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DIPLOMARBEIT

EFFECTS OF TOURIST PRESSURE ON THE FOLLICULAR CYCLES AND REPRODUCTIVE BEHAVIOUR IN FEMALE BARBARY MACAQUES (MACACA SYLVANUS)

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Verfasserin / Verfasser:	Ruth Sonnweber
Matrikel-Nummer:	9907531
Studienrichtung (lt. Studienblatt):	Biologie - Zoologie
Betreuerin / Betreuer:	Prof. Dr. John Dittami

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Abstract

In the course of the present study effects of tourist pressure on Barbary macaque females' reproductive physiology and sexual behavior were analyzed. The study was conducted on the Rock of Gibraltar in one focal group, frequently visited by tourists. Data collection was done over one reproductive season. Behavioral data were gained via focal protocols and collection of ad lib data. Endocrine profiles were evaluated from urine samples. Daily observations and urine sampling concentrated on seven focal females.

The reproductive physiology of the female Barbary macaques was monitored. Due to lack of samples it was not possible to distinguish the different cycle phases of the females. For four focals however, time points of possible ovulations respectively of follicular genesis could be evaluated. These time points were linked with the corresponding sexual behaviors occurring within the following and previous days. It was shown that sexual initiative and male interest increased during this period.

Female sexual behavior was partly affected by tourist presence. Mainly high ranking females adapted their behavior to the tourist situation and ceased being sexually active when tourists were at the site. Generally dominant females interacted more with tourists than their lower ranking peers. Overall social, agonistic and reproductive behavior was shown less in the presence of tourists, although no significant results could be gained.

Stress analyses revealed that average cortisol levels and tourist interaction rates showed no clear connection. Rank might influence stress rates. Middle ranking and dominant females expressed highest stress levels.

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1 Introduction

Human and non-human primates are close relatives and share many common behavioral and social patterns (Fuentes and Wolfe, 2002). Maybe that is one reason why interactions between these species occur often and why interacting with monkeys seems so tempting to humans. Interactions with tourists and local people in an unsupervised and unregulated way determine the daily life of the famous Barbary Macaques on the Rock of Gibraltar. These animals are the main tourist attraction and the central reason for tourists to visit the Rock. Therefore they are the town's landmark. The human recreational interests dominate the city: Gibraltar is paved with advertisements for Rock tours by bus or taxi and little shops that sell all kinds of souvenirs – from plastic monkey statues to furry stuffed monkeys, T-shirts with monkey pictures and so on and so forth. Even on the one Pound coins a Gibraltar macaque is pictured. Legends and myths tell about these animals and how they arrived in Gibraltar. The Barbary Macaques are kind of a sanctum, a heritage to the British on the Rock and as far as I experienced it in discussions with the Gibraltarians, the monkeys are considered their possession. This shows the importance of the “Rock Apes”, as these animals are often called. Nevertheless, as will be illustrated later (Chapter 1.3), the coexistence between monkeys and humans in Gibraltar is not conflict-free. Feeding the monkeys is one of the central tourist attractions, advertised by many tour operators (Fa and Lind, 1996). Tourist food is a trigger for competition among the macaques. The effects of this heightened food competition, as well as the influence on group fission and fusion dynamics were studied by Gomila (2004) in the Gibraltar population of Barbary Macaques. Hand-feeding is not the only type of interaction with the monkeys that can occur: close physical contact, which undercuts a normal individual space, direct physical contact between a monkey and a human (be it aggressive or neutral) and so on, are observable.

Human–monkey interactions are a well known phenomenon not only on the Rock of Gibraltar, but also in other regions where primate species are endemic and free or semi-free ranging. Zhao and Deng (1992) reported persistent occurrences of human-animal interactions for Tibetan Macaques (*Macaca thibetana*) in China on Mount Emei. Fuentes (2002 & 2006a) studied interactions between humans and Long-tailed Macaques (*Macaca fascicularis*) as well as other nonhuman primate species in various areas of the world e.g. on Mentawai Islands and the

Barbary Macaques in Gibraltar. In the Gibraltar population of Macaques also Fa and O'Leary (1993) conducted a study on the effects of tourists on the monkeys' time budgets in 1993, which will be discussed later on in detail (Chapter 1.3). The amount of studies on this topic, the various regions throughout the world where such studies were conducted and the interest of many scientists in it shows the importance of getting an insight in the dynamics and effects of these human–nonhuman primate interactions. The viewpoints differ: some scientists (Kao, 2003; Grossberg et al., 2003) observed the interactions from a human standpoint, whereas others (Fa, 1991b; Fa & O'Leary, 1993; Fuentes, 2002; Fuentes, 2006 a&b) concentrated on the monkeys' perspective. A rather new trend in this study area is to link the two viewpoints. Fuentes calls this the “Ethnoprimateological Approach” (Fuentes, 2006b). In Gibraltar, monkeys and humans compete over space. Studies on macaques have shown that disease transmission can occur between monkeys and humans (Honess et al., 2006). The Gibraltar macaque population depends on a daily provision of food by GONHS (Gibraltar Ornithological and Natural History Society), while the Gibraltarians depend on the monkeys economically.

In the course of the present study, the question how the persistent tourist pressure affects the Barbary females' reproductive behavior and physical reproductive ability will be highlighted. Although this study includes human behavior, its focus is on the monkeys' viewpoint. Before going into detail, some information on the Barbary Macaques in general and on the specific situation in Gibraltar will be given in the following sections.

1.1 General Information on the Barbary Macaques (Macaca sylvanus)

1.1.1 Taxonomy and Distribution

The genus *Macaca*, which belongs to the *Cercopithecidae* is one of the most successful primates with the widest geographical range (excluding humans). Apart from the Barbary macaques that are found in Northern Africa (Algeria and Morocco) and in Gibraltar, the twenty other known macaque species are distributed across South and East Asia (Thierry et al., 2004). Depending on which taxonomic criteria one accepts, two additional species of macaques can be counted: ranking the two subspecies of Pigtailed Macaques (*Macaca nemestrina nemestrina* and *Macaca nemestrina leonina*) and the two subspecies of Mentawai macaques (*Macaca pagensis pagensis*

and *Macaca pagensis siberu*) as autochthonous species the total amount of macaque species would increase to 22 (Groves, 2001). An additional species could be added or subtracted by counting seven (Fooden, 1969) instead of six (Groves, 2001) or eight (Froehlich and Supriatna, 1996) species of macaques on Sulawesi island. On a morphological and molecular basis Macaques can be classified in three main groups (Fooden, 1976; Delson, 1980; Hoelzer and Melnick, 1996 after Thierry et al., 2004): the *silenus* group, the *sinica* group and the *fascicularis* group. According to Fooden's classification (1976 in Thierry et al., 2004) Barbary Macaques belong to the *silenus* – *sylvanus* group, whereas Delson (1980) ranks them in a separate group of their own. Undisputed fact however is, that among the genus *Macaca* the Barbary Macaque is the last African representative and the most ancient taxon.

The Barbary macaques' natural habitat is the semi-deciduous mountainous forest of North Africa (Thierry et al., 2004) and the Rock of Gibraltar, which makes them the only remaining endemic primate species in Europe. The typical vegetation of wild Barbary Macaques habitats are the cedar and cedar-oak forests, the Portuguese and cork oak belts and scrub vegetation gorges in Algeria, as well as high cedar and mixed cedar forests and evergreen oak and mixed oak forests without cedar in Morocco (Taub, 1977). Habitat diversity is lower in Morocco than in Algeria. All these habitats offer food resources as well as hiding places from predators (jackals, foxes, probably raptors, as well as man). During the Pleistocene Barbary Macaques were widespread throughout Europe and North Africa. Up to the 1890's some populations were still found in Southern Spain. Later on, the populations were reduced to five main regions of Morocco and Algeria: High Atlas, Rif, Middle Atlas, Grande Kabylie and Petite Kabylie (Taub, 1977). Abegg (2004) studied the history of distribution and analyzed the preconditions that are responsible for the actual appearance of Macaque species. The distribution of the Barbary Macaques was always strongly influenced by climatic changes, alternately suppressing or promoting dispersal. Colonization, disappearances and re-colonization of Europe took place several times in history. The second main determinant that influenced the distribution of the Barbary Macaques was human pressure (hunting and competition over space). Humans are considered to be the reason that these animals were pushed to the brink of extinction in Europe.

Although the Barbary Macaques are highly adaptable to various habitats, as was illustrated by Menard (2002) or Taub (1977), the world-wide population has suffered enormous losses. The

adaptability of this species to new habitats is limited by the need for areas of retreat, like tall trees or cliffs (Cuzin, 2003 in Mouna and Camperio Ciani, 2006). In the past decades the North-African population declined from around 20 - 25 000 (Fa et al., 1984) to less than 10 000 individuals (Mouna and Camperio-Ciani, 2006). This decline in numbers is partly due to habitat loss (destruction of forests for firewood, overgrazing by livestock) and partly due to hunting by humans, as Barbary Macaques generate damage in agriculture (e.g. Menard et al., 1999; Mouna and Camperio-Ciani, 2006) and lastly the flowering trade of juvenile Macaques from Morocco to Europe. According to rough estimates, several hundred Barbary Macaques are sold and smuggled to Europe per year (van Lavieren, 2004). These numbers do not include the very small population in Gibraltar. The heartland of the world wide population of these macaques is the Middle Atlas area in Morocco (Mouna and Camperio-Ciani, 2006). But the absolute decline in numbers is apparently not the sole problem in conservation questions of this vulnerable species (IUCN, 2007), the population composition matters also. Van Lavieren (2005) showed in his survey on the Middle Atlas population, that the amount of immature individuals in this population is beneath a healthy level. Resource availability (e.g. water) and habitat loss appear to be the main reason for this.

1.1.2 Morphology, Ecology and Social Structure

The Barbary Macaques are tailless, although tail vestiges exist (Fooden, 2007). These vestiges are more pronounced in males than in females. The length varies between 4mm to 22mm. Barbary macaques are old world monkeys with a sturdy physique. Males weigh about 16 kg, while females have an average body weight of 11 kg (Singh and Sinha, 2004). The fur is grayish-brown, reddish-brown or yellow-brown. Their faces are hairless and mottled. These macaques molt from summer to winter coats to adapt to the changes in temperature and climate. Like all the macaque species, they are diurnal animals, with activity during the day (foraging, socializing...) and sleeping at night at specific roosting places. Sexual-dimorphism is pronounced, females are smaller than males. Furthermore, the males possess long canine teeth. Both sexes have large cheek pouches along the lower teeth, which allow them to store aliment of an equal volume of their stomach (Stuart and Stuart, 1996).

The diet of the Barbary Macaques is manifold. They are omnivorous animals with a high potential of adaptability to various habitat conditions (Menard and Vallet, 1996; Menard, 2004). Generally the diet consists of food taken from trees and scrubs: herbs, leaves, seeds, fruits, berries, nuts, bark, roots, but also animal prey is a typical component of their diet: caterpillars, insects and larvae. Macaques adapt their diet not only to the specific habitat (like cedar-oak forests of the Djurdjura National Park and the deciduous oak forest at Akfadou, where the forest is more dominant but less distinct in species), but also to seasonal conditions (Menard and Vallet, 1996; Menard, 2004). Results showed that in both compared habitats the Barbary Macaques alter between a folivorous phase in spring and winter and a granivorous phase in summer and autumn. This again shows the high adaptability to different ecological constraints.

Barbary Macaques live in multi male – multi female groups with balanced sex ratios (Deag, 1974). Group size in the wild varies and typically consists of some matriline and several males. According to Menard et al. (2006) wild groups of Barbary macaques can consist of up to 70 to 90 individuals and provisioned groups in rural areas can contain about 140 individuals. Groups consisting of as many as 200 individuals in provisioned semi-free ranging conditions have been reported by Kuester & Paul (1992). Barbary Macaques have a rather egalitarian hierarchical organization with philopatric females (Thierry, 2001). Egalitarian systems are favored when predation risk is low and as a consequence competition is limited. Therefore dominance hierarchies are not as pronounced as in despotic and nepotistic systems (Thierry, 2001). The frequency of aggressive encounters between group members is low (e.g. compared to Japanese macaques (*Macaca fuscata*) or the Rhesus macaques (*Macaca mulatta*)) and less severe in terms of causing physical injury. Aggression can occur bidirectionally, independent of hierarchy. Reconciliation rates are high and kinship does not play a central role as in despotic systems (Thierry, 1990). Barbary macaques form “female – bonded” (in sensu Wrangham, 1980) groups with strong matrilineal cooperative alliances. Female dominance style can be described as nepotistic; a female’s rank is inherited from her mother (Paul & Kuester, 1987; Butovskaya, 2001). There are some indications that a male’s rank is inherited from his mother (Menard and Vallet, 1996). For the females the “youngest ascendancy rule” (Kawamura, 1965) is not developed in (provisioned) Barbary Macaques dominance repertoire (Paul and Kuester, 1987). This indicates that the classic matrilineal dominance structure that is known in other macaque species (see Flack and deWaal, 2004) is not very pronounced in this species. In other words,

mothers, the matriarchs, remain dominant over their daughters until their post-reproductive phase. Younger sisters however do not exceed the older sisters in rank (Chapais, 2004). Rank reversals mostly occur in genealogies with old or dead matriarchs, respectively when the age difference between sisters is more than one year (Paul and Kuester, 1987). Adult males outrank adult females and all juveniles and subadults.

In general the Barbary Macaques' attitude is very tolerant and the spectrum of conciliatory behavioral patterns is manifold and varied (Thierry and Aureli, 2006). Post conflict reconciliation operates as a part of a homeostatic mechanism (Aureli and Schino, 2004). Aggressions can threaten social relations between individuals and increase the risk of further aggressive encounters, if not reconciled. Therefore conflict resolution plays a major role for social animals. Typical post-conflict behavior in macaques is social grooming, where one or both opponents groom. As was shown in other studies, grooming reduces heart rate and self-directed behavior (e.g. scratching), whereas both parameters are heightened in post conflict periods (without or before reconciliation) (Schino et al., 1988). Preuschoft (2004) also showed that behavioral patterns differ between egalitarian and despotic species. Reduced power asymmetries lead to a prevalence of signals of dominance, whereas signals of subordination are rather infrequent. Barbary Macaques use the rounded mouth stare threat as the principal signal for dominance, while more despotic species with higher power asymmetries like the Stumptailed Macaques often use bites.

Schiestl (2005) showed in a study on Barbary Macaques at the Affenberg Salem in Germany that females spend more time socializing, mostly with other females, than males do. Especially high ranking females initiate more social interactions with other females of the group to strengthen the affiliation. Males do not seem to express a preference for either sex, but male dominance is associated with higher rates of socializing. Interestingly, dominance in both sexes is associated with more affiliation with females.

As is typical for social groups with female philopatry, the males leave the natal group and disperse (Menard et al., 2006). In comparison to other macaque species, male Barbary Macaques and Rhesus macaques (*Macaca mulatta*) (Colvin, 1986; Bercovitch et al., 2000) have a delayed dispersal from their natal group. This holds true only for dominant individuals, but not for their subordinate peers (Paul and Thommen, 1984). Menard and Vallet (1999) reported from their

study on two populations of wild Barbary macaques, that 78% of male emigrants were older than 5 and 54% even older than 8 years, whereas only 22% of the migrating males were subadults. Sometimes these delayed dispersals can enhance to the males' reproduction in the natal group (Paul et al., 1992). These different strategies (male dispersal and female group bonding) result in different dominance styles (DeWaal, 1989) in the two sexes: females tend to have more aggressive conflicts; their hierarchies are stricter with stronger asymmetries compared to the males (Preuschoft, Paul and Kuester, 1998).

A well-known trait, specific to male Barbary macaques is called "agonistic buffering". Males "build Triads", consisting of two males and an infant. This behavior is not considered to be a form of parental investment, but the use of infants as a social tool (Deag and Crook, 1971; Paul, 1984). DNA tests have shown that there is no preference by males to use their own offspring (Kuester et al., 1992). It appears that the infant is used as appeasement in a possible tense or aggressive encounter between two males. Females Barbary macaques show allomaternal behavior with a preference for kin. The closer related a female is to an infant, the more she will invest (Paul, 2006).

1.1.3 Female Reproductive Physiology and Behavior

The principal endocrine factors that affect a female's reproduction and reproductive behavior are the two steroid hormones estrogen (E) and progesterone (P₄) (Wallen, 2001). Concentrations of both hormones vary in a characteristic way over the ovarian cycle. They in turn are regulated by the hypophysial gonadotropins LH and FSH (Hadley, 2000).

Beach (1976) proposed to divide female sexual behavior into three main components. These components are namely attractiveness, proceptivity and receptivity. Attractiveness is the stimulus affecting an initial male reaction. In macaques a principal signal for attractiveness is the swelling of the perigenital skin, which is influenced by estrogen- levels (Roberts, 1978; Moehle et al., 2005). Generally Estrogens enhance attractiveness in mammals (Nelson, 2000). Proceptivity is "the extend to which a female initiates copulation" (Nelson, 2000: 288). In Barbary Macaques this is associated with presentation behavior, i.e. when a female invites a male to copulate by presenting her tumescent anogenital swelling. Receptivity is the "stimulus value of the female for

eliciting an intravaginal ejaculation from a male” (Nelson, 2000: 288). Obviously these parameters may go hand in hand.

At an average age of three to four years females attain their sexual maturity. Males become fertile at an average age of four to five years (Fa, 1984). Mature females show multiple cycles within each reproductive season (Moehle et al., 2005). The first estrus phase of the season is the longest in duration. Even for nulliparous females a conception in the first estrus phase is possible (Kuester and Paul, 1984). Adolescent females often express prolonged follicular phases, which are linked to a phase of prolonged sexual activity (Wallen, 2001). The physiological characteristics of follicular cycles appear to be very similar among all macaque species (Kuester and Paul, 1984). Barbary macaques show an average gestation length of 164.7 days and the average cycle length is about 29.9 +/- 2.9 days. The follicular phase lasts about 15.3 +/- 1.6 days, the luteal phase lasts about 15.6 +/- 3.2 days. These data stem from the Gibraltar population and were deduced from endocrine analyses of fecal samples (Heistermann et al. 2006). Females reach menarche age at four to five years (Thierry et al., 1996). Females have vaginal bleedings after non-conceptional cycles that can last from one day to one week. Post-conceptional bleedings during pregnancy can occur (Kuester and Paul, 1984). Usually, females give birth to a single baby, although twins are born occasionally (Fooden, 2007).

Resource availability may be relevant for the sexual maturation and fertility of the provisioned Barbary macaques of Gibraltar. Comparisons of wild and captive populations of animals brought to light that food enhancement may entail an acceleration of sexual maturation (Sadleir, 1969 after Bercovitch and Harvey, 2004). Although conflicting results were gained in diverse studies in various macaque species, a general trend can be asserted: “...enhanced nutrition accelerates reproductive maturation in macaques.” (Bercovitch and Harvey, 2004:64).

Various studies on different macaque species asserted that although females show sexual activity throughout all stages of the cycles, matings occur more frequently around the periovulatory phase (Hrdy and Whitten, 1987; Aujard et al., 1998; Deschner et al., 2004). This rise in sexual activity around the time of ovulation could not be verified in one study for Barbary Macaque females, where estrogen levels did not seem to alter sexual behavior (Brauch et al., 2007b), although it had been reported in another study (Moehle et al., 2005). The discrepancy here may have been related to the unusual group composition in the study by Brauch (2007b); the troop's sex ratio was

female biased. Wallen (2001) proved that group composition can modify the individuals' sexual motivation during a female's cycle in Rhesus macaques (*Macaca mulatta*). With balanced sex ratios mating behavior and copulations increase in the follicular phase, but decrease or cease completely during other phases of a female's cycle. In contrast a single male with multiple females - situation leads to this male mating with females only during their fertile phase. The group composition in the mentioned study troop was somewhere in between and could be responsible for the altered sexual motivation. Wallen's theory (2001) says that sexual contacts can increase social conflicts. The assumption is that a mechanism is prevalent that "couples mating behavior with fertility in a complex social environment" (Wallen, 2001: 341).

Reproduction takes place seasonally, which is an adaptation to climatic fluctuations (Kuester and Paul, 1984; Paul and Thommen, 1984; Taub, 1978). In mating season, Barbary Macaque females exhibit anogenital swellings as indicators of receptivity and ovulation. Swellings develop during the fertile phase of the reproductive cycle (Wildt et al. 1977; Bercovitch 1991; Wallis 1997; Setchell & Dixon, 2001) each female goes through two to three cycles each mating season (Kuester and Paul, 1984; Moehle et al., 2005). It has been proposed that swellings enhance sexual attractiveness (Bielert et al. 1986; Nadler & Bartlett 1997). These sexual swellings develop during the follicular phase enhanced by estrogen. De-tumescence is influenced by progesterone (Wildt et al. 1977; Bercovitch 1991; Wallis 1997; Setchell and Dixon 2002).

Among different populations of Barbary Macaques the reproductive season can vary: while the reproductive period in Gibraltar is between October and February, the animals in Salem reproduce between September and January. As a consequence also the birth season can be different (Kuester and Paul, 1984). Nevertheless in each population breeding appears to be synchronized (Kuester and Paul, 1996). Within a particular population the females' timing of maximal mating effort is influenced by recent reproductive history and age. Younger females tend to conceive later than older ones and parous females without offspring from the previous season show earlier pregnancies (Kuester and Paul, 1984). Females mate with several males during all stages of their cycles and in fast succession (Taub, 1980; Small, 1990; Kuester and Paul, 1992). This extended sexual activity over a period longer than the actual fertile phase around ovulation was considered direct evidence for a female strategy to confuse paternity, which was first shown in Hanuman langurs (Heistermann et al., 2001). Taub found that estrous Barbary

females initiate consortships with about six different males a day and consort with 64% to 73% of all adult and subadult males during one estrous cycle (Taub, 1980). The highly promiscuous reproductive system puts males under steady competition. Those males, who manage to monopolize females during their fertile phase, stand to attain the highest reproductive success. Monopolizing a fertile female has the bonus of preventing other males from copulating. Male monopolizing efforts make sense either in females with high chances of conception or those whose offspring have high survival rates. These behavioral patterns lead to paternity confusion (Taub, 1980) with the effect that males tend to affiliate with the babies and do not harm them, as they could be their own offspring. In short, it reduces infanticide (Wrangham, 1980; Hrdy, 1979). Associations between male and female Barbary macaques are short-lived. Consortships do not usually exceed twenty minutes and rarely extend over one hour (Taub, 1980). Females appear to be the driving force here: males rather offer themselves to the females by displaying courtship signals or by following a pair, waiting for the female to quit the association. Females copulate with almost every male of the group, independent of age, dominance or relatedness (Taub, 1980; Kuester and Paul, 1992; Small, 1990). Although female mate choice does seem to play a role, the key issue is male competition over access to females (Kuester and Paul, 1989). Adult males avoid aggressive encounters among themselves but show aggressive behavior towards subadult males. The latter rather sneak copulations with females than compete directly with adult males (Kuester and Paul, 1992). Adult males prefer dominant females but do not discriminate between fertile and infertile females. This does not hold true for younger males. They copulate primarily with low ranking females. Older males have better access to females in general. Therefore older males are more successful in their overall reproductive efforts (Kuester and Paul, 1996). A recent study indicates that Barbary Macaques display a reproductive skew, in favor of dominant males fathering more infants (Brauch et. al, 2007a). The authors attributed this to female mate choice and challenge the presumed major role of male competition.

