Linking behaviour and physiology of female bonobos (*Pan paniscus*)

Dissertation

zur Erlangung des Doktorgrades
der Fakultät für Biologie, Chemie und Geowissenschaften
der Universität Bayreuth

vorgelegt von

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aus Augsburg

Bayreuth 2005

Die vorliegende Arbeit wurde vom Oktober 1996 bis Dezember 2001 unter der Anleitung von Prof. Dr. Dietrich von Holst und Dr. Gottfried Hohmann am Max-Plack Instutut für Verhaltensphysiologie in Sewiesen in der Abteilung von Prof. Dr. Wolfgang Wickler und am Max-Plack-Institut für evolutionäre Anthropologie in Leizig in der Abteilung von Prof. Dr. Christophe Boesch angefertigt.

Vollständiger Abdruck der von der Fakultät für Biologie, Chemie und Geowissenschaften der Universität Bayreuth genehmigten Dissertation zur Erlangung des akademischen Grades Doktor der Naturwissenschaften (Dr. rer. nat.).

Promotionsgesuch eingereicht am: 07.10.2005

Wissenschaftliches Kolloquium am: 14.12.2006

Erster Gutachter: Prof. Dr. D. von Holst

Zweiter Gutachter: Prof. Dr. K. Hodges

Only the earth endures.

Meiner Mutter – dem Engel an meiner Seite

Ein Teil dieser Arbeit wurde veröffentlicht:

Reichert, K.E., Heistermann, M., Hodges, J.K., Boesch, C. & Hohmann, G. 2002. What females tell males about their reproductive status: Are morphological and behavioural cues reliable signals of ovulation on bonobos (*Pan paniscus*)? *Ethology,* **108**, 583-600.

Content

1 Introduction

Bonobos, or pygmy chimpanzees, were recognised as being different from common chimpanzees, *Pan troglodytes*, only in 1929. However, it was not before 1933 that they were recognised as a separate species, *Pan paniscus* (Schwarz, 1929; Coolidge, 1933 (as cited in de Waal & Lanting, 1997)). It still took some more decades until the first scientific publications on wild bonobos became available (Kuroda, 1979; Nishida, 1972), probably due to their endemic distribution in the lowland rain forests south of the Congo river in the politically unstable region of the Democratic Republic of Congo (Susman, 1984). The high degree of scientific and public interest that both chimpanzee species received may be explained by the close phylogenetic relationship to humans. Both *Pan* species differ in only 1.5 % of their genome from humans. Based on morphological distinctions of the two species, bonobos were perceived as having less specialised and thus more primitive features than chimpanzees and consequently were suggested to more closely resemble the possible prototype for the common ancestor of apes and *Homo sapiens* (Zihlman *et al.*, 1978). Pygmy chimpanzees were suggested, for example to represent a potential model species for the development of pair bonds and paternal care in humans (Turke, 1984). Other studies, though, seriously questioned that pygmy chimpanzees may be a more valid model for the human ancestor than common chimpanzees (Kortlandt, 1998; Latimer *et al.*, 1981; Mc Henry & Corruccini, 1981; Shea, 1983; Stanyon *et al.*, 1986). The latter point of view has now been most widely accepted among scientists. Contrastingly, other researchers postulated that bonobos show paedomorphic traits of chimpanzees in terms of anatomy and patterns of menstrual cycles and therefore it was hypothesised that bonobos are more derived as compared to common chimpanzees (Blount, 1990; Dahl, 1985, 1986; Kuroda, 1989; Savage-Rumbaugh & Wilkerson, 1978; Shea, 1983).

Since pygmy and common chimpanzees are close relatives as well (Gagneux *et al.*, 1999; Kaessmann *et al.*, 1999), another main focus of research was to study similarities and differences between the two species regarding their ecology and behaviour (Dahl *et al.*, 1991; de Waal, 1989; Mori, 1984; Savage-Rumbaugh, 1984; Savage-Rumbaugh & Wilkerson, 1978; Stanford, 1998; Takahata *et al.*, 1999; Videan & Mc Grew, 2001; White & Chapman, 1994; Wrangham, 1993). While both species live in fission-fusion groups with males being the philopatric sex, they differ in social relationships both within and between the sexes. Despite being the dispersing sex, it is the female bonobos showing

social bonding instead of the males as it is found in chimpanzees (Furuichi, 1989; Wrangham, 1986). And while male chimpanzees usually outrank all females (Goodall, 1986), female bonobos were found to have feeding priority over males and to be co-dominant with males or even to dominate them (Furuichi, 1997; Kano, 1992; Parish, 1994). Compared to chimpanzee societies, bonobos were also perceived as being more egalitarian and less aggressive on inter- and intra-group level (de Waal, 1989, 1995b; Ihobe, 1992a; Shefferly & Fritz, 1992; Wrangham, 1986). Social status therefore was discussed to play a less important roles in bonobos compared to chimpanzees. Whereas infanticide is reported to occur in chimpanzees (Goodall, 1986), it has not yet been observed in bonobos (Furuichi *et al.*, 1998). The sexual behaviour of bonobos, however, has been perceived as being most intriguing so that the species was coined in the media as the "sexy" ape which makes love not war (de Waal, 1987, 1993, 1995a). One reason for this is that conspicuous sexual swellings that attract male attention are shown by females not only during ovarian cycles but also commonly occur during the first one or two trimesters of pregnancy and as early as one year after parturition when females are still lactating (Blount, 1990; Enomoto, 1990; Furuichi, 1992).Other, primarily female researchers employed the species as a flagship in the upcoming feministic trends in evolutionary theory (Parish, 1994; Parish & de Waal, Small 1993). This is based on the finding that bonobos appear to use sexual interactions not only in the reproductive context but also as a social tool. For example, copulations are found to take place during the major part of the female menstrual cycle, and above that, sexual interactions can be observed among all age and sex classes (Kano, 1989). Females frequently engage in same-sex sexual behaviour, the so-called genito-genital rubbing, short genital rubbing (Kitamura, 1989; White & Thompson-Handler, 1989).

Important questions on bonobos are to understand the variability of menstrual cycles and sexual swellings, especially regarding signalling of ovulation, to shed light on the context and function of genital rubbing and to investigate the importance of social status for females. To address these questions a combined approach of behavioural and morphological observations together with non-invasive faecal hormone analysis was chosen. In the following, I give further details and background information concerning these questions.

1.1 Menstrual cycles and sexual swelling patterns in bonobos

The study of reproductive parameters is one of the key approaches when trying to understand a species' biology. Unlike for chimpanzees, relatively little is known on the reproductive biology of bonobos. When comparing menstrual cycles between the two species, intermenstrual intervals of bonobos are reported to be similar or, on the contrary, longer in duration than those of common chimpanzees (average 36.0 days versus 36.2 days (Savage-Rumbaugh & Wilkerson, 1978), 49.0 days versus 37.6 days (Dahl *et al.*, 1991); bonobos: 42.0 days (Furuichi, 1987), 33.8 days (Heistermann *et al.*, 1996), chimpanzees: 35.4 days (Nadler *et al.*, 1985), 33.2 days (Wallis, 1997)). Especially the great variability of cycle duration has been emphasised in bonobos (34-55 days (Neugebauer, 1980); 27-82 days (Dahl, 1986)). Apart from the duration of cycles itself, a longer, both in absolute and relative terms, and more variable duration of tumescence of the sexual swelling has been attributed to bonobos when compared to chimpanzees (23.5 days versus 17-18 days (Dahl, 1986; Dahl *et al.*, 1991); bonobos: 3-22 days (Furuichi, 1987), 15.3 days (Savage-Rumbaugh & Wilkerson, 1978); chimpanzees: 11-17 days (Nadler *et al.*, 1985), 9.6 days (Tutin, 1979)). The physiological explanation of the greater variability in menstrual cycle duration compared to chimpanzees remains unclear. Studies on other primate species indicate that the higher variability of the follicular phase as compared to the luteal phase may contribute to the variability in the duration of the of intermenstrual intervals (Heistermann *et al.*, 1996; Rowell, 1972; Vervaecke *et al.*, 1999). The long intermenstrual intervals as well as the morphology of the sexual swelling of bonobos have been suggested to resemble those of adolescent chimpanzees and consequently to be a hint for paedomorphism in bonobos (Blount, 1990; Dahl, 1985, 1986; Savage-Rumbaugh & Wilkerson, 1978). However, a similar range of cycle duration has also been reported for common chimpanzees (25-84 d (Tutin & Mc Ginnis, 1981), 22-187 d (Young & Yerkes 1943)) although these findings are neglected in the majority of comparative *Pan* studies. Thus, duration and variability of intermenstrual intervals might be similar in both chimpanzee species. But what is the cause for the variability of menstrual cycles in the *Pan* species?

Long-term studies of female Gombe chimpanzees revealed that patterns of menstrual cyclicity are influenced by a female's reproductive history (Wallis, 1997). Intermenstrual intervals were longer in nulliparous than in multiparous females. As well, the first cycles *post partum* were found to be longer than menstrual cycles that were preceded by a series

of other cycles (Wallis, 1997). The same effect of reproductive history on cycle patterns was already suggested in 1943 by Young and Yerkes (cited in Graham, 1981). Extended *post partum* cycles during lactation do not only occur in chimpanzees but are also reported for macaques (Clarke *et al.*, 1993). While the duration of tumescence does not differ between *post partum* cycles and regular cycles in chimpanzees (Wallis, 1997), tumescence was found to last longer in lactating than in non-lactating lion-tailed macaque females (Clarke *et al.*, 1993). Although it is possible that patterns of menstrual cycles and swelling morphology are a paedomorphic trait in bonobos, the assumption that bonobos show the same influence of reproductive history on menstrual cycles as common chimpanzees therefore would be more parsimonious. One reason why this pattern has not yet become clear could be the limited sample size of most bonobo studies.

To address the variability of sexual cycles in bonobos, the degree of variability in cycle length and duration of sexual tumescence was determined. The specific questions asked in the first part of this study were (1) whether the reproductive history influences the duration of menstrual cycles in bonobos, (2) whether the duration of sexual tumescence co-varies with cycle duration, and (3) whether differences in the duration of the follicular phase or of the luteal phase correlate with the variability in cycle duration.

1.2 Sexual swellings as a signal of ovulation

In many mammalian species, mating activity is restricted to the so-called 'oestrus' period, that coincides with the fertile phase of the female ovulatory cycle. Apart from behaviour, the patterns of olfactory or morphological cues displayed by a female may also change during 'oestrus' (Dixson, 1998). For males, who are not able to detect ovulation itself, these cues can serve as indirect signals of the fertile phase. As sexual behaviour in monkeys and apes is less strictly controlled by hormones than in other mammals, the term 'oestrus' has often been considered inappropriate for these species (Dixson, 1983a; Rowell, 1972). Although, in general, signalling their readiness to mate lasts much longer than the fertile phase and is more variable in Anthropoid primates than in other mammals (Martin, 1992), the variety of female cues that can stimulate male mating activity remains the same.

One of the most obvious morphological cues of impending ovulation is the sexual swelling of many Old World primates which was already introduced above. The sexual skin around

the perineum begins to swell or redden during the follicular phase of the ovulatory cycle, showing a conspicuous maximum around the presumed time of ovulation (Dixson, 1983b; Girolami & Bielert, 1987; Hrdy & Whitten, 1986). These cyclic changes in appearance of the sexual skin which usually reflect cyclic fluctuations in the secretion of ovarian hormones during the female cycle (Clutton-Brock & Harvey, 1976; Dixson, 1983b, 1998; Rowell, 1972) markedly influence the attractivity of females to males (Bielert & Girolami, 1986). Moderate changes in the external genitalia can be observed in many non-primate mammals and prosimians during the periovulatory phase (Dixson, 1998). Yet the occurrence of exaggerated sexual swellings is mainly restricted to Old World primate species living in multi-male mating systems (Clutton-Brock & Harvey, 1976; Dixson, 1983b; Hrdy & Whitten, 1986). The duration of tumescence and of maximum tumescence of the swelling varies considerably between species, the latter ranging from 3 to more than 20 days (Aujard *et al.*, 1998; Dahl, 1986; Furuichi, 1987; Goodall, 1986, p. 444; Mc Arthur *et al.*, 1981; Nadler *et al.*, 1985; Shaikh *et al.*, 1982; Thierry *et al.*, 1995; Wildt *et al.*, 1977).

The functional significance of sexual swellings has been the subject of much discussion and several hypotheses have been suggested: (1) Sexual swellings evolved as honest signals of ovulation that increase paternity confidence for a high-ranking male and thus allocate paternal care (Hamilton, 1984). (2) By enhancing male-male mating competition, sexual swellings increase the females' chances to mate with a superior male. As a result, the females gain profit of the male's superior quality either for themselves or for their offspring (Clutton-Brock & Harvey, 1976). (3) Swellings enable females to mate with many males and therefore to confuse paternity and to minimise the risk of infanticide (Hrdy, 1979, 1981; Wolff & Macdonald, 2004). (4) Sexual swellings conceal ovulation from males. Together with the synchronisation of menstrual cycles this forces males into long-lasting consortships if they want to make sure that they copulate with the female during the fertile phase (Turke, 1984). (5) Swellings are a graded signal (Martin, 1992) that allows females to follow a mixed strategy of biasing and confusing paternity by mating with the dominant male at peak swelling and with multiple males outside peak swelling (Nunn, 1999; van Schaik *et al.*, 2000). (6) Sexual swellings inform males about female quality (Domb & Pagel, 2001; Pagel, 1994). (7) And finally, sexual swellings are suggested to serve as a social passport during inter-group transfer (Goodall, 1986, p. 483; Nishida *et al.*, 1985; Pusey, 1979). While hypotheses 6 and 7 do not explain why swellings

evolved originally, hypotheses 1-5 focus on the question of whether sexual swellings actually serve to advertise or to confuse ovulation.

Analyses of endocrine, morphological and behavioural changes across the ovarian cycle of Tonkean macaques suggested that sexual swellings are a reliable indicator of the periovulatory phase in this species (Aujard *et al.*, 1998). Compared to these macaques and also to chimpanzees, sexual swellings in bonobos (*Pan paniscus*) are characterised by a longer and more variable duration (duration of maximum tumescence in Tonkean macaques: 6-15 days (Aujard *et al.*, 1998), chimpanzees: 7-17 days (Tutin & Mc Ginnis, 1981), bonobos: 6-24 days (Dahl, 1986)). In bonobos, mating activity was found to peak at maximum tumescence (Furuichi, 1987, 1992; Kano, 1989) but females also mate when tumescence is below maximum (Kano, 1992; White, 1992). Thus, it has been concluded that sexual swellings do not allow male bonobos to assess the time of ovulation reliably (Furuichi, 1987). Heistermann *et al.* (1996) investigated the timing of ovulation with respect to maximum swelling and concluded that sexual swellings are a poor predictor of ovulation in bonobos. However, as no data on sexual behaviour were collected, this study could not explain whether or not ovulation actually affects the mating behaviour of either sex.

To shed light on the question whether sexual swellings advertise or confuse ovulation it is important to investigate mating patterns in relation to sexual swellings, including information about the female's reproductive state and especially the timing of ovulation. With only a few exceptions (e.g.Aujard *et al.*, 1998; Lindburg & Harvey, 1996), however, most studies so far either analysed mating behaviour without considering information on the precise timing of ovulation (Oi, 1996; Wallis, 1992), or investigated hormone-swelling interactions without considering behaviour (Heistermann *et al.*, 1996; Mc Arthur *et al.*, 1981; Nadler *et al.*, 1985).

The second aim of this study was to further investigate the value of sexual swellings as a signal of ovulation in captive bonobos by (i) assessing the temporal relationship between sexual swelling and ovulation and (ii) analysing whether mating activity is influenced only by the degree of sexual swelling or whether it shows further changes around the time of ovulation. Specifically, I used a combined approach of behavioural and morphological observations together with non-invasive faecal hormone analysis to determine the day of ovulation to test the following predictions: (1) If sexual swellings advertise ovulation reliably in bonobos, ovulation should be predictable from the onset of maximum

tumescence. Nonetheless, based on knowledge of the hormonal regulation of sexual swellings (Dixson, 1983b), ovulation is expected to take place closer to the end rather than the onset of maximum tumescence and the beginning of detumescence should signal that ovulation has already occurred. (2) The degree of tumescence of the sexual swelling should influence the frequency of sexual interactions and sexual interactions should be most frequent around the time of ovulation. (3) And finally, when comparing sexual interactions during the follicular and the luteal phase of the menstrual cycle, frequencies should be much lower during luteal phase as copulations are not likely to result in conception during this phase of the cycle.

1.3 Sexual interactions between females

Since several decades, the occurrence of sexual behaviour between members of the same sex has received considerable interest (reviewed in Tyler, 1984). Because of its non-reproductive context, this behaviour was first considered to be aberrant or abnormal, and assumed to be mainly observed after disturbances in individual development or under unnatural situations. However, sexual behaviour between members of the same sex is widespread throughout the vertebrates and it is most common in mammals, including both males and females. Same-sex sexual interactions are usually more frequently observed in juveniles and occur at lower frequencies among adult individuals (Dagg, 1984). Definitions of this behaviour tend to vary between studies and species. For the purpose of the present study, same-sex sexual behaviour is defined according to Vasey (1995) as any genital contact or genital manipulation between same-sex individuals. Since the stage of arousal is difficult to assess, especially for females, sexual arousal of either of the participants is almost impossible to assess in same-sex sexual behaviour. The term same-sex sexual behaviour is favoured over "homosexual behaviour" since the former neither implies any reference about general sexual orientation nor claims knowledge about the underlying psychological state of the participants (Wallen & Parsons, 1997).

In contrast to previous assumptions, the occurrence of same-sex sexual behaviour is not restricted to laboratory settings but is also common in the wild (Dagg, 1984; Fox, 2001; Sommer, 1987; Tyler, 1984; Vasey & Gauthier, 2000; Weinrich, 1980). With the advent of socio-biology, same-sex sexual behaviour started to be considered as natural behaviour, i.e. it was suggested to serve a social function instead of being maladaptive. Because sexual

signals are often exchanged outside the copulatory context, the label "socio-sexual behaviour" was proposed to cover such non-reproductive sexual patterns (Wickler, 1967). Especially in anthropoid primates, same-sex sexual behaviour received considerable attention because of possible parallels to human homosexuality (Tyler, 1984; Wallen & Parsons, 1997). In contrast to humans, however, there are no reports for non-human primates that show permanent and exclusive engagement in same-sex sexual behaviour when members of the other sex are available (Tyler, 1984; Wallen & Parsons, 1997). Thus, a direct comparison of this behaviour between humans and non-human primates is not possible (but see Kirkpatrick, 2000).

While same-sex sexual interactions among immature individuals are often assumed to serve as practice for heterosexual mating patterns, there are several hypotheses to explain the functional significance of same-sex sexual interactions among adults:

Female-female mounting was suggested to influence heterosexual mating patterns by either enhancing the mounting female's proceptivity (Parker & Pearson, 1976) or, on the contrary, reducing the receptivity of the mounted female (Tyler, 1984). However, evidence for this connection between same-sex and heterosexual interactions in primates is very weak (Vasey, 1995). Alternatively, same-sex mounting is often considered to be an expression of social dominance, especially among males, with dominant males mounting subordinate ones (Dagg, 1984; Nadler, 1990). Many authors also noted a relationship between social tension and same sex interactions in anthropoids (reviewed in Weinrich, 1980). For rhesus macaques, a relationship between same-sex sexual behaviour and alliance formation was found (Fairbanks *et al.*, 1977). Same-sex sexual behaviour in contemporary and historical human societies was also reported to result in same-sex alliances leading to benefits applicable to (future) reproductive success (Kirkpatrick, 2000). And finally, de Waal (1987) postulated that same-sex sexual interactions are a major tool in conflict resolution. It is suggested to belong to a group of different socio-sexual elements that may serve to mediate reconciliation of former opponents.

In bonobos, sexual interactions are frequently observed that do not have any direct reproductive function because of the age, sex class or the reproductive status of the participants. The adaptive significance of this socio-sexual behaviour received considerable attention because of its frequent occurrence in this species. Female bonobos show a unique type of same-sex behaviour, the so-called genito-genital rubbing (short, genital rubbing or 'gg' rubbing) (Kuroda, 1980), where females rub their genitals in

sideway movements, usually in ventro-ventral position (Kano, 1982). This behaviour is commonly observed among wild and captive animals (Hohmann & Fruth, 2000b; Idani, 1991; Parish, 1996; Thompson-Handler, 1990). With the exception of one captive group of adolescent chimpanzees (Anestis, 2004), it has not yet been described in the bonobos' close relative, or any other primate species.

