depend in part on his competitive skills; these, in turn may be related to his size (Packer, 1979a). So, maternal rank for females, and size for males can be thought of as the major single factors influencing adult rank, and both imposing ceilings on potential rank. As she grows up, a female must gain sufficient size (or age, or experience) to achieve her maternal rank; whereas a male first benefits from, then gains sufficient size that he overcomes maternal rank.

Does this help explain the regularities and exceptions in the direction of approach-withdraw interactions? For juvenile females, the outcome of approach-withdraw interactions was highly consistent with maternal rank when the interaction partners were other juvenile females, where size (age, and experience) were roughly similar. Interactions between adult females and smaller, inexperienced juvenile females were consistent in direction when both adult-female (maternal) rank and relative size favoured the same individual - that is, when the larger female also held the higher rank. When the smaller female held the higher (maternal) rank, reversals were more common. Interactions appeared to be less frequent, reflecting, perhaps, a reluctance on the part of the juvenile to initiate interactions against adult females. The juveniles appear to be disinclined or unable to "take advantage" of their maternal rank. Rowell (1966b) speculated that reversals in the predominant direction of non-agonistic interactions between a pair of animals might precede a rank change in low-intensity agonistic interactions. Walters (1980) described later transitional stages in the aggressive interactions between adult females and adolescent females of generally higher maternal rank, the end product of which is a stable relationship in which the adolescent is finally dominant. When adults interacted with juvenile females in this study, it is possible that the low-intensity approach withdraw-interaction was the contested ground of their current relationship.

Juvenile male interactions with their own class were highly consistent with size. Juvenile males were never seen to win in approach-withdraw interactions with members of larger male classes; again, size was the determining factor. In interactions with adult females, younger (smaller) males won in accordance with their mothers' ranks; whereas larger juvenile males achieved wins, in spite of their mothers' ranks, over high-ranking females.

Juvenile male interactions with juvenile females can be regarded as an earlier stage of their interactions with females in general; if males, at this age, are already able to defeat many adult females, it is not surprising that they already defeat younger, smaller females. All but one of the exceptions occurred when the juvenile female was both larger and held higher maternal rank.

The results discussed so far are strikingly similar to patterns described by Lee and Oliver (1979) in their study of juvenile rank in yellow baboons. However, a third influence on juvenile rank was absent from their study, but influenced a small number of individuals profoundly in this study: this was a change in the mother's influence, either through death or loss of rank. Again, this affected females and males differently, and the orphans differed from the offspring of the Fallen females. For juvenile females, removing the six orphans from the calculations improved the correlation between the rank order based upon maternal rank and that based upon the direction of interaction. It is clear that the position of the orphans should be reassessed individually.

Notable among the orphans was GT, ranked number two in Figures 3-2 and 3-5 and the most glaring exception to their patterns. The daughter of a high-ranking female (AI), she clearly held a position inconsistent with her late mother's rank. She was defeated by adult and juvenile females down to but not including the Fallen females and their daughters, and her reassessed rank places her accordingly.

A second orphan, PR, daughter of a low-ranking female (PX), lost behavioural rank relative to the two sisters (OP and OC) whose mother had ranked beneath her own. Her position was also adjusted downwards.

In contrast, three other female orphans, TC, IT, and XY, were all older than GT and PR at the time of being orphaned, and appear to have retained the positions their mother's ranks would predict. This suggests that older females, who were aged over three years at the time of their mothers' deaths, had made their own ranks secure; whereas the younger females, who were less than two years old at the time of being orphaned, did not yet hold secure ranks independent of their mothers.

The presence of elder siblings with, presumably, more secure ranks made no clear difference to the orphans' positions; two of the three orphan females who maintained their rank, and one of the two who lost theirs had no known elder siblings in the troop.

A final anomaly is the juvenile female HP. As HP was over three years old when she was orphaned, she could be expected to maintain her own rank as did IT, TC, and XY; but she did not. Her mother had been HH, who occupied position five in the adult female hierarchy. It was her death which immediately preceded - and may somehow have precipitated - the drastic loss of rank by the Fallen Females, DD, ZD, TH, and PH. They were previously the four highest-ranking adult females, but were the four lowest-ranking over the period of this study. It appears that HP's age and experience, which might have made her own position in the hierarchy secure after her mother's death, were outweighed by the loss of rank of females who ranked immediately above her mother. There are two possible explanations for this. If all these females - the Fallen Females, HP and her mother - were members of the same matriline, the Fallen Females might have been potential allies of HP. Thus, without their effective support, HP could not maintain her own rank. Alternatively, the Fallen Females may have all been members of the next matriline above, a separate family from HP and her mother. If the Fallen Females retained the ability to dominate the orphan HP despite their own general loss in rank, they could be thought of as having "pushed" her down (Collins, pers. comm.). HP's rank at the bottom of the juvenile female rank-order maintains her position relative to the daughters of the fallen females.

In contrast to the orphans, the fate of the four daughters of the Fallen females was consistent with their mothers' new, lower ranks, both in their interactions with their peers and with adult females. Although the eldest of these juveniles dominated some peers of higher maternal rank, she lost in all her interactions with adult females. The daughters of the Fallen females appeared "condemned by association". It was less disruptive to a juvenile female's rank if her mother died than if she lost rank, as if no allies were better than ineffectual allies.

Two examples from the long-term studies of yellow baboons at Amboseli suggest that maternal rank loss did not have the pervasive effect on a daughter's rank which was observed here, but rather that the age of the daughter when her mother lost rank was critical (Hausfater, _et_ _al_., 1982). The juvenile female who was aged one when her mother lost rank was affected more seriously than another aged three. What can account for this difference between baboons at the two sites? Compared to Alto's troop at

Amboseli, EC troop was very large (three times the size) and mortality was low. EC females probably had more opportunity to associate with and ally with close kin (Berman,1978). Thus, a female in EC troop who lost rank - or one who already occupied a low rank - may have faced not only individuals who singly held superior ranks, but whose ranks were buttressed by a larger number of surviving kin. The chances for improving or regaining lost rank could be more difficult under those circumstances.

The adjusted rank-order of juvenile females used in the remainder of this study is shown in Table 3-1. Most analyses which follow compare only the eight main juvenile female subjects with each other, and the only individual whose rank relative to the other seven is affected by this reassessment is GT.

For males, a mother's loss of rank, or her death, had little discernible effect on the male's rank. Of the orphans, the elder male, PT, interacted with other males in accordance with his size. In his interactions with adult females, he lost to adult females holding a higher rank than his late mother, and won interactions with those she had out-ranked. The younger orphan, XU, was never observed in an approach-withdraw interaction with his peers. Like PT, XU lost interactions with adult females who had out-ranked his mother, but he was never seen to interact with adult females of lower rank. However, in this, he did not differ from other small juvenile males; there were no grounds to adjust his size-based ranking.

Old (Maternal) Ranks		Reassessed Ranks	
1	TC	1	TC
2	GT	2	ER
3	ER	3	CO
4	CO	4	IT
5	IT	5	VT
6	VT	5	ZR
6	ZR	6	LL
7	LL	7	CH
8	CH	8	RD
9	RD	9	MT
10	MT	9	CL
10	CL	9	CA
10	CA	10	CD
11	CD	11	DE
12	DE	12	EO
13	EO	12	JL
13	JL	13	PM
14	PM	14	IN
15	IN	15	OP
16	PR	15	OC
17	OP	16	PR
17	OC	17	MS
18	MS	18	XY
19	XY	19	LS
20	LS	20	GT
21	DN	21	DN
22	SX	22	SX
22	ZA	22	ZA
23	PA	23	PS
24	HP	24	HP

Table 3-1. Juvenile females ranked according to their mothers′ ranks, and reassessed in light of behavioural data.

The three sons of the fallen females (DT, DC, ZG) also maintained their rank, unlike their sisters. In their interactions with both other juvenile females and with adult females, these three males resembled their peers. Changes in a mother's status appeared to be much less important than size - or associated qualities - in determining a male's rank.

Unlike females, the ranks of juvenile males are unaffected by the death of a mother, or by her loss in rank.

3.5. Summary of rank assessment

The reader should bear in mind that, in this study, a "high-ranking juvenile female" refers to the daughter of a female of high rank, with the exception of three orphans whose ranks are adjusted; while a "high-ranking juvenile male" is larger (and probably older) than his peers. These terms do not refer to dominance rank *per se*, though the ranks do correlate highly with the direction of one type of agonistic behaviour, the approach-withdraw interaction.

Chapter 4

ACTIVITY BUDGETS

4.1. Introduction

As the focus of this study was juvenile social relationships, so the recording of social interactions was given priority in the study design. However, social behaviour, even in the conspicuously gregarious baboon, may still occupy only a fraction of an animal's time. In this chapter, I briefly describe the ways juveniles allocate their time and the maintenance activities which take up most of a baboon's day.

Activity budgets are examined for evidence of seasonal differences which might have influenced social behaviour, and for differences associated with sex, rank, and age. In addition, the activity budgets are used in future chapters to generate expected scores for some behaviours, as are aspects of the data on feeding presented here.

4.2. Season and activity budgets

The mean percent of time spent in each activity in the wet season and in the dry season was calculated from the focal-animal samples of each juvenile baboon. There was a consistent pattern in activity budgets across all sixteen juveniles (dry season: $W = .83$, $p < .01$; wet season $W = .92$, $p < .01$) and there were significant differences in the amount of time devoted to each activity (dry season: $X_r^2 = 78.5$, df = 6, $p < .001$; wet season: $X_r^2 = 88.7$, df = 6, $p > .001$). Feeding was by far the most common activity, followed by the other maintenance activities: Travel and Rest. Social interaction, and Grooming each took up a much smaller amount of time, and Self grooming a minor amount (data in Appendix 2).

For each behaviour, the sixteen scores from each season were compared (see Figure 4-1). Surprisingly, there was only one significant difference between wet and dry season activities: Travel-feeding was higher in the wet season for all sixteen individuals. Grass was the food most often eaten while traveling and, as will be shown in the next section, grass made up a higher proportion of the diet in the wet season than in the dry. However, there was no difference in the total percentage of time spent feeding in the two seasons.

4.3. Sex and rank differences in activities

Data from both seasons were combined into activity budgets for males and females, shown in Figure 4-2 (data in Appendix 2). Females spent significantly more time grooming than did males, but that was the only sex difference in the percentage of time engaged in the different activities (U = 5, $p < .001$). However, if the gross categories of non-social and social behaviour are compared, males spent significantly more time in the non-social behaviours (U = 8, $p < .01$).

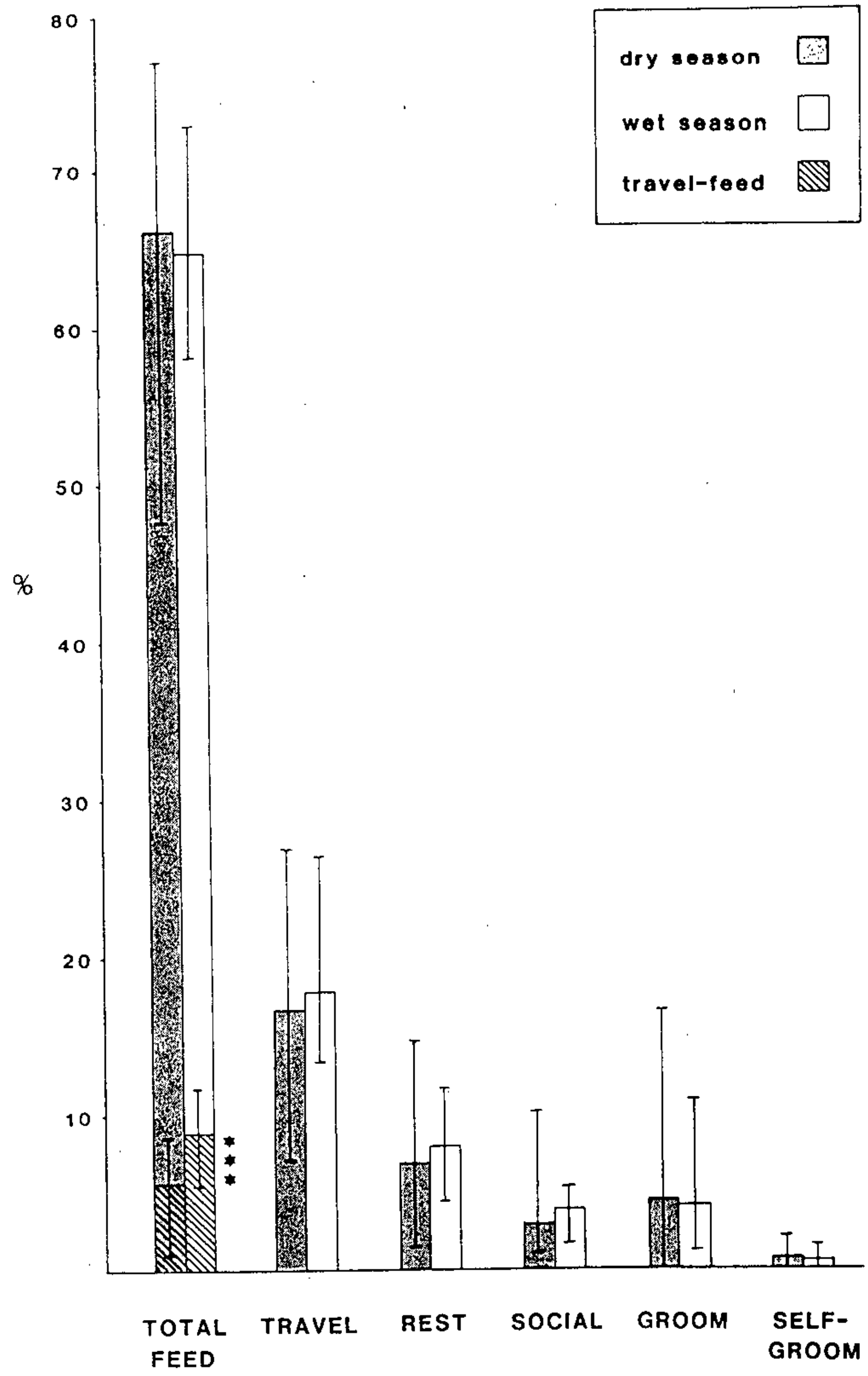


Figure 4-1. Percent of time spent in seven activities in the dry and wet seasons. **Medians and ranges of individual mean scores are shown.**

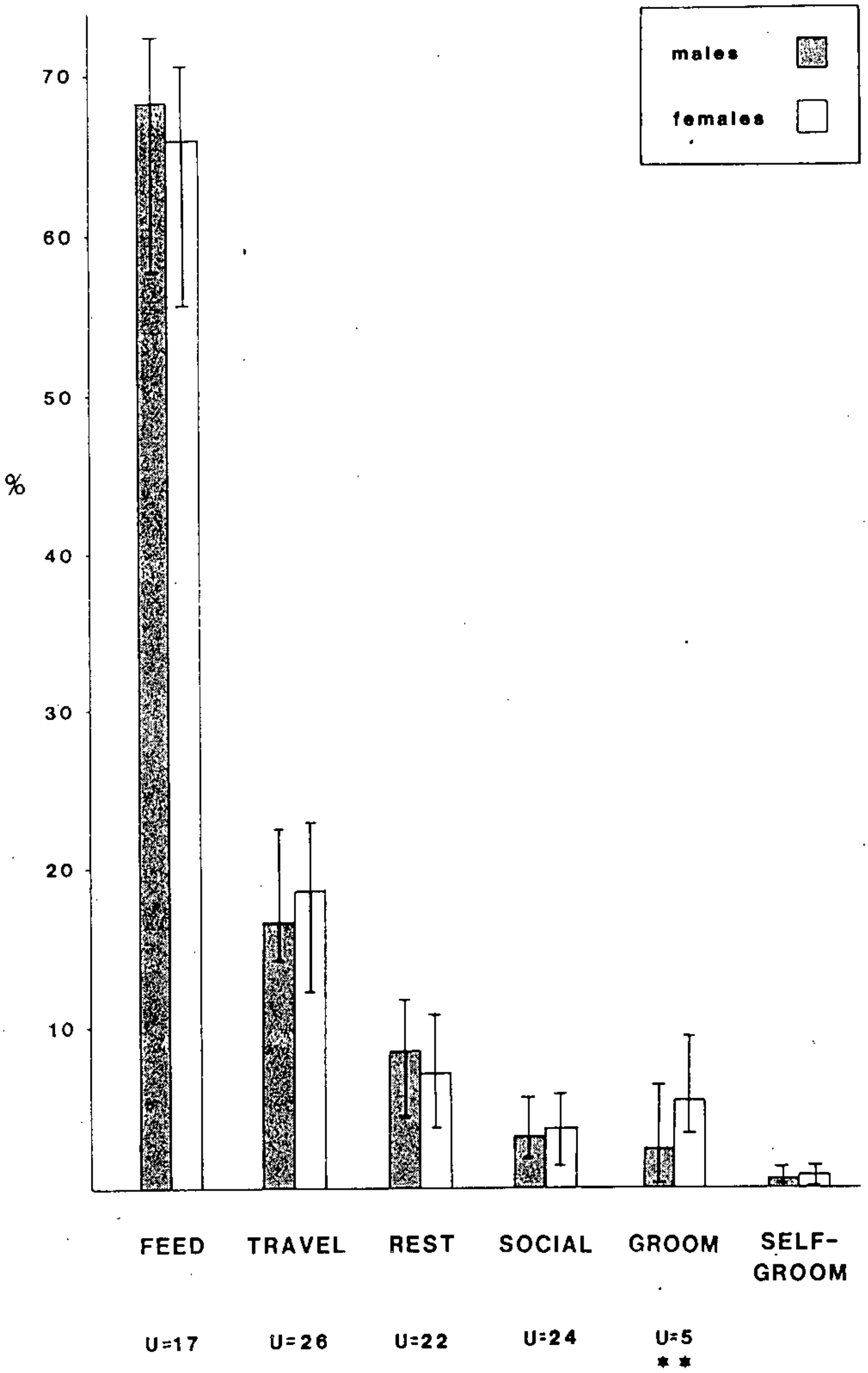


Figure 4-2. Comparison of the percent of time juvenile females and males devoted to different activities. **Medians and ranges shown, as in 4-1.**

Individual differences in time spent in each activity were not related to rank or to size.

4.4. Feeding behaviour

Although activity budgets did not vary with season, the foods eaten by juvenile baboons did. Their diet was almost entirely vegetarian; juveniles were never seen to share in the hunting and meat-eating which has been widely reported for adults, particularly males, at Gilgil (Harding, 1973; Strum, 1975, 1976, 1981, 1983). Demment (pers. comm.) identified more than two hundred plant species eaten by the neighbouring PHG troop. My classification methods were crude, noting specific names only for commonly eaten species, and otherwise noting the plant parts consumed. Appendix 3 lists twenty-one baboon foods as I recorded them during this study, and some comments on the methods of preparation. However, this degree of detail is not pertinent to the analysis which follows. Some foods were eaten so rarely ("rocks"), or during very brief periods of abundance (mushrooms, insects), that an analysis of seasonal, sexual, or individual differences would be misleading. The animals recorded eating these rare foods would be those I happened to sample on a particular day.

Figure 4-3, then, presents the feeding data in eleven food groups, showing the median proportion of feeding observations in each season which were devoted to each group. Patterns of feeding were consistent across all

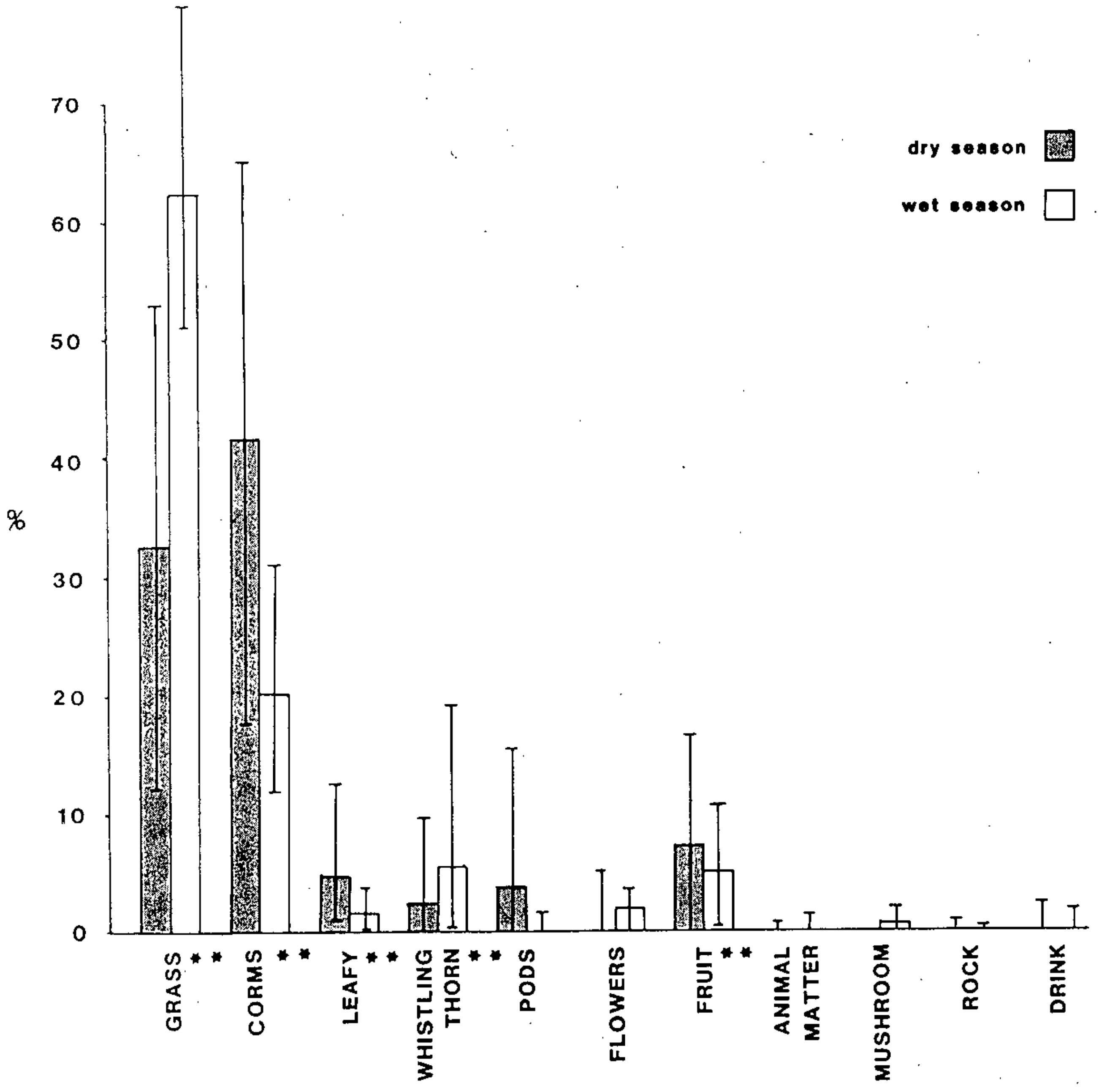


Figure 4-3. Seasonal differences in the proportion of feeding on eleven food groups. **Medians and ranges shown, as in 4-1.**

sixteen subjects (dry season: W = .78, $p < .01$; wet season: W = .81, $p < .01$; df = 10) and a significantly different amount of time was devoted to the various food groups (dry season: $X_r^2 = 124.6$, $p < .001$; wet season: $X_r^2 = 130.1$, $p < .001$; df = 10).

There are obvious seasonal changes in feeding. However, I omitted from analysis any food group which was not seen to be eaten by all sixteen subjects (these include: pods, flowers, animal matter, mushrooms, rocks, drinking); differences between individuals could have been due to observational bias. In addition, the rare foods did not contribute a high enough proportion to the scores to allow sufficient degrees of freedom in the major food groups. Changes in the rarer foods will only be commented upon.

Grasses and whistling thorn were eaten significantly more in the wet season (T = 1, T = 0, $p < .01$). In addition, of fifteen animals who were seen to eat flowers, fourteen ate more in the wet season; and mushrooms were an exclusively wet season food for the thirteen animals seen to eat them.

In the dry season, feeding on corms, on leafy vegetation, or on fruit increased significantly (T = 2, T = 15.5, T = 16; $p < .01$); and of fourteen animals seen eating pods, twelve showed increased scores in the dry season.

Sex differences in diet, which emerge in adults (Post, 1978; Rhine and Westlund, 1978; Post _et al_., 1980), were not evident in juvenile females and males (U values of between 23 and 38 for all foods tested). Measures of feeding in this study were not sufficiently sophisticated to detect the ontogeny of those adult differences. There was no correlation between rank and any feeding measure, in males or in females.

4.5. Summary

Overall activity budgets of the sixteen juveniles did not vary with season. EC troop was unusual in this respect, as seasonal changes, particularly in the time baboons spend feeding and travelling, are commonly reported (Altmann and Altmann, 1970; Nagel, 1973; Harding, 1976; Seyfarth, 1976; Oliver and Lee, 1978; Post, 1978, 1981). There are two possible explanations for this result. First, my assessment of seasonality based on rainfall may not be an accurate measure of the changes which actually affect baboon time budgets. Altmann (1980, p. 44) points out "the effect of rainfall patterns on the group movements and on the percentage of time baboons spend feeding and walking is a complicated one." However, significant differences in the foods eaten in the two seasons did emerge; this suggests that to look for an association between rainfall and activity budgets was reasonable.

An alternative explanation is that EC troop may have been buffered from seasonal fluctuations, however real, in the type or abundance of food or the availability of water. They exploited an unusually large range, and water was permanently available from cattle troughs throughout the range.

Because of the lack of an obvious impact of season on activity budgets, analyses in subsequent chapters combine wet and dry season data.

Among food groups, although grasses contributed more to the wet season diet and corms more to the dry season diet, grasses and corms were the most common foods in both seasons.

Chapter 5

PROXIMITY WITHIN THE TROOP

5.1. Introduction

The observation that two animals within a social group are frequently found close to one another may be interpreted in several ways. This proximity may be indicative of a positive relationship between the animals [illegible]), and be associated with high rates of affiliative interaction (grooming, courtship, play, etc: eg. Kummer, 1968). Alternatively, the observed proximity may result when both animals are avoiding other particular members of the social group; spacing within the group may thus come about through attempts to minimize competition, harassment, or aggression (Collins, 1984). Finally, animals may maintain proximity in order to seek or give protection, should the need arise; otherwise interacting very little.

This chapter examines which class of individual may be attractive to or attracted by juvenile baboons, and which individuals are present in the same region of the troop. It will deal with nearest-neighbour and related data, since simple proximity may be indicative of an existing relationship which requires further investigation.

5.2. Methods

During each focal animal sample, three instantaneous scores were taken, separated by fifteen-minute intervals, recording the individual baboon who was closest to the focal juvenile; this baboon was the Nearest Neighbour. Each juvenile, thus, had the opportunity to have 120 Nearest Neighbour records. In practice, the total was slightly less; since on occasions when the juvenile was more than ten metres away from any other baboon, no Nearest Neighbour was scored. For each juvenile subject, the number of times an individual baboon appeared as a neighbour was counted; that score was then expressed as a proportion of the juvenile's total Nearest Neighbour observations.

Nearest Neighbours were categorized according to age-sex class and reproductive state, and the results expressed as the proportion of the juvenile's neighbour scores contributed by that class. This proportion was divided by the expected score; that is, the proportion of that class in the troop, to allow for partner availability (see section 2.3.5. on mean troop composition). The resulting score should be equal to one if a particular class occurred as neighbours in direct proportion to its number in the troop. If greater than one, that class occurred more often than would be expected; if less than one, less often than expected.

To concentrate only on the Nearest Neighbours is to lose other valuable information, such as which individuals are frequently in the vicinity of the subject and could be available, for example, to intercede on the juvenile's behalf in the case of a dispute. In addition, the Nearest Neighbour is only relatively closer to the subject than other baboons within a ten meter radius; as the number of animals within that distance rises, the likelihood of any one neighbour being scored as the Nearest falls. Therefore, to complement the Nearest Neighbour data, Neighbour Scans were taken at the same time. During these scans, I noted the identity of all baboons, (including the Nearest Neighbour), occurring within three distance categories: zero to two metres; two to five metres; and five to ten metres. This resulted in a large number of animals who were present within ten metres at some time, whether or not they were closest to the subject.

In analysing the Neighbour Scan data, for each juvenile subject I counted the number of times another individual appeared in each of the three distance categories. To treat these three scores as equivalent in importance is to ignore the possible significance of greater proximity, and to simply add them together loses this extra information in the two closer distance categories. It seemed desirable to weight the scores from each category before summing them to create one index of proximity (P) for each individual. Various weights produced broadly similar results; however, I decided to adapt a method used by Smuts (1982). I scored the number of times a neighbour appeared in a particular distance category and multiplied the total by a constant.

The constant was the reciprocal of the mid-point of that particular distance category (see Table 5-1).

Distance category in metres	Midpoint of distance category	Reciprocal of midpoint
0 - 2	1	1.0
2 - 5	3.5	0.2857
5 - 10	7.5	0.1333

Table 5-1. Weights used to calculate the index of proximity (P-score).

The sum of the three weighted scores gave the proximity index (P) for that individual neighbour. Although the index is based on an arbitrary decision, this method distinguished most clearly between neighbours; animals who contributed more to the middle or to the most distant category. Table 5-2 shows a worked example.

		Three Fictitious Neighbours					
		A		B		C	
Distance	Weight	actual score	score x weight	actual score	score x weight	actual score	score x weight
1	1.0	10	10	5	5	5	5
2	0.2857	5	1.485	10	2.857	5	1.485
3	0.1333	5	0.667	5	0.667	10	1.333
	P-score =		12.152		8.524		7.818

Table 5-2. Calculating the proximity index (P-score). Although the three fictitious neighbours all appeared as neighbours twenty times, this method differentiates between close and more distant neighbours.

In summary, this analysis concerns two types of proximity information: the record of Nearest Neighbours and their distribution according to age-sex class and the reproductive state of females; and the index of overall proximity, or P-score.

