



Moder-ungeinteraktioner och dibeteende hos den blå markattan, *Cercopithecus mitis*

*Mother-young Interactions and Suckling Behaviour
in Blue Monkeys, *Cercopithecus mitis**

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Abstract

Mother-young interactions and suckling behaviour in blue monkeys, *Cercopithecus mitis*

The infant's first months are of vital importance for establishing relations with the mother as well as with other group members. It is also a period of learning. As a part of a larger study of the blue monkey, *Cercopithecus mitis stuhlmanni*, my study focuses on interactions between mother and offspring and suckling behaviour.

The study site was located in the forest of Kichwa Tembo Tented Camp which is a tourist lodge outside the Masai Mara National Reserve in Kenya. Data collection took place in July 2006 in collaboration with two other Swedish students and with the help of Maasai field assistants. The monkeys were observed on foot between 8:00 and 18:00 with a total observation time of 330 hours evenly spread between the ten observation hours. We could not recognize the animals individually but estimated the number of focal animals as eight mothers with offspring. While suckling behaviour was recorded continuously with regard to time and duration, general behaviour, playing and grooming was recorded each minute. My results show that the mothers had feeding peaks in the early mornings, at midday and in late afternoon. This was in contrast to the offspring's feeding rhythm whose suckling meals took place mainly in the late morning and early afternoon. The time the offspring spent foraging solid food was close to zero. The offspring spent a third of their time carried by the mother and a quarter of their time playing. Most of the playing was lone play; social play with other group members did occur but was not as common. The offspring were dependent of the mothers however very active in exploring the environment which shows both in amount of time playing and moving. The individuals in the group spent about 10 % of their daylight hours grooming each other. In general these results coincide with those of others studying guenons. I suggest though that some of the behavioural differences of the group may be due to the focal animals being lactating. Furthermore I believe that the habitat they live in, i.e. close to humans and somewhat more protected, is reflected in their behaviour. This corresponds with the low levels of antagonism observed.

Moder-ungeinteraktioner och dibeteende hos den blå markattan, *Cercopithecus mitis*

De första månaderna i en unges liv är mycket viktiga för att skapa en relation till sin moder och till andra gruppmedlemmar. Det är också en period som består av lärande. Som en del av en större studie av den blå markattan, *Cercopithecus mitis stuhlmanni*, fokuserar min studie på samspelet mellan moder och unge samt ungens dibeteende.

Studien ägde rum i den skog som omger turistlodgen Kichwa Tembo Tented Camp i utkanten av Masai Mara National Reserve i Kenya. Databesamlingen genomfördes under fem veckor i juni och juli 2006 tillsammans med två svenska studenter och med hjälp av fältassisterande massajer. Aporna observerades 8.00-18.00. Observationsperioden gav totalt 330 timmar jämt fördelade mellan de tio observationstimmarna. Vi kunde inte identifiera individerna i gruppen men den uppskattades bestå av åtta mödrar med varsin unge. Dibeteendet registrerades kontinuerligt med information om klockslag och varaktighet. Det allmänna beteendet, lek och ansning noterades varje minut. Mina resultat visar att mödrarna hade födosökstoppar tidigt på morgonen, vid lunch och under sen eftermiddag. Detta stod i kontrast till ungens födosöksrytm där digivningarna främst ägde rum sent på morgonen och under tidig eftermiddag. Ungen letade och åt fast föda i obetydlig grad. Modern bar ungen en tredjedel av observationstiden och ungen lekte under en fjärdedel av tiden. Majoriteten av lektiden var ensamlek; sociala lekar med andra gruppmedlemmar var inte lika vanligt. Ungarna var beroende av mödrarna men ändå mycket aktiva i att utforska omgivningen.

Gruppmedlemmarna ansade varandra cirka 10 % av dagen. Detta resultat överensstämmer i det stora hela med andra studier av markattor. Emellertid tror jag att vissa av de beteendeskilnader som syns i resultatet i denna grupp av markattor beror på att flera av dem var lakterande. Dessutom tror jag att denna grupps habitat, d.v.s. med närheten till människor och med ökat skydd från predatorer, påverkar deras beteende. Detta överensstämmer med den låga nivån av antagonism som observerades.

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Introduction

1.1 Description of the species

The blue monkey, *Cercopithecus mitis*, is one of at least 18 species belonging to the group of guenons (family: Cercopithecus, subfamily: Cercopithecinae). This group of Old World Monkeys diverged from the baboon, macaque and mangabey group about ten million years ago (Ruvolo 1983 in Smuts et al. 1987). The blue monkey inhabits areas in central, eastern and southern Africa (Wolfheim 1983) in countries as far south as South Africa and as north as Ethiopia (Duff & Lawson 2004). It is a rainforest species which is found both in lowland and highland habitats (Wolfheim 1983). The species is diurnal and active at day.

The species has a uni-male social system. Females stay in the group throughout their lives whilst males are forced to leave the group when reaching sexual maturity at the age of approximately six years (Smuts et al. 1987). Breeding occurs throughout the year but a peak is often noticeable in each population. This may depend on the environment, weather or social factors (increased sexuality during multi-male influxes, see below). However much is still unknown (Cords 1988). Blue monkey females give birth to one offspring only. During some breeding seasons alien males enter groups and compete for mating opportunities (Smuts et al. 1987), so called multi-male influxes. Besides competing for mating opportunities they also fight the dominant male to take over the group (Pazol 2003). Females have weak linear dominance hierarchies but antagonistic behaviour is rare within the group. Rank does not correlate with fitness benefits or reproductive success (Cords 2002a), and does not vary with changes in ecological conditions (Pazel & Cords 2005).

