universität wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

Reproductive parameters of a semi-free ranging troop of Japanese macaques

verfasst von / submitted by

Anja Böck, BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2016 / Vienna, 2016

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	A 066 827
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Anthropologie
Betreut von / Supervisor:	Ass.-Prof. Mag. Dr. Bernard Wallner, Privatdoz.

CONTENTS

I ACKNOWLEDGEMENT

It is my great pleasure to thank all those who helped me to make this master thesis possible. First of all I want to thank my advisor Bernard Wallner whose lectures intensified, if not even provoked my interest in primatology. He inspired my scientific thinking.

My sincerest thanks go to Lena Sophie Pflüger, who was at my side during the whole time. She helped me with words and deeds in so many ways. To mention just a bit of it, she helped me to find an accommodation, she guided me through all the time at the Affenberg and she supported me in the analysis. Her infectious enthusiasm was a motivation to me throughout the whole time. Without her this thesis would not have been possible and I am honoured to express my thanks to her. I appreciate her as a person and as scientist.

Furthermore I want to thank the team at the Affenberg, who helped me wherever they could. Above all my special gratitude belongs to Markus Dorner and Alexandra Werdenig for teaching me the monkeys' names and so much more. Moreover, I want to thank Peter and Svenja Gaubatz who facilitated me in many ways – whether in housing or infrastructural issues.

I also want to express my gratitude to Brigitte and Gottfried Wulz who accommodated me during my first stay at the Affenberg, although they did not know me.

Not least I thank all the people who assisted me in various ways. My friends and family, who supported me during my whole studies, who showed interest in my work and who always had an open ear for me.

II ABSTRACT

In this study 19-year data on various reproductive, demographic and climatic parameters of female Japanese macaques were analysed to achieve an extensive understanding of a semi-free ranging troops' dynamic and reproductive performance. On the one hand general pattern of female reproduction were investigated – such as birth timing, interbirth intervals, primiparity and birth rates. Those parameters have been under investigation a lot in other troops and were therefore compared with data from other provisioned as well as from wild troops. On the other hand some parameters were analysed, which have received little attention so far. The association between reproductive performance of females and climatic variables has been hardly investigated in matters of reproduction. This is especially true for sunshine.

In 1996 a total of 39 Japanese macaques were transplanted from Osaka prefecture, Japan to Austria. Although birth control was practiced, this troop has grown to 150 individuals in 2015. Hence, for nearly twenty years now sufficient amount of birth data has been accumulated. These data from the Affenberg Landskron as well as local weather records were used to examine reproductive patterns of the troop carefully.

The findings are:

(i) Regarding general patterns of female reproduction: Interbirth intervals after first-borns are greater than after any later born offspring. Furthermore, first-borns tend to be born later in the year than any later-born offspring.

(ii) Regarding climatic influences on reproductive performance: Firstly, after warmer mating seasons there seems to be a tendency towards earlier births. Secondly sunshine duration appears to influence the probability of females for receiving a young. In other words the more sunshine hours were recorded during the previous mating season, the greater was the proportion of fertile females who actually gave birth in the subsequent birth season

(iii) Regarding sex ratio: There is a trend towards a balanced sex ratio of the troop, which seems to be associated with the sex ratio of births.

Our findings concerning general patterns of female reproduction go along with previous studies. In contrast our results regarding the sex ratio of the group has not been reported in this species. Likewise not enough data is available to illuminate the association between sunshine and reproductive performance entirely. This calls for further investigation.

III DEUTSCHE ZUSAMMENFASSUNG

In dieser Arbeit werden reproduktive, demografische und klimatische Daten von weiblichen Japanmakaken analysiert. Das Ziel dabei ist es umfassendes Verständnis für die Dynamik und die reproduktiven Mechanismen einer semi-freien Gruppe zu entwickeln. Einerseits wurden generelle Parameter der weiblichen Reproduktion untersucht – wie beispielsweise der Zeitpunkt der Geburt, die Geburtsintervalle, das Alter bei der ersten Geburt oder die Geburtenraten. Diese Parameter wurden bereits in anderen semi-frei- und freilebenden Gruppen hinreichend beschrieben und konnten daher mit den Daten dieser Gruppe verglichen werden. Andererseits wurden Parameter analysiert, denen bislang noch kaum Beachtung geschenkt wurde. Dazu zählt der Zusammenhang zwischen der reproduktiven Leistung von Weibchen und klimatischen Variablen – allen voran die Sonnenscheindauer.

1996 wurden 39 Japanmakaken von Osaka in Japan nach Landskron in Österreich gebracht. Obwohl Geburtenkontrolle betrieben wurde, wuchs die Gruppe bis 2015 auf 150 Tiere an. Seither wurden reproduktive Daten der Gruppe aufgezeichnet. Diese Daten, sowie lokale Wetterdaten wurden in dieser Arbeit verwendet, um reproduktive Muster in dieser Gruppe zu untersuchen.

Das sind die Ergebnisse:

(i) Bezüglich der generellen Parameter der weiblichen Reproduktion: Das Geburtsintervall zwischen dem Erstgeborenen und dem Zweitgeborenen ist größer als zwischen spätergeborenen Jungtieren. Außerdem werden Erstgeborene meist früher im Jahr geboren als Spätergeborene.

(ii) Bezüglich klimatischer Einflüsse auf die Reproduktion: Erstens finden die Geburten nach wärmeren Paarungssaisonen eher früher statt. Und zweitens scheinen erhöhte Sonnenscheinstunden während der Paarungszeit die Wahrscheinlichkeit für

Weibchen zu erhöhen in der darauffolgenden Geburtssaison ein Jungtier zu bekommen.

(iii) Bezüglich des Geschlechterverhältnisses: Es gibt einen Trend in Richtung eines ausgeglichenen Geschlechterverhältnisses, der im Zusammenhang mit dem Geschlechterverhältnis der Geburten zu stehen scheint.

Die generellen Parameter stimmen mit den Daten vergleichbarer Gruppen von Japanmakaken überein. Im Gegensatz dazu blieb der Zusammenhang zwischen dem Geschlechterverhältnis der Gruppe während der Paarungszeit und dem Geschlechterverhältnis der darauffolgenden Geburten bisher unentdeckt. Ähnlich verhält es sich dem Einfluss des Sonnenscheins auf die Geburtenrate. Bislang sind noch nicht genügend Daten vorhanden um diesen Zusammenhang vollständig aufzuklären. Dies erfordert weitere Untersuchungen.

1 INTRODUCTION

1.1. General information about Japanese macaques

1.1.1. Taxonomy, ecology & body composition

Japanese macaques (*Macaca fuscata*) – sometimes also known as snow monkeys or red-faced macaques – belong to the family of Old World monkeys (*Cercopithecidae*). Compared to their sister group, the Apes (*Homonoidea*), Cercopithecoidea are considered to be the more successful radiation today (Geissmann, 2003). They inhabit a wide range of climate and vegetation zones in parts of Africa, Asia and in Gibraltar.

In particular, Japanese macaques belong to the genus "*Macaca*", which diverged from the human lineage 28 – 25 million years ago (see Figure 1.1: Rogers & Gibbs, 2014), leading to a difference in single-copy sequence of about 7% (Rhesus macaques: Gibbs et al., 2007).

The genus *Macaca* comprises, besides Japanese macaques, 22 other species, divided into five groups (Geissmann, 2003). These groups are the *Macaca mulatta*-group, which includes Japanese macaques, the *Macaca sylvanus*-group, the *Macaca nemestrina*-group, the *Macaca fascicularis*-group and the *Macaca sinica*-group.

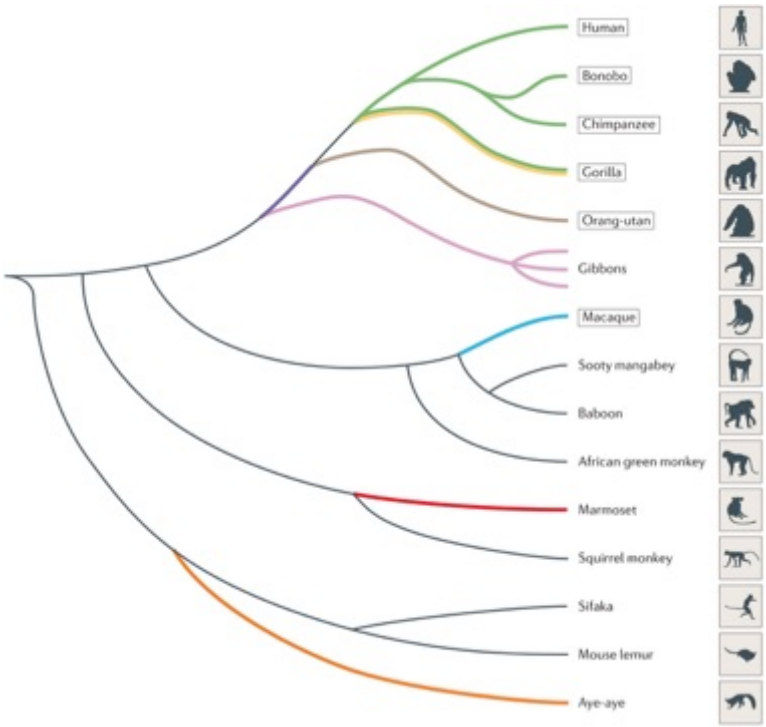


Figure 1.1: Primate phylogenetic tree
© Rogers and Gibbs, 2014

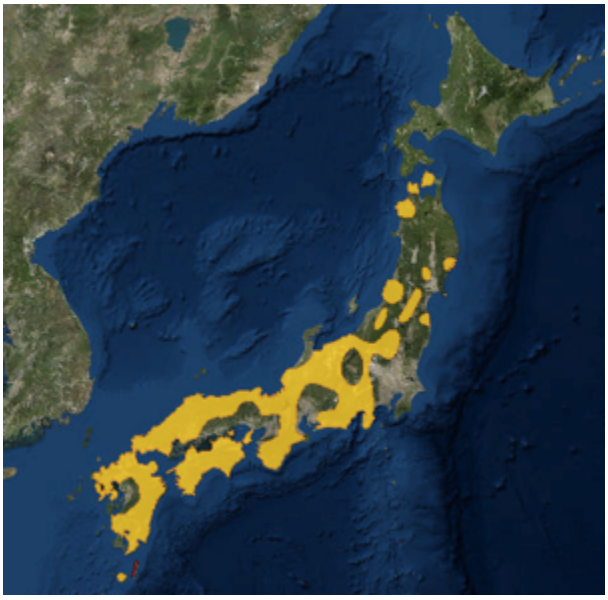


Figure 1.2: Distribution of Japanese macaques
© http://maps.iucnredlist.org/map.html?id=12552

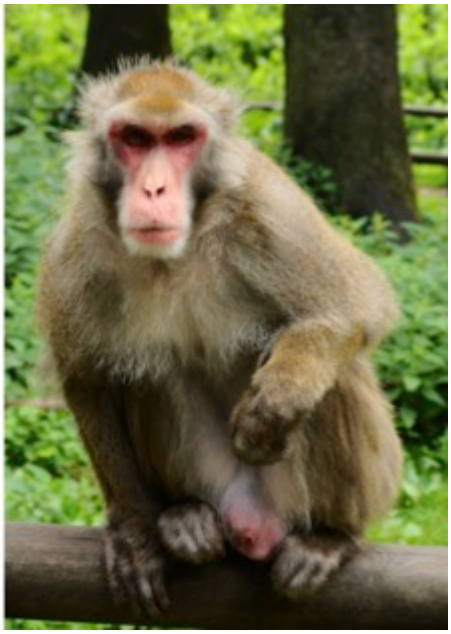
As the name suggests they are native to the Japanese archipelago and thus, the northernmost living nonhuman primates (Fooden & Aimi, 2005). They appear on three of the four large Japanese islands, namely Shikoku, Honshu and Kyushu, but not on the most northern island of Hokkaido (see Figure 1.2). Furthermore they are found on some smaller islands near the coast (Fooden & Aimi, 2005).

One population is recognized as a distinct subspecies. This population lives on the island of Yakushima and has been named *Macaca fuscata yakui*, whereas *Macaca fuscata fuscata* habits the mainland. However, most recent genetic research does not support this differentiation (Marmi et al., 2004).

Corresponding to "The IUNC-Red List of Threatened Species", Japanese macaques have been categorised as "least concern". It is estimated (Fooden & Aimi, 2005) that more than 100,000 individuals live in Japan in varying habitats, depending on the latitude and altitude. On the southern end of the populations' distribution there are subtropical forests where the temperature rarely drops below 10°C. On the northern limit of their distribution there are subarctic forests, where the temperature is below -20°C frequently and there is a lot of snow during wintertime (Hanya, 2014). In between there are cool-temperate deciduous forests, warm-temperate evergreen forests (Takasaki, 1981) and alpine grasslands (Tsuji, 2010). Nowadays, because of the high level of human habitation, Japanese macaques are absent in many lowland regions (Amagasa & Ito, 1978, cited in Fooden & Aimi, 2005).

They are semiterrestrial with females spending more time in the trees than males do (Chatani, 2003). Japanese macaques are mainly quadruped, but for shorter distances, they are able to walk and run bipedally and they are good swimmers.

Figure 1.3: Comparison of an adult female (on the left) and an adult male (on the right)
© Anja Böck



Males have higher body weight – on average females weigh 8.4 kg, whereas males weigh 11.3 kg (see Figure 1.3 for comparison of a male and a female). Additionally the median fat mass also differs between the sexes since males' median fat mass is 7% and females' is 9% (or 700g in females and 800g in males), but there are clear fluctuations in both due to seasonality in climate (Hamada et al., 2003). While body weight tends to decrease during the winter in cool habitats, in warm habitats it rather decreases in summer (Hamada et al., 1996 cited in Fooden & Aimi, 2005).

Likewise depending on the habitat and the seasonality their diet is varying. Due different and changing climate, their diet is of a great variety depending on availability (Tsuji, 2010). In general Japanese macaques are considered to be omnivorous. Although they prefer fruits, seeds, leaves, nuts, flowers, shoots, buds and bark, they have been observed eating roots, fungi, insects, spiders, eggs, molluscs, crabs (Suzuki, 1965; Tsuji, 2010), fish (Watanabe, 1989) and even frogs and lizards (Suzuki et al., 1990).

Japanese macaques can reach an age of over 30 years. However, such an old age is primarily achieved in provisioned groups, whereas in non-provisioned natural populations life spans are much shorter – e.g. 6.3 years in females according to Takahata et al. (1998a). In females it is supposed that the actual mean life span is much less than half of the greatest known. As males usually emigrate from their natal troop as soon as they have become sexually mature, their actual life span in non-provisioned groups is more difficult to assess (Fooden & Aimi, 2005).

1.1.2. Social organisation

Japanese macaques live in multimale and multifemale groups that can comprise up to 161 individuals in the wild, with a mean of 40.8 ± 28.95 individuals (Fooden & Aimi, 2005). In provisioned groups, however, the maximum size can even grow to more than a tenfold due to artificial feeding (Sugiyama & Ohsawa, 1988). Large groups, however, rather become fissured (Sugiyama, 1960; Yamagiwa & Hill, 1998).

In general home range size and population density are associated with the habitat quality in wild animals. This applies to Japanese macaques too: the higher the habitat quality, the smaller are per capita home ranges (Izumiyama et al., 2003). For example Izumiyama et al. (2003) found smaller per capita home ranges in "natural" troops compared to "rural" troops. Natural troops thereby never utilized cultivated lands. Consequently they depended more on deciduous trees, whereas rural troops utilized cultivated lands frequently. The food supply was therefore more ensured, which leaded to increased troop sizes and smaller per capita home ranges. Additionally, per captive home ranges in evergreen broadleaf forests are smaller than in deciduous broadleaf forests (evergreen: 1.4-6.4 ha/ deciduous: 7-79 ha), since evergreen forests provide food supply throughout the whole year, whereas foraging is more challenging in deciduous forests during winter (Fooden & Aimi, 2005). And in habitats with a great fruit and herb production the density of monkeys is comparably higher than in, similar habitats without a great fruit and herb production for example (Hanya et al., 2005).

Like many other mammals, Japanese macaques show sex-biased philopatry and dispersal (Pusey, 1987a; Pusey, 1987b). Females stay in their natal matrilineal organized group, whereas males emigrate once they are sexually mature. Of course there are some exceptional cases (e.g.: Inoue & Takenaka, 2008), but usually they leave their troop by an average of four years (Fukuda, 1982). Although ejaculation occurs by the time they reach 4.5 years of age (Wolfe, 1978; Takahata, 1980), males usually do not manage to sire offspring beneath an age of 8.5 years (Inoue & Takahata, 2008; Takahata, 1980). Besides the mating activity remains comparatively low until that age (Takahata, 1980). Fooden & Aimi (2005) therefore concluded, that full sociosexual maturity of male Japanese macaques occurs at an age of about 8.5 years.

This female philopatry and male dispersal causes two patterns: Firstly, usually there are more females than males in a troop. According to an analysis of 35 natural troops by Fooden & Aimi (2005), troops consist of 32% adult females, 18% adult males, 35% juveniles and 15% infants. And secondly, the hierarchy among females in a troop is quite stable among males it is more flexible (Thierry, 2000). Because males transfer between troops several times (Pusey, 1987) their social ranks changing. Accordingly within one troop of Japanese macaques there is both - an alpha male and an alpha female. Like rhesus macaques, Japanese macaques live in a despotic social system with a strict linear dominance hierarchy (Thierry, 2000). Based on the four-level classification by Thierry (2000), Japanese macaques are among those species that show the lowest level of conciliatory tendency and social tolerance. Conflicts are often aggressive and usually directed from the higher-ranking to the lower-ranking individual.

Once males leave their natal troop, they must fight their way up in the hierarchy and their rank tend to rise with length of tenure in a new troop (Takahashi, 2002a), whereas females inherit the mother's rank (Thierry, 2000). Among sisters – following the youngest-ascendancy-principle – females usually become dominant to their older sisters by the time they reach sexual maturity (Kawamura, 1958; Hill and Okayasu 1995; Kutsukake, 2000). Thus, the rank order among sisters correlates inversely with age in most of the cases (Yamagiwa, 2010). At the same time their mother remains dominant to all her daughters normally. Nonetheless studies of some smaller, free-ranging and notably unprovisioned troops reported a higher rank of the older sister compared to her younger sister, if their mother does not aid any daughter. In this regard Hill and Okayasu (1995) concluded that youngest ascendancy mainly occurs under conditions of frequent and intense aggression triggered by concentrated food resources in provisioned troops. Under these conditions mothers tend to support their younger daughters.

The above-mentioned matrilineal kin relationships result in a rank gradient of female matrilines within a troop, which means whole matrilines are dominant or submissive to others. Among higher-ranking matrilines Koyama (2003) found a higher level of social cohesion than in lower-ranking matrilines. Therefore high-ranking females spend more time grooming their close kin and they have larger grooming networks (Koyama, 2003), which is essential to maintain and tighten social relationships.

1.1.3. Reproduction & mating behaviour

In Japanese macaques' reproduction is seasonal. Mating occurs in autumn and winter, while birth is given in spring and summer – on average 171.7 days after conception (Fooden & Aimi, 2005). During the mating season their bare skin turns intensely red, whereof their synonym as "red-faced macaques" comes from. What this name not suggests, is that the hairless region of the hindquarters and nipples also increase in redness during times of mating (Figure 1.4). In females the intensity of the red colour varies within their cycles – with increasing redness during periovulatory periods (Fujita et al., 2004; Wallner et al., 2011), whereas in males the redness is more or less consistently (Enomoto, 1974). To improve the view of the red perineal skin, adult males hold their tails erect during the mating season (Wolfe 1981).

Figure 1.4: During mating season the monkeys' bare skin (face, nipples and hind quarter) turns red © Anja Böck

As already mentioned, males are considered to be adult and thus fully socio-sexually mature by an age of about 8.5 years (see Figure 1.5 for comparison of adult and adolescent males). Although they start mounting females as young as 1.5 years and ejaculation occurs by the time they reach 4.5 years of age (Wolfe, 1978; Takahata, 1980), it appears to be challenging for Japanese macaque males to sire infants beneath an age of eight (Inoue & Takenaka, 2008). By that age the frequency of mating behaviour is about five times higher than in younger males (Takahata, 1980). Proposed reasons are their lower fertility and restricted access to females (see section 1.1.3.1. Female Choice & Paternity) (Kuester et al., 1995). Because of improved nutritional conditions in a semi-captive setting, sexual maturation may be accelerated (Fooden & Aimi, 2005; Rhesus macaques: Catchpole & Van Wagenen, 1975).

Figure 1.5:
Comparison of a 13-years-old adult male (left) and an 7-years-old adolescent male (right)
© Anja Böck

In females menarche occurs in general at an age of 3.5 years (Wolfe, 1978). At about the same time those adolescent females start to develop perineal swellings expressed during the mating seasons. These swellings last for about two to three years and are not mint in adults.

Females' menstrual cycle lengths are on average 27.1 days during mating seasons, with a menstrual flow of three to five days (Fooden&Aimi, 2005). During non-mating seasons menstrual cycle is usually irregular or even suppressed (Nigi, 1975). With a mean of about two years, females seem to have 0-6 oestrous periods, which are highly variable and not synchronized among them (Fooden & Aimi, 2005). Females also display post-conceptive oestrus (Takahata, 1980; Hamada et al., 1989; Nigi et al., 1990) and copulate with multiple males during the mating season. This behaviour confuses paternity, thereby reducing the danger of infant harassment and infanticide (Soltis et al., 2000). Thus, reproductive success of males is not obvious. The complex social structure and the resulting different conditions for individuals within a group, require ingenuity to reproductively succeed. Hence different strategies appear parallel such as female choice, sperm competition, male-male-competition and alternative strategies like sneak copulation (Soltis et al., 2001).