Therefore genital rubbing is often suggested to be one of the key factors to explain the different social relationships in chimpanzees and bonobos.

The third aim of this study was to investigate, when and why female bonobos perform same-sex sexual interactions. More specifically, the following five hypotheses were tested:

(1) Genital rubbing is suggested to mediate the formation or maintenance of female-female alliances in bonobos (Parish, 1994, 1996). Bonobo females form alliances that enable them to defend themselves against male aggression, to monopolise food sources and, possibly, even to dominate males. According to kin selection theory (Hamilton, 1964), related animals should form alliances because of inclusive fitness and therefore should not need any "persuasion" to do so. For non-related animals, however, social bonds as mediated by affiliative interactions play an important role for the formation of alliances. According to Parish (1994), genital rubbing facilitates such affiliative ties between females. Therefore, genital rubbing was expected to occur more often between unrelated than related females and above that, clear preferences for certain partners should exist. The preferred partner for genital rubbing should also be preferred for other affiliative interactions like grooming. Preference for a certain partner during genital rubbing should translate in a bias during interventions in conflicts towards this partner. Interventions on behalf of a relative were expected to occur without genital rubbing. Females were further expected to share monopolisable food items mainly with their preferred partner for genital rubbing – apart from kin. Less preferred partners for genital rubbing should consequently profit less during food sharing.

(2) The sexual swelling is hypothesized to enhance female-female attractivity in bonobos and thus to reduce intra-sexual competition (Takahata *et al.*, 1996). The extended phase of tumescence is supposed to increase not only inter-sexual but also intra-sexual attractivity during the ovarian cycle. This intra-sexual attractivity is expressed by behaviours like genital rubbing. It is suggested to help to minimise competition between females for limited resources. Consequently, the rate of genital rubbing should be influenced by the degree of sexual swelling. When two females involved in genital rubbing differ in their

stage of sexual swelling, asymmetry in solicitations for genital rubbing was expected. And finally, the rate of agonistic interactions should decrease with increasing frequency of genital rubbing.

In contrast to all other explanations for genital rubbing, this idea has been uniquely suggested for bonobos and no corresponding hypothesis exists for same-sex sexual interactions in other animal species.

(3) Genital rubbing is proposed to play a central role in mediating reconciliation between former opponents (de Waal, 1987, 1993). Reconciliation, in general, is a non-violent body contact between former opponents after an agonistic interaction. Reconciliation has an important function regarding social homeostasis (de Waal & van Roosmalen, 1979) as the victim of aggression is more likely to be attacked again after a conflict and this likelihood is reduced after reconciliation (Aureli *et al.*, 1989). Furthermore, after an aggressive interaction, victims show increased levels of self-scratching and elevated heart rates that are interpreted to indicate uncertainty. After reconciliation the levels were reported to drop to baseline-levels again (Aureli & van Schaik, 1991; Smucny *et al.*, 1996). If genital rubbing is a means of reconciliation in bonobos, it should occur more often after a conflict than before. As the victim profits more immediately from reconciliation than the aggressor in terms of reduced levels of anxiety and uncertainty, solicitations for genital rubbing were expected to be shown by the victim rather than by the aggressor.

(4) Genital rubbing may also serve as a ritualised display of social status (Nadler, 1990). By means of such ritualised displays, relations between two individuals can be formally displayed and thus agonistic interactions may be avoided. Therefore, asymmetries in the performance of this behaviour are to be expected. Dominant females should take the "male position "during genital rubbing, i.e. should be in the typical mounter's top position. Further, in a female dyad with a clear dominance relationship, the rates of solicitation should be asymmetric as well. As presentations directed towards a higher ranking partner often signal submissiveness (reviewed in Wickler, 1967), solicitations for genital rubbing were expected to be mainly carried out by the low-ranking partner.

(5) Alternatively, genital rubbing was hypothesized to help to regulate social tension during group excitement, mainly during feeding events (Kano, 1982; Kuroda, 1979, 1980, 1984). If this is the case, the frequency of genital rubbing should increase in the presence of food, especially when the food is not evenly distributed. Similarly, rates of genital rubbing should also be elevated above baseline levels when social groups are reunited after

a long time of separation. Additionally, dyads that performed genital rubbing should show less agonistic interactions than dyads that did not perform genital rubbing.

1.4 Female social status

Living in a social group offers several advantages for animals, like protection from predation, better defence of food resources against neighbouring communities or optimised foraging efficiency, and easier access to mating partners (Alexander, 1974; van Schaik & van Hooff, 1983; Wrangham, 1979, 1980). For females, protection from male harassment and infanticide are further reasons to associate with other individuals (Brereton, 1995; Smuts & Smuts, 1993; Sterck *et al.*, 1997; van Schaik & Kappeler, 1997; Wrangham, 1979). Living in a group also implies costs on group members, although these costs may vary between individuals. Competition for food is one of the most important costs of group living for females but not for males because of the strong asymmetry in the reproductive effort of mammals (Emlen & Oring, 1977). The density, quality and distribution of the resource determine the mode and intensity of food competition and finally shape the social relationships between females as it is summarised in the socio-ecological model (Sterck *et al.*, 1997; van Schaik, 1996; van Schaik & van Hooff, 1983).

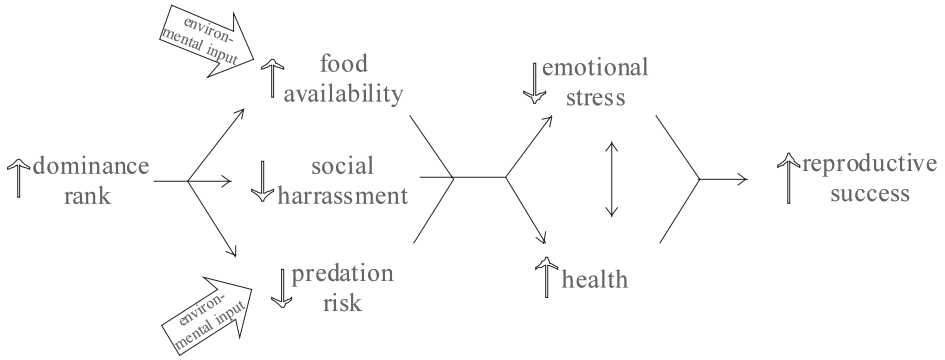

Fig. 1.1 Relationship between dominance and reproductive success. Model taken from (Ellis, 1995).

The cost of group living varies according to an individual's social position within the group. High social status translates into the power to exclude other individuals from access to resources like food, especially, when this resource is not spread evenly in the environment but occurs in discrete, monopolisable patches (Janson & van Schaik, 1988). Thus, high ranking individuals can gain a higher net food intake (van Schaik, 1989). Additionally, vulnerability to predation is reduced compared to low ranking individuals

because a high ranking individual can feed in the centre of the social group. And finally, they suffer less from harassment by other group members (Ellis, 1995). The main outcome of these effects of dominance are reduced emotional stress and good health, which in turn influence reproductive success (Fig. 1.1, (Ellis, 1995)).

Thus, the cost of group living should be smaller for high ranking than for low ranking females. The distribution and abundance of food influences the impact of dominance on reproductive success, which is maximised when resources are scarce or clumped (Ellis, 1995; Janson & van Schaik, 1988; van Schaik, 1989; van Schaik & van Hooff, 1983). There are many publications supporting this model for primates. In forest-living Hanuman langurs, physical condition correlates with dominance rank and high-ranking females are in the best condition (König, 2000). Social status together with reproductive history was found to influence the occurrence of fertile cycles in captive rhesus monkeys (Pope *et al.*, 1986). Similarly, improved nutritional state of dominant female olive baboons translates to shorter inter-birth intervals, higher infant survival and faster maturation of offspring compared to lower ranking individuals (Packer *et al.*, 1995). It has to be kept in mind that high social status can also infer negative aspects, like a greater incidence of miscarriages in this baboon species.

In addition, suppression of reproduction in subordinate mammals has been found to be mediated by high levels of aggression and harassment by high ranking individuals (Abbott, 1987; von Holst *et al.*, 2002; von Holst *et al.*, 1999). This is suggested to be the case in geladas, where the negative correlation between social status and number of offspring is argued to be a consequence of high rates of aggression towards low ranking females that disrupt their reproductive physiology (Dunbar, 1980; Dunbar & Dunbar, 1977). Female attack coalitions in yellow baboons are associated with a larger number of cycles to conception and longer inter-birth intervals in the low-ranking victims (Wasser & Starling, 1988). In African wild dogs, dominant individuals are more aggressive than subordinates and usually successful breeding is restricted to the dominant pair (Creel *et al.*, 1997). A decrease of reproductive success in subordinates attributed to social stress is also reported in other non-primate mammals, like rabbits (von Holst *et al.*, 2002; von Holst *et al.*, 1999). In general, more data supporting the link between dominance and reproductive success have been found for non-primates than for primates (excluding humans), the possible reasons for this are summarised in Ellis (1995).

Contrasting with this model, it was often assumed for chimpanzees that dominance is not important for female reproductive success (Wrangham, 1980) because they live in egalitarian societies where differences in status-dependent resource accessibility are expected to be small (Sterck *et al.*, 1997). Contrastingly, long-term data from Gombe reveal a higher lifetime reproductive success of high ranking females that is contributed to better physical condition (Pusey *et al.*, 1997). In comparison with chimpanzees, bonobo females are less solitary which has been attributed to reduced costs of foraging in parties (Furuichi, 1989; Kano, 1982; Wrangham, 1986). A higher percentage of herbaceous vegetation or leaves in the bonobo diet or larger fruit tree patches (White, 1986; Wrangham, 1986) was suggested to account for the reduced food competition. However, a comparative analysis could not support this idea (Chapman *et al.*, 1994). Actually, monopolisable food patches, like fruits of *Treculia*, play an important role in bonobo diet (Hohmann & Fruth, 2000b; Kuroda, 1984) and are mainly defended by and shared among females (Hohmann & Fruth, 1993; but see Ihobe, 1992b; Ingmanson & Ihobe, 1992; Parish, 1994; comment of B. Fruth on Stanford, 1998). Females dominate males, and support by a high ranking mother is important for a male bonobo to achieve high social status (Furuichi, 1997). Because support from the mother allows adult males to stay closer to the core of the group, this could translate into more mating opportunities for the respective male and more descendants for the high ranking mother (Furuichi, 1997). Additionally, high ranking females were shown to harass subordinate animals during mating in the wild as well as in captivity (Hohmann & Fruth, 2000a; Vervaecke & van Elsacker, 2000). This raises the question (a) if high social status confers advantages to female bonobos in situations when access to food is limited, and (b) if subordinate individuals suffer higher levels of social stress compared to high ranking animals.

The activity of the hypothalamo-pituitary-adrenocortical axis (HPA axis) has been shown to be a highly valuable indicator of disturbance. In general, a lack of predictability, lack of control and of an outlet for frustration were suggested to represent the main cause why a situation is perceived as stressful (de Boer *et al.*, 1989; Sapolsky, 1992a; Sapolsky, 1992b; Sapolsky, 1993; von Holst, 1998). Thus, the HPA axis is stimulated not only by environmental threats but also upon receiving aggression from conspecifics (Blanchard *et al.*, 2001 and references therein; Goymann *et al.*, 1999; von Holst, 1986; Wallner *et al.*, 1999). Correlates of glucocorticoid secretion and social status were assessed in many studies, focussing on males more often than on females. For example, elevated levels of

glucocorticoids have been found in subordinate baboons of both sexes (Sapolsky *et al.*, 1997; Virgin & Sapolsky, 1997), in horses (Alexander & Irvine, 1998), female rhesus monkeys (Gust *et al.*, 1993) and African elephants (Foley *et al.*, 2001), in male long-tailed macaques (van Schaik & van Noordwijk, 1986), rabbits (von Holst *et al.*, 1999) and rats (Blanchard *et al.*, 1998). Contrastingly, in many cooperative breeders with extreme reproductive skew, high ranking individuals have higher serum glucocorticoid levels than subordinates (African wild dogs: Creel *et al.*, 1997; dwarf mongooses: Creel *et al.*, 1996; marmosets: Saltzman *et al.*, 1994; Saltzman *et al.*, 1998). Other studies could not detect any difference in corticoid levels between subordinate and dominant individuals (female long-tailed macaques (van Schaik & van Noordwijk, 1986), female cynomolgous monkeys (Stavisky *et al.*, 2001), male mountain gorillas (Robbins & Czekala, 1997)).

When assessing an individual's basic glucocorticoid level it is important not to stress the subject during sample collection as this would lead to an immediate increase of corticoid secretion and thus elevate the basic hormone levels. Therefore, non-invasive methods, such as the analysis of faecal samples, are an ideal way to monitor adrenocortical activity, as they do not interfere with the study subject's well being. Furthermore, as faecal glucocorticoids represent plasma levels that are pooled over time, variability between different samples due to the circadian rhythm of hormone secretion is minimised (von Holst, 1998; Whitten *et al.*, 1998a).

Against this background, the last aims of this study were (1) to assess the female dominance hierarchy in the bonobo study groups based on the outcome of displacements, (2) to test whether females profit from high social status in terms of access to food sources when food distribution is clumped and (3) to investigate the relationship between social status and levels of faecal glucocorticoid excretion.

2 Methods

2.1 Data collection

All data for this study were collected on four captive mixed-sex groups of bonobos living in the zoos of Cologne, Stuttgart, Frankfurt and Twycross (GB). I observed these groups between October 1996 and March 1999 for periods of seven weeks to seven months (Table 2.1).

Table 2.1 Observation period and time.

Group	Observation period	Total observation time (h)	Observation time analysed° (h)
Cologne	Oct.1996–Feb.1997	443	443
Twycross	May-Jun.1997	302	293
Stuttgart	Aug.-Nov. 1997	531	506
Frankfurt	Aug.1998–Mar.1999	1068	820
Total		2344	2062

° For the analysis of behaviour, only those interactions were analysed that took part when the animals had the chance of being united as a complete group.

2.1.1 Study animals

The social composition of the study groups and information on age, reproductive status and relatedness of the animals are given in Table 2.2.

The two adult males of the Stuttgart group had been involved in severe fights in the past; therefore they joined the females alternately for a few hours every day and were kept solitary for the rest of the day. After Masikini's death in October 1997, Zorba joined the females during the whole day, but spend the night alone in a separate cage.

When observations started in Frankfurt, the animals had been split into two permanent subgroups for a couple of months. One group consisted of Salonga, her daughter and Bono, the other of Margrit, Natalie, Ukela and their daughters. As in Stuttgart, aggressive interactions in the past were the reason for the separation. The four adult females had cooperated in attacking and wounding the male on several occasions. After repeated reunification tests under constant observation, the two subgroups were reunited during daytime from October 1998 onwards.

Table 2.2 Composition of the study groups, age class, reproductive status and relatedness.

Group	Individual	Date of birth*	Age/sex class°	Reprod. status	Relatedness
Cologne	Bonnie	1976	AF	parous	
	Kamiti	21.1.1987	AF	nulliparous	
	Banya	1.2.1990	SF	menarche	daughter of Bonnie/Clyde
	Clyde	1981	AM	-	
	Kindu	23.9.1984	AM	-	son of Bonnie/Clyde
Twycross	Diatou	21.10.1977	AF	parous	
	Kichele	19.4.1989	AF	nulliparous	daughter of Diatou/Kakowet
	Kakowet	7.6.1980	AM	-	
	Jasongo	2.8.1990	IM	-	foreign orphan
	Keke	2.1.1994	IM	-	son of Diatou/Kakowet
Stuttgart	Kombote	1966	AF	parous	
	Daniela	17.6.1968	AF	parous	
	Lina	28.7.1985	AF	nulliparous	
	Chipita	1993	IF	-	foreign orphan
	Masikini	1973	AM	-	died 9.10.1997
	Zorba	1980	AM	-	
	Kirembo	10.12.1992	IM	-	son of Kombote/Masikini
	Diwani	11.8.1996	IM	-	son of Daniela/Masikini
Frankfurt	Margrit	1951	AF	parous	
	Natalie	1969	AF	parous	
	Salonga	2.5.1973	AF	parous	daughter of Margrit
	Ukela	19.12.1985	AF	parous	daughter of Natalie/Bono
	Ulindi	10.10.1993	IF	-	daughter of Natalie/Bono
	Binti	14.8.1995	IF	-	daughter of Ukela/Bono
	Cheka	18.3.1996	IF	-	daughter of Salonga/Bono
	Bono	1980	AM	-	

* Year of birth is estimated for wild born animals. All birth dates are taken from the zoo records or from the international studbook of bonobos.

° AF = adult female, SF = subadult/adolescent female, IF = infant female, AM = adult male, IM = infant male. Foreign orphan = infant was introduced to the group without mother.

Thus, with the exception of the Cologne group, all groups were one-male groups.

With regard to group size and composition, these captive groups were more similar to the smaller parties of wild-living bonobos in Lomako than to those in Wamba (Badrian & Badrian, 1984; White, 1992).

In the wild, females usually do not give birth before the age of 14 (Furuichi, 1989), in captivity, however, age at first parturition is around 9 years (Neugebauer, 1985). Consequently, the young females Kamiti and Kichele were judged to be adult although they would be grouped as adolescents in the wild. Thus, 11 adult females were present in these groups, with eight of them showing regular menstrual cycles. The other three females were pregnant or in lactational amenorrhoea (Diatou, Daniela, Lina). Two females

(Kombote/Salonga) conceived during the study period and gave birth after 230 and 237 days, respectively.

2.1.1.1 Housing conditions

The Stuttgart group inhabited two indoor enclosures of 49 m² and 11.3 m². Additionally, they had limited access to four small enclosures (20 m² in total) that were not visible for visitors or the observer. When temperature exceeded approx. 10° Celsius, access to additional outside enclosures was possible (38 m² and 30.0 m²).

The Cologne group lived in a big indoor enclosure of 145 m² with limited access to three smaller night cages of approx. 19 m² in total.

The indoor enclosure of the Twycross group measured approx. 66 m², temporary access to three small night enclosures (3 m² each) was also possible. On days without rain access to an outdoor enclosure of approx. 450 m² was possible in the afternoon.

In Frankfurt, three indoor enclosures were available (15 m², 27 m² and 32 m²), as well as four outdoor enclosures (18.5 m², 36 m² and twice 21 m²) that were opened when temperatures exceeded 10° C.

2.1.1.2 Feeding

The animals were fed 4-7 times daily with fruits and vegetables. Additionally, twigs and seeds were spread throughout the enclosure. Sometimes mash enriched with vitamins or minerals was also provided, which was usually given to each individual directly. Water was available *ad libitum* in Stuttgart and Frankfurt zoo and the Twycross outside enclosure. For the other groups, drinks were offered several times per day. Wood straw or straw was given every day to offer the possibility of nest building.

The Cologne group stayed together during all feeding events. In Twycross, all animals remained in the group during day time, but before the last feeding in the evening, Jasongo would be separated till the next morning, sometimes joined by Kakowet. Similarly, before the last meal in the evening, the male of the Frankfurt group was separated over night together with one or two adult females. After Masikini's death in Stuttgart, Zorba was separated from the females for the evening feeding as well.

2.1.2 Collection of behavioural data

In Cologne, Twycross and Stuttgart, I observed the animals on average on six days per week, whereas the Frankfurt group was observed on a daily basis with the help of a student assistant. The student assistant observed the group on one day per week. Observations began as soon as the groups were united in the morning or as soon as they had left their night cages and entered the big day enclosures. Depending on the working routine of zoo keepers, groups were observed five to eight hours per day, the student assistant observed for four hours per day on one day per week. Daily observation time included at least half of the feeding events.

All adult females, who had shown regular menstrual patterns in the past, were observed as focus animals (Altmann, 1974), independent of their current reproductive status. Young females (<10 years) were only included when menarche had occurred at least one year ago and were thus of an age when the first pregnancy could be expected. During each 30 minute focus interval, all sexual, agonistic and sociopositive interactions of the focus individual with other group members as well as the initiator and terminator of the interaction were recorded. The order of focus individuals remained the same on all observation days; however, the identity of the first focus individual changed each observation day.

In addition, sexual and agonistic interactions that involved non-focus individuals were recorded *ad libitum* (Altmann, 1974). A description of the behavioural elements that were recorded can be found inTable 2.3.

Copulation duration was measured with a digital watch and was defined as the time between the onset of pelvic thrusting after intromission and withdrawal of either participant. The occurrence of ejaculation - as inferred from the presence of seminal fluid visible on the female or male genitalia after copulation - could be recorded reliably only for the Frankfurt group.

