CHAPTER 3

FOOD FEUDS, FEMALES AND SOCIAL ORGANISATION
3.1. Introduction

A central tenet in primate socioecology is that female behavioural response to ecological pressures, especially food resources, is a key driver of variation in the social structure of primate species (Wrangham 1980; van Schaik and van Hoof 1983; van Schaik 1989; Isbell 1991; Sterck et al. 1997). Within-group competition among females is often directly related to the quality of the food resource and its distribution in time and space (Wrangham 1980; Isbell 1991). When food resources are available in a form that can be monopolised by an individual or a small group of individuals, contest competition leading to high rates of aggression between group members is predicted to occur (van Schaik 1989; Barton and Whitten 1993; Koenig 2002). An important addendum to this socioecological concept is that clumped food resources promote high within-group contest competition whereas dispersed food resources result in low levels of within-group contest competition (Barton 1993; Barton et al. 1996; Koenig et al. 1998).

Competition over food resources affects the social organisation of primate groups at multiple levels, more particularly group size, social structure and social relationships between individuals. Within-group competition typically constrains increases in group size as larger groups experience more competition over food resources than do smaller groups (Janson 1988; Janson and Goldsmith 1995). It has also been proposed that within-group contest competition strongly influences the social structure of primate groups, often giving rise to strong, stable and linear dominance hierarchies, female philopatry and matrilineal inheritance of rank (Wrangham 1980, van Schaik 1989; Sterck et al. 1997, Isbell and Young 2002). Consequently, primate social structures and female social relationships have been categorised on the basis of the patterns of within- and between-group contest competition over food (Wrangham 1980; van Schaik 1989; Sterck et al. 1997, Isbell and Young 2002).

Most studies that have tried to investigate competitive regimes and their relationship with food distribution and social structure have looked at two different or closely related species. Very few studies (apart from notable exceptions such as Koenig et al. 1998 on *Presbytis entellus*, Hanya et al. 2008 on *Macaca fuscata*, Nakagawa 2008 on *Erythrocebus patas*, and Snaith and Chapman 2008 on *Procolobus rufamitratus*) have attempted comparisons between populations or between
groups within a population. Yet, within-species as well as within-population comparative studies are crucial for two reasons. First, it is important to understand the pathways through which environmental alterations induce proximate changes in the behavioural patterns of primate groups, and second, it may be essential to determine the relative roles of phylogeny and ecological pressures in ultimately bringing about variation in primate social systems (Chapman and Rothman 2009).

Few primate taxa, as the macaques, offer themselves as a natural choice for such comparative studies. The genus *Macaca* has a highly widespread distribution and members of this group are remarkable for their ability to colonise a diverse variety of habitats (Fooden 1982; Richard et al. 1989; Thierry et al. 2004). Bonnet macaques (*Macaca radiata*) are endemic to southern India and, as discussed in Chapter 2, are typically found in large multimale-multifemale troops. In an ongoing, long-term demographic and socioecological study of one population of this species in the Bandipur National Park and the adjoining Mudumalai Wildlife Sanctuary in southern India (initiated in 1992), however, an unusually high proportion (52%) of the population was observed to consist of unimale-multifemale groups (Sinha 2005; Sinha et al. 2005; see also Chapter 2). These unimale troops were uncharacteristically devoid of juvenile and subadult males, in addition to displaying fairly extensive female emigration, previously unreported at this scale in this species (but see Singh et al. 2006). Sinha et al. (2005) posited that provisioning by tourists visiting the sanctuary or passing through it created a rich and clumped food distribution that led to the emergence of a new social organisation in this population. In their projected model (Figure 3.1), Sinha and his colleagues pointed out that these clumped and rich food resources, along with the shortage of natural food resources during the dry season, triggered a high degree of food-related competition among the typically philopatric adult females. In the more usual multimale groups, females lower in the hierarchy were more severely affected by the intense competition over food and, amongst other strategies that included elevated levels of both contact and non-contact aggression (Ram et al. 2003), resorted to emigrating from the troop either singly or in small associations. These small groups of females were eventually taken over by single males, to give rise to unimale social groups, typical of this population alone (see also Chapter 2).
The Sinha et al (2005) model is built upon two main factors: female behavioural responses to ecological pressures and male adaptive behaviour. In this study, we tested the strength of the first part of the Sinha model by examining its four main predictions in relation to food competition and female behaviour:

**Hypothesis 1:** Scarcity of natural food induces high within-group competition among females.

**Hypothesis 2:** High-quality, clumped and unpredictable resources (provisioned food of human origin) also lead to severe within-group competition among females.
Hypothesis 3: Females in larger troops face a higher degree of within-group contest competition than do females in smaller troops.