1.1.3.1. Female choice & paternity

In males social rank influences reproduction strategies greatly. High-ranking males tend to monopolize females and tend to disrupt consortships of subordinate males (e.g. Huffman,

1987; Perloe, 1992). Furthermore high-ranking males are able to keep up longer consortships with females than low-ranking males (Huffman, 1992). These dominant reproductive strategies imply the use of physical aggression (Barrett et al., 2002). Accordingly, low-ranking males have to pursue alternative strategies in order to avoid confrontations with higher-ranking males. Sneak copulation in the absence of high-ranking males therefore constitutes an efficient strategy to optimise reproductive success – for low-ranking males as well as for non-troop males (Hayakawa, 2008; Inoue & Takenaka, 2008; Rhesus macaques: Overduin-De Vries et al., 2012). In addition they benefit from a low operational sex ratio within the troop, since monopolization especially fails when the number of oestrous females per troop male is high (Takahashi, 2001; Ostner et al., 2008).

A vast amount of previous studies revealed contrasting results concerning the association between male rank and reproductive success. In this context it is of importance to distinguish mating success from reproductive success. Although high-ranking males may manage to copulate more frequently, they not necessarily sire more infants in relation to their increased mating opportunities (e.g. Inoue et al., 1993; Inoue, 1995). Females in some groups prefer mating with high-raking males only when conception already occurred (Inoue et al., 1993; Huffman, 1992). Particularly if tenure of dominant males persists for a long time, females copulate with them primarily when fertilization becomes rather unlikely (Inoue & Takenaka, 2008). One benefit of this tendency could be to increase genetic diversity among the offspring while still having the benefit of being supported by a high-ranking male. It is presumable that many females in a troop have already mated with a long-term alpha male before, who could have sired previously born infants (Inoue & Takenaka, 2008). Subsequently, these females favour novel males for mating above long-established high-ranks in following mating seasons (Takahata et al., 1999). This assumption is supported by earlier findings revealing an avoidance of breeding with the same male more than once (Inoue et al., 1990).

Moreover, females show more effort to avoid breeding with matrilineal kin (Soltis et al., 1999). Even if not yet emigrated adolescent males show sexual interest in closely related females, they usually repulse them (Enomoto, 1974). In semi-captive groups, where emigration from the troop, as well as sneak copulation with non-troop males are of course

unfeasible, studies propose an avoidance of breeding with closely relative individuals especially by females (Soltis et al., 1999; Itoigawa et al., 1981, Takahata et al., 2002).

Another factor influencing the likelihood for males to sire offspring is age. Subadult males have a far lower reproductive success in many macaque species. Adolescent males between 4.5 and 6.5 years show a reduced reproductive success in Barbary macaques (*Macaca sylvanus*; Kuester et al., 1995). In six-year-old Rhesus macaques (*Macaca mulatta*) paternity was detected in only every fourth male, whereas nearly all females at this age have already given birth (Bercovitch et al., 2003). As already mentioned also for Japanese macaque males it appears to be challenging to sire infants beneath an age of eight (Inoue & Takenaka, 2008).

To conclude, female mating preferences and partner selection appears to affect males' reproductive success essentially thereby attenuating the effect of male-male-competition in many instances (Takahata, 1982; Takahata et al., 1999; Soltis et al., 1997).

1.2. Reproductive parameters of female Japanese macaques

In accordance with Dunbar (1987), information about life history and demography of Japanese macaques provides the opportunity to attain a better understanding of the relationship between evolutionary processes and individual behaviour. Thereby, it is especially of interest which parameters or what combination of parameters, respectively, is decisive to synchronize members of a seasonal breeding species (Gouzoules et al., 1981). These parameters can be internal or environmental factors.

Particularly reproductive parameters of females have piqued primatologists' interest, since female mate choice seems to be more of a determining factor than competition among males (Soltis et al., 1997). Thus, variance of reproductive success is much lower among female compared to male Japanese macaques. According to an estimation of Fedigan et al. (1986) males' variance of reproductive success is about 2.5 times higher, whereas estimations of some other authors are even higher.

So far a wide variety of factors has been suggested to influence a females' reproductive performance – e.g. social rank (e.g. Koyama et al., 1992; Sugiyama & Ohsawa 1982), troop size (e.g. Takahata et al., 1998b), age (e.g. Itoigawa et al., 1992), previous reproductive

history (e.g. Koyama et al., 1992; Cozzolino & Schino, 1998), body weight (Hamada et al., 2003; Muroyama et al., 2006), as well as environmental factors (e.g. Cozzolino et al., 1992) such as temperature and latitude. Thereby it is especially of interest what differences occur between captive and free-ranging or provisioned and unprovisioned troop, respectively.

1.2.1. Social rank & troop size

Wrangham (1980) postulated that there exists an optimal troop size for birth rate. So, due to inter- and intragroup competition, birth rate should exhibit a humped curve against group size. In other words initially small troops birth rate should increase with troop size, because of the potential benefit of a larger troop in competition with other troops, but then – after optimal troop size has been exceeded - in larger troops birth rate should decrease with troop size, since intratroop competition may increase (Takahata et al., 1998b).

Regarding intratroop competition, the effect of females' social ranks on their reproductive performance depends strongly on a species' social system and the proportion of females within a troop. If there were fitness benefits associated with rank, it would be worth to compete for a high-rank position (Sterck et al., 1997). In some primate species like ursine howlers (*Alouatta arctoidea*) where the number of females within a troop is small, young females are occasionally evicted and the immigration of new females is deterred. In other words in those species a quite violent competition for troop membership occurs. In many diurnal primate species females are organized in a more or less stable, nepotistic dominance hierarchies, and yet all females breed practically. These species include for example vervet monkeys, cercopithecines, baboons and macaques. Concisely, competition among females manifests in a variety of ways (Mitani et al., 2012).

Following sexual selection, intrasexual competition in primate species is stronger among males than among females. Consequently reproductive success should normally be more variable in males. Nevertheless, a vast amount of previous studies revealed contrasting result concerning the association between social rank and reproductive success (see 1.1.3.1. Female choice & paternity). However it turned out as more data and studies became available that an association of the above mentioned variables apply for females too. Like in

males some studies reported increased reproductive success among high-ranking females and some studies found no association. Fedigan (1983) therefore issued two main questions:

Firstly, does a higher rank raise reproductive success? And secondly, if so, how is this achieved, or what are the mechanisms behind it, respectively? Both questions remained rather unsolved.

According to the first question different studies yielded different results. On the one hand Drickamer (1974) for example recorded increased birth rates in higher-ranking female rhesus macaques compared to lower-ranking ones. This is in line with Blomquist et al. (2010) who observed higher physiological fitness in higher compared to lower ranking females of this species. Among high-ranking female chimpanzees a significantly higher infant survival and birth rate was observed (Pusey et al., 1997). In baboons sons and daughters of high-ranking females show earlier testicular enlargement and menarche, respectively (Charpentier et al., 2008). In high-ranking bonnet macaques Silk et al. (1981) observed increased infant survival. On the contrary, Cheney et al. (1981) detected no association with birth rates or infant mortality in three groups of vervet monkeys – even in case of reduced resource availability. Also a study on Barbary macaques indicates no association between social rank and reproductive success among females (Paul & Kuester, 1990).

Despite these conflicting observations, some generalizations can be ventured probably. According to Blomquist et al. (2010) higher-ranking female rhesus macaques are indeed often younger at their first parturition and their offspring seem to have higher growth rates. However, higher-ranking females do not have shorter interbirth intervals in general, especially among macaques.

Anyhow, in Japanese macaques studies revealed contrasting results too. Takahata (1980) found no association between females' rank and sexual behaviour in free-ranging Japanese macaques, and Koyama et al. (1992) reported no significant relationship between females' rank and offspring mortality. Sugiyama & Ohsawa (1982), however, observed no increase of birth rate among high-ranking females, but only as long as troops were not provisioned. Under periods of provisioning birth rates were higher among higher- compared to lower-ranking females.

Hence, high-ranking females in social troops appear to produce more offspring and start breeding earlier under certain circumstances (Harcourt, 1987), which leads us to the next question.

Regarding to the question of what triggers a possible rank-based bias of birth rates, stress and resource availability have been considered. Low-ranking females may suffer more from social stress and/or food shortage and restricted access to water. Both could lead to a disruption of menstrual cycles, diminished fecundity, reduced infant survival (Fedigan, 1983) and later begin of parturition (Harcourt, 1987). In terms of resource availability, the influence of dominance on access to food and water depends on the distribution of both. If resources are unevenly distributes, low-ranking females may suffer more than higher-ranking females, because they are more often interrupted while feeding and generally threatened, which results in more stress for them. Consequently this may cause reduced fertility and higher infant mortality (Harcourt, 1987). In a provisioned troop of Japanese macaques, where food shortage should not be a point of concern, lower-ranking females began parturition earlier than higher-ranking females (Wolfe, 1984).

1.2.2. Age-specific fecundity

In many species – especially in larger mammals – birth rates tend to rise with age initially until a plateau is reached. This plateau maintains for a number of years and then birth rates decline markedly at the end of life (Mitani et al., 2012). This also applies to Japanese macaques.

Females usually come into oestrus at an age of about 3.5 years. Though, in those young females' sexual behaviour is considered to be immature – as they for example fail to arch their backs while males mounting them or miss to remain sitting in front of the male between mounting (Wolfe, 1978). Furthermore it was proposed that the likelihood for adolescent female of being mounted by adult males is lower than for adult females. Hence, it may be not surprising that four-year-old females rarely bare offspring irrespective of provision (or access to resources) (Itoigawa et al., 1992; Koyama et al., 1992).

According to Koyama et al. (1992) the birth rate among four-year-old females was merely 3.9%, whereas more than half of all first-born infants had a five-year-old mother. Correspondingly, the reproductive potential seems to be highest for middle-aged females between six and 19 years of age. In this context an interesting aspect is that adult males show a tendency to mate with those middle-aged females, while low-ranking subadult males rather mate with young or old females (Takahata, 1982). Additionally there might be a higher risk for five- to nine-year-old females to experience stillbirths or miscarriages. In many primates, survival is particularly at risk for first-borns or infants of young females (Mitani et al., 2012). This might be due to increased energy expenditure for young females who are still maturing (e.g.: reviewed in Bercovitch et al., 1999) or inexperience in rearing offspring (e.g.: Hiraiwa, 1981).

1.2.2.1. Post-reproductive life span

In humans menopause is conventionally described as cessation of menstrual cycle, which means consequently the end of reproductive capacity. The discontinuation of menstruation and ovulation is one component in the termination of reproductive viability (Walker and Herndon, 2008). This is, among other physiological changes, determined by a decrease of the ovarian volume (Giacobbe et al., 2004) and structural and functional changes in the reproductive hypothalamic-pituitary-ovarian axis – such as diminished estradiol (E2) and progesterone secretion and higher follicle-stimulating hormone (FSH) concentrations (Sherman et al., 1976), inter alia. It has been widely discussed whether menopause is unique for humans or not. Thereby one problem is the occurrence of various, sometimes misleading and on humans focusing definitions. In this regard vom Saal and Finch (1988) stated that a rigorous definition of menopause, thereby bringing its essential physiological features into focus, would allow a better comparison of reproductive senescence across species (citet in Walker & Herndon, 2008).

Indeed menstrual bleeding is an easily observable marker, but it is only one facet of the complex physiological mechanism that governs reproductive cyclicity. Therefore, Walker and Herndon (2008) defined menopause in primates as “the permanent, non-pathologic, age-associated cessation of ovulation”. They compared and analysed diverse biological

parameters among different primate species – such as perineal swelling, follicular depletion, menstrual bleeding and hormonal changes – to conclude that menopause is not unique to humans. Even though humans are assumed to have an outstanding long post-reproductive lifespan compared to other primates (Hawkes et al., 1998; Nozaki et al., 1995).

In Japanese macaques a decline of fecundity is well reported with a markedly decline in females over 20 years (Itoigawa et al., 1992). Hormonal data indicate an increase of basal Luteinizing hormone (LH) levels as early as females are 18 years old, marking the onset of decline in ovarian activity, while they still show normal cyclic functions at that time (Nozaki et al., 1995). Eventually at an age of 27 years there occurs a marked seasonal difference in plasma LH levels – with high levels during the breeding seasons (Nozaki et al., 1995). Within the first half of the third decade of their life females tend to cease from producing infants (Itoigawa et al., 1992; Koyama et al., 1992; Nozaki et al., 1995). Both in provisioned and unprovisioned groups, there is a time lag between the last parturition and the females' death or disappearance. Considering that the last infant is not able to survive self-dependently before an age of 1.5 years, Takahata et al. (1995) found an average post-reproductive life span of 4.5 years in a provisioned group. This refers to 16% of a females' average life span, whereas in an unprovisioned group the average post-reproductive life span was 3.6 years.

Hence, some authors assume Japanese macaques to have menopause or in other words, a period of infertility at the end of their lifespan – occurring at an age of about 27 years (Nozaki et al., 1995; Walker & Herndon; 2008). Although as already mentioned (see 1.1.1. Taxonomy, Ecology & Body composition) female Japanese macaques – especially in provisioned groups – can reach an age of over 30 years, it should be noted that an age of 27 years or older is generally a late stage in the life span of Japanese macaques and only rarely achieved in non-provisioned troops (Pavelka & Fedigan, 1999). This is an issue, which has been much under debate in humans too, as e.g. Hawkes et al. (1998) propose not early termination of fertility to be the derived characteristic of humans, but post-menopausal longevity due to low adult mortalities. Another hypothesis to explain the long post-reproductive life span is the "grandmother hypothesis" (compare Hawkes, 2004). Consistent with this hypothesis it is assumed that post-reproductive female Japanese macaques

contribute to improve the survival of their grandchildren (Nakamichi et al., 2010; MacDonald Pavelka et al., 2002).

Nevertheless a loss of fertility occurs in Japanese macaques. It occurs even though normal menstrual cycles are exhibited (Nozaki et al., 1995) and copulation behaviour is pursued in higher age (Takahata et al., 1995; Wolfe, 1978), although less frequent (Koyama et al., 1992). Thus, several causes for the cessation of reproduction come into consideration: Firstly elderly females may not be capable to maintain pregnancy – allowing for abortions are hard to notice in the field. Secondly ovulation may be absent although oestrus is exhibited (Takahata et al., 1995) and thirdly, fetal chromosomal abnormalities or physiological changes such as suboptimal uterine or hormonal environment may occur more frequently (Nozaki et al., 1995).

1.2.2.2. Parity & interbirth interval

As mentioned earlier, female Japanese macaques mostly give birth to their first infant at an age of 5 years. There is considerable evidence to assume that in non-provisioned, free-ranging troops this mean age of primiparity is higher than in provisioned troops (Mori, 1979; Sugiyama & Ohsawa, 1982) and even higher than in captive groups (Scucchi, 1984). According to Watanabe et al. (1992) and Mori et al. (1997) the mean age of primiparity increased by 3 years after a severe reduction of artificial food supply. So far the highest documented age of primiparity was 16 years (Watanabe et al., 1992; cited in Fooden & Aimi, 2005), although an age of over 8 years at first birth is not very common (Koyama et al., 1992). To some extent there seems to be a critical age for sexual maturation in female Japanese macaques, which is according to Mori et al. (1997) at an age of about 5 to 6 years. If poor nutritional conditions persist beyond this age, sexual maturation can be disproportionately delayed. However, primiparity per se, but not the mothers' age, seems to increase the likelihood for life-born infants to be abandoned (Schino & Troisi, 2005).

Even though elderly females above an age of 20 years have more sterile years than younger ones, multiparous females i.e., those who have given birth more than once, tend to have shorter interbirth intervals. That means a greater time lag occurs primarily between the first-born and the second-born infant (Koyama et al., 1992). This is consistent with many other

species, for example mountain gorillas, where the time lag between two births was positively correlated with birth order but not with maternal age *per se* (Robbins et al., 2006).

It should be noted that in wild Japanese macaque troops one-year birth-intervals are not as common as in provisioned troops. In an unprovisioned troop the mean interbirth interval was 25.1 months and Takahashi (2002b) goes even so far to suggest that the absence of a surviving infant is nearly essential for the onset of oestrous. In contrast in a provisioned troop, a one-year birth-interval was the most frequently birth-interval followed by a two-year birth-interval, whereas birth-intervals of 4 years or more were rare (Koyama et al. 1992). In primiparous females a trend has been recorded of two-year birth-intervals, while about two-third of all multiparous females gave birth in the subsequent year. Takahata et al. (1995) recognized a tendency for shorter interbirth intervals after females have given birth to a son, while there occurred longer interbirth intervals after the birth of a daughter (see Sex ratio).

Furthermore, the time of birthing seems to depend on whether a female has given birth in the previous year or not, rather than on their age or dominance rank. More precisely, multiparous females who have paused, delivered their offspring earlier in the following year (Watanabe et al., 1992; Cozzolino & Schino, 1998) – not only earlier than multiparous females who have brought an infant successfully up in the year before, but also earlier than primiparous females. Among primiparous females younger ones generally tend to give birth later in the year (Koyama et al., 1992).

1.2.3. Nutrition & climate:

The connection between food availability and reproduction is obvious, since for many non-human primates the following assumption is valid: The distribution of females is determined by the distribution of food resources, while the distribution of males is determined by the accessibility of females (Wrangham, 1980).

According to seasonal changes of food availability, the body mass of Japanese macaques varies throughout the seasons and reproduction follows an annual cyclicity (e.g. Mori, 1979; Hamada et al., 2003). Macaques usually lose weight from winter to spring whereas they gain weight from summer to autumn (Hamada et al., 2003).

However, in wild troops food availability is closely linked to the climate. In those troops differences between “high-fruit”- and “low-fruit”-mating seasons are recognized, as females tend to come into oestrus more often during “high-fruit”-mating seasons (Takahashi, 2002b). However, in captive troop, or even in provisioned troops, food supply can be kept quite stable. These improved conditions can impact reproduction enormously. Like in humans malnutrition can negatively affect a large number of reproductive parameters, such as age at menarche or interbirth interval (e.g. Bongaarts, 1980). Obviously, under provisioned conditions birth rate is higher (Takahata et al., 1998a). Compared to non-provisioned troops infant mortality is decreased, the onset of puberty is earlier and primiparous age is lower (e.g. Watanabe et al., 1992; Mori et al., 1997). In a quite extreme example adolescent females even exhibited perineal swellings during summer (Mori et al., 1997).

Physical measures, which reflect nutritional status – such as skinfold thickness, body mass or thoracic circumference – have been under investigation a lot. Generally males tend to show less remarkable seasonal fluctuations than females (Hamada et al., 2003; Muroyama et al., 2006). In females those mentioned physical measures appear to peak in late fall and early spring. Perhaps this is caused by preparation for pregnancy and lactation (Kurita et al., 2002; Muroyama et al., 2006).

As above-mentioned, in wild troops food availability is usually closely linked to the climate, whereas in captive troops, or even in provisioned troops, food supply can be kept quite stable. This may offer the possibility to investigate the effects of climate on reproductive activities separately, although it can be assumed that the influence of environmental factors on the seasonality of reproduction may be smaller in provisioned or captive troops (Cozzolino & Schino, 1998).

So far experiments demonstrated that an endogenous rhythm appears to be primarily responsible for reproductive seasonality in Japanese macaques (Fedigan & Griffin, 1996).

Obviously this endogenous rhythm has to be triggered by external factors – social factors and/or economical factors, such as photoperiod, rainfall patterns, sun exposure or temperature (Cozzolino & Schino, 1998). However, no conclusive evidence has been found to determine which of the environmental variables plays a key role (Cozzolino et al., 1992; Fedigan & Griffin, 1996).

In 1980 van Horn (citet in Cozzolino et al., 1992) proposed that latitude is the primal regulatory factor ("*zeitgeber*") for mating activities. Since of course seasonal change of day length is considered to correlate strongly with latitude, photoperiod has received most empirical support (Fedigan & Griffin, 1996). Certainly, there are other environmental factors as well, that vary along a latitudinal cline – like temperature or rainfall – but to a lesser extent. Thus, photoperiod is discussed to be the most reliable meteorological variable to compare time of parturition and consequently conception in different troops from year to year (Fedigan & Griffin, 1996).

Nonetheless, especially in troops, that have been translocated, latitude or photoperiod does not explain time of birthing. For instance, in a study of Varley & Vessey (1977) 31 Rhesus macaques were translocated within the same latitude, but the peak of birth season differed by 90 days. A laboratory study of Nozaki et al. (1990), however, revealed no impact of photoperiod on the annual cyclicity of reproduction in Japanese macaques. Consequently they argued that photoperiod do not seem to be a decisive environmental variable influencing the seasonal reproduction. This is in line with Cozzolino et al. (1992) who compared 25 provisioned troops of Japanese macaques. The authors reported an association of the beginning of the mating season with temperature only, but not with latitude. According to these findings photoperiod respectively latitude cannot be an effectual predictor for the onset of mating season. Regions on the same latitude may have completely different climates, e.g. due to altitude, distance from the sea, sun or wind exposure. Whereas Cozzolino et al. (1992) found no association of conception date with latitude, the former seems to vary in accordance with mean temperatures during fall and winter. In other words, the warmer the mating season was, the later parturition occurred and the colder fall and winter were, the earlier birthing occurred, respectively. Therefore temperature appears to be a crucial factor in determining the timing of mating.