5.3. Results

The sixteen focal juveniles were very similar in the mean number of individuals occurring in each neighbour scan (mean = 4.65, range = 4.27 - 5.23). Individual differences were not attributable to sex (U = 35, n.s.) or to rank (females: r_s = -.52; males: r_s = .08). The total number of individuals who appeared in the neighbour scans at some time was also similar. Of the 137 baboons who were ever present in the troop during this study, 88.1%, on average, were scored as neighbours of each of the juvenile subjects (range = 83.9 - 94.2%). Again, juveniles did not differ significantly in this respect by sex (U = 20, n.s.) or rank (females: r_s = -.32, n.s.; males: r_s = .37, n.s.). This mixing of the troop suggests that no baboon was absolutely excluded from being scored as a neighbour. Likewise, the large size of EC troop meant that a juvenile's opportunities to be close to particular classes of baboon were not limited by demographic factors, as can occur in smaller social units (S. Altmann, 1979; J. Altmann, 1980).

5.3.1. Age-sex class of Nearest Neighbour

Figure 5-1 shows the median class score for each age-sex class of Nearest Neighbour. Within each sex, the juveniles were similar in the distributions of age-sex classes among Nearest Neighbours (males: $W = .71$, $p < .001$; females: $W = .66$, $p < .001$), and there were significant differences between classes in their representation (males: $X_r^2 = 39.25$, $df = 7$, $p < .001$; females: $X_r^2 = 37.32$, $df = 7$, $p < .001$).

For both male and female subjects, own-sex peers are present as Nearest Neighbours most often, and with a considerably higher proportion of scores than their proportion in the troop.

Concerning peers of the opposite sex, juvenile males show a higher than expected median female neighbour score, although the converse is not true. Despite this difference in median scores, ranges show considerable overlap; opposite-sex neighbours were present roughly in proportion to their number in the troop.

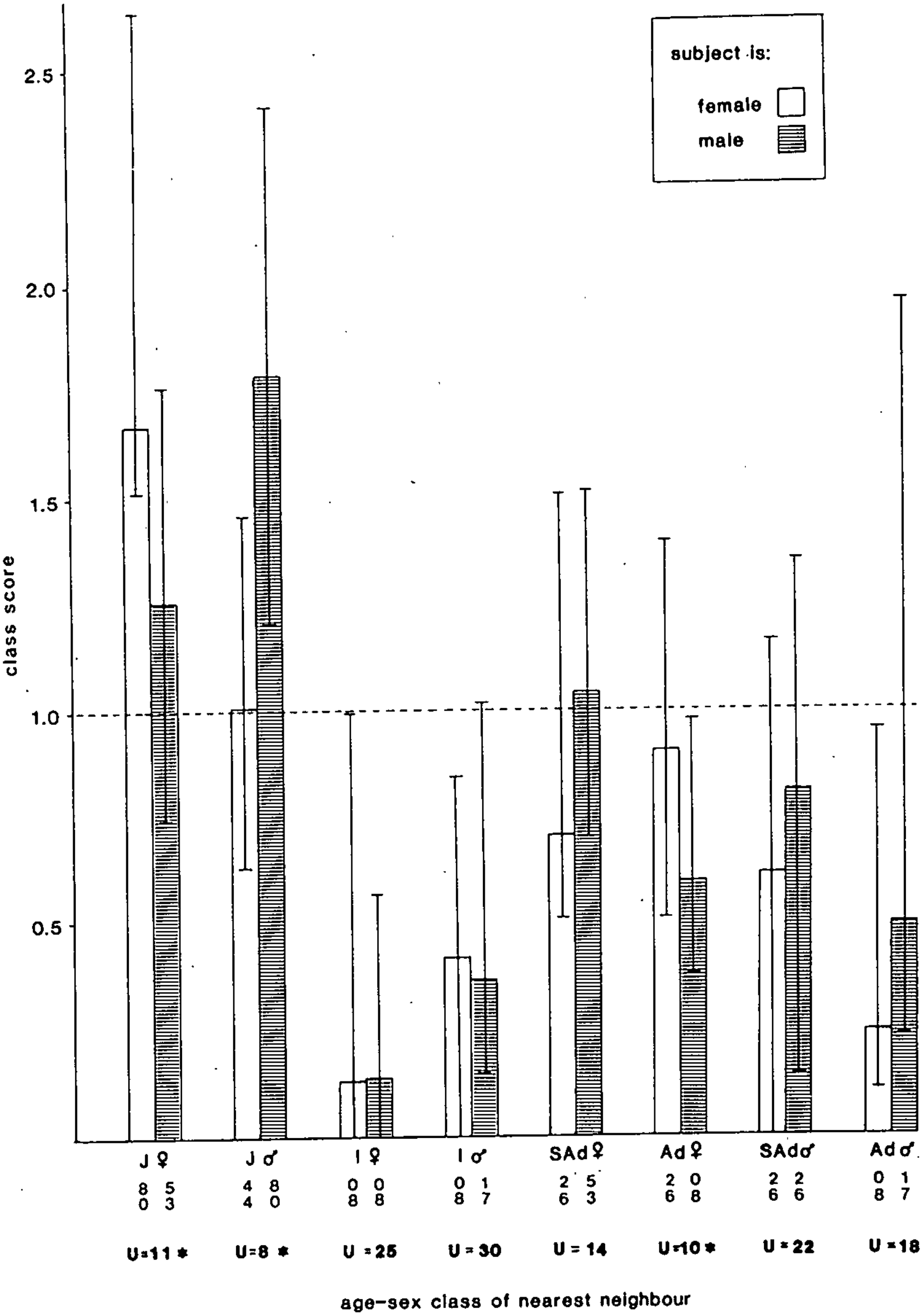


Figure 5-1. The age-sex class distribution of Nearest Neighbours for female and male juvenile subjects. The median class score is calculated to allow for the availability of that class in the troop. The dotted horizontal line at 1.0 represents the point at which that class would be represented in direct proportion to its number in the troop; underneath each column are the numbers of individual scores which fall above and below this line. Medians and ranges are shown.

The low scores of both infant classes as neighbours is marked. This may indicate that juveniles are not attracted to or attractive to infants, but this conclusion is not consistent with results presented later concerning lactating females. It is more likely that the low infant scores are an artefact of the study design: when an adult female carrying her infant was scored as the Nearest Neighbour, the infant was not considered to be an independent neighbour. Depressed infant scores would result.

Both sexes of juvenile tended to have adult and sub-adult neighbours less often than expected, with one exception discussed below.

There are some significant male-female differences in the age-sex class of neighbours. Juvenile males had male neighbours of all classes (except infant) at higher scores than did juvenile females, and this difference is significant when the neighbour class is juvenile male.

Likewise, juvenile females show significantly higher juvenile female class scores than males. However, juvenile females did not consistently show the same own-sex preference in neighbours. Although they had juvenile and adult females as neighbours significantly more often than the males, the juvenile male subjects had sub-adult female neighbours more often than did the females, a difference which is nearly significant ($p < .07$).

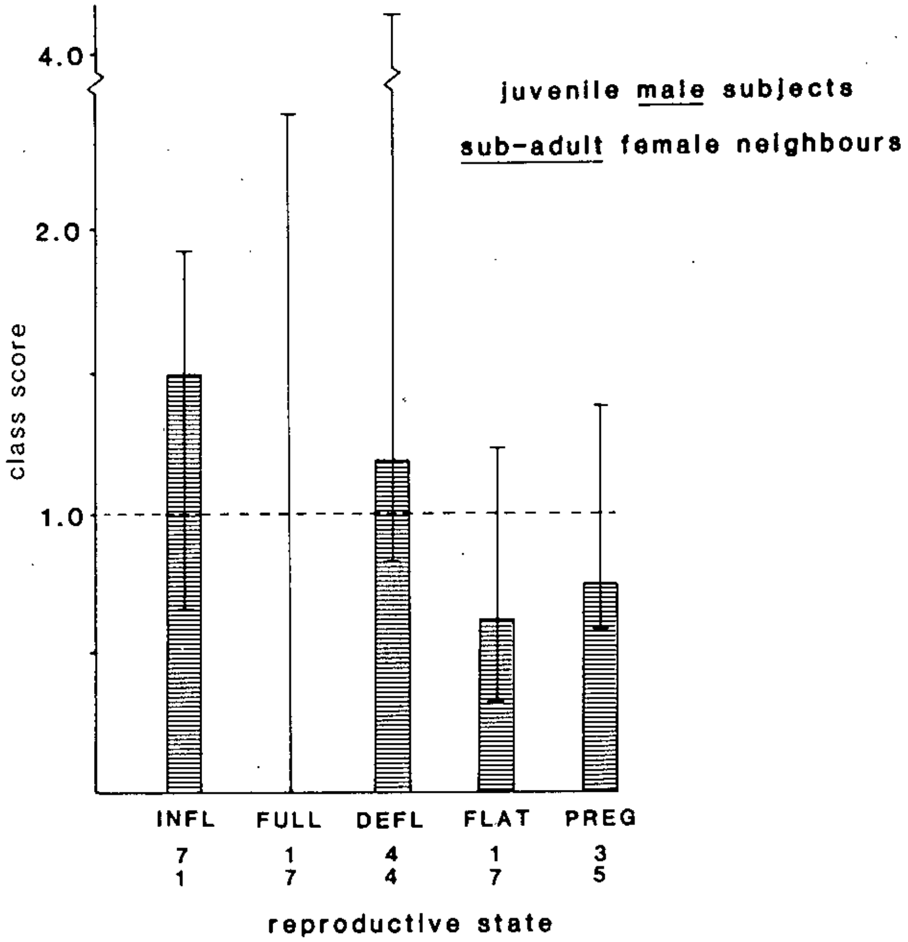
This sex difference in association with the two older female classes can be better understood when the reproductive state of the female neighbour is considered.

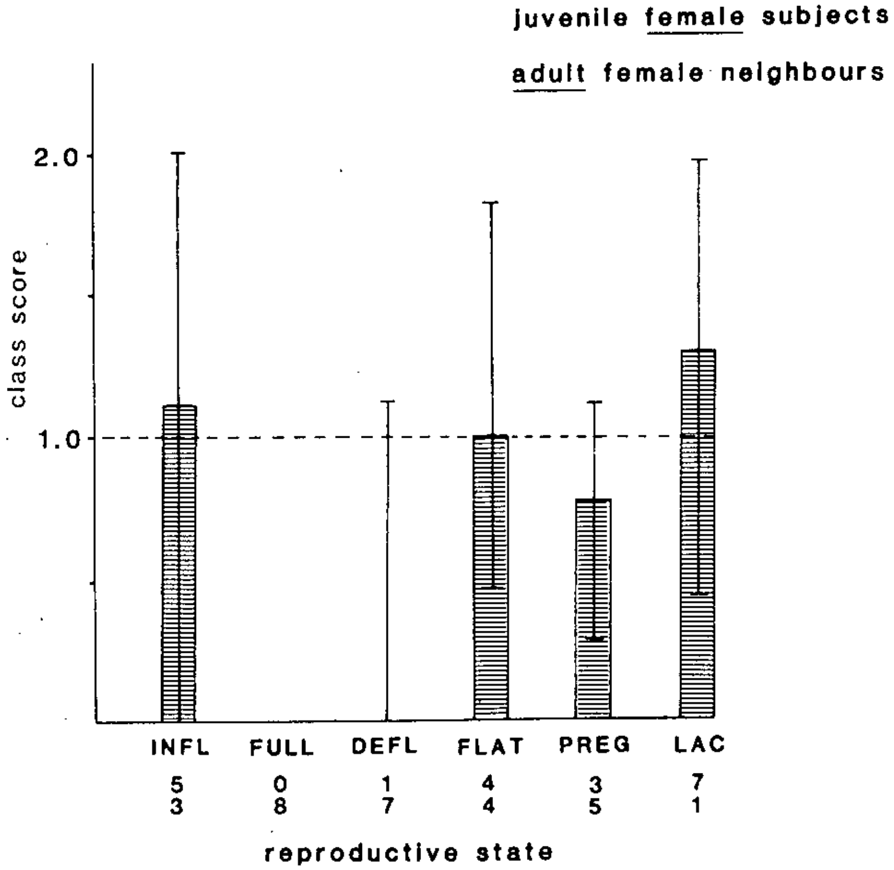
Within each sex, female and male juveniles were broadly similar with reference to the reproductive state of mature female neighbours (juvenile females with sub-adult females: $W = .40$, $p < .01$; juvenile females with adult females: $W = .48$, $p < .01$; juvenile males with sub-adult females: $W = .40$, $p < .01$; juvenile males with adult females: $W = .34$, $p < .05$). Juvenile female subjects' scores were random with respect to the neighbour's reproductive state when the neighbour-class was sub-adult female ($X_r^2 = 3.3$, df = 4, n.s.); whereas the eight juvenile females were significantly non-random with respect to the reproductive state of their adult female neighbours ($X_r^2 = 19.196$, df = 5, $p < .01$).

Conversely, juvenile males showed a significant pattern with respect to the reproductive state of their female neighbours when the neighbour class was sub-adult female ($X_r^2 = 12.775$, df = 4, $p < .02$). With adult female neighbours, the individuals' scores did not differ significantly across different reproductive states ($X_r^2 = 11.008$, df = 5, $p < .1$).

Because of these differences, Figure 5-2 represents only the two class-score distributions in which there were significant differences in the reproductive state of the female neighbour: juvenile males with sub-adult female neighbours, and juvenile females with adult female neighbours. In both diagrams, there are higher than expected scores in certain female reproductive states, but as there was considerable individual variability, these scores must be interpreted with caution. Juvenile males tend to have sub-adult females as Nearest Neighbours more often than expected in the inflating

Figure 5-2. The reproductive state of female Nearest Neighbours. Median and ranges are shown. This figure depicts only the two cases for which there were significant differences in the reproductive state of the female neighbour: juvenile males with sub-adult female Neighbours (top), and juvenile females with adult female neighbours (bottom). Once again, the horizontal dotted line represents the point at which females in that reproductive state occurred in direct proportion to their number in the troop. Underneath each column are the numbers of individual scores which fall above and below this line.


juvenile male subjects
sub-adult female neighbours
4.0
2.0
1.0
class score
INFL
FULL
DEFL
FLAT
PREG
7
1
1
7
4
4
1
7
3
5
reproductive state


juvenile female subjects
adult female neighbours
2.0
1.0
class score
INFL
FULL
DEFL
FLAT
PREG
LAC
5
3
0
8
1
7
4
4
3
5
7
1
reproductive state

state. Median scores during the flat state are lower than expected, and there are virtually no sub-adult scores during the fully swollen phase. Median scores during the deflating and pregnant states are roughly as expected.

Juvenile females have adult females as neighbours more than expected when the female is lactating.. Adult females occur as neighbours during the flat, inflating and pregnant states at roughly the level expected for their proportion in the troop, but median scores during the fully swollen and deflating states are zero.

5.3.2. Discussion

When the demographic structure and size of the group allows, juveniles' attraction to like-sexed peers emerges in many contexts; this will be discussed further in 5.3.4.

Cheney (1976) surmised that proximity could be an indication of juvenile attraction to others, even when the juvenile could not gain access to those others. She cited the example of juvenile females who stayed in the vicinity of adult females with infants, apparently waiting for an opportunity to interact, but excluded from interaction by others of higher rank.

By the same token, these age-sex class results may reflect attractions between juveniles and members of particular classes which may or may not be expressed in actual social interaction.

Juvenile males' proximity to sub-adult female neighbours suggests sexual attraction. Contrary to DeVore's conclusions (1965), immature males show the full range of male sexual behaviour (Ransom, 1971; Cheney,1978a). Baboon males are sexually precocious; by their second year, they are able to copulate (Ransom and Rowell, 1972) and ejaculate is first produced at between two and one half and three years of age (Owens, 1976). Regardless of whether the males are yet fertile (J. Altmann <u>et</u>. <u>al</u>., 1977), the likelihood of conception is extremely low for social reasons. Juvenile males discriminated between the reproductive states of sub-adult females, who become prominent as neighbours during one sexually receptive stage of the cycle. This inflating stage precedes [illegible] the fully swollen stage which coincides with ovulation. The high scores just before [illegible] the fertile stage suggest that the juvenile males are excluded or inhibited from remaining close to the females, perhaps by the presence of older, more competitively able males. Adult males consort with females at this stage (DeVore, 1965; Hausfater, 1975; Packer, 1979b), then tend to abandon the consortship at the onset of deflation (Saayman, 1970; Seyfarth, 1978a).

Juvenile males' neighbour scores with <u>adult</u> females were also highest when the female was cycling, specifically during the inflating stage, but the individual male scores are too heterogeneous to permit general conclusions. The absence of a significant pattern may not indicate lack of attraction, but instead reflect the more active interest of older males in more mature females. Sub-adult females appear to be less attractive to adult males (Ransom, 1971; K. Rasmussen, 1981), and are consorted less often (Nash, 1973; Packer, 1977); this may mean that the younger males and sub-adult females have more opportunity to gain proximity (Cheney, 1978a).

Turning to juvenile females, it is possible that their apparent discrimination according to the reproductive state of their adult female neighbours is a by-product of an attraction to infants (DeVore, 1963; Ransom and Rowell, 1971; Cheney, 1978a). Their associations with sub-adult females, who have no infants, are unaffected by the sub-adult's reproductive state.

5.3.3. Individual Neighbours

The P-scores are an overall index of proximity, based on the neighbour scan data. For each of the sixteen juveniles, the entire troop was ranked in descending order of P-scores. Figure 5-3 shows, for each subject, its twenty-five most prominent individual neighbours over the entire study.

One result is striking. A family member was the most prominent single neighbour in the troop, regardless of age-sex class, in twelve out of sixteen cases (see Table 5-3). The focal juvenile's mother, if living, was the most important adult female neighbour in every case. Brothers and sisters, if they existed, were among the most prominent

Figure 5-3. The twenty-five most prominent neighbours of each juvenile subject, as determined by their P-scores. The rows of symbols represent individual troop members, and the black vertical bars indicate the magnitude of the P-score. Very high P-scores are capped by a horizontal bar. A black arrow indicates the subject; an open arrow indicates the mother or siblings.

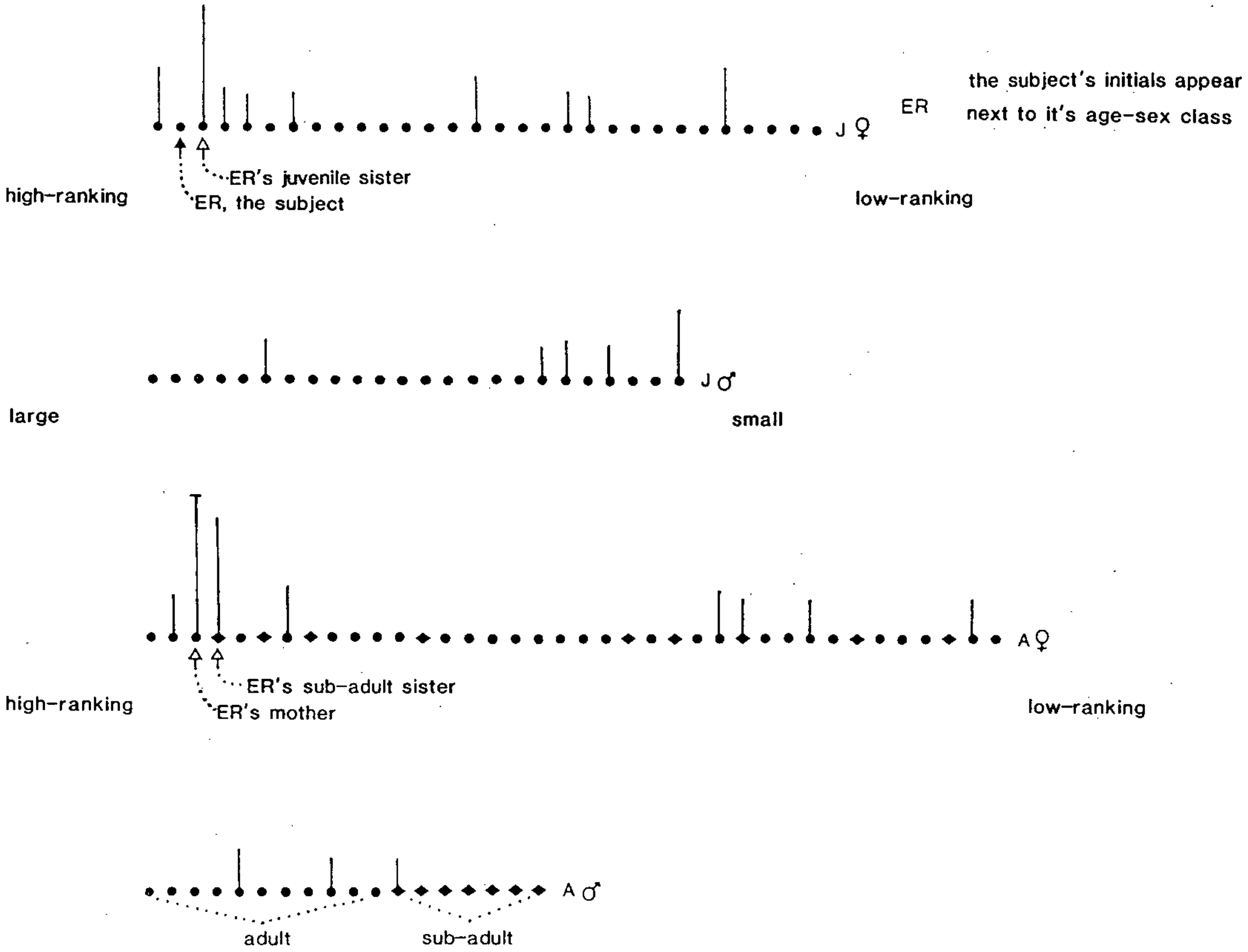
In the first row are juvenile females, arranged from left to right in descending order of maternal rank, with the exception of GT, who is placed in a lower position than her dead mother's rank.

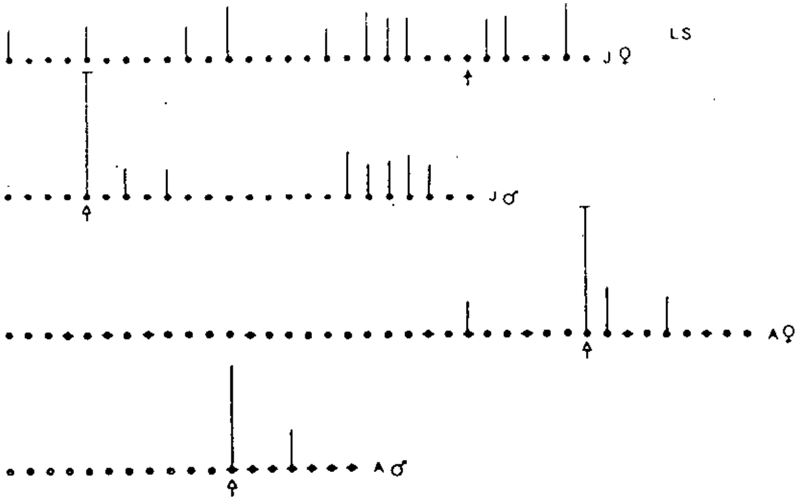
The second row shows the juvenile males, in descending order of size from left to right.

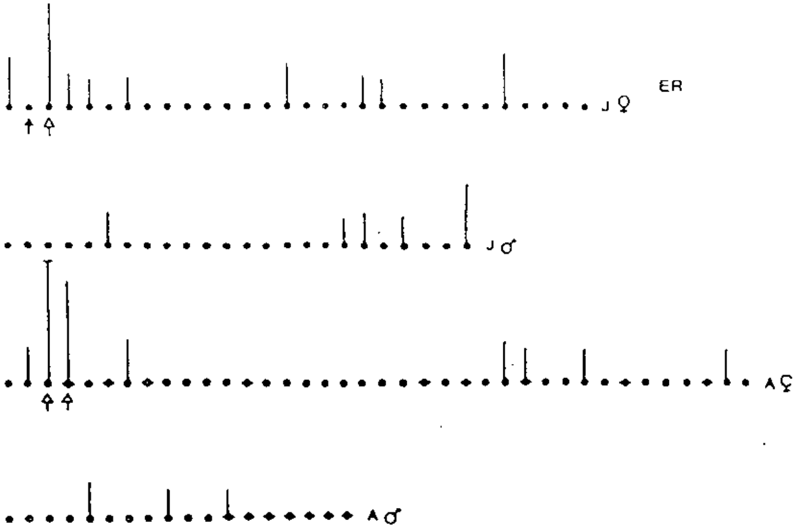
Adult and sub-adult females are shown in the third row, in descending order of agonistic rank from left to right; adults are represented by dots, sub-adults by diamonds.

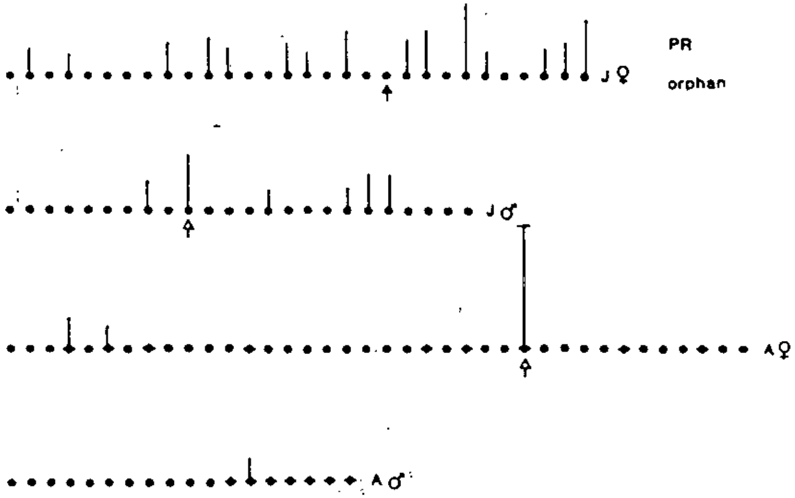
The final row depicts the adult and sub-adult males, each in an abecedarian sequence; once again, adults are indicated by dots and sub-adults by diamonds.

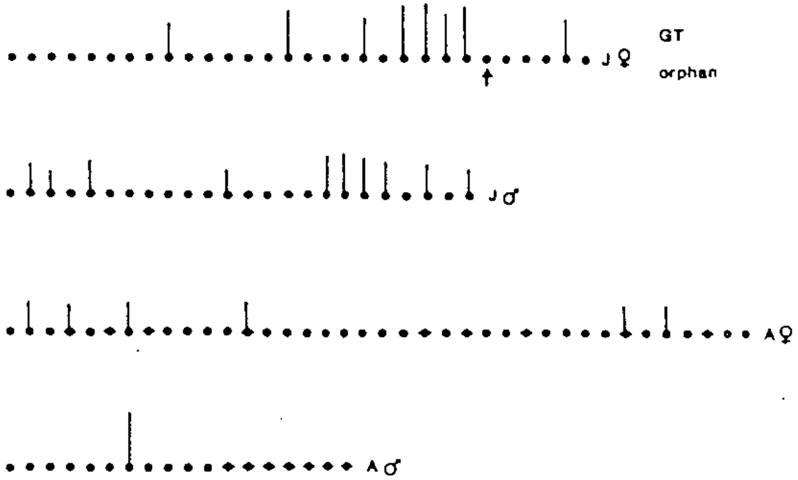
The first diagram, ER, is labelled in greater detail, as a guide. Appendix 4 gives the identities of all the baboons represented by the symbols.