Blue monkeys maintain a diverse diet; they eat mainly fruits but tend to feed on leaves and insects when food is scarce (Cords 2002b). They have cheek pouches going all the way down in their throats in which they can carry almost as much food as in their stomachs (Macdonald 1984). When foraging, the individuals spread out to avoid food competition. They often form coalitions with other primate species to search for food and to increase protection against predators (Cords 2002b).

The level of the forest canopy used by blue monkeys differs depending on the habitat and the risk of predation. Alarm calls from other members of the group to announce the presence of predators also help in avoiding predation. The monkeys are less alert within a group and tend to ignore alert calls given by other group members if the food supply is sparse (Cords 2002b). The most likely predators are larger species of eagles that specialize in hunting tree living monkeys (Macdonald 1984).

In some areas humans hunt the blue monkeys for their meat and for protecting the crops. Another threat to the species is habitat destruction, especially the clearing of the rainforest. According to the IUCN red-list from data in 1996 there is just a lower risk/least concern to the survival of *C. mitis* as a species.

1.2 Mother – offspring behaviour

The first months of an infant's life are very important for learning and gradually increasing its independence of its mother. It is also a vital period for establishing relations with the mother and other group members. Grooming is important in cultivating long-term as well

as maintaining current cooperative relationships (Cords 1997). Grooming may also help to protect the offspring from disease and ectoparasites (Altman 1980).

The mother usually carries the offspring during the first months after birth. Apart from protecting the infant from danger (Förster & Cords 2005), Altman (1980) has suggested that this phenomenon can be profitable for the mother. Since an infant is more active when not on the mother the cost for the mother, i.e. in milk production, is less the more she carries the infant. A frequently used measure of infant independence among primates is the time infants spend in physical contact with their mothers (Altman 1980, Struhsaker 1971). When an offspring starts to explore its surroundings and increase its interactions with other group members it still stays in close proximity to the mother. Blue monkey infants generally avoid spatial proximity to non-maternal adult females, whereas they associate more with other infants and large juvenile females. One assumed function of these allo-maternal interactions, i.e. infant handling, is that it is a practice for nulliparous females, i.e. females that have never given birth (Förster & Cords 2005). Another reason could be that it may have significance as an altruistic behaviour among group females and enables lactating females to increase feeding time (Stanford 1992). The behaviour is relatively common in several primate species such as blue monkeys (Förster & Cords 2005), Bolivian squirrel monkeys (Williams et al. 1994) and vervet monkeys (Struhsaker 1971).

1.3 Diurnal behaviour

Diurnal variation of behaviour may be caused by the differences in light between day and night as well as the different light intensity during daytime (Bolhuis & Giraldeau 2005). Since also temperature and relative humidity change during the day, their different degrees of impact on behaviour are not easy to distinguish.

When studying the diurnal behaviours of blue monkeys Tweheyo & Obua (2001) showed that their behaviour varied from morning to evening. In the morning 79 % of time was devoted to feeding whereas the rest of the time was used for resting and socializing. The time between 11 and 15 hours was mainly used for resting and they then resumed to feeding but not to the same extent as in the morning.

1.4 Foraging behaviour

Infant mammals often depend completely on milk during their first time of life. Oxytocin is the hormone controlling milk secretion in mammals. Mechanical stimulation of the teats at suckling stimulates additional release of oxytocin (Campbell & Reece 2002) which thereby enhances further milk secretion (Miller & Harley 1999).

In addition to receiving milk from the mother, young mammals need to learn how to select and process other kinds of food. Infant primates feed at the same time and choose increasingly the same food items as their mothers (Ueno 2005, Hauser 1993). According to a study by Querouil and Blois-Heulin (1998) young Cercopithecinae started eating other food than milk as early as four weeks of age. At week eight the intake of solid food overtook that of milk. The foraging behaviours of mothers and infants still differed at six months of age. The pattern of the infants' feeding behaviour was biting or just touching food that over time changed to picking up and eating real food. Consumption of waste occurred whatever age. Förster-Cords (2002) observed infants of five weeks swallowing food.

1.5 Parental investment and conflicts of interests

Parental investment is defined as “anything done by the parent for the offspring that increases the offspring’s chance of surviving while decreasing the parent’s ability to invest in other offspring” (Trivers 1974). Parental investment is the evolutionary product of fitness costs and benefits. The time and energy that parents invest in their offspring have costs, including reduced fecundity in the future, but also obvious benefits of improved survival of the young (Ghalambor & Martin 2001). The level of parental investment is a potential cause for a conflict between mother and offspring. While the offspring desires milk the suckling is energetically demanding for the mother. Suckling is considered as a clear form of maternal investment since it takes both the mothers’ energy and time and may increase her risk of predation. This dilemma may result in rejections by the mother. To increase the offspring’s independence and decrease the mothers’ energy expenditure physical rejections are used by the mother that results in temporary or long-term rejections of the nipple (Struhsaker 1971). Depending on the species, the restrictions by the mother have shown to differ both in frequency, first occurrence and way of appearance. Rejections can be subtle as grooming off the nipple, turning away, stretching the torso and blocking or more aggressive as pushing or biting (Förster & Cords 2002, Struhsaker 1971).

1.6 Aims of the study

In general it is difficult to observe the blue monkeys wild due to their shyness and constraints such as that the monkeys live on high trees. In our case, we had the unique opportunity to observe a habituated group that lives in a forest with relatively low trees. This made close observations of the monkeys possible, which is necessary especially for observations in suckling behaviour.

The aim of my study was to examine the mother-young and suckling behaviour in a group of wild blue monkeys. This group was used to the presence of humans due to the tourist lodge situated in the same forest. According to my knowledge, no study in suckling behaviour of wild guenons has ever been conducted. My results will therefore contribute further to the understanding of the interaction between blue monkey mothers and infants.