In contrast, Gouzoules et al. (1981) did a study on a troop of Japanese macaques, which were translocated from Kyoto to Texas. Although climatological and environmental differences were obvious, birth season remained unchanged. In this regard Fooden & Aimi (2003) proposed minimal effects on birth seasonality as long as troops are translocated within the northern hemisphere. However, when a troop was translocated to the southern hemisphere, birth season was brought forward by six months.

Fooden & Aimi (2003) also mentioned that temperature generally decreases as latitude increases in Japan. In higher latitudes winter starts earlier. Of course winter is the poorest food season for Japanese macaques and so, the offspring has to reach a minimum level of development before. Thus, earlier birth seasons in troop in higher latitudes may be not surprising. This is consistent with Nozaki et al. (1992; citet in Fooden & Aimi, 2003), who concluded that the beginning of the mating season depends on both, temperature and photoperiodicity. Correspondingly, Fedigan & Griffin (1996) reported that the further south a troop of Japanese macaques is located in Japan, the later in the year conception and parturition occurred.

However, this does not apply for extreme latitudes. On the very north of the Japanese macaques' appearance, mean time of birth is later than predicted. Perhaps the prolonged winter is one reason, but according to Fooden & Aimi (2003) this needs to be under further investigation. And at the very south end of the Japanese macaques' distribution, winters are quite mild and therefore they may be less relevant for infant survival (Fooden & Aimi, 2003).

This is consistent with the results of Cozzolino & Schino (1998): neither temperature nor rain influenced the timing of birth in a troop of Japanese macaques in the Rome zoo, where the mean temperature in fall and winter varied from 9.6 to 13°C. In contrast, they found a correlation of temperature and mean conception date in a comparative study of intergroup variation, where the mean temperature in fall and winter varied from 4 to 11.2°C (Cozzolino et al., 1992; Cozzolino & Schino, 1998).

Endothermal animals in general have to bring up appreciable energy costs to keep body temperature constant. Since Japanese macaques are the northernmost living non-human primates (Fooden & Aimi, 2005) it may be especially challenging for them during autumn and winter, so during mating season (Hanya et al., 2007). When temperatures are low,

thermoregulatory costs are considered to be high. It is known that physiological costs of thermoregulation can be lowered by behaviour. This is called behavioural thermoregulation. Japanese macaques for example tend to decrease travelling and feeding time under cold conditions to save energy presumably (Hanya, 2004). More generally, behavioural thermoregulation includes adjustment of posture [Yellow baboons (*Papio cynocephalus*): Stelzner & Hausfater, 1986], as well as huddling [Japanese macaques: Hanya et al., 2007; Schino & Troisi, 1998; long-tailed macaques (*Macaca fascicularis*): Schino & Troisi, 1990; ring-tailed lemurs (*Lemur catta*): Kelly et al., 2016] and sunbathing [ring-tailed lemurs: Kelly et al., 2016; vervet monkeys (*Chlorocebus aethiops*): Danzy et al., 2012]. Huddling and adjustment of posture refer to the principle of decreased body surface/volume ratio. In this way thermal radiation can be reduced. Accordingly, when it is cold, the body posture of Japanese macaques tends to be more curled (Hanya et al., 2007). When weather is clear and sunbathing is possible Japanese macaques huddle less often. They prefer sunbathing instead (Hanya et al., 2007). This is true for ring-tailed lemurs (*Lemur catta*) as well (Kelly et al., 2016). Danzy et al. (2012) described more sunbathing on mornings after cooler nights in vervet monkeys. Accordingly, Hanya et al. (2007) proposed that the increment of skin temperature is higher after sun bathing than after huddling. Thus, sunbathing might have an energetic effect that is not negligible and therefore an impact on reproduction in primates and thus also in macaques.

1.3. Sex ratio of offspring

How parents split investment between their offspring and what are the consequences of this division have become a popular domain in evolutionary biology. While for example Sulloway (1996) paid special attention to the birth order, Trivers & Willard (1973) spotlighted the sex ratio. They proposed that “natural selection might favour the ability to adjust progeny sex ratio in relation to the parents’ ability to invest in their offspring” (Brown & Silk, 2002). More precisely, they assumed that the physical condition of the mother might affect whether she invests comparatively more in sons or more in daughters to maximize her own lifetime reproductive success (Brown, 2001).

Although reproductive success of male mammals is more variable than in females, many species, including humans, are observed to show a sex ratio of 1:1 (Fisher's principle; Fisher, 1930). In male Japanese macaques reproductive success is more variable too (see 1.2. Reproductive Parameters of Female Japanese macaques**;** cf. Fedigan et al., 1986). Under good conditions they can produce a large number of grand offspring, whereas under adverse conditions they can go completely empty-handed. In females, in contrast, reproductive success is not as fluctuating as in males. Accordingly, in polygynous species females who can afford, so those in good physical condition, should bias their investment towards sons to maximize their own reproductive success (Gomendio, 1990). However, mothers in poor physical conditions should invest more in daughters than in sons.

This bias towards one sex may be manifested in the birth sex ratio *per se* and/or in the maternal effort during pre- and postnatal life of the offspring (Brown, 2001). Concerning sex ratio *per se*, what means the intrauterine development and sex differentiation, more females are born under poor conditions, since male embryos seem to be more vulnerable (Kraemer, 2000). Concerning postnatal investment the frequency and duration of nipple contact may be an appropriate measure for the mothers' expenditure, since suckling on the nipples is often a non-nutritive contact and though contraceptive (Tanaka, 1992). Accordingly, Gomendio (1990) reported higher frequencies of nipple contact with daughters in low-ranking mothers compared to sons, whereas the reverse is true for high-ranking mothers.

Thus, it could be assumed that lower-ranking females tend to have longer interbirth intervals after they gave birth to a daughter and high-ranking females tend to have longer interbirth intervals after they gave birth to a son. Due to conflictive results, this assumption could have not been confirmed so far (Brown, 2001). Additionally, high-ranking mothers may benefit more from daughters, since rank is inherited and sons will emigrate (Gomendio, 1990).

In this context there are two point of concern: Firstly, there might be too little attention on sample size. As Brown and Silk (2002) noted for non-human primates that the magnitude of the difference of the sex ratios at birth in high- compared to low-ranking females declines as sample size increases. And this means that the mean difference of the sex ratios at birth of high- and low-ranking females is actually zero. Secondly, in practice physical conditions of mothers are not directly measured in many cases, but indirectly estimated from social rank.

Still, there is reason to suppose that, higher-ranking females are indeed heavier (cf. Small, 1981) and that larger and higher-ranking females give birth to larger infants (Bowman & Lee, 1995).

Silk & Brown (2008) focus on local resource competition and enhancement biasing the sex ratio of the offspring instead of maternal investment. Therefore, sex ratio at birth tends to be biased towards the more beneficial and helpful sex in cooperatively breeding primates (Griffin et al., 2005). In primate species, that do not breed cooperatively, birth sex ratio seems to be linked to dispersal – which means in troops with female dispersal, more females are born and conversely (Silk & Brown, 2008). In addition, group size may play a role in terms of local resource competition as well.

2 RESEARCH AIM

The aim of the thesis was to shed light into reproductive patterns in a semi-free ranging troop of Japanese macaques. More specifically, I aimed to compare those findings with previous literature and especially with data from free-ranging troops. In addition climatic parameters were taken into account, which so far received little attention in reproductive issues in Japanese macaques.

The present thesis aimed to investigate:

1) Firstly, general patterns of female reproduction, such as maternal age, interbirth intervals and parity, were examined. It was of particular interest, whether reproductive patterns of females differ highly from females in wild and non-provisioned troops. Due to improved nutritional conditions on the Affenberg compared to the wild, I expected the following differences: shorter interbirth-intervals and lower maternal age at the first birth in this provisioned troop compared to non-provisioned troops in Japan.

2) Secondly, I wanted to investigate whether climatic factors play a role in terms of reproduction in this troop of Japanese macaques. As the diet of the monkeys is constant throughout the year, nutritional effects on reproduction may be small. This enabled me to consider climatic effects separately. Here I focused on the impact of temperature, rainfall and sunshine duration during autumn and winter (mating season) on the subsequent birth rate and birth timing. I expected earlier births after cold winters and later births after warm winters, respectively. So far no direct link between birth rates/birth timing and rainfall or sunshine duration has been reported in previous study. However, observations in the field suggest the importance of sun for Japanese macaques as the most-northern living non-human primate species.

3) Thirdly, I aimed to investigate whether the sex ratio of births varies greatly throughout the years and if so, following which pattern. Considering, that nutritional conditions have always been stable, I did not expect a great variation of sex ratios at birth. Considering Fisher's principle of a balanced sex ratio, no large deviation from a groups' sex ratio of 1:1 was expected. Possible variations of birth sex ratios between the years were investigated in relation to climatic, weather and group conditions during the prior mating seasons.

3 MATERIAL & METHODS

3.1. Study site, environment & climate:

The monkeys in this study are a troop of Japanese macaques housed semi-free at the Affenberg Landskron, Carinthia, Austria (GPS: 46.6439014° 13.8994263°). In 1996 they were captured together and transplanted from Osaka prefecture, Japan (GPS: 34.6937° 135.50216°). Back then the group consisted of 38 monkeys, 23 females of different ages and 15 males, who were not older than four years. Since that time they have been kept in a four-hectare enclosure. The population density increased from 9.0 monkeys per hectare in 1997 to 37.5 individuals per hectare in 2015.

Every year from April to October the Affenberg Landskron (Affenberg Zoobetriebsgesellschaft mbH) opens its doors for visitors, who can walk through the enclosure within the scope of guided tours solely. Any interaction with the monkeys, such as feeding or touching, is strictly prohibited. Guided tours take visitors on a pathway, bordered on both sides, through one-third of the park. The remaining two-thirds of the enclosure provide a place of retreat for the monkeys.

Carinthia, were the monkey park is located, lies in the moderate temperature zone of central Europe. It has a continental climate with hot summers and cold winters. During winters the landscape is covered by snow frequently. This is similar to Osaka prefecture, the monkeys' original homeland. For this analysis monthly weather records were obtained from the Central Institute for Meteorology and Geodynamics (ZAMG). Records from September to March for each mating season (see Figure 3.1) were used. The weather station (GPS: 46.6181° 13.8738°) is near the Affenberg Landskron – only about 3.5 kilometres away as the crow flies. It is situated in a plain at 493 meters above sea level, which is about 140 meters below the Affenberg.

During the study period from 1996 to 2015 the average temperature from September to March varied between 2.8°C and 6°C with a mean ±SD of 4.2°C ±0.92°C. Throughout the entire period the temperature curves followed a clear pattern with lowest temperatures in December, January and February. Sunshine duration followed a similar pattern, with

comparatively few sunshine hours in November, December and January, whereas the amount of rainfall did not follow such a clear pattern and varied strongly over the years (see Figure 3.1). The average amount of rainfall was between 44.4mm and 141.3mm with a mean ±SD of 82.4mm ± 28mm. The average sunshine duration per month ranged between 113 hours and 162 hours with a mean ±SD 139.9 hours ± 17.42 hours.

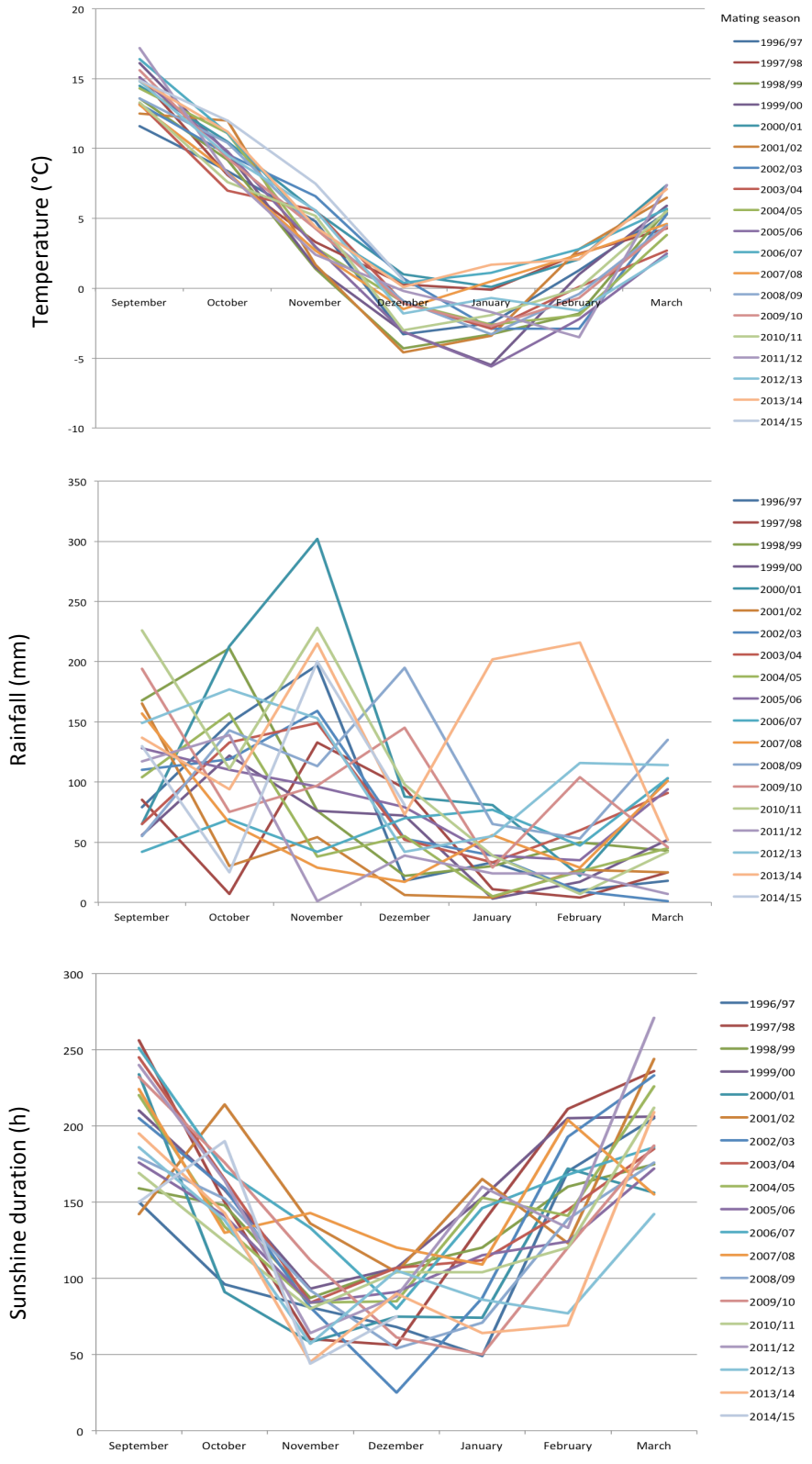


Figure 3.1: Mean temperature, rainfall and sunshine duration recorded during each mating season from the year 1996 to 2015

3.2. Nutrition

The enclosure contains a small stream, deciduous and coniferous trees as well as shrubbery and grassland. This environment enables the monkeys to forage for themselves. Nevertheless foraging becomes less feasible during wintertime, when the area is usually covered with snow and deciduous trees have no leaves. Therefore, and especially in order to preserve the environment in the enclosure, the monkeys have been provisioned from the outset. This food supply consists of mostly regional vegetables (mainly carrots and potatoes), fruits (mainly apples) and wheat or pellets (pressed plant fibres), respectively. The food is spread over a wide area in the enclosure by the animal care staff every day. Depending on the size of the troop, the amount of provisioned food is adjusted. Per adolescent or adult individual an average daily requirement of 900 kcal is expected and for each juvenile individual beneath an age of three years a daily requirement of 400 kcal is calculated (compare with: Hill, 1997; Hanya, 2003). Currently (1.September 2015) there are 150 monkeys in the park. Thus, the animal care staff provides a daily food supply of 170 kg fruits, vegetables and weed.

3.3. Group composition

3.3.1. Group size

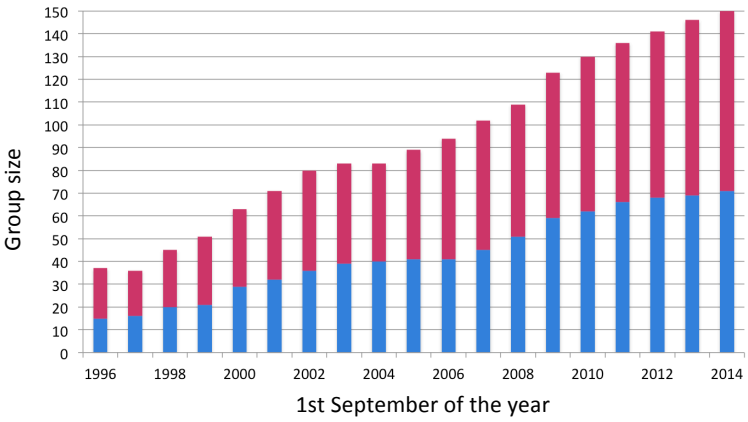


Figure 3.2: Number of individuals, males (blue) and females (pink), living in the Affenberg Landskron on the 1. September of each year

Within 19 years - from 1996 to 2015 - the troop size has grown from 39 to 150 monkeys in the park. During the whole period, no individual has been taken out from the group and merely one group foreign, two-year-old male has been integrated into the group in 2003. This male, whose name was “Junior”, died in 2009 by the age of 8.

Over the years the troop size steadily increased (see Figure 3.2). Given that 1. September is around the onset of the mating season, this date is selected as reporting date for this study. The number of females varied from 20 to 79, with a mean ± SD of 49.89 ± 18.79. The number of males varied from 15 to 71, with a mean ± SD of 43.21 ± 18.59. Correspondingly, the sex ratio of the whole troop (defined as number of males per female) has a mean ± SD of 0.847 ± 0.0761 males per female, with a minimum of 0.682 males per female, a maximum of 0.943 males per female. Currently (1. September 2015) the troop consists of 71% adults, 12% adolescents and 17% juveniles. The mean age of the whole troop increased by nearly five years since 1996 – from 4.28 years to 9.31 years in 2015. On average females are older than males (see Figure 3.3).

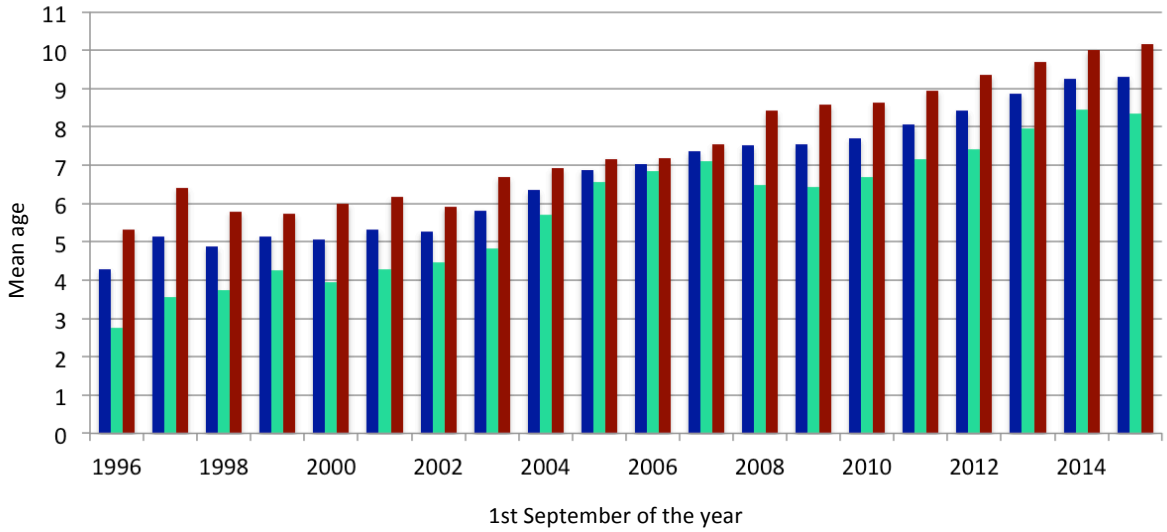


Figure 3.3: Mean age of the whole troop (blue) and of females (red) and males (green) only

Assuming that females are not sexually mature before an age of 3 years, the number of sexually mature females varied from 16 to 65, with a mean ± SD of 38.11 ± 16.47. Furthermore, assuming that males are not sexually mature before an age of 3 years too (compare 3.3.4. Paternity), the number of sexually mature males varied from 8 to 59, with a mean ± SD of 30.58 ± 15.82 (see Figure 3.4). The operational sex ratio (ratio of mature males to mature females) therefore lies between 0.50 and 0.91, with a mean ± SD of 0.773 ± 0.118 mature males per mature female.