1.2 The Gibraltar Situation

How the ancestors of the Barbary Macaques came to inhabit the Rock of Gibraltar remains unclear. Shaw and Cortes (2004) assume that animals were brought as pets by migrating North-African people on their way to Spain. The theory is based on Arabic texts, which seem to be the

most reliable sources of information on that topic at the present time. Recent genetic analyses have revealed that the population is composed of animals originating from Morocco and Algeria (Modolo, 2004). Legend has it that the British brought the Barbary macaques to Gibraltar. These animals once gave warning to the British of a nightly attack of the Spanish. Ever since, the British have been in charge of the monkeys under the premise that Gibraltar will remain British as long as monkeys inhabit the Rock.

Under the guidance of the UK – military, which lasted more than five decades (Fa and Lind, 1996), information on census and population composition tended to be unreliable and incomplete. Due to diseases and anthropogenic interferences the population required restocking with animals from Morocco several times. This happened for the last time after the Second World War, when the population had shrunk to three animals (Fa, 1984; Fa, 1991). In the 1920s first complaints by citizens about interfering Rock-apes were reported, when official counts noted a total of 10 animals. As Shaw and Cortes (2004) state, it is unlikely that these few animals could have provided a noteworthy cause for alarm. In the following decades population management was controlled by the military. By 1946 two groups, the Princess Caroline Troop and the Apes Den Troop existed. Regulation of overpopulation was assured by culling (Fa, 1984). Group splitting and exploration of formerly unused areas followed. As the Army offered daily provisioning to the macaques on the Upper Rock, the monkeys concentrated there. Feeding sites were moved and resulted in formation of the “Middle Hill” group. In the 1980’s culling of animals was stopped which resulted in an explosion of the population and led to repeated group splitting: Apes Den group, Royal Anglian Way I and II, Prince Phillips Arch, Cable Car, Middle Hill, Caletta, Rock Gun and the group at Farrington Barracks (Möhr, 1998;. personal observation and communication with Eric Shaw).

Today the animals are under the care of the Gibraltar Ornithological and Natural History society (GONHS). Two ape-keepers supply the monkeys with food and water on a daily basis and keep the tourist sites clean. A variety of vegetables and fruits are offered; occasionally seeds or peanuts are distributed. Although officially restricted, feeding, especially hand feeding of the monkeys by tourists, locals and tour operators is common and occurs daily. Culling was reestablished as a management tool as the government wants to keep the number of animals at

around 300. In addition some females have been implanted with hormonal contraceptive devices. Apes Den is the only group where no females were implanted at the time of the study.

All groups apart from Middle Hill are “tourist groups”, visited on a daily basis throughout the year. In 2005 about 7.8 million tourists visited Gibraltar according to government records (<http://www.lowtax.net/lowtax/html/gibraltar/jgiecon.html>, 08.09.2008). Core tourist troops are the Apes Den, the Royal Anglian Way and the Prince Phillips Arch group. The Apes Den troop is mainly visited by Gibraltarians and “bus-tourists”, whereas the Prince Phillips Arch group is mainly visited by “taxi- tourists”. At the Royal Anglian Way group, the taxi and bus tourists merge. The Middle Hill group lives in a restricted area where only interactions with military people can occur (personal observations and communication with Eric Shaw). Maybe this is the reason why this specific troop is best studied. Almost all studies on reproductive and social behavior were conducted in this specific group. Only few studies have focused on tourists groups; specifically, no studies on reproductive physiology and behavior have been carried out on these groups.

1.3 Human – Monkey Interactions and Implications on Social Life and Physical Health

Human – monkey interactions occur frequently on the Rock of Gibraltar. Here, the primary threat for macaque conservation is not habitat destruction or predation as known in Morocco and Algeria, but tourism and culling. The following section gives an overview on studies on human – monkey interactions.

Fa and O’Leary (1993) found that diurnal activity patterns of the macaques are highly influenced by tourists. The data discussed in their paper stem from two study periods – one from observations in 1979/80 and the second from 1991. With the rise of tourist numbers over the time span between the two study periods (probably due to the opening of the border to Spain in 1985) the monkeys’ daily time budgets changed: feeding activity was relatively low (4.6%) in 1979/80. Eleven years later there was a strong increase in feeding (7.3%). Simultaneously the amount of time spent for socializing (grooming, being groomed ...) diminished. The authors attributed this to the higher tourist numbers: more tourists meant more food. In turn foraging or fights over provisioned food decreased. In contrast, wild populations of Barbary Macaques spend from 24%

(Menard, 2004) up to 50% (Fa and O'Leary, 1993) of their time foraging and feeding. Compared to other macaque species this is still a low level, considering that for instance Lion-tailed Macaques (*Macaca silenus*) spend up to 55% of their time foraging and feeding (Menard, 2004).

A further study by Fa (1991b) revealed that higher tourist numbers were linked with more severe aggression in the response of the monkeys. Biting, a very aggressive way a monkey can interact with humans, increased with visitor numbers. A certain degree of habituation did however take place. Over a four-year period (1985 to 1989) a decline in bite rates was registered, "*reflecting a drop in visitor density response*" (Fa, 1991b:43). Women were been reported to have been bitten more often than men. Younger humans were bitten more often than their older peers. Compared to other enclosures where Barbary Macaques can be visited the aggression rates in Gibraltar are comparably high, which most likely can be attributed to the high tourist numbers, the small home range of the monkeys and the low level of visitor education (Fa, 1991b).

According to Fa and O'Leary (1993) most food-related interactions were initiated by humans (human-initiated and macaque-initiated interactions ratio = 3.2: 1). Interaction rates rose with tourist numbers, although the monkeys can decide and choose not to interact in certain cases (Fa and O'Leary, 1993). Tourist visitation peaks were recorded between 12:00 to 13:00h and 15:00 to 16:00h. Reportedly the monkeys ignored humans' interaction attempts in the evening hours (around 17:00) and concentrated on socializing with group members before heading for their roosting places. Fuentes (2006b) verified the results. Although group composition changed over the years, the basic dynamics in human-animal interaction seem to remain constant. Looking at these dynamics in more detail on a troop-specific level slight differences emerge: within the population, troops with disproportional high respectively low interaction rates occurred. The Prince Phillips Arch troop showed the highest rate with 1.1 interactions per minute, whereas the neighboring troop at the Cable Car station has the lowest interaction rate with 0.13 interactions per minute. Apes Den was the other troop with frequent human interactions. As was suggested by Fuentes, a study on focal animals and their taxi driver/bus driver interactions was conducted during the mating seasons of 2004/2005 and 2005/2006. It could be shown that specific animals (mostly high-ranking) "adopted" specific bus-drivers and received most of the food they distributed. At Prince Phillips Arch a comparable effect could not be confirmed for individual taxi drivers. Low-ranking and dominant animals were found to acquire equal amounts of food

and had similar numbers interactions at Prince Phillips Arch (Schiestl and Sonnweber, unpublished data).

These extensive interactions with humans have an impact on the group size. Gomilla (2004) analyzed the fission and fusion events in the Barbary Macaque population in Gibraltar in connection with tourist pressure and tourist feeding behavior. He argued that the availability of indiscriminately distributed tourist food can heighten intra-group competition over food. This in turn can weaken the group cohesion, provoking group fission. The study revealed that intra-group conflicts (between neighboring individuals) increased whenever food was offered by tourists. Conciliatory tendencies decreased, although this was not significant due to low sample size (Gomilla, 2004).

Fuentes (2006a) and Fa (Fa & O'Leary, 1993) both mentioned their concerns about the probability of disease transmission between humans and macaques as a consequence of close contact. Transmission could occur in both directions: from humans to monkeys or vice versa. Numerous potential zoonotic diseases in macaques have been described (Honess et al., 2006). The transmission of a disease does not necessarily happen by direct body contact (bites, scratches...); it can also result from contact with contaminated body fluids, blood or waste matter. Honess et al. (2006) studied the health of the Barbary Macaque population in recent years. Despite the high interaction rates between the macaques and tourists in Gibraltar transmission seems to be rare.

1.4 Hypotheses and Questions

In the present study, effects of tourism on reproductive behavior and reproductive ability were investigated. Due to the high tourist pressure at the Apes Den site, the ovarian capacities of the females were expected to be compromised. The term “*ovarian capacity*, defined as the total number of follicles which can be stimulated under maximal ovarian stimulation with FSH” (Kwee et al., 2003: 1422), is often used in research on in vitro fertilization. It describes the ovarian ability to stimulate the development and growth of a follicle, which can be fertilized under hormonal (such as Estrogen, Inhibin B, Progesterone, FSH and LH) control. Therefore variations in estrogen (E) and progesterone (P₄) concentrations throughout the cycle are

necessary. The higher these fluctuations are, the higher the ovarian capacity is classified. The ovarian capacity is expected to be higher in young females than in older ones (Hadley, 2000).

Furthermore cycle phase was expected to have an effect on the expression of sexual behavior (Brauch et al., 2007b; Kuester and Paul, 1996; 1984; Engelhardt et al., 2004 in long-tailed macaques). As the study group was highly female biased, a link between the estrogen concentrations and sexual behavior was predicted (Wallen, 2001). A peak in sexual behavior was expected around the time of ovulation, when estrogen levels are high. Female sexual initiatives (such as presentations) were assumed to be independent of female rank (Kuester and Paul, 1984). In contrast, inspections by males were expected to occur more often in higher ranking females throughout the whole study period, whereas in lower ranking females more inspections were predicted for the fertile phase (Wallen, 2001). In “tourist specialists” lower rates of presentation and inspection rates were expected as due to tourist interaction behavior less time for sexual activity is available (Fa and O’Leary, 1993). “Tourist specialists” are animals than spend more than average time, interacting with tourists.

Copulation, intromission and mounting rates were assumed to be higher in dominant females than in low ranking peers (Kuester and Paul, 1996, Brauch, 2007). Higher ranking females were expected to receive more social copulations than their lower ranking peers (personal communication with Prof. Dr. Dittami). Dominant, older males do not discriminate between females at fertile and infertile stages but copulate mostly with dominant, older females (Kuester and Paul, 1996). It was found that males are able to discern a female’s fertile phase and show most ejaculatory copulations during that phase (Brauch, 2007b). Therefore a higher proportion of social copulations in dominant females can be expected, as they receive copulations during all cycle stages. As females are the most important resource for males (Wrangham, 1980), males can use social copulations as a bonding tool. Especially during consortships an increase of social copulations is expected (Caldecott, 1986; Kuester and Paul, 1992).

Reproductive success was predicted to be influenced by the females’ stress levels. High Cortisol concentrations were assumed to affect reproductive success negatively (Deutsch and Lee, 1991). The HPA-axis (hypothalamic-pituitary-adrenal-axis) is the major control system of stress (Hadley, 2000). Furthermore it regulates processes such as digestion, the immune system and sexuality. Direct and feedback interactions between the hypothalamus, the pituitary gland and the

adrenals modulate hormone production and secretion of the glucocorticoids (i.e. Cortisol, Corticosterone). Stress can be induced as social stress or physical stress (both activating the HPA-axis but on different pathways). Cortisol was used as a stress marker in the present study.

In hierarchically organized animals, rank can affect an individual's social stress. Rank was assumed to impact average stress level. Literature suggests (Diezinger and Anderson, 1986) that individuals with medium rank have highest stress levels. Other results showed that dominant animals have highest stress levels (Easley et al., 1987; te Boekhorst et al., 1991), whereas other studies found that subordinate animals were the most stressed (Pavani et al., 1991). But there are also indications that rank is overrated in the role it plays for stress (scratch rates not connected with rank) (Knöpfler, 2005).

Higher stress levels were expected for females with high tourist interaction rates. It was expected that animals with high Cortisol levels would show high tourist interaction and tourist feeding rates. For tourists proximity no effect on stress levels was expected, as it was assumed that all individuals had more or less equivalent exposure to tourists.

The actual presence or absence of tourists was assumed to impact the animals' social, reproductive and agonistic behavior. Furthermore an effect of the amount of tourists present was expected for all behavioral categories. Especially an increase in aggressive encounters was expected for high tourist numbers at the site (Fa and O'Leary, 1993; Fuentes, 2006b).

2 Material and Methods

2.1 Study site

Gibraltar has been a part of Great Britain since 1713 and was formally declared a colony in 1830. It is situated in south-western Europe, bordering the famous Strait of Gibraltar in southern Spain. This is where the Mediterranean Sea and the North Atlantic Ocean merge, making this location an important strategic point in Europe, inducing the British colonisation. In total, Gibraltar measures 6.5 sq km with a coastline of 12 km that surrounds the peninsula. The lowest point is at sea level; the highest point is at 426 m. The climate is Mediterranean with cold and rainy winters and warm, dry summers. Gibraltar consists mostly of city and rock without crops or arable land. Only limited freshwater resources are available. Therefore, large natural rock water catchments were installed, but are no longer used for drinking water collection nowadays (Rosenberg, 2005).

The Rock itself stretches over 5 km in north-south direction and 1 – 1.5 km in east-west direction. In the North, the Rock is linked to the Spanish continent by an Isthmus. The eastern and northern cliff sides are almost vertical, whereas the southern and western sides are less steep. The vegetation is rather Maquis-form with some more open areas covered in lower scrubs (garigue) (Möhr, 1998). The variation in scrub types on the Rock of Gibraltar is very high due to geography and geology (alkaline soil). So far, 530 different plant species have been described. The geology of Gibraltar is very similar to North Africa. Typical North African species can also be found on the peninsula. The main flowering season is during March and May (Linares, 1999).

Because the vegetation is not sufficient to supply enough food to the population the Barbary Macaques are provisioned on a daily basis by the staff of GONHS. This also keeps the different groups at the specific tourist sites. At the time the study was conducted, the population was split into six different groups (Figure 1): the Farrington Barracks group, the Middle Hill group (the only group not accessible to tourists, as the territory is located in a restricted military zone), the Royal Anglian Way group I and II, the Prince Phillips Arch group and the Apes Den group. Apes Den was chosen as the study group due to good accessibility, good overview of the territory and the fact that the troop was highly frequented by tourists.

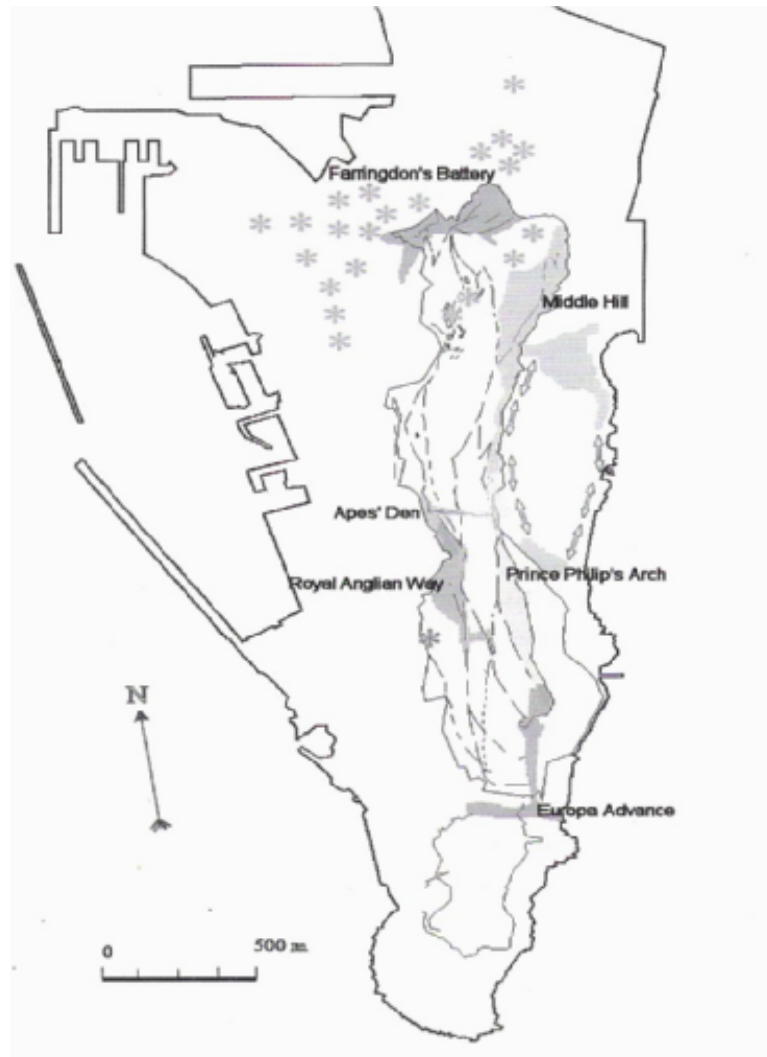


Figure1: Distribution of the Gibraltar macaque groups (Graphic from Shaw and Cortes, 2006).

2.2 Animals and Focal Females

The overall population in 2004 consisted of about 350 animals, with a female biased sex ratio, unlike what Deag (1974) describes in wild populations. The Apes Den group, where the study was conducted had a sex ratio female : male = 13:3 at the beginning of the study (13:9 at the end). The group at Apes Den consisted of 35 animals at the beginning of the study period and grew to 41 individuals as males immigrated during the study (Sonnweber, unpublished census, 2005). The group consisted of 13 adult females, 3 respectively 7 adult males, 3 subadult females, 3 to 5 subadult males, 3 juvenile females, 5 juvenile males and 5 female babies (Table 1 for

males and Table 2 for females). The classification of age was graded after Burton (1972). An overview of the group's individuals is given below; the focal females are highlighted in pink. As background information on the individuals was sparse and no ranking order was available, focal females were chosen to represent all age classes within the mature females. No animals of the Apes Den troop had contraceptive implants. All individuals on the Rock were trapped on an irregular basis. This was used to collect basic data (weight, height, veterinary inspection ...) and to mark the animals with tattoos.

Table 1: Overview of the males at Apes Den during the study period. The resident males were already present in the group at the beginning of the study. Except for Mystery Male, who came later, the immigrant males entered the group around January 2005. Some individuals were marked with tattoos (in brackets), the letter indicates the troop of birth (A for Apes Den, C for Cable Car/ Prince Phillips Arch, W for Anglian Way), the number the sequence of trapping.

Resident adult males	Immigrant adult males	Immigrant subadult males
Clio	Castro	Dino (C26)
Smartie (A5)	James (C3)	Paul (W22)
Jerry (A8)	Sean (C7)	
	Mystery Male	

Table 2: Overview of the females and their offspring at Apes Den during the study period. The first column shows all adult females. The seven focal females are highlighted in pink. The columns “infants 1999” – “infants 2004” show all infants born to these females. The rows indicate the matriline. Deceased individuals are marked in red. The group consisted of 35 (December 2004) respectively of 41 (February 2005) individuals. All females classified “adult females” were considered fertile, as no contraceptive implantations were made in females of this group.

Adult Females	infants 1999	infants 2000	infants 2001	infants 2002	infants 2003	infants 2004
Mercedes	Posh (A9)					
Bloody Mary						
Arthemis		Salma				
Athene (A14)		Steven	Amanda			Princess
Venus		Daniel	infant deceased	infant deceased	Kevin	Ruth
Tris			Blondy	Theo (A15)	April	
Sandy (A4)		Aristotel	Emily	Ryan (A33)	Marcus (A18)	Sophie
Chery		Livia				
Makeup (A3)				Eddy (A16)	Artist	Irene
Punta						Heather
Zora						
Posh (A9)					Spice	
Lea						
Livia						

Information on kinship among the focal animals was not available, but observations by the staff of GONHS suggest that Sandy, Makeup and Zora are siblings and daughters of Athene (evaluation of the ranking order support these assumptions). Posh is known to be Mercedes’ daughter. The genealogy of Venus and Artemis is largely unknown. It is also unclear of how many matriline the group consists. The only matriline that can be considered as confirmed is the dominant kin of Athene. Mercedes and Posh form another lineage, but whether there is any relation to any of the other adult females remains unclear. As other groups originated from Apes Den, for instance the Prince Phillips Arch group, it is possible that matriline may have split. Basic information of the individual focal females is summarized below, focusing on reproductive success in the past.

Mercedes is the oldest female not only of the group, but also of the whole population on the Rock. She was born in 1980, which made her 24 years at the beginning of the study. Despite her age she still expressed cycles and anogenital swellings. Her only known offspring is Posh, born in 1999. Later conceptions and births may have occurred but were not observed.

Arthemis, born in 1986, also had only one known daughter (in 2000), who died. Afterwards no conceptions, pregnancies or miscarriages were documented. If she has other relatives in the group is unclear.

Venus, born in 1990 gave birth to her first infant in 2000. According to reports from the staff of GONHS she had had offspring before that, who did not survive. In 2001 and 2002 she gave birth to an infant each year who did not survive. The cause of death is not known in both cases. In 2003 (Kevin) and 2004 (Ruth), she gave birth to two more children who survived. Venus and her son Kevin died in 2006, but this was after this study was finished. Whether she had siblings in the group is unclear. Possibly there is some relationship to Tris and/or Athemis, but these are just suggestions after observations over a long period of time.

Sandy, born in 1993 is probably the daughter of Athene and a member of the dominant matriline. According to information by the staff of GONHS and personal observations, Makeup and Zora could be her sisters. From 2000 to 2004 Sandy gave birth to one offspring every year and all children survived.

Makeup, born in 1995 had a single infant in 2000 but did not give birth to any further surviving offspring. No further information on possible pregnancies, miscarriages etc. was available. She is a member of the dominant matriline of the troop.

Zora, born in 1997 had no known offspring. Most likely she is the sister of Sandy and Makeup and daughter of Athene, which makes her part of the dominant matriline.

Posh, born in 1999 is the daughter of Mercedes which makes her a member of a low ranking matriline. She gave birth to an infant in 2003, which was her only child when the study started.

A ranking order was gained by using ad libitum and focal protocol data of dyadic, same sex conflicts between all adult animals of the group and analyzed with MathMan 1.0 (Noldus, Wageningen, The Netherlands) (Table 3). These data were collected over the whole study period.

Males who immigrated to Apes Den during the study period were not included in the calculations as the process of migration took place slowly and aggressive attacks by females and males of the troop must be attributed to the “invasion” of an outsider and not to intra-group conflicts. The ranking order was calculated separately for the two sexes. An overview is given in the table below (Table 3). Focal animals are marked in pink. Apart from Posh, who is the tenth female in the dominance hierarchy, all focal females are high or medium ranked. Six of the seven females gained rank numbers in succession, from rank place 2 to rank place 7. As mentioned before, this was a coincidence as no ranking order was available at the beginning of the study.

Table 3: Ranking order of the adult animals of the Apes Den troop. Calculated with MathMan 1.0 (Noldus, Wageningen, The Netherlands). Immigrated males are missing in the order, as they immigrated slowly during the study period. Dominance rank for males and females was calculated separately. Focal females are highlighted in pink.

Rank	Females	Males
1	Athene	Smartie
2	Sandy	Jerry
3	Makeup	Clio
4	Zora	
5	Mercedes	
6	Arthemis	
7	Venus	
8	Bloody Mary	
9	Tris	
10	Posh	
11	Punta	
12	Livia	
13	Lea	

2.3 Hormonal Profiles

Urine samples of the focal females were collected on a daily basis. A total of 231 samples were gathered during the study period. 16 to 37 urine samples were collected per individual. On average 26.14 samples per individual were analyzed. The urine was soaked up with a sponge and stored and frozen in salivettes for hormone analysis at the University of Vienna.

Urine samples were analyzed for concentrations of estrogen (E), progesterone (P₄), as well as cortisol levels and creatinine concentrations. Hormone concentrations were gathered through measuring the steroid metabolites with enzyme immunoassays (EIA) on microtitre plates using biotinylated steroids as labels (method described by Möstl & Palme, 2004). Creatinine values were analyzed after the standard Jaffe method (Slot, 1965). Estrogen and progesterone levels were analyzed to gain information on the female ovarian cycle; cortisol was measured for stress level monitoring. All hormone evaluated concentrations were corrected with creatinine values. Creatinine is a degradation product of the muscles. As muscle mass can be assumed to be more or less constant, without daily fluctuations, the Creatinine concentration in the urine is a marker for the urine's dilution. By multiplication of the hormone concentration with the Creatinine value, dilution effects of the urine can be excluded from results. Some sample points had to be excluded, as Creatinine concentrations were too low and dilution effects could not be eliminated.