Materials and Methods

The Masai Mara National Reserve (MMNR) in the northern part of the Serengeti-Mara ecosystem in south-western Kenya was formed in 1965 and makes out an area of 1,368 km² (Brotten & Said 1995, Norton-Griffiths 1995). The temperature is relatively constant with a monthly mean maximum temperature of 27 - 28°C, and with minimum temperatures varying from 16°C in October to March to 13°C during May to August. Rain usually follows a bimodal pattern with long rains from March to May and short rains in November and December. The main dry period is from mid-June to mid-October, with a lesser dry spell in January and February. Rainfall in the MMNR average 1,200 mm per year (Sinclair 1995).

2.1 Study site: Kichwa Tembo Tented Camp

The Kichwa Tembo Tented Camp is situated outside the western border of the MMNR at the base of the Oloololo escarpment alongside the Sabaringo River (35° E, 1.2° S, 1620 m.a.s.l.). The lodge is surrounded by the Sabaringo forest which occupies an area of 24 ha. The entire Sabaringo forest is protected since 13 years ago by an electric fence that prevents larger herbivores like elephants and hippopotamus to enter the area. The fence may even reduce the number of predators, although leopards, hyenas and snakes might cross it easily. Within the lodge area there are 34 tents and a few houses for tourists, a restaurant and bar with adherent kitchen, a pool, a reception, the main office, two management houses and a staff quarter with adherent football field. In the south-eastern corner of the forest is a more private lodge situated, the Bateleur Camp. A wooden fence separates the two lodges. New tents are under construction in both lodges. We were allowed to follow the monkeys all over the fenced area with the exception of the Bateleur Camp. When a focal animal moved in to the Bateleur Camp or over the fences surrounding the lodge we stopped the observation.

Perhaps due to the decreased predation pressure, several large animals besides the blue monkey inhabits the area, like red-tailed monkey, *Cercopithecus ascanius*, warthog, *Phacochoerus aethiopicus*, banded mungo, *Mungos mungo*, tree hyrax, *Dendrohyrax Dorsalis*, in addition to several bird species. The forest is a semi-dry deciduous forest, dominated by *Diospyros abyssinica*, *Euclea divinorum* and *Teclea nobilis*. The tallest trees are approximately 20 metres and there is a dense undergrowth of different bushes (*Erythrococca*, *Strychnos* etc.). Vines are frequent as well. The area around the staff quarters are visibly affected by the staff's presence, i.e. of paths and garbage. Open trash bins are to be found around the lodge in which leftovers and other eatable things are put.

2.2 Focal animals

The focal group of blue monkeys, *Cercopithecus mitis stuhlmanni*, consisted of approximately 50 individuals. We could not recognize the individual animals but estimated there to be eight lactating females with one offspring each. The rest of the group consisted of about twelve non-lactating females, one dominant male and many juveniles.

2.3 Animal observations

The monkeys were used to the vicinity of tourists and tolerated our presence when observing them. After habituating the monkeys for ten days, we conducted data collection from 1st to 27th of July 2006. Recordings of the monkeys' behaviours were made on foot between 8:00 and 18:00 by one to three parallel working observation teams. Depending on the habitat, each team consisted of two to three observers and one writer who recorded all data on a paper sheet. Each team observed one lactating female together with their offspring. If the focal animal was lost, that particular observation was stopped and a new observation with a different focal animal was started. The observations lasted in average 3:55 h (range 30 min – 9.5 h). Recordings shorter than 30 min were discarded. No upper time limit was used. A total of 165 hours evenly spread between the ten observations hours were made on the two categories of monkeys (lactating and offspring), i.e. 330 hours.

2.3.1 Behavioural recordings

Interval recordings of the focal animal's behaviour were made each minute. The behaviours were: foraging, carried on mother, standing, sitting, lying, moving, playing, self-grooming, grooming, receiving grooming, other social behaviour or missing observation. In case of playing and grooming, the partner was recorded as itself, mother, offspring, other adult, other infant or juvenile.

2.3.2 Behavioural definitions

<u>Behaviour</u>	<u>Definition</u>
Foraging	Chewing, gathering or manipulating potential food.
Carried on mother	Offspring carried by mother with or without suckling.
Standing	Standing up on four limbs alternatively upright on its rear limbs.
Sitting	Sitting on its bottom.
Lying	The monkey's torso leaning against an object.
Moving	Walking, running or jumping at a certain direction with all four limbs in motion.
Playing	Undirected movements with another individual or by itself.
Self-grooming	Manipulating own fur with hands, such as scratching and picking.
Grooming other	Manipulating other monkey's fur by mouth or hands.
Receiving grooming	Manipulation of the focal animal's fur by other monkey's mouth or hands.
Other social behaviour	Antagonistic or sexual behaviour.
Missing observation	Behaviour was not able to identify or monkey was out of sight.

2.3.3 Suckling behaviour

Suckling behaviour was recorded continuously whenever it occurred. The time and duration was recorded with a stop watch and registered by the writer. A suckling meal could consist of several bouts. Meal duration was recorded as time on the nipple; pauses in between bouts were excluded when analysing.

When the infant made an effort of trying to put the nipple in its mouth without actual suckling taking place it was recorded as a suckle attempt. Additionally, all durations of

nipple in mouth which were shorter than ten seconds were recorded as suckle attempts. Actual milk suckling and mere nipple holding with mouth could not be discriminated by visual observation. As a result, we recorded suckling as contact between the infant's mouth and the mother's nipple for longer time than ten seconds.