Specifically, for genital rubbing, the identity of the interaction partners, their position, the initiator (the individual who presented her genitalia to the partner) and the specific context (during feeding/after aggression) were recorded. Although both females perform sideway movements during genital rubbing, their behaviour typically is not completely symmetrical (Kitamura, 1989). Consequently, the mounter was defined to be the more active partner, i.e. the female who moved her genitals with greater amplitude, whereas the mountee was

defined as the more passive individual who moved less. In case of genital rubbing taking place on the ground, the mounter usually assumes the top position. Additionally, this definition also allowed determination of the mounting female for other postures than described by Kuroda (1980), e.g. when genital rubbing is carried out while both females were hanging from a branch or a rope.

Table 2.3 Ethogram of the analysed behavioural elements.

Context	Behaviour	Description
food	taking food	A takes food out of hand / foot / mouth of B or from food pile in front of B (from distance < 30 cm) & stays next to B or leaves slowly; no sign of aggression.
	giving food	A actively offers / passes food to B.
	stealing food	A takes food from B and runs away.
	cofeeding	A + B (or more individuals) feed simultaneously on the same monopolisable food item / pile within arm's reach & turned ± towards each other.
	begging	A stretches out an extremity (hand with palm up or foot) towards B (while B is eating) from a distance ≤ 2 m or is staring into B's face or hands that hold the food from a short distance (≤ 30 cm) for ≥ 5 sec.
neutral	grooming	A searches through skin or fur of B using hands and/or mouth to remove parasites, dead skin, etc.
	approaching	A is approaching B to ≤ 2 m distance & remains in this range for ≥ 5 sec.
agonism	displacing	A approaches B who reacts by retreating (within ≤ 2 sec) (passive: B gives way to A).
	driving away	A approaches B at high speed, B runs away; vocalisation possible, no body contact.
	chasing	Like driving away, but A additionally runs after B for ≥ 2 m; vocalisation possible, no body contact.
	kicking / hitting	A kicks B with legs or slaps B with hands (no play face), usually with vocalisation.
	biting	A bites B.
	body contact aggression	Mutual kicking / hitting / biting of A and B, or a clear direction not recognisable.
	charging display	A suddenly charges closely past B or aimed at no one particular, usually with pilo-erection (de Waal, 1988a), may be accompanied by A dragging or shoving an object.
sex	genital inspection	A visually inspects B's genitals (distance ≤ 30 cm), may be accompanied by touching, poking, sniffing or licking; usually in direction male to female.
	sexual solicitation	A presents genitalia in the direction of B; ventral presentation: A is sitting & leaning back or lying on the back with legs spread apart to display the erected penis or the sexual swelling to B; dorsal presentation: A is standing quadrupedally with back facing to B & keeping eye contact with B.
	genital rubbing (gg-rubbing)	Females A and B rub genitals in lateral movements , usually in ventro-ventral position with A clinging arms and legs to B, may also occur in dorso-ventral position (Kuroda, 1980).
	copulation	A mounts B with intromission & pelvic thrusts, may occur in ventro-ventral or ventro-dorsal position.

2.1.3 Collection of behavioural data during feeding experiments

In Frankfurt, it was possible to carry out feeding experiments during which one big item of food was offered when no other dispersed food was available. In total, 21 experiments were conducted at a rate of 2 experiments per week. These experiments represented situations of a clumped food contest when individuals should actively compete for access to the monopolizable food item. Contrastingly, normal feeding events represented a dispersed food situation when competition for the evenly spread out small food items would not pay off. The keepers of the other zoos did not agree to the running of the experiments since they feared increased aggression within the groups.

A loaf of dry bread (750 g) or a whole watermelon (3-4 kg) was the monopolisable food item of choice, because this food is highly appreciated by the animals but rarely handed out by the care-givers (C. Knott, pers. comm.). This food was hidden in one of the three inside enclosures during absence of the animals. The food item was either covered with wood wool or placed behind a visual barrier that did not allow immediate detection when the animals entered the enclosure. Thus, the order of animals entering the experimental area was unlikely to influence the identity of the animal first taking possession of the food. When all dispersed food was eaten and some time had passed to guaranty motivation to take part in the experiment, access to the experimental enclosure with the hidden food was allowed.

All sexual and agonistic interactions as well as interactions related to food acquisition that happened during the first 15 minutes after the first animal had taken hold of the food were recorded *ad libitum* using a dictaphone and a video camera. For control, animals were observed for the same interactions and period of time 24 hours after the onset of the experiment. This corresponds to the matched-control method introduced by de Waal &Yoshihara (1983).

The identity of the food owner was recorded together with details on the initiation, duration and termination of ownership. Peering, extending a hand or foot and pouting of an individual towards the food owner were classified as begging behaviour. Co-feeding of the food owner with another individual, passing food to another individual, taking and stealing food from an owner (in the later case only if no overt defence or aggression by the food owner was observed) were classified as food sharing.

Additionally, the state of male sexual arousal was recorded during the first 15 minutes of the feeding experiment as well as during the control phase. The occurrence of partial and full penile erection was scan-sampled every minute during the feeding experiment as well as during the control phase (*sensu* Altmann, 1974).

2.1.4 Scoring of the genital swelling

Visual markers of reproductive condition were recorded in the morning and late afternoon of each observation day. More specifically, details of the appearance of wrinkles, turgidity, shine and colour of the genital and the peri-anal area as well as the presence or absence of labial occlusion (Dahl, 1986) and menstrual bleeding were recorded. Additionally, the degree of sexual swelling was scored according to a 3 step rating system ranging from 1 (no tumescence: deep wrinkles in labia, swelling wobbly) to 3 (maximum tumescence: no wrinkles on labia, maximum firmness) as had been described for wild bonobos by Furuichi (1987).

2.1.5 Collection of faecal samples

To assess the female endocrinological state non-invasively by analysing the excretion pattern of respective hormones (Heistermann *et al.*, 1996), faecal samples were collected from all adult females. In order to avoid the influence of diurnal variation in excretion patterns, samples were only collected in the morning. The collection of faeces instead of urine was favoured because it did not need immediate recovery of the excrement after voiding which would require separation of the group and therefore disturb the animals. Defecation was recorded during observation of the group and the sample collected later, when the group had to shift cages because the keepers wanted to clean the enclosure or spread food. Only samples not contaminated with water or urine were taken. Samples were collected in commercial freezer bags and mixed by kneading to ensure that steroids were distributed evenly in the faeces. An approximately walnut sized aliquot was transferred into a clean film canister and stored at –20 °C until further analysis. This yielded in 3-4 samples per female and week for the groups of Stuttgart, Cologne and Twycross as a result of losses of samples due to normal activity of the animals (e.g. samples could not be identified properly anymore after straw had been moved through the enclosure during charging displays, etc.). It was possible to increase successful sampling frequency for the Frankfurt group by feeding each adult individual with another type of indigestible seed

(e.g. sesame seed, millet) or red root, which allowed easy identification of individual faecal samples. Thus, 5-6 samples per female and week could be collected in this group.

2.2 Data analysis

2.2.1 Analysis of behavioural data

Only interactions among adult individuals and only those observations were analysed that had been recorded during presence of the whole group. Thus, results were not biased by artificially reduced choice of potential interaction partners. For most analyses of dyadic interactions, rates per dyad, day and hour were calculated for the respective types of behaviour using the programme SPSS for Windows, version 8.0. Values of interaction rates are given as mean ± standard deviation (SD). As not all animals or dyads showed all behaviours investigated (e.g. the two females of the Cologne group were not observed to copulate), sample numbers can be smaller than the total number of possible dyads.

Following Beach (1976), female sexual interactions were categorised according to proceptivity, attractivity and receptivity. Female solicitations were attributed to proceptive behaviour, male solicitations, male genital inspections, successful female solicitations and copulations to attractivity and successful male solicitations were qualified as receptive behaviour.

To assess the influence of the presence of food on behaviour, the periods of 15 minutes before and after the onset of regular feeding were defined to represent the context of dispersed feeding. The time before the actual feeding was included into the analysis because the animals could see the preparation of food (e.g. cutting of food, keepers passing by with the food etc.) and reacted to it by giving food calls and by increased activity. Actual feeding time for specific meals could differ as much as one to two hours from day to day. As setting up the feeding experiment required less preparation and took place at least one hour before the experiment, the clumped food context comprised only the first 15 minutes after the start of the feeding experiment. All remaining periods of time were contributed to the context "no food".

Similarly to the food context, time windows of 15 minutes before or after a conflict were defined to represent the pre- or post-conflict intervals, which were compared regarding the occurrence of genital rubbing between the opponents.

For the determination of dominance hierarchies within groups, only cases where a clear winner and loser of the interaction could be determined were taken into analysis, all cases with unclear outcome were excluded.

To assess dyadic dominance relationships, a dyadic dominance index was calculated according to the following equation (Cavigelli, 1999):

Dyadic dominance index $DDI_{AB} = \frac{(A\,displaces\,B)}{(A\,displaces\,B)+(B\,displaces\,A)}$

This index was calculated for displacements as well as for the three types of agonistic interactions recorded. As in most primate and other mammalian species females and males form separate dominance hierarchies (e.g. chimpanzees (Goodall, 1986), hyenas (East & Hofer, 2001), rabbits (von Holst *et al.*, 1999)), only interactions among adult females were analysed.

To assess the overall competitive ability of an animal within the group, total dominance indices were calculated according to the following equation:

Total dominance index $TDI_A = \frac{\sum_{n=1}^{i} (A\,displaces\,Y_i)}{\sum_{n=1}^{i} ((A\,displaces\,Y_i)+(Y_i\,displaces\,A))}$.

2.2.2 Analysis of swelling data

Since morning and evening scores of sexual swelling were highly related (Cramer coefficients of association 0.9 - 1.0 for each female), only morning data were used for further analysis. When using the swelling score of Dahl (1986), not all females reached all swelling stages which made the analysis of many swelling stages impossible. Therefore, only the degree of sexual swelling scored according to rating system ranging from 1 (no tumescence) to 3 (maximum tumescence) as had been described for wild bonobos by Furuichi (1987) was used for further analysis. With this rating system, all swelling stages were reached in every menstrual cycle. Thus, a high degree of objectivity and inter-animal comparability in rating swelling changes was provided. As well, comparisons with other studies became possible.

When applying Furuichi's swelling scores, the period of maximum sexual swelling was defined as lasting from the first day of occurrence to the last day seen in a given swelling cycle. In other words, short periods of lower tumescence (< 3 days) within the phase of

maximum tumescence were ignored, if the swelling score did not drop below stage 2. Since observations were done on six days per week for the groups of Cologne, Twycross and Stuttgart, duration of swelling phases of individuals of these groups may include an error of one day. Because of the daily observation of the Frankfurt group, this is not the case for the females of this group.

2.2.3 Hormone analysis

All hormone analyses were carried out by me at the Department of Reproductive Biology, German Primate Centre (DPZ), Göttingen. In total, 1040 faecal samples were lyophilised, pulverised, extracted and analysed. The analysis of the excretion pattern of sex hormones followed the protocol previously published by Heistermann (1996), the analysis of the cortisol-metabolite 11-oxoetiocholanolone was carried out according to the protocol by Bahr (2000).

2.2.3.1 Sample preparation

Nutrition, the health status of an animal, and other factors were shown to result in a considerable variability in the water content of faeces (Wasser *et al.*, 1988), therefore samples were lyophilised at -30° C (Christ, Alpha II – 12) before further processing. All solid, inert material (e.g. undigested seeds) was removed from the dried sample by carefully pulverising the sample with a mortar and passing it through a commercial sieve. The resulting faecal powder was transferred into plastic tubes and stored at –20° C till extraction.

2.2.3.2 Extraction

Two types of extractions were carried out. Methanol extractions were carried out for later analysis of immunoreactive pregnandiol, oestrogen and 11-oxoetiocholanolone. Oestrogen excretion was additionally analysed in samples extracted with ether.

2.2.3.2.1 Methanol extraction

The extraction procedure followed the protocol given by Möhle (1995) & Heistermann *et al.* (1996) with small changes. Aliquots of the faecal powder (0.07-0.15 g) were weighed into 15-ml polypropylene screw-top vials (Fa. Sarstedt), 5 ml methanol (40 %, v:v) were

added and vortexed for 15 minutes. After centrifugation at 5000 rpm (5 minutes at room temperature), the supernatant was decanted into a glass vial, closed with a polypropylene lid and stored at –20° C till further analysis. The faecal pellet was discarded.

To determine efficiency of different extraction series (max. 72 samples per series), 50 µl ^{3}H-progesterone (approx. 5000 cpm/50 µl in 100 % ethanol; NEN Du Pont, Bad Homburg, Germany) were added to 10 samples per extraction series and incubated for 10 minutes at room temperature. The subsequent steps of the extraction were carried out together with the other, not tritium-marked samples.

100 µl of each tritium-marked extract were transferred into scintillation tubes, 3 ml scintillation liquid were added and the radioactive decay of the tracer was counted for 60 s. Mean (± SD) efficiency for all extraction series (n = 21) was 60.9 ± 4.9 %, with a range from 51.3 % to 69.6 %.

2.2.3.2.2 Ether extraction

Apart from the method mentioned above, an alternative oestrogen-specific extraction was tested following a protocol kindly provided by Prof. Möstl and Dr. Palme (Institute for Biochemistry and Veterinary Medicine, University of Vienna). Here, for the determination of extraction efficiency, the tracer hormone was added to each sample of an extraction series.

Aliquots of faecal powder (0.05-0.10 g) were weighed into 30-ml polypropylene screw-top vials and 20 µl ^{3}H-oestradiol tracer (approx. 5000 cpm) were added. After incubation for 10 minutes, 0.7 ml *aqua bidest*. was added, the tube was thoroughly mixed by hand and incubated for another 10 minutes. Then 10 ml diethylether / n-hexane (1/4, v:v) were added and the mixture was vortexed for 10 minutes. Following snap freezing of the aqueous phase, the supernatant organic phase was decanted into a glass vial. This first extraction step removed water soluble contamination factors.

The organic phase was evaporated to dryness under nitrogen, reconstituted in 0.5 ml choloroform / n-hexane (6/4, v:v) and re-extracted with 0.5 ml 1 M KOH by vortexing for 2 minutes and subsequent centrifugation (3000 rpm, 10 min, 4°C). This second extraction step separated oestrogens from other steroids by turning the phenolic A ring of the oestrogens into a water-soluble salt. Thus, only oestrogens dissolved in the KOH phase. 300 µl of this KOH phase were recovered and combined with 15 µl glacial acetic acid to

re-establish the normal form of the phenolic A ring. After appropriate dilution, this extract could be directly taken into enzyme immunoassay.

Mean extraction efficiency of all 28 series was 59.3 ± 4.0 % (range 53.8 % - 66.2 %).

2.2.3.3 Enzyme immunoassays

Hormone concentrations were quantified using competitive enzyme immunoassays.

2.2.3.3.1 Quantification of immunoreactive oestrone-3-glucuronide

Faecal methanol extracts were analysed for their content of immunoreactive oestrone-3-glucuronide (iE1C) with an antibody produced by rabbits against oestrone-3-glucuronide-BSA (bovine serum albumin). Cross-reactivity of this antibody is shown in Table 2.4.

Table 2.4 Specific cross-reactions of the oestrone-3-glucuronide antibody at 50 % binding.

Steroid	% Cross-reactivity
oestrone-3-glucuronide	100.0
oestrone	71.0
oestrone-3-sulfate	17.0
17β-oestradiol	0.9
17β-oestradiol-3-sulfate	0.2
17β-oestradiol-3-glucuronide	<0.1
pregnandiol-3-glucuronide	<0.1

The standard curve covered 1.9 – 250 pg/well. Faecal extracts were directly taken into assay after appropriate dilution with assay buffer (follicular and luteal phase 1:8, pregnancy 1:20). Extracts were analysed in duplicates along with the standard and quality controls. The E1C antibody was diluted 1:200000. Oestrone-glucuronide bound to alkaline phosphatase was used as the labelled marker hormone in a dilution 1:4000. After over-night incubation of extracts and standards with label and antibody at 4 °C, bound steroids were separated from free steroids by washing with wash buffer. The addition of 150 µl phosphatase substrate (20 mg/15 ml buffer) started an enzymatic reaction that caused a change in colour which was measured with a photometer (Dynatech, MR 5000, wave length: 405 nm, referential filter: 630 nm). The steroid concentration in the samples was interpolated from standard curve values using the programme Mikro Tek (Microtec Laboratory systems GmbH).

Variation of measurements within and between assays was investigated by replicate determination of quality control pools (at 30 % and 70 % binding). Intra-assay coefficients of variation gave values of 2.6 (n = 15) and 4.0 (n = 17), inter-assay coefficients were 14.3 (n = 41) at 30 % binding, 16.7 (n = 41) at 70 % and 17.8 for faecal control pools (n = 27). The sensitivity limit - determined as 90% binding - was 8 pg/tube for E1C. Validation of the assays for the faecal extracts was assured by testing for parallelism in which the slope of curves produced by serial dilutions of extracts were compared to that of the standard curve. Following probit transformation of the data, the slopes of the lines were compared and found not to differ significantly (ANCOVA df = 2, F = 1.771, p = 0.20). For accuracy see Möhle (1995).

2.2.3.3.2 Quantification of immunoreactive oestradiol

Faecal ether extracts were analysed for immunoreactive oestradiol (E_2) with a commercial monoclonal mouse antibody raised against 17β-oestradiol-BSA (Dunn Labortechnik GmbH, Asbach, Germany). Table 2.5 shows the specificity of this antibody.

Table 2.5 Specific cross-reactions of the estradiol antibody at 50 % binding.

Steroid	% Cross-reactivity
17β-oestradiol	100.0
oestrone	<0.1
oestriol	<0.1
cortisol	<0.1
testosterone	<0.1
progesterone	<0.1

The antibody was diluted 1:12000. Oestradiol bound to alkaline phosphatase was used as the labelled marker hormone in dilution 1:3000. Faecal ether extracts were diluted 1:5 with assay buffer and then directly taken into assay. The standard curve covered 0.49 – 125 pg/well. Extracts were analysed in duplicates along with the standard and quality controls as described above. Serial dilutions of faecal extracts gave displacement curves that did not differ from the standard curve after probit-transformation (ANCOVA df = 5, F = 10.413, p = 0.43). Intra-assay coefficients of variation gave values of 3.8 (n = 15) and 7.2 (n = 17), inter-assay coefficients were 11.3 (n = 28) at 30 % binding, 16.0 (n = 28) at 70 % and 18.3 for faecal control pools (n = 23).

2.2.3.3.3 Quantification of immunoreactive pregnandiol

The amount of immunoreactive pregnandiol (iPd) in the methanol extracts was assessed using an assay with an antibody produced by rabbits against pregnandiol-glucuronide-BSA. While the antibody was originally produced to cross-react with pregnandiol-glucuronide, using a pregnandiol standard for the standard curve allowed quantification of unbound iPd. The antibody was added to the plate in a dilution of 1:200000 and biotin-labelled marker hormone in a dilution of 1:120000. The cross-reactivity of the iPd antibody can be taken from Table 2.6.

Table 2.6 Specific cross-reaction of the pregnandiol antibody at 50 % binding.

Steroid	% Cross-reactivity
pregnandiol	100.0
pregnandiol-3-glucuronide	500.0
20α-hydroxyprogesterone	205.0
17α-hydroxyprogesterone	1.0
progesterone	1.0
oestrone	<0.1
oestradiol	<0.1

Depending on the reproductive status, samples were diluted 1:2 (follicular phase) to 1:40 (pregnancy). The standard curve covered 39-10000 pg/well.

The assay was pipetted as described previously. After over-night incubation, 150 µl/well streptavidin-peroxidase (20 µl/15 ml assay buffer) were added. After incubating for 30 minutes (room temperature, in darkness) and washing again, 150 µl peroxidase-substrate were added. Samples were incubated in darkness at room temperature until the colour of the solution changed to blue. The reaction was stopped by acidifying with 50 µl/well 4N NH_2SO_4 and the extinction was measured as described above. Serial dilution of faecal extracts yielded displacement curves that did not differ from the standard curve (probit transformation, ANCOVA df = 3, F = 1.599; p = 0.23). At 30 % and 70 % binding, intra-assay coefficients of variation gave values of 6.1 (n = 15) and 14.1 (n = 17), inter-assay coefficients were 15.0 (n = 63) and 16.6 (n = 63), respectively. The sensitivity limit - determined as 90% binding - was 150 pg/tube.