2.4 Behavioral Data Collection

Behavioral data were collected using focal animal sampling (Martin & Bateson, 1993). Focal protocols lasted 20 respectively 40 minutes and were collected on a daily basis. Per day two of the seven focal females were observed for 40 minutes, the remaining five females for 20 minutes. Females were selected for observation in random order during all hours of the day. Bad weather conditions or inaccessibility of a certain female on individual days limited behavioral observations. An average of 80.87 (SD 4.34) hours of observations per female was collected, resulting in a total observation time of 161.74 hours. Additionally ad libitum data on mating and agonistic behavior were collected.

Focal protocols were split into units. One unit lasted 30 seconds. A stop watch gave a signal after the duration of one unit. With this method, it was possible to measure the duration of certain behavioral traits such as feeding duration, duration of social interactions and so forth. Some behavioral categories were recorded taking the duration into account; others were monitored according to their frequency (mountings, copulations, human directed behavior...). Behavioral patterns that were noted were classified as social, sexual/ reproductive and aggressive behavior, as well as human directed behavior. The following behaviors were recorded and analyzed:

Feeding: was defined the intake, chewing or swallowing of provisioned or foraged food. Duration was measured. “Eating tourist food” was analyzed as a separate behavior.

Proximity: when the focal females was in spatial proximity with one or more individuals. Proximity was defined as the distance of one monkey arm length or shorter between two individuals (touching distance). Body contact was rated as (close) proximity. Individuals who were involved were identified and noted. The duration of proximity was analyzed.

Grooming/ being groomed: social grooming received or given by the focal female. The groomer uses both hands, whereby one hand parts the fur of the animal being groomed, the other hand or the mouth of the groomer is used to remove particles. Grooming can also be done with just one hand; this hand then alternates between the two tasks. Grooming of an individual by the focal animal was rated as “grooming”. When another animal groomed the focal female this was noted as “being groomed”. When the active groomer removed the fur-parting hand from the recipient, a grooming bout was considered to have ended. The identity of the interaction partner was noted. Duration of this behavior was taken into account.

Human proximity: was defined as spatial proximity between a monkey and a human. Distances of one human arm length or less between the human and the monkey were rated as human closeness. Duration was noted.

Human interaction: was noted when any type of interaction, apart from feeding, between the focal female and a human occurred. Both, monkeys and humans initiated interactions. Friendly (patting, stroking ...) and aggressive (scratching, biting, threatening ...) behavior was observed. Frequency was noted.

Human feeding: was defined as the actual feeding of an animal by a human. Snatching of food from humans by a monkey was noted separately. Frequency was analyzed.

Presentation: when a female turns her anogenital region with an Archd back towards another animal offering it for inspection this was noted as a presentation. When presenting to a male, this behavior was considered to be sexual behavior. When presenting to another female it was classified as a sign of subordination. This behavioral pattern was sometimes accompanied by motivating the male to copulate by touching him or pulling him towards the female. This

behavior was recorded in frequency. Additionally the male's identity was written down and analyzed.

Inspection: is the exploration of the female's genitals by a male. This could happen either by touching, smelling or visually. The type of exploration was not distinguished in data collection. Frequency was recorded.

Mounting: was defined as the climbing up on the female's hind legs by the male with the intention to mate. Mountings were recorded according to their frequency. The male's identity was noted.

Intromission: insertion of the male's penis into the female's vagina. Frequency and interaction partner were noted.

Copulation: was recorded when the male started to perform pelvic thrusts. Ejaculatory (reproductive) and non-ejaculatory copulations (social) were distinguished. Ejaculatory copulations were recognizable by ejaculation-pauses and sperm plug. The copulating male was identified and frequency of copulations was noted.

Active/ passive aggression: any aggressive behavior a focal female received or showed. Threats, displacements, chasings, bites and other aggressive behavior were distinguished. The involved animals were identified and recorded. Frequency of aggressive encounters was noted.

Apart from behavioral patterns information on weather conditions, time of day and amount of tourists present were recorded.

2.5. Data Analysis

2.5.1 Hormone Data Analysis

The ovarian capacity, defined as fluctuation of the delta values of estrogen and progesterone concentrations, was measured. Ovarian capacity is defined as the ovaries' ability to produce and secrete hormones. Delta values were gained by subtracting two subsequent hormone values. The positive difference between them was taken as the delta value. Four females (Sandy, Mercedes, Artemis and Posh) had sufficient sample points for this analysis.

Female steroid hormones were analyzed in order to monitor cycles in addition with fluctuations in sexual behavior. According to Beach (1976), female sexual activity and male interest increase around the fertile phase. Therefore hormone levels during time spans with elevated sexual activity were looked at in order to detect follicular development and possible ovulations. Ovulation could occur with or without production of a gamete. A hormonal indication for an ovulation was defined as a three fold increase in estrogen concentration without corresponding changes in progesterone levels followed by a progesterone increase. Only data points within a time span of three or less days were included in this analysis. When a three fold increase in estrogen within three days or less was accompanied by parallel increases in progesterone concentrations and subsequent decreases in both steroid hormones, follicular development was assumed not to have ended in ovulation and was classified as a disturbed follicular genesis or atresia.

In cases where females gave birth to an infant at a known date, post-conceptional ovulation events were analyzed. These were defined as total decreases in estrogen levels accompanied by low but not zero progesterone values. As average Barbary macaque pregnancies last approximately 165 days, a known birth date makes the calculation of the likely date of conception possible.

Cortisol was used as a marker to monitor stress levels. Individual differences in average Cortisol concentrations were calculated. Connections with focal rank and tourists interaction rates were analyzed.

2.5.2 Behavioral Data Analysis

All data were analyzed using SPSS 15.0 (SPSS Inc., Chicago, IL, USA). Data were tested for normal distribution. Differences between “tourists – present” and “tourists – absent” situations were analyzed using Wilcoxon or T-Test. Correlations of specific behavioral and hormonal parameters were evaluated using Spearman or Pearson correlation coefficients. As different amounts of observation hours with or without tourists present were collected for each focal individual, frequencies of the different behavioral patterns were controlled for observation time. Therefore on an individual level behaviors are shown in “sum per minute”. In calculations representing all focal females together, frequencies are illustrated in “sum per hour”.

Social, reproductive/sexual and agonistic behaviors were evaluated separately. All categories of behavior were analyzed in “tourists – present” and “tourists – absent” situations. Individuals were tested, as to whether they adapt their behavior to the tourist situation at the site. For results a difference between the two scenarios was found, individual differences were analyzed.

Also partial correlations between the amount of tourists present and modifications in behavior were analyzed. To avoid any bias these calculations were controlled for rank.

A descriptive analysis of the distribution of ejaculatory and non – ejaculatory copulations among the females in dependence of their rank was done. As no cycles could be reliably monitored this could not be done in relation to cycle phases, but only around the day of ovulation in case it could be monitored.

Finally the reproductive success of the focal females was described. Reproductive success was defined as the survival of an infant until October 2006. Reproductive success was discussed in relation to rank, age, hormonal profile and sexual performance of the females.

3 Results

Due to lack of urine samples over several days for each individual no cycles could be evaluated reliably. Estrogen and progesterone fluctuations were used to calculate ovarian capacity among focal females. Endocrine data were analyzed in order to detect time points of possible ovulations and follicular genesis. These hormonal data were linked with variations in sexual behavior over the study period. Furthermore absolute hormone concentrations during the study period were analyzed. The relationship between tourists' presence/ absence and animals' behavior modification was evaluated.

3.1 Ovarian Capacity

To analyze ovarian capacity, delta values in estrogen and progesterone concentrations were calculated for all individuals (Appendix 1). Fluctuations within single females over the study period were taken as a marker for the ovaries' ability to develop reproductive cycles (personal communication with Dr. Machatschke). Subject Zora was excluded from detailed analysis as not enough samples (16) were available. For subjects Makeup and Venus no reliable analysis was done due to a lack of samples. The remaining four females were used to illustrate differences in ovarian capacity.

Comparing individual ovarian capacities over time showed that Posh had high variation in estrogen concentrations (Figure 2). The highest fluctuation in estrogen concentrations was 64.45 ng/ μ g within two days (4th of February 2005 – 6th of February 2005) apart from the variation in estrogen of 317 ng/ μ g between the 8th of February 2005 to the 11th of February 2005. This last modification in estrogen was most likely caused by a pregnancy. In comparison to Sandy and Mercedes her delta – progesterone values were low. From 23rd of January 2005 to 24th of January 2005 a fluctuation of 163.76 ng/ μ g was measured. Apart from the last two sample points on the 11th and 13th of February 2005 this was the highest variation in progesterone. For approximately two weeks (30.12.2004 - 12.01.2005) no urine samples could be collected and therefore no information on ovarian function could be illustrated.

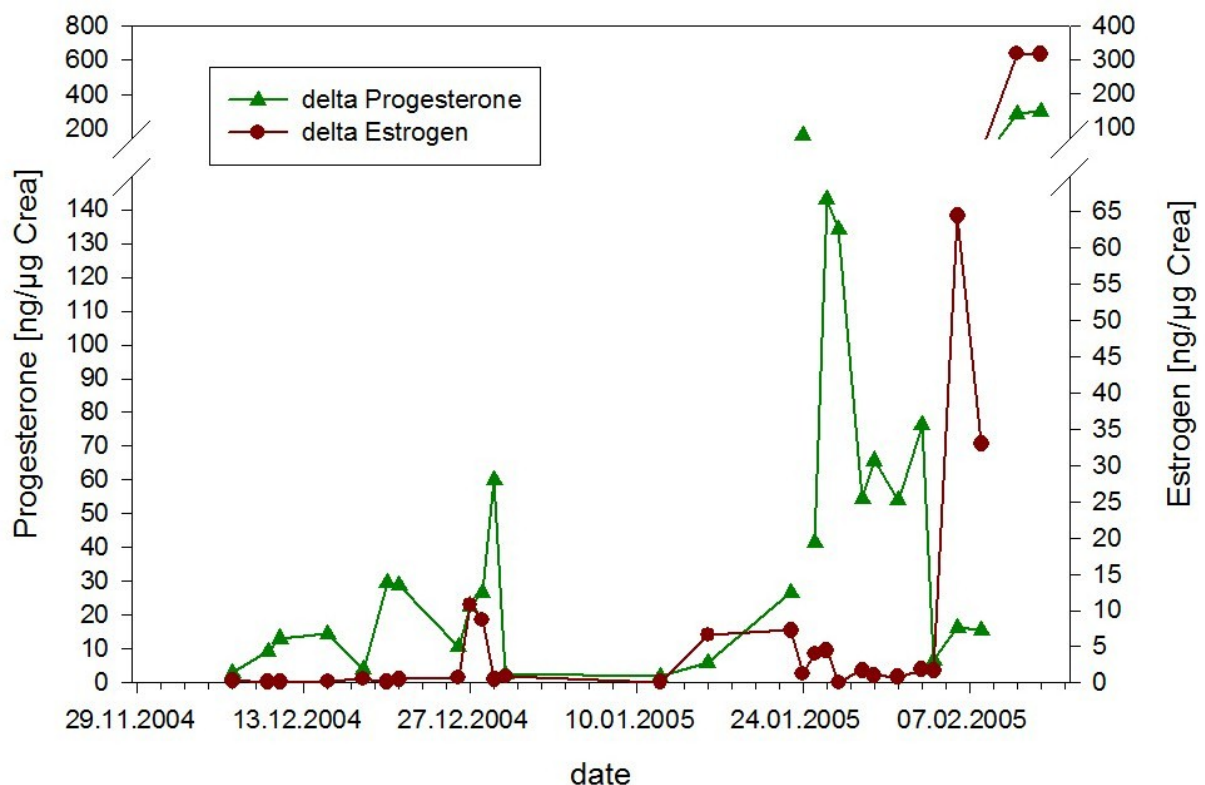


Figure 2: Delta values of urinary E and P4 concentrations during the study period for Posh. P₄ concentrations are shown on the first Y- axis, E levels on the second Y- axis.

The range of fluctuations in delta-estrogen values analyzed for Posh was similar to the one in Sandy (Figure 3). Maximum variation for estrogen concentration was 17.31 ng/ μ g within two days. Apart from that peak, fluctuations ranged around 5 to 8 ng/ μ g. Her highest fluctuation for progesterone peaked at 777.64 ng/ μ g within three days. Apart from this enormous fluctuation the other variations in progesterone concentration were relatively high as well. Between 4th of January 2005 and 16th of January 2005 no samples were collected, therefore, no information on ovarian activity for this period is available.

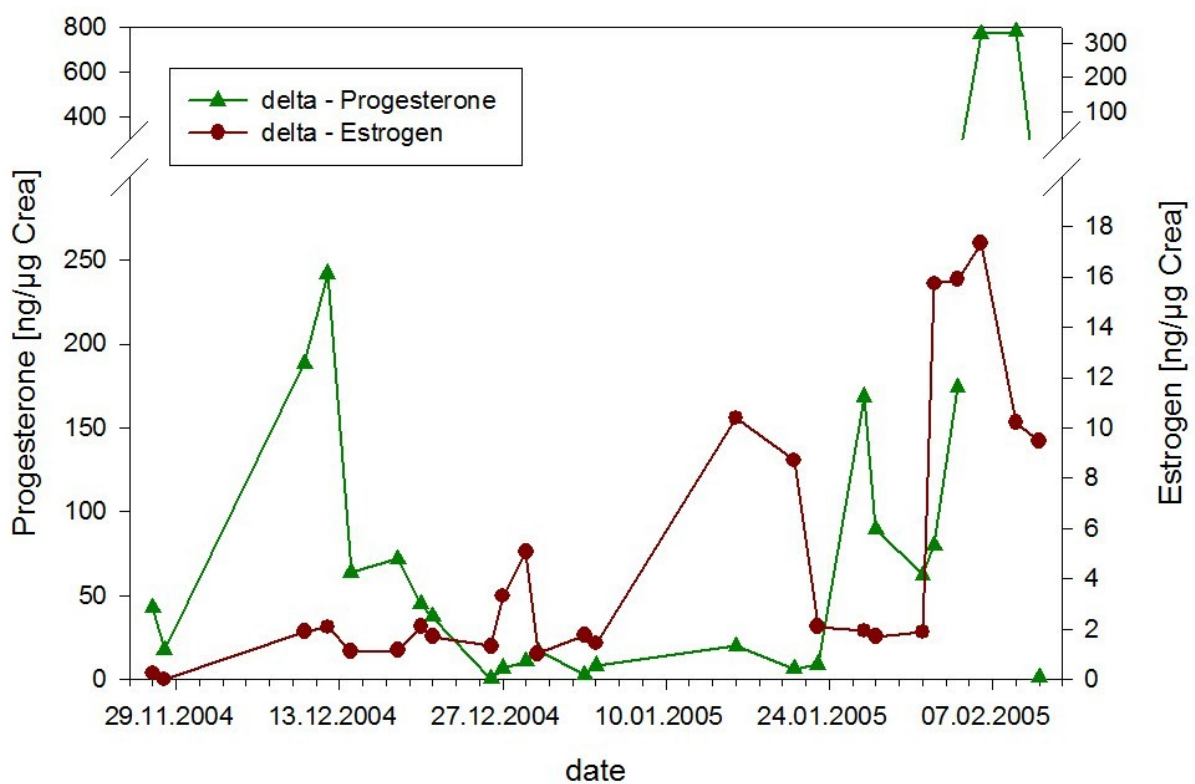


Figure 3: Delta values of urinary E and P₄ concentrations during the study period for Sandy. P₄ concentrations are shown on the first Y- axis, E levels on the second Y- axis.

Mercedes showed high fluctuations in both estrogen and progesterone concentrations (Figure 4). The highest variance within one day was found for estrogen with a fluctuation of 45.67 ng/ μ g. The highest progesterone variation within one day was calculated as 251.98 ng/ μ g. Estrogen and progesterone concentrations appeared to fluctuate almost in synchrony. Between the 19th of December 2004 and the 4th of January 2005 and from the 15th of January 2005 until the 23rd of January 2005 no samples could be gathered. Therefore, no information on ovarian activity over these time spans was available.

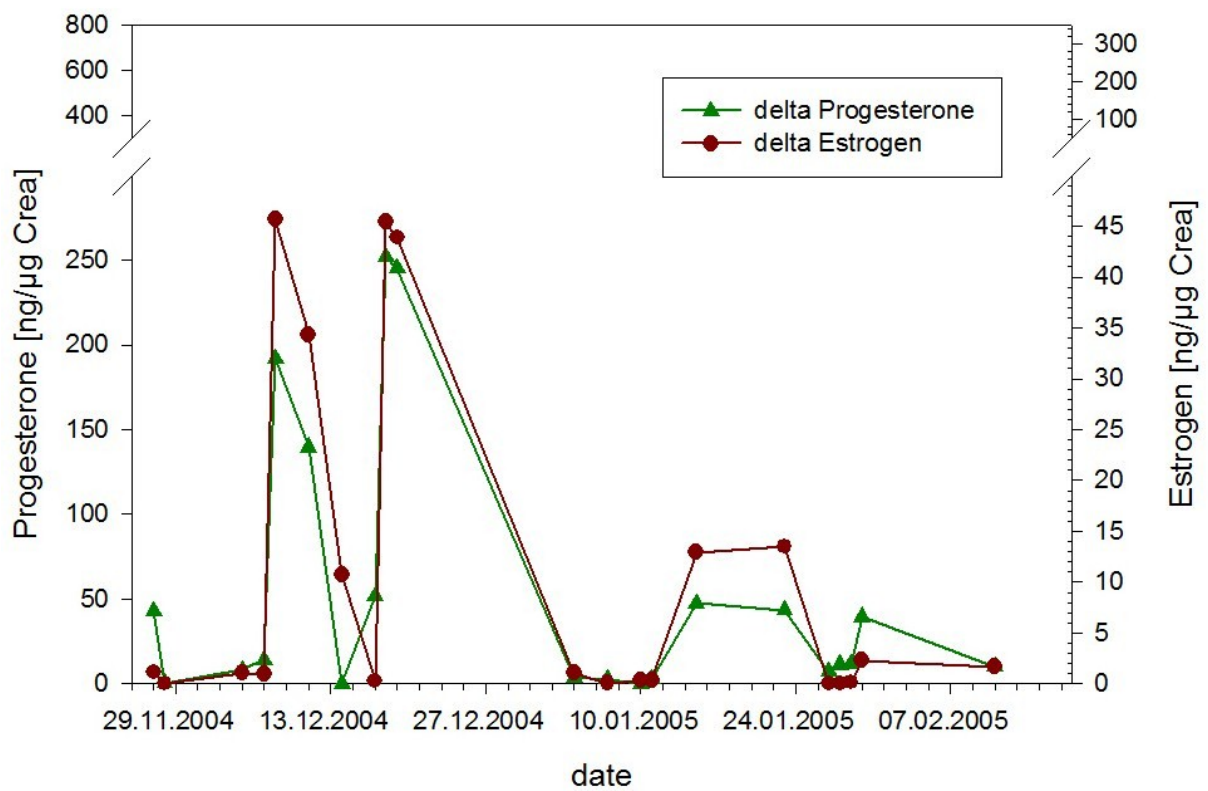


Figure 4: Delta values of urinary E and P4 concentrations during the study period for Mercedes. P₄ concentrations are shown on the first Y- axis, E levels on the second Y- axis.

Compared to the other focal individuals, Artemis showed low fluctuations in both estrogen and progesterone concentrations (Figure 5). Estrogen levels showed no higher fluctuations than 5.04 ng/ μ g within two days. Progesterone fluctuations were low with a peak of 55.78 ng/ μ g change within three days. Another fluctuation in both estrogen (2.88 ng/ μ g) and progesterone (20.75 ng/ μ g) concentrations was found in January 2005. These fluctuations were not as high as the ones in December 2004.

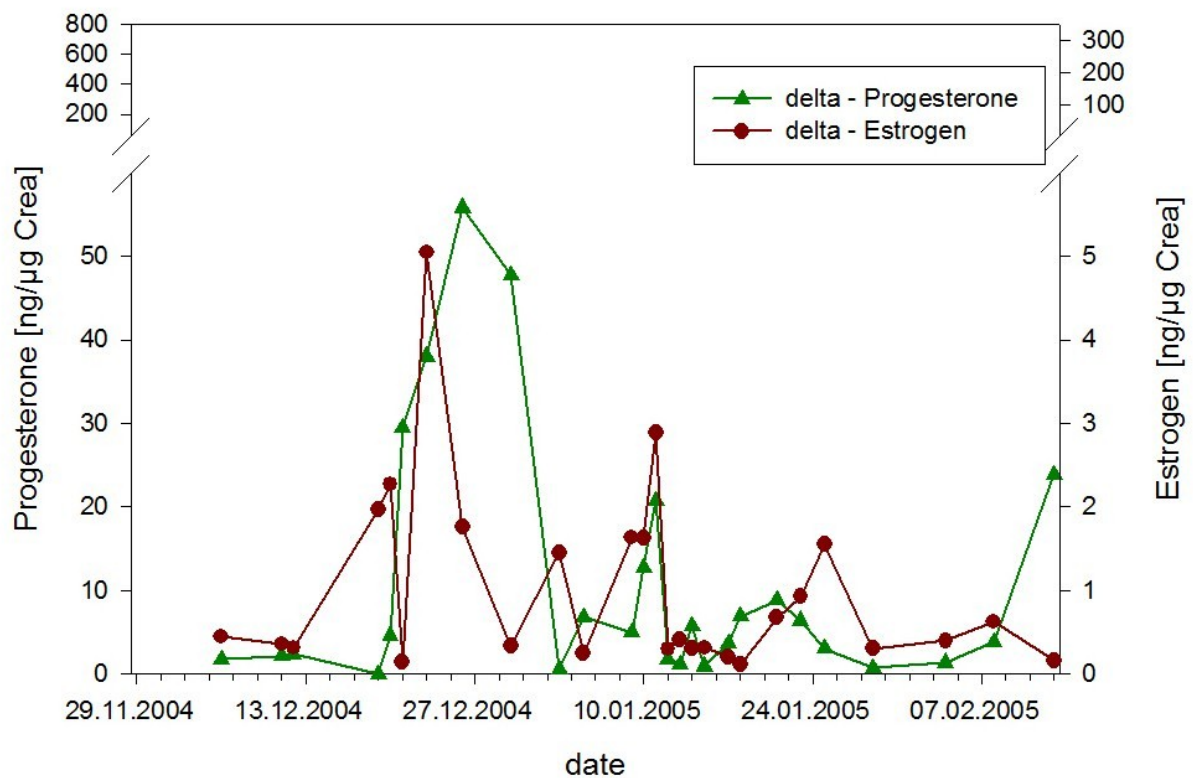


Figure 5: Delta values of urinary E and P4 concentrations during the study period for Artemis. P₄ concentrations are shown on the first Y- axis, E levels on the second Y- axis.

3.2 Hormones and Sexual Behavior

Patterns of sexual behavior were correlated with hormonal profiles. All behavioral data were plotted in the graphs, independent of urine sample collection on the same day. For these figures absolute concentrations of estrogen and progesterone in ng/ μ g Creatinin instead of delta – values are depicted.