2.4 Data analysis

2.4.1 Statistical analysis of animal observations

The results are presented as means \pm standard error of the means (SE), in some cases without SE. Since none of the data was normally distributed statistical significance was tested with either the non-parametric Mann-Whitney Test or the non-parametric Kruskal-Wallis Test.

Results

3.1 Mother and offspring general behaviour

There was an apparent difference between the percentage of time mothers and offspring spent on different general behaviours (fig. 1). Mothers preferred sitting whereas offspring favoured being carried by the mother. Compared to offspring mothers spent more time foraging ($W=6896$, $P<.001$, Mann-Whitney Test), standing ($W=6131$, $P<.001$), sitting ($W=7061$, $P<.001$) and lying ($W=5442$, $P=.0036$) whilst offspring spent more time on other behaviours, which include playing, grooming and other social behaviours. Moving did not differ between mother and offspring.

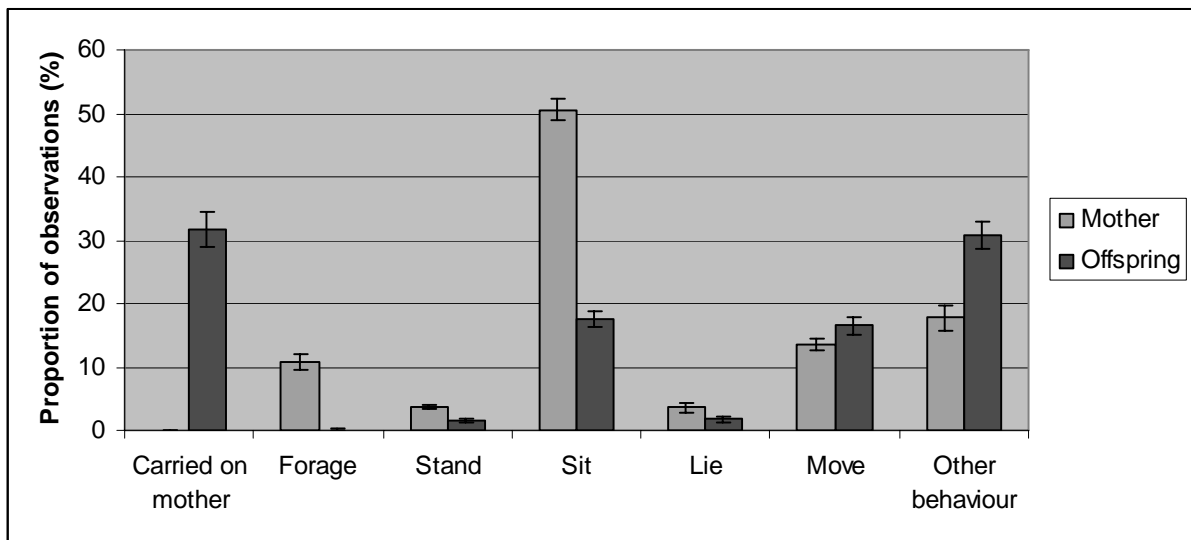


Figure 1 Percent of time spent by mothers and offspring on the general behaviours. Other behaviour includes playing, grooming and other social behaviours.

3.2 Daily rhythm

3.2.1 Mothers' daily rhythm

Figure 2 and 3 show the animals' activities hour by hour. We performed statistical analysis by pooling hours 8-10 to early morning, hours 11-14 to midday and hours 15-17 to late afternoon. Mothers moved mostly in the early morning and late afternoon ($H=17.46$, $P<.001$, Kruskal-Wallis Test, fig. 2). In contrary showed sitting ($H=7.32$, $P=.026$), lying ($H=5.35$, $P=.069$, Kruskal-Wallis Test; $H=8.58$, $P=.014$, Kruskal-Wallis Test adjusted for ties) and other behaviour ($H=7.73$, $P=.021$, Kruskal-Wallis Test) the opposite pattern, i.e. these behaviours were more frequent during the day than in the morning and afternoon. We failed to show significance of a difference in foraging frequency during the day.

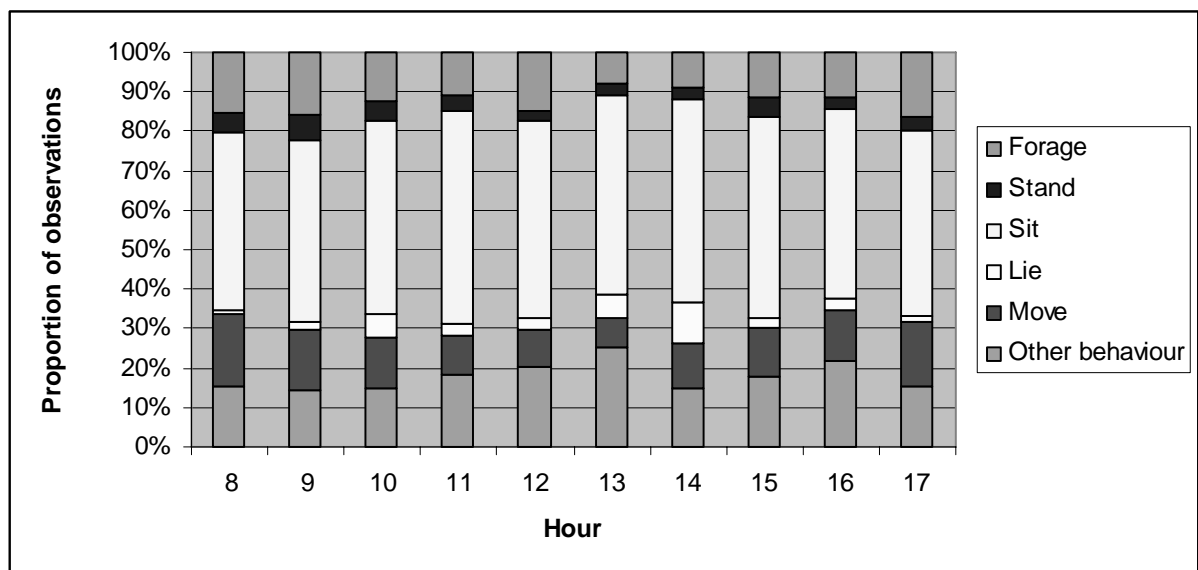


Figure 2 Mothers' daily rhythm. Proportion of time mothers spent on the different behaviours in each hour. Other behaviour includes playing, grooming and other social behaviour.