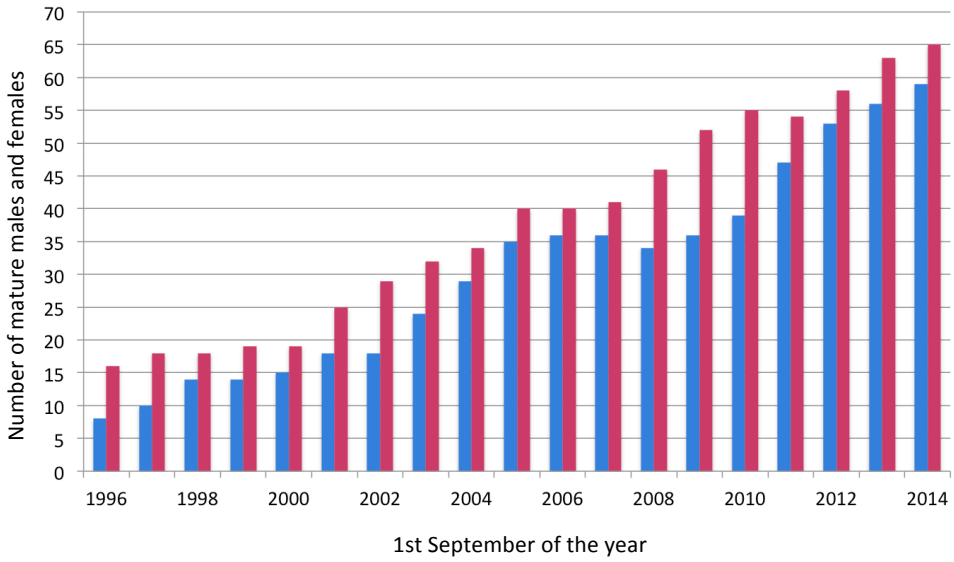


Figure 3.4: Number of mature individuals, males (blue) and females (pink), living at the Affenberg Landskron of each year (sample date = September, 1st)

3.3.2. Birth rates

Throughout the whole period since the foundation of the Affenberg Landskron, 182 births were documented in 19 birth seasons. Of these, 94 were male and 88 were female infants. Stillbirths and miscarriages are hard to recognize in the wild and this is true for the semi-free ranging troop at the Affenberg Landskron too. Over the whole period 16 infants (nine males and seven females) were reported, that died during their first half-year of life (compare Takahata et al., 1995). The remaining 166 births (85 males and 81 females) are defined as live births in this analysis.

In each birth season between one and 15 infants were born and survived at least a half year (see Figure 3.5). There is no year without at least one live birth. On average live-born offspring increases the troop size by 10.8 per cent with a standard deviation of 6.48 per cent, compared to the troop size at the onset of the mating season in the previous year. The minimum growth of the troop size happened in 1997, when the troop size was increased by only 2.7 per cent, and the troop size was increased maximum by 27.8 per cent in 1998.

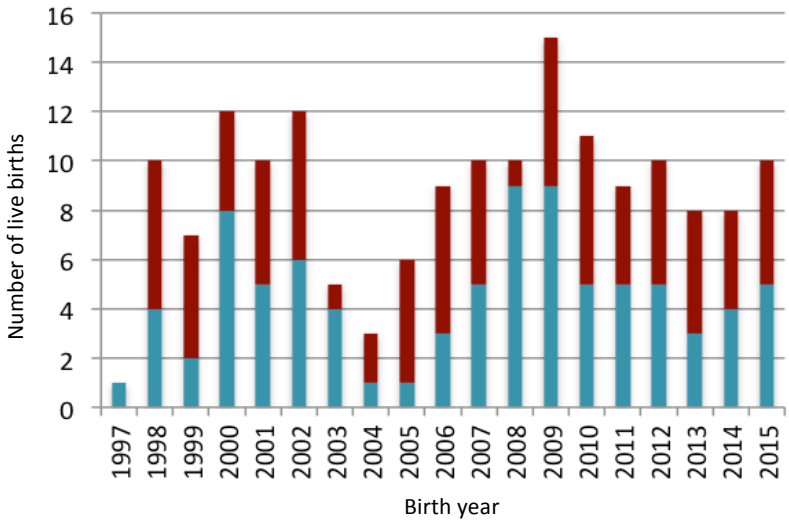


Figure 3.5: Number of live-born males (blue) and females (red) in every birth season

All 182 births occurred between February and August (see Figure 3.6), bearing in mind that 177 of these occurred in March, April, May and June and overall, only five births took place in February, July and August. Most of the births occurred in April and May, more specifically in late April and throughout the whole May (see Figure 3.7).

Two live-born females were born in May, but the exact date is unknown, so they are not included in Figure 3.7. To deduce an approximate conception date from birth dates, I expected a mean gestation duration of 172 days according to Fooden & Aimi (2005).

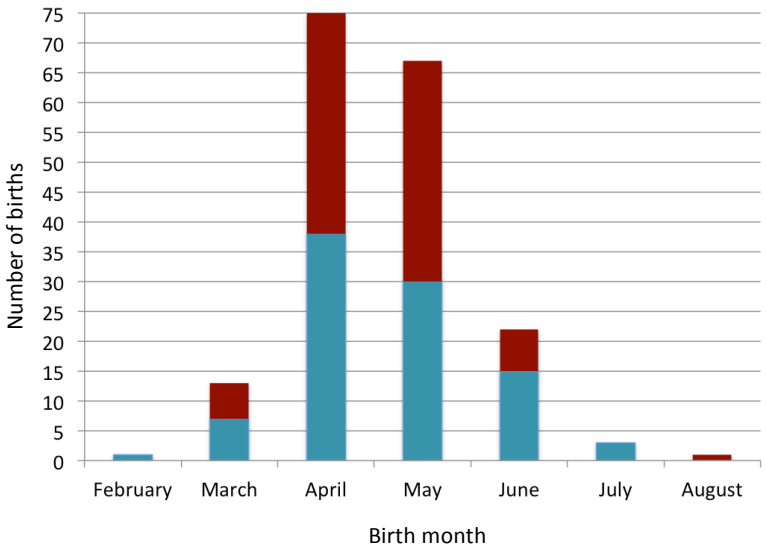


Figure 3.6: Number of all births per month (blue: male new-borns, red: female new-borns)

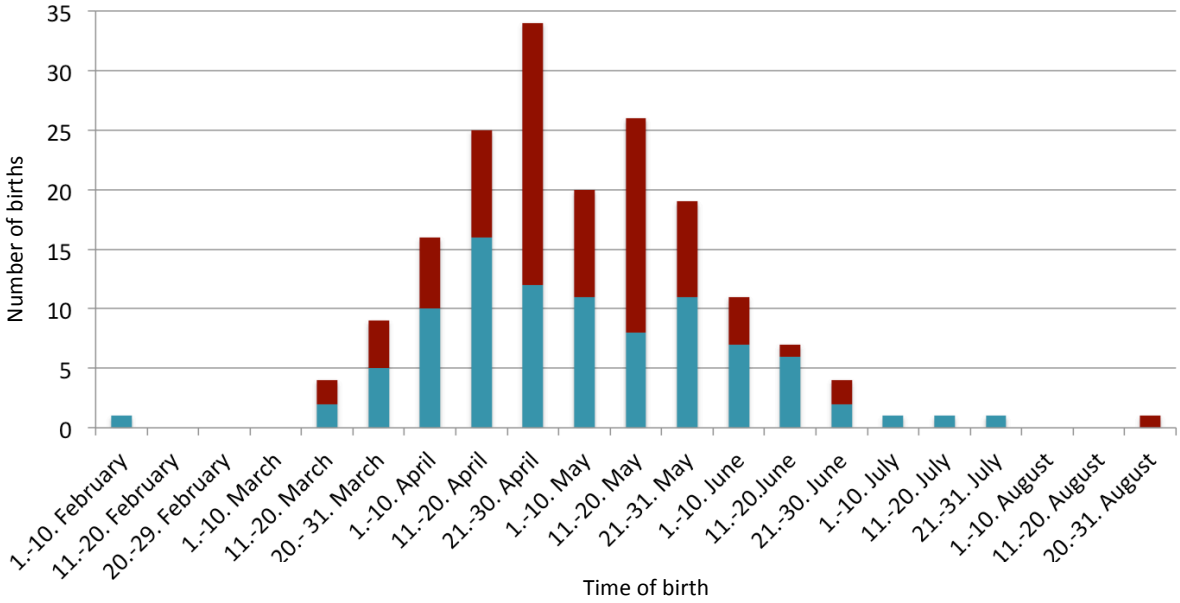


Figure 3.7: Number of new-born male (blue) and female (red) offspring per one-third of each month

3.3.3. Sterilisation & matrilines:

To control the troop's population growth, since 2000 a total of 54 females have been sterilised during ten non-mating periods. In contrast to hormonal contraceptives, these ovarial ligations are highly appropriate to avoid significant manipulation of mating behaviour and physiology. In doing so particular attention was paid to ensure that existing matrilines remain intact. Accordingly, females usually had raised two offspring before they were sterilised, except when the matriline was small. In those cases, females were not sterilised to prevent any extinction of female bloodlines.

Currently (1. September 2015) the Affenberg Landskron houses eleven intact matrilines, consisting of at least one fertile female. On average these eleven intact matrilines are made up of 6.63 females with the smallest matriline consisting of two females and the largest matriline consisting of eleven females alive. All together there are 26 mature and not sterilised females in the troop – in each matriline at least one and a maximum of five.

All those matrilines go back on females transplanted from Japan to Landskron, Austria in 1996. Today four of these native Japanese females are still alive (Sissy, Amanda, Anastasia and Chita) and they are estimated to be between 23 and 29 years old. However, three other females from Japan are still alive as well, but they have no intact matriline any more (Kathi,

Michaela and Tanja). Besides, three of those 15 males, who were brought to the Affenberg Landskron in 1996, are still alive too.

3.3.4. Paternity

In 2011 paternity was determined by the Institute of Zoology, University of Graz (Radler, 2014). Therefore DNA was extracted from hair samples as well as from saliva. Subsequently 8 microsatellite loci – three direpeats and five tetrarepeats – were analysed, using macaque and human specific primers. Thus, 43 paternities could be determined. 19 different males sired these 43 offspring. On average one of them sired 2.26 offspring. However, the two most successful males sired five offspring. Two of these 43 fathers were only 3.5 years at their first successful conception. They were the youngest. Overall the oldest detected father was 12.5 years at procreation. On average fathers were 6.75 years at the procreation (see Figure 3.8).

Although no individual has been taken out from the group and merely one group foreign, two-year-old male has been integrated into the group in 2003, nearly all determined parent pairs were not kin - with three exceptions. These parents were two pairs being aunt and nephew or uncle and niece, respectively, and one parent pair was more closely related, but the exact degree of relationship could not be found.

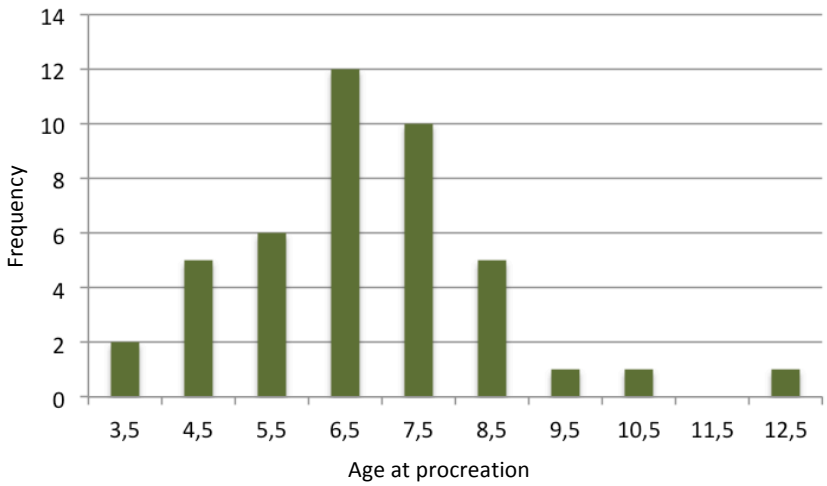


Figure 3.8: Age of all 43 identified fathers at procreation

3.4. Data processing & analysis:

I analysed reproductive parameters in a birth-controlled troop of Japanese macaques in Landskron, Austria. For that purpose I used data from the aforementioned weather station, as well as records from the Affenberg Landskron itself. From the beginning, all important information has been recorded by the animal care staff – such as births, deaths, veterinary treatments, injuries et cetera. Since the park's staff knew the monkeys from the outset, all troop members have been individually identified.

These raw data were provided from the Affenberg Landskron. All data processing and statistics were done in Microsoft Excel: Mac 2011 and IBM SPSS Statistics Version 20. Depending on the question the sample and the sample size changed. This happened especially due to new-borns whose exact birth date, sex or mother were not known or due to including or excluding those females who were transplanted from Japan to Austria in 1996, depending on the type of question. For more details see below.

3.4.1. Animal selection for the analysis of maternal age

For analysis of maternal age only females who were born at the Affenberg Landskron were included. Accordingly, 19 female Japanese macaques that were transplanted from Japan to Landskron in 1996 were excluded. This exclusion was done for two reasons: Firstly, some of these females had been already mature when they came to Austria and their reproductive history was not known. For the same reason they were excluded from the analysis of the age at sterilisation. Secondly, females who were juvenile in 1996 were excluded since the onset of reproduction could be influenced by the stress of transplantation. This resulted in 56 mothers who were involved in the analysis of maternal age.

3.4.2. Interbirth intervals & parity

For the analysis of interbirth intervals females, who originally came from Japan, were excluded too. This results in a sample size of 37 interbirth intervals between the first-born and the second-born offspring and 37 interbirth intervals between any further offspring.

According to the association between the time of birth (birth months as well as thirds of birth months) and parity, only female were included who gave their first birth at the Affenberg Landskron as well. In general in all analysis regarding parity females who were born in Japan were excluded, as it remained unknown whether those females have had already given birth in Japan before. This resulted in a sample size of 59 first births and 78 further births.

The association between parity and the time of birthing was analysed in two alternative ways. Firstly, the month of birth *per se* was used, no matter if this birth occurred at the beginning, in the middle or at the end of the month. Secondly, the association between the time of birthing and parity was analysed in more detail. Therefore each month was divided into thirds.

Concerning the offspring's sex, every offspring, whose sex has been known, was included – that included those who died soon after they were born (no names) and offspring of females from Japan. The sample size for interbirth interval analysis (N=107) was smaller than the number of births (N=185), because after the last-born offspring there is no interbirth interval of course and in three cases the sex of those offspring who died after birth was not known.

Throughout non-parametric statistical tests were used. To analyse, if the interbirth intervals after first-borns and later-borns differ in length, a Mann-Whitney-U-test was performed. A Mann-Whitney-U-test was also carried out to find a possible link between parity and birth timing.

3.4.3. Birth rate & timing

To analyse whether birth timing is associated with the temperature during the previous mating season, birth months were divided into thirds. Every birth date was encoded as following: the decade represented the birth month and the unit position represented the third of the month in which births occurred. For example a birth occurred on the 15th of April this was encoded as 46.66. Then, a mean for each birth season was calculated. In this analysis all documented births with known birth dates were included. Subsequently Spearmen's correlation coefficient was calculated.

All females were included in the analysis of birth rates. Fertile females were defined as females who are already mature, but not sterilised or in other words all females who could potentially conceive. Sterilisations were usually performed before the onset of the mating season to avoid abortions. That means for example the number of mature and fertile females differed for the first time during the mating season 2000/2001, because two females were sterilised in 2000.

Another factor of concern in this regard may be lactation. Some females may still breastfeed their offspring during the mating season following the birth. These females might have not been able to conceive. Taken this into account, two analyses were conducted. The first analysis included those probably lactating females, whereas for the second one, those females were excluded. In other words, for the second, females who had given birth to an offspring in any birth season and who paused then in the next birth season were excluded. Females, who gave birth in two subsequent birth seasons, were probably not lactating during the mating season in between and were thus not excluded from the analysis.

To analyse, whether there is a link between the proportion of fertile females who actually gave birth in each birth season and the weather situation during the foregoing mating period, Spearmen's correlation coefficients were calculated.

3.4.4. Sex ratio

The sex ratio of the group was calculated in three different ways. However, the record date was always September, the 1st. Firstly, the variable sex ratio was defined as males per female in the group. Therefore all individuals were included – juveniles, adolescents and adults. Secondly, the operational sex ratio was calculated by the ratio of mature males per mature females. According to the paternity records (see section 3.3.4. Paternity, Radler et al., 2014), some males in the troop fathered their first offspring at an age of 3.5. The youngest females gave birth to their first offspring at an age of four years. Taking these data into account, both males and females were defined as mature at the age of at least three years. Thirdly, a ratio of mature males per fertile females was calculated, although all mature, but sterilised females show ordinary mating behaviour too. Males therefore could not recognize, if a

female is fertile or not. However, to see if something was missed and for the sake of completeness I calculated this third kind of sex ratio, composed of fertile individuals only.

The sex ratio of births was defined as new-born males per new-born female. All new-borns were included, thus also those new-borns who died soon after birth. In 1997 only one male offspring was born and thus no sex ratio of new-borns could be calculated for this particular year. The final data therefore covers a period from the birth season in 1998 to the birth season in 2015.

While the troop size was between 38 and 150 individuals, the number of births fluctuated between one and 15 births each year. Besides, the sex ratio of births was calculated from completely new individuals each year – only those who where born. However, the sex ratio of the group was to a large extent composed of the same monkeys from the previous and the next year (plus new-borns and minus fatal casualties). Consequently, the sex ratio of the group deviated much less than the sex ratio of births. For that reason these variables were z-transformed. A Spearmen's correlation should give information about a possible association between the sex ratio of the group during mating season and the sex ratio of births.

3.4.5. Weather data

Besides the data from the Affenberg itself, weather data from the ZAMG weather station were used. A monthly average of diverse parameters is public. There is still no data for 2015 available. On this account the birth season of 2015 is not included in this analysis. For the average rain in mm, the average temperature in °C and the average sunshine duration in hours during each mating season, monthly records from September, October, November, December, January, February and March were used. Besides the ordinary averages, weighted averages have been calculated. These variables have been weighted by the number of offspring sired in certain months of the mating season. That means, given the date of birth, the date of conception was estimated. The average temperature, rainfall and sunshine duration of each month were therefore multiplied by individuals that have been sired an infant in this month.

4 RESULTS

4.1. Maternal age

Over 19 birth seasons 75 females gave birth to 185 infants, including those who died within their first half-year of life and those whose sex remained unknown. Of the 75 known mothers 22 gave birth to only one infant and for 18 of them reproduction is limited, because they were sterilised or died. The other 53 mothers gave birth to two or more infants. More precisely, there are 19 mothers with two offspring, 21 with three offspring, seven with four offspring, five mothers with five offspring and one with six offspring.

19 mothers were born in Japan. So their age at their first birth is not known. The mean age of the remaining 56 mothers was 4.73 ± 0.694 years at their first birth. Of them, 37 females gave birth to two or more infants. On average they were 6.65 ± 0.907 years old at the birth of their second infant. Furthermore those 22 females, who gave birth to at least three infants, were 8.05 ± 0.928 years old at the birth of their third infant. At the fourth birth the mean age of the mothers was 9.33 ± 0.943 years and at the birth of their fifth infant 10.2 ± 1.17 years (see Figure 4.1). The youngest mothers were four years old (22 females) and the oldest mothers were 12 years old (two females).

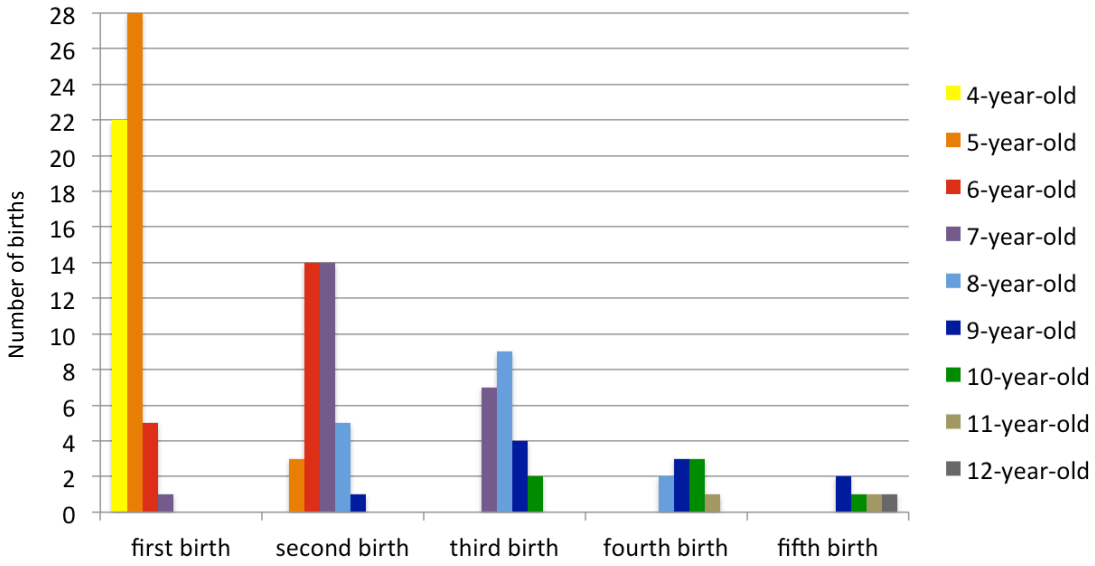


Figure 4.1: Age of females when giving birth to their first, second, third, fourth and fifth offspring

According post-reproductive lifespan no conclusions can be drawn, since in general females were sterilised in early years. The oldest females were twelve at their sterilisation, while the youngest were four years old (see Figure 4.2). Currently there are no unsterilised females over an age of eleven years in the troop.