Hypothesis 4: Certain individuals/classes of females in larger troops face relatively higher aggression due to this competition for food than do other females within these troops.

3.2. Methods

3.2.1. Study Site and Study Groups
The study site, including the Provisioned Area and the Forested Area, in the Bandipur National Park, Karnataka state and the four study troops have already been described in great detail in Sections 2.1 and 2.2 of Chapter 2. It should suffice to just mention here that two troops of the study troops – one multimale (MM1) and one unimale (UM1), also referred to as the Provisioned Troops – inhabited the provisioned area, while two troops – again, one multimale (MM2) and one unimale (UM2), also referred to as Forest Troops – inhabited the forested area. Troops UM1 and UM2 consisted of a single adult male and 5 and 3 adult females respectively while Troops MM1 and MM2 had 5 and 4 adult males and 8 and 9 adult females respectively, at the beginning of the study period.

3.2.2. Data Collection
Following the habituation and successful identification of all individuals in the study troops, quantitative data collection was conducted using 10-minute focal animal sampling of all adult individuals chosen randomly without replacement (Altmann 1974). Focal animal sampling was conducted from 0600 h to 1800 h and each observation day was, divided into three sessions: morning (0600 – 1100 h), afternoon (1100 – 1500 h) and evening (1500 – 1800 h). The total number of focal animal samples was comparably distributed for all individuals across the three sessions over the entire study period. The results of this study are based on 506.6 h of focal animal sampling data collected on the 27 adult females in the four study troops, with a mean (± SE) of 17.5 ± 0.1 hours of observation on each female.
We constructed dominance hierarchies separately for the adult males and females in each troop and ranked each of these individuals on the basis of the outcome of dyadic approach-retreat interactions, observed during the habituation period; such behavioural interactions were continuously monitored throughout the study period for any subsequent changes in hierarchal positions. We assigned numerical ranks ‘1’ upwards to the individuals within each hierarchy beginning with the lowest-ranked individuals. The females in all the troops presented transitive linear hierarchies without any rank ties.

Monthly rainfall data was collected from the local Forest Department records and the study period was divided into two seasonal phases based on the annual rain cycle. The average rainfall sharply declined (58.5 ± 13.9 mm) from December to May and hence, this period was considered the dry season while June to November was considered the wet season due to a clear increase in average rainfall (144.27 ± 22.3 mm) during this period.

Availability of natural food over the two seasonal phases was assessed by laying 83, 10 m x 10 m quadrats, randomly placed over the study area (Cox, 1990); these quadrats were continuously monitored twice every month for changes in estimated abundance of various components of the vegetation. A list of all the documented food species utilized by the study troops is given in Appendix I. The 83 quadrats together covered approximately 2% of the total study area. All trees and bushes in every plot were identified, and subsequently monitored for the abundance of leaves (green and dry), fruits, flowers (including buds), pods and grass (green and dry) (See below) twice every month. Within each quadrat, grass abundance was also estimated using a 1 m x 1 m wooden frame with 25 threaded cells (Sutherland 2006). This frame was tossed randomly into the quadrat from three different randomly chosen points on the periphery of the plot, and the number of cells that covered green grass versus dry grass. Each of the cells of the frame represented 4%. Thus, if all the cells in the frame were found to cover more than fifty percent of green grass, the availability estimate of that particular sample was considered as 100% (4% x 25 cells). In every quadrat at least three such sampling occasions were conducted at every period of monitoring, preferably from different sides of the tree or shrub foliage, and estimates of all samples for a particular monitoring occasion were averaged to arrive at a more unbiased availability status for an individual quadrat. A similar frame was used to estimate the abundance
of fruits, leaves, flowers and pods, but unlike the grass counts, the frame was used as a viewfinder to estimate approximate abundance. Again, for every tree of large bush within the quadrat, at least three samples were taken using the frame as a viewfinder. Thus the presence of any of the above mentioned vegetation component across all the 25 cells of the 1m x 1m wooden frame was considered as a representation of 100% abundance for that component, and subsequent percentages were assigned according to the number of cells the component covered. The abundance of all vegetation components recorded during a month (two occasions), were finally averaged to arrive at a consolidated estimate for that particular month.