3.2.2 Offspring's daily rhythm

Offspring's daily rhythm did not show the same clear pattern as the mothers' did (fig. 3). However, offspring did lie more at midday than in the early morning and late afternoon ($H=5.35$, $P=.069$, Kruskal-Wallis Test; $H=8.58$, $P=.014$, Kruskal-Wallis Test adjusted for ties). The remaining behaviours did not show any significant differences when comparing morning, midday and afternoon.

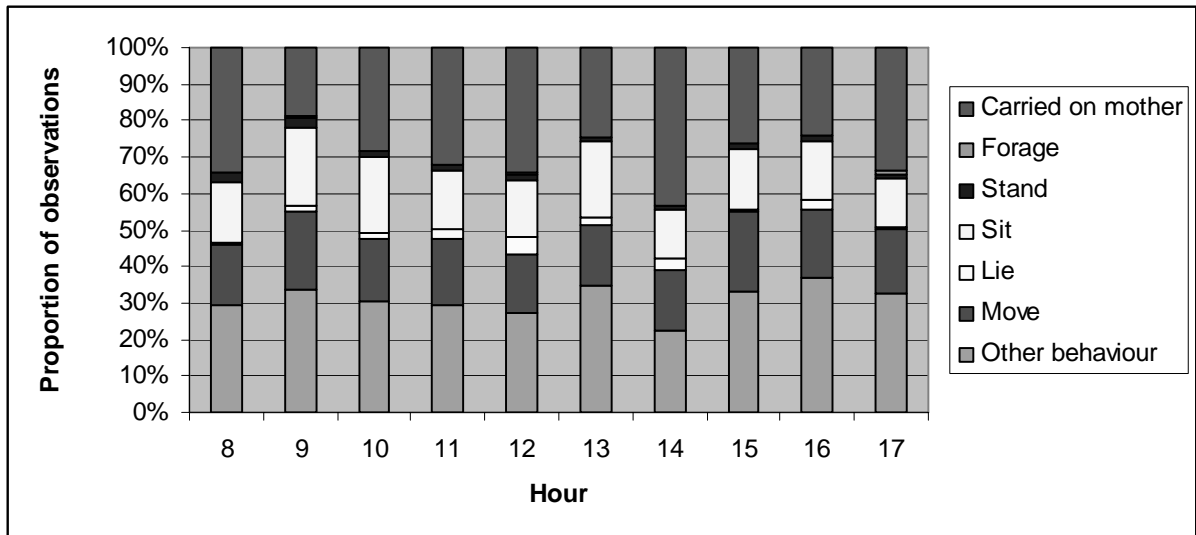


Figure 3 Offspring's daily rhythm. Proportion of time offspring spent on the different behaviours in each hour. Other behaviour includes playing, grooming and other social behaviour.

3.3 Other behaviour

Offspring spent approximately a quarter of their time playing while mothers hardly played at all ($W=2599$, $P<.001$, Mann-Whitney Test, fig. 4). Most of the playing offspring did by itself ($92.4\pm 1.82\%$) whereas social play accounted for $7.6\pm 0.34\%$ ($W=6810$, $P<.001$). Mothers performed more grooming than offspring did ($W=6519$, $P<.001$) and they also did more self-grooming ($W=6289$, $P<.001$). Frequencies of receiving grooming did not differ between mother and offspring. Mothers did groom more than they received ($W=5574$, $P<.001$) while the opposite was true for offspring ($W = 3137$, $P<.001$).

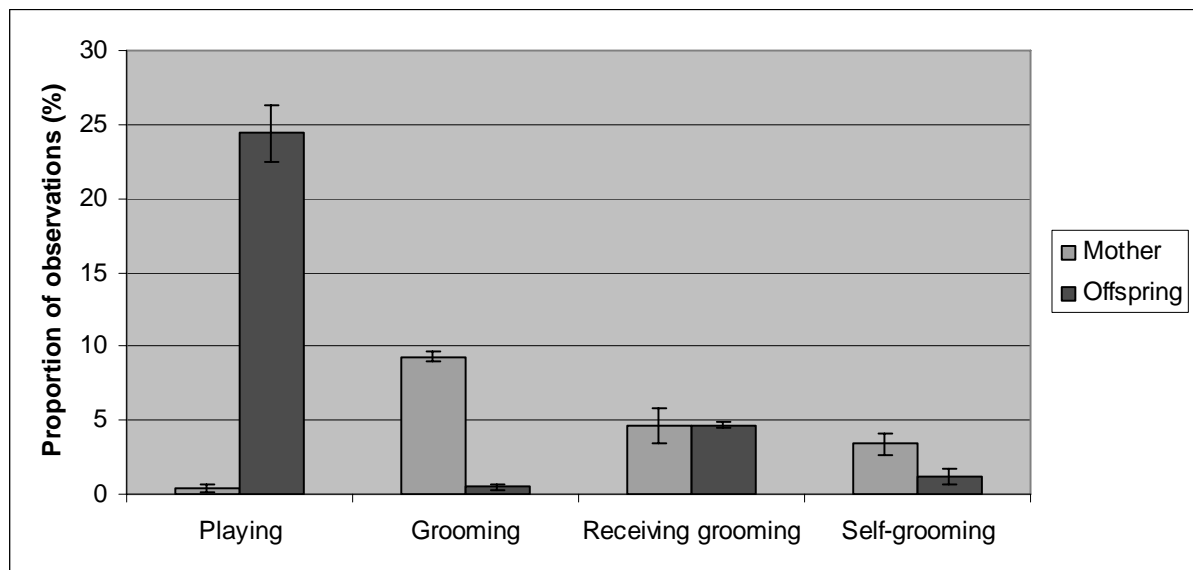


Figure 4 Percent of time spent on playing, grooming, receiving grooming and self-grooming.