2.2.3.3.4 Quantification of immunoreactive 11-ketoetiocholanolone

A rabbit antibody raised against 11-ketoetiocholanolone-17-CMO-BSA (kindly provided by Prof. Möstl) was used to measure the amount of immunoreactive 11-ketoetiocholanolone (= 11,17-dioxoandrostane = DOA) in the faecal methanol extracts. The antibody was added to the assay in a dilution of 1:65000 and the biotin-labelled marker hormone in a dilution of 1:2240000. The cross-reactivity of the DOA antibody can be taken from Table 2.7. For further cross reactions see Palme & Möstl (1997).

Table 2.7 Specific cross-reaction of the 11-ketoetiocholanolone antibody at 50 % binding.

Steroid	% Cross-reactivity
11-ketoetiocholanolone	100.0
pregnanolone	37.00
11-hydroxyetiocholanolone	3.3
11-ketoandrosterone	<1.0
etiocholanolone	<1.0
pregnanediol	<1.0
pregnanetriol	<1.0
cortisol	<1.0
tetrahydrocortisol	<1.0

Depending on the reproductive status, samples were diluted 1:80 (ovarian cycles) to 1:150 (pregnancy). The standard curve covered 0.45-125 pg/well. The assay was pipetted as described previously. Incubation with substrates for the biotin-labelled marker hormone was the same as described for the pregnandiol assay. Serial dilution of faecal extracts yielded displacement curves that did not differ from the standard curve (probit transformation, ANCOVA df = 6, F = 0.517; p = 0.79). At 30 % and 70 % binding, intra-assay coefficients of variation gave values of 5.15 (n = 17) and 8.93 (n = 17), inter-assay coefficients were 10.92 (n = 23) and 17.14 (n = 23), respectively. The sensitivity limit was 0.40 pg/tube.

2.2.4 Duration of menstrual cycles

The duration of intermenstrual intervals was defined to last from the first day of menstruation to the day before onset of the consecutive menstruation (Rowell, 1972; Strassmann, 1996). Published data from previous studies were treated the same with the exception of cycles extracted from Furuichi (1987) on wild bonobos (n = 6). Here, inter-swelling intervals were calculated from Fig. 1 of Furuichi's publication as menstruation is

usually difficult or impossible to observe in the wild (Furuichi, 1987; G. Hohmann, pers. comm.). An inter-swelling interval was defined to last from the first day of detumescence of sexual swelling to the last day of maximum tumescence in the following cycle (Wallis, 1997). Therefore, cycle duration refers to both, intermenstrual intervals and inter-swelling intervals.

2.2.5 Determining ovulation and the follicular and luteal phase

The excretion pattern of immunoreactive pregnandiol (iPd) was used to identify the follicular and luteal phase of the menstrual cycle. In primates, the follicular phase is typically marked by low levels of circulating gestagens, whereas the luteal phase is characterised by high levels of these hormones. The significant postovulatory increase in iPd excretion was defined by an increase above the threshold level of two standard deviations above the mean of the five preceding samples (Royston, 1983). Apart from being a significant increase, iPd also had to show a sustained rise, i.e. at least three consecutive samples had to show iPd levels above the threshold to indicate the onset of the postovulatory phase of the ovarian cycle.

The presumed day of ovulation was set to three days prior to the day of the defined faecal iPd increase taking into account a previous study on captive bonobos (Heistermann *et al.*, 1996). Fig. 2.1 exemplifies how ovulation was determined for any menstrual cycle. Due to possible variability in the temporal relationship between ovulation and the post-ovulatory faecal progestin increase, data on timing of ovulation is expected to have an error of ± 1 day.

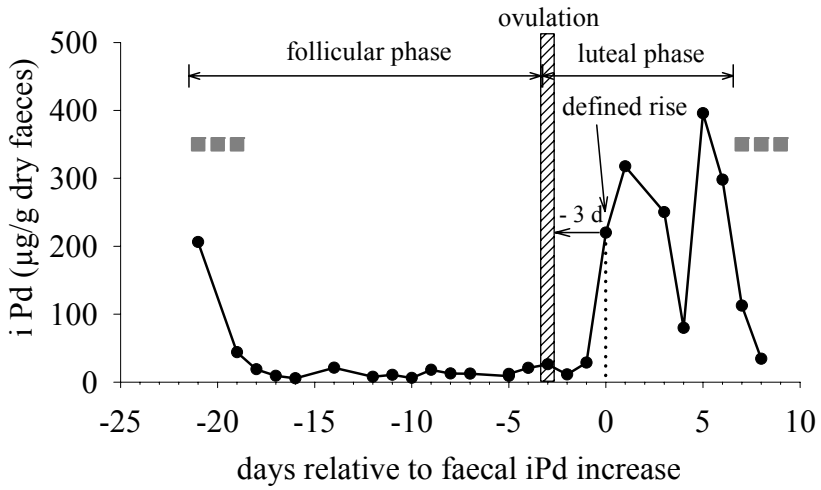

Fig. 2.1 Determination of the day of ovulation and calculation of the follicular and luteal phase of the menstrual cycle. Grey squares indicate days with menstrual bleeding.

The fertile phase of an ovarian cycle was determined to comprise the day of ovulation plus the three preceding days, as copulations can lead to conception in a window of time spanning the functional life of the spermatozoa and the ruptured egg (France, 1981; Gomendio & Roldan, 1993a, 1993b).

The follicular phase was determined to last from the first day of menstruation to the day prior to ovulation. The luteal phase comprised the day of ovulation to the day before the next menstruation (Fig. 2.1).

2.2.6 Validation of the 11-ketoetiocholanolone assay

11-Ketoetiocholanolone (or 11,17-dioxoandrostane = DOA) has been identified as the major cortisol metabolite excreted into urine and faeces in common marmosets, long-tailed macaques and chimpanzees (Bahr *et al.*, 2000). Therefore, it was decided to use this assay to address the the relationship between social status and levels of glucocorticoid excretion. However, Bahr *et al.* (2000) have not tested whether excreted iDOA is a biologically meaningful indicator of the activity of the HPA axis. Therefore, before applying this methodology to bonobos, the assay was validated. The first step was to show that faecal iDOA has physiological relevance as an indicator of stress in chimpanzees. This was achieved by investigating the change of excreted hormone levels after administration of exogenous ACTH (adrenocorticotrophic hormone) which is known to stimulate the HPA axis leading to an increased release of glucocorticoids. In the second step, the physiological relevance of faecal iDOA in bonobos was tested in three approaches. Firstly, the impact of anaesthesia on glucocorticoid levels was assessed in individuals who needed sedation. Previous studies have shown that anaesthesia activates the HPA axis (e.g. chimpanzees: (Whitten *et al.*, 1998b)), most probably due to the disorientation just before the loss of consciousness (Sapolsky, 1982). Secondly, it was investigated whether the reunification of a social group that had been separated for several months influenced basal glucocorticoid levels. Assuming that this reunification represents a period of increased social tension and possibly high social stress, because animals have to confirm or defend their social rank, it was expected that this would result in an increase of individual glucocorticoid levels when compared to the time before reunification. And thirdly, I evaluated whether glucocorticoid levels were higher in pregnant females as compared to non-pregnant subjects as glucocorticoid levels are known to be raising constantly during pregnancy in apes and humans, peaking shortly before parturition (Cavigelli, 1999).

2.2.6.1 Validation for chimpanzees

Faecal samples following an ACTH challenge were available from one adult male common chimpanzee (*Pan troglodytes*) living together with one female in the zoo of Halle, Germany. The challenge was carried out by Dr. N. Bahr who kindly provided those samples for further analysis. The chimpanzee was anaesthetised with ketamine and injected i.m. with 25 IU of ACTH. During 48 hours following treatment, all faecal samples were collected. Samples collected four and three days before treatment were used as base line values.

2.2.6.2 Validation for bonobos

Three different approaches to validate the assay for bonobos were taken:

(1) The Frankfurt zoo offered the opportunity to investigate the impact of sedation on glucocorticoid levels when the animals had to be anaesthetised for a routine health check, withdrawal of blood for medical analysis and microchip implantation. Daily faecal samples of three adult females were analysed for the excretion pattern of iDOA ten days before and after anaesthesia.

(2) The same group of animals had been split into two subgroups for several months when I started with the data collection. After approximately six weeks of observation, the group was reunited for a couple of hours on two days before the reunification became permanent for the rest of the study period (from October 1998 on). Individual iDOA levels during reunification where compared to the week before and after.

(3) Faecal glucocorticoid levels of samples collected during pregnancy were compared to non-pregnant periods. Samples collected during pregnancy were available from Diatou, Kombote, Lina and Salonga.

2.2.7 Analysis of 11-ketoetiocholanolone levels

To investigate the relationship between social rank and adrenocortical activity, two faecal samples per week and female were analysed for the excretion of iDOA. Because of the diurnal excretion pattern of glucocorticoids, only samples shed before noon were used for this analysis. Since Bahr *et al.* (2000) found that peak radioactivity in chimpanzee faeces was detected after 22 hours, the excretion patterns of iDOA were corrected for a time lag of one day.

2.2.8 Statistical analysis

Unless otherwise indicated, all interactions were analysed on a dyadic level. More specifically, rates of interactions were compared between different contexts by comparing rates per dyad using non-parametric tests for related samples (Wilcoxon signed rank pair test, Friedman-ANOVA test). All statistical analyses were carried out using the programme Statistica (StatSoft Inc. (1999), Tulsa, USA), the α-level of significance was 0.05 (two-tailed). Because of the relatively small sample size, all p values given resemble exact probabilities (Siegel & Castellan 1988; Mundry 1998).

Some females contributed more than one data set of menstrual or swelling cycles to this study. The respective values were assumed to be independent when females had either changed their reproductive status (nulliparous to parous, normal menstrual cycles to lactation cycles), or when several years had passed between the phases of data collection. To evaluate the influence of reproductive status on duration of cycles, mean values per female and reproductive status were compared using the Kruskall-Wallis test. When relating the duration of cycles to maximum tumescence or to follicular/luteal phase, a high intra-individual variability became obvious, that rendered the use of median or mean values for these correlations questionable. On the other hand, working with individual cycles would bias results because of over-representation of certain females. For these reasons, permutation or randomisation tests were carried out. Repeatedly, one data pair per female was selected and Spearman correlation coefficients were calculated, until either all possible combinations had been calculated (permutation test) or until 10000 bootstraps of randomisation had been carried out.

To assess whether genital rubbing translates into food sharing, correlations between matrixes were analysed with the programme MatMan (Version 1.0, Noldus Information Technology, Netherlands).

To compare glucocorticoid levels between individuals, mean values ± SD were calculated for each female. If a female had changed her reproductive status in the course of the study (e.g. from lactational amenorrhoea to menstrual cycles), mean iDOA values were calculated for each reproductive phase. Log-transformation of hormone data resulted in normal distribution. Therefore, all hormone values were transformed before being put to test and parametric statistical procedures were applied. The α-level of significance was 0.05.

3 Results

3.1 Variability of menstrual cycles and swelling patterns

This first part of the study investigates the variability of menstrual cylces and patterns of sexual swelling in bonobos. It is analysed, first, whether the duration of menstrual cycles is influenced by a female's reproductive history, second, whether the duration of sexual tumescence co-varies with cycle duration, and third, whether the duration of the follicular phase or of the luteal phase correlates with the duration of menstrual cycles.

3.1.1 Influence of the reproductive status

Mean duration of all cycles cited was 39.41 ± 7.86 days (N = 27 observation periods, range of means 25.7 - 54.0 days). The duration of cycles was found to vary significantly in dependence on the reproductive status of the female (nulliparous: 37.45 ± 6.91 days; parous & non-lactating: 35.44 ± 5.59 days; lactating: 48.18 ± 5.24 days; Kruskal Wallis test: KW = 10.235; N = 27; $p < 0.01$; Fig. 3.1). During lactation, cycles lasted significantly longer than when females were not lactating (parous/non-lactating: n = 11; lactating: n = 7; Kruskall Wallis post hoc multiple comparison; z = 2.990; $p < 0.01$; Fig. 3.1).

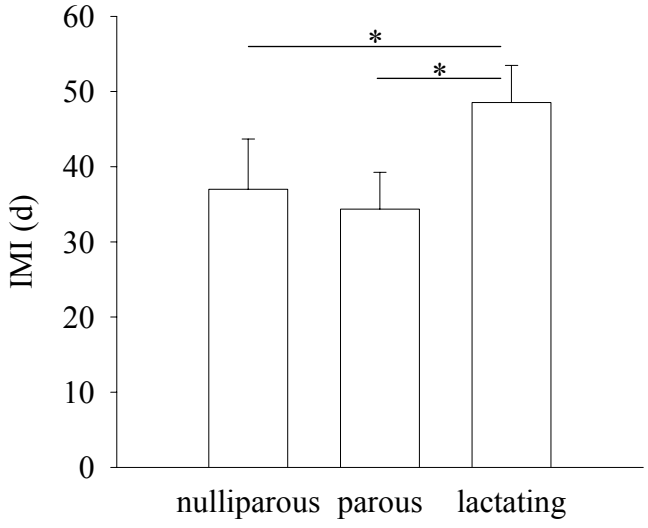

Fig. 3.1 Duration of menstrual cycles in nulliparous, parous, and lactating parous bonobo females. $N_{nulliparous} = 9$, $n_{parous} = 11$, $n_{lactating} = 7$; * = $p < 0.05$, Kruskall Wallis post hoc multiple comparison. IMI = intermenstrual interval.

Cycles of nulliparous females did not differ significantly from parous females (parous/non-lactating: n = 11; nulliparous: n = 9; Kruskall Wallis post hoc multiple comparison;

$z = 0.342$; $p > 0.50$; Fig. 3.1), but were significantly shorter than those of lactating females (nulliparous: $n = 9$; lactating: $n = 7$; Kruskall Wallis post hoc multiple comparison; $z = 2.593$; $p < 0.01$; Fig. 3.1). When excluding the elder females Kosana, Kitty and Lannie from the nulliparous group so that this group is more representative of young females during adolescent sterility, the difference between parous and nulliparous females became bigger but did still not gain significance (parous/non-lactating: 35.44 ± 5.59 days; N = 11; nulliparous: 40.26 ± 6.93 days; N = 6; Mann-Whitney U test; $z = 1.206$; $U = 21$; n.s.).

3.1.2 Intermenstrual intervals and maximum swelling

Data on intermenstrual intervals (IMI) were available from three of the four study groups over a period of 409 days in total. In the fourth group (Stuttgart), none of the three adult females contributed data on intermenstrual intervals to the study, as they were either conceiving right at the onset of the study (females Kombote and Lina) or were in early lactational amenorrhoea and therefore acyclic (female Daniela). In total, data on 18 intermenstrual intervals were recorded of 7 different females.

To assess the influence of the reproductive status on cycle duration, published data from Furuichi (1987) on wild specimen and from Dahl (1986), Vervaecke *et al.* (1999), Thompson-Handler (1990) and Heistermann *et al.* (1996) on captive animals were added to the data set described above. Table 3.1 gives an overview on cycle duration, age and reproductive history of all females. Both Vervaecke *et al.* (1999) and Thompson-Handler (1990) published data that were extracted from long term records of zookeepers. One female of Dahl's publication (1986) was excluded from this comparison because of her unclear reproductive history.

When assessing the association of cycle duration and swelling patterns, data from Dahl (1986) were excluded from the analysis since a different methodology of scoring the genital swelling was used compared to the other studies. This resulted in a total number of 58 cycles of 16 females.

Table 3.1 Female age, reproductive status and cycle duration (intermenstrual interval, IMI).

Female	Year of birth[1]	Age at data collection (years)[2]	Reproductive history	No. of cycles[3]	IMI ± SD (days)	Ref.[4]
Bonnie	1976[w]	?	Parous	5 (6 mo.)	35.60 ± 3.13	2
		20	Parous	3 / 1	25.70 ± 0.60	1
Catherine	??	16-17	Parous	9	36.11 ± 4.37	3
Daniela	1968[c]	10-21	Nulliparous+other	32	32.72 ± 5.85	3
		?	Parous	14 (2 yrs)	42.71 ± 4.14	2
Dzeeta	1970[w]	14-17	Parous	21	31.00 ± 3.45	3
		?	Parous	73 (16 yrs) / 3	30.71 ± 3.63	2 / 6
Hermien	1978[w]	8-10	Nulliparous	3	53.33 ± 14.19	3
		?	Parous	5 (5 yrs) /1	43.20 ± 8.47	2 / 6
Hortense	1978[w]	9-10	Nulliparous	4 /1	34.00 ± 2.45	3
Kame		35-40 yr	Lactating	2	49.50 ± 3.50	4
Kamiti	1987[w]	10	Nulliparous	1 / 1	40	1
Kichele	1889[c]	8	Nulliparous	1 / 1	38	1
Kitty	1951[w]	34-35	Nulliparous	13	31.92 ± 4.11	3
Kosana	1980[w]	?	Nulliparous	8 (2 yrs) / 1	31.88 ± 3.36	2 / 6
Lannie	??	30-31	Nulliparous	13	31.69 ± 6.72	3
Laura	1967[c]	14	Lactating	7	40.28 ± 10.50	5
Lorel	1969[c]	13	Lactating	10	50.5 ± 10.50	5
Margrit	1951[w]	27-37	Parous	33	37.33 ± 7.08	3
		48	Parous	6 / 5	32.7 ± 4.10	1
Mitsu		30-35 yr	Lactating	2	42.00 ± 2.80	4
Natalie	1969[w]	13-21	Nulliparous	67	35.31 ± 8.93	3
		29	Lactating	3 / 3	48.00 ± 8.50	1
Salonga	1973[c]	7-8	Nulliparous	9	40.89 ± 15.7	3
		26	Nactating	2 / 2	53.00 ± 2.80	1
Sen		35-40 yr	Parous	2	42.00 ± 0	4
Ukela	1985[c]	14	Lactating	2 / 2	54.00 ± 15.60	1
total				366 / 21		

1 c = born in captivity, w = wild born

2 age at study of swelling pattern

3 No. cycles for relationship of IMI and swelling: in parentheses: the time interval from which data were originally taken. Behind slash: No. cycles for correlation of cycle phases & cycle duration.

4 references: 1 = this study, 2 = (Vervaecke *et al.*, 1999), 3 = (Thompson-Handler, 1990), 4 = (Furuichi, 1987), 5 = (Dahl, 1986), 6 = (Heistermann *et al.*, 1996).

Cycle length varied between 24 and 65 days, the period of maximum tumescence between 1 and 24 days (Fig. 3.2). Using a randomisation test, one cycle per female per observation period was chosen randomly and the relation between duration of the cycle and of the phase of maximum tumescence was assessed by calculating the Spearman coefficient of correlation. After 10000 bootstraps a mean correlation coefficient of 0.668 (n = 16) was

obtained, with the 95 % interval of confidence ranging from 0.505 to 0.826, i.e. menstrual cycle duration and duration of maximum tumescence show a highly positive correlation.

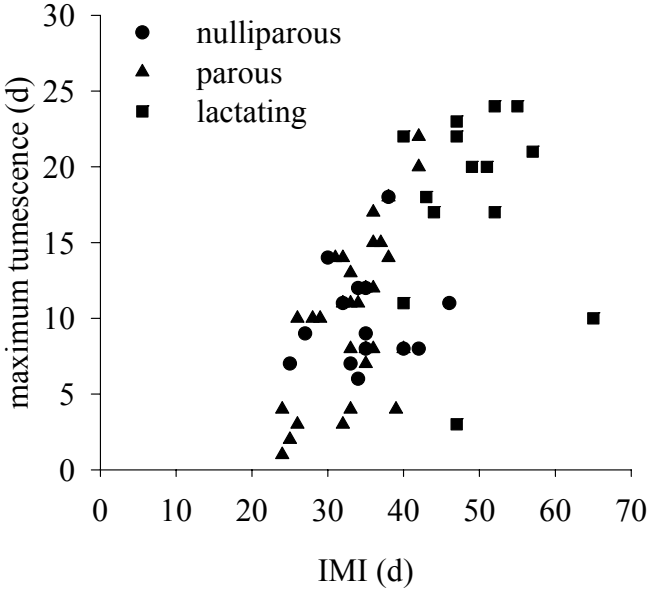

Fig. 3.2 Duration of maximum sexual tumescence and cycle duration in bonobo females. Individual cycles of nulliparous, parous and lactating females are shown; $n_{nulliparous} = 14$, $n_{parous} = 30$, $n_{lactating} = 14$. IMI = intermenstrual interval.