No attempts were made, however, to quantify the availability of the human-origin food provisioned by tourists or available as garbage, nor was an attempt made to quantify the proportion of time different study individuals spent on different food species. Detailed estimation of dependency on different food species and of actual availability of different resource types was not undertaken, since the overall goal of this estimation was to validate whether the general vegetation abundance undergoes a reduction during phases of low rainfall, i.e. during the summer months. Thus it must be noted that, while the estimates do not reflect actual variation of particular food species across seasonal phases, the study area being largely a dry-deciduous forest, it is assumed that if the larger vegetation fluctuations are strongly synchronized with rainfall, the key food species will follow similar patterns of fluctuations as well.

3.2.3. Behaviours Analysed
We recognised two types of feeding regimes – provisioned foraging, when individuals fed or foraged on human-origin food, and natural foraging, when individuals foraged and fed on natural vegetation. The proportion of time spent by individuals on feeding and dyadic aggressive interactions over food resources were the two most important behaviours analysed in relation to the type of food consumed.

The actual time spent foraging on different food sources was recorded during focal animal sampling on each individual and the proportion of time spent feeding on natural food was calculated as:
Formula 3.1: Proportion of time spent feeding on natural/provisioned food (N/P) by individual (ι), is given by summing the total observed time spent foraging or feeding on the particular resource type, N or P, divided by the total hours spent feeding on both the types of food resources, P and N, for individual (ι).

\[
\text{Prop}(N, \iota) = \frac{\sum_{t \in \text{time}} F_{t,N}(\iota)}{\sum_{t \in \text{time}} F_{t,N}(\iota) + \sum_{t \in \text{time}} F_{t,P}(\iota)}
\]

Competition over food was measured through the frequency of dyadic agonistic interactions that occurred in feeding contexts. Aggressive interactions were categorised in terms of contact and non-contact aggression. Non-contact Aggression (NCAN) included all acts of gestural or vocal displays of aggression and comprised nine different agonistic acts. Contact Aggression (CAN), in contrast, included all acts of direct physical contact between the interacting individuals and constituted six different acts of physical aggression, including (For details of different behaviours categorized into NCAN and CAN, please see Appendix 1). Total Aggression (TA) was defined as the cumulative frequency of all aggressive acts (NCAN + CAN) displayed by an individual. Two other behaviours that were important measures of feeding competition were Aggressive Approach (AR) and Feeding Supplant (FS). When one individual approached another individual engaged in feeding, with a resultant aggressive interaction between the two or a retreat on the part of the feeding individual, it was labeled Aggressive Approach. When an individual displaced another feeding individual from the food source and the aggressor fed on or from the same food source, it was labeled Feeding Supplant. A feeding supplant not only resulted in a cost due to a wasted effort to obtain food on the supplanted individual’s part but also added to the foraging pressure on that individual; hence, we considered it a direct measure of the way in which food competition impedes individuals from obtaining food resources. We calculated the frequencies of the different categories of aggressive behaviour as:
Formula 3.2: where ‘a’ represents a particular or a cumulative behaviour directed by individual ‘ι’ towards individual ‘y’, ‘N’ the number of times behaviour ‘a’ was observed and ‘T’ the combined observation time (in h) for individuals ‘ι’ and ‘y’.

3.2.4. Data Compilation and Analysis
All data were tabulated in Microsoft Excel 2007 spreadsheets. Conventional non-parametric tests such as Spearman’s correlation, Wilcoxon signed-rank test and Mann-Whitney U-test (Sokal and Rohlf 1995) as well as two novel distribution-free, randomised tests (Pairs and Matched pairs tests, Ram et al. 2003) were used for within-troop and between-troop comparisons of behavioural performance. R and Kr tests (Mantel tests) were used to compare patterns of distribution of aggression at the troop-level (Hemelrijk 1990). All the tests were coded in Mathcad (version: 14.0, Parametric Technology Corporation) and all randomisation tests were conducted with 10,000 permutations. All tests, except correlations, were one-tailed unless mentioned otherwise while significance was calculated at 5% probability threshold.