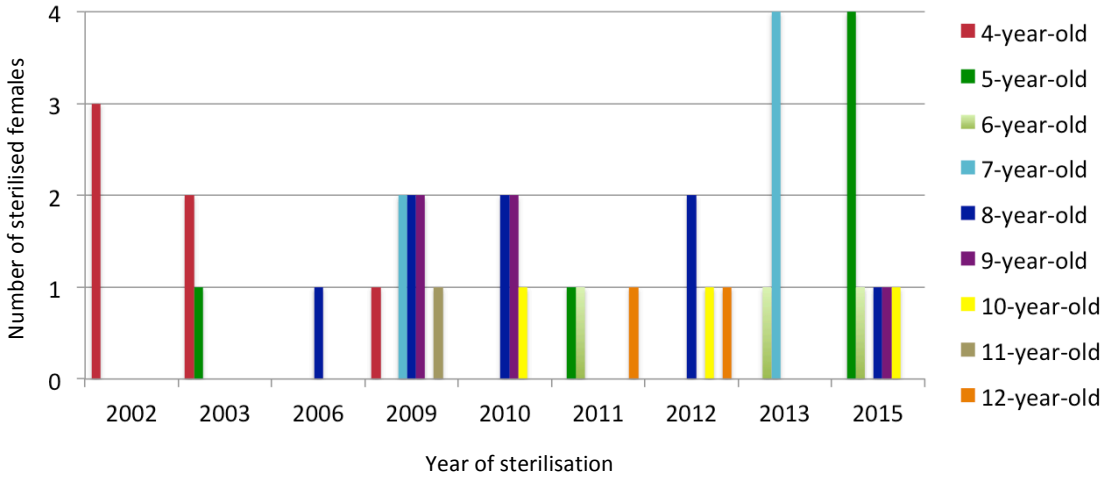


Figure 4.2: Overview of all sterilisations on the Affenberg Landskron (age of females at sterilisation and year)

4.2. Interbirth intervals & parity

For the analysis of interbirth intervals only those mothers were included, who were born in Austria. A two-year interval between two births was most common (54.05%, N=40), followed by a one-year interval (40.54%, N=30) and a three-year interval (5.41%, N=4). The interval between two births has never been greater than three years (see Figure 4.3).

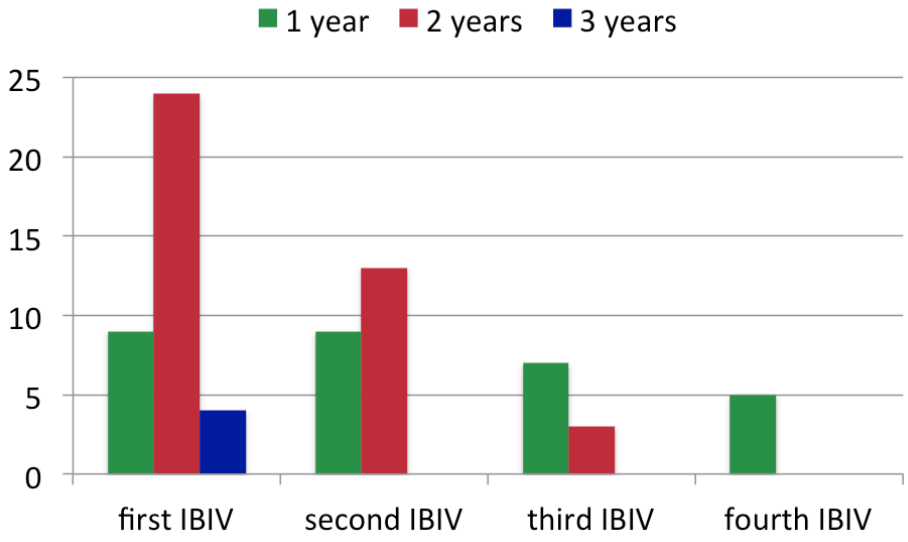


Figure 4.3: Number of one-year-Interbirth-Intervals (IBIV), two-year-IBIVs and three-year-IBIVs for each Interbirth Interval: between first offspring and the second, between the second and the third, the third and the fourth and between the fourth and the fifth offspring (N=74 interbirth intervals)

The mean interbirth interval was 1.65 years, but there revealed a difference of interbirth intervals with respect to parity (number of pregnancies or births, respectively). The interbirth interval in primiparous females (between first and second offspring) is greater than in multiparous females (between any further offspring). That means only 24.32% (9/37) of all primiparous females gave birth to their second offspring in the following year, while 64.86% (24/37) gave birth two years later again and 10.81% (4/37) actually paused for two birth seasons. However, in multiparous females a one-year interbirth interval was the most common. 56.76% (21/37) of all multiparous females gave birth to their next offspring in the following year and only 43.24% (16/37) paused for one birth season. There was no interbirth interval greater than two years in multiparous females. The difference between the interbirth intervals among primiparous and multiparous females was significant (Mann-Whitney's-U=430.5; N1=37, N2=37; p=0.002).

Moreover, primiparous females delivered their first offspring later in the year than any further offspring (see Figure 4.4) or in other words, first-borns tend to be born later in spring than their younger siblings.

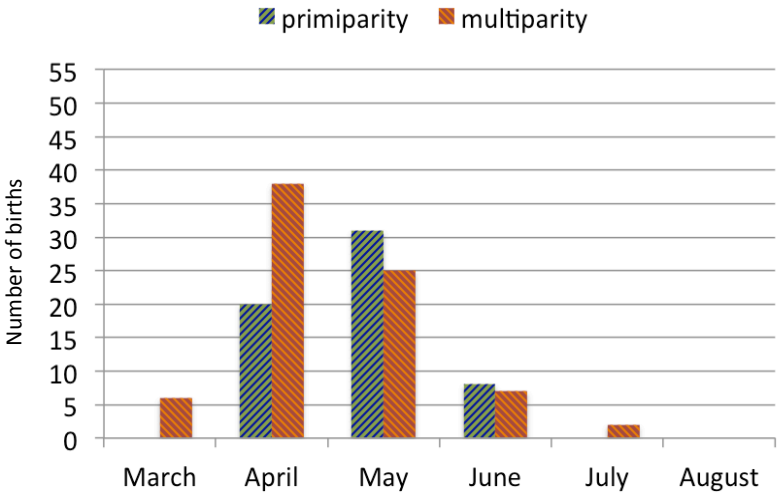


Figure 4.4: Comparison of the date of birth of first-borns (primiparity) and later-borns (multiparity) (N=137)

This difference is significant when birth months are compared (Mann-Whitney's -U=1770.5; N1=59, N2=78; p=0.013), but also when birth date is pulled up more precisely and months were divided into thirds (Mann-Whitney's-U=1619.5; N1=59, N2=78; p=0.003).

Concerning the offspring's sex, there seems to be no association between the length of the following interbirth interval and the sex of the offspring (chi-square=1.959; p=0.375; df=2). After the birth of sons the mean interbirth interval ± STD was 1.54 ± 0.532 years (N=57) and after the birth of daughters the mean interbirth interval ± STD was 1.68 ± 0.581 years (N=50) (compare Figure 4.5).

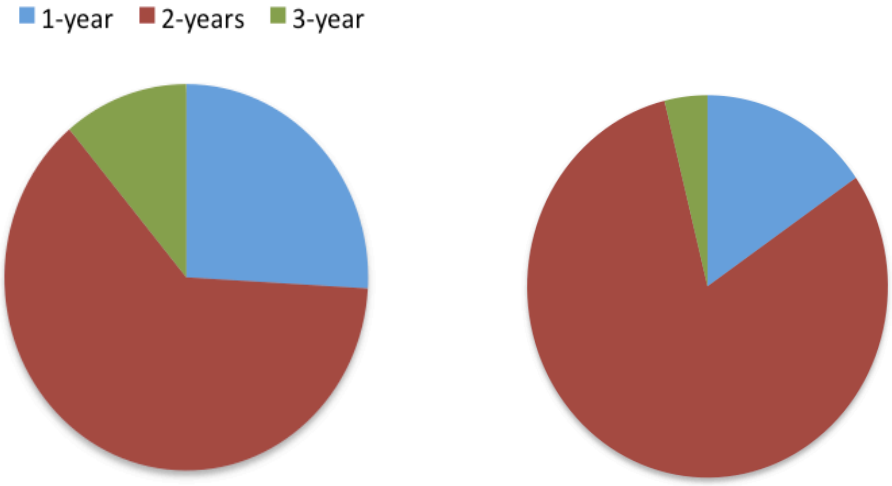


Figure 4.5: Length of interbirth intervals after the birth of daughters (left; N=50) and sons (right; N=57)

4.3. The influence of climatic factors on birth rates & timing

Temperature during mating seasons seems to influence the timing of consequent births (see Figure 4.6). There is a tendency towards earlier births after warmer mating seasons (Spearmen's-correlation-coefficient (CC)= -0.407; p=0.094).

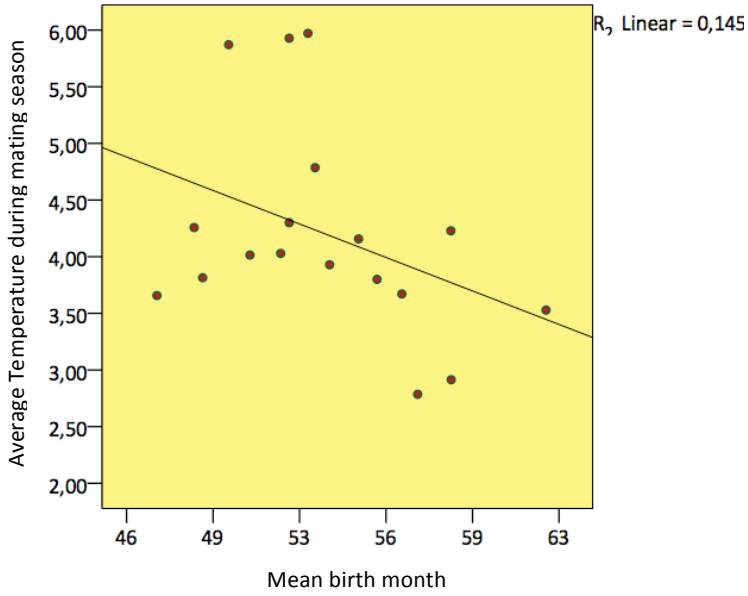


Figure 4.6: Association between temperatures during mating season (September to March) and birth timing (mean birth month in thirds, e.g. 46.6 = birth between 11th and 20th of April); CC= -0.407; p= 0.094; N=18 birth seasons

Regarding birth rates, throughout the years the number of births per season varied from one to 15 (see 3.3.2. Births). Due to sterilisation the group of potential mothers was kept quite small and stable (see Figure 4.7).

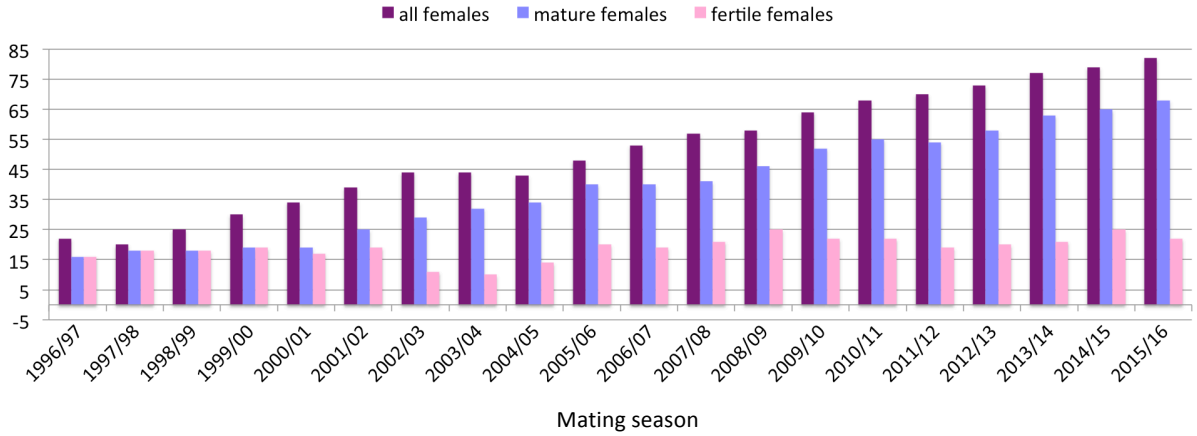


Figure 4.7: Number of all females, mature females and only fertile females (defined as mature and not sterilised) in the troop on September, the 1st, of each year

It should be mentioned that the birth rate could have been higher in each mating season, since some mature and not sterilised females (below mentioned as fertile females) paused for one, two or even more seasons. The percentage of fertile females, who paused, or in other words, who did not give birth although they were already mature, but not sterilised, varied throughout the years. In some years nearly every female, who potentially could have conceived, gave birth and in other years just one third of them.

More precisely the maximum was reached in the first birth season on the Affenberg Landskron in 1997 when only one offspring was born. That means 93.75% of all fertile females did not give birth in 1997. On the contrary a minimum of nearly two-thirds (63.64%) of all fertile females gave birth in 2003 (see Figure 4.8).

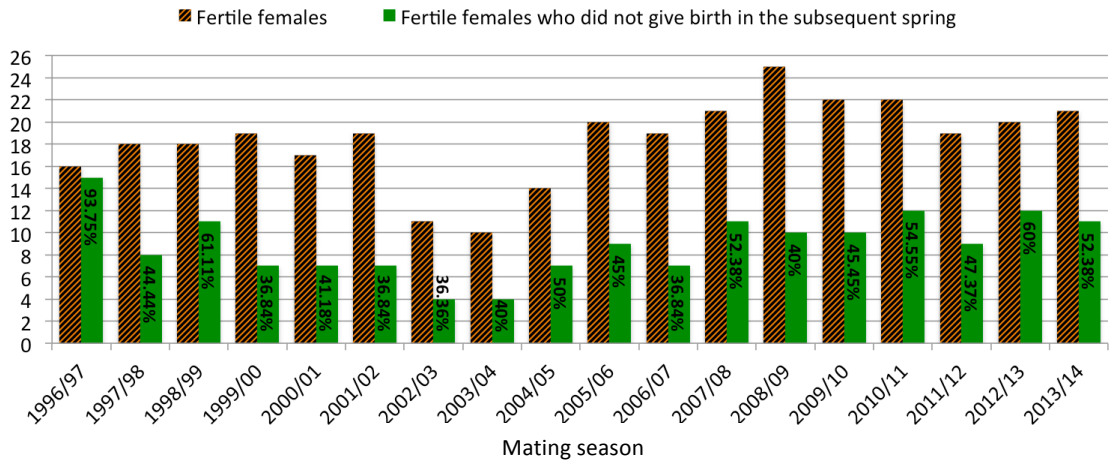


Figure 4.8: The number of fertile females in comparison to the number of fertile females, who gave not birth in the following spring/summer

To make an attempt at understanding and explaining this difference, diverse variables were taken into account. Besides demographic variables, climatic parameters were analysed. Neither the number of visitors in the park, nor nutrition was included in this analysis. Firstly, visitors become rare at the Affenberg Landskron after school holidays at the beginning of September. Additionally, from first of November to the end of March visitors are not allowed to enter the Affenberg, which covers for most of the mating seasons. Secondly, nutrition did not vary throughout the year. The animal care staff adjusted the food amount according to the group size and the type of food was kept stable (for details see section 3.2. Nutrition).

The only parameter that correlates significantly with the percentage of females who had been fertile during mating season, but still did not give birth in the subsequent spring/summer, is the sunshine duration (Spearmen's-correlation-coefficient (CC)=-0.545; p=0.019). The more hours the sun was shining during mating season (September, 1st to March, 31st), the greater was the proportion of fertile females who actually gave birth next year (see table 4.1). For further explanation of the other variables in table 4.1 and 4.2 see section 3.2. Data processing.

Table 4.1: Correlation between the proportion of fertile females who did not give birth and variable parameters of the previous mating seasons

		Group Size	Sex Ratio	Opera-tional Sex Ratio	Sex Ratio with fertile females only	Average Tempera-ture [°C]	Average Rain [mm]	Average Sun [h]	Average Tempera-ture weighted [°C]	Average Rain weighted [mm]	Average Sun weighted [h]
Percentage of fertile females who did not give birth	**CC**	0.215	0.224	0.160	0.137	-0.194	0.360	-0.545	0.070	0.249	-0.348
	p	0.392	0.372	0.525	0.589	0.441	0.142	0.019*	0.781	0.318	0.157

Some females may have been lactating as they gave birth in the previous year, but paused in the subsequent year. For that reason those females were excluded in the second analysis. Females who gave birth in two subsequent birth seasons were kept in the analysis, reasoning that they were surely not lactating during the mating season in between (see table 4.2). Again, sunshine duration was significantly correlated with the proportion of fertile and surely not lactating females who did not give birth (Spearmen's-correlation-coefficient (CC)=-0.542; p=0.02).

Table 4.2: Correlation between the proportion of fertile and surely not lactating females who did not give birth and variable parameters of the previous mating seasons

		Group Size	Sex Ratio	Operational Sex Ratio	Sex Ratio with fertile females only	Average Temperature [°C]	Average Rain [mm]	Average Sun [h]	Average Temperature weighted [°C]	Average Rain weighted [mm]	Average Sun weighted [h]
Percentage of fertile and surely not lactating females who did not give birth	CC	0.093	0.242	-0.337	0.071	-0.084	0.302	-0.542	-0.037	0.385	-0.454
	p	0.714	0.33	0.172	0.78	0.741	0.223	0.020*	0.883	0.114	0.059

4.4. Sex ratio

Sex ratio of births varied throughout the years - from 0.4 new-born males per new-born female in 1999 and 2005 to 9 new-born males per new-born female in 2008. Although, birth rate is associated with sunshine duration, the sex ratio of births is not linked to sunshine. However, there seems to be a connection between the sex ratio of the group during the mating season and the sex ratio of the new-borns in the consequent spring/summer. If there has been an overspill of males during the mating season, more daughters were born next

year and *vice versa*. Although this correlation is not significant (Spearmen's-correlation-coefficient=-0.352; N=18; p=0.152), there appears to be a tendency towards a balanced sex ratio in the group (see Figure 4.9). This does not apply when the operational sex ratio of the group (mature males per mature females) is used (Spearmen's-correlation-coefficient (CC)= -0.117; N=18; p=0.644). Also, such a trend is not observed when sex ratio of only fertile individuals (without sterilised females) is used (CC=-0.158; N=18; p=0.531).

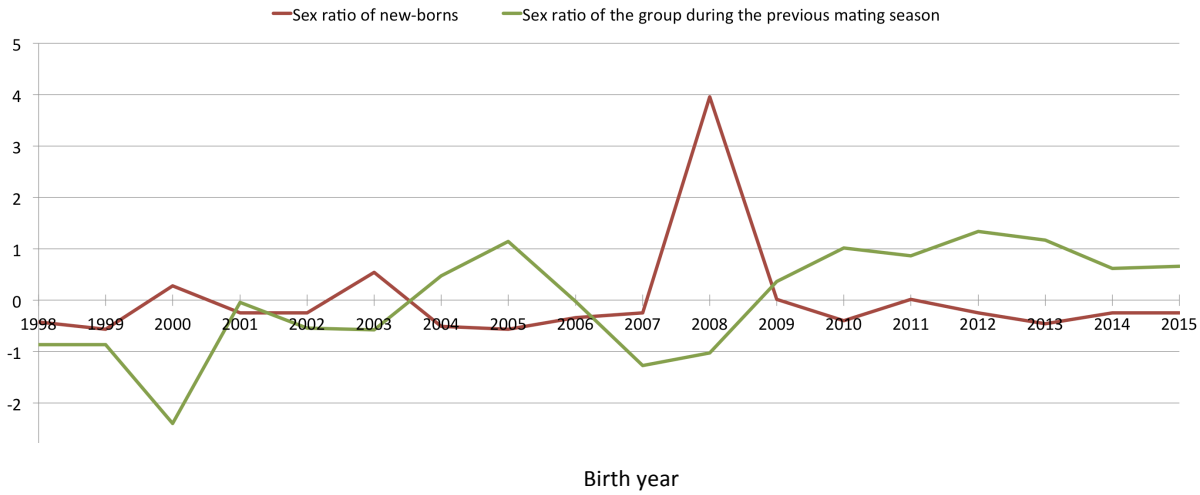


Figure 4.9: Comparison of the sex ratio of new-born offspring during one mating season (red; z-transformed) and the sex ratio of the whole group (green) during the previous mating season

5 DISCUSSION

The aim of this thesis was to achieve an extensive understanding of the dynamic and reproductive performance of a semi-free ranging troop of Japanese macaques at the Affenberg Landskron. Reproductive features – such as birth timing, interbirth intervals and birth rates – were analysed, also whether they are associated with demographic or climatic factors.

On the one hand some of these parameters have been previously investigated in other Japanese macaque troops – e.g. general patterns of female reproduction, such as maternal age, interbirth intervals and parity. Consequently I wanted to compare those parameters in this group at the Affenberg with previous literature and especially with data from free-ranging troops of Japanese macaques.

On the other hand some parameters have received little attention so far. Sunshine duration, for example has been hardly investigated with regard to reproduction. Since Japanese macaques are the northern most living non-human primates and the temperature drops regularly to minus degrees during their mating season, it may be challenging to bring up required costs for thermoregulation and mating behaviour. All the more interesting are the findings of this thesis.