3.1.3 Determination of cycle phases from hormone excretion patterns

The secretion levels of oestrogens and progestins depend on the phase of the menstrual cycle. Therefore, analysis of the excretion patterns of metabolites of these hormones was used to follow menstrual cycle phases in female bonobos. Fig. 3.3 shows the excretion pattern of immunoreactive oestrone-conjugate (iE1C) and pregnandiol (iPd) of the female Margrit during the whole study period. Because of the high day-to-day variability in oestrogen excretion it was difficult to objectively determine the pre-ovulatory oestrogen peak in most cycles. This was true for iE1C as well as for immunoreactive oestradiol (data not shown). As well, extraction with 80 % instead of 40 % methanol did not yield different results (data not shown). This high day-to-day variability was seen in all oestrogen profiles of all females. In contrast, the cyclic excretion pattern of iPd allowed the objective determination of a postovulatory progestin increase in all menstrual cycles analysed (Fig. 3.3).

As a consequence, the assessment of the time of ovulation was solely based on the pattern of faecal progestin excretion, a procedure which has been shown to be reliable for assessing female reproductive status and timing of ovulation in a variety of other primate

(Carosi *et al.*, 1999; Heistermann *et al.*, 2001; Strier & Ziegler, 1997) and non-primate mammalian species (Foley *et al.*, 2001; Schwarzenberger *et al.*, 1997).

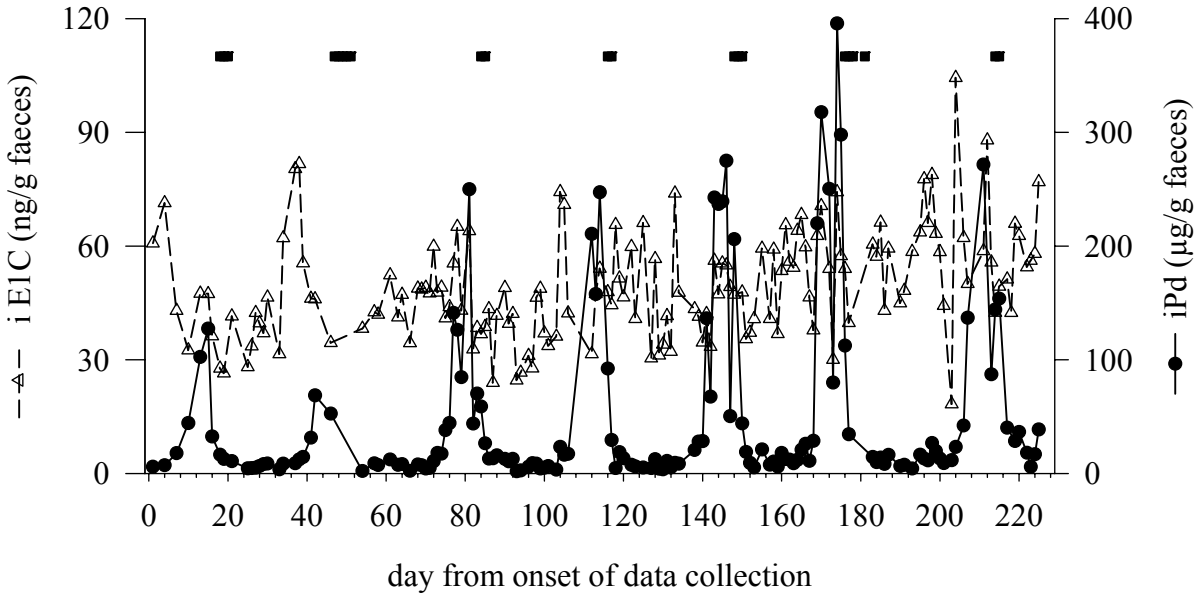

Fig. 3.3 Excretion pattern of immunoreactive oestrone-conjugate (iE1C) and pregnandiol (iPd) during consecutive menstrual cycles of the bonobo female Margrit. Black squares indicate days with menstrual bleeding.

3.1.4 Duration of intermenstrual intervals and follicular and luteal phase

To assess which phase of the menstrual cycle is responsible for the high variation of cycle duration, I investigated the relationship between duration of follicular or luteal phase and the intermenstrual interval. Data collected for this study were combined with data from a previous study (Heistermann *et al.*, 1996), which resulted in 21 complete individual cycles of 11 females. Fig. 3.4 shows the influence of the length of the follicular and the luteal phase on cycle duration. Again, the length of the intermenstrual interval showed a great variability (range 26-65 days). Similarly, the follicular phase varied between 16 and 54 days, but the luteal phase showed much less variation (7-17 days). Because females contributed different numbers of cycles, a permutation test was carried out where each cycle of each female was combined with each cycle from each other female (n = 176 permutations) and the respective Spearman coefficients of correlation were calculated. The duration of the follicular phase showed a highly positive correlation with the length of the menstrual cycle (mean $r_s = 0.966$, range 0.950-0.986, n = 11; Fig. 3.4a), whereas, no correlation between duration of the luteal phase and the menstrual cycle could be detected (mean $r_s = -0.214$, range (-0.474)-0.187, n = 11; Fig. 3.4b).

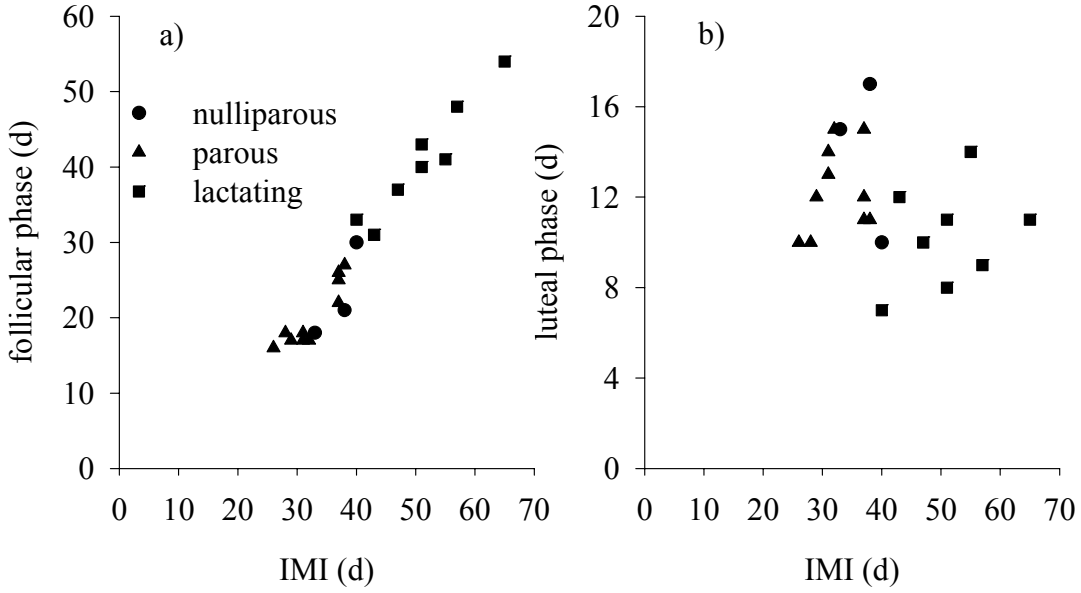

Fig. 3.4 Duration of (a) follicular phase and (b) luteal phase and cycle duration in bonobo females. Individual cycles of nulliparous, parous and lactating females are shown; $n_{nulliparous} = 3$, $n_{parous} = 10$, $n_{lactating} = 8$. IMI = intermenstrual interval.

3.2 Reliability of sexual swellings as a signal of ovulation

The investigation whether sexual swellings reliably advertise ovulation in bonobos is the focus of the second chapter of this study. If sexual swellings in deed advertise ovulation reliably, the onset of maximum tumescence should predict when ovulation is likely to occur. It is expected that ovulation takes place closer to the end rather than the onset of maximum tumescence and it should not occur after the onset of detumescence. Secondly, the degree of tumescence of the sexual swelling is expected to influence the frequency of sexual interactions which should be most frequent around the time of ovulation. Finally, sexual interactions are expected to occur at a higher rate during the follicular compared to the luteal phase of the menstrual cycle.

3.2.1 The timing of ovulation during maximum tumescence

To assess how reliably sexual swellings advertise ovulation, I analysed the variability of the duration of maximum swelling and the timing of ovulation relative to this phase. Females were tumescent (scores 2 and 3) during 38-75 % of the menstrual cycle (range 13-38 d in 26-65 d cycles, n = 23). Within this period, the duration of maximum tumescence

lasted on average 16.0 ± 6.8 days (range 3-30 d, Fig. 3.5) and was highly variable both within and between individuals. Detumescence lasted 1-21 days (mean 5.9 ± 2.4 days).

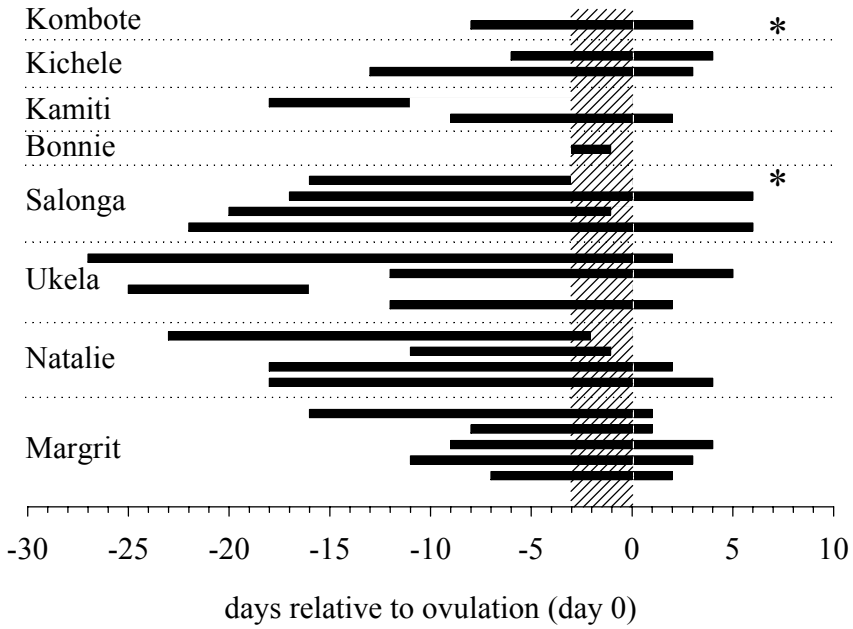

Fig. 3.5 Duration and timing of maximum swelling relative to the day of ovulation (day 0). Horizontal bars represent the period of maximum swelling and are ordered chronologically with each female's latest swelling cycle being on top. The shaded area highlights the fertile phase which comprises the day of ovulation plus the three prededing days. * = conception cycles.

Hormone analysis showed that ovulation never occurred in the first half of the maximum swelling period. In 16 of 23 cases (69.6 %) it took place in the second half of maximum swelling, and in the remaining seven cases after the onset of detumescence (30.4 %, in 5 of 8 females; Fig. 3.5). The occurrence of ovulation after maximum swelling was not due to those cycles with one faecal sample missing at the period of the progestin rise. Maximum swelling began 3-27 days before ovulation (mean 14.3 ± 6.5 d) and ended on average 0.7 ± 5.1 days thereafter (range –16 to 6 d). In two cases, more than 10 days passed between the end of maximum swelling and ovulation (Fig. 3.5). In all cases where ovulation occurred after maximum swelling, the swelling was still in the stage of detumescence.

3.2.2 Patterns of sexual swelling and sexual behaviour

3.2.2.1 Influence of the swelling phase on copulations

In total, 411 copulations were analysed with respect to the phase of swelling or menstrual cycle. Copulation frequencies differed significantly between swelling stages (Friedman ANOVA, $F_r = 12$; $n = 6$; $p < 0.01$; Fig. 3.6, all copulations). Although the mean copulation rate increased more than fivefold with advancing tumescence, multiple post-hoc comparison analysis revealed that only the increase from non-tumescence to maximum tumescence was significant ($z = 2.394$; $n = 6$; $p < 0.05$).

To assess whether all copulations have the same probability of ejaculation, it was investigated whether any specific minimum copulation duration is necessary for ejaculation to occur. In total, copulation duration could be analysed in 468 cases (observed in all groups). Copulation duration varied between 1 and 37 s, with a mean of 11.8 ± 7.1 s. The analysis of the occurrence of ejaculation was carried out for the Frankfurt group only, since in the other groups, the greater distance to the animals proved to yield problems when determining whether ejaculation had occurred.

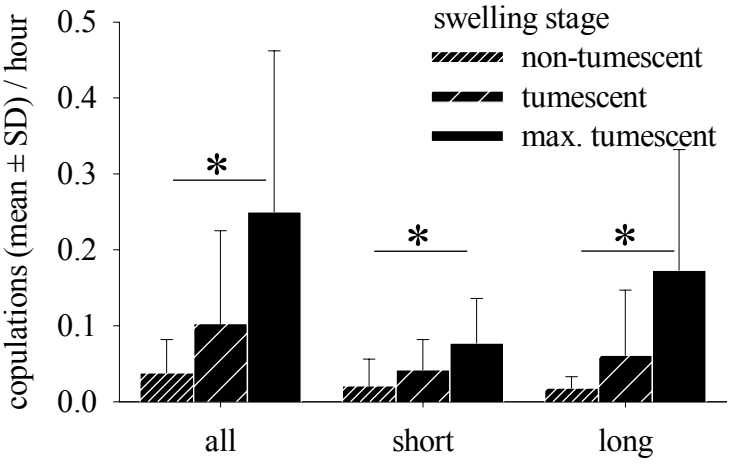

Fig. 3.6 Mean rates (± SD) of all copulations, short copulations (≤ 7 s) and long copulations (> 7 s) per hour in relation to stages of sexual swelling. * = Friedman ANOVA, $n = 6$, $p < 0.05$.

Assessing copulation frequency is only one way to investigate the influence of sexual swelling on mating behaviour; another parameter would be the probability of ejaculation. Mounts with intromission may also serve social functions (de Waal, 1987; Thompson-Handler, 1990) and in many primate species repeated mounts are required to achieve

ejaculation (e.g. Lindburg & Harvey, 1996). As there is no hint yet that bonobos are 'repeated mounters', it was assumed that bonobo males need a certain number of pelvic thrusts to achieve ejaculation (Dixson, 1998; Goodall, 1986; Wikelski & Bäurle, 1996) or, as an indirect measure, a certain copulation duration. Accordingly, copulations were divided into three classes regarding their duration (1 - 7 s, 8 - 14 s, 15 - 21 s) and the distribution of ejaculations across these classes was tested (only Frankfurt group).

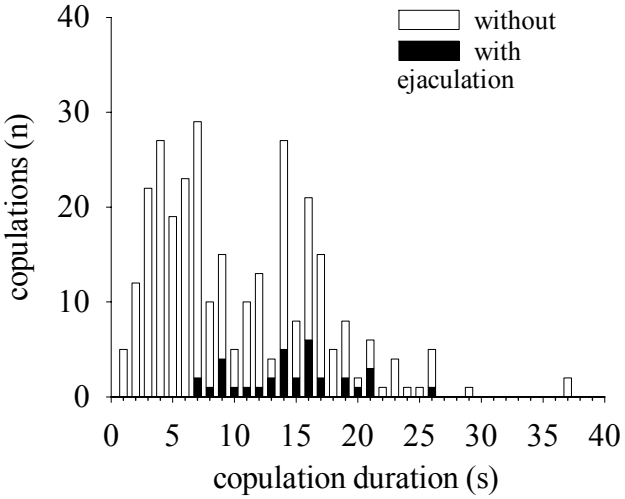

Fig. 3.7 Copulation duration and occurrence of ejaculation in the Frankfurt group. Ejaculation was inferred from the presence of seminal fluid on female or male genitals after copulation.

In 12.7 % of copulations in the Frankfurt group, ejaculation occurred as inferred from seminal fluid on the female or male genitals after copulation. Minimum copulation duration for ejaculation to occur was 7 seconds (Fig. 3.7). Of 301 copulations of known duration, the majority (88.7 %) lasted 1-21 seconds. Based on the distribution of copulations, copulations were divided into three categories of varying duration, 1-7 s, 8-14 s and 15-21 s, respectively.

Table 3.2 Distribution of copulations with ejaculation among different classes of copulation duration. Data from Frankfurt group only.

Copulation duration (s)	Copulations with ejaculation	All copulations observed
1-7	2	137
8-14	15	84
15-21	16	65
Sum	33	286

Ejaculations were observed less frequently in short copulations (≤ 7 s) and more frequently in long copulations (> 7 s) than would be expected by chance (chi-square test, $\chi^2 = 25.58$; df = 2; $p < 0.001$; Table 3.2).

On this basis, I separated short (≤ 7 s) from long (> 7 s) copulations and compared the influence of the swelling stage on the frequencies of both copulation types in all groups (Fig. 3.6). The frequencies of both short and long copulations were found to differ significantly between swelling stages (Friedman ANOVA, n = 6; short copulations: $F_r = 8.43$; $p < 0.05$; long copulations: $F_r = 9.33$; $p < 0.01$), with a significant increase in frequency from non-tumescence to maximum tumescence for both types (both: Friedman post hoc comparisons; $z = 2.394$; n = 6; $p < 0.05$). The increase in copulation frequency was much more pronounced in long copulations than in short ones (factor 9.6 versus 3.7; Fig. 3.6). When comparing the frequencies of short and long copulations during the three swelling stages, their rates did not differ when the swelling was non-tumescent or tumescent (Wilcoxon Matched Pairs Signed Rank test, non-tumescent: n = 5, T = 10, $p > 0.60$; tumescent: n = 6, T = 12, $p > 0.80$). Yet during maximum tumescence, long copulations occurred at a significantly higher frequency than short copulations (n = 6, T = 21, $p < 0.05$).

3.2.2.2 Influence of the swelling phase on other sexual interactions

The degree of sexual swelling did not significantly alter the frequency of total female solicitations (Friedman-ANOVA, n = 8; $F_r = 2.89$; $p > 0.30$; Fig. 3.8) nor did it influence the rate of successful female solicitations (Friedman-ANOVA, n = 6; $F_r = 5.2$; $p > 0.10$; Fig. 3.8). Male sexual behaviour increased tendentiously with advancing swelling. While this increase was not significant for male solicitations (Friedman-ANOVA, n = 8; $F_r = 5.87$; $p < 0.10$; Fig. 3.8), the rate of successful male solicitations changed significantly across swelling cycles (Friedman-ANOVA, n = 6; $F_r = 8.33$; $p < 0.05$; Fig. 3.8). Male solicitations were accepted by females significantly more often during maximum tumescence than during non-tumescence (Friedman multiple post hoc comparison, $z = 2.394$; n = 6; $p < 0.05$; Fig. 3.8).

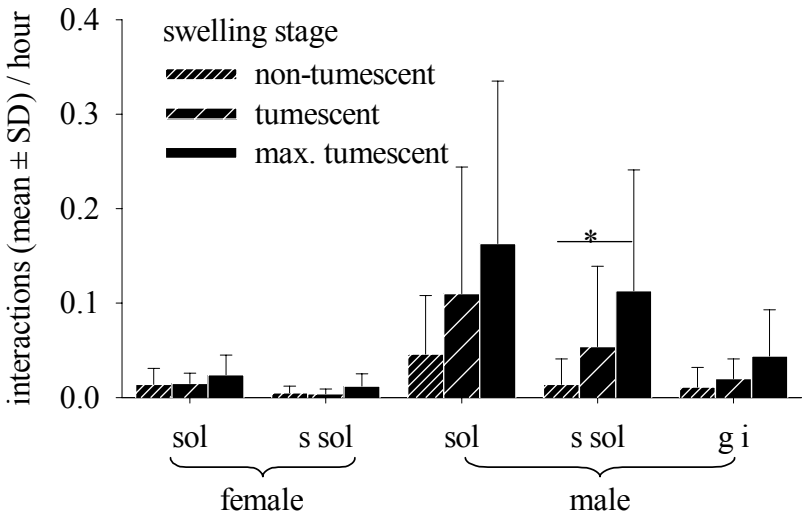

Fig. 3.8 Mean rates (± SD) of sexual interactions per hour in relation to stages of sexual swelling. sol = solicitation, s sol = successful solicitation, gi = genital inspection. * = Friedman ANOVA, $p < 0.05$.

In general, males solicited females at a significantly higher rate than females solicited males (Mann-Whitney U test; male solicitations: 0.11 ± 0.04, $n = 8$; female solicitations: 0.02 ± 0.01, $n = 8$; $W_x = 43$; $p < 0.01$).

Although males inspected female genitals more frequently when these were more tumescent, this did not reach statistical significance (Friedman-ANOVA, $n = 9$; $F_r = 4.47$; $p > 0.15$; Fig. 3.8).