In order to examine possible interactions between follicular cycles and the expression of sexual behavior, the patterns of endocrine changes were plotted together with the patterns of reproductive behavior for each focal female. According to the previously set definitions, hormonal fluctuations were looked at to detect potential ovulations respectively follicular acitivity. These hormone characteristics were linked and interpreted with the distribution of frequencies in female sexual initiative and male interest. All these analyses were done on an individual basis. First female proprioceptive behavior and attractiveness (presentations and male inspections) were evaluated and are depicted in the middle part of the following figures for each focal female. For this analysis only intersexual presentations and inspections were used. Preliminary correlations revealed a positive connection between females' presentations and males' inspections. This correlation was independent of tourists' presence (Spearman: $r = 0.673$, $p \leq 0.001$) or tourists' absence (Spearman: $r = 0.71$, $p \leq 0.001$). Presentations and inspections are both presented in the same figures.

Mountings, intromissions and copulations are shown in the lowest part of the figures and were related to hormone values as well. Reproductive (ejaculatory) and social copulations (non ejaculatory) were not distinguished in these analyses. A differentiation of these two kinds of copulations will be discussed in a separate section (Chapter 3.3.1 and Chapter 3.3.2). Therefore frequencies of this behavior include both types of copulations. Females are discussed in descending ranking order.

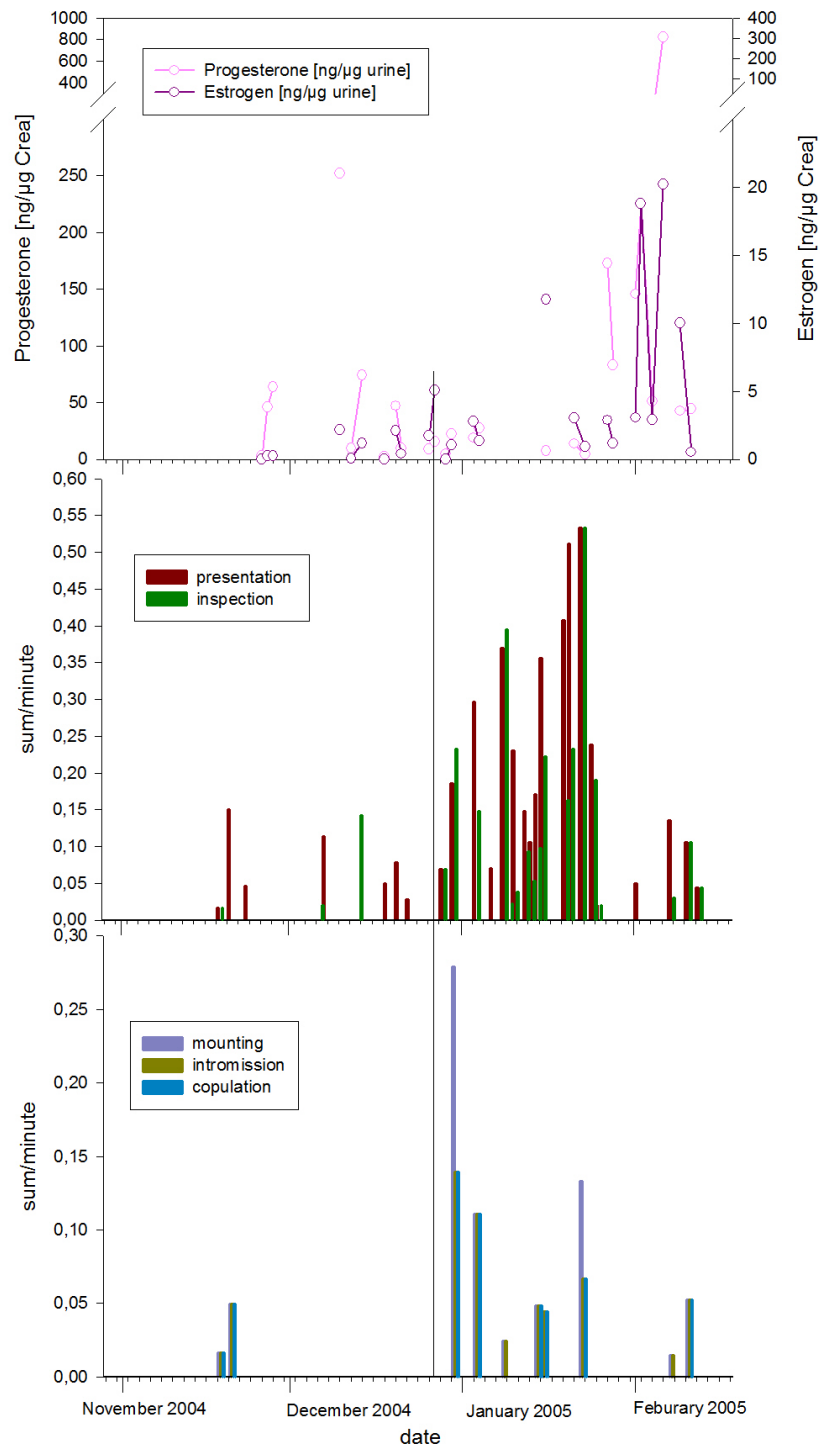


Figure 6: Endocrine data and sexual behaviors of Sandy. Urinary progesterone (light pink circles) and estrogen (dark pink circles) concentrations (in ng/μg Creatinin) are plotted in the upper section of the figure. The middle and the lowest picture show frequencies of sexual behaviors. The vertical line shows the time point of a potential ovulation.

For Sandy a three fold increase in estrogen with subsequent progesterone increase could be found on the 27th of December 2004 (Figure 6). In the graph this event is marked with a black line, connecting the corresponding behavior in the lower parts of the figures. This hormonal pattern could indicate an ovulation. Sexual behavior, which is plotted in bars in the middle and lower part of the picture, increased markedly within the following days. Most copulations could be observed on the 31st of December 2004. This increase in female sexual initiative and male interest support the theory that an ovulation had occurred around that time.

In general Sandy, the highest ranking female among the focal individuals and second ranking female among the whole group showed high rates of sexual behavior (Figure 6). Especially in the end of December 2004 and in January 2005 presentations rates (red bars in the middle section of the figure scaled in sum per minute) and male interest increased. Highest presentation and inspection rates were recorded in mid and end January 2005 when few hormone values exist. Further peaks in mountings, intromissions and copulations occurred during this period. This is an indication that another ovulatory event could have taken place during that time. Knowing that Sandy gave birth to an infant in August 2005 it is likely that hormone fluctuations in February 2005 indicate a post-conceptual ovulation or physiological changes associated with pregnancy. While estrogen concentrations decreased completely, progesterone values remained rather high. This hormonal pattern corresponds with the preset definition of a post-conceptual cycle.

Regarding absolute hormone values, in comparison to the other females, estrogen concentrations in Sandy stayed rather low with a maximum of 18.78 ng/ μ g Cr. Progesterone levels reached maxima at 820.2 ng/ μ g Cr on the 6th of February 2005 during the post-conception ovulation. This was the highest measured progesterone value among all females.

In general presentations towards males and inspection rates of males were high compared to the other focal females. For both behaviors the highest value was over 0.5 times per minute. Presentation rates were mostly higher than inspection rates, or occurred with equal frequency. Sandy had relatively high rates of mountings, intromissions and copulations. Most often all three behaviors occurred in succession, but some males only mounted. Intromissions were always followed by copulations. At the end of the study period in February 2005 in Sandy's post-conceptual period, medium rates of reproductive behavior were observed.

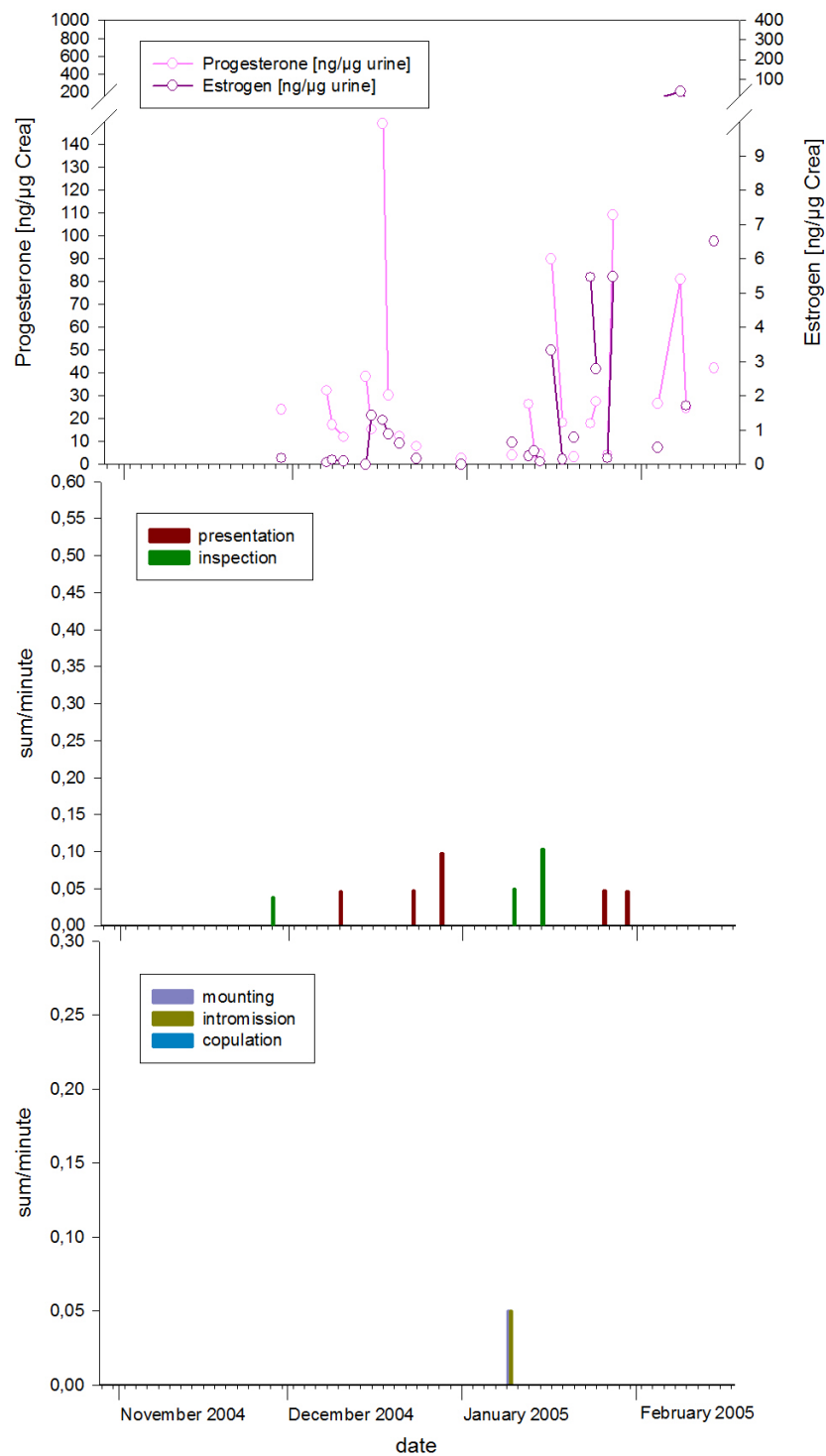


Figure 7: Endocrine data and sexual behaviors of Makeup. Progesterone (light pink circles) and estrogen (dark pink circles) concentrations (in ng/μg Creatinin) are plotted in the upper section of the figure. The middle and the lowest picture show frequencies of sexual behaviors. No follicular phases were documented.

For Makeup no potential ovulation could be monitored during the whole study period (Figure 7). In the end of January 2005 increases in estrogen and progesterone values, occurring in fast succession could be monitored. Three estrogen peaks, followed by complete decreases were accompanied with corresponding progesterone increases within ten days. These endocrine changes could not have led to an ovulation. Behavioral observations did not indicate that ovulatory events were taking place around this time. After the mating season she did not give birth to an offspring.

In general sexual behavior was observed in low frequencies compared to her peers and was distributed scattered over the study period. No core time of sexual activity, whether initiatives from her side, nor interest by males, could be evaluated. Presentations were never followed by an inspection through a male, which was the case in Makeup's female peers most of the time. During focal protocols no copulation was observed. Only mountings and intromissions occurred in early January 2005.

Absolute estrogen and progesterone concentrations were rather low compared to the other focal females. Estrogen concentrations remained around a baseline level, apart from slight increases in late January 2005 and a single peak in February 2005. The highest estrogen concentration was 34.08 ng/ μ g Cr, measured on the 8th of February 2005. Progesterone concentrations remained low over the whole study period with three peaks in January 2005 and a single increase in December 2004. This was the highest progesterone value reaching 149.1 ng/ μ g Cr on the 17th of December 2004. Apart from Artemis and Venus, these were the lowest measurements among the focal females.

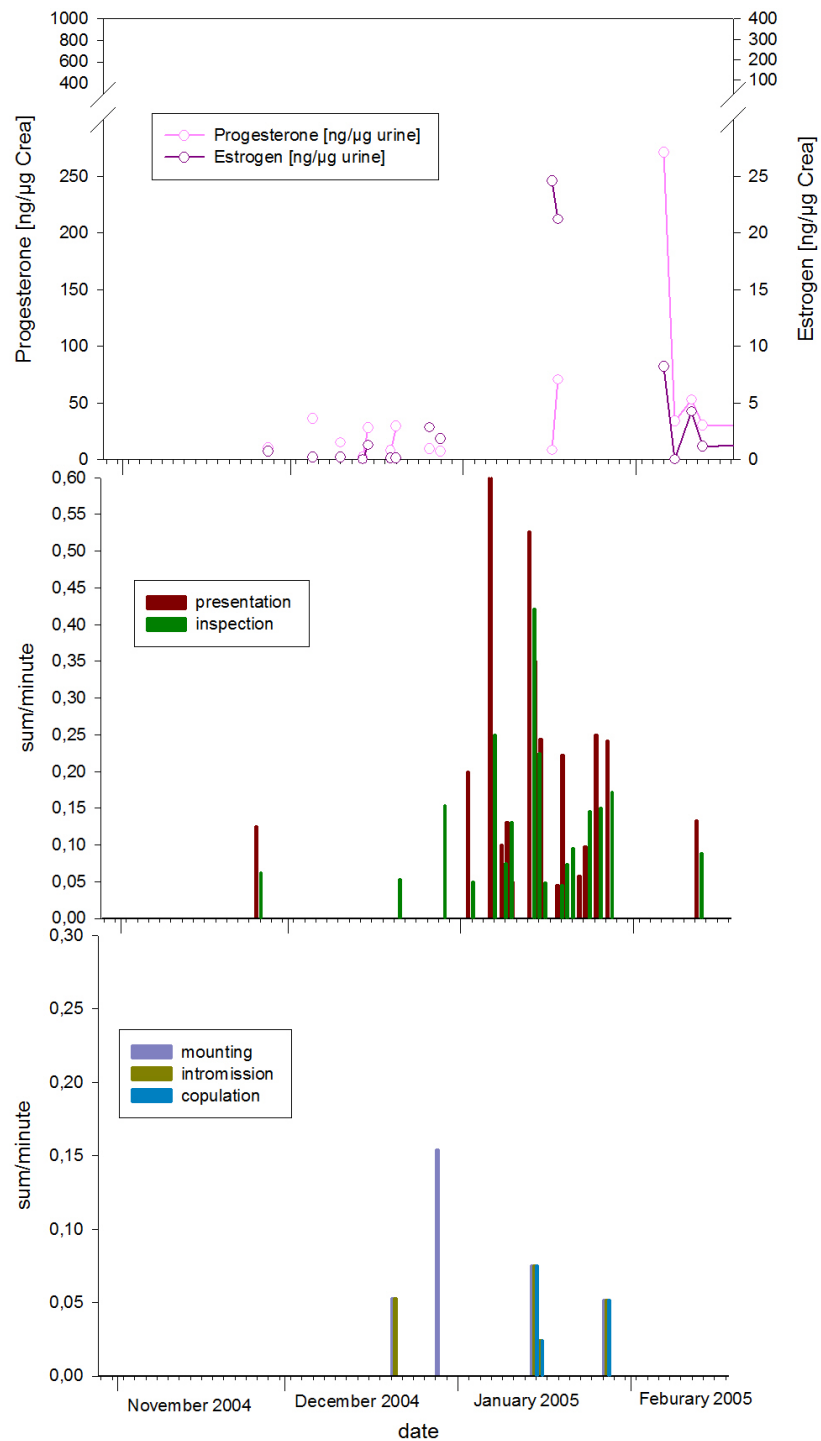


Figure 8: Endocrine data and sexual behaviors of Zora. Progesterone (light pink circles) and estrogen (dark pink circles) concentrations (in ng/μg Creatinin) are plotted in the upper section of the figure. The middle and the lowest picture show frequencies of sexual behaviors. No follicular phases were documented.

An evaluation of ovulatory events was not possible for Zora due to lack of samples (Figure 8). Especially in January 2005 hardly any urine samples could be collected for this individual. The only samples available for this month reveal a high concentration in estrogen. January 2005 was the core time of sexual activity for Zora. The only copulations recorded in focal protocols were noted in mid and end January. Therefore one can assume that an ovulation could have occurred during that phase. No information on surviving offspring is available, as Zora died in spring of 2005.

While overall presentation and inspection rates were high, copulations, intromissions and mountings showed average counts. Outside of the core sexual activity phase, presentations and inspections were observed occasionally. Regarding the absolute values of the samples that could be gathered, she had average concentrations in both estrogen and progesterone.

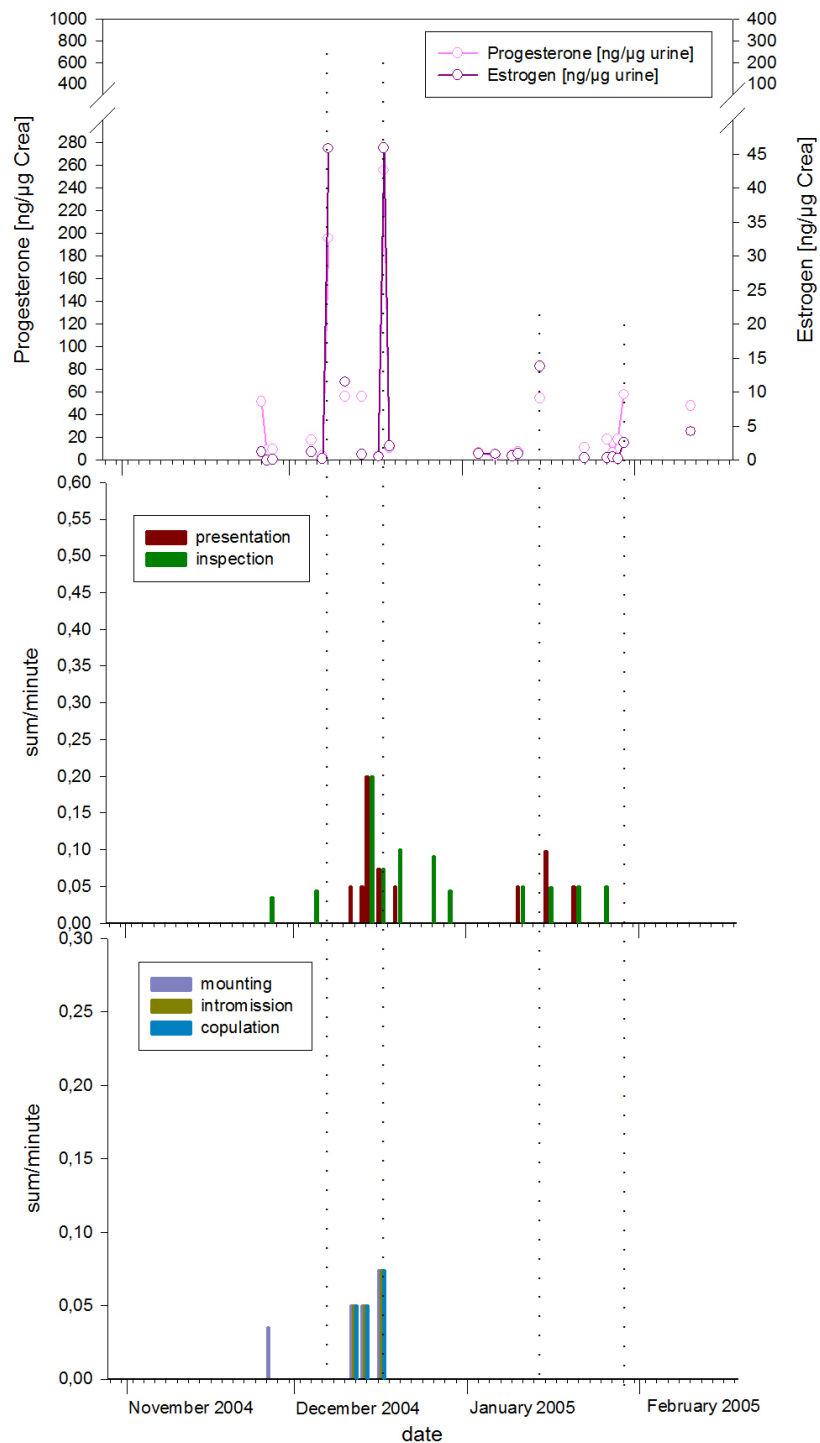


Figure 9: Endocrine data and sexual behaviors of Mercedes. Progesterone (light pink circles) and estrogen (dark pink circles) concentrations (in ng/μg Creatinin) are plotted in the upper section of the figure. The middle and the lowest picture show frequencies of sexual behaviors. The dotted lines show the time points of follicular activity.

Hormonal profiles of Mercedes showed four three fold increases in estrogen values over the whole study period (Figure 9). In the figure these are marked with dotted lines, as they did not fit the definition of a potential ovulation. The first and second peaks occurred in December 2004 within ten days. These estrogen peaks were accompanied by progesterone increases. Subsequently estrogen decreased completely, while progesterone remained around 50ng/μg urine after the first disturbed follicular genesis. After the second estrogen peak and decrease no further samples could be collected for two weeks. Shortly before the second increase in estrogen sexual behaviors occurred more frequently. The only copulations observed in focal protocols were recorded during this period. This suggests that ovulatory activity might have occurred then. After the reproductive season Mercedes did not deliver an infant.

After the third and fourth estrogen peaks no further urine samples could be collected within the following weeks. While the third estrogen peak corresponded with increases in presentation and inspection behavior right before and right after the elevation, the fourth peak was not connected to any sexual behavior. No mountings, intromissions or copulations were observed around these estrogen peaks.

Mercedes was inspected without a preceding presentation from late November to the beginning of December 2004. Later inspections around ovulatory events were connected with presentations. However rates of both behavioral categories were average to low compared to the other focal females with the exception of Makeup. At the end of November 2004 mountings occurred without a following intromission or copulation. All observed mountings occurred within the first two weeks of December 2004 and were linked with copulations. After mid December 2004 no further sexual intercourse was observed in focal protocols for Mercedes.

As sample density was rather low, no exact information on follicular development could be gathered. Regarding absolute values progesterone concentrations were average while estrogen levels were rather high. Progesterone peaked at 195.6 mg/μg Cr on the 8th of December 2004. On that day and on the 18th of December 2004 estrogen concentrations increased to over 45 ng/μg Cr.