3.4 Grooming

The individuals spent a noticeable amount of time grooming each other. However, adult females and immatures differed visibly in frequency of events (fig. 5). Compared to offspring, mothers spent more time grooming adults ($W=6018$, $P<.001$, Mann-Whitney Test) and juveniles ($W=5838$, $P<.001$). Mothers also spent appreciably more time grooming their offspring than vice versa ($W=6379$, $P<.001$).

Mothers received approximately equal grooming from other adults that they performed on them (n.s.). There was a statistical tendency that they performed more grooming on infants than they received ($W=5007$, $P=.0871$) whereas there was no statistical difference in performing and receiving grooming from juveniles. Offspring received more grooming from adults ($W=5314$, $P<.001$) and juveniles ($W=5531$, $P<.001$) than they self performed on them. There was almost no grooming between infants in the group.

Mothers received more grooming from adults than offspring did ($W=5668$, $P<.001$).

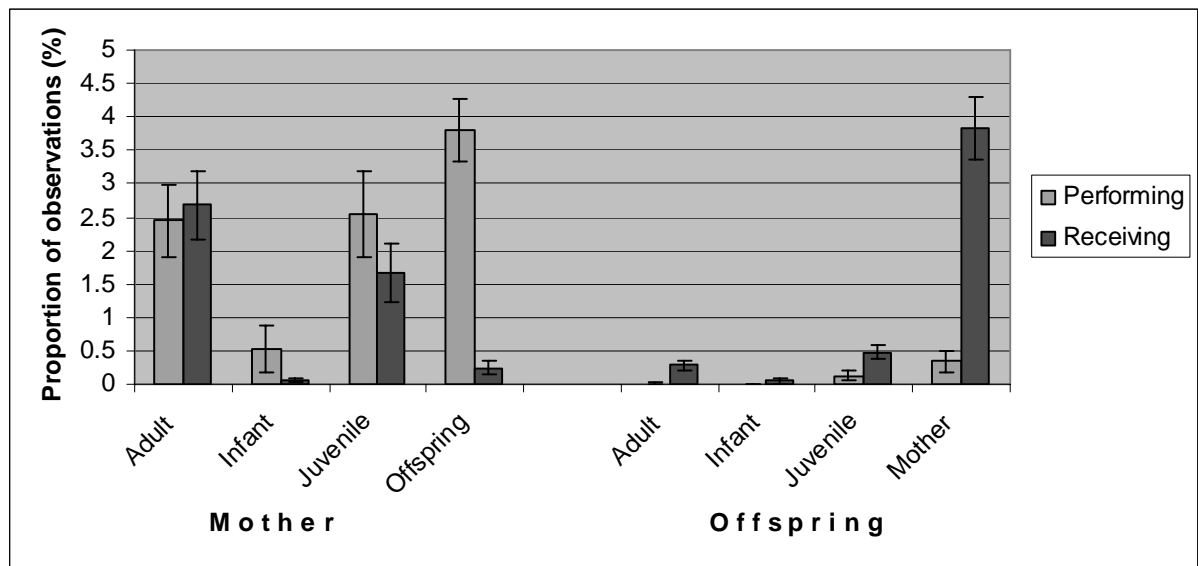


Figure 5 Percent of total time mothers and offspring spent grooming and receiving grooming respectively from group members.

3.5 Suckling behaviour

Figure 6 shows the offspring's suckling behaviour hour by hour. We performed statistical analysis by pooling hours 8-10 to early morning, hours 11-14 to midday and hours 15-17 to late afternoon. Offspring suckled more often during midday than in the early morning and late afternoon ($H=6.55$, $P=.038$, Kruskal-Wallis Test). However, we failed to show significance of the daily rhythm of suckling attempts and average meal durations.