3.3. Results

3.3.1 Seasons, Rainfall and Food Abundance
Rainfall was highly seasonal in the study area and the gross abundance of green leaves, fruits, pods, and green grass increased significantly with rainfall (Spearman’s correlation, N = 8; green leaves: $r_s = 0.857$, P = 0.007; fruits: $r_s = 0.752$, P = 0.028; pods: $r_s = 0.775$, P = 0.024; green grass: $r_s = 0.881$, P = 0.004; Figure 3.2). Only the abundance of flowers was not found to be significantly correlated with mean monthly rainfall ($r_s =$0.690, P = 0.06). A point to be noted is that while the availability of green grass and green leaves scaled to nearly 60% and 78% respectively, in terms of the sampled percentage of abundance in the peak availability period, fruits, flowers and pods constituted less than 10% of the sampled abundance.
3.3.2 Feeding Regimes

The adult females of the study troops UM2 and MM2 in the forested area spent significantly more time feeding on natural food than on human-origin food (Wilcoxon signed-rank test; UM2: \( T = 21, N = 3, P = 0.026 \); MM2: \( T = 45, N = 9, P = 0.008 \)). In the provisioned area, however, only the females in the unimale troop UM1 spent a significantly higher proportion of time foraging on natural food (\( T = 21, N = 6, P = 0.014 \)); the females of the multimale troop MM1, in contrast, spent comparable time foraging on the two kinds of food (MM1, \( T = 32, N = 9, P = 0.26 \)).
When the proportion of time spent foraging on natural and provisioned food was compared across the two seasons, however, the females of MM1 were found to significantly shift their foraging and feeding to provisioned food in the dry season (T = 5, N = 9, P = 0.04) while the females in the other three troops (UM1, UM2 and MM2) continued to spend more time foraging on natural resources (UM1: T = 21, N = 6, P = 0.9; UM2: T = 21, N = 3, P = 0.9; MM2: T = 45, N = 9, P = 0.9). In the wet season, only the females of troops MM1, UM2 and MM2 spent significantly more time foraging and feeding on natural food (MM1: T = 40, N = 9, P = 0.04; UM2: T = 21, N = 3, P = 0.03; MM2: T = 36, N = 9, P = 0.012). The females in the unimale troop UM1 surprisingly spent almost comparable time foraging on both kinds of food in this season (UM1: T = 14, N = 6, P = 0.08).

3.3.3 Feeding Competition

3.3.3.1 Hypothesis 1 - Scarce Natural Resources and Feeding Competition: The frequency of aggressive interactions, related to feeding competition, significantly escalated among females in both multimale troops MM1 and MM2 during the dry season while feeding principally on natural food (Figure 3.3a; Matched pairs test; MM1: N = 72 dyads; Non-Contact Aggression, NCAN, P = 0.0003; Contact Aggression, CAN, P = 0.002; Total Aggression, TA, P = 0.0005; Aggressive Approach, AR, P = 0.001; Feeding Supplants, FS, P = 0.002; MM2: N = 56 dyads; NCAN, P = 0.003; CAN, P = 0.0004; TA, P ≤ 0.0001; AR, P = 0.0002; FS, P = 0.0003). The frequencies of different kinds of aggression displayed by the females in the two smaller unimale troops did not, however, differ between the dry and wet seasons (Figure 3.3b; UM1: N = 20 dyads; NCAN, P = 0.4; CAN, P = 0.2; TA, P = 0.2; AR, P = 0.9; FS = 0.8; UM2: N = 6 dyads; NCAN, P = 0.07; CAN, P = 0.1; TA, P = 0.07; AR, P = 0.7; FS, P = 0.6).
Figure 3.3a: Aggressive behaviours displayed by females of the two multimale troops MM1 and MM2 during feeding and foraging on natural resources in the wet and dry seasons. The bars represent mean frequencies with standard errors and * represents statistically significant differences across seasons (Matched pairs test, $P \leq 0.05$). NCAN: Non-contact Aggression, CAN: Contact Aggression, TA: Total Aggression, AR: Aggressive Approach, FS: Feeding Supplant