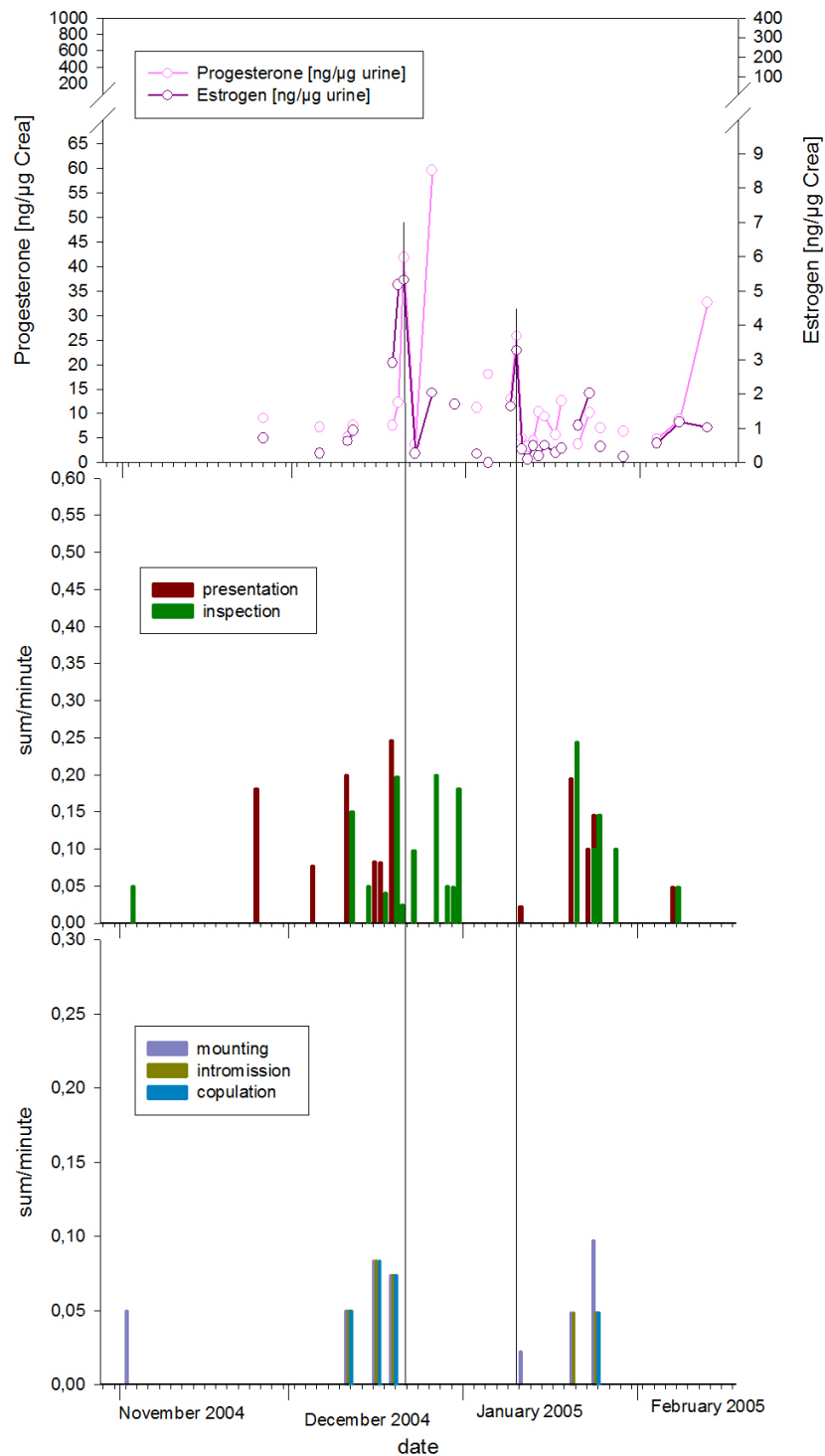


Figure 10: Endocrine data and sexual behaviors of Artemis. Progesterone (light pink circles) and estrogen (dark pink circles) concentrations (in ng/μg Creatinine) are plotted in the upper section of the figure. The middle and the lowest picture show frequencies of sexual behaviors. The vertical lines show the time points of potential ovulations.

Arthemis showed high presentation rates (Figure 10). From the end of November 2004 until early January 2005 inspections without prior presentation occurred. Otherwise her presentations were linked with inspections by males. Highest presentation and inspection rates were associated with the first possible ovulation around the 21st of December 2004. This ovulatory event is highlighted with a black line, linking the corresponding sexual activity in the lower parts of the figure. After twenty days a second peak in estrogen could be monitored. While estrogen levels decreased completely afterwards, progesterone values remained high. This second potential ovulation was not accompanied with increases of presentations, inspections or copulations. Only at the end of January 2005 an increase in sexual activity could be found, but no appropriate hormone fluctuations were noted, that could indicate a further ovulation.

Arthemis' absolute estrogen concentrations were the lowest of all. 5.31 ng estrogen/ μ g Creatinin on the 21st of December 2004 was the highest measured concentration. Progesterone concentrations remained low during the whole study period as well. Concentration peaked at 59.57 ng/ μ g Cr on the 26th of December 2004. Although concentrations were low both hormones fluctuated notably. For Artemis no extended periods without sample collection occurred.

Mounting, intromission and copulation rates for Artemis were average. Mounting, intromission and copulation rates peaked on the 20th of December 2004, shortly before estrogen concentrations were highest. Reproductive behavior in general occurred mostly when estrogen concentrations were elevated. After the 20th of December 2004 until the 25th of January 2005 no copulations were observed. Only mountings without intromissions or copulations were recorded for Artemis in this period. In February none of these reproductive behaviors were observed. Artemis did not deliver an infant after the reproductive season.

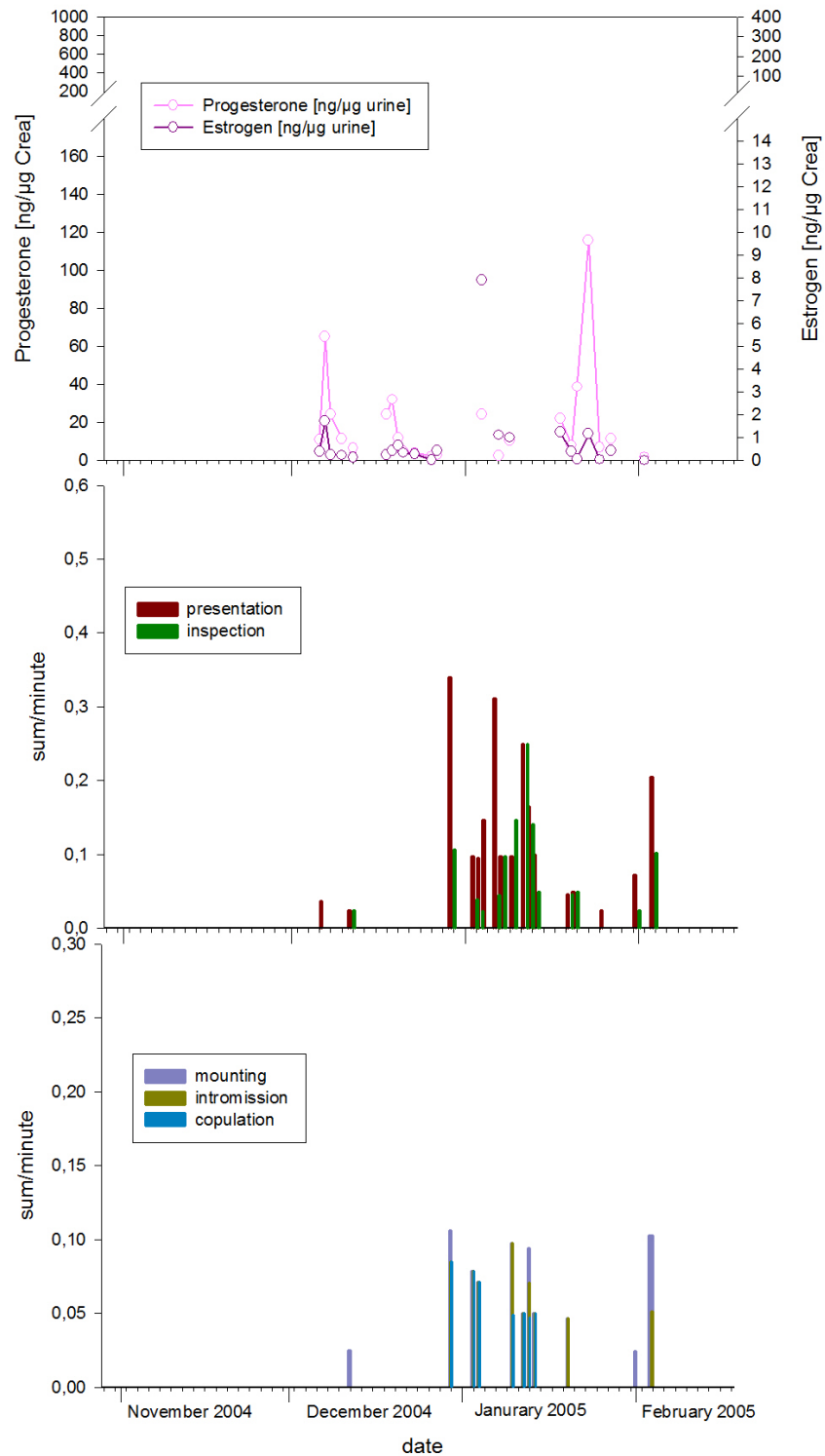


Figure 11: Endocrine data and sexual behaviors of Venus. Progesterone (light pink circles) and estrogen (dark pink circles) concentrations (in ng/μg Creatinin) are plotted in the upper section of the figure. The middle and the lowest picture show frequencies of sexual behaviors. No ovulatory event was documented.

Absolute estrogen and progesterone concentrations in Venus were low during the study period (Figure 11). Progesterone concentrations did not exceed 120ng/μg Cr and estrogen levels were under 8ng/μg Cr, apart from a single data point in January 2005. No three fold increases in estrogen could be monitored over the study period. Conversely, two increases in progesterone, one in December 2004, the second in January 2005 were evaluated. These increases were accompanied with slight elevations in estrogen values. Afterwards estrogen decreased completely, while progesterone concentrations stayed up. Nevertheless these data points do not fit the preset definition of a potential ovulation. Furthermore these hormone fluctuations were not linked with increases in sexual activity, which supports the conclusion that no ovulation took place.

In January 2005 a urine sample shortage exists. During this month sexual behavior peaked. In this period Venus showed high presentation rates. Males inspected her with average frequencies compared to her female peers. Many presentations were not accompanied by an inspection through a male. A notable increase in copulatory activity was recorded in late December 2004 through mid January 2005. Sexual initiative and male interest increased as well. This suggests that ovulation might have occurred during that phase, when hardly any urine samples were available.

Overall for Venus average rates of mountings, intromissions and copulations were found. In mid December 2004 mountings occurred without following intromissions or copulations. After the mating season Venus gave birth to a female infant in August 2005. Male interest and her sexual initiative were elevated in early February. As no urine samples could be collected in February 2005, information on hormonal fluctuation indicating a pregnancy is not available.

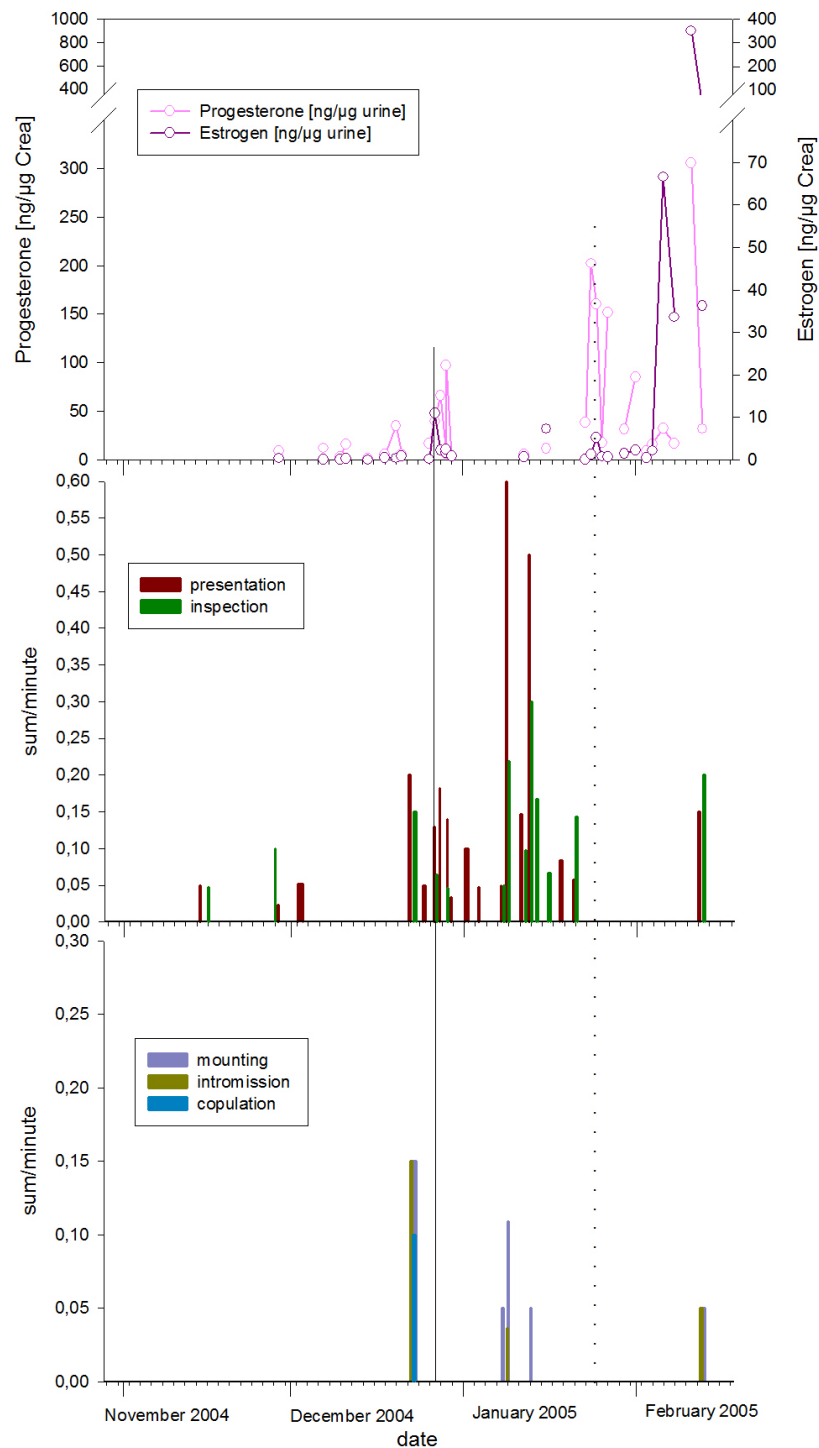


Figure 12: Endocrine data and sexual behaviors of Posh. Progesterone (light pink circles) and estrogen (dark pink circles) concentrations (in ng/μg Creatinin) are plotted in the upper section of the figure. The middle and the lowest picture show frequencies of sexual behaviors. The vertical line shows the time point of a potential ovulation; the dotted line shows the time point of a follicular activity.

Regarding the hormonal profiles of Posh, one three fold increase in estrogen on the 27th of December 2004 with a subsequent progesterone elevation and estrogen decrease could be found (Figure 12). This indicates an ovulation. Four days before the estrogen increase, copulations were observed. Also an elevation in presentation and inspection behavior was noted in this period. Surprisingly, components of sexual activity (proprioceptive behavior and inspections) increased thereafter in January 2005.

Thirty days later, which is approximately the average cycle length in Barbary macaque females, an irregular ovulation occurred. However, this ovulatory event was not linked to an increase in sexual activity. Three days before the estrogen elevation some presentations and inspections were observed, but no copulations occurred in focal protocols. Therefore from the behavioral perspective the occurrence of an ovulation is unlikely. Posh gave birth to an infant in late July 2005, which supports the likelihood of an ovulation in late January 2005.

Posh showed average presentation and inspection rates. Before the end of December 2004 very few presentations and inspection occurred, but no other sexual behavior. From late December 2004 until mid January 2005 a core period for activity could be found, but was linked to a hormone sample shortage. Hardly any copulations could be observed over the whole study period during focal protocols. Ovulatory events and presentation respectively inspection rates did not show a clear connection.

Absolute estrogen levels were rather low compared to her female peers, apart from a notable increase at the end of the study period on the 11th of February 2005 to 350.66 ng/μg Cr. Absolute progesterone concentrations were at a medium level. Only at the end of January 2005 peaks in progesterone concentrations were found, possibly linked to her pregnancy.

3.3 Social and Reproductive Copulations

Social (non ejaculatory) and reproductive (ejaculatory) copulations were differentiated. A copulation followed by an ejaculation was rated as a reproductive copulation, copulations without ejaculation were noted as social copulations.

3.3.1 Social and Reproductive Copulations around Ovulation

For focal individuals, where a potential ovulation respectively follicular activity (potentially with atresia) could be found over the study period an evaluation of the distribution of social and reproductive copulations in relation to the day of the ovulatory event was carried out. The day of ovulation was taken as point zero. The distribution of social and reproductive copulations over five days before and five days after this starting point were looked at. An overview is given in Table 4. More detailed graphs can be found in the Appendix 2.

Table 4: Absolute numbers of two types of copulation relative to day of follicular activity. Individuals are shown in descending rank order. Social copulations are highlighted in pink, reproductive copulations are marked in blue. According to the definitions, the type of follicular activity is mentioned (ovl for potential ovulation and fol for disturbed follicular genesis or atresia). Numbers include data from focal protocols and ad lib data.

	type	Social copulations										Reproductive copulations											
		Days relative to ovulation																					
		-5	-4	-3	-2	-1	0	1	2	3	4	5	-5	-4	-3	-2	-1	0	1	2	3	4	5
SAN	ovl	0	0	0	0	0	0	2	2	1	0	2	1	0	0	0	0	0	0	0	0	0	0
MU	None																						
ZOR	None																						
MER	fol	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
	fol	0	0	1	0	1	1	0	0	1	0	0	0	4	1	0	3	0	0	1	0	0	0
	fol	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	fol	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ART	ovl	0	2	1	1	2	0	0	0	0	0	4	0	2	0	0	4	2	0	0	0	0	3
	ovl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
VEN	None																						
PO	ovl	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	fol	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0

Overall numbers of copulations around the time of ovulatory events were rather low among all females (Table 4). Sandy had a single reproductive copulation, five days before her potential ovulation. Afterwards she received only social copulations.

Around the time of Mercedes' first irregular ovulation, three copulations were observed (two social and one reproductive). Nine reproductive and four social copulations were observed around the time of the second disturbed follicular genesis. Four days and one day before day zero frequencies of reproductive copulations were highest. Social copulations were at a low level during the whole period.

Highest frequencies of both, social and reproductive copulations, around the time of possible ovulations were recorded for Arthemis, but only for the first one. In sum eleven reproductive and ten social copulations were recorded during this eleven day period. One day before the potential ovulation reproductive copulations were highest, but also social ones occurred. The day of the potential ovulation she had two reproductive copulations, but no social ones. After day zero no copulations were noted until the fifth day, when three reproductive and four social copulations were seen. Around the second suggested ovulation, no social and no reproductive copulations were noted.

Posh hardly ever copulated in the eleven day period around her potential ovulation. Only two social copulations were observed. In the five days before and on the actual day of her irregular ovulatory event only reproductive copulations were recorded. No further copulations were observed for this eleven day period.

3.3.2 Type of Copulation in Relation to Female Rank

As only percentages of social versus reproductive copulations within each individual were analyzed, all copulation information (also ad libitum data) that had been collected was used.

A comparison of social and reproductive copulations revealed that high ranking females received a higher percentage of social copulations (Wilcoxon $n = 7$, $z = -2.366$, $p = 0.18$) than low ranking females (Figure 13). The percentage of reproductive copulations was significantly higher in low ranking females (Wilcoxon $n = 7$, $z = -2.197$, $p = 0.028$). Sandy received almost 60% of copulations without ejaculation. For Makeup only social copulations were observed. Zora had a higher percentage of social copulations than Sandy. Mercedes and Venus had equal percentages of social and reproductive copulations. Posh and Arthemis received higher percentages of reproductive copulations than social ones. Posh, the lowest ranking female had the highest percentage of reproductive copulations of all focal females.

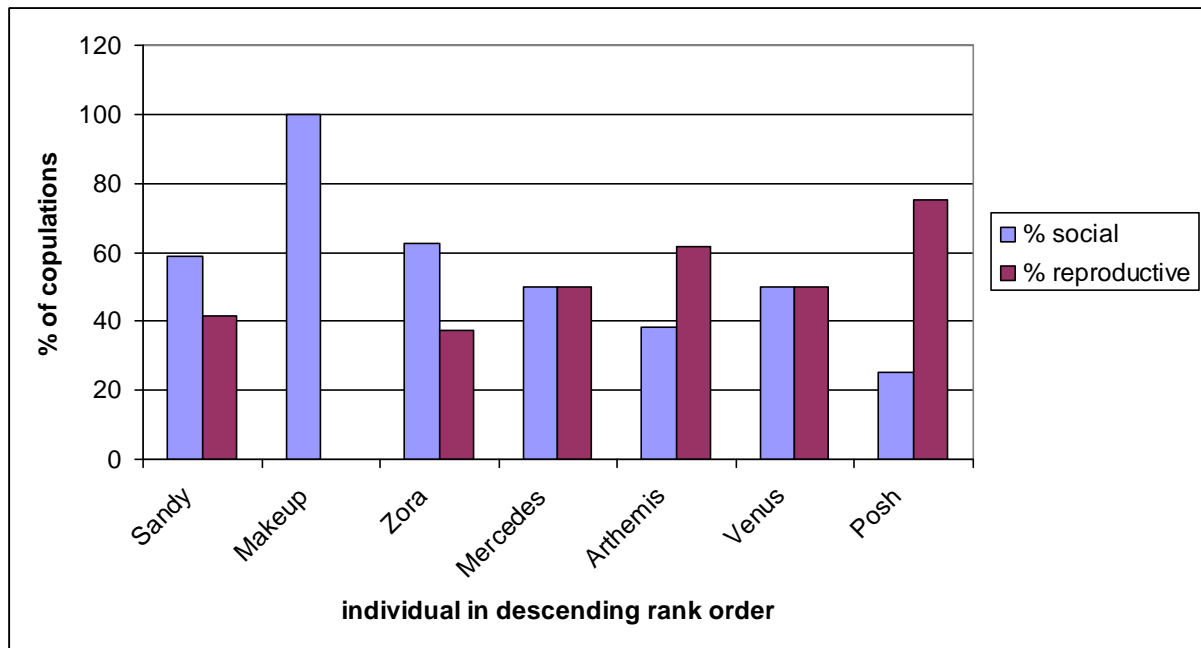


Figure 13: Percent of social and reproductive copulations. Females are plotted in descending rank order. Percentages of social copulations are shown in blue and reproductive are represented by dark red columns.

3.4 Reproductive Success

Three of the seven focal females gave birth to an infant after the reproductive season that survived until April 2006 (Table 5). All three had had infants before. All infants born after the study period were female.

Table 5: Reproductive success of the focal females. Three of the seven focal females gave birth to an infant that survived until April 2006 after the reproductive season.

focal female	infant	sex of infant	primiparous
Sandy	yes	female	no
Makeup	no	--	--
Zora	no	--	--
Mercedes	no	--	--
Arthemis	no	--	--
Venus	yes	female	no
Posh	yes	female	no

3.5 Stress Analysis

The secretion of cortisol in urine was used as a marker for stress physiology in the focal females. For correlation analysis daily Cortisol concentrations were compared with the amount of tourists present. Daily Cortisol levels correlated with tourist numbers for none of the focal females (Spearman $r = 0.18$; $p = ns$).

For correlations analyses between rank and stress levels, average Cortisol concentrations for each female were calculated. Female rank was positively correlated with higher Cortisol levels (Spearman $r = -.253$, $p \leq 0.001$) (Figure 14). In the figure females are shown in descending rank order. Artemis, Venus and Posh, the three lower ranking females show low Cortisol levels. Artemis had the lowest average concentration of all focal females. Mercedes, the fifth ranking female of Apes Den showed the highest average stress levels. Zora, fourth in rank, showed the second highest average Cortisol concentration. Sandy, the second ranking female had higher average stress levels than Makeup, the third ranking female.