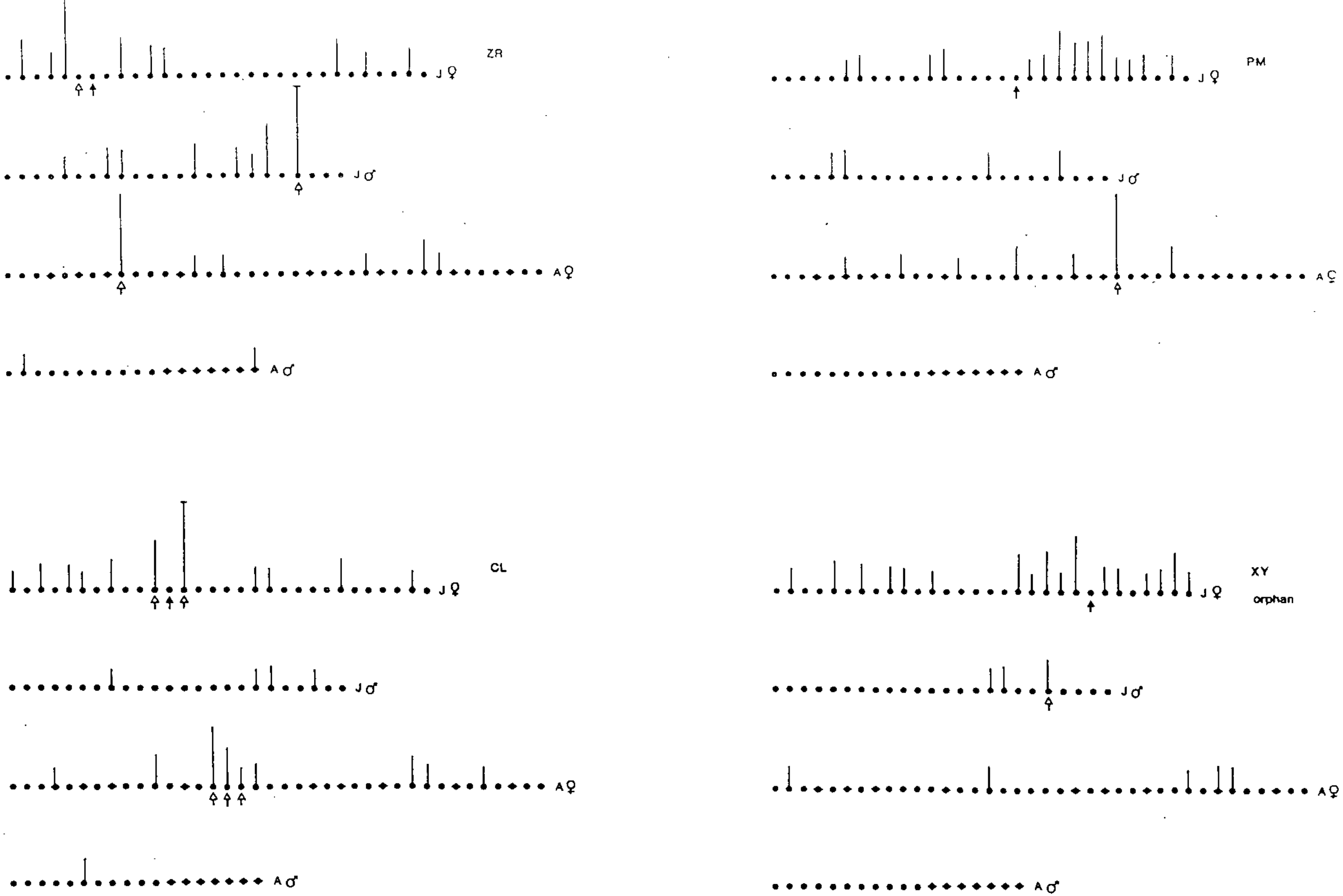

the subject's initials appear
next to it's age-sex class
ER
J ♀
ER's juvenile sister
high-ranking
ER, the subject
low-ranking
J ♂
large
small
A ♀
ER's sub-adult sister
high-ranking
ER's mother
low-ranking
A ♂
adult
sub-adult

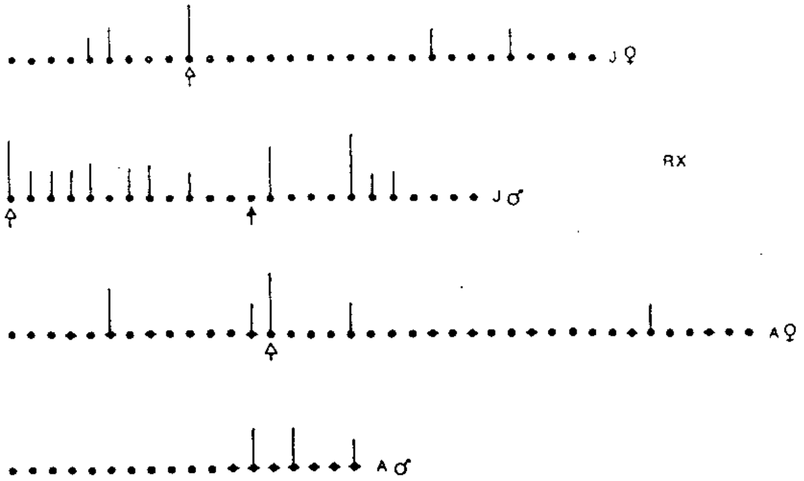

J♀
LS
J♂
A♀
A♂

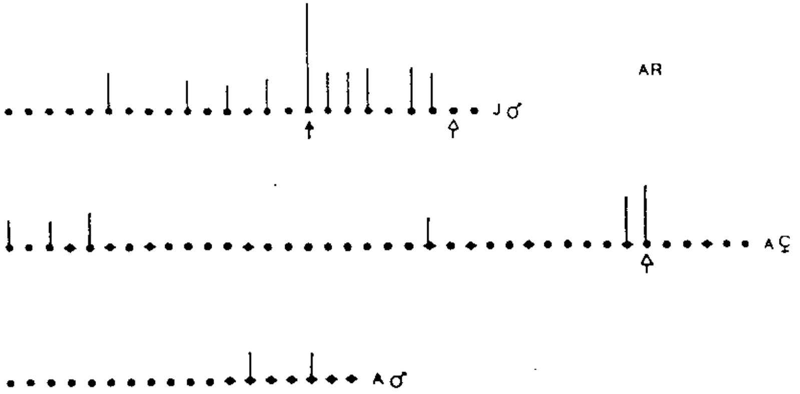

J♀
ER
J♂
A♀
A♂

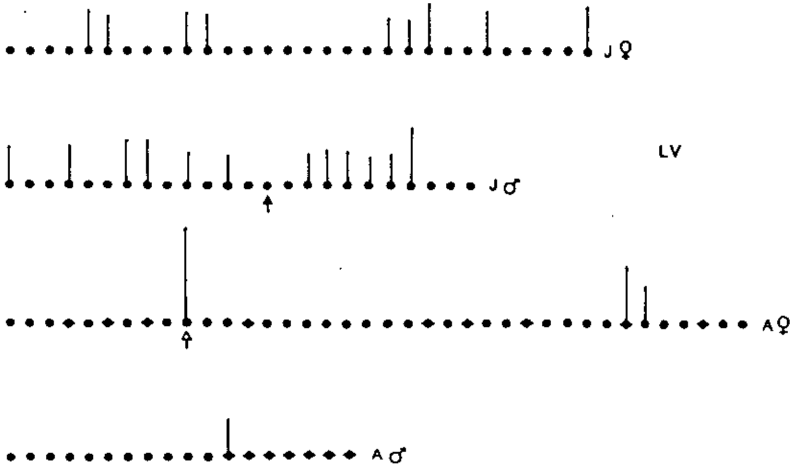

J♀
PR
orphan
J♂
A♀
A♂

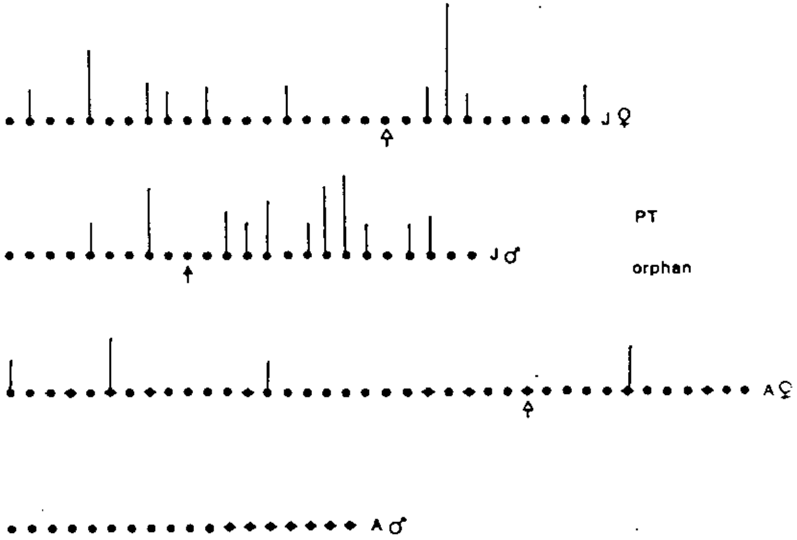

J♀
GT
orphan
J♂
A♀
A♂

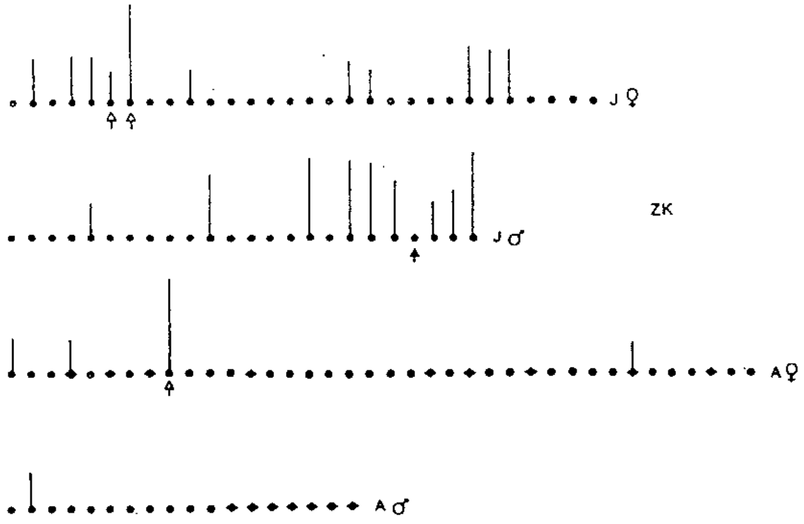

ZR
J♀
J♂
A♀
A♂
PM
J♀
J♂
A♀
A♂
CL
J♀
J♂
A♀
A♂
XY
orphan
J♀
J♂
A♀
A♂

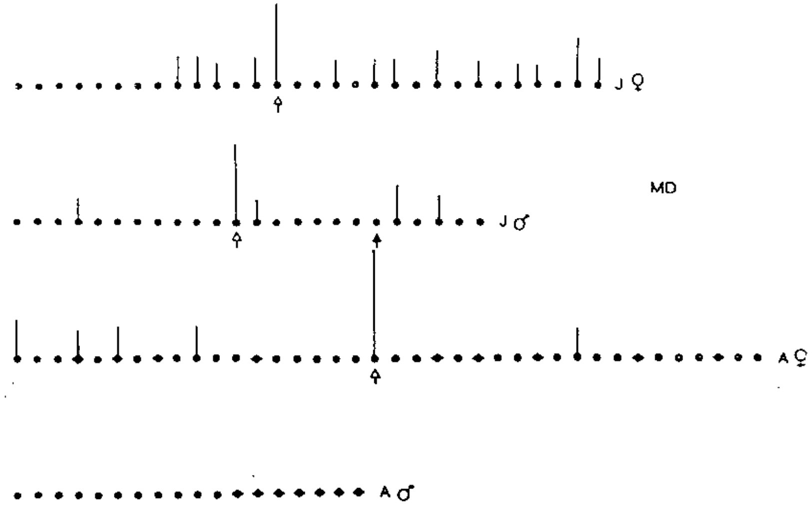

J♀
RX
J♂
A♀
A♂

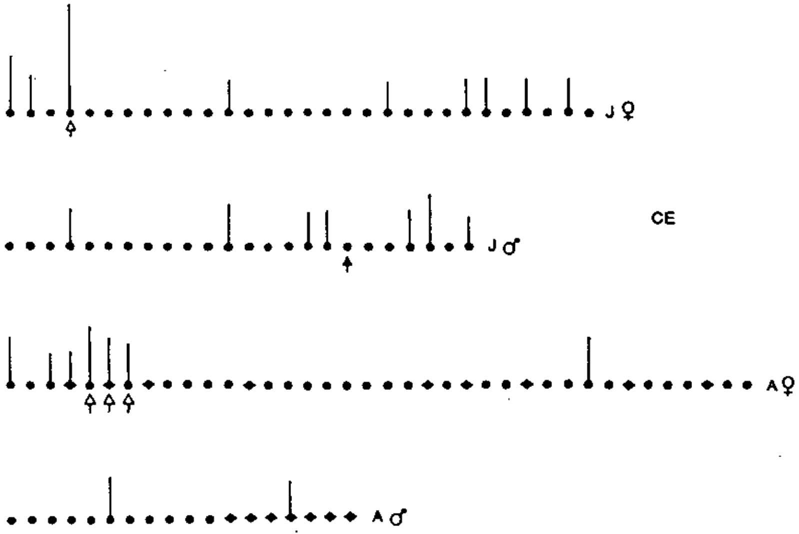

J♀
AR
J♂
A♀
A♂

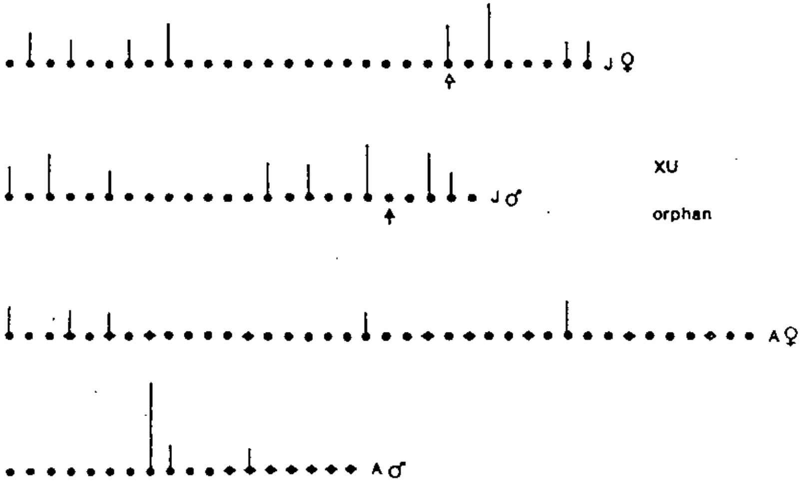

J♀
LV
J♂
A♀
A♂


J♀
PT
orphan
J♂
A♀
A♂


J♀
ZK
J♂
A♀
A♂


J♀
MD
J♂
A♀
A♂


J♀
CE
J♂
A♀
A♂


J♀
XU
orphan
J♂
A♀
A♂

Subject	Mother	Sister(s)	Brother(s)
Cicily	1	1*, 2, 1	-
Euphoria	1*	1, 2	-
Galatea	-	-	-
Lisa	1	-	1*, 2
Pomona	1*	-	-
Pyrrha	-	1*	1
Xylia	-	-	1
Zora	1	19, (1)	1*
Archimedes	1	-	1*
Caesar	1	1*, 1, 4	-
Livy	1*	-	-
Midas	1*	1	1
Plutarch	-	1*, 3	-
Rex	1	1	2
Xuthus	-	3	
Zeke	1	1*, 11, (6)	-

Table 5-3. The prominence of family members as neighbours, based on ranked P-scores within each age-sex class. A * indicates that family member was also the most prominent neighbour of any age-sex class. Brackets enclose the scores of one juvenile female, the putative cousin of siblings Zeke and Zora. Her scores were more typical of a sister than the scores of the putative sister.

neighbours in their age-sex classes. (Two exceptions were Zora and Zeke, sibling subjects whose putative sister ranked nineteenth and eleventh as a neighbour, respectively, among members of her age-sex class: juvenile female. Their putative cousin, much closer in age, was a more prominent juvenile female neighbour, ranking first and sixth, respectively.) This means that, whether or not family members interacted frequently, they were very often in the same region of the troop.

Prominent neighbours among non-family members did not follow clear-cut patterns. There was a tendency for juvenile female subjects to have neighbours from their own class whose maternal rank was relatively close to their own. However, even low-ranking PM, who shows this pattern quite clearly, still had several prominent high-ranking neighbours. When neighbours are re-arranged according to age, patterns of association vary even more, with both old and young females in proximity as neighbours.

Juvenile females had relatively few individual adult female neighbours. Here, neighbours again tended to be clumped in rank for some individuals, such as LS, CL, and ER. This was due to the mother's presence, and that of adjacently-ranked adult females, who could well have been close relatives. By contrast, the orphan GT, with no known relatives in the troop, had fairly low neighbour scores with adult females of very disparate ranks, not only those who shared her own low rank. An attraction of similar-ranked animals to one another does not explain these proximity patterns.

Turning to juvenile males and their own-class neighbours, some subjects had neighbours of similar size, rather than similar maternal rank, the converse of the female pattern. However, though this may apply, for example, in the cases of ZK and CE, there are too many exceptions to generalize.

Patterns of adult female proximity to juvenile males are again dominated by the mother's presence. In some cases, (eg. CE), females of adjacent rank were also prominent neighbours, but this is not a convincing explanation for all adult female scores.

In the previous section, the preference of both male and female juveniles for Nearest Neighbours of their own age-sex class was noted. By examining the twenty-five most prominent neighbours, it can be shown that this is a tendency which increases with age. Table 5-4 shows each subject, and the proportion of his or her juvenile neighbours who were the same sex as the subject. Dividing this proportion by the expected - the proportion of all potential neighbours who were the same sex as the subject - produces a relative proximity index. If this index is greater than one, it indicates that own-sex neighbours were more common than their representation in the troop. The eight older juveniles showed a significantly more pronounced tendency to have own-sex peers as neighbours than did the eight younger juveniles ($U = 9$, $p < .02$).

	Subject	Own-sex Neighbours	Other-sex Neighbours	Proportion Own-sex	Preference Index
Young					
Females	GT	8	10	.444	.812
(.547)	PR	14	5	.737	1.347
	LS	11	8	.579	1.059
	ER	9	5	.643	1.176
Males	MD	5	14	.263	.606
(.434)	CE	7	8	.467	1.076
	XU	8	8	.500	1.152
	ZK	8	11	.421	.970
Old					
Females	CL	11	4	.733	1.340
(.547)	PM	13	4	.765	1.399
	XY	16	3	.842	1.539
	ZR	9	8	.529	.967
Males	PT	11	10	.524	1.207
(.434)	LV	12	9	.571	1.316
	AR	10	6	.625	1.440
	RX	12	5	.705	1.624

Table 5-4. Juvenile proximity to [illegible] own-sex neighbours. For each juvenile subject is shown the number of juvenile neighbours within the first twenty-five which are the same sex and the opposite sex as the subject. In the fourth column is the number of same-sex neighbours as a proportion of all juvenile neighbours. The expected values for these scores, being the proportion of own-sex juveniles in the troop, are shown in brackets on the left. The preference index is calculated by dividing the figure in column four by these expecteds; a score greater than one indicates a tendency to have own-sex neighbours.

When juveniles had neighbours of the opposite sex, these baboons tended to be of a similar size to the subject. Figure 5-4 shows all the juveniles arranged according to size, with lines connecting each juvenile subject with his or her three most prominent opposite-sexed neighbours, excluding siblings. There are relatively few neighbours of widely disparate size.

Adult males were conspicuously rare as neighbours. In fact, only seven of the sixteen juveniles had an adult male within the top twenty-five neighbours, as ranked by their P-scores. Initially, this suggests that adult male presence was unlikely to have a major social impact.

On closer examination, however, adult male neighbour scores reflect a long-term pattern. Table 5-5 compares data from this study with the two previous studies of this troop. Nicolson (1982) provides data on seven infants who were later to become the young juvenile subjects in this study. An individual adult male who was present within two meters of the infant for more than 20% of the infant's total male neighbour scores was designated an Associate. This proximity reflected a relationship between the male and the infant, not simply an effect of a relationship between the male and the infant's mother: when scores were compared with the mother present and absent, male scores remained high, or even increased in the mother's absence.

Smuts (1982), studying the troop over the same period, identified special male associates of adult females,

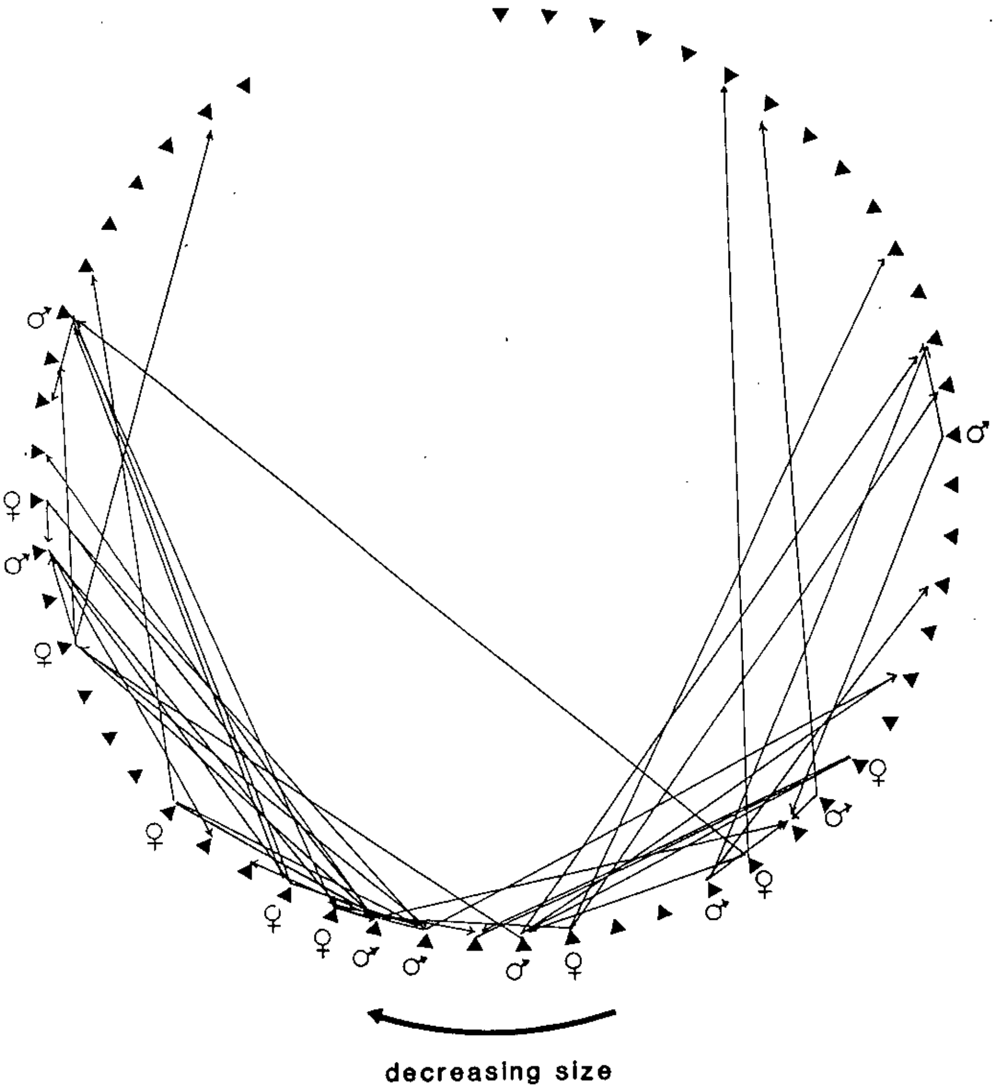


Figure 5-4. The main juvenile subjects' three most prominent opposite-sexed neighbours. All the troop's juveniles are arranged, clockwise, in order of decreasing size. Male and female subjects are indicated, and arrows lead from the juvenile subject to the neighbours.

Juvenile	Mother	Male * Associate in Infancy	Mother's ** Male Associate	Juvenile's*** Male Associate
Cicily	Cybele	-	-	Hector
Euphoria	Eudora	Hector (Virgil) (Agammemnon)	Hector (Virgil) (Agammemnon)	Hector
Galatea	(Antigone)	Sherlock (Agammemnon) (Achilles)	Sherlock (Agammemnon) (Achilles)	Sherlock
Lisa	Louise	(Virgil)	(Virgil)	none
Pomona	Pallas	-	-	none
Pyrrha	(Pandora)	(Virgil)	(Virgil)	none
Xylia	(Xanthe)	-	-	none
Zora	Zena	-	-	Alexander
Archimedes	Artemis	-	-	none
Caesar	Circe	Hector	Hector (Virgil)	Hector
Livy	Leda	-	-	none
Midas	Medea	(Achilles) (Adonis)	(Achilles) (Adonis)	none
Plutarch	(Pandora)	-	-	none
Rex	Rhea	-	-	none
Xuthus	(Xanthe)	Sherlock	Sherlock	Sherlock
Zeke	Zena	-	-	Alexander

Table 5-5. Persistence of adult male association through time. Names in brackets indicate animals who have died or left the troop before my study. A dash indicates no data available.

* Nicolson (1982) studied these juveniles subjects in their infancy, and identified the adult males who contributed more than 20% of the infant's total adult male proximity scores.

** Smuts (1982) identified adult females' important adult male associates based on a proximity index and grooming scores.

*** This study.

determined by a combination of grooming and proximity scores. The match between the infant's and the mother's associates is clear.

Turning to the present study, based on data collected between six and eighteen months later, the consistency is marked. If the adult male associate of infancy was still in the troop, he remained the juvenile's most prominent adult male neighbour, and this independent relationship persisted despite a mother's death. If, on the other hand, the male had died or left the troop, the juvenile had no prominent adult male neighbours at all.

Three juveniles included in this study, but not in the two previous studies, had adult male neighbours. Juvenile female Cicily had adult male Hector as a neighbour; he had been in the troop long enough to have been a potential father. Siblings Zora and Zeke both had adult male Alexander as a neighbour; he had been in the troop long enough to have been a potential father to Zeke, but not to his elder sister.

5.3.4. Discussion

In a series of papers on rhesus monkey mothers and infants, Hinde and his colleagues employed an index which demonstrated which partner in a dyadic relationship was primarily responsible for maintaining proximity. This index has been used to assess changes in a relationship over time (Hinde and Proctor, 1977), to compare individual dyadic relationships at the same stage of development (Hinde and Spencer-Booth, 1971), and to examine preferences for one partner over another (Hinde, 1977). This is clearly a much more subtle method of analysis than those presented here.

In this chapter, I have dwelt on a measure of simple proximity because the size of EC troop was such that many dyads were never observed to interact, let alone interact frequently enough to ascribe responsibility for maintaining proximity. Proximity measures tell us nothing about the quality of relationships; they can only hint at their existence. High proximity should be viewed as a signpost pointing to particular age-sex class and dyadic associations which require further investigation. In this light, several results in this chapter stand out.

Family. It is clear that members of a family are often occupying the same area of the troop, within ten metres of on another. As it was not unusual for the whole troop to be spread across a square kilometer, this close spacing was conspicuous. Family members may be expected to interact frequently, grooming one another, or passively feeding together. Over short distances, family members may be better able to monitor each other's activity and give or solicit aid. Alternatively, the observed pattern might occur as entire families, sharing similar maternally-based rank within the troop, successfully compete for or are excluded from preferred sites. For juveniles, whose social rank may be more labile than that of their mothers, a mother's close presence may help confirm the juvenile's status relative to others. Certainly, the mother is the individual primarily responsible for the high adult female class scores found in the previous section. None of the orphans have as high scores with any individual adult female as other juveniles have with their mothers.

However, there is also frequent proximity with other family members, and this is not only an attraction siblings share for their mother. Following the death of a mother, the tendency for family members to frequent the same area of the troop persists, and it is possible that older siblings fulfill some aspects of a mother's role. The orphan female PR's conspicuously high proximity score with her sub-adult sister suggests this possibility.

<u>Older females</u>. Association patterns outside the immediate family do not all follow consistent patterns, but this is not surprising. Baboons will be in close proximity for many reasons. Thus, the association of juvenile males with sub-adult females during particular reproductive states suggests sexual interest. Juvenile females are known to show great interest in infants (DeVore, 1963; Ransom and Rowell, 1972; Cheney, 1976), and their associations with adult females who are lactating probably reflects this interest.

Cheney (1978a) suggested that adult females of high rank are attractive to juvenile females because of the presumed benefits to the juvenile which could result from a strong social bond with the elder female. Competition from higher-ranking peers, however, can exclude lower-ranking juveniles from interacting with the most attractive (highest-ranking) partners and restrict their interactions to females of similar rank to their own. In this chapter, proximity measures could be expected to reflect the attraction to high rank, even if the juvenile female was prevented from actually interacting with those females. However, there was no evidence for this in these results. In the case of a few subjects, adult female neighbours held ranks close to that of the the juvenile´s mother, but this was by no means general.

Peers. J. Altmann (1980) contrasted the study troop at Amboseli with the majority of long-term primate field studies (such as this one) which are carried out on large, expanding populations which experience low mortality. The effects of the demographic conditions at Amboseli on "an infant´s options" for association were similar to those discussed by Blurton-Jones and Konner (1973) and Draper (1976) on the composition of !Kung children´s play groups. This point was also made by Cheney (1976), whose study of juvenile chacma baboons was carried out on a small troop. Altmann speculated that demographic limits on the range of individuals available as social partners could delay the emergence of sex differences in a small cohort of immatures.

During this study, EC troop contained around forty juveniles, more than the total membership of many baboon troops. From the demographic point of view, immatures in EC troop had a wide "choice" of associates, and patterns of peer association appear to change during the juvenile years.

Among peers of the same sex, similar rank of female neighbours, and similar size of male neighbours seems to characterize the association patterns of some subjects, though not all. Similar size, once again, is a feature of opposite-sexed neighbours. And it is clear that there is a tendency for juveniles to have their own-sexed peers as neighbours, and that this tendency strengthens with age. One might predict, therefore, that bi-sexual juvenile playgroups would consist of animals of roughly the same size, and that mixed play would be more common in the younger juveniles, with single-sex groups more common in older animals.

Adult males. Associations between adult males and lactating females and their infants were noted in early studies (Hall, 1963; DeVore, 1963; Rowell et al., 1968) and were often attributed to the generally protective role the adult male was thought to fulfill. However, Ransom and Ransom (1971) described "special relationships" between particular pairs of baboons, among them, particular males and infants. They concluded that certain preferential associations of males and infants "consisted of the widening of the attachment between the male and female to include the female´s infant at birth" (p. 183). Since then, many authors have observed the repeated association of individual adult males and infants. Where the information was available, a common feature of many of these associations is that the male had usually been resident in the troop for long enough to be a potential father of the infant (Packer, 1980; Collins, in press), and sometimes was judged the probable father (J. Altmann, 1980; Busse and Hamilton, 1981; Stein and Stacey, 1981; Smuts, 1982).

Adult male-infant interactions may be characterized by proximity, care-taking (Ransom and Ranson, 1971), or grooming (J. Altmann, 1980). There are, in addition a variety of behaviours which are alternately described as protective (Busse and Hamilton, 1981) or exploitative of the infant (Packer, 1980); in light of the male's possible kinship with the infant, these interpretations have aroused controversy. The latter behaviours occur in the context of interactions between adult males, during which one male picks up and carries an infant, possibly to protect it from a potentially infanticidal male or, alternatively, "using" the infant to gain a competitive advantage over the other male (a form of "agonistic buffering", Deag and Crook, 1971). In a review of the topic, Collins (in press) suggests that baboons "learn to be cautions of any male who (is) protecting an infant. . . Conversely, the protecting males would learn the increased effectiveness of their agonistic interactions when paired with a black infant". Exploitation and protection could both characterize the relationship.

In EC troop, an adult male's "special relationship" with an adult female was a better predictor of his relationship with her offspring than behavioural estimates of paternity (Smuts, 1982); special bonds were not formed with infants unless a special bond existed with the mother first. Nevertheless, Nicolson (1982) concluded that the adult male-infant bonds developed into relationships which were independent of the relationships those males had with the youngsters' mothers. This point is further strengthened by the persistence of these adult male-juvenile associations into this study, after the mother's death in two cases. As in J. Altmann's study (1978), these males, or "godfathers", as she called them, are likely fathers of the youngsters who were found in close proximity to them. In both Altmann's and Nicolson's studies, the godfather relationship was also characterized by grooming, and caretaking. Smuts found that association with males brought benefits to immatures, both through the male's active intervention on behalf of the immature, and passively, when proximity to the male deterred aggression from others.