What I found in all brevity:

(i) Regarding general patterns of female reproduction I found that, interbirth intervals after first-borns are greater than after any later born offspring. Furthermore, first-borns tend to be born later in the year than any later-born offspring.

(ii) Concerning the influence of climatic factors on the birth rate and timing, two findings are noteworthy. Firstly, after warmer mating seasons there seems to be a tendency towards earlier births. And secondly, sunshine duration appears to influence the birth rate greatly. The more sunshine hours were recorded during the previous mating season, the greater was the proportion of fertile females who actually gave birth in the subsequent birth season. In other words, sunshine during fall/winter seemed to higher the probability to receive an offspring in the following spring/summer.

(iii) In terms of the sex ratio of new-borns, an association to the sex ratio of the whole group during the previous mating season has been recognized. If there has been an overspill of males during the mating season, more daughters were born next year and *vice versa*. This points to a trend towards a balanced sex ratio of the troop.

Our findings regarding general patterns of female reproduction go along with previous studies. In contrast the influence of sunshine duration went unnoticed so far. Likewise our results regarding the sex ratio of the group, which seems to be balanced by the sex ratio of subsequent births has not been reported in this species.

5.1. General pattern of female reproduction

First of all, it goes without saying that the selection of the parameters has been dependent on the fact that sterilisations have been carried out. Since females usually were sterilised in early years after they have given birth at least once, some reproductive parameters could not be investigated in the present thesis. Those parameters are, for example, age-specific fecundity, post-reproductive life span, reproductive success or rank-association differences of reproductive performance. No female was older than twelve years at any birth. This goes along with the fact, that the oldest females were twelve at their sterilisation. However, in other provisioned troops of Japanese macaques the highest birth rates were recorded between an age of five and 19 years. In these troops birth rates decreased rapidly above an age of 20 (Koyama et al., 1992; Itoigawa et al., 1992).

In contrast, the age at first birth could have been investigated. In this regard, differences arose in the Austrian group under investigation compared to other provisioned troops. According to Koyama et al. (1992) four-year-old females accounted for merely six per cent of all recorded first births, whereas more than half of all first-born infants had a five-year-old mother. Similar findings have been revealed by Itoigawa et al. (1992). It is commonly known, that improved nutritional conditions can decrease the age of primiparity (Mori, 1979; Sugiyama & Ohsawa, 1982; Watanabe et al., 1992; Mori et al., 1997). However, in two troops investigated by Itoigawa et al. (1992) and Koyama et al. (1992) four-year-old females rarely bared offspring irrespective of provision. In accordance, most females of the troop in Landskron were five years at their first birth. However, the percentage of four-year-old primipara was much higher. At the first birth 50% of all mothers were five years old, but still, 39.3% were four years old. Since miscarriages and stillbirths were not included in this analysis, this is even more remarkable. At this point, however, it should be mentioned, that the troops investigated by Koyama et al. (1992) and Itoigawa et al. (1992) were free-ranging. Maybe additional stress factors made the difference, such as predators or the intrusion of non-troop members.

Still, the young age of primipara in this troop at the Affenberg Landskron is striking. Particularly since five- to nine-year-old females might have a higher risk to experience stillbirths or miscarriages (Koyama et al., 1992). Both are hard to recognize in the wild and in semi-free troops. It cannot be assumed that the documentation of stillbirths was complete

at the Affenberg, not to mention miscarriages. Hence, with an age of only four years nearly four out of ten females managed to successfully maintain a pregnancy and raise a child for at least six months. This leads to the assumption that the living conditions are favourable at the Affenberg Landskron.

In general, interbirth intervals in provisioned troops of free-ranging Japanese macaques are usually shorter than in unprovisioned troops. For example Takahashi (2002b) documented a mean interbirth interval of 25.1 months in an unprovisioned troop, while Itoigawa et al. (1992) found a mean interbirth interval of 18.7 months in a provisioned troop. In another provisioned troop investigated by Koyama et al. (1992) a one-year interval was most common, whereas interbirth intervals of four years or more were rare. This is in line with findings revealed from the troop at the Affenberg Landskron: The interval between two births has never been greater than three years. Still, the most common interval was a two-year interval (54.05%), followed by a one-year-interval (40.54%). Also the mean interbirth interval of 1.65 years or 19.8 months is consistent with previous findings in provisioned troops, but shorter than in unprovisioned troops. These findings are less surprising given the fact that improved nutritional conditions can improve reproductive performance of females, i.e. higher birth rates, decreased infant mortality, an earlier onset of puberty and a lower primiparous age (e.g.: Watanabe et al., 1992; Mori et al., 1997; Takahata et al., 1998).

As described in other studies (Koyama et al., 1992; Itoigawa et al., 1992) an association between parity and the length of interbirth intervals was found in the investigated troop. While a one-year-interval occurred in more than half of all multiparous females, only every fourth primiparous female gave birth to their second offspring in the following year.

The offspring's sex does not explain differences of interbirth intervals. This is in contrast to Takahata et al.'s (1995) findings. Age, also, is assumed to have little impact on interbirth intervals, because females were sterilised in about the same age and relatively young, considering that fecundity remains high until an age of 19 (Koyama et al., 1992; Itoigawa et al., 1992).

Besides, parity seemed to influence the timing of births. First-borns tend to be born later in spring than their younger siblings. The birth timing of multiparous females peaked in middle and late April, while most primiparous gave birth between the end of April and the end of

May. Koyama et al.'s (1992) findings are consistent as long as multiparous females who had not given birth in the previous year are considered. Those females give birth earlier, which means in early May. Females with an infant from the previous year did not receive their young earlier than primiparous females. Taking all births at the Affenberg into accounts, whether or not mothers came from Japan, births peaked in late April (34/180), followed by mid May (26/180) and mid April (25/180). However, it is striking, that females at the Affenberg gave birth earlier than those in the troop described by Itoigawa et al. (1992) and Koyama et al. (1992). Although climate is similar in Landskron, Austria, and Kyoto prefecture, Japan, the latitude is different (Landskron: 46.64°/Kyoto: 35°). There is a tendency, described by Fooden & Aimi (2005), towards earlier births as latitude increases. This may serve to maximize the time for infants before the onset of the following winter to reach a sufficient level of development. Consistently, in a captive troop of Japanese macaques in the Rome zoo, where the temperature during the winter was warmer and thus not as challenging as in Japan and Austria, the mean birth date was the 26th of July (Cozzolino & Schino, 1998). Additionally photoperiod strongly varies along latitude. This may explain those variations, although previous studies resulted in conflicting results regarding the association between birth timing and latitude or photoperiod, respectively (e.g.: Varley & Vessey, 1977; Cozzolino et al., 1992; Gouzoules et al., 1981; Fooden & Aimi, 2003; Fooden & Aimi, 2005). Another causation for earlier births at the Affenberg compared to other provisioned, but free-ranging troops could be that, females may physiologically benefit from lowered stress levels due to the absence of predators and/or the lack of intrusion of non-troop members.

5.2. The influence of climatic factors on birth rates & timing

In the wild food availability is closely linked to climate. Under provisioned conditions nutrition can be kept stable throughout the year. Differences of reproductive performance of females therefore are in all probability not explained by nutritional variations. Thus, provisioning provides the advantage to investigate climatic impacts on reproductive features without any bias caused by food availability.

Many studies compared variation of birth seasons between different troops, but hardly any study investigated fluctuations within one troop. Cozzolino & Schino (1998) found no

association between the mean birth date and the mean temperature during fall and winter in a captive troop of Japanese macaques in the Rome zoo. But in great contrast to the troop at the Affenberg Landskron the temperature in Rome was much warmer, and therefore not similarly challenging. It ranged between 9.6°C and 13°C in Rome, while in Landskron the mean temperature ranged between 2.8°C and 6°C. Maybe this difference explains why birth dates and mean temperatures during mating seasons seem to be associated in Landskron, but not in Rome. After warmer mating seasons there is a tendency towards earlier births in Landskron. In contrast Cozzolino et al. (1992) described a positive correlation between temperature during fall and winter and birth dates in a comparative study of 25 Japanese macaque troops. However, considering that thermoregulation during cold winter periods demands high energetic costs, it might be more challenging to require additional energy for gestation. Hence, it becomes plausible, that births are delayed after cold winter periods.

Besides temperature, a striking impact of sunshine on the reproductive performance of females was found. The more hours the sun was shining throughout the mating season, the more fertile females gave birth in the subsequent birth season. Those who were sterilised were not included in this analysis. This positive correlation is significant whether or not potentially lactating females were included. So far not enough data has been available to illuminate this association entirely. However, it can be assumed that sunshine duration during fall and winter influences reproductive patterns in a primate species that has to cope with exceptional low temperatures during gestation periods. Sun is an important energy supplier and by sunbathing energy for thermoregulation may be saved. Additionally, the sun is also important for intrauterine development.

Further, it is known, that physiological costs of thermoregulation can be lowered by behaviour, such as huddling, adjustment of posture, reducing activity to save energy or sunbathing. This behavioural thermoregulation has been described for various mammals (e.g.: Japanese macaques: Schino & Troisi, 1990; Hanya, 2004; Yellow baboons: Stelzner & Hausfater, 1986; ring-tailed lemurs: Kelly et al., 2016; vervet monkeys: Danzy et al., 2012). For Japanese macaques the following has been reported so far: Firstly, when temperatures are low, their body postures are more curled. And secondly, they prefer sunbathing above huddling, when the sun is shining (Hanya et al., 2007). These findings are consistent with observations (not documented) on the Affenberg in Landskron. During cold winter periods

they sat upright and stretched their underside towards the sun. They seem to maximize the area exposed to the sun (Figure 5.1.). In this posture the skin of the underside is clearly visible, leading to the assumption that their pelage is lighter in this region than on back and side, where the skin is not so readily apparent. This may also be an explanation for their curled body posture under cold conditions. Besides their stretching behaviour towards the sun and their permeable fur on the abdominal region, their skin on the underside is in places dark (Figure 5.1).

Figure 5.1: Sun exposure behaviour of the investigated troop during wintertime

Here is to note that these assumptions are solely based on routine daily observations and have not been investigated on the Affenberg so far. The findings in the present thesis, however, are calling for a consideration of the interplay between sun duration, stretching behaviour and anatomical as well as physiological features in future investigations. In general, there is not enough evidence available to get the full picture, but there are important pieces provided by previous investigations. Danzy et al. (2012) for example described that vervet monkeys tend to sunbath more on mornings after cooler nights than after warmer nights. Further Hanya et al. (2007) proposed that the increment of skin temperature is higher after sunbathing than after huddling in Japanese macaques. In the

group at the Affenberg Landskron sunshine hours are positive correlated with the percentage of females who received a young in the following birth season. This association becomes even more notable, since sunshine is usually highly correlated to rainfall. When it rains, the sun does usually not shine and *vice versa*. However, there was no significant association between rainfall and the percentage of females who received a young. This suggests that the sun is decisive. Besides, other factors like visitor numbers or nutrition could not have an influence, since the Affenberg is closed for visitors during wintertime and nutrition has been kept stable throughout the years.

Taking all those evidence together, sunbathing might have an energetic effect that is not negligible. Thus, sunshine seems to have an impact on reproductive performance in female Japanese macaques. In the present study data from 18 years were analysed, which is not sufficient to give a clear view, but the observed association is noteworthy and requires further investigation.

Furthermore, in humans Waldie et al. (2000) found that pre-natal sunlight affects body height at birth. This is verisimilar, since vitamin D, which is primarily derived from sun exposure, is crucial for the skeletal development (Pasco et al., 2008). Vitamin D statuses of mothers during gestation periods therefore seem to affect bone growth and mineralisation of the infant. Additionally, intrauterine vitamin D levels seem to have an impact on muscle development. There is also evidence to assume that an insufficiency of intrauterine vitamin D may cause a variety of other diseases later in life – e.g. cardiovascular and autoimmune diseases (Pasco et al., 2008). However, Pasco et al. (2008) concluded that maternal vitamin D supply is crucial for the offspring's growth and development. This is another evidence of how important the sun is during gestation.

Regarding the weather data *per se*, the weather station is merely 3.5 kilometres away from the Affenberg Landskron as the crow flies. Therefore, it cannot be assumed that the sunshine hours differed strongly. Besides, the weather station is located 141 metres below the Affenberg. Although it can therefore be assumed that the average temperature is slightly lower on the Affenberg than at the weather station, the fluctuations should be the same.

5.3. Sex ratio

Trivers & Willard (1973) supposed that a mother invests comparatively more in sons or more in daughters, in order to maximize her own lifetime reproductive success and this is influenced by her physical condition. Since males can potentially produce much more offspring, females in polygynous species who can physiologically afford, should bias their investment towards sons (Gomendio, 1990). This bias may already be manifested intrauterine – e.g. miscarriages or stillbirths – or postnatal – e.g. abandoning offspring.

In seasonal breeding species, females could experience increased intrasexual competition among mating partners, if the sex ratio of the group is skewed. For example Ménard & Vallet (1993: unpublished data, compare Thierry et al., 2004) described a very high level of sexual competition among females in a troop of Barbary macaques consisting of only one male, but five females. This male was not able to monopolize all females during mating season. Consequently, after only one year, this group reached a balanced sex ratio through immigration of foreign males. Ménard (in Thierry et al., 2004) concluded that the composition of a troop could result from a trade-off between two different strategies of females: to maximize access to food on the one hand and to maximize access to mating partners on the other hand.

As already mentioned nutrition may not play a crucial role at the Affenberg, since it has been kept stable through provisioning. Regarding the competition for access to males: The troop of Japanese macaques at the Affenberg Landskron lived semi-free. Immigration of foreign males was therefore not possible and becomes likewise negligible as an influencing variable in terms of the groups' sex ratio. Dispersal, as described by Silk & Brown (2008), may not play a decisive role in this troop for the same reason.

The only individuals, who were new to the troop, were the new-borns. So, apart from deaths, new-borns are crucial for the sex ratio of the entire troop. The impact of new-borns of a current season on the whole groups' sex ratio became smaller of course, as the group size increased. This was because the number of births did not increase proportionally to the group size, since sterilisations were practiced. For that reason z-transformations were operated. The correlation between the sex ratio of the entire troop during the previous mating season and the sex ratio of all births during the following birth season was not

significant. Still, there is a noteworthy trend apparent, that calls for future investigation. It might be a successful strategy of the investigated troop to counterbalance the troops' sex ratio via 1:1 through the sex ratio of subsequent births.

6 CONCLUSIO & OUTLOOK

The importance of climatic, demographic and life-history variables should not be undervalued for reproductive parameters in primates. The present thesis contributes to a better understanding of these parameters, also in relationship to evolutionary processes and individual behaviour. In this study 19-year data on various reproductive, demographic and climatic parameters of female Japanese macaques were analysed to achieve an extensive understanding of the troops' dynamic and reproductive performance. On the one hand this study succeeded to gain important insights for the Affenberg itself. Improved reproductive performance of females at the Affenberg compared to other semi-free ranging troops and wild troops argue for good living conditions.

On the other hand it was possible to reveal new associations in reproductive issues of Japanese macaques. The sex ratio of the entire group may influence the sex ratio of the births and increased sunshine duration seems to higher the probability of females to receive a young. Both necessarily need to remain observed in the coming years and both need to be under further investigation. Monitoring of behaviour is required to analyse for instance under which condition Japanese macaques prefer sunbathing above huddling or whether there appear sex differences or not. If these relationships are clear, one can get a more complete impression of the importance of sun exposure for Japanese macaques. Further physiological studies may be necessary to analyse energetic benefits.

REFERENCES

Barrett, G.M., Shimizu, K., Bardi, M., Asaba, S., Mori, A., 2002. Endocrine Correlates of Rank, Reproduction, and Female-Directed Aggression in Male Japanese Macaques (Macaca fuscata). Hormones and Behavior 42, 85–96. doi:10.1006/hbeh.2002.1804

Bercovitch, F.B., Lebron, M.R., Martinez, H.S., Kessler, M.J., 1999. Primigravidity, body weight, and costs of rearing first offspring in rhesus macaques. American Journal of Primatology 46, 135–144. doi:10.1002/(SICI)1098-2345(1998)46:2<135::AID-AJP3>3.0.CO;2-X

Bercovitch, F.B., Widdig, A., Trefilov, A., Kessler, M.J., Berard, J.D., Schmidtke, J., Nürnberg, P., Krawczak, M., 2003. A longitudinal study of age-specific reproductive output and body condition among male rhesus macaques, Macaca mulatta. Naturwissenschaften 90, 309–312. doi:10.1007/s00114-003-0436-1

Blomquist, G.E., Sade, D.S., Berard, J.D., 2010. Rank-Related Fitness Differences and Their Demographic Pathways in Semi-Free-Ranging Rhesus Macaques (Macaca mulatta). Int J Primatol 32, 193–208. doi:10.1007/s10764-010-9461-z

Bongaarts, J., 1980. Does malnutrition affect fecundity? A summary of evidence. Science 208, 564–569. doi:10.1126/science.7367878

Bowman, J.E., Lee, P.C., 1995. Growth and threshold weaning weights among captive rhesus macaques. Am. J. Phys. Anthropol. 96, 159–175. doi:10.1002/ajpa.1330960205

Brown, G.R., 2001. Sex-biased investment in nonhuman primates: can Trivers & Willard's theory be tested? Animal Behaviour 61, 683–694. doi:10.1006/anbe.2000.1659

Brown, G.R., Silk, J.B., 2002. Reconsidering the null hypothesis: Is maternal rank associated with birth sex ratios in primate groups? PNAS 99, 11252–11255. doi:10.1073/pnas.162360599

Catchpole, H.R., Van Wagenen, G., 1975. Reproduction in the rhesus monkey, Macaca mulatta. The rhesus monkey 2, 117–140.

Charpentier, M.J.E., Tung, J., Altmann, J., Alberts, S.C., 2008. Age at maturity in wild baboons: genetic, environmental and demographic influences. Mol. Ecol. 17, 2026–2040. doi:10.1111/j.1365-294X.2008.03724.x

Chatani, K., 2003. Positional behavior of free-ranging Japanese macaques (Macaca fuscata). Primates 44, 13–23. doi:10.1007/s10329-002-0002-z

Cheney, D.L., Lee, P.C., Seyfarth, R.M., 1981. Behavioral correlates of non-random mortality among free-ranging female vervet monkeys. Behav Ecol Sociobiol 9, 153–161. doi:10.1007/BF00293587

Cozzolino, R., Cordischi, C., Aureli, F., Scucchi, S., 1992. Environmental temperature and reproductive seasonality in Japanese macaques (Macaca fuscata). Primates 33, 329–336. doi:10.1007/BF02381194

Cozzolino, R., Schino, G., 1998. Group Composition Affects Seasonal Birth Timing in Captive Japanese Macaques. International Journal of Primatology 19, 857–866. doi:10.1023/A:1020345413644

Danzy, J., Grobler, J.P., Freimer, N., Turner, T.R., 2012. Sunbathing: a behavioral response to seasonal climatic change among South African vervet monkeys (Chlorocebus aethiops). African Primates 7, 230–237.

Drickamer, L.C., 1974. A Ten-Year Summary of Reproductive Data for Free-Ranging <i>Macaca mulatta</i> Folia Primatologica 21, 61–80. doi:10.1159/000155596

Dunbar, R.I.M., 1987. Demography and reproduction.

Enomoto, T., 1974. The sexual behavior of Japanese monkeys. Journal of Human Evolution 3, 351–372. doi:10.1016/0047-2484(74)90198-5

Fedigan, L., Griffin, L., 1996. Determinants of reproductive seasonality in Japanese macaques, in: Evolution and Ecology of Macaque Societies. Cambridge University Press, Cambridge, pp. 368–387.

Fedigan, L.M., 1983. Dominance and reproductive success in primates. American Journal of Physical Anthropology 26, 91–129.

Fedigan, L.M., Fedigan, L., Gouzoules, S., Gouzoules, H., Koyama, N., 1986. Lifetime Reproductive Success in Female Japanese Macaques. Folia Primatologica 47, 143–157. doi:10.1159/000156271

Fisher, R.A., 1930. The Genetical Theory of Natural Selection: A Complete Variorum Edition. OUP Oxford.

Fooden, J., Aimi, M., 2005. Systematic Review of Japanese Macaques, Macaca fuscata. Fieldiana Zoology 1–198. doi:10.3158/0015-0754(2005)104[1:SROJMM]2.0.CO;2

Fooden, J., Aimi, M., 2003. Birth-season variation in Japanese macaques, Macaca fuscata. Primates 44, 109–117. doi:10.1007/s10329-002-0011-y

Fujita, S., Sugiura, H., Mitsunaga, F., Shimizu, K., 2004. Hormone profiles and reproductive characteristics in wild female Japanese macaques (Macaca fuscata). Am. J. Primatol. 64, 367–375. doi:10.1002/ajp.20086

Fukuda, F., 1982. Relationship between age and troop shifting in male Japanese monkeys. Japanese Journal of Ecology 32, 491–498.

Geissmann, T., 2003. Vergleichende Primatologie, Springer-Lehrbuch. Springer Berlin Heidelberg, Berlin, Heidelberg.

Giacobbe, M., Pinto-Neto, A.M., Costa-Paiva, L.H.S., Martinez, E.Z., 2004. Ovarian volume, age, and menopausal status. Menopause 11, 180–185.