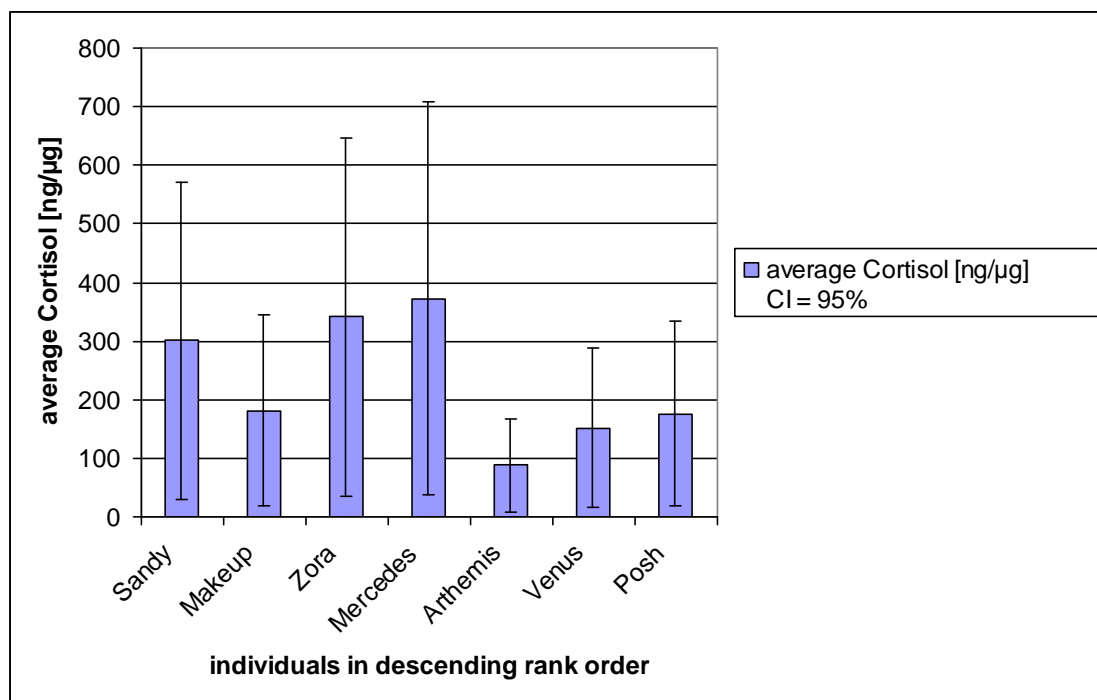


Figure 14: Average Cortisol levels over the study period in connection with rank. Dominant females showed significantly higher stress levels than the low ranking females (Spearman $r = -.253$, $p = 0.001$). Confidence interval was at 95%.

3.6 Behavior and Tourists

The only type of behavior that was shown significantly less in the presence of tourists compared to tourists' absence was feeding (Figure 15). Feeding was noted when the animals consumed provisioned food (by GONHS, not by tourists). Foraging was rated when animals made use of natural food resources (not tourists). The animals fed or foraged significantly more when no tourists were at the study site (Wilcoxon $n = 258$, $z = -3.435$, $p \leq 0.001$). This does not hold true for all females. Sandy, Makeup and Zora showed less feeding activity in the presence of tourists. Their subordinate peers Mercedes, Artemis, Venus and Posh did not alter their feeding behavior in dependence of tourist presence. Venus had the highest feeding rates in absence of tourists. Overall the highest feeding activity was shown by Posh. Sandy showed low feeding rates both when tourists were present and absent.

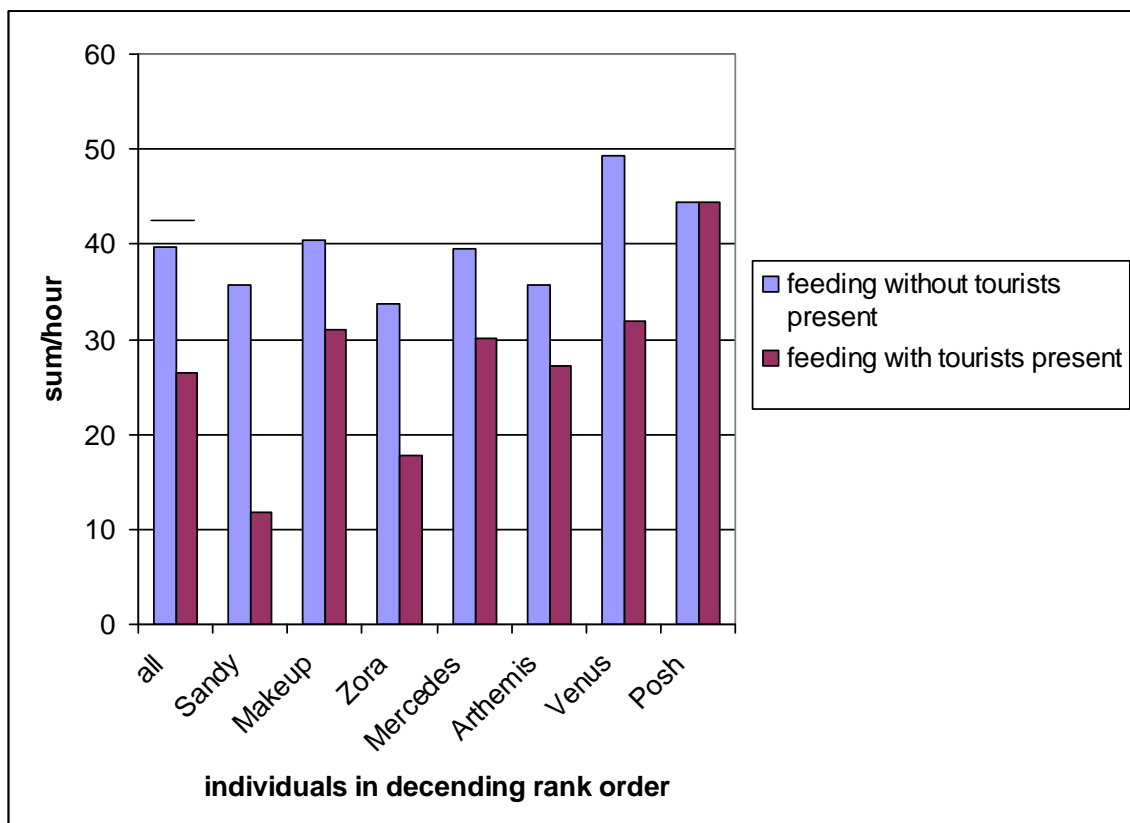


Figure 15: Feeding activity when tourists were present or absent. Females are plotted in descending rank order. Feeding behavior in the presence of tourists is shown in dark red, in the absence of human in blue. Total feeding activity was significantly lower when tourists were present.

3.6.1. Rank and Tourist Interactions

Correlation analysis revealed a relationship between female rank and all three noted categories of tourist contact behavior (Figure 16). Dominant females were more often in human proximity (Spearman $r = -.042$, $p = .000$), interacted more (Spearman $r = -.016$, $p = .049$) and were fed more often by tourists (Spearman $r = -.053$, $p = .000$) than subordinate individuals. For all three human contact behaviors, Makeup showed highest rates. Venus was never involved in human feeding although, apart from Makeup, she showed the highest rates of interactions with humans. Her human closeness rates were lowest of all females.

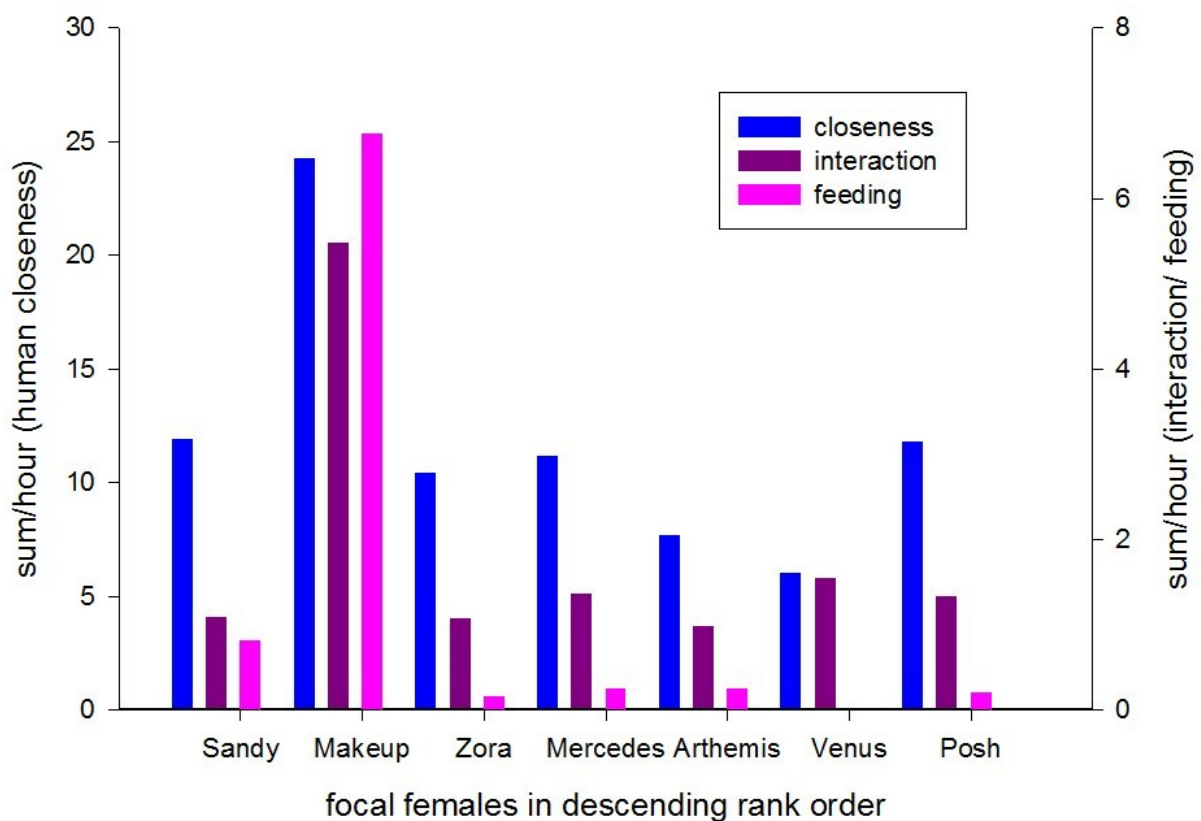


Figure 16: Human interaction rates in connection with female rank. Frequencies of the behavioral categories are shown in sum/hour. Human closeness (blue) is depicted on the left Y-axis, interaction (pink) and feeding (dark pink) behavior on the right Y-axis.

3.6.2 Social Behavior

Calculations on social behavior in “tourists- present” and “tourists – absent” situations showed no significant (Wilcoxon $p = ns$) differences in the expression of the animals’ social interactions (Figure 17). Neither grooming behavior nor proximity between the individuals was significantly altered in either situation. No connection between the females’ rank and their social behavior was found in relation to tourists presence/absence (Spearman $p = ns$). However on a descriptive level active grooming was shown more often than passive grooming (being groomed). Correlations revealed that the amount of tourists present was connected to the amount of “being groomed” (Spearman, $r = 0.135$, $p = 0.28$).

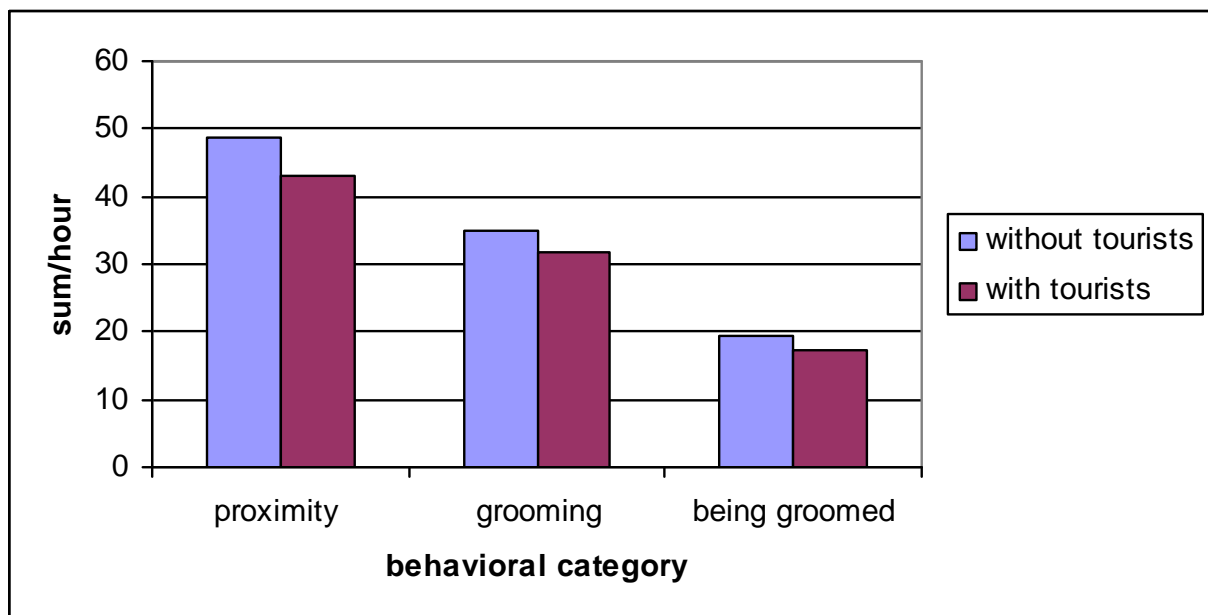


Figure 17: Social behavior in “tourists-present” and “tourists-absent” situations. Values represent the frequencies of the different behavioral patterns per hour. Blue columns represent animals’ behavior in the absence of tourists, dark red columns shown behavior in tourists-present-situations. Data of all focal females were taken for analysis. No significant differences of social behaviors in either situation could be found.

3.6.3 Reproductive Behavior

None of the females’ reproductive behavioral categories (presentation, inspection, mounting, intromission and copulation) were influenced significantly (Wilcoxon $p = ns$) by the presence or

absence of tourists (Figure 18). Presentations and inspections occurred more often than mountings, intromissions or copulations in either tourists' absence or presence. Inspections were shown slightly more when tourists were present. All the other reproductive behavioral patterns were observed more frequently in tourists' absence situations. With no tourists at the site, intromissions were shown slightly more often than copulations. These results did not show significant differences.

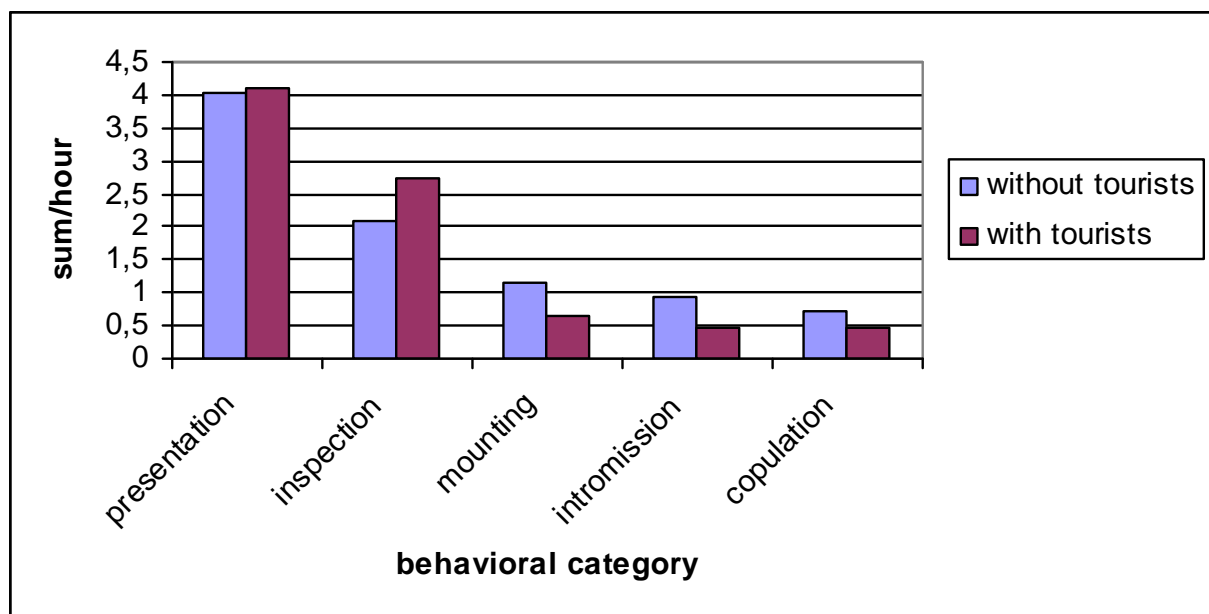


Figure 18: Reproductive behavior in “tourists – present” and “tourists – absent” situations. Values represent the frequencies of the different behavioral patterns per hour. Blue columns represent animals' behavior in the absence of tourists, dark red columns shown behavior in tourists-present-situations. Data of all focal females were taken for analysis. No significant differences of reproductive behavior in either situation could be found.

3.6.4 Agonistic Behavior

The presence or absence of tourists did not influence the amount of focal females' agonistic behavior significantly (Wilcoxon $p = ns$) (Figure 19). In absolute numbers both active and passive aggression occurred slightly more frequently when no tourists were at the site than in tourists' presence. When controlled for rank, the amount of aggressive encounters correlated with the amount of tourists present at the site (partial correlation: $r = -0.135$, $p = 0.31$). Higher ranking females showed less aggressive behavior when many tourists were at the site than when few or

no tourists were around. Lower ranking females did not adapt their aggressive behavior to the tourist situation. No further correlations for the amount of tourists and any behavioral category were found.

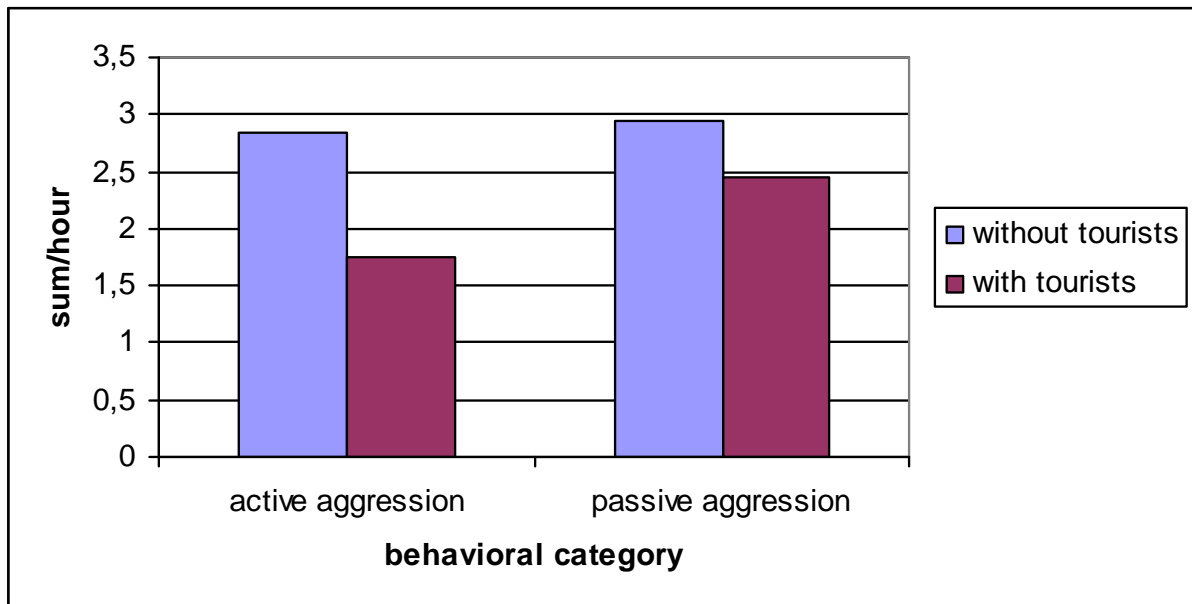


Figure 19: Agonistic behavior in “tourists–present” and “tourists–absent” situations. Values represent the frequencies of the different behavioral patterns per hour. Blue columns represent animals’ behavior in the absence of tourists, dark red columns shown behavior in tourists-present-situations. Data of all focal females were taken for analysis. No significant differences of aggressive behavior in either situation could be found.

4 Discussion and Conclusions

Provisioning *per se* can increase direct competition over food and heighten the amount of aggressive encounters, as was shown in Japanese macaques (Hill, 2004). Competition increases if the food is offered in smaller areas than natural food resources would be distributed. In Gibraltar not only GONHS provides food. In addition tourist groups represent a considerable resource. Feeding is not the only way tourists interact with the monkeys. As was shown in the present study the Barbary females' social and reproductive behavior was partly affected by tourist pressure.

The females' social behavior diminished slightly, albeit not significantly, when tourists were at the site compared to "no – tourists present" situations. Fa and O'Leary (1993) found significant differences in the expression of social behavior depending on tourist presence. In the present study, the absence of significant results may be explained by the type of data collection. By comparing "no tourists present" and "tourists present" situations, the actual amount of tourists at the site was neglected. It is likely that the animals' behavior is not as strongly influenced when only a few tourists are at the site. Therefore, a comparison of the two scenarios may have led to the loss of significant results. Correlation analysis revealed that a connection between the number of tourists present and the modification of social behavior existed. The study was conducted during mating season in winter when less tourists visit the sites than in summer. Thus, the need to adapt social behavior to tourists visiting Apes Den may have been less pressing.

Feeding on natural and provisioned food sources decreased significantly when tourists were at Apes Den. In Fa and O'Leary's study (1993) an increase in feeding activity in correlation with a peak in tourist numbers was demonstrated. This phenomenon held true not only over a short observation period but for the extended total study time of an eleven year period. This result appears to contradict effects presented in the present study. Fa and O'Leary included the consumption of tourist food to their "feeding" parameter so it may have been a simple case of: more tourists with food leading to more monkeys eating more. Foraging and feeding on provisioned food by GONHS was recorded separately in this present study. Fluctuations in tourist numbers within one or several days are smaller than increases in tourist numbers over the years.

Fa and O'Leary (1993) came to the conclusion that fights over food became unnecessary when tourists were present due to the higher food availability. The present study confirmed these results to certain extent. With increasing tourist numbers the amount of aggressive encounters among the animals decreased, when correlation was controlled for rank. Nevertheless Fa (1991b) also showed that with higher tourist numbers aggressions became more severe, especially towards tourists. However, a habituation effect was observed. After four years, fewer incidents of biting were observed in Fa's study. Severity of aggression in connection with the number of tourists was not analyzed in this study. Monkey bites were reported at the Gibraltar hospital and observed by the staff of GONHS (Eric Shaw pers. comm., pers. observations). Even though juveniles tended to be more mobile and socially curious, they were less frequently involved in close human contact situations than adults (Fa and O'Leary, 1993; Sonnweber, 2004 unpublished data). Of the adults the females were the ones who showed more aggressive responses, like threats towards humans. This was not really surprising as the study was conducted during summer, shortly after the birth season. Tourists are attracted to babies and juveniles and the mothers defend their offspring. Male Barbary Macaques do not seem to perceive humans as an actual threat and were hardly ever involved in aggressive situations. Another possible explanation could be that for females, food is the most important resource whereas for males females are more significant (Wrangham, 1980). This should lead to females being more motivated to gain access to high calorie nourishment, which in turn can lead to more aggression. According to Preuschoft et al. (1998), Barbary macaques have two sex-specific temperaments. As a hierarchical matrilineal society, females show a stricter ranking order that is enforced by more aggression. Hence, it could be a side effect of the males more tolerant attitude that they show less aggression towards tourists.