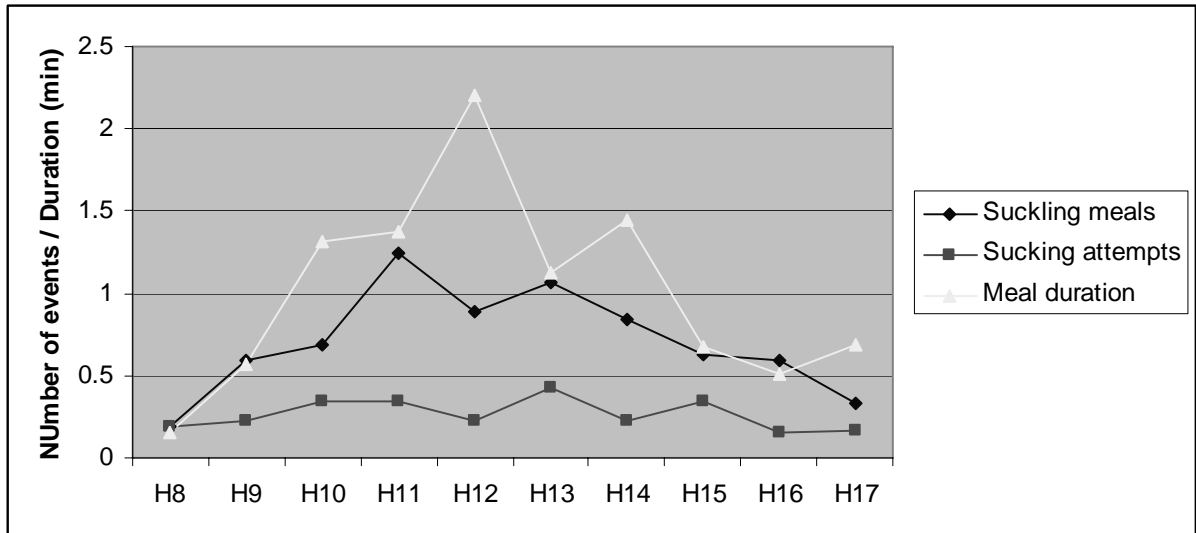


Figure 6 Number of suckling meals (minimum 10 sec.) and sucking attempts (maximum 9 sec. of sucking) as well as average durations of meals during each hour of the day.

3.6 Other social behaviour

Other social behaviour which includes sexual and antagonistic behaviour happened very seldom during our study. Of the few observations we did see in this group of primates there were more antagonistic than sexual actions. Mothers were seen performing other social behaviours during $0.026 \pm 0.02\%$ of their time whereas offspring used $0.027 \pm 0.02\%$ of their time.

Discussion

4.1 Mother and offspring general behaviour

My results show that there was a noticeable difference between the percentage of time mothers and offspring spent on the different general behaviours. While offspring spent a fifth of their time playing and a third being carried by the mothers, mothers spent almost half their time sitting. This can be compared to other studies of guenon infants that spent almost their entire time on their mother the first week after birth and then gradually increased its independence to their mother (Förster and Cords 2002, Lee 1984, Struhsaker 1971). Playing is important as a way to create social bonds with other group members, practise for adult social interaction and get to know the environment. Playing is uncommon among adults where social relations are already established (Poirier & Smith 1974), which was also shown in this study. Additionally, Poirier and Smith (1974) point out that playing helps to increase an infant's muscular coordination. Most of the playing in my study was lone play; social play with other group members did occur but was not as common. Lee (1984) observed more social play than lone play in a group of wild vervet infants which contrasts with studies on captive vervet monkeys where infants showed both high rates of lone and social play.

Why do then mothers spend as much as 50 % of their time sitting? The blue monkey females in Pazol & Cords (2005) showed that they spent 40 % of their daylight hours resting (i.e. non-moving without any activity). One reason for these numbers could be that sitting, and resting, is an excellent way of saving energy. It is also a good position for observing the surroundings.

Except for sitting did mothers and offspring differ in time spent foraging. Mothers spent much more time foraging on food objects, which is understandable since small offspring's larger energy intake comes from milk. They do not need to forage in the same extent as the mothers as well as they need to learn what food to select. Standing and lying were also more common behaviours for mothers than for offspring however took only a small part of the mothers' time.

4.2 Diurnal behaviour

While offspring's daily rhythm did not show any particular pattern, the rhythm of mothers did. They moved more in the morning and afternoon while they sat and lied down more at midday. This behaviour coincides with that of Adeyemo (1997) whose green monkeys were more active in the morning and evenings as well. According to Cords¹ blue monkeys spend the night in one place. They spend the daylight hours normally somewhere else which may be the reason for the high moving frequencies in the morning and afternoon.

While the blue monkeys in the study by Tweheyo & Obua (2001) rested between 11 and 15 hours my study did not support their results of the feeding rhythm. The reason for my

¹ Marina Cords, verbal communication in June 2006.

females not using mainly morning and afternoon for feeding does probably depend on the feeding opportunities given to them from the kitchen at lunch time (Linderoth, in preparation).

4.3 Grooming

The individuals in the present population spent about 10 % of their daylight hours grooming each other. This is slightly more than in Pazol and Cords (2005) whose adult blue monkeys spent less than 7 % of their days grooming each other. The reason for this difference might be that my adult monkeys were all lactating, in contrast to the ones in Pazel's and Cords' study. Grooming helps the individual to keep clean as well as to stay protected from disease and ectoparasites (Altman 1980). The grooming frequency may well then depend on the environment and the presence of parasites. Grooming is also important in creating and maintaining relationships with other group members as well as with the mother (Cords 1997). In blue monkeys, the relationships among females are important for effectively defending food resources and their territory from neighbours (Cords 2002a). To keep strong bonds in a group the socializing frequency should be of a certain level. The grooming frequency could then depend on the group size; a smaller group may need less grooming to keep the affiliations strong. This is supported by the fact that the group size of the present group was estimated to be 50 individuals. According to Wolfheim (1983) most guenons live in groups of 10 to 40 members. Moreover, grooming has been associated with reducing stress (Shutt et al. 2007). Their result indicated that it is the giving rather than the receiving of grooming that is associated with lower stress levels.

Mothers performed grooming more often than their offspring. An infant's first months are very important for establishing relations in the group and learn how to manage everyday situations. It is then natural that an adult have more time for grooming than an immature. In spite of a distinct difference in frequency of events, mothers and offspring had each other as their favourite grooming partner. These results partly coincide with Cords (1999) where infants most often had their mothers as their preferred grooming partner. The mothers, however, typically had another adult as their top-ranked partner. The mothers in Cord's study did nevertheless prefer grooming their offspring more than they did other immatures in the group. The relation between mother and infant is very important and creating a strong bond is partly done through grooming (Cords 1999).