Gibbs, R.A., Rogers, J., Katze, M.G., Bumgarner, R., Weinstock, G.M., Mardis, E.R., Remington, K.A., Strausberg, R.L., Venter, J.C., Wilson, R.K., others, 2007. Evolutionary and biomedical insights from the rhesus macaque genome. Science 316, 222–234.

Gomendio, M., 1990. The influence of maternal rank and infant sex on maternal investment trends in rhesus macaques: birth sex ratios, inter-birth intervals and suckling patterns. Behav Ecol Sociobiol 27, 365–375. doi:10.1007/BF00164008

Gouzoules, H., Gouzoules, S., Fedigan, L., 1981. Japanese monkey group translocation: Effects on seasonal breeding. Int J Primatol 2, 323–334. doi:10.1007/BF02693482

Griffin, A.S., Sheldon, B.C., West, S.A., Crespi, A.E.B.J., Whitlock, E.M.C., 2005. Cooperative Breeders Adjust Offspring Sex Ratios to Produce Helpful Helpers. The American Naturalist 166, 628–632. doi:10.1086/491662

Hamada, K., Suginami, H., Matsuura, S., 1989. [Changes in plasma estradiol, progesterone and LH level in the menstrual cycle of the adult female Japanese monkey during the mating season]. Jikken Dobutsu 38, 187–194.

Hamada, Y., Hayakawa, S., Suzuki, J., Watanabe, K., Ohkura, S., 2003. Seasonal variation in the body fat of Japanese macaques *Macaca fuscata*. Mammal Study 28, 79–88. doi:10.3106/mammalstudy.28.79

Hamada, Y., Watanabe, T., Iwamoto, M., 1996. Morphological variations among local populations of Japanese macaque (Macaca fuscata), in: Variations in the Asian Macaques. Tokai University Press, pp. 97–115.

Hanya, G., 2014. Japanese Macaques: Habitat-Driven Divergence in Social Dynamics, in: Yamagiwa, J., Karczmarski, L. (Eds.), Primates and Cetaceans, Primatology Monographs. Springer Japan, pp. 99–114.

Hanya, G., 2004. Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: Effects of food and temperature. Am. J. Primatol. 63, 165–177. doi:10.1002/ajp.20049

Hanya, G., 2003. Age differences in food intake and dietary selection of wild male Japanese macaques. Primates 44, 333–339. doi:10.1007/s10329-003-0047-7

Hanya, G., Kiyono, M., Hayaishi, S., 2007. Behavioral thermoregulation of wild Japanese macaques: comparisons between two subpopulations. Am. J. Primatol. 69, 802–815. doi:10.1002/ajp.20397

Hanya, G., Zamma, K., Hayaishi, S., Yoshihiro, S., Tsuriya, Y., Sugaya, S., Kanaoka, M.M., Hayakawa, S., Takahata, Y., 2005. Comparisons of food availability and group density of Japanese macaques in primary, naturally regenerated, and plantation forests. Am. J. Primatol. 66, 245–262. doi:10.1002/ajp.20142

Harcourt, A.H., 1987. Dominance and fertility among female primates. Journal of Zoology 213, 471–487. doi:10.1111/j.1469-7998.1987.tb03721.x

Hawkes, K., 2004. Human longevity: The grandmother effect. Nature 428, 128–129. doi:10.1038/428128a

Hawkes, K., O'Connell, J.F., Jones, N.G.B., Alvarez, H., Charnov, E.L., 1998. Grandmothering, menopause, and the evolution of human life histories. PNAS 95, 1336–1339.

Hayakawa, S., 2008. Male–female mating tactics and paternity of wild Japanese Macaques (Macaca fuscata yakui). Am. J. Primatol. 70, 986–989. doi:10.1002/ajp.20580

Hill, D.A., 1997. Seasonal variation in the feeding behavior and diet of Japanese macaques (Macaca fuscata yakui) in lowland forest of Yakushima. Am. J. Primatol. 43, 305–322. doi:10.1002/(SICI)1098-2345(1997)43:4<305::AID-AJP2>3.0.CO;2-0

Hill, D.A., Okayasu, N., 1995. Absence of "Youngest Ascendancy" in the Dominance Relations of Sisters in Wild Japanese Macaques (Macaca fuscata yakui). Behaviour 132, 367–379.

Hiraiwa, M., 1981. Maternal and alloparental care in a troop of free-ranging Japanese monkeys. Primates 22, 309–329. doi:10.1007/BF02381573

Huffman, M.A., 1992. Influences of Female Partner Preference on Potential Reproductive Outcome in Japanese Macaques. Folia primatologica; international journal of primatology 59, 77–88. doi:10.1159/000156645

Huffman, M.A., 1987. Consort Intrusion and Female Mate Choice in Japanese Macaques (Macaca fuscata). Ethology 75, 221–234. doi:10.1111/j.1439-0310.1987.tb00655.x

Inoue, E., Takenaka, O., 2008. The effect of male tenure and female mate choice on paternity in free-ranging Japanese macaques. Am. J. Primatol. 70, 62–68. doi:10.1002/ajp.20457

Inoue, M., 1995. Application of paternity discrimination by DNA polymorphism to the analysis of the social behavior of primates. Hum. Evol. 10, 53–62. doi:10.1007/BF02437514

Inoue, M., Mitsunaga, F., Nozaki, M., Ohsawa, H., Takenaka, A., Sugiyama, Y., Shimizu, K., Takenaka, O., 1993. Male dominance rank and reproductive success in an enclosed group of Japanese macaques: with special reference to post-conception mating. Primates 34, 503–511. doi:10.1007/BF02382661

Inoue, M., Takenaka, A., Tanaka, S., Kominami, R., Takenaka, O., 1990. Paternity discrimination in a Japanese macaque group by DNA fingerprinting. Primates 31, 563–570. doi:10.1007/BF02382539

Itoigawa, N., Negayama, K., Kondo, K., 1981. Experimental study on sexual behavior between mother and son in Japanese monkeys (Macaca fuscata). Primates 22, 494–502. doi:10.1007/BF02381241

Itoigawa, N., Tanaka, T., Ukai, N., Fujii, H., Kurokawa, T., Koyama, T., Ando, A., Watanabe, Y., Imakawa, S., 1992. Demography and reproductive parameters of a free-ranging group of Japanese macaques (Macaca fuscata) at Katsuyama. Primates 33, 49–68. doi:10.1007/BF02382762

Izumiyama, S., Mochizuki, T., Shiraishi, T., 2003. Troop size, home range area and seasonal range use of the Japanese macaque in the Northern Japan Alps. Ecol Res 18, 465–474. doi:10.1046/j.1440-1703.2003.00570.x

Kawamura, S., 1958. The matriarchal social order in the minoo-B Group. Primates 1, 149–156. doi:10.1007/BF01813701

Kelley, E.A., Jablonski, N.G., Chaplin, G., Sussman, R.W., Kamilar, J.M., 2016. Behavioral thermoregulation in Lemur catta: The significance of sunning and huddling behaviors. Am. J. Primatol. n/a–n/a. doi:10.1002/ajp.22538

Koyama, N.F., 2003. Matrilineal Cohesion and Social Networks in Macaca fuscata. International Journal of Primatology 24, 797–811. doi:10.1023/A:1024676705433

Koyama, N., Takahata, Y., Huffman, M.A., Norikoshi, K., Suzuki, H., 1992. Reproductive parameters of female Japanese macaques: Thirty years data from the arashiyama troops, Japan. Primates 33, 33–47. doi:10.1007/BF02382761

Kraemer, S., 2000. The fragile male. BMJ 321, 1609–1612.

Kuester, J., Paul, A., Arnemann, J., 1995. Age-related and individual differences of reproductive success in male and female barbary macaques (Macaca sylvanus). Primates 36, 461–476. doi:10.1007/BF02382869

Kurita, H., Shimomura, T., Fujita, T., 2002. Temporal Variation in Japanese Macaque Bodily Mass. International Journal of Primatology 23, 411–428. doi:10.1023/A:1013895830970

Kutsukake, N., 2000. Matrilineal rank Inheritance varies with absolute rank in Japanese macaques. Primates 41, 321–335. doi:10.1007/BF02557601

MacDonald Pavelka, M.S., Fedigan, L.M., Zohar, S., 2002. Availability and adaptive value of reproductive and postreproductive Japanese macaque mothers and grandmothers. Animal Behaviour 64, 407–414. doi:10.1006/anbe.2002.3085

Marmi, J., Bertranpetit, J., Terradas, J., Takenaka, O., Domingo-Roura, X., 2004. Radiation and phylogeography in the Japanese macaque, Macaca fuscata. Molecular Phylogenetics and Evolution 30, 676–685. doi:10.1016/S1055-7903(03)00247-1

Mitani, J.C., Call, J., Kappeler, P.M., Palombit, R.A., Silk, J.B., 2012. The Evolution of Primate Societies. University of Chicago Press.

Mori, A., 1979. Analysis of population changes by measurement of body weight in the Koshima troop of Japanese monkeys. Primates 20, 371–397. doi:10.1007/BF02373390

Mori, A., Yamaguchi, N., Watanabe, K., Shimizu, K., 1997. Sexual Maturation of Female Japanese Macaques Under Poor Nutritional Conditions and Food-Enhanced Perineal Swelling in the Koshima Troop. International Journal of Primatology 18, 553–579. doi:10.1023/A:1026363206561

Muroyama, Y., Kanamori, H., Kitahara, E., 2006. Seasonal variation and sex differences in the nutritional status in two local populations of wild Japanese macaques. Primates 47, 355–364. doi:10.1007/s10329-006-0184-x

Nakamichi, M., Onishi, K., Yamada, K., 2010. Old grandmothers provide essential care to their young granddaughters in a free-ranging group of Japanese monkeys (Macaca fuscata). Primates 51, 171–174. doi:10.1007/s10329-009-0177-7

Nigi, H., 1975. Menstrual cycle and some other related aspects of Japanese monkeys (Macaca fuscata). Primates 16, 207–216. doi:10.1007/BF02381418

Nigi, H., Hayama, S., Torii, R., 1990. Copulatory behavior unaccompanied by ovulation in the Japanese monkey (Macaca fuscata). Primates 31, 243–250. doi:10.1007/BF02380945

Nozaki, M., Mitsunaga, F., Shimizu, K., 1995. Reproductive senescence in female Japanese monkeys (Macaca fuscata): age- and season-related changes in hypothalamic-pituitary-ovarian functions and fecundity rates. Biol. Reprod. 52, 1250–1257.

Nozaki, M., Mori, Y., Oshima, K., 1990. Effects of Artificial Manipulation of Photoperiod on Reproductive Seasonality of the Female Japanese Monkey. The Japanese journal of animal reproduction 36, 219–223. doi:10.1262/jrd1977.36.219

Ostner, J., Nunn, C.L., Schülke, O., 2008. Female reproductive synchrony predicts skewed paternity across primates. Behavioral Ecology 19, 1150–1158. doi:10.1093/beheco/arn093

Overduin-De Vries, A. m., Massen, J. j. m., Spruijt, B. m., Sterck, E. h. m., 2012. Sneaky Monkeys: An Audience Effect of Male Rhesus Macaques (Macaca mulatta) on Sexual Behavior. Am. J. Primatol. 74, 217–228. doi:10.1002/ajp.21988

Pasco, J.A., Wark, J.D., Carlin, J.B., Ponsonby, A.-L., Vuillermin, P.J., Morley, R., 2008. Maternal vitamin D in pregnancy may influence not only offspring bone mass but other aspects of musculoskeletal health and adiposity. Medical Hypotheses 71, 266–269. doi:10.1016/j.mehy.2008.01.033

Paul, A., Kuester, J., 1990. Adaptive significance of sex ratio adjustment in semifree-ranging Barbary macaques (Macaca sylvanus) at Salem. Behav Ecol Sociobiol 27, 287–293. doi:10.1007/BF00164902

Pavelka, M.S.M., Fedigan, L.M., 1999. Reproductive termination in female Japanese monkeys: A comparative life history perspective. American Journal of Physical Anthropology 109, 455–464.

Perloe, S.I., 1992. Male mating competition, female choice and dominance in a free ranging group of Japanese macaques. Primates 33, 289–304. doi:10.1007/BF02381191

Pusey, A.E., 1987a. Dispersal and philopatry. Primate societies 250–266.

Pusey, A.E., 1987b. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology & Evolution 2, 295–299. doi:10.1016/0169-5347(87)90081-4

Pusey, A., Williams, J., Goodall, J., 1997. The Influence of Dominance Rank on the Reproductive Success of Female Chimpanzees. Science 277, 828–831. doi:10.1126/science.277.5327.828

Radler, C., 2014. Genetic analysis of paternity and relationship quality in Japanese macaques (*Macaca fuscata fuscata*) (Master thesis), University of Graz, Graz, Austria.

Robbins, A.M., Robbins, M.M., Gerald-Steklis, N., Steklis, H.D., 2006. Age-related patterns of reproductive success among female mountain gorillas. Am. J. Phys. Anthropol. 131, 511–521. doi:10.1002/ajpa.20474

Rogers, J., Gibbs, R.A., 2014. Comparative primate genomics: emerging patterns of genome content and dynamics. Nature Reviews Genetics 15, 347–359. doi:10.1038/nrg3707

Sapolsky, R.M., 2005. The Influence of Social Hierarchy on Primate Health. Science 308, 648–652. doi:10.1126/science.1106477

Schino, G., Troisi, A., 2005. Neonatal abandonment in Japanese macaques. American journal of physical anthropology 126, 447–452.

Schino, G., Troisi, A., 1998. Mother-infant conflict over behavioral thermoregulation in Japanese macaques. Behav Ecol Sociobiol 43, 81–86. doi:10.1007/s002650050469

Schino, G., Troisi, A., 1990. Behavioral thermoregulation in long-tailed macaques: Effect on social preference. Physiology & Behavior 47, 1125–1128. doi:10.1016/0031-9384(90)90362-8

Scucchi, S., 1984. Interbirth intervals in a captive group of Japanese macaques. Folia primatologica 42, 203–208.

Sherman, B.M., West, J.H., Korenman, S.G., 1976. The Menopausal Transition: Analysis of LH, FSH, Estradiol, and Progesterone Concentrations During Menstrual Cycles of Older Women. The Journal of Clinical Endocrinology & Metabolism 42, 629–636. doi:10.1210/jcem-42-4-629

Silk, J.B., Brown, G.R., 2008. Local resource competition and local resource enhancement shape primate birth sex ratios. Proceedings of the Royal Society of London B: Biological Sciences 275, 1761–1765. doi:10.1098/rspb.2008.0340

Silk, J.B., Clark-Wheatley, C.B., Rodman, P.S., Samuels, A., 1981. Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques (Macaca radiata). Animal Behaviour 29, 1106–1120. doi:10.1016/S0003-3472(81)80063-2

Small, M.F., 1981. Body fat, rank, and nutritional status in a captive group of Rhesus Macaques. Int J Primatol 2, 91–95. doi:10.1007/BF02692303

Soltis, J., Mitsunaga, F., Shimizu, K., Nozaki, M., Yanagihara, Y., Domingo-Roura, X., Takenaka, O., 1997. Sexual selection in Japanese macaques II : female mate choice and male-male competition. Animal behaviour 54, 737–746.

Soltis, J., Mitsunaga, F., Shimizu, K., Yanagihara, Y., Nozaki, M., 1999. Female mating strategy in an enclosed group of Japanese macaques. Am. J. Primatol. 47, 263–278. doi:10.1002/(SICI)1098-2345(1999)47:4<263::AID-AJP1>3.0.CO;2-F

Soltis, J., Thomsen, R., Matsubayashi, K., Takenaka, O., 2000. Infanticide by resident males and female counter-strategies in wild Japanese macaques (Macaca fuscata). Behav Ecol Sociobiol 48, 195–202. doi:10.1007/s002650000224

Soltis, J., Thomsen, R., Takenaka, O., 2001. The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, Macaca fuscata. Animal Behaviour 62, 485–494. doi:10.1006/anbe.2001.1774

Stelzner, J.K., Hausfater, G., 1986. Posture, microclimate, and thermoregulation in yellow baboons. Primates 27, 449–463. doi:10.1007/BF02381890

Sterck, E.H.M., Watts, D.P., Schaik, C.P. van, 1997. The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41, 291–309. doi:10.1007/s002650050390

Sugiyama, Y., 1960. On the division of a natural troop of Japanese monkeys at takasakiyama. Primates 2, 109–148. doi:10.1007/BF01659166

Sugiyama, Y., Ohsawa, H., 1988. Population Dynamics and Management of Baited Japanese Monkeys at Takasakiyama. Primate Research 4, 33–43. doi:10.2354/psj.4.33

Sugiyama, Y., Ohsawa, H., 1982. Population Dynamics of Japanese Monkeys with Special Reference to the Effect of Artificial Feeding. Folia Primatologica 39, 238–263. doi:10.1159/000156080

Sulloway, F.J., 1996. Born to rebel: Birth order, family dynamics, and creative lives. Pantheon Books, New York, NY, US.

Suzuki, A., 1965. An ecological study of wild Japanese monkeys in snowy areas. Primates 6, 31–72. doi:10.1007/BF01794458

Suzuki, S., Hill, D.A., Maruhashi, T., Tsukahara, T., 1990. Frog- and lizard-eating behaviour of wild Japanese macaques in Yakushima, Japan. Primates 31, 421–426. doi:10.1007/BF02381113

Takahashi, H., 2002a. Changes of dominance rank, age, and tenure of wild Japanese macaque males in the kinkazan a troop during seven years. Primates 43, 133–138. doi:10.1007/BF02629673

Takahashi, H., 2002b. Female reproductive parameters and fruit availability: factors determining onset of estrus in Japanese macaques. Am. J. Primatol. 57, 141–153. doi:10.1002/ajp.10041

Takahashi, H., 2001. Influence of fluctuation in the operational sex ratio to mating of troop and non-troop male Japanese macaques for four years on Kinkazan Island, Japan. Primates 42, 183–191. doi:10.1007/BF02629635

Takahata, Y., 1982. The Socio-Sexual Behavior of Japanese Monkeys. Zeitschrift für Tierpsychologie 59, 89–108.

Takahata, Y., 1980. The reproductive biology of a free-ranging troop of Japanese monkeys. Primates 21, 303–329. doi:10.1007/BF02390462

Takahata, Y., Huffman, M.A., Bardi, M., 2002. Long-Term Trends in Matrilineal Inbreeding Among the Japanese Macaques of Arashiyama B Troop. International Journal of Primatology 23, 399–410. doi:10.1023/A:1013843814131

Takahata, Y., Huffman, M.A., Suzuki, S., Koyama, N., Yamagiwa, J., 1999. Why dominants do not consistently attain high mating and reproductive success: A review of longitudinal Japanese macaque studies. Primates 40, 143–158. doi:10.1007/BF02557707

Takahata, Y., Koyama, N., Huffman, M.A., Norikoshi, K., Suzuki, H., 1995. Are daughters more costly to produce for Japanese macaque mothers?: Sex of the offspring and subsequent interbirth intervals. Primates 36, 571–574. doi:10.1007/BF02382877

Takahata, Y., Suzuki, S., Agetsuma, N., Okayasu, N., Sugiura, H., Takahashi, H., Yamagiwa, J., Izawa, K., Furuichi, T., Hill, D.A., Maruhashi, T., Saito, C., Saito, S., Sprague, D.S., 1998a. Reproduction of wild Japanese macaque females of Yakushima and Kinkazan Islands: A preliminary report. Primates 39, 339–349. doi:10.1007/BF02573082

Takahata, Y., Suzuki, S., Okayasu, N., Sugiura, H., Takahashi, H., Yamagiwa, J., Izawa, K., Agetsuma, N., Hill, D., Saito, C., Sato, S., Tanaka, T., Sprague, D., 1998b. Does troop size of wild Japanese macaques influence birth rate and infant mortality in the absence of predators? Primates 39, 245–251. doi:10.1007/BF02557737

Takasaki, H., 1981. Troop size, habitat quality, and home range area in Japanese macaques. Behav Ecol Sociobiol 9, 277–281. doi:10.1007/BF00299883

Tanaka, I., 1992. Three phases of lactation in free-ranging Japanese macaques. Animal Behaviour 44, 129–139. doi:10.1016/S0003-3472(05)80762-6

Thierry, B., 2000. Covariation of conflict management patterns across macaque species. Natural conflict resolution 106–128.

Thierry, B., Singh, M., Kaumanns, W., 2004. Macaque Societies: A Model for the Study of Social Organization. Cambridge University Press.

Trivers, R.L., Willard, D.E., 1973. Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring. Science 179, 90–92. doi:10.1126/science.179.4068.90

Tsuji, Y., 2010. Regional, Temporal, and Interindividual Variation in the Feeding Ecology of Japanese Macaques, in: D.Sc, N.N., Nakamichi, M., D.Sc, H.S. (Eds.), The Japanese Macaques, Primatology Monographs. Springer Japan, pp. 99–127.

Varley, M.A., Vessey, S.H., 1977. Effects of geographic transfer on the timing of seasonal breeding of rhesus monkeys. Folia Primatol. 28, 52–59.

Vom Saal, F.S., Finch, C.E., 1988. Reproductive senescence: phenomena and mechanisms in mammals and selected vertebrates. The Physiology of Reproduction.

Waldie, K.E., Poulton, R., Kirk, I.J., Silva, P.A., 2000. The effects of pre- and post-natal sunlight exposure on human growth: evidence from the Southern Hemisphere. Early Hum. Dev. 60, 35–42.