3.2.3 Sexual behaviour and the fertile phase

Next, it was investigated whether the frequency of sexual interactions during maximum tumescence is influenced by the female reproductive status, i.e. the fertile phase of the ovarian cycle. For all sexual interactions recorded, frequencies - shown during maximum tumescence - did not differ significantly between the non-fertile and the fertile phase of the ovarian cycle (Fig. 3.9, Wilcoxon Matched Pairs Signed Rank test; all copulations: $n = 5$, $T = 13$, $p > 0.15$; short copulations: $n = 5$, $T = 11$, $p > 0.40$; long copulations: $n = 5$, $T = 14$, $p > 0.10$; female solicitations: $n = 6$, $T = 18$, $p > 0.15$; female successful solicitations: $n = 5$, $T = 12$, $p > 0.30$; male solicitations: $n = 6$, $T = 14$, $p > 0.50$; male successful solicitations: $n = 5$, $T = 12$, $p > 0.30$). However, male genital inspections tended to occur more frequently in the non-fertile than in the fertile phase of maximum tumescence ($n = 6$, $T = 20$, $p < 0.10$; Fig. 3.9). Long copulations were significantly more frequent than short copulations in the non-fertile phase and tended also to increase in

frequency in the fertile phase (Wilcoxon Matched Pairs Signed Rank test, non-fertile: n = 6, T = 21, $p < 0.05$; fertile: n = 5, T = 15, $p < 0.10$; Fig. 3.9).

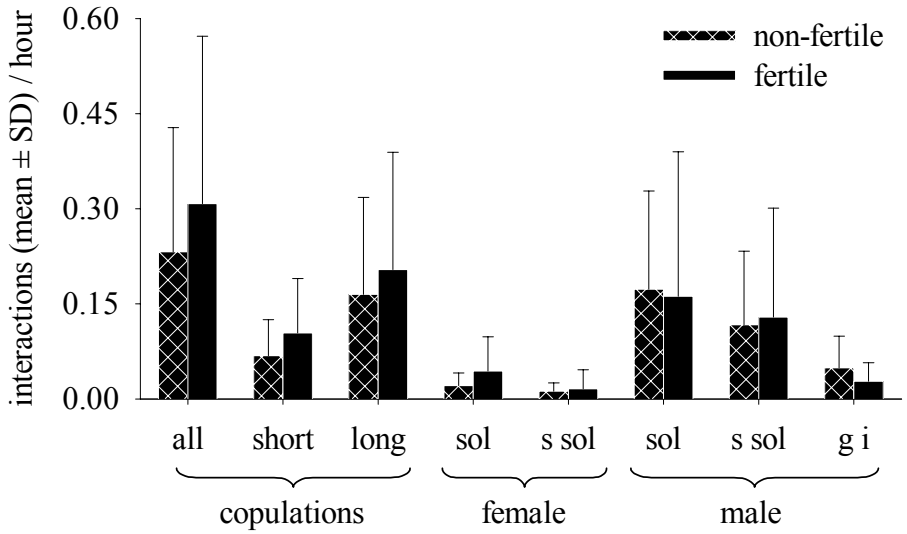

Fig. 3.9 Mean rates (± SD) of sexual interactions per hour outside and inside the fertile phase during maximum tumescence. The fertile phase comprises the day of ovulation plus the three preceding days. Abbreviations see legend Fig. 3.8. Wilcoxon signed rank test, ns.

When analysing behavioural changes between the non-fertile and the fertile phases outside the maximum swelling period, statistical tests were not always possible as not all individuals contributed enough data to this analysis. However, to the extent that tests were possible, sexual interactions did not become more frequent either during the fertile phase outside maximum tumescence when compared to the non-fertile phase (data not shown).

3.2.4 Sexual interactions during the follicular and the luteal phase

To evaluate if males can detect whether ovulation is still impending or has already occurred in a given ovarian cycle, frequencies of sexual interactions were compared between the follicular and the luteal phase. Sexual interactions were not found to differ significantly between the two phases (Fig. 3.10, Wilcoxon test, all copulations: n = 5, T = 14, $p > 0.12$; short copulations: n = 5, T = 12, $p > 0.30$; long copulations: n = 5, T = 12, $p > 0.30$; female solicitations: n = 5, T = 11, $p > 0.40$; female successful solicitations: n = 4, T = 5.5, $p = 1.0$; male solicitations: n = 7, T = 23, $p > 0.15$; male successful solicitations: n = 5, T = 13, $p > 0.18$). Only male genital inspection showed a tendency to be less frequent during the luteal phase (n = 8, T = 31, $p < 0.10$; Fig. 3.10).

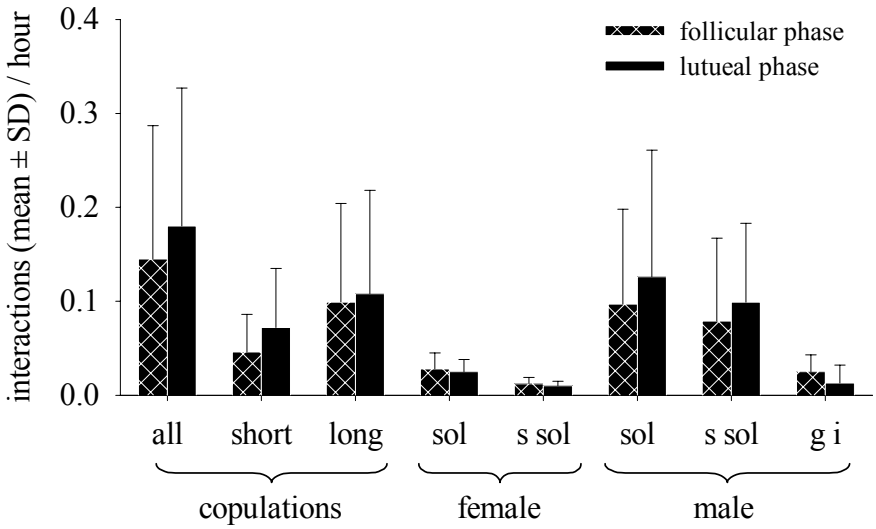

Fig. 3.10 Mean rates (± SD) of sexual interactions per hour during the follicular and the luteal phase of the ovarian cycle. Abbreviations see legend Fig. 3.8. Wilcoxon signed rank test, ns.

3.3 Context and function of sexual interactions between females

To assess the context and function of sexual interactions between female bonobos is the focus of this chapter. More specifically, it is investigated whether genial rubbing serves to mediate the formation or maintenance of female-female alliances, to enhance female-female attractivity and thus to reduce intra-sexual competition, to mediate reconciliation between former opponents, to display social status or to reduce social tension. The predictions resulting from these hypotheses are summarized in Table 3.3.

Table 3.3 Possible functions of genito-genital rubbing (gg) and consecutive predictions.

Hypothesis	Predictions
Alliance formation	
1	Frequency of gg is higher between non-kin than between kin.
2	Preferred gg partner is also preferred grooming partner.
3	Intervention in conflict occurs on behalf of the preferred gg partner.
4	Monopolisable food is shared mainly with preferred gg partner.
Competition reduction	
1	Frequency of gg increases with advancing tumescence.
2	The less tumescent partner in a dyad solicits the more tumescent female for gg.
3	Frequency of suffering from aggression decreases with advancing tumescence.
Reconciliation	
1	Frequency of gg is higher between non-kin than between kin.
2	Frequency of gg is higher after conflict than before.
3	After a conflict, mainly the victim solicits gg.
Display of status	
1	Frequency of gg is higher between non-kin than between kin.
2	Position during gg is status-dependent, dominant individual is more often in top position.
3	Solicitation for gg mainly by the lower ranking individual.
Tension regulation	
1	Frequency of gg is higher between non-kin than between kin.
2	Frequency of gg increases in presence of food (food distribution!).
3	Dyads involved in gg are not involved in aggression in same context.

3.3.1 Influence of relatedness

Genital rubbing was observed 626 times in 11 of the 13 possible female-female dyads (Table 3.4).

The rate of genital rubbing was not evenly distributed among the different dyads of each social group. Two mother-daughter dyads were not seen to perform genital rubbing, Diatou-Kichele and Natalie-Ukela (Table 3.4). Statistical analysis showed that genital rubbing was not equally distributed among non-kin and kin dyads in those groups where females could choose between related and unrelated partners (Cologne: $\chi^2 = 159.41$, $df = 1$, $p < 0.001$; Frankfurt: $\chi^2 = 107.23$, $df = 1$, $p < 0.001$). In these two groups, related dyads were less often involved in genital rubbing than unrelated dyads. The same pattern was observed when focussing on the distribution of genital rubbing during the first 15 minutes of the feeding experiment carried out with the Frankfurt group ($\chi^2 = 116.36$, $df = 1$, $p < 0.001$). However, genital rubbing was not evenly distributed in the Stuttgart group either, where all female dyads were unrelated ($\chi^2 = 28.67$, $df = 2$, $p < 0.001$).

Table 3.4 Distribution of genital rubbing between female dyads.

Zoo	Dyad	Related-ness[#]	n genital rubbing (total)	n genital rubbing (experiment)
Cologne	Bonnie-Kamiti	No	41	-
	Bonnie-Banya	Yes	1	-
	Kamiti-Banya	No	283	-
Twycross	Diatou-Kichele	Yes	0	-
Stuttgart	Kombote-Daniela	No	17	-
	Kombote-Lina	No	40	-
	Daniela-Lina	No	6	-
Frankfurt	Margrit-Natalie	No	25	6
	Margrit-Ukela	No	87	26
	Margrit-Salonga	Yes	4	1
	Natalie-Ukela	Yes	0	0
	Natalie-Salonga	No	14	6
	Ukela-Salonga	No	108	22

#: Relatedness: yes = mother-daughter dyad, no = not related.

For further analysis, the dyads Bonnie-Banya and Kamiti-Banya were excluded from analysis since Banya reached menarche only during the course of the study and genital rubbing at this age could serve other functions than in adult life (note the high frequency of genital rubbing between Banya and Kamiti compared to other dyads). This left 342 cases of genital rubbing among 9 adult female dyads for analysis.

3.3.2 Formation or maintenance of alliances

3.3.2.1 Preferred partners for genital rubbing and grooming

To assess whether preferred partners for genital rubbing were identical with those for grooming, it was investigated whether each female's genital rubbing or grooming activities differed significantly from random distribution. The preference for a specific partner can only be tested when females can choose between several partners. Therefore, only the study groups of Stuttgart and Frankfurt were analysed. All occurrences of genital rubbing and active grooming observed during focus observations (not during the feeding experiment) were analysed.

As expected based on previous findings for genital rubbing (chapter 3.3.1), females discriminated between possible partners for genital rubbing and grooming. All seven females included in the analysis deviated significantly from random distribution in their choice of partners for genital rubbing and grooming (Chi square test, Table 3.5).

However, the female who was a preferred partner for genital rubbing for a certain individual was never also groomed preferentially (Table 3.5).

Table 3.5 Distribution of genital rubbing and grooming among female dyads.

Female	Partner	Genital rubbing (n)	χ	P	Active grooming (minutes)	χ	P
Margrit	*Natalie*	19	64.63	***	378	476.98	***
	Ukela	61			75		
	Salonga	3			18		
Natalie	Margrit	19	20.22	***	477	505.64	***
	Ukela	0			1326		
	Salonga	8			629		
Ukela	Margrit	61	79.88	***	135	969.84	***
	Natalie	0			934		
	Salonga	86			179		
Salonga	Margrit	3	134.01	***	138	798	***
	Natalie	8			924		
	Ukela	86			270		
Kombote	*Daniela*	17	9.28	**	333	166.5	***
	Lina	40			73		
Daniela	Kombote	17	5.26	*	639	1.04	ns
	Lina	6			603		
Lina	Kombote	40	25.13	***	270	387.88	***
	Daniela	6			960		

Underlined: preferred partner for genital rubbing, italics: preferred grooming partner. Chi square-test, *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

3.3.2.2 Alliance formation during the feeding experiments

During the feeding experiment in the Frankfurt group, three of the four adult females and the male were able to establish first ownership of the monopolisable food item solitarily, without the help of an alliance partner (Table 3.6). With the male usually being the first individual who entered a re-opened enclosure and the female Margrit the last one (data not shown), this shows that the first animal entering the enclosure was not necessarily the one taking first possession of the food. During the experiments, it was never observed that two individuals defended the food in a co-operative way. No other cases of alliance formation were observed either. The low ranking female Ukela was the only female who never succeeded in achieving initial ownership of the food (Table 3.6). One of the infants was able to get the food item as the first possessor, but the food was taken from her within a few seconds (data not shown). The analysis of ownership during the first 15 minutes of the experiment differed significantly from chance ($\chi^2 = 82.74$, $df = 4$, $p < 0.001$; Table 3.6).

The low ranking female Ukela was in possession of the food a much shorter period of time than the other three adult females and the adult male.

Table 3.6 Individual success in obtaining possession of the main piece of food during the feeding experiments.

Individual	First ownership (n)	Keeping > 120 sec (%)	Total ownership[a] (n)	Total owner duration[a] (min)
Margrit	4	100	5	74.9
Natalie	3	100	6	61.9
Salonga	5	80	8	86.1
Ukela	-	-	1	0.1
Bono	8	75	8	84.6

a) Sum over the first 15 minutes of all 21 experiments.

3.3.2.3 Alliance formation in the context of conflicts

During both routine observations and the feeding experiments, a total of 1158 dyadic conflicts were observed in the four study groups, in 597 of them both participants were adults. In 49 of those adult conflicts a third individual intervened (8.21 %). Only two interventions occurred in 65 female-female conflicts (3.08 %), whereas 47 interventions were observed in 532 female-male conflicts (8.83 %). In all those inter-sexual conflicts, females intervened on behalf of the female, never on behalf of an adult male. The majority of interventions during adult inter-sexual conflicts (32 interventions in 67 conflicts) were observed in the Cologne group with the two males whereas no intervention was observed in the Twycross group. Because of the low occurrence of interventions in most groups it was not possible to test the distribution statistically. Although statistical testing is not possible, these data suggest that females do not support their preferred same-sex sexual partner in female-female agonistic encounters.

3.3.2.4 Food sharing during the feeding experiment

While an adult female was in possession of the food, 52 cases of genital rubbing were observed. Of those, 42 cases involved the food owner, whereas only 10 cases were observed among two bystanders (Table 3.7). Thus, genital rubbing was not distributed by chance between the food owner and the bystander females ($\chi^2 = 18.84$, $df = 1$, $p < 0.001$;Table 3.7).

Table 3.7 Distribution of genital rubbing between food owner and bystanders.

Owner	Genital rubbing with food owner	Genital rubbing among bystanders
Margrit	21	0
Natalie	6	8
Ukela	0	0
Salonga	15	2

In owner-bystander dyads, sexual solicitations were not randomly distributed but genital rubbing was significantly more frequently initiated by the food owner than by a bystander ($\chi^2 = 6.0$, df = 1, $p < 0.001$; Table 3.8). Note however, that the main body of data comes from cases where either Margrit or Salonga were food owners. For each dyad, the female responsible for initiation of genital rubbing was the same during the feeding experiment as well as outside the experimental context, i.e. during routine observation.

Table 3.8 Initiation of genital rubbing in owner-bystander dyads.

Owner	Bystander	Initiation of genital rubbing by owner	bystander	unknown
Margrit	Natalie	3	1	1
	Salonga	1	0	0
	Ukela	13	1	1
Natalie	Margrit	0	1	0
	Salonga	1	2	2
Salonga	Natalie	0	0	1
	Ukela	10	0	4

To assess whether genital rubbing and begging translate into food sharing, matrix correlations were carried out. This showed that dyadic genital rubbing did not correlate with food sharing (mantel test, 10000 permutations, $t = 1.441$, $p > 0.18$) but correlated positively with begging (mantel test, 10000 permutations, $t = 2.473$, $p < 0.05$, Table 3.9).

Table 3.9 Distribution of genital rubbing, begging and food sharing during the feeding experiments.

	Genital rubbing with				Begging by				Sharing with			
Owner	Mar	Nat	Uke	Sal	Mar	Nat	Uke	Sal	Mar	Nat	Uke	Sal
Margrit	-	5	15	1	-	1	30	8	-	0	16	0
Natalie	1	-	0	5	0	-	9	12	3	-	28	9
Ukela	0	0	-	0	0	0	-	0	0	1	-	0
Salonga	0	1	14	-	2	3	48	-	4	1	28	-

Females who begged more towards the food owner did not receive more food than females with fewer begging events (mantel test, 10000 permutations, $t = 1.721$, $p > 0.18$; Table 3.10).

Table 3.10 Begging and begging success (=food sharing in a time window of 5 minutes after the begging).

	Margrit		Natalie		Ukela		Salonga	
Owner	beg (n)	% success	beg (n)	% success	beg (n)	% success	beg (n)	% success
Margrit	-	-	1	0	30	16.7	8	0
Natalie	0	-	-	-	9	55.6	12	33.3
Ukela	0	-	0	-	-	-	0	-
Salonga	2	0	3	0	48	33.3	-	-

Females who received food after genital rubbing tended to receive food after begging as well (mantel test, 10000 permutations, $t = 1.732$; $0.05 < p < 0.10$; Table 3.11).

Table 3.11 Genital rubbing (gg) and success (=food sharing in a time window of 5 minutes after genital rubbing).

	Margrit		Natalie		Ukela		Salonga	
Owner	gg (n)	% success	gg (n)	% success	gg (n)	% success	gg (n)	% success
Margrit	-	-	5	0	15	20.0	1	0
Natalie	1	0	-	-	0	-	5	60.0
Ukela	0	-	0	-	-	-	0	-
Salonga	0	-	1	0	14	21.4	-	-

Looking at individual levels, it becomes obvious that the female Ukela was very successful in obtaining food from all other females after begging and genital rubbing although she was hardly able to monopolise the food item herself. In contrast to Ukela, Margrit and Natalie showed an extremely low rate of begging and genital rubbing with food owners and never obtained food afterwards. Salonga was successful in obtaining food from Natalie after begging in 33 % of cases (Table 3.10) and after genital rubbing in 60 % of cases (Table 3.11).

3.3.3 Reduction of female-female competition

To test whether the frequency of genital rubbing increases with advancing stages of tumescence, frequencies of genital rubbing during the different swelling stages of a female were compared. Although the mean frequenciy of genital rubbing increased at higher stages of tumescence, this effect did not reach statistical significance (Friedman ANOVA, $n = 7$; $F_r = 2.89$, $p > 0.20$, Fig. 3.11). Five females performed genital rubbing most frequent when in maximum tumescence, the other two females showed similar values during non-tumescence and maximum tumescence.

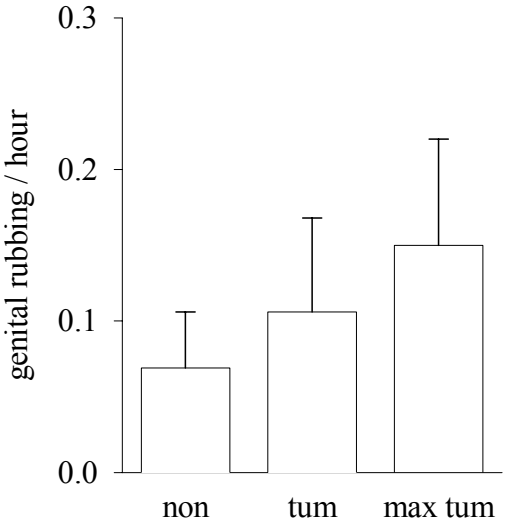

Fig. 3.11 Frequency (mean ± SD) of genital rubbing and degree of tumescence. Non = sexual swelling not tumescent, tum = sexual swelling at intermediate stage, max tum = swelling maximum tumescent. Friedman-ANOVA, ns.

However, this approach oversimplifies the influence of sexual tumescence, as it does not pay credit to the swelling status of both interacting females simultaneously. Consequently, rates of genital rubbing were compared in dyads during times when both partners were in maximum tumescence with times when both were below maximum tumescence. In five dyads where phases of maximum tumescence overlapped, three showed higher rates of genital rubbing during maximum tumescence (0.11 ± 0.11 interactions/h) than during non-maximum tumescence (0.04 ± 0.03). No significant difference could be detected (Wilcoxon signed rank test, $n = 5$, $T = 12$, $p > 0.30$).

While it is difficult to assess the influence of the degree of tumescence of both females on the dyadic rate of genital rubbing, this approach becomes easier when investigating the relative degree of tumescence during solicitation for genial rubbing. It is expected that the less tumescent female solicits the more tumescent female, while no asymmetry in the direction of solicitation should be found when both females are at the same stage of tumescence. As expected, there was no difference in the direction of solicitations when both females were in the same stage of tumescence (Wilcoxon signed-rank test, $n = 6$, $T = 18$, $p > 0.15$; Fig. 3.12). However, no difference in solicitation direction was found when either of the females was at a higher stage of tumescence (ind1<ind2: $n = 6$, $T = 18$, $p > 0.15$; ind1>ind2: $n = 6$, $T = 17$, $p > 0.20$; Fig. 3.12). In four of the seven dyads, mainly one female, irrespective of the relative degree of tumescence performed the solicitations.