Compared to offspring, mothers spent four times as much time grooming others, i.e. not auto-grooming. Mothers groomed adults just about as much as they received grooming from other adults. Moreover, mothers groomed juveniles in the same degree however it was not returned in the same extent. Except for just strengthening the bonds with other group members, this could also be a mother-offspring situation. The juvenile may be an offspring of the mother which no longer spends all time with her but a strong connection between them is still apparent. This could not be determined though since the relationships in the group had not been able to establish.

The offspring received more grooming from adults, juveniles and mothers than they self carried out. In blue monkeys it is relatively common that nulliparous females, i.e. juveniles, practice infant handling with infants in the group (Förster & Cords 2005). As mentioned, blue monkey infants associate more with infants and juvenile females than with non-maternal adult females (Förster & Cords 2005). Although offspring received more grooming from adult females than from juveniles they themselves groomed the juveniles more often than they did adults. In addition, compared to offspring, mothers received more grooming from adults.

Mothers practised self-grooming more often than offspring did. Offspring did however receive a considerable amount of grooming especially from its mother. Furthermore, mothers do not need to spend as much time exploring the environment and getting to know other group members. It is therefore reasonable that an offspring is not as active in self-grooming.

4.4 Suckling behaviour

Most of the suckling events in this study took place in the late mornings and early afternoons with peaks at 11 and 13 hours. There was a steady rise from morning until around 11 hours and a steady downfall from 13 hours. At 12 hours there was a dip, maybe due to the activities of the monkeys when gathering food from the lodge's staff canteen (Linderoth, in preparation). At 12 hours, lunchtime, the staff threw their leftovers in trash bins and there was a rise in foraging frequency by mothers. Since there was nutritious food, mainly ugali made from corn flour, available (Linderoth, in preparation) which did not need much energy to forage the mothers often took the opportunity to feed. During feeding mothers may not be eager to let the offspring suckle.

A reason for the low frequency of suckling meals in the early mornings and late afternoons may be that suckling might take place at night. I assume that when it is dark the offspring stay close to the mother, i.e. is carried, for protection. In this position and especially when the mother itself is resting it is most likely easier for the infant to suckle. If it does suckle at night it does not need to suckle in the early mornings or late evenings which might explain the lower suckling activities.

Sucking attempts followed in the morning the same pattern as that of suckling meals; increasing throughout the day with a dip at 12 hours. After 15 hours the attempts became fewer and there seemed to be a small disunity between the mother and the offspring in that the number of suckling meals declined and the number of suckle attempts increased. However, at 14 hours the meal durations were longer than normal. The mother was at this time lying down more than usual and may have allowed more suckling. The offspring would following suckling have plenty of energy for playing, a behaviour which also increased around 16 hours.

In my study, every time the offspring was on the nipple more than ten seconds we recorded a suckling meal. The reason for this was that shorter suckling bouts are less likely to lead to milk ingestion since milk flow in many mammal species does not begin immediately (Whittemore 1980 in Cameron 1998). Different ways of studying milk transferred from mother to offspring in mammals have been tried. Examples of these are comparing time spent suckling and growth, weighing before and after suckling and observing the frequency and bout time. When comparing the different behaviour-sampling methods, suckle bout frequency and total suckling time was shown to be the only method that correlated with estimated milk intake, although differing between species and studies (Cameron 1998). If possible, the infant's suckling behaviour should also be taken into consideration when estimating the milk intake in mammals since infants of many species suckle despite no milk being present (Wolff 1968). In such non-nutritive sucking, when there is no milk flow, the sucking rate is characterized by being increasingly high local. Nutritive sucking, i.e. milk transfer from mother to offspring, is characterized by a low constant suckling rate (Tanaka 1992, Wolff 1968). A reason for being on the nipple in spite of no milk transfer is that it may satisfy other requirements than nutritional (McVittie 1978). When distressed, offspring often seek their mothers and therefore suckling may also satisfy social and emotional needs (Carson & Wood-Gush 1983). Additionally, even if milk transfer is taking

place, Cameron (1998) points out that an analysis of milk composition is required if energy transfer from mother to offspring, rather than amount of milk, is to be determined. Milk yield, quality and composition vary between individuals (Oftedal 1985) in response to environmental conditions and with time and experience (reviewed in Oldham & Friggens (1989). There is also variation between infants' ability to suckle. This could depend on the sex of the infant, age (i.e. experience), size (larger infants tend to be more efficient) and individual differences between mother-infant dyads (Cameron 1998).

4.5 Maternal behaviour and parent-offspring conflict

Trivers (1974) was the first to suggest that evolutionary interests of parents and their young were not the same, an idea which has been termed parent-offspring conflict. Basically, it means that offspring try to benefit in an evolutionary sense from a higher level of parental care than what is optimal for the parents, since parents have to allocate resources to both present and future offspring. In primates, milk provisioning is the largest part of parental expenditure and thereby the resource causing most conflicts between mother and offspring. Conflicts may result in rejections of the nipple which increase with the age of the offspring (Förster & Cords 2002, Lee 1984). In my study, the decreased nursing frequency around 12 hours might be an expression of a conflict between nursing and foraging.

The level of antagonistic behaviour in this population of blue monkeys was very low and no aggressive behaviours were seen between mothers and offspring. Contrary there were high rates of grooming between mother and offspring and no apparent conflicts in the sucking behaviour. This coincides with the behaviour of blue monkeys in general where conflict occurrence has shown rare, especially within the group. Males do occasionally fight for mating opportunities and females have been observed fighting other groups for their territories. On the other hand, groups often form coalitions with other primate species (Cords 2002). One explanation for the low antagonism is the diverse diet (Pazol & Cords 2005). Instead of competing the individuals spread out when foraging to avoid food competition.

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