Figure 3.3b: Aggressive behaviours displayed by females of the two unimale troops UM1 and UM2 during feeding and foraging on natural resources in the wet and dry seasons. The bars represent mean frequencies with standard errors and * represents statistically significant differences across seasons (Matched pairs test, $P \leq 0.05$). NCAN: Non-contact Aggression, CAN: Contact Aggression, TA: Total Aggression, AR: Aggressive Approach, FS: Feeding Supplant
3.3.3.2 Hypothesis 2: High Quality, Clumped Resources (Provisioned Human-origin Food) and Feeding Competition: The females of all four study troops exhibited significantly more aggression while feeding or foraging on provisioned food in comparison to that on natural food (Figures 3.4a and 3.4b; Matched pairs test; MM1: NCAN, \( P \leq 0.0001 \); CAN, \( P \leq 0.0001 \); TA, \( P \leq 0.0001 \); AR, \( P \leq 0.0001 \); FS, \( P = 0.001 \); MM2: NCAN, \( P \leq 0.0001 \); CAN, \( P \leq 0.0001 \); TA, \( P \leq 0.0001 \); AR, \( P \leq 0.0001 \); FS, \( P \leq 0.0001 \); UM1: NCAN, \( P = 0.0004 \); CAN, \( P = 0.003 \); TA, \( P = 0.0002 \); AR, \( P = 0.047 \); FS, \( P = 0.08 \); UM2: NCAN, \( P = 0.01 \); CAN, \( P = 0.02 \); TA, \( P = 0.01 \); AR, \( P = 0.2 \); FS, \( P = 0.07 \)). It is noteworthy that neither did feeding supplants differ across feeding regimes for females in the two unimale troops nor was there a significant difference in aggressive approach displayed by the females of troop UM2.

Figure 3.4a: Aggressive behaviours displayed by females of the two unimale troops UM1 and UM2 during feeding and foraging on natural and provisioned resources. The bars represent mean frequencies with standard errors and * represents statistically significant differences across foraging regimes (Matched pairs test, \( P \leq 0.05 \)). NCAN: Non-contact Aggression, CAN: Contact Aggression, TA: Total Aggression, AR: Aggressive Approach, FS: Feeding Supplant
3.3.3.3 Hypothesis 3: Group Size and Feeding Competition: The females in the two larger multimale troops displayed higher levels of all types of aggressive interactions than did females in the two smaller unimale troops, regardless of their food sources (Figures 3.5a and 3.5b; Pairs test; UM1 – MM1: N = 6 and 9; NCAN, P ≤ 0.0001; CAN, P = 0.001; TA, P ≤ 0.0001; AR, P = 0.001; FS, P = 0.002; UM2 – MM2: N = 3 and 9; NCAN, P ≤ 0.0001; CAN, P ≤ 0.002; TA, P = 0.0001; AR, P = 0.02; FS, P = 0.04). Significantly, these results also held true when analysed separately for feeding regimes and seasonal phases, except under conditions of natural foraging in the wet season, when food was relatively more abundant (data not shown).
Figure 3.5a: Aggressive behaviours displayed by females of the unimale troop UM1 and the multimale troop MM1 during feeding and foraging in the provisioned area. The bars represent mean frequencies with standard errors and * represents statistically significant differences across the two troops (Matched pairs test, $P \leq 0.05$). NCAN: Non-contact Aggression, CAN: Contact Aggression, TA: Total Aggression, AR: Aggressive Approach, FS: Feeding Supplant

Figure 3.5b: Aggressive behaviours displayed by females of the unimale troop UM2 and the multimale troop MM2 during feeding and foraging in the forested area. The bars represent mean frequencies with standard errors and * represents statistically significant differences across the two troops (Matched pairs test, $P \leq 0.05$). NCAN: Non-contact Aggression, CAN: Contact Aggression, TA: Total Aggression, AR: Aggressive Approach, FS: Feeding Supplant
3.3.3.4 **Hypothesis 4: Within-troop Feeding Competition in Relation to Dominance Status:** An analysis of all dyadic aggressive interactions during competition over food in all the study troops indicated that virtually all the aggression was directed by dominant females towards their subordinate counterparts, with subordinate individuals displaying negligible levels of aggression towards dominant females (Aggression received by dominants from subordinate females vs. aggression received by subordinates from dominant females: matched pairs test; $N = 133$ dyads across four troops; NCAN, $P \leq 0.0001$; CAN, $P \leq 0.0001$; TA, $P \leq 0.0001$; AR, $P \leq 0.0001$; FS, $P \leq 0.0001$). Again, these results were consistent for individual troops in both seasons and under the two feeding regimes (data not shown).