Aggressive encounters among the animals were mild. In a study of a provisioned group of Barbary macaques with tourist contact at the Affenberg Salem (Schiestl, 2005), severe aggression between the animals was very rare. Between females only 1% of all observed agonistic encounters involved actual attacks. Mild ritualized aggression predominated. Between males the amount of escalated aggression was low as well, without a single serious injury. These data were collected outside of the mating season, when aggression levels were low (Kohpal, 1986; Paul, 1984). Also in this study threats and displacements were observed far more often than more severe types of aggressive behavior during the whole study period. This is typical for the

egalitarian organized Barbary macaques (Thierry, 2001). Most aggression directed towards humans was limited to threats. Interestingly, some tourists, not knowing the actual meaning of a threat, copied the animal's behavior, which apparently was not perceived as an aggressive attack by an animal (pers. observations). Unfortunately, monkey-initiated respectively tourist-initiated interactions were not discriminated in data collection. A collection of such information could offer the possibility for better understanding of the dynamics in monkey-human interactions.

Fuentes (2006b) demonstrated that at Apes Den, interaction rates between humans and Barbary macaques were highest among all sites on the Rock of Gibraltar. The present work showed that stress levels and the amount of tourist were positively correlated. Cortisol and tourist contact rate did not correlate significantly. For human feeding, human interaction or human proximity no connection with stress levels were found, although an equal trend was expected. The fact, that only a few focal females were involved in human feeding activities could have influenced this outcome. A connection between female rank and frequency of tourist interactions was found. Venus for instance was never fed directly by humans. Makeup on the other hand could be considered the classical "tourist animal". Tourist animals are defined as individuals who show over-average tourist interaction rates. Furthermore they actively search out groups of humans and beg for food.

This theory is supported by results of the "bus driver study" (Sonnweber, 2004 unpublished data). While some individuals had "adopted" specific bus drivers that fed them, other animals did not initiate contact with the tour operators. Human proximity on the other side was not expected to influence stress levels. The study was conducted in winter season when the amount of tourists visiting the Rock was low compared to summer seasons. The Barbary Macaques are habituated to humans since a long time. Therefore it was expected to be unlikely that the animals got stressed by rather low tourist numbers at the sites. Studies during summer season on stress levels might give another picture. In core tourist visitation times, a single individual may be surrounded by hundreds of humans at once. An elevation in stress levels could be expected during this season therefore. This possibility has to be taken into account in the interpretation of the results of the present thesis, as stress exposure during summer season can affect the reproductive physiology during winter season indirectly as long term effects.

Stress levels in general were not evenly distributed. Highest average cortisol concentrations were found in the higher ranking females. This result was unexpected. A former study at Affenberg Salem had shown that middle ranking Barbary macaques show highest stress levels (Knöpfler, 2005). Scratching rates were taken as a stress marker. Scratching rates did not correlate significantly with dominance in Knöpfler's study, but on a descriptive level the highest stress levels were found for middle ranking females. Mastrepieri et al. (1992) used scratching as one of the indicators for the "emotional state" of an animal. Aureli (1992) stated that scratching rates are an appropriate parameter for stress and tension levels in primates. Results on highest stress levels in dependence of rank varied in different studies. In Egret monkeys for instance, higher ranking animals show lower scratching rates (Pavani et al., 1991). Male baboons (Easley et al., 1987) and chimpanzees (te Boekhorst et al., 1991) on the other hand express higher scratching rates in dominant individuals. In Rhesus macaques, a study revealed that highest scratching rates in females were found in middle ranking animals (Diezinger and Anderson, 1986).

Although on a descriptive level the results on cortisol levels may appear to peak for the mid ranking females one should keep in mind that the first four depicted females (Sandy, Makeup, Zora and Mercedes) represent the high ranking group (rank numbers two through five out of a total of thirteen females). Mercedes, not a "tourist animal" per se but also not a peripheral individual, showed the highest average Cortisol concentrations followed by Zora and Sandy. Sandy, the second ranking female in the Apes Den troop had the second highest average Cortisol levels. She was a female with high tourist interaction rates and a core "tourist animal". Zora, fourth ranking was a core animal of the group but not as involved in tourist interactions as Sandy. Third ranking Makeup showed average stress levels. This is interesting as she was the ultimate "tourist animal". Artemis the sixth in the hierarchy had the lowest average Cortisol concentrations. Her middle rank would have led to the assumption that high stress levels could be expected. Possibly the low stress levels in Artemis can be explained by low tourist interaction. By comparison, mid-ranking Venus and low ranking Posh had low cortisol concentrations.

Referring to the study by Knöpfler (2005) the highest stress levels were expected for mid ranking animals. The discrepancy between the results in Salem and Gibraltar could be an indication that individual personality structure plays a major role in stress management. Capitanio (2004) found in a study on various species that the individuals' personalities are very influential on their stress

levels. Barbary macaques are classified as one of the more tolerant macaque species (Thierry and Aureli, 2006). Social organization in turn is responsible for the emphasis on developing and the possibility to reveal individual personalities (Butovskaya, 2004). The personality structure of an animal could affect its way of behaving and reacting in stressful situations. Hence, for an egalitarian species individual temperament may be as important as rank or other factors for individual stress levels.

Further studies that link physiological (cortisol levels) and behavioral (scratching rates) stress markers could help to better understand these dynamics and to explain the role of rank and/or personality in individual stress reaction. In laboratory experiments, Orangutans' stress levels measured in cortisol values and scratch rates were disassociated (Elder and Menzel, 2001). Whether scratching is a reliable parameter for stress in macaques remains to be studied.

The analysis of ovarian capacity was limited to four individuals due to sample shortage. Posh was the youngest female among the focal individuals and low ranking. At the beginning of the study she was four to five years old. This has been described as the average menarche age in Barbary macaque females (Thierry et al., 1996). After the reproductive season 2004/2005 Posh gave birth to an infant. In 2003 Posh gave birth to her first child when she was around three to four years. In the following season she did not have any surviving offspring. Whether she had been impregnated and had had a miscarriage or lost her infant after birth is not known. Paul and Kuester (1996) found that young primiparous females often skip one birth season. This was explained by the high costs of lactation that were hard to bear for these young, not completely developed females. Posh was very young when she gave birth to her first infant. First reproduction at a young age has been described for dominant Barbary macaque females (Roberts, 1978; Paul and Thommen, 1984; Paul and Kuester, 1988) and for Japanese macaques (Sugiyama and Ohsawa, 1982). Posh however was very low-ranking. But accelerated sexual maturation is known in provisioned, food-enhanced groups of Barbary Macaques (Bercovitch and Harvey, 2004). Hormone fluctuations in Posh were partly lower than expected. As the youngest female, she was expected to show highest fluctuations in both estrogen and progesterone concentrations (Hadley, 2000). In humans natural phases of sub-fecundity respectively sterility are known during puberty, lactating periods, pregnancies and in the peri-menopausal times (Dunson et al., 2002). According to results from Salem, females from seven to twelve years show highest

fertility (Paul et al., 1993). A decline in fecundity is observable at ages from 13 to 19 years and from 20 to 25 years. Compared to Sandy and Mercedes progesterone variations were rather low. Baseline estrogen concentrations on the other hand were high. At the end of the study period (mid February 2005) estrogen and progesterone peaked. The estrogen value was the highest among all focal females. Posh gave birth to a female infant in August 2005. Therefore it can be assumed that these hormone peaks represent a pregnancy.

Interestingly, apart from a peak in February 2005, Mercedes had estrogen fluctuations as high as or higher than Posh, although Mercedes was the oldest individual. A study demonstrated that in ageing human women who still develop menstrual cycles heightened concentrations in FSH serum are prevalent. Estradiol concentrations were as high respectively higher than in their younger peers (Hansen et al., 2004). FSH elevations seem to serve as a compensatory factor to maintain dominant follicle development (as only few primordial follicles remain in the pool). This could explain the high estrogen concentrations in Mercedes as well. Older females in Barbary macaques often cease reproduction but still develop menstrual cycles (Paul and Kuester, 1996). Again this could be the case for Mercedes. At the time of the study she was already 24 years of age, which is rather old for Barbary Macaque females. Among the Gibraltar population Mercedes is the oldest female that ever inhabited the Rock (Eric Shaw, per. comm.) Nevertheless she still developed cycles and a sexual swelling. Although a decline in fecundity could be prevalent, macaque females can live long periods after their last infant's birth (Gagliardi et al., 2007). According to Paul et al. (1993) Barbary macaque females show an age-related decline in fertility and an increase in inter-birth intervals and cease to reproduce at approximately 25 years of age. Post-reproductive periods over five years are not uncommon for provisioned groups. Information on Mercedes' reproductive life shows that Posh was her only surviving offspring since 1999. Whether she gave birth to any other infants is not known. Therefore it would also be possible that the cessation of reproductive success might have other reasons than her age.

Sandy showed similar fluctuations to Posh with a peak of progesterone and estrogen fluctuations in February 2005. These values were notably higher than fluctuations during the rest of the study period. Possibly this indicates a pregnancy. The exact date of Sandy's delivery is not known, but according to the staff of GONHS it fell into late August. At Affenberg Salem females typically give birth from April to June (Küster & Paul, 1984; Paul & Küster, 1988; Paul & Thommen,

1984). It is conspicuous that in Gibraltar the birth season is more spread out and lasts until late October. This cannot be explained by provisioning, as the population in Salem receives additional food on a daily basis as well. The seasonal changes in climate in Gibraltar are smaller compared to both Salem and the Atlas mountains. The quality of the food in Gibraltar is heavily influenced by the tourist food (mostly high in sugar and fat) and is available year round. These factors might play a role in the extended birth season.

Arthemis showed very low fluctuations in both her progesterone and estrogen delta values. Her absolute values were very low compared to the other focal females as well. She had no offspring and there are no indications of any previous or later pregnancies. A side effect of low quality nutrition and stress over a long period of time is the loss of fertility and the cessation of reproductive ability (Ellison, 2001). Census data of the Gibraltar population of Barbary macaques show that some females, although sexually active and of reproductive age, never had any offspring or very few. A possible explanation for this situation might be the easy access to low quality tourist food throughout the year and the potentially permanent high stress levels. These reasons for infertility are very unlikely for Artemis. She showed the lowest average Cortisol levels of all focal females and her tourist interaction rate was low. Reproductive behavior and males' interest were relatively high. Therefore it can be assumed that she was possibly naturally infertile.

Due to the low amount of samples, no development of reliable hormonal profiles and specifically the timing of ovulation and discrimination of follicular and luteal phase were possible. Estrogen concentrations often vary very rapidly. Determination of ovulation via progesterone concentrations (after Brauch et al. 2007a) could not be examined due to the lack of samples. Therefore hormone fluctuations that could indicate a possible ovulation were defined. Following these definitions nine potential ovulatory events could be detected in four different focal females (Sandy, Mercedes, Artemis and Posh). For other focal females follicular activity could be documented although it could not be classified as an ovulation. Possibly these endocrine changes showed disturbed follicular genesis respectively atresia in these individuals. This does not mean that these females did not cycle or produce fertile follicles and ovulated, but that they were just missed in hormone collection. Posh and Sandy were the only females for whom the likelihood that the correct days of ovulation have been detected is given. This is possible as their birthing

dates are known and fit with the proposed ovulation. In Sandy's hormonal profile even a potential post-conceptual ovulation could be evaluated. For the rest of the focal females including their sexual activity could help with the interpretation of the hormonal profiles and thus support or falsify the proposed time of potential ovulation (Beach, 1976).

Beach (1976) proposed to take sexual performance into account when trying to monitor a female's cycle. As was shown in the present study, female presentations and male inspections were often linked. Attractiveness and proceptivity therefore seem to be synchronized to a high degree. Highest sexual activity was observed in December 2004 and January 2005 in most females. The two lower-ranking females (Venus and Posh) extended their sexual behavior into February 2004. An interesting aspect was the immigration of the six novel males beginning in January 2005. The core-time when the females were sexually active was around late December 2004 and January 2005. Venus and Posh were both lower-ranking individuals and could be found at the periphery. Their second peak in sexual behavior in February 2005 could have been influenced by this immigration. Before only three males were resident in Apes Den, but thirteen mature females were in the group. Females mostly conceive during their first cycle (Kuester and Paul, 1984). Therefore the timing of the immigration would have been expected to happen earlier. Except for Castro (the alpha male of Prince Phillips Arch before migration) none of the immigrating males entered the core of the Apes Den group for a long time. Copulations between the novel males and females of Apes Den occurred mostly at the periphery.

Mercedes, the oldest female on the Rock, expressed relatively high rates of presentations and inspections. Rates of mountings, intromissions and copulations were high as well. In contrast to her peers sexual activity started one month earlier, in November 2004. Considering her age her overall high rates of sexual behavior are astounding. It was shown that older Barbary macaque females, who were defined as females older than nineteen years, reduce interactions with their group peers and self-directed behavior becomes more prevalent (Grieger, 1984). This effect could not be observed in Mercedes. She not only contributed actively in social and reproductive life in the Apes Den group but even was the first to show sexual initiative.

As was reported, maximal mating effort is influenced by reproductive history and the female's age (Kuester and Paul, 1984). Younger females usually conceive later, while parous females without offspring from the former season tend to have earlier pregnancies. This was not the case

at Apes Den. Compared with the birth season in Salem, Posh and Lea gave birth very late (August 2005), but at Apes Den with its extended birthing period these two young females were the first to give birth. Sandy, Venus, Tris and Punta all delivered later. Tris who did not have an infant from the former season but had had children before, delivered later than her younger peers Posh and Lea.

In general, reproductive success in the troop was rather low. Of the thirteen adult females only six gave birth to an infant after the mating season. Discrimination between reproductive and social copulations showed no connection between observed types of copulation and reproductive success. Sandy who had more social than reproductive copulations became pregnant. Posh who had only few copulations but most of them reproductive delivered as well. A connection between reproductive copulations and reproductive success was expected. During mating season, Barbary macaques establish consortships (Caldecott, 1986). In this period, they tend to withdraw from the group which in turn made observations difficult. Therefore, the lack of observed reproductive copulations may be an artifact caused by the animals copulating most when they were out of sight.

Compared to data from Middle Hill (census data), the only group with restricted tourist access, the amount of successful pregnancies was very low. While all Middle Hill females gave birth to an infant almost every year when they reach fertility, Apes Den females have fewer babies. Some, like Makeup, did not give birth to an infant for many years. Again, persistent intake of presumably low quality food and possible high stress levels in connection with tourist pressure may have played a role.

The amounts of social and reproductive copulations at Apes Den were comparably low as well. Middle Hill data showed that females copulate twice as often or more around the time of ovulation than their female peers at Apes Den (Brauch, 2007b). A main reason could be that the females at Apes Den spent more time interacting with tourists, so that they have less time for reproduction. The data collection at Apes Den was conducted by a single person, while data in Middle Hill were collected by up to four people, resulting in more observations for each individual.

Only partly a connection between estrogen and progesterone concentrations, respectively the phase around ovulation and sexual behavior was found for the focal females at Apes Den. Also copulations were not influenced by these females' cycle phase. This result confirms the outcome of a study conducted at Middle Hill in Gibraltar (Brauch et al., 2007b). This effect could be induced by group composition. The Apes Den group as well as the Middle Hill group was highly female biased. As was mentioned before group composition can impact the copulatory behavior (Wallen, 2001). Group composition in general was very untypical for Barbary macaques (Deag, 1974). The group consisted of very few males at the beginning of the study and was female biased. During the study period several males immigrated into the group without notable fights with the resident males. Only one matriline (matriarch: Athene) was known in Apes Den, although at least one further matriline (matriarch: Mercedes) was assumed to exist.

An effect of tourist pressure on the reproductive behavior and the reproductive physiology in female Barbary macaques seems to exist. It was found that reproductive behavior in some females is highly reduced. Although no significant results for differences between "tourists present" and "tourists absent" situations could be gained, certain individuals clearly adapted their reproductive performance to the tourists' presence. Physiological effects were not conspicuous. Further studies that compare tourist troops and non – tourist troops could answer some of these questions.

Since the law against feeding the monkeys was introduced, not a single reported incident of feeding was prosecuted. Also, no wardens are employed to monitor and supervise the Rock and to interfere regulatory. The current situation on the Rock for both humans and non human primates can be improved only by visitor education and better schooling of the tour operators. At the moment, a petition against monkey culling is going on, collecting signatures of people to support the project. Public press in Gibraltar plays a major role in information transfer and promoting the petition. Unfortunately, rumors emerged of taxi and bus drivers that have fed the monkeys in order to save them from starving. The wrongdoing of these people therefore gets justified and supported in public. It is absolutely necessary to inform and educate both the taxi/bus drivers and the public that their way of treating the monkeys induces lots of problems. Culling is not used only as a management tool for population control but also to "extinct problem apes". Those monkeys that bite, steal and snatch from tourists and tour operators get reported and

are at risk to be taken out of population. A vicious circle is kept up this way, since feeding and training the monkeys to “do funny things” like “give me five” creates new monkeys that learn to link people with food and that interacting with humans gets treated with rewards. It is necessary to mention that not all bus and taxi drivers act that way. Nevertheless, an installation of wardens that monitor bus and taxi drivers as well as private visitors and education programs for people that work on the Rock would improve the situation very likely. As habituation to the actual tourist situation took place successfully, a reversal to better conditions for both humans and monkeys would function as well.

5 Zusammenfassung

Die Studie beschäftigte sich mit den Auswirkungen des Tourismus auf die Reproduktionsphysiologie und das Sexualverhalten weiblicher Berberaffen (*Macaca sylvanus*). Die Daten hierfür wurden in einer Fokusgruppe der Population in Gibraltar, die häufig von Touristen besucht wird erhoben. Verhaltensdaten in Form von Fokusprotokollen und ad lib. Daten wurden täglich gesammelt, Hormonprofile mittels Urinproben erstellt. Die Studie wurde an sieben Fokusweibchen durchgeführt.

Die Reproduktionsphysiologie der Weibchen konnte nur teilweise ausreichend untersucht werden. Aufgrund von Probenmangel war es nicht möglich, Zyklusphasen der Fokustiere nachzuvollziehen. Für vier Weibchen konnten jedoch mögliche Ovulationszeitpunkte eruiert werden. Diese wurden mit dem Sexualverhalten einige Tage vor beziehungsweise nach dem möglichen Ovulationszeitpunkt korreliert und interpretiert.

Es zeigte sich, dass weibliche Berberaffen ihr Verhalten teilweise an die Touristensituation anpassen. Hierbei spielt jedoch auch der jeweilige Rang des Weibchens eine Rolle. Generell interagierten höherrangige Weibchen öfter mit Touristen als niederrangige. Allgemein wurde sowohl soziales, agonistisches wie sexuelles Verhalten in Anwesenheit von Touristen weniger oft gezeigt. Es konnten jedoch keine signifikanten Ergebnisse gewonnen werden.

Eine Analyse der Stresslevels der Weibchen zeigte keinen klaren Zusammenhang mit der Frequenz der Touristeninteraktionen. Mittlerrangige und das dominante Weibchen zeigten die höchsten Stresslevels.

6 Literature

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7 Appendix

Appendix 1: Delta values for P₄ and E for all individuals

individual	date	Delta-PROG [ng/μg]	Delta-EST [ng/μg]
Arthemis	06.12.2004	1,767333	0,44757825
Arthemis	11.12.2004	2,16326075	0,36146888
Arthemis	12.12.2004	2,44983086	0,31508876
Arthemis	19.12.2004	0,02115027	1,96496431
Arthemis	20.12.2004	4,66429801	2,2695535
Arthemis	21.12.2004	29,5467273	0,14159408
Arthemis	23.12.2004	38,0111578	5,04223833
Arthemis	26.12.2004	55,7823103	1,76044054
Arthemis	30.12.2004	47,7425652	0,33298348
Arthemis	03.01.2005	0,63920044	1,45156109
Arthemis	05.01.2005	6,81654826	0,24849891
Arthemis	09.01.2005	4,98176718	1,63498387
Arthemis	10.01.2005	12,7774194	1,63303337
Arthemis	11.01.2005	20,7529326	2,88283982
Arthemis	12.01.2005	1,78156064	0,30205639
Arthemis	13.01.2005	1,21400539	0,40728873
Arthemis	14.01.2005	5,84311495	0,30587345
Arthemis	15.01.2005	0,94705462	0,31773851
Arthemis	17.01.2005	3,74366776	0,20724148
Arthemis	18.01.2005	6,93947205	0,11157536
Arthemis	21.01.2005	8,85176355	0,67935263
Arthemis	23.01.2005	6,42452737	0,93108555
Arthemis	25.01.2005	3,08740593	1,55012851
Arthemis	29.01.2005	0,76545953	0,30851121
Arthemis	04.02.2005	1,41495517	0,40057524
Arthemis	08.02.2005	3,83621133	0,62675945
Arthemis	13.02.2005	23,8943258	0,16370185
Makeup	07.12.2004	8,28952948	0,12649742
Makeup	08.12.2004	14,936601	0,07706812
Makeup	10.12.2004	5,51747505	0,03293737
Makeup	14.12.2004	26,4526159	0,09290066