If the adult male's presence can benefit a juvenile, it might be expected that these males would become more prominent in their association with orphans. Among my orphaned subjects, Pyrrha had lost her male associate, Virgil, and had no adult male associate during this study. Xylia and Plutarch were too old to have been included in the infant study; neither of them had adult male associates in this study. However, for two young orphans, Xuthus and Galatea, the adult male Sherlock was such a constant neighbour that he ranked first and second in their respective neighbour rankings out of the entire troop.

Results presented here suggest that a male's association with an immature baboon, even if it has been in part exploitative, may outlast the period when the male could benefit from that exploitation. The complement to Collins' explanation may apply: if a baboon learns as an infant that the proximity of a particular male confers protection, the juvenile might maintain proximity with the male in later years. In that case, the male may only be a passive partner in the relationship. If, on the other hand, this is a durable social bond which persists into the juvenile period, it could represent the continued investment by a male in his likely offspring.

Chapter 6

SOCIAL GROOMING

6.1. Introduction

Social grooming is the most conspicuous and time-consuming affiliative behaviour among monkeys. For most age-sex classes of baboon, grooming occupies more time than all other social activities combined.

The distribution of grooming among members of the social group has been used, together with information on proximity, to identify affiliative relationships. Grooming is particularly frequent between members of the same matriline (macaques: Sade, 1965; baboons: Cheney, 1978a); indeed, presenting for grooming is the most reliable measure used to identify mother-daughter pairs when kinship is unknown (Walters, 1981). Females of high rank attract grooming (Seyfarth, 1976; Cheney, 1978a), as do those with young infants (DeVore, 1963; Ransom and Rowell, 1972; Altmann, 1980). Grooming is frequent during sexual consortships (Zuckerman, 1932; Saayman, 1971; Rowell, 1972a; Packer, 1979b), when males groom more actively than usual. But it is also a feature of long-term "special relationships" between males and females outside a sexual context (Smuts, 1982).

Observers of primates will have the intuitive sense that grooming, like play, is something a monkey does because it "likes" it. Sade (1965) acknowledged, "grooming seems to serve a variety of functions, although a common element is the relaxing effect on the participants". However, the functional consequences of grooming for the groomer and the groomed are disputed.

The animal being groomed enjoys immediate benefits, some of which may have consequences for fitness. As dirt and dead skin are picked from the skin surface, ecto-parasites which could carry disease are removed, and wounds are cleaned (Simonds, 1965). Hutchins and Barash (1976), reacting against what they felt to be primatologists' over-emphasis of the social functions of grooming, have stressed these hygienic benefits. They demonstrated that areas of the body which are inaccessible to the individual are those most often groomed by another. Additional benefits may result from the reduction of stress.

The benefits to the groomer, however, whether of an immediate or ultimate nature, are more difficult to identify. This point, and the observed distribution of grooming which favours matrilineal kin, has led many researchers to treat grooming as an altruistic behaviour (Kurland, 1977; Silk, 1982), evolved through kin selection (Wilson, 1975). For this to be the case, not only must the recipient benefit in ways which enhance reproductive success, but the donor of the altruistic act must suffer a cost, also ultimately reflected in reproductive terms (Hamilton, 1964). Although the former is plausible, the latter has not been demonstrated.

The main cost postulated for the groomer is loss of time which could be used more profitably (Dawkins, 1976), specifically in feeding (Silk, 1982). Dunbar and Sharman

(1984) have tested the hypothesis that time is spent grooming at a cost to feeding time. From the activity budgets of eleven populations of baboons, they examined correlations between time spent feeding and social time (95% of which was assumed to be spent grooming). An inverse relationship between the two would support the hypothesis. No significant correlation was found. Instead, feeding time was inversely correlated with time spent resting. They concluded that extra time required for feeding could be drawn from reserve resting time, and that grooming could not be said to have a cost in feeding terms.

Kurland (1977) has put forth additional arguments for the cost of grooming, such as the expenditure of energy by the groomer. However, that cost seems trivial in its ultimate consequences. He also suggests the groomer may suffer from the build-up of hair boluses in the caecum and consequent gastrointestinal pathology. This may be a risk in captive populations when a source of bulk is missing from the diet, but it is unlikely to be an historically important cost.

Rather than regard grooming as an altruistic activity with direct fitness consequences, many researchers have treated it as a behaviour which initiates or maintains social relationships. In long-lived, highly social primates, it is these relationships which may have the most important consequences for the groomer's fitness.

Seyfarth (1983) summarizes a model which was developed to predict the distribution of grooming (Seyfarth, 1977; Cheney, 1977), and has since been extended to a wider range of primate interactions (Seyfarth, Cheney and Hinde, 1978). In this model, an individual attempts to groom animals with whom a strong social relationship will be beneficial: in some cases these will be kin; in some cases, potential sexual partners; or in some cases, animals of higher rank who may reciprocate by forming alliances with the groomer. Whenever the desirable grooming parter is widely attractive to many other individuals, as in the last case, competition will restrict the access of lower-ranking groomers. These animals will groom the highest-ranking animals available to them. Thus, the observed pattern of grooming will be confined largely to similarly-ranked animals, who will often be close relatives.

The pattern of grooming predicted resembles that which would be expected as a result of kin selection; but the value of the model is that it also accomodates the many exceptions to kin-grooming which are observed. The attractiveness of high rank and the attractiveness of kin are not mutually exclusive explanations for the distribution of grooming; the emphasis is on the possible benefits the groomer might gain from social relationships with others.

The analysis which follows concentrates first on sex and rank differences in juvenile participation in grooming. Next, the distribution of grooming is analysed, and some features are discussed which may make a grooming partner "attractive". Finally, it has been suggested that individuals who receive grooming might reciprocate by forming aggressive alliances with their groomers. Patterns of alliance formation are briefly compared with patterns of grooming.

6.2. Methods

Information on grooming was drawn from both *ad libitum* and focal-animal data. While taking the daily census of the troop or searching for juvenile subjects, I noted every pair of grooming baboons and the direction of the grooming. As I could not assume that all animals in the troop were equally visible, this data is used to examine the identity of grooming pairs, and not to calculate the frequency of interaction. Nevertheless, although individuals are not equally conspicuous, grooming itself is a conspicuous activity of long duration which was easy to notice as I moved around the troop. Therefore, it seemed likely that if I observed a particular pair of baboons grooming together often, this observation did actually reflect a high frequency of grooming for that pair. *Ad libitum* data may also indicate the prevalent direction of grooming in any pair.

During focal-animal samples social grooming was one category of activity recorded on the minute (instantaneous sampling). From these data, the activity budgets were constructed (Chapter 4), making it possible to compare the proportion of time juvenile subjects devoted to grooming.

Using only this measurement of time, it is not possible to distinguish, for example, between animals who groomed only a few individuals for long periods and those who briefly groomed many others. Greater detail of grooming interactions was available in the information recorded during the minute (continuous sampling) during focal animal samples; from these data, each episode of grooming, or grooming bout, could be extracted.

In this study, a grooming bout commenced when one baboon began grooming another, and ended when both individuals switched to another activity. During an interaction, all grooming might be performed by one partner, or the two animals might repeatedly alternate roles as groomer and groomee ("reciprocal grooming", Sparks, 1967); either case counted as a single grooming bout. Solicitations for grooming (Rowell, 1972b), which often initiate grooming or a change of grooming roles, were included in the bout. Events which briefly interrupted grooming - a mild alarm, the approach of another animal - were not scored as terminating the bout, provided grooming was resumed immediately.

The bouts were analyzed in various ways. Rates of interaction express the number of bouts per unit time (in this case, per half-hour sample). Separate rates of giving and receiving grooming were calculated by asking in how many bouts did the subject groom another; and in how many bouts was the subject groomed? If reciprocal grooming occurred within one bout, that bout would be counted in both totals. For this reason, the sum of the rates at which grooming was given and received would exceed the total rate of grooming interactions actually observed.

Mutual grooming (Sparks, 1967), in which two animals simultaneously groom one another was never observed. Grooming bouts were almost always dyadic; the occasional triadic bout always took the form of two baboons simultaneously grooming a third. For purposes of analysis, these were regarded as two dyadic bouts.

6.3. Rates of interaction

6.3.1. Results

Although both sexes participated in grooming, it was more a female than a male activity, as it is for adults (baboons: Bolwig, 1959; Washburn and DeVore, 1961; macaques: Sade, 1965; Lindburg, 1973). In Chapter 4 (Activity Budgets), grooming emerged as the only activity in which the sexes differed; females spent a significantly higher proportion of their time involved in grooming ($U = 5$, $p < .01$). To put this into perspective, all eight juvenile females spent more time in grooming interactions than in all other social activities combined ($T = 0$, $p < .01$). For all but one of the eight male subjects, the reverse was true ($T = 4$, $p < .05$).

A female's greater overall participation in grooming was entirely due to her grooming of others (see Figure 6-1). When rates of grooming interaction are examined, females and males were groomed at similar rates. However, females groomed others at significantly higher rates than did males

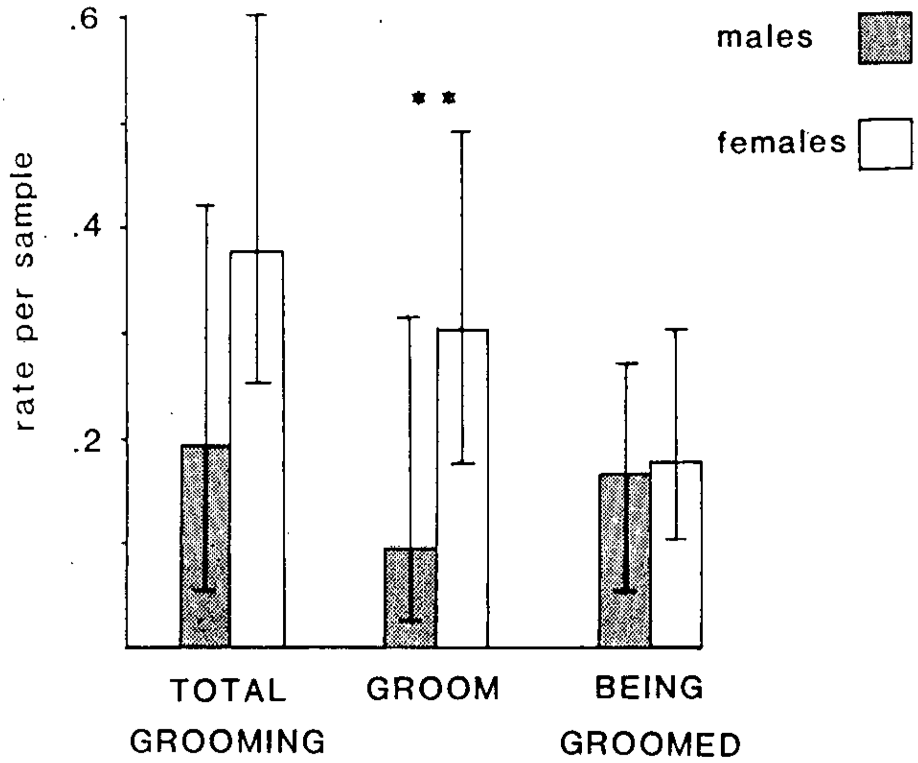


Figure 6-1. Rates of juvenile male and female grooming. Medians and ranges are shown.

(U = 4, $p < .01$). All females groomed others more than they were groomed themselves (T = 0, $p < .01$); for seven of the eight males, the reverse was true (T = 4, $p < .05$).

These patterns of male-female differences in grooming are similar, whether one looks at rates of grooming interactions, or at the proportion of time spent grooming and being groomed. There was an exception, however, which points to sex differences in patterns of grooming: the relationship between social rank and grooming behaviour differed according to which of these measures was used.

All correlations between high rank and measures of grooming interaction were positive (see Table 6-1). That is, for both sexes, there was some tendency for high-ranking animals to both groom and be groomed more than low ranking, whether the measurement is the rate at which the behaviours occur, or the proportion of the animal's time they occupy. However, only two of the correlations are significant, and males and females differed in the aspects of grooming which were influenced by rank. High-ranking males spent a greater proportion of their time grooming others than did low-ranking males - but the number of interactions was not significantly greater. In contrast, high-ranking females were groomed a significantly greater number of times than low-ranking, but they did not spend more time being groomed than did low-ranking females.

	Interaction Rate	Proportion of Time
Male rank correlated with:		
Grooming others	.45	.84 **
Being groomed	.11	.58
Female rank correlated with:		
Grooming others	.67	.41
Being groomed	.75 *	.50

Table 6-1. Spearman rank order correlations between juvenile rank and different measures of grooming. (In this table, two stars - ** - indicate significance at the $p < .02$ level.)

Maternal rank did not affect any measure of male grooming, nor did size affect any measure of female grooming.

6.3.2. Discussion

The results on participation in grooming interactions generally confirm the findings of other studies. They show that grooming behaviour, and the grooming of others in particular, is primarily a female activity. It has been suggested that grooming occupies more time than is necessary for its hygienic function, and has acquired an additional importance in initiating and maintaining relationships. If so, juvenile females, who will remain in the troop of their birth throughout life, have more to gain by investing in relationships with fellow troop members.

Males, by contrast, will emigrate from the troop. Grooming members of the natal troop cannot contribute directly to the strengthening of long-term relationships, as it can for females. The males will form their adult relationships with a completely new set of partners. Although skills used in establishing these adult relationships may be shaped in the course of the male's development in his natal troop, research to demonstrate this is yet to be done.

Concerning the relationship between the amount of grooming behaviour and high rank, the correlations are all positive. However, only two are significant. Males of higher rank (that is, older males) were groomers more often. Because rank relative to their peers was associated with size and age, it is not clear whether older males were competing more effectively with their smaller peers for opportunities to groom. It is more likely that grooming others is one behaviour by which older males and cycling sub-adult females maintained contact.

Among females high rank was also associated with greater amounts of grooming behaviour. But here, it was the role as the groomed partner in the interaction which was significantly correlated with rank. High-ranking females, regardless of age, attracted more grooming from others.

The males who groomed more did so in absolute terms - a greater proportion of their time was devoted to grooming.

But their rate of grooming interactions did not differ significantly from that of smaller males. This suggests that, as males grow older, they devote more of their time to grooming in longer bouts.

By contrast, although high-ranking females were not groomed for any greater length of time, their rate of being groomed was significantly greater than that of lower-ranking females. This suggests that the bouts themselves were shorter, perhaps as a consequence of a greater number of interruptions, evidence which would suggest greater competition for access to high-ranking females (Seyfarth, 1977; Cheney, 1978a).

Participation in grooming by the orphans was consistent with their places in the rank order (see 3.4.). Orphan male PT was the largest juvenile male subject; he out-ranked the others in agonistic interactions, and he also both gave and received the most grooming (highest rates of interaction). The other male orphan, XU, was one of the two smallest males in the sample. He groomed very little, but was groomed slightly more than the other male his size. An orphan male's participation in grooming, then, was most influenced by his size (or age), despite the fact that, in losing his mother, he lost a potentially important grooming partner.

Female orphans also participated in grooming in accordance with their (adjusted) ranks. The three orphan females, PR, XY, and GT (ranked fifth, sixth, and eighth in the sample of eight), were involved in the fewest grooming interactions, as both groomers and recipients. The most interesting of the three was the orphan GT, the daughter of a high-ranking female. GT was comparable in both age and maternal rank with another subject, ER. ER held an agonistic rank in keeping with her mother's rank; she was groomed the greatest number of times, and groomed others third most. By contrast, GT held the lowest agonistic rank, and was both groomed and groomed others less than any juvenile female in the sample. She apparently lost not only high rank, but the attractiveness which seems to go with it.

6.4. The distribution and context of grooming

Seyfarth's model has been chiefly used to examine the influence of dominance rank on the distribution of grooming among female primates (e.g. Fairbanks, 1980; Silk, 1982). But its initial assumptions are more general. It is assumed that an animal is attracted to a grooming partner because of the benefits which could result from a relationship with that partner. Some grooming occurs which does not conform to the pattern of kinship and high-rank, and the presumed benefits are more difficult to assess and more various. It is tempting to regard these grooming interactions as exceptions to the overall pattern. Simonds, however, makes a distinction which is useful in examining these "exceptions". He distinguishes three types of grooming (1974, p. 186):

1) relaxed social grooming between individuals who

already have a strong attractive bond between them.

2) soliciting grooming, which allows individuals to remain close for a temporary activity.

3) tension grooming, which serves to deflect an imminent attack

Although these need not be mutually exclusive categories, the divisions acknowledge a difference between enduring attractions between animals (type one) and transitory affinities or contexts in which grooming occurs (types two and three). That is, there may be qualities of an animal which remain attractive over time (such as close kin relationships or high rank). Alternatively, an animal may be temporarily attractive to others during short periods (such as infancy, or certain phases of the female reproductive cycle). Finally, the immediate social context may draw two animals together to groom (alliances during fights, or troop alarms). These three situations will influence the choice of grooming partner.

The question "who did juveniles groom?" is difficult to answer in a quantitative manner. Grooming occupied a substantial amount of juvenile social time. However, the number of grooming bouts observed per individual was small, and the large troop presented many potential grooming partners. This meant, in terms of analysis, that to groom another individual once was to groom that individual more than expected.

This is further complicated by the variation in the number of focal grooming bouts recorded for each juvenile, which ranged from two to twenty-four. Thus, the juvenile male who participated in only two bouts gave 100% of his grooming to his family. The juvenile female who groomed her family in six of her twenty-four bouts gave "only" 25% of her grooming to family members and the majority to non-family members. It would be misleading to compare individual juveniles for the proportion of grooming with different classes of partner. It is necessary to take a more descriptive approach to the data. Despite the disadvantages to this approach, clear patterns do emerge.

6.4.1. Grooming within the family

Across the troop as a whole, grooming was concentrated within families (close maternal kin) or between animals who were close in maternal rank. Figure 6-2 shows every *ad libitum* observation of grooming between baboons of known or putative maternal rank (adult males and troop members for whom no kinship assignment could be made are excluded). Frequencies of interaction cannot be calculated from these data, yet all pairs who were repeatedly observed grooming together had similar maternal ranks. Within a family, many of the possible pairs of family members were observed grooming at some time. Family dyads comprised 2.4% of the possible dyads in the troop, but they accounted for 531 of the 905 grooming observations, or 58.7%.

The distribution of grooming within EC troop concurs with results reported by others (e.g. Sade, 1965 for macaques; Seyfarth, 1977; Cheney, 1978a for baboons). The pattern resembles that predicted

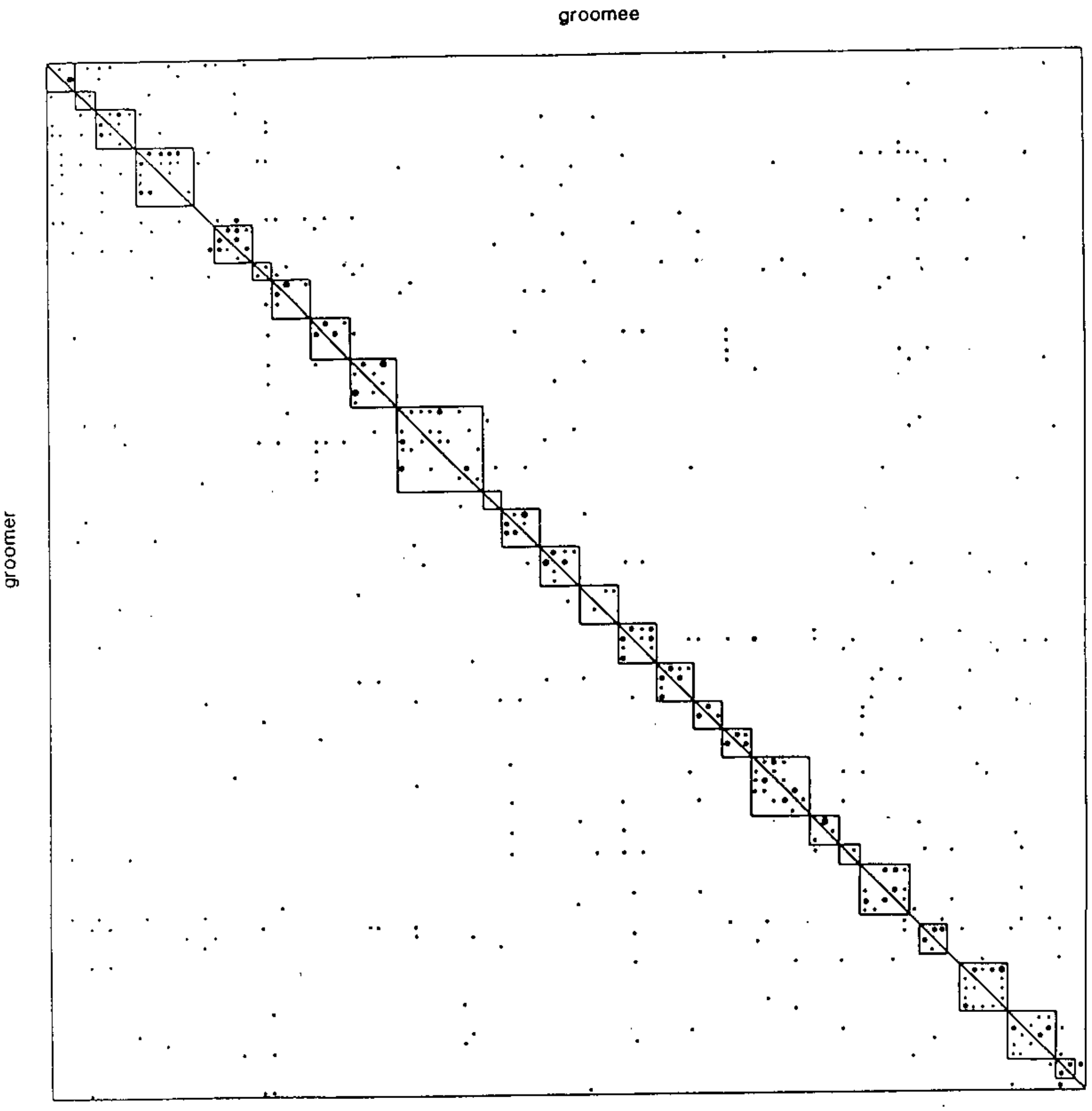


Figure 6-2. Ad libitum grooming observations between baboons of known maternal rank. One-hundred & twenty-six members of the troop are arranged in descending order of maternal rank from top to bottom, as groomers, and from left to right, as recipients of grooming. The squares drawn along the diagonal enclose grooming between members of the same family. The 905 observations are represented by dots: the smallest dot represents one or two observations; the middle-sized dot, three to eight; and the largest dot, nine or more observations of grooming between a pair of animals.

by Seyfarth's model, in which access to attractive, high-ranking grooming partners is prevented by competition and grooming is restricted to those holding similar ranks. Equally, this pattern could be the product of straightforward attractiveness and availability of family members, themselves, as grooming partners.

To what extent did the focal juvenile subjects groom within the family? Family members were clearly prominent as grooming partners. There were forty-two dyads in the troop which comprised a focal juvenile and a family member. In twenty-seven of these dyads, both baboons were observed to groom one another at some time during the study. In twelve pairs, grooming occurred in one direction, but was not seen to be reciprocated. In five pairs, no grooming was observed (two of these pairs involved putative elder siblings, three involved newborn infants). All juveniles were groomed by their mothers, if living; all but one were seen to groom their mother in return.

Data drawn from the focal animal samples give some idea of the amount of grooming exchanged with family members (see Table 6-2). It is necessary, however, to ignore the variation in individual contributions to the data. Less than 3% of all potential grooming dyads in the troop consisted of a juvenile subject and a family member. Yet, these dyads accounted for over one half of juvenile female grooming and over one-third of juvenile male grooming. Likewise, family members accounted for nearly three-quarters, and one half of grooming received by

Subject	Number of dyads in the troop which were:		Juvenile grooms:		Juvenile is groomed by:	
	Family	Non-family	Family	Non-family	Family	Non-family
females						
ER	3.0	113.1	14	3	9	3
ZR	3.1	108.6	6	13	8	3
CL	6.1	105.3	12	7	5	1
PM	1.4	112.0	5	6	6	1
PR	3.0	110.0	6	1	6	0
XY	1.0	113.5	1	9	0	6
LS	3.4	110.3	11	2	8	1
Total	21.0	772.8	55	41	42	15
Family comprises:	2.6% of troop		57.3% of grooming given		73.7% of grooming rec´d	
males						
PT	3.0	112.0	2	12	4	7
RX	3.4	110.4	3	2	3	3
LV	1.2	111.6	0	3	1	7
AR	2.0	111.0	1	0	2	0
CE	4.0	109.2	1	3	3	2
MD	3.0	108.8	1	0	4	2
XU	1.0	112.5	1	0	2	5
ZK	3.5	115.5	3	3	8	1
Total	21.1	891.0	12	23	27	27
Family comprises:	2.3% of troop		34.3% of grooming given		50.0% of grooming rec´d	

Table 6-2. Proportion of potential grooming dyads which include family members and the proportion of focal grooming exchanged with family members. Individual raw scores are shown. Female GT, who had no living family members, is excluded.

juvenile females and males, respectively.

The use of raw scores in these calculations preclude statistical analysis. However, family members are clearly responsible for a much larger proportion of observed grooming than their representation in the troop. The data suggest that a greater share of a female's grooming is limited to her family than is the case for males. However, in both the female and the male totals, grooming by family members exceeds juvenile grooming of family members. It is possible that juvenile grooming of non-family members is not reciprocated, and that the juveniles are more successful in eliciting grooming from their relatives.

6.4.2. Grooming with mature females

In Chapter 5, juvenile proximity to unrelated mature females - sub-adult and adult - was influenced more by the female's reproductive state than by her dominance rank. Juvenile males tended to have sub-adult but not adult females as neighbours, while the reverse was true for juvenile females. These same patterns recur in grooming.

Table 6-3 shows, for all juvenile males in the troop, every observation of grooming between juvenile males and sub-adult females recorded during both ad libitum and focal observations. It is necessary, as in the previous section, to ignore the differences between individuals. Nevertheless, it appears that sub-adult females who are at the inflating stage of their reproductive cycle are over-represented as

	Juvenile grooms female					Female grooms juvenile				
	Sub-adult female reproductive state									
Juvenile	Preg	Infl	Full	Defl	Flat	Preg	Infl	Full	Defl	Flat
IC		1					1			
TB										1
OV		2								
DT							1			
PE					3		1			2
NP		1					1			
CR		2					1			1
ZG		1		1	1		1		1	1
DM										
PT		1			1		1			
DK										1
MR										
RX		2					1			
LV		1					2			
PD										
AR		2					2			
DC		1					2			
CE										
MD										
XU							1			
ZK										
Total	0	14	0	1	5	0	15	0	1	5
% of obs.	0	70	0	5	25	0	71	0	4.8	23.8
% of class	15	43	3	11	28	15	43	3	11	28

Table 6-3. Juvenile male grooming interactions with sub-adult females, listed according to the reproductive state of the female. Reproductive states are abbreviated as follows: Preg (pregnant); Infl (inflating); Full (fully swollen); Defl (deflating); Flat (flat). The total in each column is shown both as a raw score and as a percentage of the total observations. The final row, ´% of class´, refers to the proportion of the study which sub-adult females spent in various reproductive states.
The males are listed in descending order of rank (size).

grooming partners. Inflating females accounted for 70% of interactions in which the juvenile groomed and 71% of those in which the female groomed, although only 43% of sub-adult female time was spent in this state.

Similarly, Table 6-4 shows all juvenile female-adult female grooming. Again, one reproductive state, lactating, is over-represented among the adult females.

In Chapter 5, these female classes emerged as neighbours more often than expected, but it was not possible to determine whether the juvenile or the neighbour was primarily responsible for the proximity. The grooming results, although based on a much smaller amount of data, do suggest which member of the dyad was more active in maintaining contact with the other. The grooming between juvenile males and sub-adult females appears to be reciprocal; females who were inflating predominate, whether they were grooming the males or being groomed. By contrast, it appears that juvenile females were the more active partners in grooming interactions with lactating adult females. The juvenile´s attraction to adult females who were lactating was not reciprocated; it was not reflected in the scores when grooming roles were reversed.

The attractiveness of young infants has been widely remarked upon (DeVore, 1963; [illegible] Cheney, 1978a), and appears to be the basis for juvenile female preferences for grooming lactating females. In addition, juveniles, like older females, have been observed directing their grooming to

	Juvenile grooms female						Female grooms juvenile					
	Adult female reproductive state											
Juvenile	Lac	Preg	Infl	Full	Defl	Flat	Lac	Preg	Infl	Full	Defl	Flat
TC	4	4					1					
ER	2											
CO												
IT	7		1									
VT		1										
ZR	2	1					1	1				
LL	1					1		1				1
CH	3											
RD												
MT					1							
CL	5		1									
CA												
CD						1						
DE	1											
EO	2	1	1									
JL												
PM	3											
IN												
PR												
OP	4											
MS	3											
XY	6						1					
LS								2				
GT	1	2	1									
DN												
SX			1		1				1			
ZA												
PA												
HP	4	1	2			1						
Total	48	10	7	0	2	3	3	4	2	0	0	4
% of obs.	66	13	20				23	31	46			
% of class	44	34	22				44	34	22			

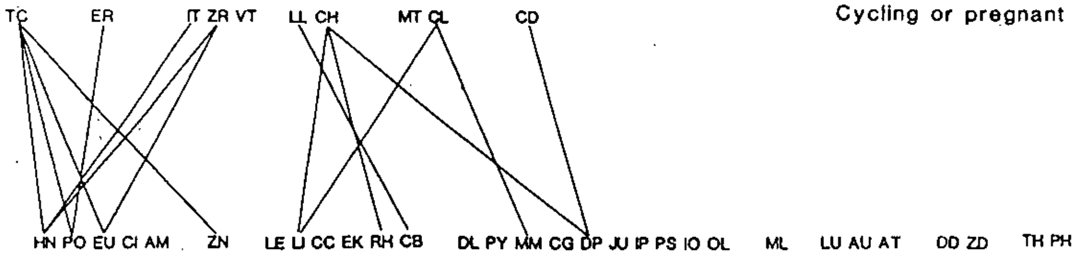
Table 6-4. Juvenile female grooming interactions with adult females, according to the adult's reproductive state. Juveniles are listed in descending order of rank. Details as in Table 6-3, with the addition of 'Lac' (lactating).

adult females of high rank. The interaction of these two attractions, one temporary (the presence of a young infant), the other long-term (high rank), should produce a different distribution of grooming, depending upon the reproductive state of the adult female. Juvenile females would be expected to groom;

1) higher-ranking females with infants (lactating)
2) higher-ranking females without infants (other cycle states)
3) lower-ranking females with infants (lactating)

In other words, there should be a wider range in the ranks of the lactating females groomed by juvenile females than in the ranks of the cycling and pregnant females. Figure 6-3 shows juvenile female grooming of adult females in different cycle states. For clarity, the juveniles are split into higher-ranking and lower-ranking halves. The higher-ranking juveniles groomed higher-ranking adult females who were cycling or pregnant. When the recipient was lactating, the adult females were of much more diverse ranks. Grooming of cycling and pregnant females by lower-ranking juvenile females was directed entirely up-rank, except for that given to one of the Fallen females by two juveniles of the Fallen female group, and the orphan GT. Grooming of lactating females, once again, covered a wider spectrum of rank.