Walker, M.L., Herndon, J.G., 2008. Menopause in Nonhuman Primates? Biol Reprod 79, 398–406. doi:10.1095/biolreprod.108.068536

Wallner, B., Aspernig, D., Millesi, E., Machatschke, I.H., 2011. Non-lactating versus lactating females: a comparison of sex steroids, sexual coloration, and sexual behavior in Japanese macaques. Primates 52, 69–75. doi:10.1007/s10329-010-0221-7

Watanabe, K., 1989. Fish: a new addition to the diet of Japanese macaques on Koshima Island. Folia Primatol. 52, 124–131.

Watanabe, K., Mori, A., Kawai, M., 1992. Characteristic features of the reproduction of Koshima monkeys,Macaca fuscata fuscata: A summary of thirty-four years of observation. Primates 33, 1–32. doi:10.1007/BF02382760

Wolfe, L., 1978. Age and sexual behavior of Japanese macaques (Macaca fuscata). Arch Sex Behav 7, 55–68.

Wolfe, L.D., 1984. Female rank and reproductive success among arashiyama B Japanese macaques (Macaca fuscata). Int J Primatol 5, 133–143. doi:10.1007/BF02735737

Wolfe, L.D., 1981. Display behavior of three troops of Japanese monkeys (Macaca fuscata). Primates 22, 24–32. doi:10.1007/BF02382554

Wrangham, R.W., 1980. An Ecological Model of Female-Bonded Primate Groups. Behaviour 75, 262–300. doi:10.1163/156853980X00447

Yamagiwa, J., 2010. Research History of Japanese Macaques in Japan, in: D.Sc, N.N., Nakamichi, M., D.Sc, H.S. (Eds.), The Japanese Macaques, Primatology Monographs. Springer Japan, pp. 3–25.

Yamagiwa, J., Hill, D.A., 1998. Intraspecific variation in the social organization of Japanese macaques: Past and present scope of field studies in natural habitats. Primates 39, 257–273. doi:10.1007/BF02573076

APPENDIX

Table A-1: Mean temperature (in °C) for each month of the mating season from 1996 - 2015

	Temperature (°C)						
Mating season	September	October	November	Dezember	January	February	March
1996/97	11,6	8,4	4,8	-3,3	-2,5	1,3	5,4
1997/98	15,1	8,1	3,3	0,3	-0,1	2,5	4,3
1998/99	13,6	9,2	1,4	-4,3	-3,3	-1,8	5,6
1999/00	16,1	9,7	1,5	-3,1	-5,5	1	5,9
2000/01	14,5	10,5	5,5	1	0,1	2,1	7,4
2001/02	12,5	12	1,7	-4,6	-3,4	2,8	6,5
2002/03	13,2	9,6	6,6	0,7	-2,9	-2,9	5,3
2003/04	13,2	7	5,6	-1	-2,9	0,1	2,7
2004/05	14,3	11,1	2,9	-1	-2,6	-1,9	3,8
2005/06	15,1	9,8	3	-3,1	-5,6	-2,2	2,5
2006/07	16,4	11,1	4,3	0,4	1,1	2,8	5,7
2007/08	13,1	8,3	2,7	-1,5	0,5	2,4	4,6
2008/09	13,6	10,4	4,3	-0,9	-3,3	-0,4	4,5
2009/10	15,6	9,3	4,3	-1,1	-2,7	-0,7	4,4
2010/11	13,3	7,6	5,2	-3	-1,9	0	5,5
2011/12	17,2	8,2	2,4	-0,2	-1,7	-3,5	7,4
2012/13	14,8	9,5	5,6	-1,8	-0,7	-1,6	2,3
2013/14	14,9	11,2	4,4	0,1	1,7	2,1	7,1

Table A-2: Mean amount of rainfall (in mm) for each month of the mating season from 1996 - 2015

	Rainfall (mm)						
Mating season	September	October	November	Dezember	January	February	March
1996/97	79	149	197	18	33	10	18
1997/98	85	7	133	95	11	4	25
1998/99	168	211	76	22	30	50	43
1999/00	56	122	76	72	3	17	52
2000/01	65	213	302	88	81	22	103
2001/02	165	30	54	6	4	27	25
2002/03	110	119	159	53	39	9	1
2003/04	65	133	149	52	33	60	91
2004/05	104	157	38	55	5	26	45
2005/06	128	110	96	79	39	35	94
2006/07	42	69	42	70	77	47	103
2007/08	157	66	29	17	56	29	101
2008/09	55	143	113	195	65	53	135
2009/10	194	75	97	145	29	104	46
2010/11	226	111	228	98	39	7	42
2011/12	117	139	1	39	24	24	7
2012/13	149	177	153	42	55	116	114
2013/14	137	94	215	73	202	216	52

Table A-3: Mean sunshine duration (in hours) for each month of the mating season from 1996 - 2015

	Sunshine duration (h)						
Mating season	September	October	November	Dezember	January	February	March
1996/97	150	96	81	68	49	170	205
1997/98	256	150	60	56	136	211	236
1998/99	159	148	87	107	120	160	175
1999/00	210	158	93	107	153	205	206
2000/01	234	91	58	75	74	172	156
2001/02	142	214	136	104	165	123	244
2002/03	205	159	81	25	87	193	233
2003/04	245	165	84	107	112	145	185
2004/05	220	134	84	85	153	141	226
2005/06	176	141	84	91	115	124	172
2006/07	251	171	133	80	146	168	186
2007/08	224	130	143	120	109	204	155
2008/09	179	152	92	54	71	139	176
2009/10	232	176	112	61	50	120	187
2010/11	169	124	80	104	104	120	212
2011/12	240	164	64	88	160	133	271
2012/13	186	138	57	105	86	77	142
2013/14	195	143	45	90	64	69	209

Table A-4: Group size, number of females and males, sex ratio and the number of mature females and males on the 1st September of each year

September 1st	**Sex ratio (m/f)**	**Males**	**Females**	**Group size**	**Mature males**	**Mature females**
1996	0,682	15	22	37	8	16
1997	0,800	16	20	36	10	18
1998	0,800	20	25	45	14	18
1999	0,700	21	30	51	14	19
2000	0,853	29	34	63	15	19
2001	0,821	32	39	71	18	25
2002	0,818	36	44	80	18	29
2003	0,886	39	44	83	24	32
2004	0,930	40	43	83	29	34
2005	0,854	41	48	89	35	40
2006	0,774	41	53	94	36	40
2007	0,789	45	57	102	36	41
2008	0,879	51	58	109	34	46
2009	0,922	59	64	123	36	52
2010	0,912	62	68	130	39	55
2011	0,943	66	70	136	47	54
2012	0,932	68	73	141	53	58
2013	0,896	69	77	146	56	63
2014	0,899	71	79	150	59	65
2015	1,123	73	82	155	61	68

Table A-5: Mean age of the troop, mean age of males and females only

September 1st	Mean age of the whole troop	Only males	Only females	Group size
1996	4,2837	2,7666	5,3181	37
1997	5,1388	3,5625	6,4	36
1998	4,8777	3,75	5,78	45
1999	5,1274	4,2619	5,7333	51
2000	5,0555	3,9483	6	63
2001	5,3169	4,2812	6,166	71
2002	5,2625	4,4722	5,9091	80
2003	5,8133	4,8333	6,6818	83
2004	6,3434	5,7	6,919	83
2005	6,882	6,5488	7,1666	89
2006	7,0319	6,8415	7,1792	94
2007	7,3529	7,1	7,5526	102
2008	7,5092	6,4804	8,4138	109
2009	7,5488	6,4322	8,578	123
2010	7,7077	6,6935	8,6324	130
2011	8,0735	7,1515	8,9429	136
2012	8,422	7,4265	9,3493	141
2013	8,8767	7,9638	9,6948	146
2014	9,2667	8,4437	10,0063	150
2015	9,3129	8,3493	10,1707	155

Table A-6: Number of offspring born in each month and the percentage of share in all births

Time of Birth	Frequency	Males	Females	%
1.-10. February	1	1	0	0,6
11.-20. February	0	0	0	0
20.-29. February	0	0	0	0
1.-10. March	0	0	0	0
11.-20. March	4	2	2	2,2
20.- 31. March	9	5	4	5
1.-10. April	16	10	6	8,9
11.-20. April	25	16	9	13,9
21.-30. April	34	12	22	18,9
1.-10. May	20	11	9	11,1
11.-20. May	26	8	18	14,4
21.-31. May	19	11	8	10,6
1.-10. June	11	7	4	6,1
11.-20.June	7	6	1	3,9
21.-30. June	4	2	2	2,2
1.-10. July	1	1	0	0,6
11.-20. July	1	1	0	0,6
21.-31. July	1	1	0	0,6
1.-10. August	0	0	0	0
11.-20. August	0	0	0	0
20.-31. August	1	0	1	0,6

Table A-7: Number and sex of all new-borns over the years

Birth year	Sex ratio at birth (m/f)	Number of new-borns	Male new-borns	Female new-borns
1997		1	1	0
1998	0,667	10	4	6
1999	0,400	7	2	5
2000	2,000	12	8	4
2001	1,000	10	5	5
2002	1,000	12	6	6
2003	2,500	7	5	2
2004	0,500	6	2	4
2005	0,400	7	2	5
2006	0,833	11	5	6
2007	1,000	12	6	6
2008	9,000	10	9	1
2009	1,500	15	9	6
2010	0,714	12	5	7
2011	1,500	10	6	4
2012	1,000	10	5	5
2013	0,600	8	3	5
2014	1,000	10	5	5
2015	0,714	12	5	7

Table A-8: All identified parent couples and the age of every father and the mothers

Name of offspring	Mothers' name	Mothers' age at birth	Fathers' name	Fathers' age at conception
Gustav	Nora	3,5	Double-U	3,5
Julius	Anastasia	14,5	Double-U	3,5
Lena	Minni	3,5	Schlumpfi	4,5
Leopold	Chita	8,5	Willi	4,5
Luca	Barbara	6,5	Gustav	4,5
Nikolaus	Amanda	7,5	Mickey	4,5
Victoria	Sissy	8,5	Oskar	4,5
Anastasia II	Anastasia	10,5	Max	5,5
Dolores	Anastasia II	6,5	Adrian	5,5
Funki (Marc)	Josefine	6,5	Stefan	5,5
Hilde	Christina	3,5	Felix	5,5
Lisa	Mona	5,5	Schüchi	5,5
Villach	Kathi	6,5	Max	5,5
Alexander	Pia	7,5	Ludwig	6,5
Alois	Rosi	12,5	Schüchi	6,5
Berta	Josefine	4,5	Double-U	6,5
Christina	Victoria	3,5	Schüchi	6,5
Coco	Berta	3,5	Alois	6,5
Daniel	Iris	3,5	Herkules	6,5
Florentine	Rudolfine	8,5	Alois	6,5
Karl-Vinzenz	Rosi	10,5	Oskar	6,5
Laura	Anastasia	11,5	Max	6,5
Maria	Betty	5,5	Herkules	6,5
Thomas	Barbara	7,5	Junior	6,5
Werner	Anastasia II	9,5	Nikolaus	6,5
Alexandra	Betty	10,5	Carlos S.	7,5
Alice	Christina	6,5	Nikolaus	7,5
Beate	Lisa	4,5	Herkules	7,5
Benjamin	Sissy	10,5	Max	7,5
Felix	Kathi	8,5	Ralph	7,5
Friderike	Nils-Gerlos	3,5	Herkules	7,5
Fritz	Rudolfine	6,5	Adrian	7,5
Hanna	Barbara	5,5	Herkules	7,5
Markus	Betty	9,5	Nikolaus	7,5
Sabrina	Anastasia	13,5	Oskar	7,5
Alina	Anke	4,5	Double-U	8,5
Carlos S.	Krümel	7,5	Oskar	8,5
Leonardo	Lisa		Adrian	8,5
Siegfried	Christina	7,5	Nikolaus	8,5
Silvio	Dolores	5,5	Julius	8,5
Anke	Maridi	9,5	Ralph	9,5
Melanie	Mona	10,5	Schüchi	10,5
Sarah (Anita)	Beate	4,5	Double-U	12,5

Table A-9: Age of all mothers at their first, second, third, fourth and fifth birth

	First birth	Second birth	Third birth	Fourth birth	Fifth birth
4-year-old	22	0	0	0	0
5-year-old	28	3	0	0	0
6-year-old	5	14	0	0	0
7-year-old	1	14	7	0	0
8-year-old	0	5	9	2	0
9-year-old	0	1	4	3	2
10-year-old	0	0	2	3	1
11-year-old	0	0	0	1	1
12-year-old	0	0	0	0	1

Table A-10: Age oft he females at the time they were sterilised from 1996 to 2015

	2002	2003	2006	2009	2010	2011	2012	2013	2015
4-year-old	3	2		1					
5-year-old		1				1			4
6-year-old						1		1	1
7-year-old				2				4	
8-year-old			1	2	2		2		1
9-year-old				2	2				1
10-year-old					1		1		1
11-year-old				1					
12-year-old						1	1		

Table A-11: Frequency of one year-, two year- and three-year-interbirth intervals between first offspring and second offspring, between second offspring and third offspring, asf.

	first IBIV	second IBIV	third IBIV	forth IBIV	fifth IBIV
1 year	11	18	10	6	1
2 years	38	16	3	0	0
3 years	4	0	0	0	0

Table A-12: Frequency of one year-, two year- and three-year-interbirth intervals after the birth of sons and daughters

	First IBIV		Second IBIV		Third IBIV		Fourth IBIV		Fifth IBIV	
IBIV	after daugh-ters	after sons	after daugh-ters	after sons	after daugh-ters	after sons	after daugh-ters	after sons	after daugh-ters	after sons
1-year	7	4	7	11	4	6	1	4	0	1
2-years	17	21	8	8	3	0	0	0	0	0
3-year	3	1	0	0	0	0	0	0	0	0

Table A-13: All females with two or more offspring, including the offspring's sex (1=male/2=female) and the interval after every birth in years (IBIV=interbirth interval)

	First born	First IBIV	Second born	Second IBIV	Third born	Third IBIV	Fourth born	Fourth IBIV	Fifth born	Fifth IBIV
Alice	1	2	2							
Alina	1	2	1							
Amanda	1	2	1	1	2					
Anastasia	2	1	2	1	1	1	2	1	1	1
Anastasia II	2	1	1	1	2	2	1	1	1	
Anke	1	1	2	2	1					
Annegret	1	2	1							
Augustine	1	2	1	1	2					
Barbara	2	2	2	1	1	1	1	1	1	
Beate	2	2	2							
Betty	2	1	2	2	2	2	1	1	2	
Bum Bum	1	2	1	2	1	1	1			
Caroline	2	2	1	1	1					
Chita	1	2	1	1	1					
Christina	2	3	2	1	1					
Claudia	2	1	1							
Dolores	1	2	2	2	1					
Elfriede	2	3	2							
Elli	2	2	1							
Esther	1	2	2							
Friderike	2	2	2							
Gisela	1	2	1							
Gusti	1	2	2	1	1					
Heidi	1	2	1							
Hilde	2	2	2							
Ilvy	1	2	1	1	2					
Iris	1	2	2	2	1	1	2			
Josefine	2	1	2	2	1	1	1	1	1	
Kathi	2	2	1	2	1					
Krümel	2	2	2	1	1					
Lena	2	2	2	1	2	1	1	1	1	
Lilly	1	1	2	2	2	1	1			
Lisa	2	2	1	1	2					
Magdalena	1	1	1							
Marianne	2	3	2							
Maridi	2	2	1	2	2					
Maya	1	2	1	2	1					
Melanie	1	2	2							
Michaela	2	1	1	2	1					
Mona	2	2	1	1	2	2	2			
Nicky	2	2	1	1	2					
Nils-Gerlos	2	2	1	1	2					
Olga	2	1	2							

	First born	First IBIV	Second born	Second IBIV	Third born	Third IBIV	Fourth born	Fourth IBIV	Fifth born	Fifth IBIV
Pauline	1	2	2	1	2	1	2			
Pia	1	2	1	2	1					
Rosi	2	2	1	1	1	1	1			
Rudolfine	2	2	1	2	2					
Sabine	1	2	2	2	2	1	1			
Sabrina	1	1	1	2	1					
Sissy	2	2	1							
Svenja	1	2	2	2	1					
Villach	1	3	1							
Wilma	1	2	1							

Table A-14: Number of first-born offspring (primiparity) and later-born offspring (multiparity) in each third of all months during birth season

Birth date	Encoded as	Primiparity	Multiparity
1. -10. March	31	0	0
11. -20. March	32	0	3
21. -31. March	33	0	3
1. -10. April	41	4	7
11. -20. April	42	4	16
21. -30. April	43	12	15
1. -10. May	51	7	11
11. -20. May	52	12	7
21. -31. May	53	11	6
1. -10. June	61	3	4
11. -20. June	62	4	2
21. -30. June	63	1	1
1. -10. July	71	0	1
11. -20. July	72	0	0
21. -31. July	73	0	1

Table A-15: Number of mature females during each mating season and how many of them did not give birth in the subsequent spring/summer (number and percentage)

Mating Season	Mature females	Mature females who did not give birth in the subsequent birth season	Percentage of mature females who did not give birth
1996/97	16	15	0,938
1997/98	18	8	0,444
1998/99	18	11	0,611
1999/00	19	7	0,368
2000/01	19	9	0,474
2001/02	25	13	0,520
2002/03	29	22	0,759
2003/04	32	26	0,813
2004/05	34	27	0,794
2005/06	40	29	0,725
2006/07	40	28	0,700
2007/08	41	31	0,756
2008/09	46	31	0,674
2009/10	52	40	0,769
2010/11	55	45	0,818
2011/12	54	44	0,815
2012/13	58	50	0,862
2013/14	63	53	0,841

Table A-16: Number of fertile females during each mating season and how many of them did not give birth in the subsequent spring/summer (number and percentage)

Mating Season	Fertile Females	Fertile Females who did not give birth in the subsequent birth season	Percentage of fertile females who did not give birth
1996/97	16	15	0,9375
1997/98	18	8	0,4444
1998/99	18	11	0,6111
1999/00	19	7	0,3684
2000/01	17	7	0,4118
2001/02	19	7	0,3684
2002/03	11	4	0,3636
2003/04	10	4	0,4000
2004/05	14	7	0,5000
2005/06	20	9	0,4500
2006/07	19	7	0,3684
2007/08	21	11	0,5238
2008/09	25	10	0,4000
2009/10	22	10	0,4545
2010/11	22	12	0,5455
2011/12	19	9	0,4737
2012/13	20	12	0,6000
2013/14	21	11	0,5238

Table A-17: Number of fertile and surely not lactating females during each mating season and how many of them did not give birth in the subsequent spring/summer (number and percentage)

Mating Season	Fertile & surely not lactating females	Fertile & surely not lactating females who did not give birth in the subsequent birth season	Percentage of fertile & surely not lactating females who did not give birth in the subsequent birth season
1996/97	14	13	0,9286
1997/98	17	7	0,4118
1998/99	10	3	0,3000
1999/00	13	1	0,0769
2000/01	11	1	0,0909
2001/02	17	5	0,2941
2002/03	11	4	0,3636
2003/04	9	3	0,3333
2004/05	11	4	0,3636
2005/06	14	3	0,2143
2006/07	13	1	0,0769
2007/08	14	4	0,2857
2008/09	21	6	0,2857
2009/10	19	7	0,3684
2010/11	17	7	0,4118
2011/12	12	2	0,1667
2012/13	14	6	0,4286
2013/14	17	7	0,4118

Table A-18: Group size, sex ratio, operational sex ratio (OSR = mature males per mature female), operational sex ratio of fertile individuals [mature males/(mature females minus sterilised ones)] and mean weather data for each mating season (1st September)

Mating Season	Group size	OSR	OSR of fertiles	Sex ratio of the group (m/f)	Average temperature [°C]	Average rainfall [mm]	Average sunshine [h]
1996/97	37	0,500	0,500	0,682	3,671	72,000	117,000
1997/98	36	0,556	0,556	0,800	4,786	51,429	157,857
1998/99	45	0,778	0,778	0,800	2,914	85,714	136,571
1999/00	51	0,737	0,737	0,700	3,657	56,857	161,714
2000/01	63	0,789	0,882	0,853	5,871	124,857	122,857
2001/02	71	0,720	0,947	0,821	3,929	44,429	161,143
2002/03	80	0,621	1,636	0,818	4,229	70,000	140,429
2003/04	83	0,750	2,400	0,886	3,529	83,286	149,000
2004/05	83	0,853	2,071	0,930	3,800	61,429	149,000
2005/06	89	0,875	1,750	0,854	2,786	83,000	129,000
2006/07	94	0,900	1,895	0,774	5,971	64,286	162,143
2007/08	102	0,878	1,714	0,789	4,300	65,000	155,000
2008/09	109	0,739	1,360	0,879	4,029	108,429	123,286
2009/10	123	0,692	1,636	0,922	4,157	98,571	134,000
2010/11	130	0,709	1,773	0,912	3,814	107,286	130,429
2011/12	136	0,870	2,474	0,943	4,257	50,143	160,000
2012/13	141	0,914	2,650	0,932	4,014	115,143	113,000
2013/14	146	0,889	2,667	0,896	5,929	141,286	116,429

Figure A-1: The Sex ratio (raw data) of new-borns of each birth season opposed to the sex ratio (raw data) of the whole troop during the previous mating season