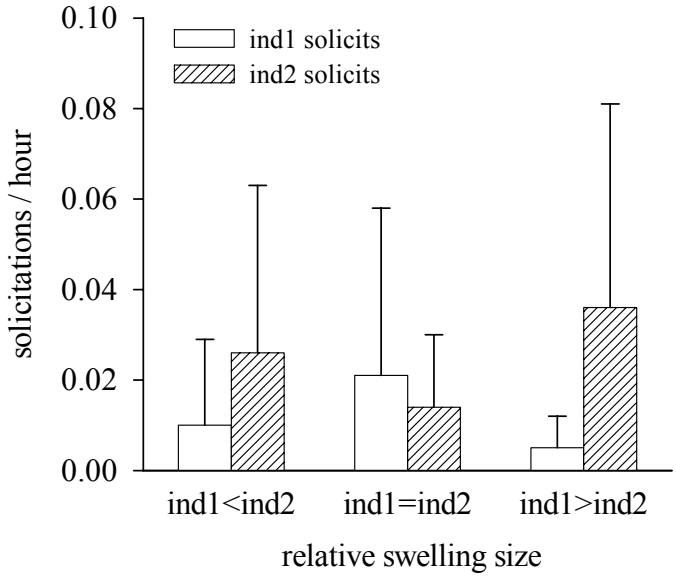

Fig. 3.12 Frequency (mean ± SD) of solicitation for genital rubbing and relative swelling size. Ind1<ind2: swelling of female 1 < swelling female 2, ind1=ind2: swelling of female 1 = swelling female 2, ind1>ind2: swelling of female 1 > swelling female 2. Wilcoxon signed-rank test, ns.

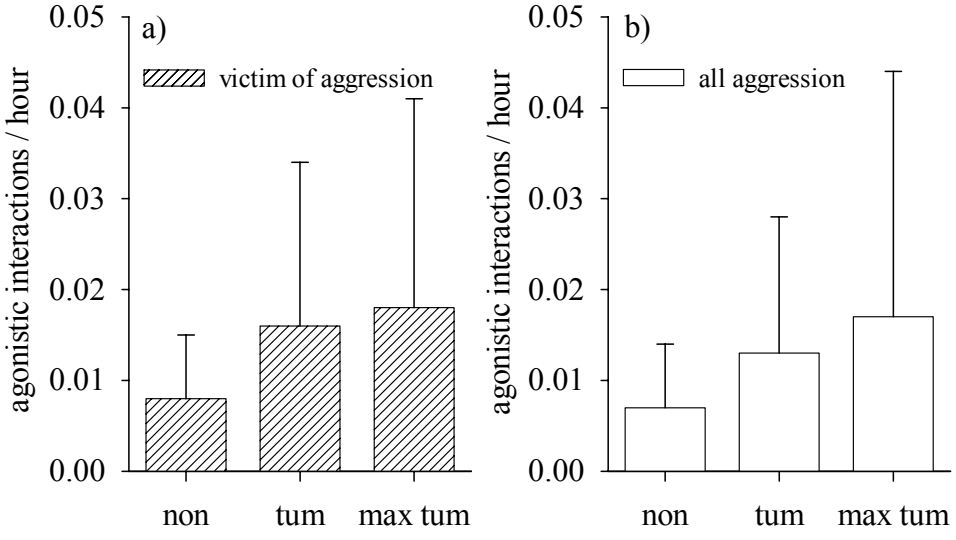

Fig. 3.13 Frequency of agonistic interactions and degree of tumescence. (a) Frequency (mean ± SD) of being a victim of other females' agonistic attacks and (b) frequency (mean ± SD) of all agonistic interactions a female is involved in. Friedman-ANOVA, ns.

Additionally, the degree of tumescence did not influence the amount of aggression a female received from other females, i.e. there was no significant difference in the frequency of received aggression between different swelling stages (Friedman ANOVA, $n = 5$; $F_r = 0.737$, $p > 0.70$; Fig. 3.13a). Note that only five of the eight females with

ovarian cycles received aggression at all. This result did not change when all aggressive interactions were summed up for each female, irrespective of whether she was the victim of aggression or the aggressor (Friedman ANOVA, n = 8; $F_r = 0.483$, $p > 0.60$; Fig. 3.13b).

3.3.4 Reconciliation between former opponents

A total of 1158 conflicts was observed in the four study groups, 51.6 % (n = 597) of these occurred between adult individuals. The majority of conflicts between adults (n = 532, 89.1 %) involved a male and a female, whereas only 10.9 % (n = 65) involved two females. Male-female conflicts occurred significantly more often than female-female conflicts ($\chi^2 = 236.45$, df = 1, $p < 0.001$).

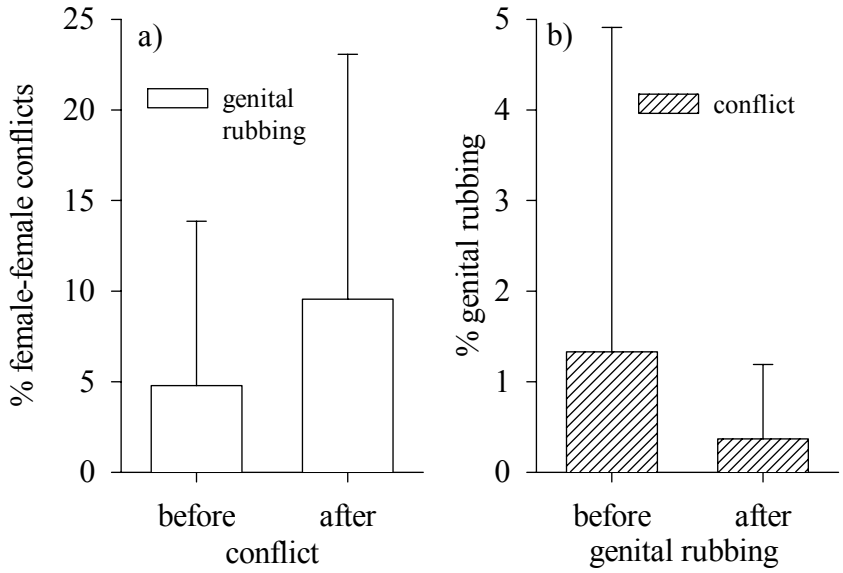

Fig. 3.14 Genital rubbing and conflicts. (a) Occurrence (mean ± SD) of genital rubbing between opponents in the pre- and post-conflict interval and (b) of conflicts between same-sex partners in the interval before and after genital rubbing. Wilcoxon signed-rank test, ns.

As described before (chapter 3.3.1), 626 cases of genital rubbing were observed in 11 of 13 possible female-female dyads. 65 female-female conflicts were observed in 12 of 13 dyads. However, only in five dyads genital rubbing of former conflict partners was observed within 15 minutes after the conflict ($n_{\text{genital rubbing}} = 9$). When analysing the occurrence of genital rubbing between female conflict partners in the pre- versus post-conflict interval, genital rubbing did not show a higher rate after the conflict than before (Wilcoxon signed-rank test, n = 5, T = 12.5, $p > 0.20$, Fig. 3.14a). Similarly, a female was not more likely to

be involved in a conflict with her same-sex partner before than after genital rubbing (Wilcoxon signed-rank test, n = 3, T = 2, p > 0.50, Fig. 3.14b).

The solicitor of post-conflict genital rubbing could be determined only in two cases. Both times it was the (subordinate) victim of aggression who presented to the former opponent. In one case, Natalie presented to Salonga, and in the other case the adolescent female Banya presented to Kamiti.

3.3.5 Signal of social status

Calculating the displacement index for each dyad assessed dominance relationships as it is described in more detail in chapter 3.4.1. In 276 cases of genital rubbing observed in 9 different female-female dyads, the female performing the movements could be identified; it was the dominant interaction partner in 245 cases (88.8 %). With the exception of one dyad (Bonnie-Kamiti), the dominant female in a given dyad took the male position most frequently. On average, dominant females were in the male position in 84.3 ± 23.4 % of genital rubbing, the subordinate female in 15.1 ± 23.8 % (Fig. 3.15a); this difference is highly significant (Wilcoxon signed-rank test, n = 9, T = 43, p < 0.01).

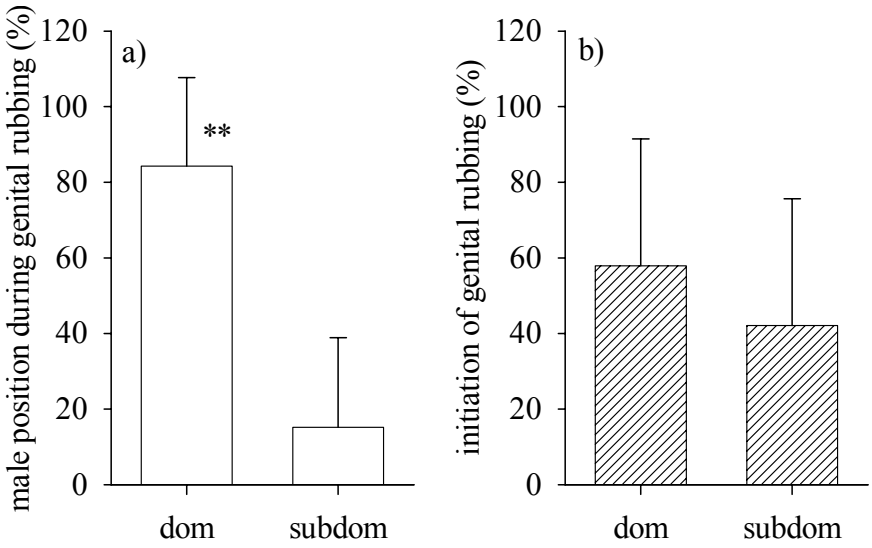

Fig. 3.15 Social status and performance of the male position during (a) genital rubbing and (b) initiation of genital rubbing. Wilcoxon signed pair test, **: p < 0.01.

The initiator of genital rubbing could be determined in 240 cases. On average, dominant females were responsible for the initiation of genital rubbing in 57.9 ± 33.6 % of the observed cases, the subordinate female in 42.1 ± 33.6 %, this difference was not significant (Wilcoxon signed rank test, n = 9, T = 29, p > 0.4; Fig. 3.15b). This result remained the

same, when only those dyads with strong dominance relationships (see chapter 3.4.1) were analysed, i.e. when dyads with bi-directionality in displacements were excluded (dominant solicitations: 57.2 ± 38.8, subordinate: 42.8 ± 38.8; Wilcoxon signed rank test , n = 6, T = 13; p > 0.60).

3.3.6 Regulation of social tension

This analysis was carried out on the Frankfurt group only, as a clumped food condition was not given in the other groups.

The presence of food influenced the frequency of agonistic interactions among adults. During 643.1 hours of observation outside the feeding context, 210 incidences of inter-and intra-sexual aggression were observed (0.33 interactions/h). In the presence of food, the rate of conflicts increased, reaching 0.47 interactions/h in the dispersed feeding context (55 cases in 115.8 hours) and 6.42 interactions/h in the clumped feeding context (34 cases in 5.3 hours). Statistical analysis showed that the presence of food had a significant influence on the rate of conflict in all adult partner combinations (Friedman ANOVA, $F_r = 7.0$, n = 8, $p < 0.05$; Fig. 3.16a). *Post hoc* analysis revealed that the respective interactions increased significantly from the no food- to the clumped food-context (Friedman post hoc comparison, z = 2.394; $p < 0.05$; Fig. 3.16a).

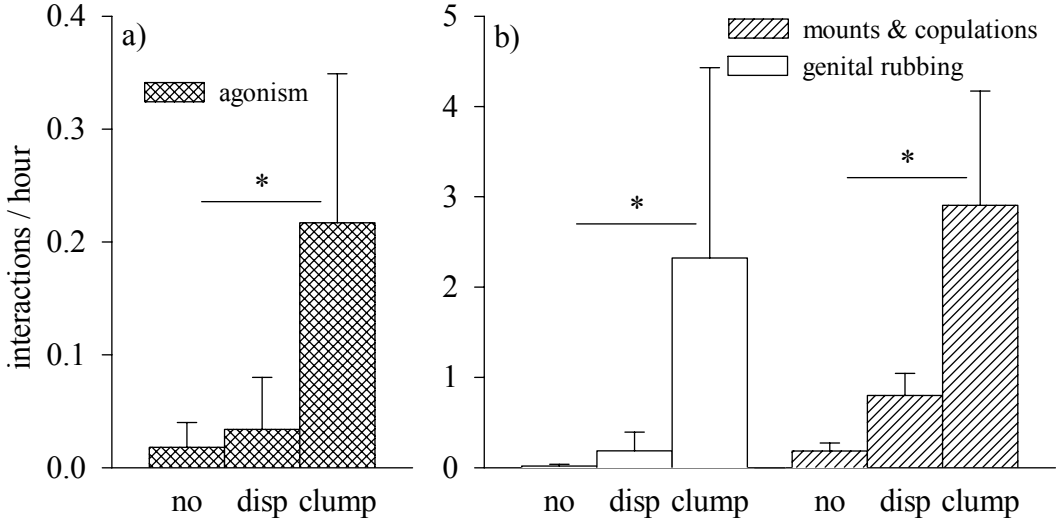

Fig. 3.16 Frequency (mean ± SD) of (a) agonistic and (b) sexual interactions in different feeding contexts. No = outside feeding, disp = dispersed feeding context, clump = clumped feeding context. *: $p < 0.05$ (Friedman-ANOVA post hoc comparison).

A total of 231 cases of genital rubbing were analysed with respect to the food context. This corresponded to rates of 0.09/h (n = 61), 0.94/h (n = 109) and 11.51/h (n = 61) in the no-food, dispersed food and clumped food context, respectively (Fig. 3.16b). Analysis of the dyadic frequencies of genital rubbing revealed that rates increased significantly in the presence of food (Friedman ANOVA: $F_r = 8.4$, $n = 5$, $p < 0.05$; Fig. 3.16b). Genital rubbing was significantly more frequent in the clumped food- than in the no food-context (Friedman post hoc comparison, $z = 2.394$; $p < 0.05$; Fig. 3.16b).

The same increase was observed in heterosexual interactions, namely mounts and copulations (no food: 0.72 interactions/h (n = 463), dispersed food: 3.24 interactions/h (n = 375), clumped food: 11.51 interactions/h (n = 61)). The dyadic rate of heterosexual interactions increased significantly in the food context (Friedman ANOVA: $F_r = 8.0$, $n = 4$, $p < 0.05$; Fig. 3.16b), with the significant increase taking place between the no food- and the clumped food-context (Friedman post hoc comparison, $z = 2.394$; $p < 0.05$).

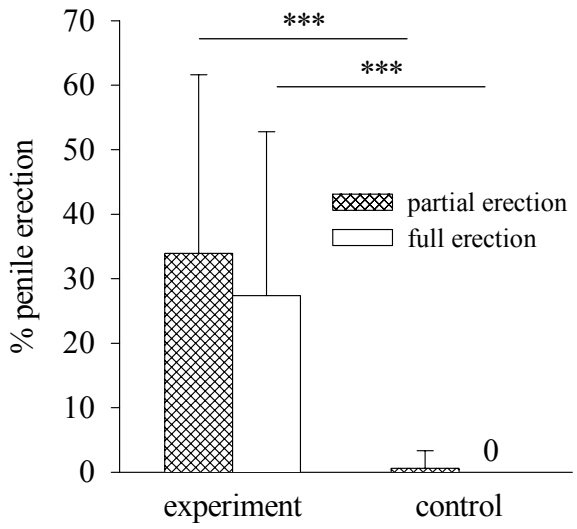

Fig. 3.17 Penile erection during the first 15 minutes of the feeding experiment and during control phases. ***: Wilcoxon signed rank test, $p < 0.001$.

Additionally, excitement during the feeding experiment could also be inferred from male sexual arousal. When analysing the percent of scans with partial or full penile erection during the feeding experiment, highly significant differences were found between the experiment and the control phase on the next day (Wilcoxon signed rank test, $n = 21$, partial erection: $T = 231$, $p < 0.001$; full erection: $T = 231$, $p < 0.001$; Fig. 3.17).

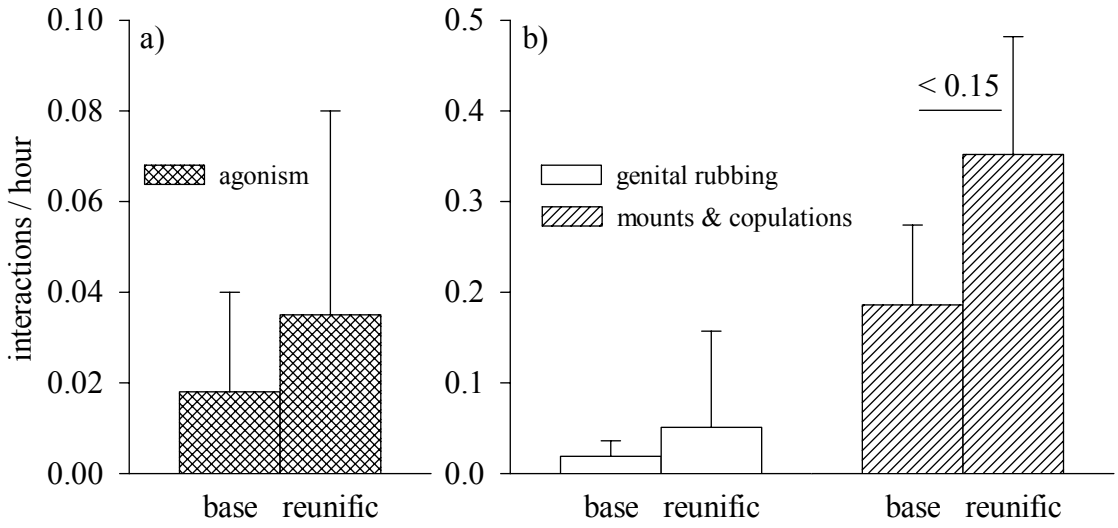

Fig. 3.18 Frequency (mean ± SD) of (a) sexual interactions and (b) agonistic interactions during normal observation days and around the time of group reunification. Base = baseline values during non-feeding, reunific = reunification days. Wilcoxon signed-rank test, n.s..

The reunification of the Frankfurt group after separation for several months was also expected to represent a phase of social tension. A total of 7 agonistic interactions, 7 cases of genital rubbing and 31 copulations and mounts were observed among adults during the 17.5 hours of temporary reunification (distributed over 5 days). However, dyadic rates of agonistic, same-sex sexual and heterosexual interactions outside feeding time were not found to differ significantly between the reunification period and baseline values (Fig. 3.18a: agonistic interactions: $n = 9$, $T = 22$, $p > 0.60$, Wilcoxon signed rank test; Fig. 3.18b: genital rubbing: $n = 5$, $T = 9$, $p > 0.80$; copulations/mounts: $n = 4$, $T = 10$, $0.10 < p < 0.15$). Although the male mounted all four females at a higher frequency during the reunification phase than during baseline levels, this effect did not become significant, most probably because of the small sample size and the weak increase (ranging from factor 1.6 to 2.8).

To test whether the performance of genital rubbing in tense situations may reduce the probability of conflict with a potential competitor, it was investigated whether, in a tense situation, genital rubbing and conflicts occurred in the same dyads. In two of three cases of aggression between females during the feeding experiments, no genital rubbing was observed between the opponents in the same experiment. Both cases of aggression were observed between Natalie and Salonga (Table 3.12). Contrastingly, when an aggressive conflict was observed between Margrit and Ukela during one experiment, the two females

also performed genital rubbing six times. During most experiments, however, genital rubbing took place without overt aggression between females. Thus, a statistical investigation, whether genital rubbing negatively correlates with aggression in tense situations was not possible.

Table 3.12 Distribution of genital rubbing and aggression within dyads during the feeding experiments. The occurrence of genital rubbing per dyad and experiment is given in numbers. Occurrence of aggression in a specific dyad is highlighted in grey.