As food supplants directly measure the effect of food competition in hindering individuals from obtaining food resources, the distribution of feeding supplants was investigated, with respect to the dominance status of the interacting individuals, in all the study troops under different seasonal conditions and feeding regimes. No significant relationship was observed for any of the multimale troops or unimale troops, over the wet season. In the multimale troops MM1 and MM2 however, subordinate females in the dominance hierarchy were supsplanted more often that more dominant females (Kr test; MM1: $N = 72$ dyads; natural foraging, Kr = 50, $P = 0.19$; provisioned foraging, Kr = 76, $P = 0.0006$; MM2: $N = 72$ dyads; natural foraging, Kr = 48, $P = 0.06$; provisioned foraging, Kr = 157, $P = 0.007$) in the dry season; significant only under conditions of provisioning (Figure 3.6a and 3.6b).

Interestingly when the nature of distribution of this effect was compared against the rank distances of troop females: in MM1, females were supsplanted more often by closer ranking dominant females than more distant females (MM1: provisioned foraging; $R = -0.41$, $P = 0.01$; natural foraging; $R = -0.95$, $P = 0.57$), but only under conditions of provisioning. In direct contrast to this result, in MM2, lower ranking females were supsplanted by more distant ranking females, i.e. supplants received were found to be higher across more distant female-female dyads ((MM2: provisioned foraging; $R = 0.45$, $P = 0.004$; natural foraging; $R = 0.33$, $P = 0.04$), but under both feeding regimes.
Figure 3.6: Distribution of feeding supplants received, among adult females in relation to the dominance hierarchy in the multimale troops (a) MM1 and (b) MM2 in the dry season. Each column represents a single female and each data point, a unique pair of interacting females. The frequency of feeding supplants during dyadic interactions is plotted on the Y-axis.

3.4. Discussion

Variation in primate social structures has traditionally been linked to four major determinants – diet, predation, infanticide avoidance and demography – with some studies stressing the relative importance of one set of factors over others (Wrangham 1980; van Schaik and van Hoof 1983; Terborgh and Janson 1986; Kappeler and van Schaik 2002; Chapman and Rothman 2009). Countering these socioecological models, some authors have emphasized the role of phylogeny in constraining social structures in primates (Struhsaker 1969; DiFiore and Rendall 1994; Thierry et al. 2000). Investigating the nature and causes of intraspecific social variation may permit a separation of the influences of ecology from those of phylogeny although few studies on wild primates can be controlled sufficiently to test for specific determinants (but see Pochron and Wright 2003, Hanya et al. 2008). In the more recent past, the concept of behavioural plasticity as a mechanism of social variation has increasingly received more attention (Struhsaker 2000; Chapman and Rothman 2009; Strier 2009). Many studies, both implicitly and explicitly, have recommended the need to recognise and understand the ways in which primate species respond adaptively to changes in their environment and the differences between species in this ability to make behavioural alterations (Jones 2005; Strier 2009).
The results of the current study not only confirm the critical function of food resources in governing female social relationships in bonnet macaques but also underscore the role of behavioural flexibility in a species that permits individuals to adjust their behaviour to current ecological conditions. The direct effect of group size on contest competition is evidenced in the results of this study, which show that only females in the large multimale troops displayed high levels of food-related aggression in the dry season. Hence, scarcity of food does induce a high degree of contest competition among female bonnet macaques but only when they are in large aggregations. Several authors have noted that provisioning conditions dramatically increase contest competition among female primates (Southwick et al. 1976; Mori 1977; Hill 1999; Ram et al. 2003). The increase in aggression among females over provisioned food relates to the nature of the food resource – provisioned human food is typically richer in calorific value than natural food, clumped in distribution and usually unpredictable temporally (Hill 1999; Saj et al. 1999). Provisioned food, therefore, directly affected the degree of contest competition among the study females, irrespective of group size, and this influence was most apparent during the dry season, when there was a shortage of natural food.