Figure 6-3. The effect of adult female rank and reproductive state on juvenile female grooming. Juveniles (top row) and adults (bottom row) are arranged in descending order of rank, from left to right. For clarity, the juveniles are divided into higher-ranking (a and b) and lower-ranking (c and d) halves. A line leading from the juvenile to the adult represents at least one occasion on which the juvenile groomed the adult.


Cycling or pregnant
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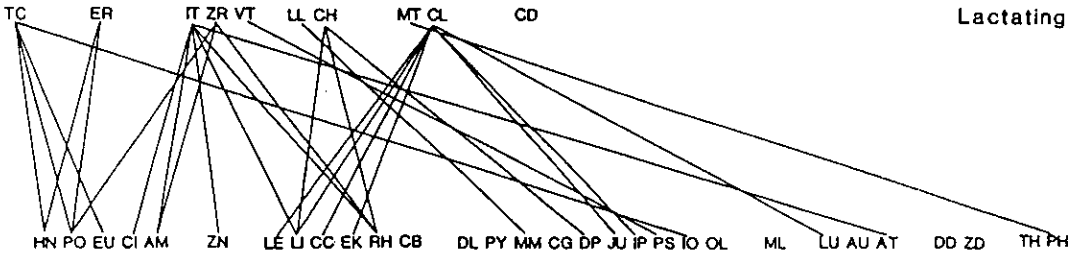
Lactating
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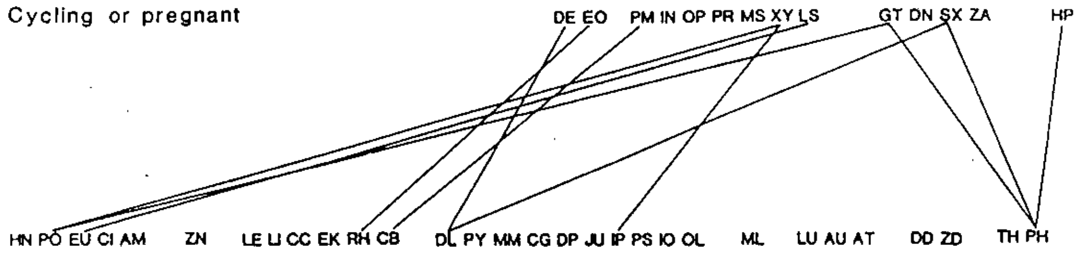
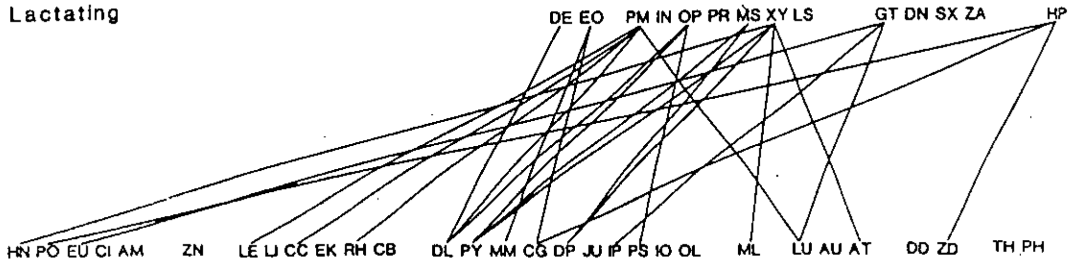
HN PO EU CI AM ZN LE LI CC EK RH CB DL PY MM CG DP JU IP PS IO OL ML LU AU AT DD ZD TH PH


Cycling or pregnant
DE EO PM IN OP PR MS XY LS GT DN SX ZA HP
HN PO EU CI AM ZN LE LI CC EK RH CB DL PY MM CG DP JU IP PS IO OL ML LU AU AT DD ZD TH PH


Lactating
DE EO PM IN OP PR MS XY LS GT DN SX ZA HP
HN PO EU CI AM ZN LE LI CC EK RH CB DL PY MM CG DP JU IP PS IO OL ML LU AU AT DD ZD TH PH

6.4.3. Grooming with mature males

In other studies, grooming characterized the relationships between infants and special males or "godfathers" (J. Altmann, 1980; Nicolson, 1982). Although results in the previous chapter suggested that these adult male-infant relationships persisted into the juvenile period (Table 5-5), grooming between these classes was extremely rare.

Mature males groomed juveniles on only four occasions; all involved three sub-adult males and their putative younger siblings.

On thirteen occasions, involving ten pairs, juveniles groomed mature males. In all cases, the juvenile was female. Five pairs consisted of the female and her putative sub-adult brother. Of the remaining five pairs, three consisted of the female and the adult male identified as a "special male" (see 5.3.3.). These were: RD and male BZ, a relationship identified by both Nicolson (1982) and Smuts (1982), although RD was not a focal animal in this study; and CL and male HC, and ER and male HC, relationships which were identified in all three studies.

6.4.4. Grooming and alliances

Grooming between a pair of monkeys is thought to increase the likelihood that they will support one another in other ways, particularly in the formation of aggressive alliances. Since high-ranking individuals tend to be more successful in conflicts, this could underlie their attractiveness as grooming partners.

Cheney (1977) made a useful distinction between two types of allied aggression. In the first, a coalition, the ally joins an aggressor who is already threatening or attacking a third animal. The assistance of the ally does not demonstrably alter the outcome of the interaction. In the second type, an aid, the ally intervenes on behalf of the victim of aggression, potentially influencing the outcome of the interaction. Therefore, aiding carries a greater risk to the ally; it is this sort of assistance which is postulated as a benefit to the groomer.

Aids to juveniles in this study were rare. Table 6-5 shows all instances of aids, drawn from all data sources, disregarding the identity of the individual partners.

Juvenile's ally	Number of interactions	%	Number of pairs
Family			
Mother	6	14%	5
Elder sibling	21	49%	18
Younger sibling	1	2%	1
Cousin (putative)	4	9%	2
Non-family			
Adult male	3	7%	3
Adult female	2	5%	2
Juvenile male	4	9%	4
Juvenile female	2	5%	2
	----		----
	43		37

Table 6-5. Aggressive alliances; aids given to juveniles by family and non-family members.

Three-quarters of all observed aids were given by family members. All of the family members observed aiding juveniles were also groomed by them at some point during the study. In contrast, I never observed grooming between any of the non-family allies and the recipients of their aid. It cannot be said that a grooming relationship was later reciprocated by aiding.

Grooming and polyadic aggression were closely associated, however, on many occasions. A juvenile appeared to "use" grooming to maintain proximity to an individual who out-ranked his or her attacker, as in the following example:

> Juvenile female ZR approaches infant female RD. RD screams, and ZR chases her. RX, RD's elder brother, attacks ZR. ZR escapes and runs ten metres to where high-ranking adult female HN is resting. ZR grooms her. RX follows, but stops five metres away. He threatens ZR. She shuffles behind HN and grooms more rapidly, not looking at RX. RX leaves. HN has not gestured or looked at RX.

HN provided "passive aid" to ZR, at no risk to herself. Presumably, the possibility that HN would actively intervene dissuaded RX from his threats.

6.4.5. Discussion

No single explanation accounts for the distribution of grooming, but various features, some of a long-term nature and others transitory, seemed to attract grooming.

The most prominent and enduring bonds, as expressed by grooming, were among close maternal relatives. Juveniles received a larger proportion of their grooming from family members than they gave in return. Aggressive aids to juveniles were also given primarily by relatives.

High rank was the second long-term characteristic which attracted grooming. High-ranking juveniles received more grooming, and juvenile females directed their grooming to adult females of high rank.

Other qualities were transitory. Thus, the high rate of grooming received by high-ranking (older) juvenile males appeared to be part of the reciprocal interactions by which they and sub-adult females maintained proximity when the female was in the inflating stage of her sexual cycle. For both partners, this seemed to be a precursor to adult consort behaviour, in which grooming plays an important part (Saayman, 1971); as opposed to the heterosexual grooming which takes place outside a sexual context as part of a "special relationship" between adults (Seyfarth, 1978b;

Smuts, 1982). Young, pre-transfer males would not be expected to invest large amounts of time in relationships in their natal troops. However, grooming in a sexual context may enhance chances for opportunistic copulations.

Young infants temporarily increased their mothers' attractiveness as grooming partners. Cheney (1978a) argued that infants "constitute a major mechanism for the formation of social relationships", by which the juvenile female may establish relationships with unrelated high-ranking females which may persist after the infant matures. In this study, however, the presence of an infant seemed to override the attractiveness of high rank. Even high-ranking juvenile females groomed lactating mothers of diverse ranks, although their grooming of non-lactating mothers was limited to those who held similar ranks to their own.

Finally, situations of a very temporary nature were conducive to grooming, such as when a juvenile gained protection by "using" grooming to maintain proximity to another individual. The choice of the grooming partner in these cases was hardly random - the juvenile groomed an individual of sufficiently high rank to deter his or her aggressor in every case - but I saw no evidence that the juvenile cultivated these relationships in other circumstances.

It remains puzzling why individuals should groom in the absence of reciprocity, whether given in kind or in alliances. It may be, as Cheney suggested of coalition behaviour (1977), that the juvenile initially directs its behaviour to the highest-ranking individuals, and then gradually ceases to interact with distantly-ranked animals who do not reciprocate. An alternative explanation is that juveniles groom high-ranking individuals who reciprocate by <u>not</u> aggressing against the juvenile in the future (Silk, 1982). To test that possibility, it would be necessary to demonstrate that grooming in such cases reduced the likelihood of aggression in future interactions.

Chapter 7

APPROACH-WITHDRAW INTERACTIONS

7.1. Introduction

Baboons are popularly characterized as highly aggressive animals (Washburn and Hamburg, 1968; Jolly, 1972). Certainly fights, when they occur, can be protracted and noisy, often drawing many animals into the conflict. But it is relatively rare that a dispute between two baboons escalates through threats into physical attacks. The majority of conflicts between baboons are not overtly aggressive and do not attract the attention of other members of the troop. These conflicts are generally resolved by one animal simply moving away from the other. These interactions, here called approach-withdraw interactions, are of interest precisely because they do not escalate into physical aggression. They demonstrate to the observer how two animals interact unassisted by other individuals, and are probably a more accurate reflection of stable dominance relationships than interactions whose outcome is, or could be, influenced by the intervention of others.

For this reason, I decided to use the approach-withdraw interaction to rank juvenile males and juvenile females, and as was shown in Chapter 3, the direction of these interactions shows great consistency. When juvenile males interact, the smaller male is generally

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For this reason, I decided to use the approach-withdraw interaction to rank juvenile males and juvenile females, and as was shown in Chapter 3, the direction of these interactions shows great consistency. When juvenile males interact, the smaller male is generally the one to move away at the approach of the larger; whereas, among females, the agonistic rank of the juvenile´s mother influences which others move away at her approach.

This chapter first examines the rates at which individual animals were involved in approach-withdraw interactions, both as winners and as losers. Regardless of the identity of the interaction partner, these rates tell us something about what life was like for that animal. For example, were some juveniles more likely than others to lose a resource, and was this difference attributable to either rank or sex? The next section identifies the partners in the interaction. For example, did juvenile baboons single out members of particular age-sex classes to supplant, and avoid the members of another distinct class, or were approach-withdraw interactions distributed randomly across all age-sex classes?

The baboon who moves away from another may abandon a resource; indeed, in most cases, it appears that gaining a desirable resource is the goal of the baboon who approaches. The nature of the disputed resource is discussed. Lastly, the interaction may have effects beyond the change in possession of a resource. Just as grooming can be viewed as a behaviour with obvious hygienic benefits which also functions to initiate or maintain relationships, a supplant may allow the dominant animal to gain a resource and - without particular risk - reinforce the asymmetries of the relationship. This possibility is examined in the final section.

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7.2. Methods

The approach-withdraw interaction was the most common agonistic interaction recorded in this study. When discussing the broad category of approach-avoidance behaviours, primate researchers have not reached consensus on the definition of terms. The extent to which the definitions used here overlap with those of other studies may be seen in Table 7-1.

An approach-withdraw interaction was scored whenever the following criteria were met:

> 1) one animal, A, moves towards or orients towards another animal, B.
> 2) very shortly, B moves away, or alters course if already moving.

In addition, B may look at, or towards A before moving away. B may also show mild submissive gestures (tail up, grin, crouch, etc) but no vocalizations, threats, or overt aggressive gestures are given by either animal.

This sequence would be recorded as an approach-withdraw interaction in which A wins and B loses. In addition, the interaction will be one of two types. In a Supplant, B is in possession of what I judged to be a resource (food, a shaded resting spot, a grooming partner, etc.) and loses that resource by moving away; animal A may or may not replace B at the resource. In the second type, an Avoid, no obvious resource is involved. In their 'purest' forms, the two types are easy to distinguish: during a supplant, the approach is clearly directed towards the

Study	Behaviours included in category		
	'Loser' loses a resource		No resource involved
	Winner does not replace loser at resource	Winner takes resource from loser	
Rowell 1966b	Non-agonistic approach-retreat interactions		
	not included	Supplant	Avoid
Seyfarth 1976	Approach-retreat interactions		
		(resource limited to other animals)	
Post 1978	Spatial Displacement		
Lee and Oliver 1979	Supplant		Avoid
	(not included in analysis)	(resource limited to food)	
Altmann 1980	(not included)	Spatial displacement	not described
Packer 1979b	(not specified)		Supplant
This study	Approach-Withdraw		
	Supplant		Avoid

Table 7-1. Comparison of terms used to describe behaviours in the broad category of 'approach-avoid' interactions.

resource, not the animal in possession of it (as noted by J. Altmann, 1980). During an avoid, the loser may be responsible for the entire interaction, moving out of the path of a winner who appears not to have even noticed the loser's presence. However, it is the behaviour of both partners which amounts to a supplant.

Rather than 'winner and loser', some researchers use the labels 'donor and recipient' or 'actor and receiver' for the two interacting animals, implying that the active animal is necessarily the winner. In my definition of an approach-withdraw interaction, either the winner or the loser may be giving or receiving gestures: whether A supplants B, or B avoids A, A is labelled the winner.

All interactions of either type are treated as dyadic interactions, although the 'resource' may sometimes be a third animal, such as a grooming partner. The following example:

> ZR approaches CL, who is grooming adult female LU. CL glances toward ZR, leaves, and sits five meters away. ZR grooms LU. LU leaves ZR, and approaches CL, who resumes grooming.

was recorded as a supplant interaction in which ZR won and CL lost, despite the fact that the 'resource' walked away!

In Chapter 3, rank orders based on the direction of approach-withdraw interactions were compared to those based on juvenile male size and juvenile female maternal rank in order to justify use of the latter measures to approximate dominance rank. The analysis which follows focuses on the rates of interaction, the identity of the interaction partners, the possible cost of being supplanted, the nature of the disputed resources, and the selectivity of the winners regarding the resources.

7.3. Results

7.3.1. Rates of interaction

There was a tendency, though not a significant one, for females to be involved in approach-withdraw interactions at higher rates than males (Figure 7-1, U = 16).

These general rates, however, take no account of the outcome of the interaction. When the rates are broken down according to whether the subject animal was the winner or loser in the interaction, sex differences again emerge, but now females are found to be involved more frequently in interactions in which they lost than were males (U = 8, $p < .01$). In interactions in which the juvenile subject was the winner, there was no appreciable difference, only a suggestion that males won at higher rates.

7.3.2. Interaction partners

The rates of interaction with each age-sex class of partner were calculated for each juvenile baboon. The rates were divided by that animal's individual mean troop composition, to allow for the availability of interaction

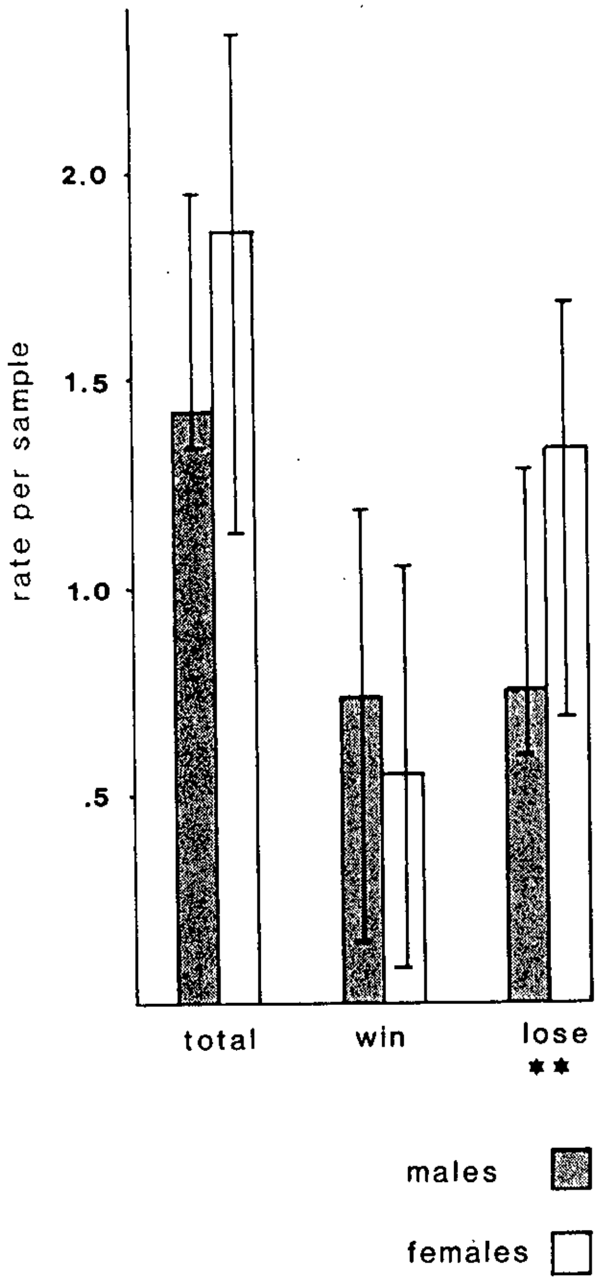

Figure 7-1. Rates of approach-withdraw interactions, comparing sexes. Medians and ranges are shown.

partners of a particular class. (The individual mean troop composition, described in full in Section 2.3.5., expresses the mean number of baboons of each age-sex class and reproductive state over the particular forty days in the study on which a given focal juvenile was sampled.) Figure 7-2 shows, for males and females, the rates at which the juveniles were winners and losers in approach-withdraw interactions.

Looking first at interactions in which the juvenile won, males and females did not supplant or elicit avoids from the age-sex classes at random (males: $X_r^2 = 18.7$, $p < .011$; females: $X_r^2 = 11.98$, $p < .01$; both df = 5). Both classes defeated juvenile females at a high rate, but never defeated subadult or adult males. Turning next to juvenile losses, when juvenile males lost in approach-withdraw interactions, the age-sex class of the winner differed in a consistent pattern from random ($X_r^2 = 34.78$, $p < .001$), with their own class and sub-adult males winning at high rates. However, in interactions in which females were losers, the age-sex class of the winner differed significantly from random ($X_r^2 = 37.50$, $p < .001$, df = 7). with the two juvenile classes winning at very high rates.

Significant sex differences between females and males in the rates at which they won and lost with different classes are starred in the figure. Juvenile males won at a significantly higher rate than juvenile females against juvenile males. When the juvenile was the loser, females lost at higher rates to infant males. They also lost at

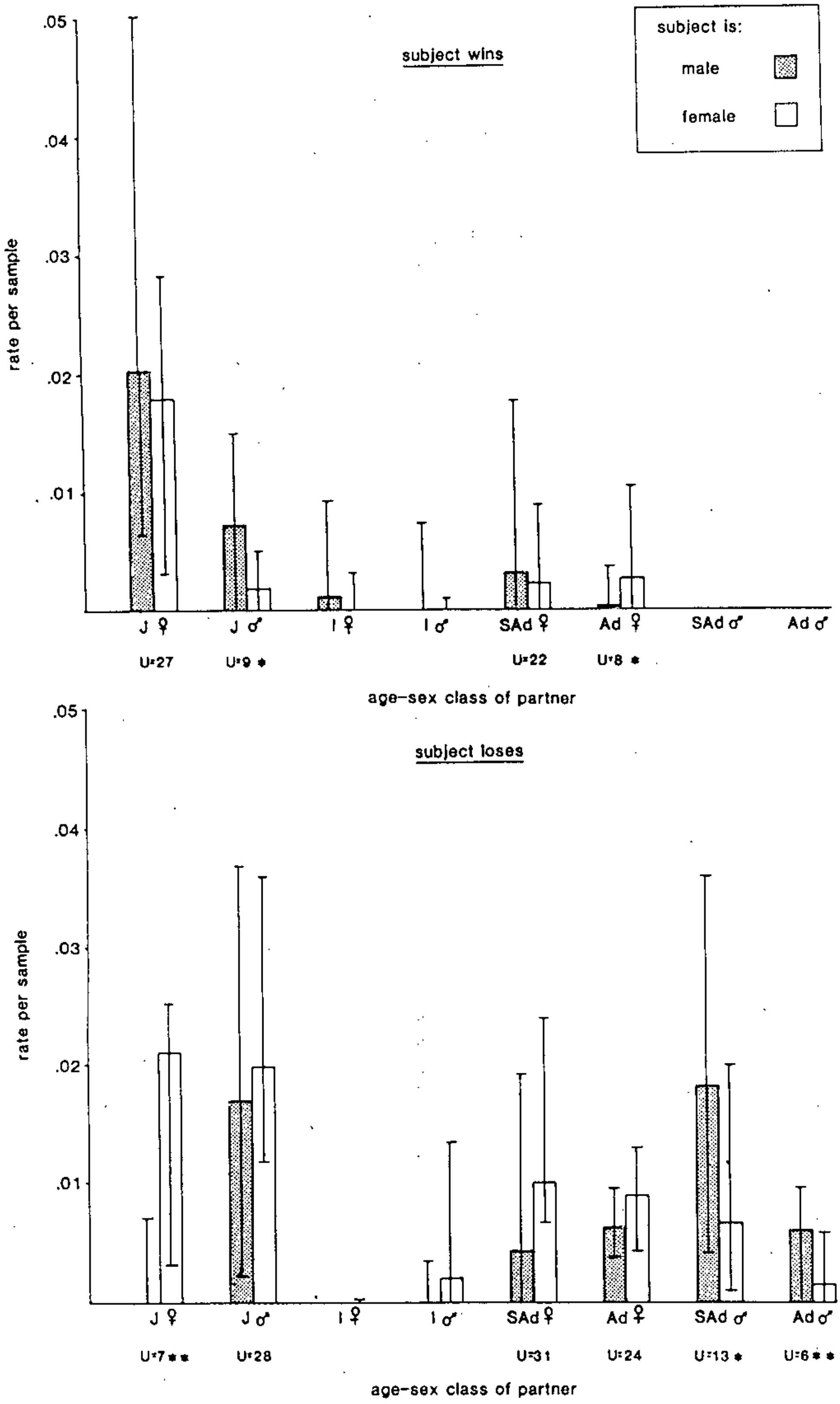

Figure 7-2. Rates of approach-withdraw interactions in which juveniles won and lost. The rates are calculated per half-hour focal-animal sample, and are adjusted for the number of individuals in each age-sex class. Medians and ranges are shown.

higher rates to all three female classes (significant with their own class) than did juvenile males; while juvenile males lost at significantly higher rates to the two older male classes than did females.

7.3.3. The effects of rank

Several studies have found a correlation between dominance rank and rates of approach-withdraw interactions (Rowell, 1966b; Bernstein, 1969; Lindburg, 1971; Deag, 1977; Bramblett, 1978; Post, 1978; Lee and Oliver, 1979). This is not a surprising result if the entire social group is included in the ranking, or if the rates are based on interactions within one internally-ranked sub-set of the troop. For example, if a group of ten animals can be arranged in a linear hierarchy according to the direction of supplants, the animal ranked number one is able, by definition, to supplant nine other animals; the animal ranked number ten is able to supplant none. Some correlation between frequency of winning interactions and high rank would be expected. Only if the number of potential partners is taken into account can this correlation be used to demonstrate whether high-ranking animals have more inclination, as well as more opportunity to defeat others.

High rank within the juvenile class does not necessarily result in high rank in the troop as a whole. One would not predict a correlation between juvenile rank and overall rates of approach-withdraw interactions. For example, a high-ranking juvenile male may lose to other juvenile males at a low rate, but this fact may be obscured in the overall scores if he also loses at a high rate to a larger male class, such as sub-adult males.

Table 7-2 shows the correlations between juvenile rank and rates of winning and losing.

	Juvenile wins	Juvenile loses
males n = 8	.67 *	-.45
females n = 8	.62	-.52

Table 7-2. Correlations between juvenile rank and rates of approach-withdraw interactions.

It is surprising that for both male and female juveniles, high ranks within their respective age-sex classes were associated with high rates of winning, regardless of the identity of the interaction partner. To a lesser extent, high rank conferred some protection as well; high rank was associated with lower rates of losing.

This result is better understood by looking at the relationship between rank and rates of approach-withdraw interactions with different age-sex classes (Table 7-3). The overall association between rank and rates is only reflected in scores with certain classes. Higher-ranking juvenile males showed significantly higher rates of winning against their own class, and tended to win at higher rates against sub-adult females. Lower-ranking males showed significantly higher rates of losing to both juvenile classes, but significantly lower rates of losing to sub-adult males.

	Age-sex class of interaction partner					
	Juvenile Females	Juvenile Males	Sub-adult Females	Sub-adult Males	Adult Females	Adult Males
Subject wins						
Juvenile Males						
agonistic rank	.10	.95 **	.70		.38	
maternal rank	-.21	.00	.04		.48	
Juvenile Females						
agonistic rank	.71	.33	.30		.10	
size rank	.30	-.07	.25		.37	
Subject loses						
Juvenile Males						
agonistic rank	-.78 *	-.92 **	-.06	.74 *	.68	-.09
maternal rank	-.05	-.16	-.44	-.07	-.39	.33
Juvenile Females						
agonistic rank	-.53	.11	-.53	-.52	-.25	.37
size rank	.29	.50	.02	-.25	.04	.22

Table 7-3. Correlations between rates of approach-withdraw interaction with all age-sex classes and juvenile rank. Two alternative rank orders are used for both male and female juveniles. Agonistic rank refers to the rank order based upon the direction of approach-withdraw interactions. Agonistic rank approximates maternal rank for females and size rank for males. The alternative rank orders are based upon the maternal ranks of the juvenile males and the relative sizes of the juvenile females. Interactions with infant classes are excluded.

Concerning juvenile females, none of the correlations were significant. Higher-ranking females tended to show higher rates of winning against their own class and lower rates of losing to their own class and to both sub-adult classes.

7.3.4. Discussion

In EC troop, the rate of losses suffered in approach-withdraw interactions rose sharply as a youngster grew up. Nicolson (1982) found that infants less than 41 weeks old were supplanted (a sub-category of my approach-withdraw interactions) at a rate of .06 times per 100 minutes. Between 41 and 72 weeks of age, the rate rose to .39 times per 100 minutes, as infants became more independent of their mothers. During this study, the comparable figure was 1.87 times per 100 minutes, nearly a five-fold increase. The juvenile, no longer in constant proximity to its mother, and perhaps not yet large enough to assert itself, may be more vulnerable to this type of low-intensity agonism than at any time in its life.

Juvenile females lost at nearly twice the rate of juvenile males. In a study of toque macaques, Dittus (1977) found that juvenile females were threatened more than any other age-sex class, and their access to contested resources was thus limited. (Threats were broadly defined as "behaviour that caused the respondent to alter its spatial position or behaviour in avoidance"; and so include all approach-withdraw interactions).

shortage, juvenile females suffered greater mortality, so-called "behaviourally-induced starvation", than other age-sex classes. Dittus (1979) related this discrimination against younger animals and against females in particular to the reproductive value of males and females at different ages.

During this study, females did not die more often than males, and there was no evidence of the extreme food shortage experienced by the toque macaques. But patterns of approach-withdraw interactions indicate that females and low-ranking individuals could be at a severe disadvantage in times of resource scarcity (Wrangham, 1981).

Patterns of wins and losses with different age-sex classes, and the relationship between rates of interaction and rank suggest interesting changes with age. In the distribution of losses (Figure 7-2), individual juvenile male scores were too heterogeneous for partner-class differences to be meaningful. However, some of the variation between juvenile males appears to be due to a correlation between class scores and rank (size), suggesting an association with male development.