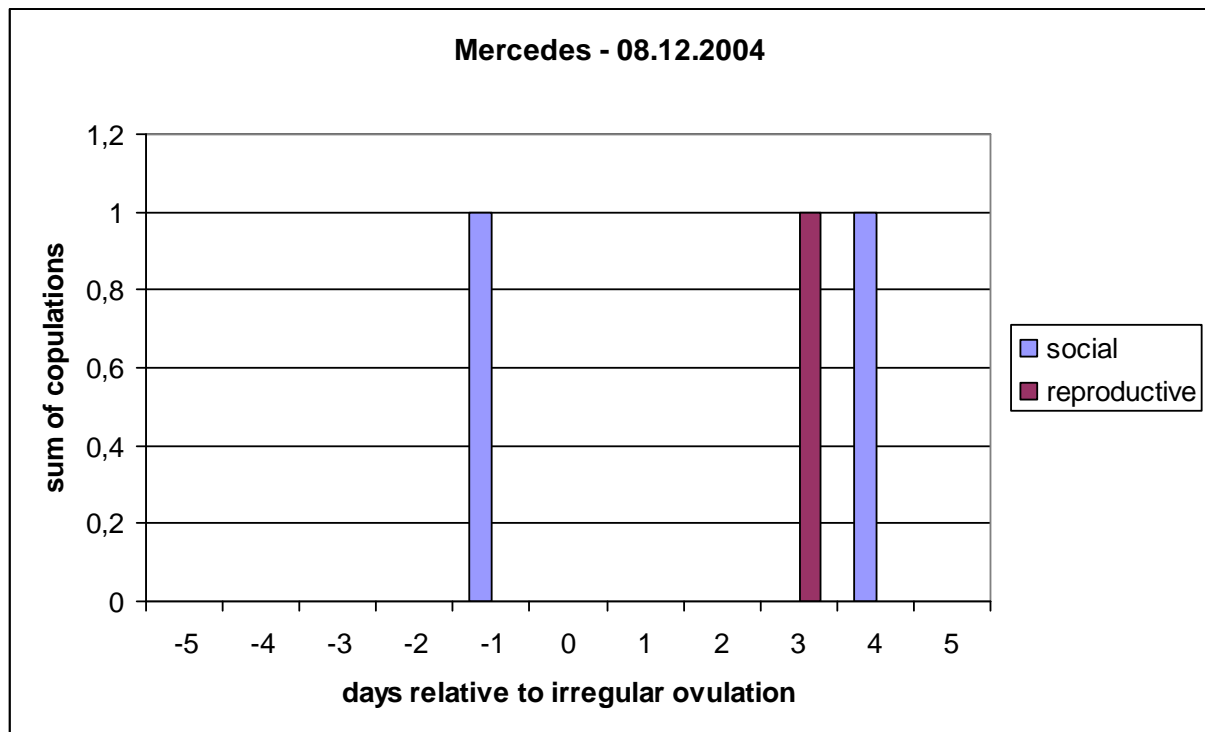
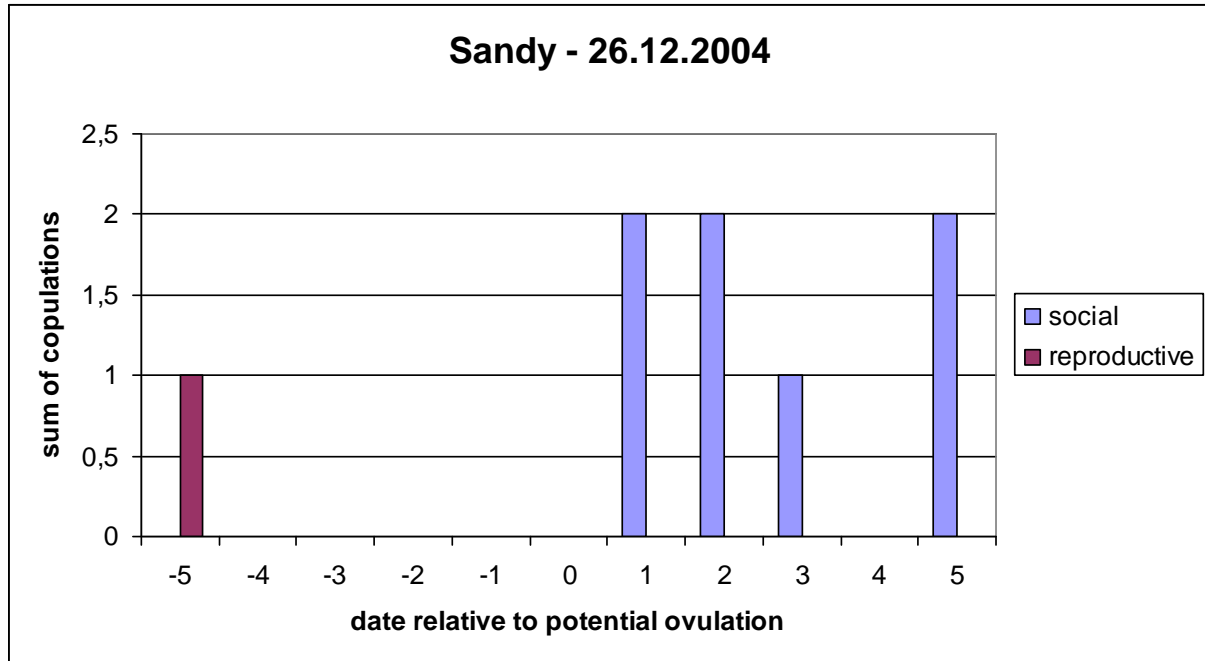
Makeup	15.12.2004	23,0192077	1,41831173
Makeup	17.12.2004	133,832935	0,13165264
Makeup	18.12.2004	118,880032	0,41390257
Makeup	20.12.2004	17,9831733	0,26706995
Makeup	23.12.2004	4,37863497	0,43205081
Makeup	31.12.2004	5,4738423	0,17363576
Makeup	09.01.2005	1,55450532	0,63768012
Makeup	12.01.2005	22,3880556	0,39730133
Makeup	13.01.2005	21,2043834	0,14612776
Makeup	14.01.2005	0,83562799	0,31220259
Makeup	16.01.2005	17,2619718	4,81000175
Makeup	18.01.2005	85,7103375	3,25578926
Makeup	20.01.2005	71,7581845	3,19769682
Makeup	23.01.2005	15,1782387	0,65254676
Makeup	24.01.2005	14,7244669	4,67676167
Makeup	26.01.2005	9,68006842	2,68597811
Makeup	27.01.2005	23,4008203	2,59868846
Makeup	04.02.2005	105,073699	5,30698483
Makeup	08.02.2005	82,4861388	5,00103288
Makeup	09.02.2005	54,230595	33,5994064
Makeup	14.02.2005	56,1913793	32,3770462
Mercedes	27.11.2004	43,0251009	1,15500559
Mercedes	28.11.2004	0,53792604	0,04815337
Mercedes	05.12.2004	8,29931038	1,0830583
Mercedes	07.12.2004	14,15255	0,9563106
Mercedes	08.12.2004	192,079665	45,6696915
Mercedes	11.12.2004	139,717164	34,3338121
Mercedes	14.12.2004	0,00099659	10,7314472
Mercedes	17.12.2004	52,1015443	0,29111988
Mercedes	18.12.2004	251,977297	45,4117365
Mercedes	19.12.2004	245,16846	43,8797701
Mercedes	04.01.2005	3,89753482	1,07301575
Mercedes	07.01.2005	2,70938233	0,08448089
Mercedes	10.01.2005	0,18028886	0,29724789
Mercedes	11.01.2005	2,68786627	0,3697646
Mercedes	15.01.2005	47,5588889	12,8924

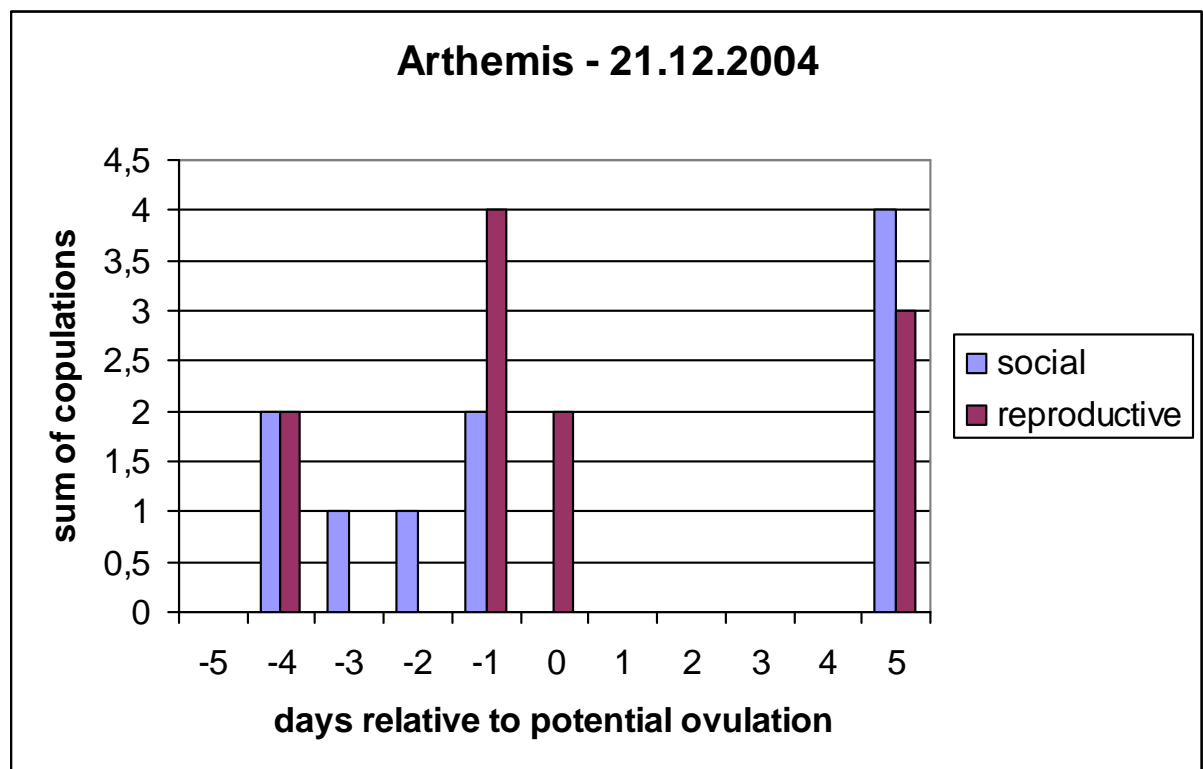
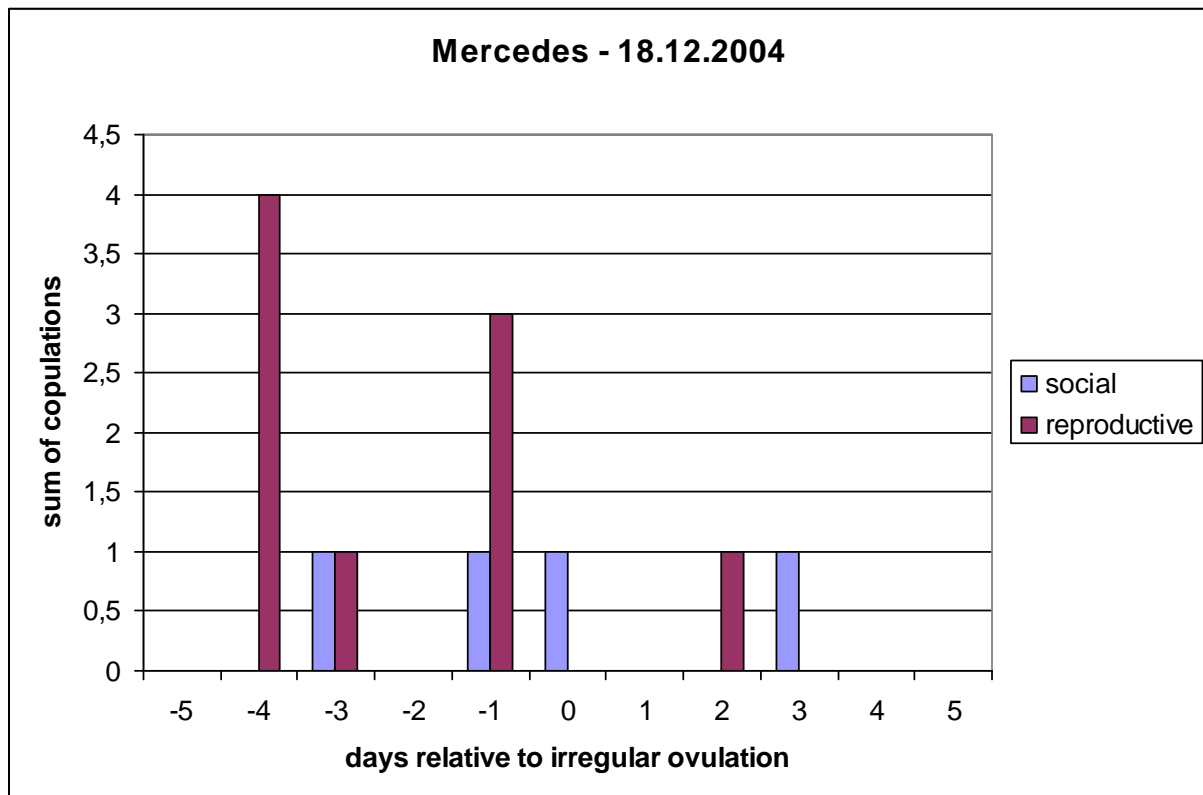
Mercedes	23.01.2005	43,6175516	13,5131819
Mercedes	27.01.2005	7,19234403	0,04751424
Mercedes	28.01.2005	11,4701055	0,0365682
Mercedes	29.01.2005	11,6008021	0,15950058
Mercedes	30.01.2005	39,7680284	2,29980982
Mercedes	11.02.2005	10,160299	1,67074191
Posh	07.12.2004	3,02138221	0,32960873
Posh	10.12.2004	9,28039886	0,09750389
Posh	11.12.2004	13,1376923	0,08992308
Posh	15.12.2004	14,5698845	0,22866154
Posh	18.12.2004	3,98333321	0,55439033
Posh	20.12.2004	29,6623734	0,15162563
Posh	21.12.2004	29,0010422	0,49748095
Posh	26.12.2004	10,6610631	0,7304031
Posh	27.12.2004	22,817234	10,770513
Posh	28.12.2004	26,8205263	8,66388187
Posh	29.12.2004	60,0295985	0,53932935
Posh	30.12.2004	2,60485641	0,91765147
Posh	12.01.2005	1,92645775	0,14369519
Posh	16.01.2005	5,95522944	6,61029716
Posh	23.01.2005	26,8166232	7,26904309
Posh	24.01.2005	163,763853	1,26328159
Posh	25.01.2005	41,5882353	3,99534848
Posh	26.01.2005	142,973171	4,49689157
Posh	27.01.2005	134,205314	0,05114739
Posh	29.01.2005	54,5608314	1,7554555
Posh	30.01.2005	65,8114984	1,02223855
Posh	01.02.2005	53,9478792	0,8278966
Posh	03.02.2005	76,1685238	1,79543037
Posh	04.02.2005	6,77333151	1,64960068
Posh	06.02.2005	16,2863095	64,4542876
Posh	08.02.2005	15,5357465	33,0106557
Posh	11.02.2005	288,561937	317,071691
Posh	13.02.2005	305,325	314,401671
Sandy	27.11.2004	43,0176688	0,25676755
Sandy	28.11.2004	17,6738583	0,01319372

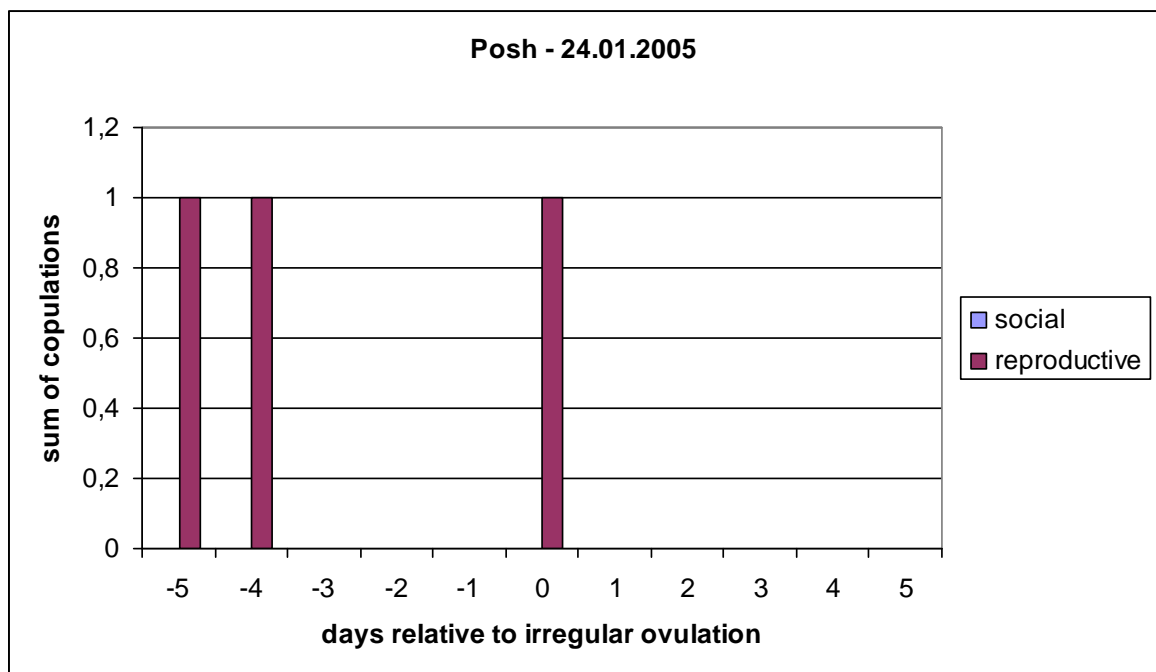
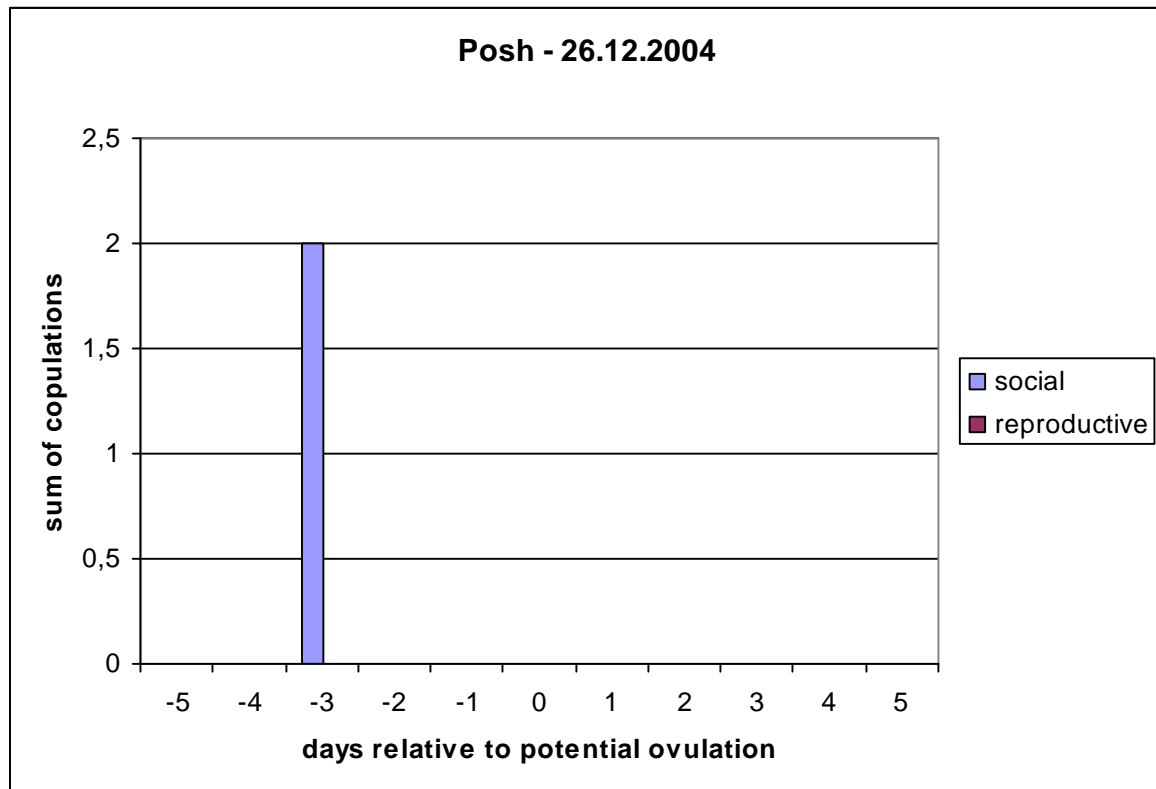
Sandy	10.12.2004	188,113285	1,90506515
Sandy	12.12.2004	241,978413	2,08736746
Sandy	14.12.2004	64,096817	1,10917384
Sandy	18.12.2004	71,8712157	1,17610638
Sandy	20.12.2004	44,9954859	2,11468605
Sandy	21.12.2004	37,5614675	1,71734122
Sandy	26.12.2004	0,61812997	1,32982056
Sandy	27.12.2004	6,93520177	3,3321133
Sandy	29.12.2004	10,8419151	5,05927869
Sandy	30.12.2004	17,0438995	1,03715789
Sandy	03.01.2005	3,05009074	1,75673291
Sandy	04.01.2005	8,51625616	1,44487782
Sandy	16.01.2005	20,1764286	10,3922003
Sandy	21.01.2005	6,37452381	8,70499429
Sandy	23.01.2005	9,22776557	2,09692051
Sandy	27.01.2005	168,460944	1,93355282
Sandy	28.01.2005	89,7107596	1,70464282
Sandy	01.02.2005	62,5196618	1,89510752
Sandy	02.02.2005	80,0171829	15,7216536
Sandy	04.02.2005	174,428082	15,8917438
Sandy	06.02.2005	768,999294	17,3137741
Sandy	09.02.2005	777,637374	10,2207374
Sandy	11.02.2005	1,57321711	9,46564516
Venus	07.12.2004	54,0271126	1,33202925
Venus	08.12.2004	40,9462796	1,49118685
Venus	10.12.2004	12,8844109	0,01964005
Venus	12.12.2004	4,74181485	0,08397653
Venus	18.12.2004	17,6142916	0,10567831
Venus	19.12.2004	7,88744409	0,1969847
Venus	20.12.2004	20,142122	0,215288
Venus	21.12.2004	7,08106462	0,31414893
Venus	23.12.2004	0,88869032	0,06958249
Venus	26.12.2004	1,6438169	0,24225916
Venus	27.12.2004	0,41878933	0,38724282
Venus	04.01.2005	21,5088732	7,50394507
Venus	07.01.2005	21,6076275	6,80898358

Venus	09.01.2005	7,81859059	0,10829373
Venus	18.01.2005	11,7498103	0,23456413
Venus	20.01.2005	14,1007076	0,85272691
Venus	21.01.2005	30,6599181	0,31788734
Venus	23.01.2005	77,2584386	1,09312039
Venus	25.01.2005	109,12541	1,11985732
Venus	27.01.2005	4,60525592	0,39507732
Venus	02.02.2005	9,60978493	0,42752
Venus	11.02.2005	167,711412	54,5474737
Zora	05.12.2004	25,7571024	0,505541
Zora	08.12.2004	19,5102745	8,88557882
Zora	10.12.2004	40,6104412	8,89643382
Zora	14.12.2004	12,7527216	0,17395833
Zora	15.12.2004	25,6106511	1,2519084
Zora	19.12.2004	19,9746079	1,13547882
Zora	20.12.2004	21,7904801	0,02256826
Zora	26.12.2004	19,9822881	2,72605297
Zora	28.12.2004	2,41080685	1,01603243
Zora	17.01.2005	1,22718085	22,7295833
Zora	18.01.2005	62,2243673	3,3539357
Zora	06.02.2005	200,558088	13,0235441
Zora	08.02.2005	237,457556	8,15598529
Zora	11.02.2005	19,13299	4,23216107
Zora	13.02.2005	22,8038862	3,10316107

Appendix 2: Figures of the distribution of social and reproductive copulations relative to the day of potential ovulations. Individuals are shown in descending rank order.







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Curriculum vitae

Surname/ First name	Sonnweber Ruth
Address	Nordbahnstrasse 44/28 1020 Vienna, Austria
Nationality	Austria
Date of birth	30 October 1980
Work experience	
Dates	March 2007 – August 2007 Employee at the University of Vienna as a research assistant
Dates	June 2003 – June 2004 Employee in the Department for realization of clinical studies – secretary and administrative work Wyeth Whitehall Export GmbH, Storchenteg 1, 1150 Vienna, Austria
Education and training	
Dates	February 2007 – March 2007 Census work on the Barbary macaque population in Gibraltar (in cooperation with Mag. Gisela Schiestl)
Dates	November 2005 – February 2006 Field work in Gibraltar on Barbary macaques (<i>Macaca sylvanus</i>) – development and testing of a new 3D- method of tumescence analysis of female sexual swellings (in cooperation with Mag. Gisela Schiestl)
Dates	October 2004 – February 2005 Field work for diploma thesis
Dates	June 2004 – July 2004 TBA course in Kenya with field projects and seminars in savannah ecology
Dates	October 1999 Matriculation and Inscription at the University of Vienna, Austria
Dates	August 1991 – June 1999 A – level Akademisches Gymnasium Innsbruck, Angerzellgasse, 6020 Innsbruck, Tyrol, Austria
Dates	August 1989 – June 1991 Primary school (3rd und 4th form) in Hall, Tyrol, Austria
Dates	August 1987 – June 1989 Primary school (1st und 2nd form) in Absam, Tyrol, Austria