A closer examination of aggression levels among the study females showed that during the wet season, under conditions of natural foraging, females in the larger multimale troops did not exhibit higher levels of aggressive interactions over food than did females in the smaller unimale troops. The aggression level differences between the two kinds of troops only arose under conditions of constrained food availability (provisioned feeding and dry season). Therefore, while females in larger groups did show increased levels of competition during food-constrained conditions, competition levels clearly decreased during periods of food abundance. Females in the smaller unimale groups showed escalated levels of aggression only under provisioning; indicating that while group size may have an additive effect on the degree of competition over certain resources, the degree of competition for food clearly depends on the quality of the food resource and its distribution pattern in space and time.

The most noteworthy results of this study concern the patterns of aggression displayed by females in relation to their dominance status. To begin with, much of the aggression displayed by
females was unidirectional, with little or no aggression being directed by subordinate females towards dominant individuals, a feature typical of bonnet macaques (Sinha 2001). Further in the larger multimale troops, a correlation between the absolute dominance rank and the frequency with which a female was supplanted was strongly correlated, with subordinate dominance rank conferring to higher frequencies of supplants, but only in the dry season and only under conditions of provisioned foraging and feeding. Interestingly further, under these same conditions (provisioned foraging in the dry season), in troop MM1 subordinate females were supplanted more often by more closely ranked females, than more distant females, while in MM2 contrastingly, subordinate females received more frequent supplants from more distant ranking females.

Thus, it seems that while the lowest ranking females withstand the worst of food-related aggression in large forest troops, the lowest ranking females in large provisioned troops do not face such adversity. In their study on the social strategies of bonnet macaque females in a single troop that alternated between conditions of provisioning and natural foraging, Ram et al (2003) observed that individuals preferentially directed their aggression towards higher ranked subordinates only when they were provisioned. The authors speculated that this could be either because closely ranked individuals are the greatest competitors or because lower ranking individuals space themselves away from higher ranking individuals, thereby avoiding direct conflict (Ram et al. 2003). We extend this position by arguing that, in this study, a different environmental factor comes into play. Troops in the provisioned area achieved a greater spatial spread during foraging and feeding than did troops in the Forested Area (pers. obs.), possibly due to the low predation pressure in the former zone (see Chapter 2). A larger area to forage would enable lowest ranking females to forage further away from very dominant members, thus avoiding costly conflicts over food resources (Barton 1993). Bonnet macaque females form strong matrilineal dominance hierarchies; close ranking individuals are, therefore, most likely to be close kin, and travel and forage together. Hence, much of the aggression among females in the provisioned area occurred between dominant matriarchs and their close kin. This, of course, could be in addition to the enhanced competition over human-origin food that prevailed in this area. In the forested area, in comparison, individuals foraged more cohesively and therefore, lower ranking individuals were more likely to be in conflict with higher ranking individuals.
Also this patterning of feeding supplants with respect to the dyadic rank distance seemed to manifest strongly under both natural and provisioned foraging and feeding regimes in the dry season, for only MM2. This is possibly because a large troop size faces higher levels of competition across both, periods of natural resource scarcity as well as when feeding and foraging on provisioned foods, i.e. perhaps for MM1 only provisioned resources were highly clumped during the dry season and for MM2 both types of resources were highly clustered (additionally with provisioned foods being highly unpredictable) in the dry season.

It follows, therefore, that relatively lower ranking females in forest-living multimale troops in this particular population in the Bandipur National Park are subjected to high aggression levels and thus face major constraints in finding sufficient food resources, especially during periods of natural scarcity. In such a scenario, a possible, albeit extreme, strategy for such traditionally philopatric females could be to break out from their respective natal troops and settle down in other, often smaller, resource patches that can sustain a relatively smaller group of females, an observation made earlier by Sinha et al. (2005). Such single females or small groups of females could then be susceptible to take-overs by single males, thus giving rise to unimale troops, a model suggested by Sinha et al. (2005) to explain the appearance of this unique form of social organisation in only this particular population of bonnet macaques. The second prediction of this model, however, remains to be tested as we did not examine the contribution of individual male behaviour in the development of such unimale troops. Recent work on genetic polymorphism and behavioural traits in macaques (Chakraborty et al. 2010) lend credence to the Sinha et al. (2005) premise that individual temperament and personality may hold the final key to the conundrum of intraspecific variation in social structures, at least in primates. Nonetheless, our study provides valuable insight into how ecological factors might drive social change in animal populations and, more importantly, clarify the extent to which individual animals can potentially adjust their behaviours in accordance with rapidly changing ecological as well as social environments.
3.5. References