Since juvenile male rank is so closely correlated with size, it is simplest to set aside individual differences for the moment and summarize these results as if they described one hypothetical juvenile male growing up. In his interactions with other males a small male loses at a high rate to larger members of his own peer group. As he grows larger, he defeats his younger male peers in relation to their size, but also suffers more than they do from defeats by sub-adult males. Here, the distinction by age-sex class is misleading; he is by now a large juvenile male, and the sub-adult males who defeat him at higher rates than his smaller peers are, in effect, the same animals who defeated him when they were juveniles. The pattern is one of male interaction according to size, with males interacting at high rates with those close in rank - defeating slightly smaller ones and losing to those slightly larger. This may be due to males of similar sizes associating preferentially, yet that was not borne out in the juvenile males' neighbours (P-scores, Figure 5-3).

As discussed in Chapter 5 (Proximity), there was also a tendency for the older juvenile males to associate more with their own sex than did younger juvenile males. This may explain the early changes in approach-withdraw patterns with females. The juvenile male, when young, loses to juvenile females in relation to his - not their - size. As he grows larger, he spends less time in proximity to female age-mates; he ceases to lose to them, although he does not defeat them at any higher rates. He spends time in proximity to sub-adult females, and supplants them at higher rates than he did when younger. Sub-adult females do not supplant him more than they do younger peers; however, adult females do.

It appears that the young juvenile male loses in his interactions with some juvenile females. With increasing size, he is gradually able to defeat them, and later, their sub-adult sisters. The adults are the final female class that the male will be able to defeat as he grows older. The high rates at which adult females defeated the larger juvenile males in particular may indicate their efforts to delay this process.

In Chapter 3 (Rank), it was suggested that immature males are initially unable to defeat adult females in approach-withdraw interactions; then defeat those who their mothers out-rank, and finally, as large juveniles or sub-adults, are able to defeat all adult females. The oldest male subjects of this study were younger than those males who in Chapter 3 were able to defeat adult females.

With the two age-sex classes sub-adult males and adult females, correlations between juvenile male rank and rates of losing are positive, the reverse of the general pattern in which high rank conferred some protection against losing. Juvenile male proximity scores with both of these classes were low. It seems possible that members of both these age-sex classes have an interest in delaying the rise of juvenile males; sub-adult males because the large juveniles will soon enter the sub-adult cohort, and adult females, because juvenile males will soon compete against them with increasing success.

In contrast to the males, female rank, correlated as it is with maternal rank, is not expected to change with time; older females cannot represent a stage which the younger ones will attain eventually. And correlations with female size (Table 7-3) did not suggest changes related to age, as they do in males.

However, the rates of interaction lend weight to conclusions reaches in Chapter 3. The correlations of high rank with high rates of winning and low rates of losing are best with the juvenile female's own peers, less correlated with sub-adult females, and only weakly correlated with adult females. In Chapter 3, juvenile females were defeated only by females who out-ranked their mothers, yet they appeared in most cases to be unable, or disinclined to defeat adult females which their mothers out-ranked.

7.4. Context and cost of supplants.

So far in this chapter, I have examined the approach-withdraw interaction first from the point of view of the individual: how often he/she is involved in this type of interaction, and how these rates vary according to season or the sex of the subject. Following this, the next section concentrated on the pair of animals interacting, the importance of the age-sex class of the partner, and how rates of interaction varied in relation to dominance rank.

Finally, in this chapter, I will examine details of the supplant interaction itself: the context in which supplants occur and the possible costs of being supplanted. Avoids, the other sub-category of approach-withdraw interactions, may have a trivial cost in energy expended, but they are excluded from the following analysis which centres on resources which change ownership during supplants.

Whenever possible, for each supplant interaction, I recorded the initial activity (and food, if feeding) of the loser which was terminated by the start of the interaction. I recorded the distance the loser moved away from the winner after being supplanted, and the loser's subsequent activity (and food); if the loser was still moving away after ten seconds, the subsequent activity was listed as "travelling". As defined here, a supplant is a dispute over ownership of a resource; so it is important to determine whether the winner actually did take over the resource (food, resting site, grooming partner) held by the loser. And so I noted whether the winner replaced the loser at the resource; e.g. if the initial activity of the loser had been feeding on grass, I noted whether or not the winner fed on grass at the same site after the supplant.

7.4.1. Results

For all supplants recorded during focal samples, Table 7-4 shows that the winner did indeed replace the loser at the resource in most cases, regardless of its type. When the winner did not utilize the resource, it is interesting that nevertheless she/he often inspected it, lending credence to the assertion that during a supplant it is the resource and not the animal in possession of it, which is approached (Altmann, 1980).

Does the winner replace the loser at resource?		
Yes	639	97.4%
No, but inspects	13	2.0%
No	4	0.6%
	656	100.0%

Table 7-4. Replacements after supplants.

The winner nearly always gains a resource; but we may ask how selective is he/she? Or, taking the loser's point of view, is an animal equally likely to be supplanted during all activities?

To answer this question, I calculated the proportion of all supplants which occurred during each category of activity. It was clear that the vast majority (88.4%) occurred during feeding. However, as feeding was the most frequent activity (see Chapter 4), supplants could still have occurred at random with respect to activity of the animal supplanted. So, for each individual, the percent of time spent in each activity was re-calculated from the activity budget (Chapter 3), omitting Travel (It was rare that a travelling animal was in possession of a route which might be considered a "resource", possibly a path along a narrow ledge would be an example. An animal deflected from its path by another was scored as having avoided the other). These new scores represented the amount of time each animal spent in "supplantable" activities.

Figure 7-3 shows the percent of time spent in each supplantable activity, compared with the percent of supplants which occurred during each activity. If an animal

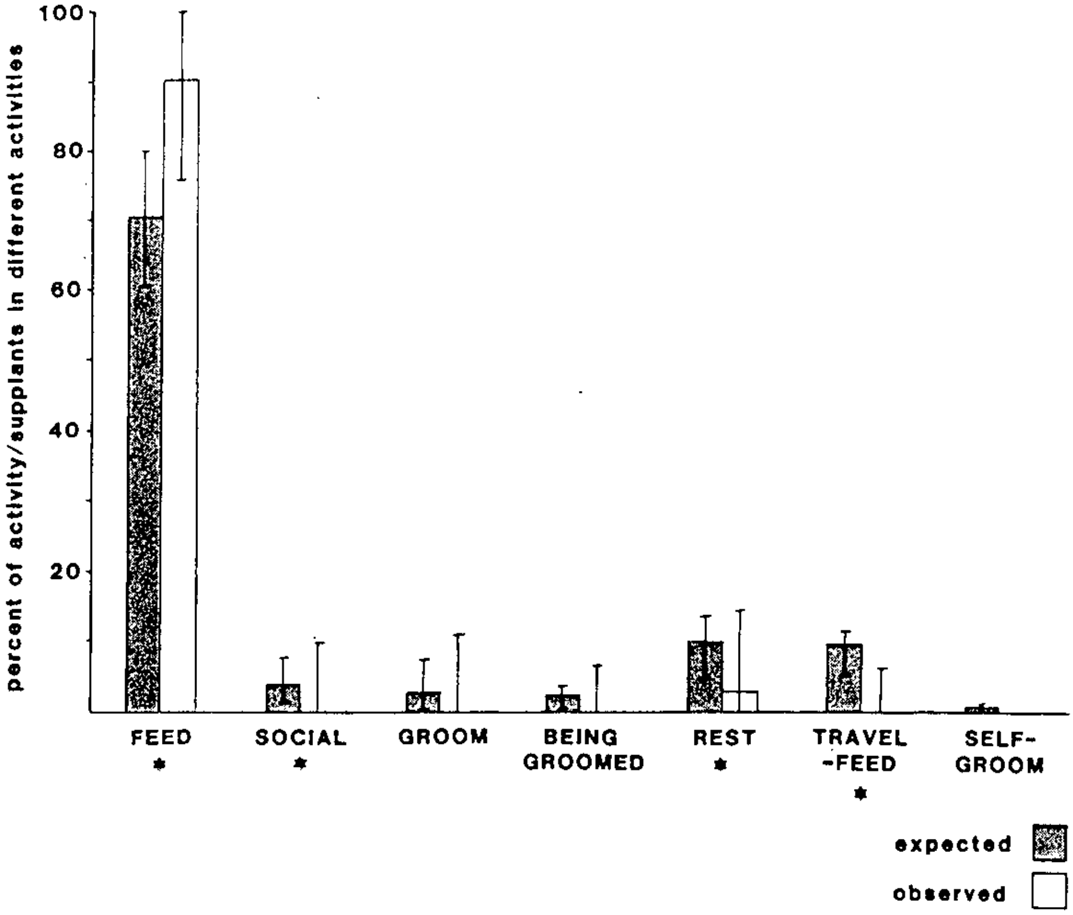

Figure 7-3. Median percent of supplants which occurred during different activities. This is compared with the percent of time devoted to each activity, which provides an expected distribution for the former. Significant differences are starred.

was equally likely to be supplanted during any activity, these scores should be very similar. (Since the activity budget and the supplants were taken from the same samples on the sixteen main focal animals, it was not necessary to consider seasonal changes in activity - but it was possible to include only those supplants in which the focal animal was the loser in the interaction). For each animal, the difference between expected and observed in the seven activities was calculated. There is a consistent pattern throughout, suggesting that an animal is more vulnerable to supplants during some activites than others. (X_r^2 = 67.27, df = 6, $p < .001$).

An animal feeding stands a significantly greater than expected chance of being supplanted; the chances are lowered for all other activities, but only significantly so for social interacting, resting, and travel-feeding (Sign test, $p < .01$).

The winner, therefore, appeared to supplant selectively with regard to the activity of the loser. In the 90% of supplants which concerned food, was she/he similarly selective regarding the food the loser was eating? The same methods as above were used to look at selectivity over foods, specifically. Figure 7-4 shows the percent of feeding time spent eating different classes of food, derived again from the activity budgets of the focal animals. If feeding supplants occured at random with respect to the food being eaten by the loser before the supplant, these scores should be similar to the percent of feeding supplants

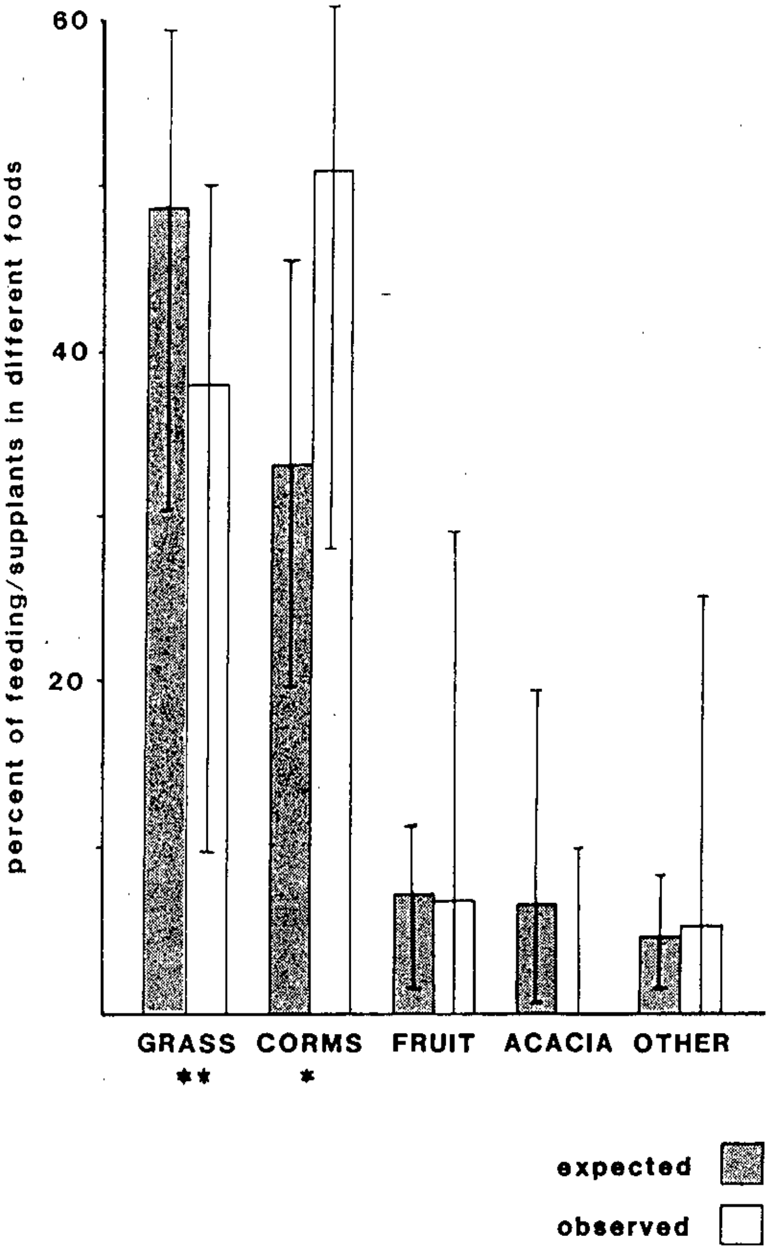

Figure 7-4. Median percent of feeding supplants which occurred over different foods. This is compared to the percent of time spent eating these foods, which provides an expected distribution for the former. Significant differences are starred.

which occur over different foods. However, there were significant differences in the likelihood of being supplanted from different foods ($X_r^2 = 21.05$, df = 4, $p < .001$). The clearest difference concerned the food classes Grass and Corms, which were the two most prominent foods, both in the diets and in the supplant interactions. Animals eating grass were less likely than expected to be supplanted (Sign test, $p < .004$), while those at corm-digging sites were more likely to be supplanted ($p < .02$).

So far, it is clear that the winner did actually benefit, nutritionally in most cases, from supplanting another, and that he/she showed some selectivity in choice of resources.

But what did the loser actually lose? Table 7-5 shows the first activities of the losers within ten seconds of being supplanted from a feeding site.

Feeding	336	52.9%
Travelling	214	33.7%
Resting	54	8.5%
Social Interaction	30	4.7%
Self-grooming	1	0.2%
Social Grooming	0	0.0%
	---	-----
	635	100.0%

Table 7-5. Losers' activities following a feeding supplant

In nearly half the supplants, the loser of a feeding site did not resume feeding again immediately. However, this figure varied depending upon the disputed food. Figure 7-5 shows the subsequent

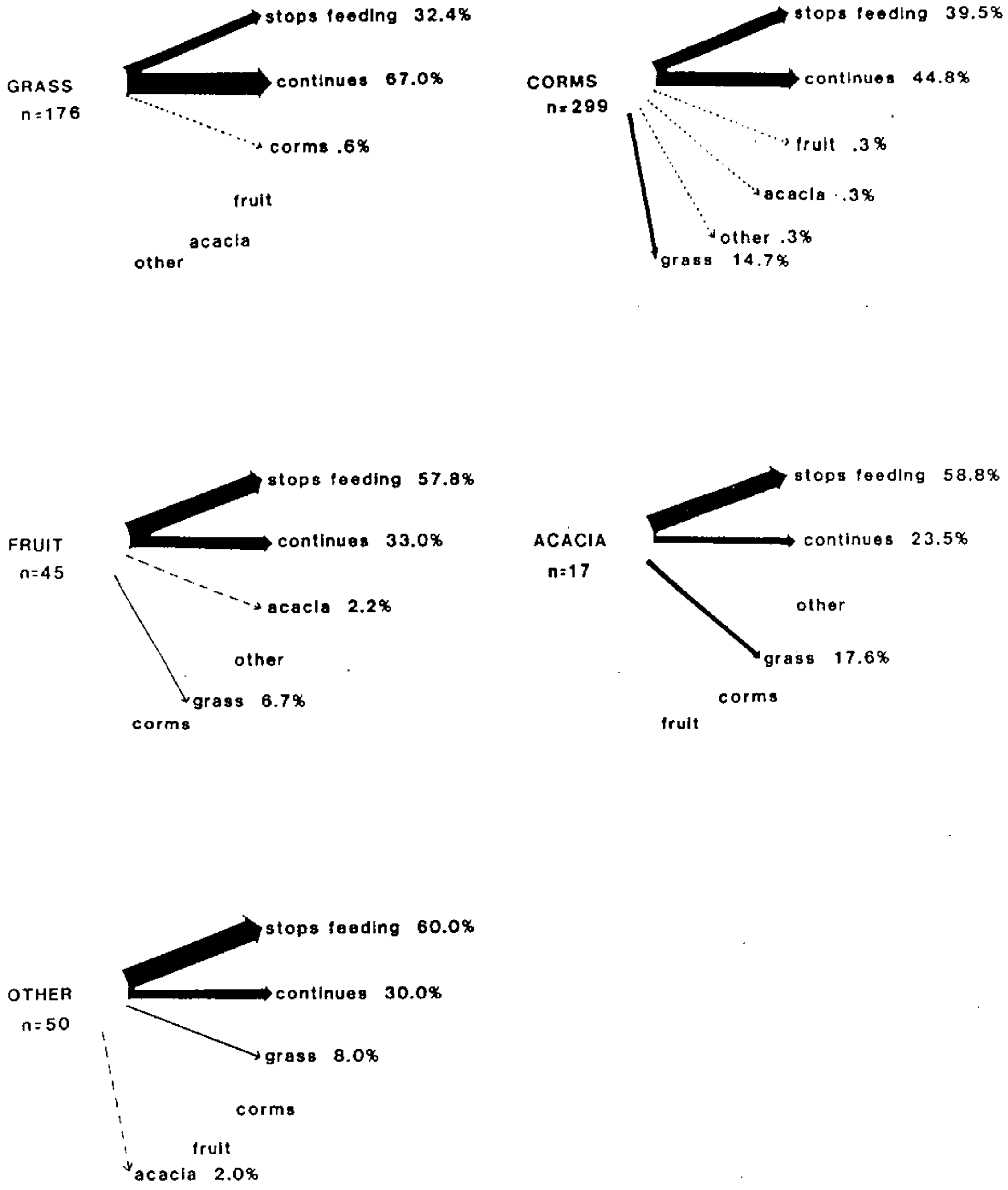

Figure 7-5. Subsequent food eaten following a feeding supplant. In the centre of each wheel is the food being eaten originally, before the loser is supplanted. The arrows show the percent of those supplants after which the loser: stops feeding altogether, continues feeding on the same type of food as the original food, or switches to another food class. The four alternative food classes, listed below the horizontal in each wheel, are shown here without any attempt to gauge their availability in the vicinity of the original food.

activities of the losers after being supplanted from a given food class. The subsequent activities "stops feeding" and "continues (feeding on the same food as before the supplant)" give the best idea of the cost of being supplanted. If we can assume that a baboon would have continued feeding at a particular site if not for the interruption of a supplant, then the loser is able to continue feeding on its "preferred" food in between 23.5% and 67% of cases, depending on the food class. Even when the loser has been feeding on grass, the most common and, one assumes, abundant item in the diet, only 67% continue feeding on grass afterwards. As food classes make up a smaller part of the diet, it is less likely that a supplanted baboon will locate another feeding site of the same type, and the rate at which losers stop feeding altogether rises also.

It seems unlikely that the energetic gain will justify the cost of supplanting another baboon over grass. It was the most common food in all the study animals´ diets; and, as has been shown, an animal supplanted from grass was more likely to continue feeding on the same food than an animal supplanted from any other food group. And the loser travelled a significantly shorter distance to resume feeding on grass than to resume feeding on corms, the other major category of supplants (Kolmogorov Smirnov two-sample test: $D = .237$, $p < .001$. See Figure 7-6.), so it was not difficult to locate another site. Indeed, watching the baboons on a large, grassy plain where most members of the troop were

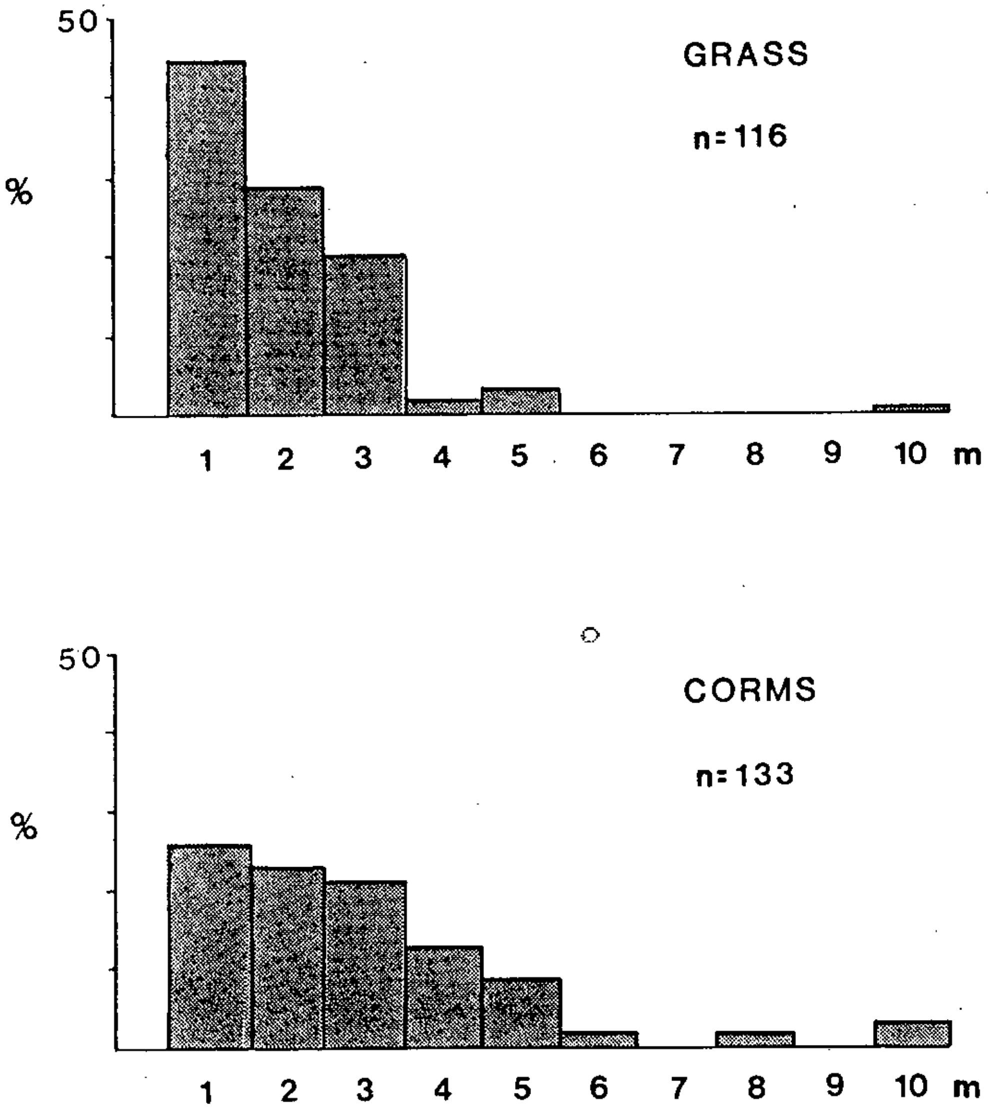

Figure 7-6. Distance travelled following a supplant before feeding on the same food again. Only the two major food types, Grass and Corms, are shown. The loser must travel significantly further after losing a digging site.

eating grass, an interaction such as this one between two juvenile males seemed inefficient on the part of the winner:

> <u>minute 11</u>. PD approaches AR, who is digging for corms. AR leaves, and feeds on grass one metre away. PD replaces AR at site, digs.
> PD approaches AR, who is travelling. AR avoids, continues travelling.
> <u>minute 12</u>. PD approaches AR, who is feeding on grass. AR leaves, charges juvenile female LS three metres away. PD feeds on grass at AR's old site.
> <u>minute 13</u>. PD approaches AR, who is feeding on grass. AR leaves, feeds once again on grass one metre away. PD replaces AR at the site and feeds on grass.

PD initially took a valuable feeding site (corm) from AR, forcing AR to feed on a less preferred food. But PD then repeatedly supplanted AR from grass, even abandoning a (presumably) more valuable digging site to do so. It would seem that PD used the supplant for social gain, even at nutritional expense, and for many supplants this appeared to be the main result.

If supplants can serve this double function, under what circumstances can baboons be expected to impose energetic cost upon themselves by supplanting another animal? It seemed possible that, between two animals of widely disparate rank, it would be unnecessary to reinforce rank difference, and that, in general, supplants should occur over more favoured food items. However, in relationships at smaller rank differences, where there might be ambiguity and a threat of future rank reversals, it would be worthwhile for a baboon to be less selective about the quality of food in a supplant.

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Ideally, this question should be tested by calculating the ratio of supplants over more favoured to less-favoured foods for each baboon with each of its interaction partners, to allow for individual differences. As the rank difference decreases, the proportion of supplants over the less-favoured food would be expected to rise. Unfortunately, the large size of EC troop meant that even with over 600 supplants recorded, each dyad contributed very few interactions. Even so, the idea was worth testing by some means, since it appeared a plausible explanation for supplants which yielded marginal apparent benefit.

Grass and corms were chosen as the less and more favoured supplant foods. All supplants between juvenile males and between juvenile females were selected. At each rank difference, grass supplants as a proportion of the total supplants (grass plus corm) were calculated. In Figure 7-7, the proportions are shown in relation to the median proportion of grass supplants across all rank differences. The proportion of grass supplants fell with increasing rank difference, and the change was significant both for females (r_s - .75, p < .01) and for males (r_s = .90, p < .01).

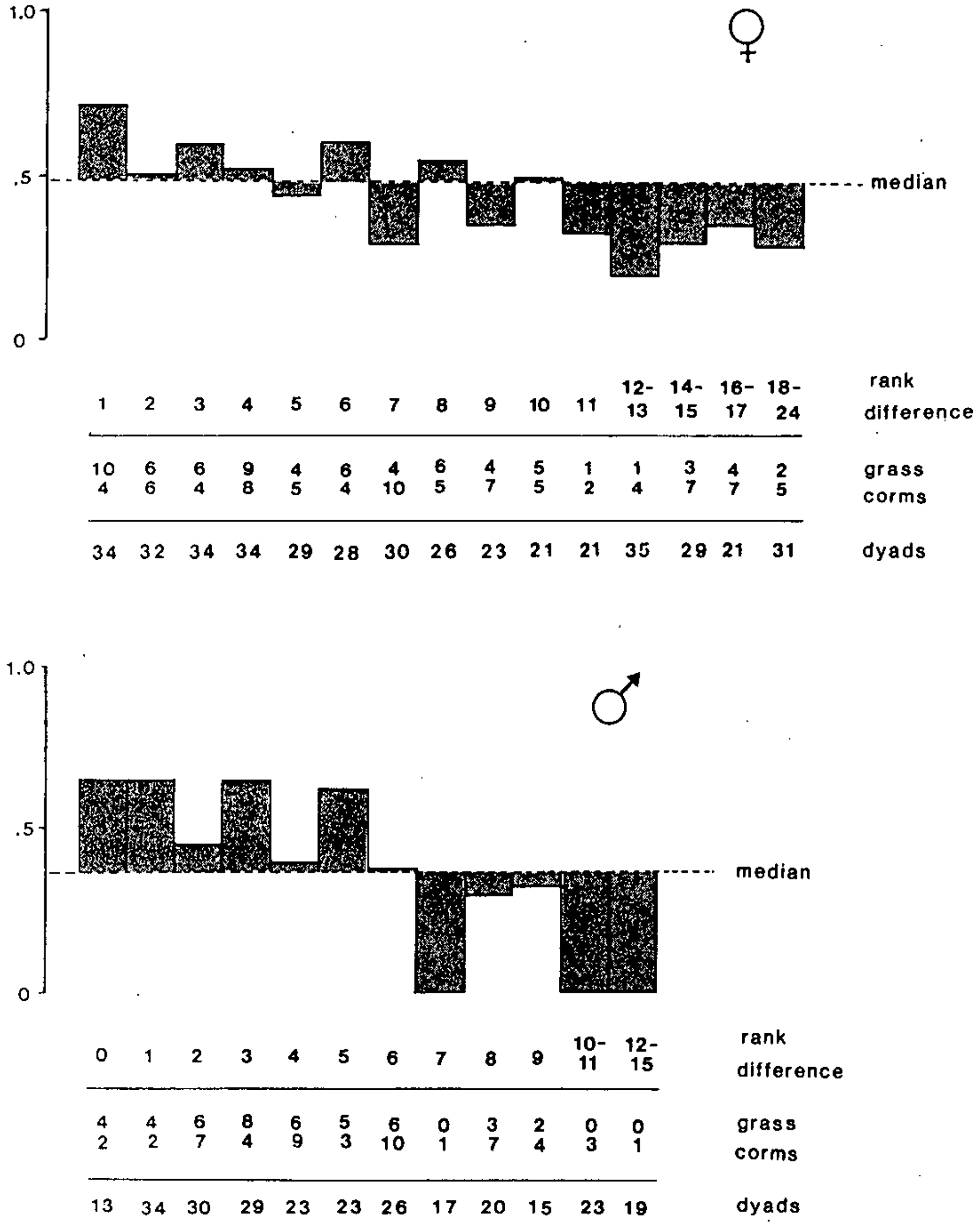


Figure 7-7. Supplant foods at different rank distances. This figure includes only supplants over either grass or corms, between two members of the same age-sex class. At each rank difference, a bar represents the proportion of all supplants which concerned grass. The bars are shown either above or below the dotted line, which is the median proportion over all rank differences in that age-sex class. The actual number of grass and corm supplants is shown below the figure. 'Dyads' refers to the number of pairs of animals who could potentially have contributed to those scores.

7.4.2. Discussion

Several studies report interactions, such as unprovoked attacks and aggressive displays, the primary purpose of which appears to be the reassertion of rank over another individual (Struhsaker, 1967; Rowell, 1974; Bygott, 1979; Walters, 1980). Often, the observer only has a subjective impression that this is the case.

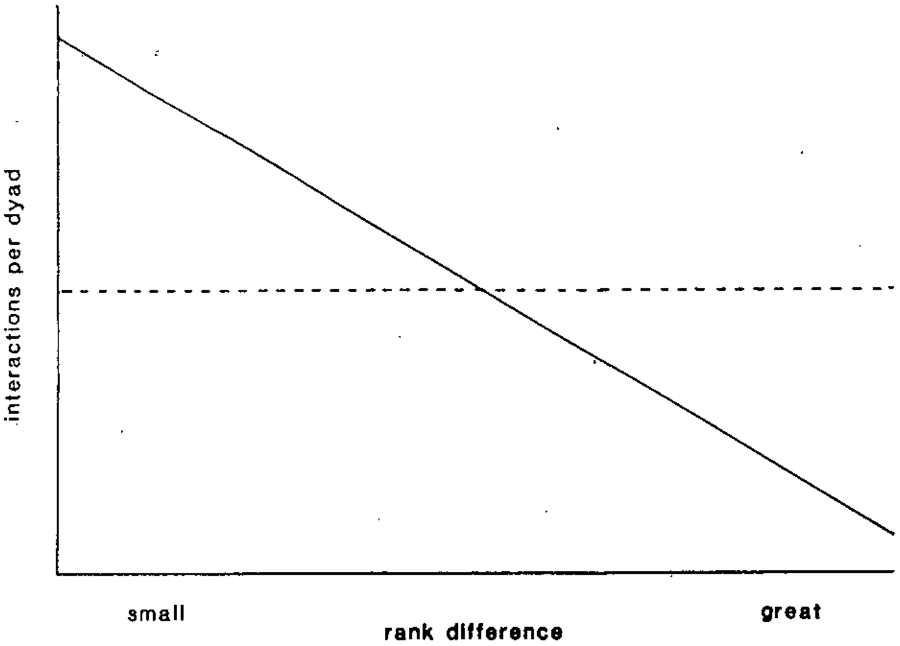
Concerning supplants, it is suggested here that they can serve a double function. First, the winner gains a resource from the loser. Second, the winner reinforces the rank relationship between them, at no great risk because of the small chance of escalation. Since all supplants are of essentially the same form, interactions which are primarily of the first type cannot be distinguished from those of the second except by looking for evidence of selectivity in the animal's interactions. There were three suggestive pieces of evidence in this chapter.

First, the age-sex classes supplanted members of particular other classes. The selective supplanting of one class by all others may only indicate that the losers are generally poor competitors. The selective supplanting of two different classes by different sets of winners suggests a social component to the supplant. So, juvenile females lost more often than males in interactions with all female classes. And juvenile males lost more often than females in interactions with sub-adult and adult males, and at high rates with their own class.

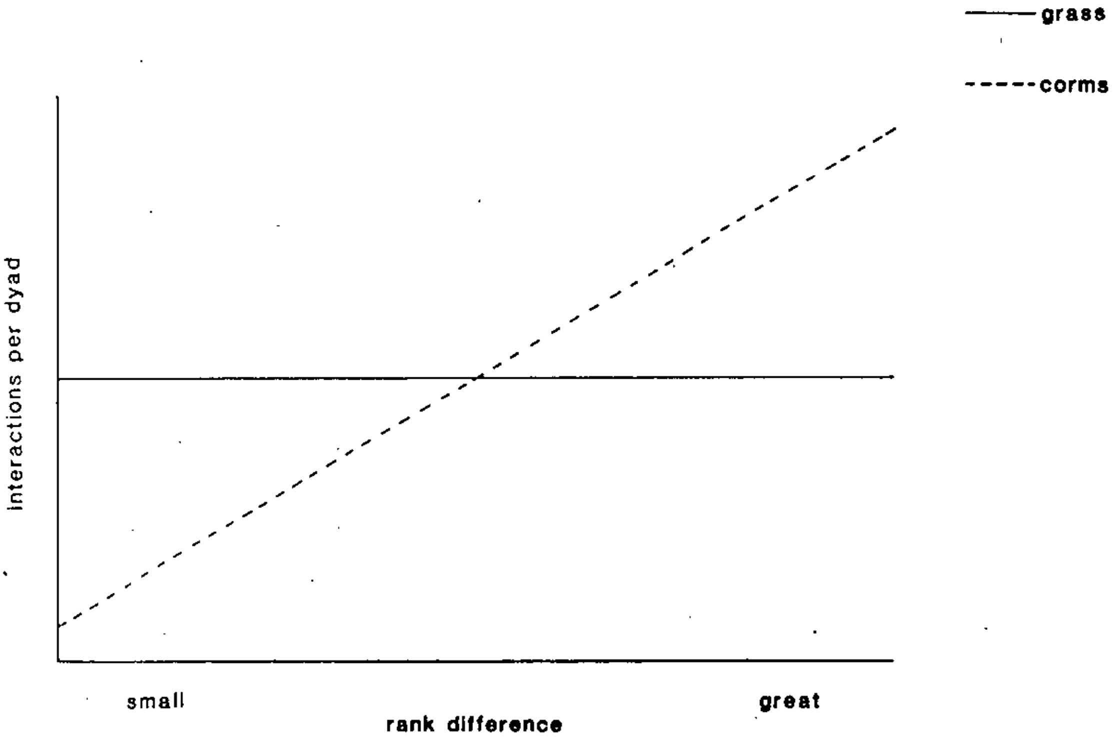
Second, the larger (higher-ranking) juvenile males lost at higher rates to sub-adult males and adult females. This suggests that the winners were not choosing the easiest individuals to supplant from the resource, but often supplanted those who presented the greatest future threat.

Finally, results presented here suggest that baboons supplanting at close rank are less selective about the resource, and are simply taking an opportunity to reinforce the existing asymmetries in a relationship. There is, however, an alternative explanation which interprets the results purely in terms of the value of the resource itself (Packer, pers. comm.). It can be argued that the effort expended in gaining a resource is related to its value (Clutton-Brock and Harvey, 1976; Popp and DeVore, 1979); the more valuable the resource, the more worthwhile it will be to contest its ownership. Likewise, the more valuable the resource, the harder the owner will defend it (Popp and DeVore, ibid.). The owner is often at an advantage at holding a resource, even against a more dominant animal, unless that animal is very much more dominant (Kummer, 1974). Thus, a baboon will only risk supplanting another from a valuable resource (a corm-digging site) when it greatly out-ranks the holder of that site.

The two competing explanations attribute the occurence of grass and corm supplants at different ranks either to the social value of the supplant or, alternatively, to the value of the resource. Is it possible to distinguish between them? The explanations make different assumptions which can be tested. The social value explanation assumes that grass supplants yield marginal nutritional benefit, and that corm-digging sites are not so valuable that a supplant can only be successful if the animals hold widely disparate ranks. One would predict, therefore, that the frequency of grass supplants would fall with increasing rank difference, and that the frequency of corm supplants would remain relatively constant. By contrast, the resource value explanation assumes that grass is sufficiently valuable to justify supplanting, but that corm-digging sites are of so much more value that supplants are only attempted at large rank differences. One would predict, under this explanation, that the frequency of grass supplants should remain relatively constant at all rank differences, but the frequency of corm supplants should rise with increasing rank difference. In other words, is the decrease in the proportion of grass supplants with increasing rank distance due primarily to the decreasing frequency of grass supplants or to the increasing frequency of corm supplants? Figure 7-8 shows the changes, as predicted by the two explanations, in the frequencies of the two types of supplants with increasing rank difference. Figure 7-9 shows the data from Figure 7-7 expressed as the frequency of grass supplants and the frequency of dig supplants per dyad at each rank distance.



social value



resource value

Figure 7-8. Frequency of grass and corm supplants at different rank distances, as predicted by the social value explanation and the resource value explanation.

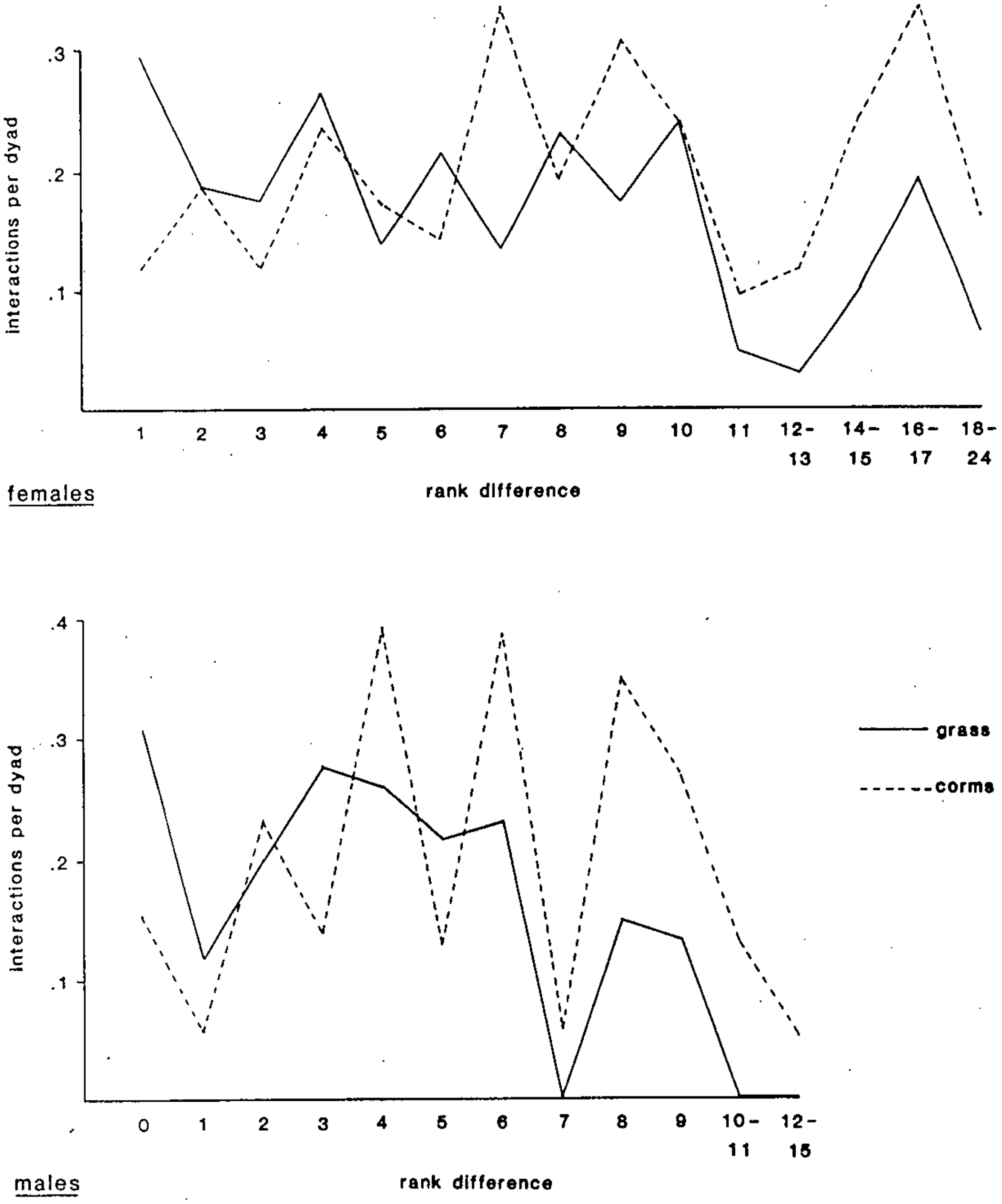


Figure 7-9. Frequency of grass and corm supplants at different rank distances, for males and females.

Table 7-6 shows the correlations between rank distance and rate of interaction.

	Grass	Corms
males	.6690*	.1509
females	.5574*	-.2129

Table 7-6. Correlations between the frequency of two types of supplant and rank distance.

There is no significant correlation between rates of corm supplants and rank distance. However, for both males and females, there is a significant correlation between the frequency of supplants over grass and rank distance. It is the fall in frequency of grass supplants with increasing rank which is responsible for the change in the proportions of grass to corm supplants, supporting the social value explanation.

This final result is pertinent to one aspect of the long debate on dominance. When we observe repeated and consistent dominance interactions between pairs of animals in a group, it is convenient to create a linear order in which each individual holds a rank. Bernstein (1981) and others have questioned whether the rank order is any more than a construction in the observer's mind, or whether animals actually rank one another.

Seyfarth provides the best evidence that monkeys not only distinguish between animals who are either higher- or lower-ranking than themselves, but also rank those other individuals. In two studies (1976, 1980), he showed that adult female baboons and adult female vervets responded differently to the grooming solicitations of other females. A rank order of their grooming preferences was consistent with the dominance ranks Seyfarth had assigned. He suggested possible benefits for individuals who distinguish the relative ranks of others (Seyfarth, 1977). High-ranking animals compete more effectively and have freer access to resources. Lower-ranking animals may be able to share some of those advantages by forming strong social bonds with those of high rank. They should therefore cultivate relationships with not just high<u>er</u> ranking, but the high<u>est</u> ranking individuals, if bonds are reflected in the formation of alliances, greater tolerance at preferred feeding sites, and so on. If grooming and other friendly interactions contribute to the formation of bonds, the distribution of these interactions should reflect the animal's ranking of the group.

Results presented here suggest that the distribution of agonistic behaviour, too, reflects the baboon's ability to assess relative rank. Rank changes generally occur between individuals of close rank. Observed cases of rank change in female baboons involved, or implicated, females or matrilines of adjacent rank (Nash, 1973; 1974; Smuts, 1980; in prep.). Likewise, among males, if size is the most important component in determining (juvenile) rank, males of similar size are a more likely source of future rank reversals than those of disparate size. In both sexes, it should benefit a baboon to rank other individuals not only according to the benefits high-ranking individuals could confer, as suggested by Seyfarth's results, but for the threat closely-ranked individuals pose.

Chapter 8

CONCLUDING REMARKS

A major theme in this thesis has been the persistence of a female baboon's direct and indirect influence beyond infancy and into the juvenile years of her offspring's life. Many juvenile relationships evident in this study had their origins in infancy, when the newborn's experience of the complex social environment of the troop is entirely mediated through its mother.

The first, of course, concerns the mother, herself. Despite the juvenile's complete nutritional and locomotive independence, the mother remains a vitally important social partner. This is true of daughters, whose relationships with their mothers persist into adulthood. But it is also true of sons, although they are within only a few years of leaving the troop and might be expected to contribute less to close relationships in the natal troop. The juvenile's mother was frequently found in the same area of the troop as her offspring, and she thus was available as a potential or actual ally in the juvenile's aggressive encounters. And although juveniles groomed widely outside the family, they appeared to be most successful in soliciting grooming within the family, particularly from their mothers.

Many of the juvenile's social relationships broadly reflect the mother's own relationships. Her older offspring will have been among the first and most frequent interaction partners with a new infant. This early familiarization with close kin initiates strong bonds - life-long for females - and, with them the opportunities for beneficial kin-directed behaviour. Although peers in the troop may share the same father, and therefore be as closely related as uterine siblings (Altmann, 1978b), the common association of the latter with their mother ensures that one set of close kin are familiar with one another. These maternally-related siblings form the closest relationships juveniles have with immatures of other age groups.

Relationships with siblings were characterized by proximity and grooming, and siblings were the source of the majority of aids observed. The bond between siblings was more than a coincident attraction for the mother; it endured between orphan siblings after a mother's death, and may have decreased the social costs of being orphaned.

Special relationships between adult males and adult females led to the formation of independent adult male-infant bonds (Nicolson, 1982; Smuts, 1982). For five of the juvenile subjects of this study, those bonds were still evident in proximity scores. In cases where those "special males" were no longer in the troop, the juvenile had no prominent adult male neighbour. The few bouts of grooming between juveniles and adult males were between these special pairs, but the juvenile was the active partner in these grooming bouts. There were very few examples of adult males aiding juveniles. If the juvenile benefitted from association with an adult male, the nature of the benefit was likely to be reduced aggression received from others in the vicinity of the male, or passive male tolerance of the juvenile at preferred feeding sites. For the two youngest orphans, whose special male from infancy was a conspicuously frequent neighbour, this passive protection may have been very valuable.

An adult female's associates tend to be those similar in rank (Seyfarth, 1977) who may also be close relatives. Some juveniles showed a tendency to associate with adult females who held ranks close to their mothers', but proximity and grooming with mature females was influenced to a greater extent by the female's reproductive stage. Juvenile males associated with and groomed sub-adult females in the inflating and deflating phases of their sexual cycle, and were groomed in return.

Juvenile females were attracted to lactating mothers, both as neighbours and as grooming partners. Interaction with such mothers appeared to be a means of interacting with the infants; the juvenile female did not appear to be using the presence of an infant as an opportunity to interact with unrelated females of higher rank (in contrast to Cheney, 1979a). In fact, juvenile grooming of lactating mothers covered a wider spectrum of adult female rank than grooming of non-lactating females, which was directed primarily up rank.

The mother's influence was most pervasive in affecting her offspring's rank, which in turn affected relationships the juvenile formed with other troop members, and the direction and frequency of the interactions. There were clear sex differences in the effect of maternal rank on offspring. Daughters were effectively limited in their interactions with others by their mother's rank. The frequency of winning or losing approach-withdraw interactions, attractiveness as a grooming partner, and access to other attractive grooming partners, were all influenced by the juvenile female's (maternal) rank.

In contrast, male size - or the age and experience which went with it - was the overriding factor which influenced the direction of interactions with peers. Juvenile males were influenced by their mother's ranks in their interactions with adult females, and in some interactions with younger females, but as they grew older, it appeared that they were no longer constrained by their mother's position in the adult female hierarchy; with increasing size males dominated females who out-ranked their mothers.

The process and timing of immature female rank acquisition in baboons is more, not less complicated by the results of this study. Cheney (1977) found that aiding behaviour was frequent during her study of chacma baboon juveniles. High-ranking mothers aided their offspring more often and with more success than did low-ranking mothers, and this appeared to be a major factor in the acquisition of juvenile rank. In contrast, both Lee and Oliver (1979) studying juveniles, and Walters (1980) studying sub-adults, concluded that direct aggressive intervention by the mother was not necessary to secure an immature female's rank.

In this study, aiding was seen so rarely that I am tempted to agree with the latter conclusion. But if rank acquisition does not require frequent active intervention by the mother, her presence still appears to be essential up to a certain age. Here, the data on the orphan and offspring of the Fallen females has been used to investigate aspects of the timing of rank acquisition and sex differences in this process.

The death of a mother or her loss in rank had no discernible effect on the rank of sons, underscoring the preeminence of size (age, or experience) in determining male rank. By the time a son was old enough to survive physically the loss of the mother, his independent rank was secure.

Juvenile females appeared to secure their own ranks, independent of their mothers, during their third year; the death of the mother before a female was two years old resulted in rank loss, whereas females whose mothers died after their third birthday retained the ranks consistent with their mother's rank. The effect of a mother's loss of rank was more damaging, and all daughters of the Fallen females appeared to have dropped in rank along with their mothers. It is puzzling that there was so little evidence of alliances in the study, yet the absence of a mother had a profound effect on rank. Her loss not only altered her daughter's agonistic rank from that which would be expected, but it altered the daugher´s participation in affiliative interactions. Orphaned females groomed less, and were less attractive as grooming partners.

The female hierarchy of a troop, despite its appearance of stability, is a dynamic structure, as evidenced by the rank changes which do occasionally occur. If high rank is correlated with higher reproductive success, females might be expected to try and improve their position in the troop. Yet the costs to a female of doing so may be greater than any possible increment to her lifetime reproductive success. In this study, when females fell in rank, entire families, not simply individuals, fell together. This means that the female seeking to improve her rank must come to dominate the entire family which out-ranks her. Female efforts seem, instead, to be concentrated on consolidating and transmitting to their daughters the position they already hold, rather than improving it. Juvenile females are already participating in upholding that structure, as well as securing an independent place within it. That they were supplanted in particular by the females of all age-sex classes suggests that older, higher-ranking females are actively perpetuating the existing rank order across generations by supplanting their daughters´ peers. The juvenile females themselves were also selective in their supplanting: supplants of a "social" rather than a "nutritional" nature were more prevalent at close rank differences; close ranking individuals and their families are the most likely source of rank reversals (Nash, 1973, 1974;

Smuts, 1980).

The supplants between juvenile males who were close in rank were also more often of a "social" nature. Males, like females appeared to expend effort to reinforce assymetries in relationships with those individuals who posed the greatest threat of rank reversals. It is not immediately clear why this should be so, nor why juvenile males should be subject to specific competition from older males and adult females. Juvenile males, after all, will make little contribution to the future structure of relationships within the troop, unlike the females. The males will transfer out of the troop; a male must become integrated into at least two troops in his lifetime, and it will be the post-transfer relationships in other troops which determine how successful he will be at mating.

An insight may be gained from Wrangham's model of the evolution of matrilineal ("female bonded") primate groups (1980). He argued that although many factors will influence adult reproduction, different key resources are uniquely valuable to the two sexes as adults. For breeding males, fertile females are the resource which sets limits to their reproductive success. In baboons, male competition for access to females and behaviour patterns used to guard them from rival males have received much attention (Packer, 1979b). Latterly, maintaining a relationship with a particular female has been recognized as another component of male reproductive strategy (Smuts, 1982). In short, adult male strategy is primarily dependent upon affiliative and agonistic relationships with both females and males; social competition to a social end. In contrast, the key resource for females is an environmental rather than a social one. Wrangham concluded that sufficient food to sustain reproduction is the key resource which sets limits on female reproductive success; in other words, social competition to a nutritional end.

But it appears that the situation is nearly reversed during the juvenile period. Juvenile females compete to secure a social position which will enhance their access to resources as adults. Males, while young, compete with other troop members for access to resources before they transfer to a new troop and there compete for a social position.

Males and females begin to diverge in size during the juvenile period. The males have ahead of them their adolescent growth "spurt"; they also continue growing for a longer period than do females. Prior to transfer, the dominance rank of young males increases rapidly when they attain full size, and size correlates with post-transfer male rank (Packer, 1977). The rank order among pre-transfer males, therefore, seems to reflect current competition in the natal troop for resources which ensure and could accelerate the process of growth.

With increasing age, males compete more and more effectively against female troop members. While increasing size is certainly a factor in this, relative size is not; juvenile males dominated females larger than themselves, including their own sisters. As a baboon mother has only a limited number of years during which she may invest in her sons, as opposed to life-long contact with her daughters (Clutton-Brock, _et al._, 1981), she may be preferentially assisting sons to dominate both other troop members and their sisters.

Many questions are unanswered in this study; in particular, the timing and process of juvenile female rank acquisition is unresolved. For humanitarian reasons, field studies seeking to use the disruption of this process as a means to understand its mechanism must remain opportunistic.

Other issues raised by the results of this study centre around the influence of a baboon mother and the alternative strategies by which an adult female enhances her personal and inclusive fitness. Adult females differ in their ability to assist and defend their offspring, and they may adjust the sex ratio of their offspring accordingly. For primates, research has emphasized female differences associated with rank. A low-ranking female may experience lower reproductive success; she will pass both her low rank and the reproductive disadvantages associated with it to her daughters, who remain in the troop. In contrast, juvenile and sub-adult males appear already to be emancipated from the effects of maternal rank; in any case, they will transfer to another troop, away from any remaining constraints of their mother's low status. Low-ranking females might be expected to give birth to sons, and high-ranking females to daughters; there is evidence that this is the case (Altmann, 1980; Silk et al., 1981; Simpson and Simpson, 1982). But results of this study indicate that a mother's death can also drastically affect the future of her daughters. Age, as well as rank, will be a factor which influences a mother's ability to assist her offspring. We may soon have life-time reproductive data on the females of a few primate groups. It is possible that the sex ratio of offspring becomes biased towards sons as an ageing female becomes less likely to survive the two to three years necessary to secure a daughter's rank within the troop.

The long-term consequences of juvenile experience will be difficult to disentangle from the many other complex factors which impinge upon the individual. The life-spans of baboons and their researchers are similar enough that we must often rely on a composite picture of baboon relationships based on a few years in the lives of many individuals. But the diversity of these individuals and the relationships they form will be best appreciated through studies of sufficient length that the details of the animal's history, kinship, and past relationships can be taken into account.

Philip Whitfield 1984

REFERENCES

Alexander, B.K. 1970. Parental behavior of adult male Japanese monkeys. Behaviour 36:270-285.

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49:227-265.

Altmann, J. 1978a. Infant independence in yellow baboons. In: The Development of Behavior: Comparative and Evolutionary Aspects, ed. G.M. Burghardt and M. Bekoff. New York: Garland.

Altmann, J. 1978b. Age cohorts as paternal sibships. Behav. Ecol. Sociobiol. 6:161-164.

Altmann, J. 1980. Baboon Mothers and Infants, Cambridge, Mass: Harvard University Press.

Altmann, J., S.A. Altmann, G. Hausfater, and S.A. McCuskey. 1977. Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. Primates 18: 315-330.

Altmann, S.A. 1970. The pregnancy sign in savannah baboons. Lab. Anim. Digest 6:6-10.

Altmann, S.A., and J. Altmann. 1970. Baboon Ecology: African Field Research. Chicago: University of Chicago Press.

Altmann, S.A. and J. Altmann. 1979. Demographic constraints on behavior and social organization. In: Ecological Influences on Social Organization, ed. I.S. Bernstein and E.O. Smith. New York: Garland STPM.

Angst, W. 1975. Basic data and concepts on the social organization of Macaca fascicularis. In: Primate Behavior: Developments in Field and Laboratory Research, vol. 4, ed. L.A. Rosenblum. New York: Academic Press.

Bateson, P. 1983. Optimal outbreeding. In: Mate Choice, ed. P. Bateson. Cambridge: Cambridge University Press.

Berman, C.M. 1978. The development of social relationships in free-ranging infant rhesus monkeys. PhD Thesis. Cambridge.

Bernstein, I.S. 1969. Stability of the status hierarchy in a pigtail monkey group (Macaca nemestrina). Anim. Behav. 17:452-458.

Bernstein, I.S. 1970. Primate status hierarchies. In: Primate Behavior, vol. 1, ed. L.A. Rosenblum. New York: Academic Press.

Bernstein, I.S. 1981. Dominance: the baby and the bathwater. Brain Behav Sci 4(3):419-429.

Blankenship, L. and S. Qvortrup. 1974. Resource management on a Kenya ranch. Ann. of the S. Afr. Wild. Manage. Assn. 4:185-190.

Blurton-Jones, N.G. and M.J. Konner. 1973. Sex differences in the behavior of Bushman and London two- to five-year-olds. In: Comparative Ecology and Behavior of Primates, ed. J. Crook and R. Michael. New York: Academic Press.

Boelkins, R.C., and A.P. Wilson. 1972. Intertroop social dynamics of the Cayo Santiago rhesus (Macaca mulatta) with special reference to changes in group membership by males. Primates 13:125-140.

Bolwig, N. 1959. A study of the behavior of the chacma baboon. Behaviour 14:136-163.

Bramblett, C.A. 1978. Is the concept of ´control group´ valid? A quantitative comparison of the behavior of caged baboon groups. Am. J. Phys. Anthropol. 49(2):217-226.

Busse, C., and W.J. Hamilton III. 1981. Infant carrying by male chacma baboons. Science 212:1282-1283.

Bygott, J.D. 1979. Agonistic behavior, dominance and social structure in wild chimpanzees of Gombe National Park. In: The Great Apes, ed. D.A. Hamburg and E.R. McCown. Menlo Park: Benjamin/Cummings.

Byles, R.H., and M.F. Sanders. 1980. Morphological variation in a population of Kenyan olive baboons. Am J. Phys. Anthropol. 52: 210.

Byles, R.H., and M.F. Sanders. 1981. Genetic variation in olive baboons (abstr.). Am J. Primatol. 1(3):334.

Chapais, B., and S.R. Schulman. 1980. An evolutionary model of female dominance relations in primates. J. Theoret. Biol. 82: 47-89.

Cheney, D. 1976. The social development of immature male and female baboons. Ph.D. thesis, Cambridge University.

Cheney, D.L. 1977. The acquisition of rank and development of reciprocal alliances among free-ranging immature baboons. Behav. Ecol. Sociobiol. 2(3):303-318

Cheney, D.L. 1978a. Interactions of immature male and female baboons with adult females. Anim. Behav. 26:389-408.

Cheney, D.L. 1978b. The play partners of immature baboons. Anim. Behav. 26:1038-1050.

Cheney. D.L., P.C. Lee, and R.M. Seyfarth. 1981. Behavioral correlates of non-random mortality among free-ranging female vervet monkeys. Behav. Ecol. Sociobiol. 9:153-161.

Clutton-Brock, T.H., and P.H. Harvey. 1976. Evolutionary rules and primate societies. In: *Growing Points in Ethology*, ed. P.P.G. Bateson. Cambridge: Cambridge University Press.

Clutton-Brock, T.H., S.D. Albon, and F.E.Guinness. 1981. Parental investment in male and female offspring in polygynous mammals. *Nature* *289*:487-489.

Collins, D.A. 1981. Behaviour and patterns of mating among yellow baboons (*Papio* *c*. *cynocephalus*, *L*. 1766). PhD Thesis. University of Edinburgh.

Collins, D.A. 1984. Spatial pattern in a troop of yellow baboons (*Papio cynocephalus*) in Tanzania. *Anim*. *Behav*. *32*(2):536-553.

Collins, D.A. in press. Interactions between adult male and infant yellow baboons (*Papio* *c*. *cynocephalus*) in Tanzania.

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.

Dawkins, R. 1976. *The Selfish Gene*. Oxford: Oxford University Press.

Deag, J.M. 1977. Aggression and submission in monkey societies. *Anim*. *Behav*. *25*:465-474.

Deag, J.M., and J.H. Crook. 1971. Social behavior and agonistic buffering in the wild Barbary macaque, *Macaca sylvanus*. *Folia Primatol*. *15*:183-200.

DeVore, I. 1963. Mother-infant relations in free-ranging baboons In: *Maternal Behavior in Mammals*, ed H.L. Rheingold. New York: Wiley.

DeVore, I. 1965. Male dominance and mating behavior in baboons. In: *Sex and Behavior*, ed. F.A. Beach. New York: Wiley.

DeVore, I., and S. L. Washburn. 1964. Baboon ecology and human evolution. In: *African Ecology and Human Evolution*, ed. F.C. Howell and F. Bourliere. Chicago: Aldine.

DeVore, I., and K.R.L. Hall. 1965. Baboon Ecology. In: *Primate Behavior: Field Studies of Monkeys and Apes*, ed. I. DeVore. New York: Holt.

DeWaal, F.B.M. 1977. The organization of agonistic relations within two captive groups of Java monkeys (*Macaca fascicularis*). *Z*. *Tierpsychol*. *44*:225-282.

Dittus, W.P.J. 1975. Population dynamics of the toque monkey, (*Macaca sinica*). In: *Socioecology and Psychology of Primates*, ed. R.H. Tuttle. The Hague: Moulton.

Dittus, W.P.J. 1977. The social regulation of population density and age-sex class distribution in the Toque monkey. Behaviour 63:281-322.

Dittus, W.P.J. 1979. The evolution of behaviors regulating density and age-specific ratios in a primate population. Behaviour 69: 265-302.

Draper, P. 1976. Social and economic constraints on child life among the !Kung. In: Kalahari Hunter-gatherers, ed. R.B. Lee and I. DeVore. Cambridge, Mass: Harvard University Press.

Drickamer, L. 1974. A ten-year summary of reproductive data for free-ranging Macaca mulatta. Folia Primatol. 21:61-80.

Dunbar, R.I.M. 1980. Determinants and evolutionary consequences of dominance among female gelada baboons. Behav. Ecol. Sociobiol. 7:253-265.

Dunbar, R.I.M., and E.P. Dunbar. 1977. Dominance and reproductive success among female gelada baboons. Nature 266:351-353.

Dunbar, R.I.M., and M. Sharman. 1984. Is social grooming altruistic? Z. Tierpsychol. 64:163-173.

Fairbanks, L.A. 1980. Relationships among adult females in captive vervet monkeys: testing a model of rank-related attractiveness. Anim. Behav. 28:853-859.

Gartlan, J.S. 1964. Dominance in East African monkeys. Proc. E. Afr. Acad. 2: 75-79.

Gartlan, J.S. 1968. Structure and function in primate society. Folia. Primatol. 8:89-120.

Gouzoules, H. 1975. Maternal rank and early social interactions of the infant stumptail macaque, Macaca arctoides. Primates 16: 405-418.

Gouzoules, H. 1980. A description of genealogical rank changes in a troop of Japanese monkeys. Primates 21(2):262-267.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28:1140-1162.

Groves, C.P. 1972. Phylogeny and classification of primates In: Pathology of simian primates, part 1, ed. M. F iennes. Basel: Karger.

Hall, K.R.L. 1963. Variations in the ecology of the chacma baboon Papio ursinus. Symp. Zool. Soc. Lond. 10:1-28.

Hall, K.R.L. 1965. Social organization of the Old World monkeys and apes. Symp. Zool. Soc. Lond. 14:265-289.

Hall, K.R.L., and I. DeVore. 1965. Baboon social behavior. In:

Primate Behavior: Field Studies of Monkeys and Apes, ed. I. DeVore. New York: Holt.

Hamilton, W.D. 1964. The genetical theory of social behavior, parts I and II. J. Theor. Biol. 7(1):1-51.

Haraway, D. 1978. Animal sociology and a natural economy of the body politic. Part II: The past is the contested zone: Human nature and theories of production and reproduction in primate behavior studies. Signs 4(1):37-60.

Harding, R.S.O. 1973. Predation by a troop of olive baboons (P. anubis). Am. J. Phys. Anthropol. 38:587-591.

Harding, R. S. O. 1976. Ranging patterns of a troop of baboons (Papio anubis) in Kenya. Folia Primatol 25:143-185.

Hasegawa, T., and M. Hiraiwa. 1980. Social interactions of orphans observed in a free-ranging troop of Japanese monkeys. Folia Primatol. 33:129-158.

Hausfater, G. 1975. Dominance and reproduction in baboons (Papio cynocephalus): a quantitative analysis. Contributions to Primatology, vol. 7. Basel: Karger.

Hausfater, G., J. Altmann, and S. Altmann. 1982. Long-term consistency of dominance relations among female baboons (Papio cynocephalus). Science 217:752-755.

Hendrickx, A.G., and D.C. Kraemer. 1969. Observations of the menstrual cycle, optimal mating time, and preimplantation embryos of the baboon, Papio anubis and Papio cynocephalus. J. Reproduct. Fertil. Suppl. 6:119-128.

Hill , W.C.O. 1970. Primates: Comparative Anatomy and Taxonomy. 8: Cynopithecinae. Edinburgh: Edinburgh University Press.

Hinde, R.A. 1976. Interactions, relationships and social structure. Man 11:1-17.

Hinde, R.A. 1977. On assessing the basis of partner preferences. Behaviour 62;1-9.

Hinde, R.A. 1978. Dominance and role - two concepts with dual meaning. J. Soc. Biol. Struct. 1;27-38.

Hinde, R.A., and Spencer-Booth, Y. 1967. The behaviour of socially living rhesus monkeys in their first two and a half years. Anim. Behav. 15:169-196.

Hinde, R.A., and Spencer-Booth, Y. 1971. Towards understanding individual differences in rhesus mother-infant interaction. Anim. Behav. 19:165-173.

Hinde, R.A., and J. Stevenson-Hinde. 1976. Towards understanding relationships; dynamic stability. In: Growing Points in

Ethology, ed. P.P.G. Bateson and R.A. Hinde. Cambridge; Cambridge University Press.

Hinde, R.A., and L.P. Proctor. 1977. Changes in the relationships of captive rhesus monkeys on giving birth. *Behaviour* *61*(3-4);304-321.

Hinde, R.A., and S. Datta. 1981. Dominance; an intervening variable. *Brain Behav. Sci.* *4*(3);442.

Hrdy, S.B. 1981. *The Woman That Never Evolved*. Cambridge: Harvard University Press.

Hrdy, S.B., and G.C. Williams. 1983. Behavioural biology and the double standard. In: *Social Behaviour of Female Vertebrates*, ed. S.K. Wasser. New York: Academic Press.

Humphrey, N.K. 1976. The social function of intellect. In: *Growing Points in Ethology*, ed. P.P.G. Bateson and R.A. Hinde. Cambridge: Cambridge University Press.

Hutchins, M., and D.P. Barash. 1976. Grooming in primates: implications for its utilitarian function. *Primates* *17*:145-150.

Jay, P.C. 1965. The common langur in North India. In: *Primate Behavior*, ed. I. DeVore. New York: Holt.

Jolly, A. 1966. Lemur social behaviour and primate intelligence. *Science* *153*:501-506.

Jolly, C.F., and F.L. Brett. 1973. Genetic markers and baboon biology. *J. med. Prim.* *2*:85-99.

Kaufmann, J.H. 1967. Social relations of adult males in a free-ranging band of rhesus monkeys. In: *Social Communication Among Primates*, ed. S.A. Altmann. Chicago: University of Chicago Press.

Kawai, M. 1965. On the system of social ranks in a natural troop of Japanese monkeys, I and II. In: *Japanese Monkeys: A Collection of Translations*, ed. S.A. Altmann. Published by the editor.

Kawamura, S. 1965. Matriarchal social ranks in the Minoo-B troop: a study of the rank system of Japanese monkeys. In: *Japanese Monkeys: A Collection of Translations*, ed. S.A. Altmann. Published by the editor.

Koford, C.B. 1963. Rank of mothers and sons in bands of rhesus macaques. *Science* *141*:356-357.

Koyama, N. 1967. On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. *Primates* *8*:189-216.

Koyama, N. 1970. Changes in dominance rank and division of a wild Japanese monkey troop in Arashiyama. *Primates* *11*:335-390.

Kummer, H. 1967. Tripartite relations in hamadryas baboons. In: Social Communication Among Primates, ed. S.A. Altmann. Chicago: University of Chicago Press.

Kummer, H. 1968. Social organisation of Hamadryas baboons. Bibl. Primatol. vol. 6. Basel: Karger.

Kurland, J.A. 1977. Kin Selection in the Japanese monkey. Contributions to Primatology. vol. 12. Basel: Karger.

Lee, P.C. 1983. Species, Study Sites, and Methods. In: Primate Social Relationships. ed. R.A. Hinde. Oxford: Blackwell Scientific Publications.

Lee, P.C., and J.I. Oliver. 1979. Competition, dominance, and the acquisition of rank in juvenile yellow baboons (Papio cynocephalus). Anim. Behav. 27:576-585.

Lindburg, D.G. 1971. The rhesus monkey in North India: an ecological and behavioral study. In: Primate Behavior, vol. 2. Academic Press: New York and London.

Lindburg, D.G. 1973. Grooming behavior as a regulator of social interactions in rhesus monkeys. In: Behavioral Regulators of Behavior in Primates, ed. C.R. Carpenter. Lewisburg: Bucknell University Press.

Maples, W.R. 1972. Systematic reconsideration and a revision of the the nomenclature of Kenya baboons. Am. J. Phys. Anthro. 36:9-20.

Marsden, H.M. 1968. Agonistic behaviour of young rhesus monkeys after changes induced in social rank of their mothers. Anim. Behav. 16:38-44.

Missakian, E.A. 1972. Genealogical and cross-genealogical dominance relations in a group of free-ranging monkeys on Cayo Santiago Primates 13:169-180.

Moore, J. 1978. Dominance relations among free-ranging female baboons in Gombe National Park, Tanzania. In: Recent Advances in Primatology, vol. 1. ed. D.J. Chivers and J. Herbert. London: Academic Press.

Moore, J., and R. Ali. 1984. Are dispersal and inbreeding avoidance related? Anim. Behav. 32:94-112.

Mori, A. 1975. Intra-troop spacing mechanisms of wild Japanese monkeys of the Koshima troop. Primates 16:107-140.

Nagel, U. 1973. A comparison of anubis baboons, hamadryas baboons, and their hybrids at a species border in Ethiopia. Folia. Primatol. 19:104-165.

Nash, L.T. 1973. Social behavior and social development in baboons, Papio anubis, at Gombe Stream National Park. PhD Thesis, University of California, Berkeley.

Nash, L.T. 1974. Parturition in a feral baboon, Papio anubis. Primates 15:279-285.

Nicolson, N.A. 1982. Weaning and the development of independence in olive baboons. PhD Thesis, Harvard.

Nie, N.H. 1970. SPSS: Statistical Package for the Social Sciences. New York: McGraw-Hill.

Nowell, L.H., and A.G. Heidrich. 1978. Factors affecting dominance relationships in adult female baboons. In: Recent Advances in Primatology, vol. 1, ed. D.J. Chivers and J. Herbert. London: Academic Press.

Oliver, J.I., and P.C. Lee. 1978. Comparative aspects of the behaviour of juveniles in two species of baboon in Tanzania. In: Recent Advances in Primatology, vol. 1. ed. D.J. Chivers and J. Herbert. London: Academic Press.

Owens, N.W. 1973. The development of behaviour in free-living baboons. PhD Thesis. Cambridge.

Owens, N.W. 1975. A comparison of aggressive play and aggression in free-living baboons, Papio anubis. Anim. Behav. 23:757-765.

Owens, N.W. 1976. The development of sociosexual behaviour in free-living baboons, Papio anubis. Behaviour 62(3-4):241-259.

Packer, C. 1975. Male transfer in olive baboons. Nature 225:220.

Packer, C. 1977. Reciprocal altruism in Papio anubis. Nature 265: 441-443.

Packer, C. 1979a. Inter-troop transfer and inbreeding avoidance in Papio anubis. Anim. Behav. 27:1-36.

Packer, C. 1979b. Male dominance and reproductive activity in Papio anubis. Anim. Behav. 27:37-45.

Packer, C. 1980. Male care and exploitation of infants in Papio anubis. Anim. Behav. 28:512-520.

Popp, J.L. and I. DeVore. 1979. Aggressive competition and social dominance theory: synopsis. In: The Great Apes, ed. D.A. Hamburg and E.R. McCown. Menlo Park: Benjamin/Cummings.

Post, D.G. 1978. Feeding and ranging behavior of the yellow baboon (Papio cynocephalus). PhD Thesis, Yale.

Post, D.G. 1981. Activity patterns of the yellow baboon (Papio Cynocephalus) in the Amboseli National Park, Kenya. Anim. Behav. 29: 357-374.

Post, D.G. 1982. Feeding behavior of yellow baboons (Papio cynocephalus) in the Amboseli National Park, Kenya. Int. J. Primatol. 3(4):403-430.

Post, D.G., G. Hausfater, and S.A. McCuskey. 1980. Feeding behavior of yellow baboons (*Papio cynocephalus*): Relationship to age, gender, and dominance rank. *Folia Primatol*. *34*:179-195.

Ransom, T.W. 1971. Ecology and behavior of the baboon, *Papio anubis*, at the Gombe Stream National Park, Tanzania. PhD Thesis, University of California, Berkeley.

Ransom, T.W. 1981. *Beach Troop of the Gombe*. East Brunswick: Associated University Presses.

Ransom, T.W., and B.S. Ransom. 1971. Adult male-infant relations among baboons (*Papio anubis*). *Folia Primatol*. *16*:179-195.

Ransom, T.W., and T.E. Rowell. 1972. Early social development of feral baboons. In: *Primate Socialization*, ed. F. Poirier. New York: Random House.

Rasmussen, D.R. 1979. Correlates of patterns of range of use of a troop of yellow baboons (*Papio cynocephalus*) 1. Sleeping sites, impregnable females, births and male emigration and immigration. *Anim*. *Behav*. *27*:1098-1113.

Rasmussen, D.R. 1981. Communities of Baboon Troops (*Papio cynocephalus*) in Mikumi National Park, Tanzania. *Folia Primatol*. *36*:232-242.

Rasmussen, K.L.R. 1981. Consort behaviour and mate selection in yellow baboons (*Papio cynocephalus*) (abstract). *Am*. *J*. *Primatol* *1*(3):350.

Rhine, R.J., and B.J. Westlund. 1978. The nature of a primary feeding habit in different age-sex classes of yellow baboons (*Papio cynocephalus*). *Folia Primatol*. *30*:64-79.

Rhine, R.J., Forthman, D.L., Stillwell-Barnes, R., Westlund, B.J., and Westlund, H.D. 1979. Movement patterns of yellow baboons (*Papio cynocephalus*): the location of subadult males. *Folia Primatol*. *32*:241-251.

Rhine, R.J., G.W. Norton, W.J. Roertgen, H.D. Klein. 1980. The brief survival of free-ranging baboon infants (*Papio cynocephalus*) after separation from their mothers. *Int*. *J*. *Primatol*. *1*(4):401-409.

Richards, S.M. 1974. The concept of dominance and methods of assessment. *Anim*. *Behav*. *22*:914-930.

Robinson, B.N., G.D. Anderson, E. Cohen, W.F. Gazdzik, L.C. Karpel, A.H. Miller, and J.R. Stein. 1980. Sir: Scientific Information Retrieval. Evanston: Sir Inc.

Rowell, T.E. 1966a. Forest living baboons in Uganda. *J*. *Zool*. London, 149:344-364.

Rowell, T.E. 1966b. Hierarchy in the organization of a captive baboon group. *Anim Behav*. *14*:430-443.

Rowell, T.E. 1967. A quantitative comparison of the behaviour of a wild and a caged baboon group. Anim. Behav. 15:499-509.

Rowell, T. 1969. Long-term changes in a population of Ugandan Baboons. Folia Primatol. 11:241-254.

Rowell, T.E. 1972a. Female reproductive cycles and social behaviour in primates. Adv. in the Study of Behaviour. vol. 4:69-105.

Rowell, T.E. 1972b. Social Behaviour of Monkeys. Harmondsworth: Penguin Books.

Rowell, T.E. 1974. The concept of social dominance. Behav. Biol. 11:131-154.

Rowell, T.E., N.A. Din, and A. Omar. 1968. The social development of baboons in their first three months. J. Zool. 155:461-483.

Saayman, G.S. 1971. Grooming behaviour in a troop of free-ranging chacma baboons. Folia Primatol. 16:161-178.

Sade, D.S. 1965. Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. Amer. J. Phys. Anthro. 23:1-18.

Sade, D.S. 1967. Determinants of dominance in a group of free-ranging rhesus monkeys. In: Social Communication among Primates, ed. S.A. Altmann. Chicago: University of Chicago Press

Sade, D.S. 1972. A longitudinal study of social behaviour in rhesus monkeys. In: The Functional and Evolutionary Biology of Primates, ed. R. Tuttle. Aldine, Chicago.

Sade, D.S., K. Cushing, P. Cushing, J. Dunaif, A. Figueroa, J. Kaplan, C. Lauer, D. Rhodes, and J. Schneider. 1977. Population dynamics in relation to social structure on Cayo Santiago. Yrbk. Phys. Anthrop. 20(1976):253-262.

Schulman, S.R. and B. Chapais. 1980. Reproductive value and rank relations among macaque sisters. Am. Nat. 115(4):580-593.

Seyfarth, R.M. 1975. Social relationships among adults in a troop of free-ranging baboons (Papio cynocephalus ursinus). PhD thesis, Cambridge.

Seyfarth, R.M. 1976. Social relationships among adult female baboons. Anim. Behav. 24:917-938.

Seyfarth, R.M. 1977. A model of social grooming among adult female monkeys. J. Theoret. Biol. 65:671-698.

Seyfarth, R.M. 1978a. Social relationships among adult male and female baboons, I: Behaviour during sexual consortship.

Behaviour 64(3-4):204-226.

Seyfarth, R.M. 1978b. Social relationships among adult male and female baboons. II: Behaviour throughout the female reproductive cycle. Behaviour 64:227-247.

Seyfarth, R.M. 1980. The distribution of grooming and related behaviours among adult female vervet monkeys. Anim. Behav. 28: 798-813.

Seyfarth, R.M. 1983. Grooming and social competition in primates. In: Primate Social Relationships, ed. R.A. Hinde. Oxford: Blackwell Scientific Publications.

Seyfarth, R.M., D. Cheney, and R.A. Hinde. 1987. Some principles relating social interaction and social structure among primates. In: Recent Advances in Primatology, vol 1. ed. D.J. Chivers and J. Herbert. London: Academic Press.

Siegel, S. 1956. Non-parametric Statistics for the behavioral Sciences: International student edition. Tokyo: McGraw-Hill Kogakusha.

Silk, J.B. 1982. Altruism among female Macaca radiata: explanations and analysis of patterns of grooming and coalition formation. Behaviour 79:162-188.

Silk, J.B. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. Am. Nat. 121:56-66.

Silk, J.B., C. Clark-Wheatly, P. Rodman, and A. Samuels. 1981a. Differential reproductive success among female Macaca radiata: a longitudinal analysis. Anim. Behav. 29:1106-1120.

Silk, J.B., A. Samuels, and P. Rodman. 1981b. Hierarchical organisation of female Macaca radiata in captivity. Primates 22(1):85-95.

Simmonds, P.E. 1965. The bonnet macaque in South India. In: Primate Behavior, ed, I. DeVore. New York: Holt, Rinehart and Winston.

Simmonds, P.E. 1974. The Social Primates. Harper & Row, New York.

Simpson, M.J.A. 1973. The social grooming of male chimpanzees. In: Comparative Ecology and Behaviour of Primates, ed. R.P. Michael and J.H. Crook. London: Academic Press.

Simpson, M.J.A. and A.E. Simpson. 1982. Birth sex ratios and social rank in rhesus monkey mothers. Nature, 300(5891):440-441.

Smuts, B. 1980. Changes in dominance relationships among adult female baboons. Paper presented at the Annual Meeting of the Animal Behaviour Society. Fort Collins, Colorado. June 9-13, 1980.

Smuts, B. 1982. Special relationships between adult male and female olive baboons (Papio anubis). PhD thesis, Stanford Univesity.

Smuts, B. 1983. Dynamics of "Special Relationships" between adult male and female olive baboons. In: Primate Social Relationships. ed. R.A. Hinde. Oxford: Blackwell Scientific Publications.

Smuts, B. In prep. Loss of high rank in adult female baboons.

Sparks, J. 1967. Allogrooming in primates: a review. Primate Ethology, ed. D. Morris. Aldine: Chicago.

Stein, D. M., and P.B. Stacey. 1981. A comparison of infant-adult male relations in a one-male group with those in a multi-male group for Yellow Baboons (Papio cynocephalus). Folia Primatol. 36:264-276.

Struhsaker, T.T. 1967. Ecology of Velvet monkeys (Cercopithecus aethiops) in the Masai-Amboseli Game Reserve, Kenya. Ecology 48:891-904.

Stoltz, L.P., and G.S. Saayman. 1970. Ecology and behaviour of Baboons in the Northern Transvaal. Ann. of the Transvaal Museum 26(5):99-143.

Strum, S.C. 1975. Primate predation: interim report on the development of a tradition in a troop of Olive baboons. Science 187:755-757.

Strum, S.C. 1976. Primate predation and bioenergetics. Science 191:314-317.

Strum, S.C. 1983. Baboon cues for eating meat. J. Hum. Evol. 12:327-336.

Sugiyama, Y. 1976. Life history of male Japanese monkeys. Adv. Stud. Behav. 7:255-284.

Symons, D. 1978. Play and Aggression: A Study of Rhesus Monkeys. New York: Columbia University Press.

Trivers, R.L. 1972. Parental investment and sexual selection. In: Sexual Selection and the Descent of Man. ed. B. Campbell. London: Heinemann.

van-Lawick Goodall, J. 1971. In The Shadow Of Man. Houghton Boston, Mass.

Walters, J. 1980. Interventions and the development of dominance relationships in female baboons. Folia Primatol. 34: 61-89.

Walters, J. 1981. Inferring kinship from behaviour: maternity determinations in yellow baboons. Anim. Behav. 29:126-136.

Washburn, S.L., and I. DeVore. 1961a. The social life of baboons. Sci. Am. 204:62-71.

Washburn, S.L., and I. DeVore. 1961(b). Social behaviour of baboons and early man. In: Social Life of Early Man. ed. S.L. Washburn. Chicago: Aldine.

Washburn, S.L., and D.A. Hamburg. 1968. Aggressive behaviour in old world monkeys and apes. In: Primates: Studies in Adaptation and Variability. ed. P.C. Jay. New York: Holt, Rinehart & Winston.

Wasser, S.K. 1983. Reproductive competition and cooperation among female yellow baboons. In: Social Behavior of Female Vertebrates. New York: Academic Press.

Wilson, E.O. 1975. Sociobiology: The New Synthesis. Cambridge: Harvard University Press.

Wrangham, R.W. 1980. An ecological model of female-bonded primate groups. Behaviour 75:262-299.

Wrangham, R.W. 1981. Drinking competition among vervet monkeys. Anim. Behav. 29:904-910.

Yamada, M. 1963. A study of blood relationships in the natural society of the Japanese macaque. Primates. 4:43-65.

Yamada, M. 1966. Five natural troops of Japanese monkeys in Shodoshima Island, (1): distribution and social organisation. Primates. 7:315-362.

Zuckerman, S. 1932. The Social Life of Monkeys and Apes. Kegan Paul, London.

Appendix 1.

KEY TO BABOON NAMES AND INITIALS

Name	Initials	Name	Initials
Achilles	AC	Electra	EK
Alexander	AA	Erato	ET
Andrus	AX	Eryx	EX
Archimedes	AR	Eudora	EU
Argus	AG	Euphoria	ER
Aristotle	AS	Europa	EP
Artemis	AT	Galatea	GT
Athena	AN	Hadrian	HA
Aurora	AU	Handel	HD
Bacchus	BA	Hector	HC
Boz	BZ	Helen	HN
Caesar	CE	Hera	HH
Calliope	CO	Hermes	HS
Calypso	CP	Hespera	HR
Cera	CA	Hippo	HI
Cercerus	CU	Hippocrates	GR
Chaos	CS	Iacchus	IA
Charybdis	CY	Icarus	IC
Chloe	CH	Iolanthe	IO
Cicero	CR	Iona	IN
Cicily	CL	Iphigenia	IP
Circe	CI	Isadora	IS
Clea	CC	Isis	II
Cressida	CD	Ithaca	IT
Cybele	CB	Jackie O	JK
Cygne	CG	Jocasta	JO
Daedalus	DS	Julia	JL
Damocles	DC	Juno	JN
Danae	DN	Justine	JU
Danko	DK	Laertes	LA
Dante	DT	Leda	LE
Daphne	DP	Lesbos	LB
Delphi	DL	Levon	LN
Demetrius	DM	Ligeia	LG
Despoena	DE	Lily	LL
Dido	DD	Lisa	LS
Diodorus	DO	Livy	LV
Dionysius	DI	Louise	LU
Drachma	DR	Lycus	LC
Echo	EO	Lydia	LY

Name	Initials
Lysistrata	LI
Maia	MA
Mars	MR
Medea	MM
Medusa	MS
Melia	ME
Melina	ML
Midas	MD
Minerva	MN
Minos	MO
Minthe	MT
Moussaka	MK
Myrine	MY
Neis	NE
Nemesis	NM
Neptune	NP
Niobe	NB
Nysa	NY
Octavia	OC
Olympia	OL
Ophelia	OP
Orpheus	OR
Ouzo	OZ
Ovid	OV
Pallas	PS
Pan	PN
Pandora	PX
Pasithea	PA
Pegasus	PE
Phaedra	PH
Phoebe	PO
Pleiades	PX
Plutarch	PT
Pomona	PM
Poseidon	PD
Priapus	PP
Psophis	PI
Psyche	PY
Pyrrha	PR
Rex	RX
Rhea	RH
Rhesus	RS
Rhoda	RD
Sherlock	SK
Socrates	SC
Sparta	SP
Sphinx	SX
Terpsichore	TC
Thalia	TH
Thespia	TS
Tiberius	TB
Triton	TN
Urania	UR
Vesta	VT
Vesuvius	VS
Vulcan	VU
Xuthus	XU
Xylia	XY
Zagreus	ZG
Zandra	ZD
Zarathustra	ZA
Zena	ZN
Zeke	ZK
Zimmerman	ZM
Zizi	ZI
Zoo	ZO
Zora	ZR
Zorba	ZB

Appendix 2

JUVENILE ACTIVITY BUDGETS BY SEASON AND SEX

	All juvenile subjects		Both seasons combined	
	Dry season	Wet season	Males	Females
Feeding	61.6 (41.4 - 72.6)	55.76 (50.9 - 65.1)	60.9 (53.9 - 63.0)	57.7 (47.6 - 64.)
Travel-feed	5.53 (0.76 - 8.47)	8.68 (5.4 - 11.5)	6.36 (3.9 - 9.31)	7.73 (6.4 - 8.65)
Rest	6.57 (1.37 - 14.5)	7.78 (4.24 - 11.6)	8.61 (4.5 - 11.73)	7.12 (3.9 - 10.8)
Social	2.65 (0.91 - 10.0)	3.83 (1.65 - 5.2)	3.25 (1.9 - 5.7)	3.61 (1.5 - 5.83)
Groom	4.12 (0.0 - 16.58)	3.89 (1.1-10.73)	2.31 (0.3 - 6.49)	5.62 (3.49 - 9.4)
Self groom	0.53 (0.0 - 1.9)	0.4 (0.0 - 1.4)	0.5 (0.4 - 1.3)	0.63 (0.08 - 1.3)

Median percentage of time spent in six activities; ranges in brackets

Appendix 3

FOODS EATEN BY JUVENILES IN EBURRU CLIFFS TROOP

Grass spp (including *Cynodon dactylon* or ′star grass′, and ′onion grass′)	The blades are plucked singly or in handfuls, and the tender bases of the blades eaten, or the seed heads stripped off between the teeth. Perhaps due to short processing time, this is the most common food eaten during the behaviour ′travel feed". Grasses are eaten throughout the year, with an increase during the wet season.
Corms	The corms of grasses or sedges are dug up and eaten. Though used throughout the year, corm digging is more common in the dry season.
Mushrooms.	Eaten during short periods of abundance.
Prickly pear (*Opuntia vulgaris*).	The fruits of this introduced plant are knocked to the ground and rolled briskly to remove the spines before eating. Opuntia was eaten in both seasons, but was only available in the southern part of EC troop′s range (Marula).
Whistling thorn (*Acacia drepanolobium*).	These small trees could generally support only one feeding baboon at a time. Baboons fed on galls and on the young green leaves.
Leleshwa (*Tarchonanthus camphoratus*).	
Acacia xanthophloea.	Young leaves, flowers, and pods eaten. One tree could support many baboons feeding together at one time.
Acacia tortilis	
Termites spp.	The winged reproductives were caught as they flew or when they landed. Termites represented a rich food source for a limited amount of time, perhaps one day only.
Sodom apple (*Solanum incanum*).	Both the yellow fruits and insect galls were plucked from these short bushes and eaten.
Euphorbia candalabrum	The long, tough leaves were knocked down, the tough outer skin stripped away with the teeth and the moist inner tissue eaten. This was generally a dry season food, when it seemed to be an alternative to drinking water.
Rocks.	In one particular part of the range, baboons

Appendix 3

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Rocks.	In one particular part of the range, baboons

	chewed small pieced of soft lava, or scraped fragments from outcroppings with their lower incisors.
Other Animal Matter.	On two occasions, juveniles were seen eating birds: once, a nestling, and a second time, parts of the next itself which may have contained a nestling or an egg.

Miscellaneous categories: bark, leaves, berries, fruit, pods, flowers.

Over 200 plant food species were recorded for neighbouring PHG troop by M. Demment (Nicolson, 1982)

Appendix 4

KEY TO FIGURE 5-3.

● J♀
TC ET IT ZR CH MT CA DE JL IN OP XY GT SX PA
ER CO VT LL RD CL CD EO PM PR MS LS DN ZA HP

● J♂
IC OV PE CR DM DK RX PD DC MD ZK AG
TB DT NP ZG PT MR LV AR CE XU HA PP

● ● ● ◆ ● ◆ ● ◆ ● ● ● ● ◆ ● ● ● ● ● ● ● ● ◆ ● ◆ ● ● ◆ ● ● ● ● ◆ ● ● ● ◆ ● ● A♀
HN EU CI AM ZN LI EK CB DL MM DP JU PS NB ML AU AT ZD TH
PO EP SP NM LE CC RH MN PY CG JN IP IO OL LU NY DD SX PH

● ● ● ● ● ● ● ● ● ● ● ◆ ◆ ◆ ◆ ◆ ◆ ◆ A♂
AC AS HD HS TN LN GR OR VS
AA BZ HC SK ZM BA PN SC VU