Experiment	Margrit-Natalie	Margrit-Ukela	Margrit-Salonga	Natalie-Ukela	Natalie-Salonga	Ukela-Salonga
1	-	4	-	-	-	-
2	-	2	-	-	-	-
3	-	3	-	-	3	1
4	1	6	1	-	-	-
5	-	-	-	-	-	3
6	-	-	-	-	1	-
7	-	2	-	-	-	-
8	-	-	-	-	-	-
9	1	1	-	-	-	1
10	1	1	-	-	-	-
11	3	3	-	-	-	-
12	1	2	-	-	-	-
13	-	2	-	-	-	-
14	-	-	-	-	-	1
15	-	-	-	-	-	4
16	-	-	-	-	-	-
17	-	-	-	-	-	7
18	-	-	-	-	-	2
19	-	-	-	-	1	-
20	-	-	-	-	-	2
21	-	-	-	-	-	1

Similarly, during normal feeding events, genital rubbing and aggression occurred only rarely simultaneously (Table 3.13).

Table 3.13 Number of days with female-female aggression, genital rubbing or both during the dispersed feeding context of the Frankfurt group.

Dyad	Only aggression	Only genital rubbing	Both
Margrit-Natalie	0	7	0
Margrit-Ukela	2	22	2
Margrit-Salonga	0	0	0
Natalie-Ukela	-	-	-
Natalie-Salonga	3	4	1
Ukela-Salonga	1	25	0

3.4 Behavioural and endocrine parameters of female social status

The fourth topic this study addressed is the impact of social status for female bonobos. First, the female dominance hierarchy in the bonobo study groups is determined based on the outcome of displacements. Second, it is tested whether females profit from high social status in terms of access to food sources when food distribution is clumped. Third, the relationship between social status and levels of glucocorticoid excretion is investigated. The glucocorticoid analysed here is 11-ketoetioncholanolone.

3.4.1 Dominance hierarchies

To determine dominance hierarchies, the degree of unidirectionality of displacements and agonistic interactions is usually calculated. However, agonistic interactions were observed only rarely between the females of the four study groups. With the exception of one female-female dyad (Natalie-Salonga), less than 5 interactions involving chasing or body contact were recorded in each possible dyad. Therefore, dyadic dominance indices (DDI) were merely based on displacements.

Table 3.14. Dyadic dominance indices (DDI) as calculated from displacements among adult females. In each dyad, the dominant female is listed first.

Group	Dyad	DDI	N displacements
Cologne	Bonnie-Kamiti	0.91	11
Twycross	Diatou-Kichele	1.00	18
Stuttgart	Kombote-Daniela	0.94	17
	Kombote-Lina	0.99	70
	Daniela-Lina	0.92	64
Frankfurt	Salonga-Margrit	0.53	43
	Natalie-Salonga	0.62	26
	Margrit-Natalie	0.80	15
	Margrit-Ukela	0.53	19
	Salonga-Ukela	0.86	43
	Natalie-Ukela	1.00	15

As can be seen from Table 3.14, eight of 11 dyads showed a clear directionality of displacements with DDI $\geq$ 0.8. Yet for the Frankfurt group, one dominance relationship was weak (DDI = 0.62, Natalie-Salonga) and two female dyads, Salonga-Margit and Margrit-Ukela, had very weak dominance relationships with dominance indices being close to 0.5. When including all other agonistic elements to further clarify the relationships of these dyads, the dyadic dominance index increased slightly to 0.59 in one dyad (Margrit-Ukela), whereas it remained the same for the other (Salonga-Margrit) because

only displacements were observed in this dyad. Including all agonistic elements further changed the weak dominance relationship between Natalie and Salonga towards bi-directionality (DDI = 0.50). For all other dyads, dominance relationships did not change when all agonistic elements were combined (data not shown).

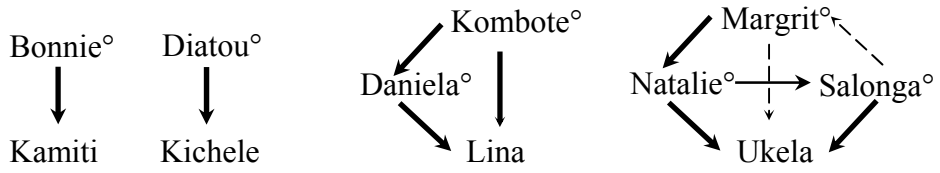

Fig. 3.19 Dominance relationships calculated from displacements indices. Arrows indicate relationships by pointing towards the lower ranking individual. Bold arrows: DDI > 0.8, thin arrows: 0.6 < DDI < 0.8, dotted arrows: 0.5 < DDI < 0.6. ° = high ranking, as established by total dominance indices TDI (i.e. sum of displacements for each female).

The dyadic dominance relationships based on displacements added up to linear dominance hierarchies in the groups of Cologne, Twycross and Stuttgart, but not in Frankfurt (Fig. 3.19).

Because of this lack of linearity, females were grouped as either high or low ranking according to their total dominance index (TDI), i.e. the ratio of how often they won displacements over the total number of displacement interactions they were involved in, irrespective of the identity of the interaction partner. More specifically, the females Bonnie, Diatou, Kombote, Daniela, Margrit, Natalie and Salonga with a TDI > 0.5 were considered as high ranking, whereas Kamiti, Kichele, Lina and Ukela with TDI < 0.5 were regarded as low ranking. In the groups with at least three adult females, high rank corresponded to being dominated by one female at maximum, low ranking females were dominated by at least two females (Fig. 3.19).

3.4.2 Status-dependent access to monopolisable food sources

To address whether high social status pays in better access to restricted resources, individual success of obtaining possession of a monopolisable food source during the feeding experiment was investigated. Fig. 3.20a shows the total percentage of individual ownership duration over the first 15 minutes of all feeding experiments of the Frankfurt group, when social excitement was highest. All three high ranking females were successful in obtaining possession of the food item while Ukela, the low ranking female, owned the food only once for < 10 s. Note that the male Bono was as successful in monopolizing the

food item as the high ranking adult females. Ownership duration during the first 15 minutes of the experiment differed significantly from equal distribution (chi square test, $\chi = 82.73$, df = 4, $p < 0.001$).

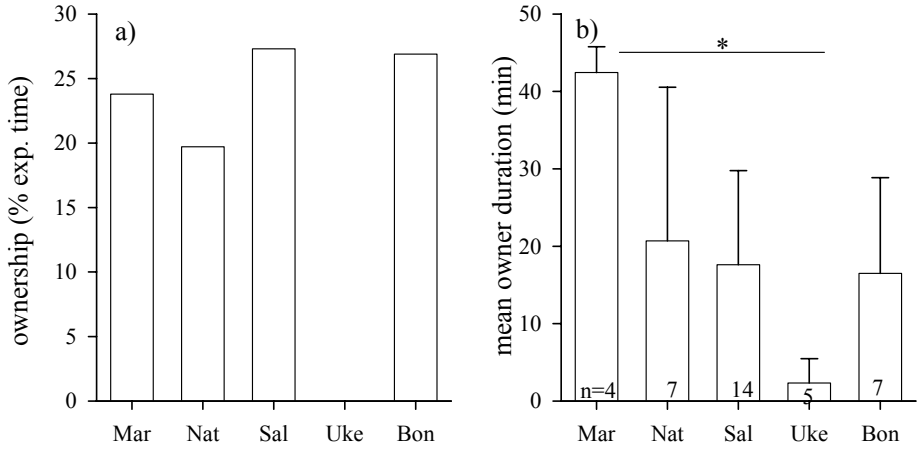

Fig. 3.20 Duration of ownership of monopolisable food items during the feeding experiments. (a) Total duration during the first 15 minutes and (b) mean (± SD) ownership duration in all experiments. *: Kruskal-Wallis test, $p < 0.05$.

Another approach to compare the status dependent capability to monopolise food is by investigating how long different individuals were able to "defend" the food source during the whole duration of the experiments. More specifically, only those data were included, when an animal possessed at least a quarter of the food source and ate it till it was either finished or until the food was taken by another individual (i.e. not being put aside). Possession bout duration differed significantly between adult individuals (Kruskal Wallis test, KW = 15.01; n = 37; $p < 0.01$, Fig. 3.20b). Margrit was on average more successful in keeping the food in possession than any other adult, yet the difference in possession bout duration was significant only between Margrit and Ukela (Kruskal Wallis post hoc comparison, Margrit: 42.46 ± 3.31 min, n= 4, Ukela: 2.32 ± 3.15 min; n = 5, Z = 2.807, $p < 0.05$).

3.4.3 Validation of the 11-ketoetiocholanolone assay

Since the analysis of immunoreactive 11-ketoetioncholanolone (= 11, 17-dioxoandrostane, DOA) as an indicator of the HPA activity has not yet been validated, the assay was validated first by showing that fecal iDOA is an indicator of stress in chimpanzees and bonobos.

3.4.3.1 Chimpanzee

After ACTH application, excreted glucocorticoid levels increased 10-fold from a baseline value of 0.40 ± 0.28 µg/g faeces to 4.27 µg/g after 22 hours (Fig. 3.21). Five hours after ACTH injection, the iDOA excretion level was at an intermediate stage. On the second day after the challenge, iDOA levels started to decline. Unfortunately, sampling had been stopped before excreted levels of iDOA reached baseline levels again.

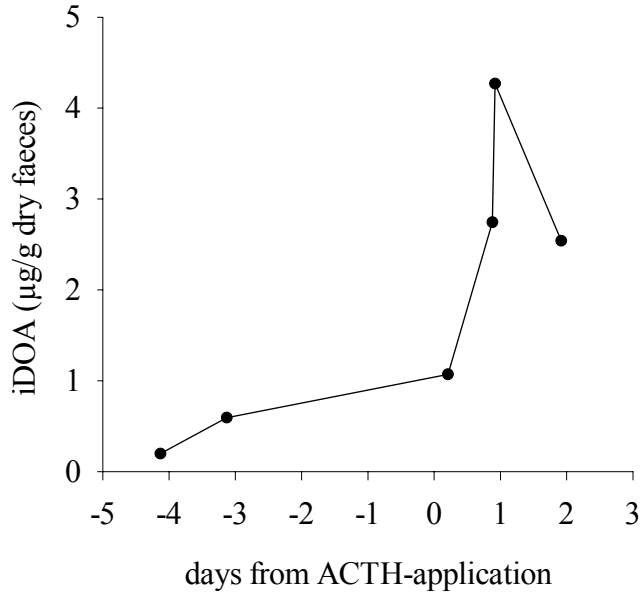

Fig. 3.21 Change in faecal 11-ketoetiocholanolone (iDOA) excretion after challenge with 25 IU ACTH (day 0) in a male common chimpanzee.

3.4.3.2 Bonobo

First, it was investigated whether the measurement of faecal iDOA can detect the effect of anaesthesia as a stressor in bonobos. Mean individual baseline levels during the week before anaesthesia varied between 0.96 ± 0.30 and 2.86 ± 1.44 µg iDOA/g faeces in the three females for whom daily samples could be collected before and after sedation. Anaesthesia and the subsequent handling resulted in a 3- to 7-fold increase of excreted iDOA levels in all individuals (Fig. 3.22a). In two females glucocorticoid excretion peaked on the first day after the treatment, in the third female on the second day.

Mean faecal glucocorticoid concentrations in the three females differed significantly between the periods before (days –7 to -1), during (days 0 to +2) and after treatment (days +3 to +9; Friedman ANOVA, $F_r = 6$; $n = 3$; $p < 0.05$; Fig. 3.22b).

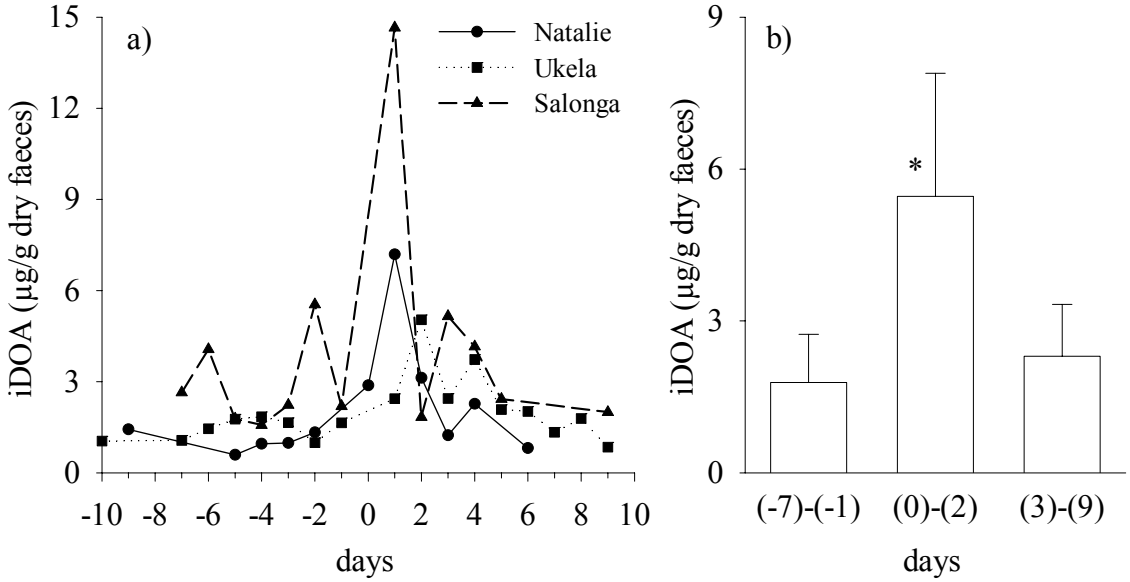

Fig. 3.22 Changes in faecal 11-ketoetiocholanolone (iDOA) excretion after anaesthesia of the Frankfurt group. (a) Individual excretion patterns of three female bonobos and (b) mean ± SD values of the periods before, during and after the treatment. Day of anaesthesia = day 0. *: $p < 0.05$, Friedman ANOVA.

Second, I assessed whether social reunification is a stressful event that can be measured with the iDOA assay. In contrast to anaesthesia, reunification of the former subgroups did not lead to increased adrenocortical activity in either of the females of the Frankfurt group (Fig. 3.23a). Mean individual baseline values during the week before the first reunification varied between 1.07 ± 0.55 and 3.77 ± 2.05 µg iDOA/g faeces in the four females. Note the initial high level of iDOA in the female Margrit (Fig. 3.23a). Individual glucocorticoid excretion did not change during or after reunification. Thus, when comparing periods before (days -15 to –7), during (days –6 to 2) and after reunification (days 3 to 8), mean faecal iDOA concentrations did not differ significantly (Friedman ANOVA, $F_r = 5$; $n = 4$; $p > 0.15$; Fig. 3.23b).

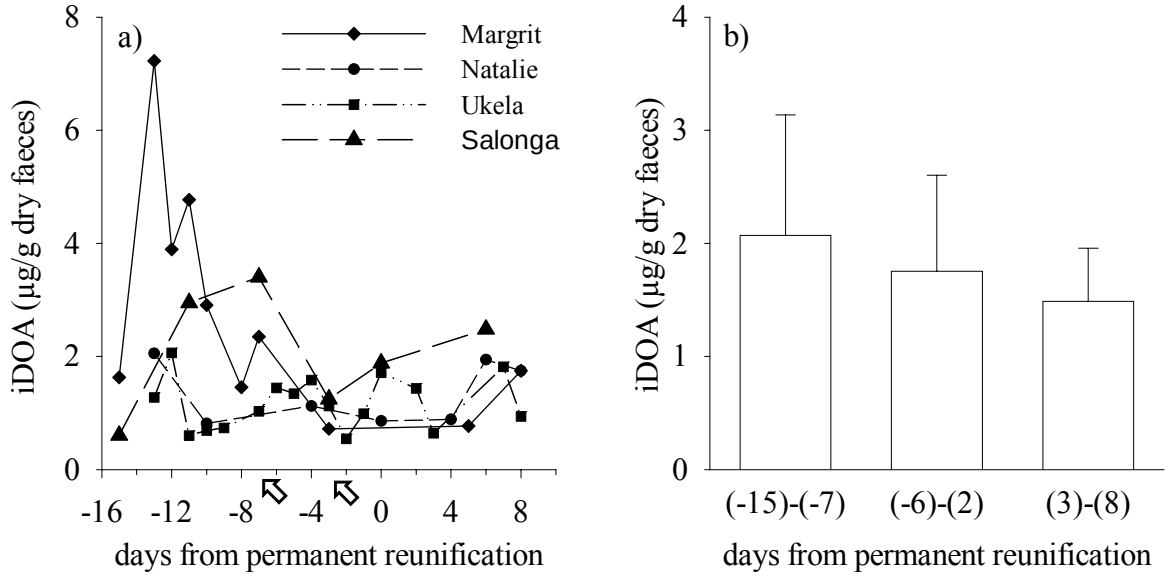

Fig. 3.23 Changes in faecal 11-ketoetiocholanolone (iDOA) excretion after reunification of the Frankfurt group. (a) Individual excretion patterns, (b) mean ± SD values of the periods before during and after reunification. Arrows: temporary reunification. Friedman ANOVA, n.s..

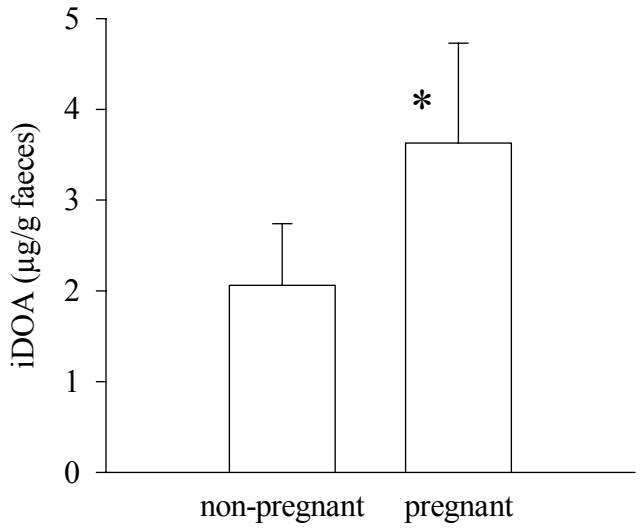

Fig. 3.24 11-Ketoetiocholanolone (mean ± SD) excretion in non-pregnant and pregnant females. The group of non-pregnant females combines females in lactational amenorrhoea and females with ovarian cycles. *: $p < 0.05$, T test.

Third, it was assessed whether iDOA analysis can detect elevated adrenocortical activity during pregnancy. Four out of eleven females observed were pregnant during at least part of the sampling time. For only three out of four pregnant females samples before conception were available which rendered a statistical comparison with each female as her own control impossible. Comparing mean faecal glucocorticoid concentrations of pregnant

females with values of non-pregnant females (combining both other females and observation periods when the pregnant females were not pregnant) revealed a significant difference between the two groups (T test, $n_{non\text{-}pregnant} = 10$; $n_{pregnant} = 4$; $T = -2.833$; $df = 12$; $p < 0.05$; Fig. 3.24).

3.4.3.3 Summary of the validation

Non-invasive analysis of faecal iDOA was found to be a valid tool to measure adrenocortical activity in chimpanzees as shown by ACTH administration and in bonobos as shown by the elevated glucocorticoid excretion after anaesthesia and during pregnancy. Reunification of a formerly separated group, however, was not accompanied by elevated iDOA levels.

3.4.4 Social status and adrenocortical activity

Samples collected during anaesthesia in the Frankfurt group (incl. samples collected until one week thereafter) were excluded from the comparison of mean levels of glucocorticoid excretion between high- and low-ranking individuals as this treatment was shown to significantly increase the excretion of glucocorticoids (chapter 3.4.3.2).

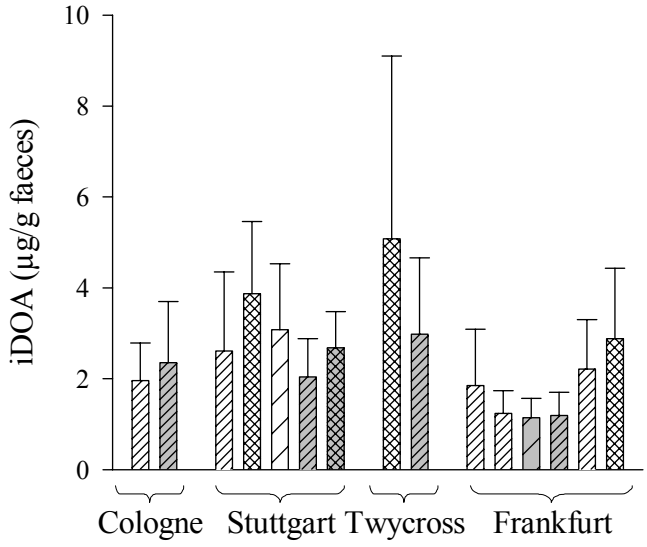

Fig. 3.25 Mean glucocorticoid excretion (± SD) calculated per female and reproductive status. White bars represent high ranking, grey bars low ranking females. Narrow stripes indicate females with ovulatory cycles, broad stripes females in lactational amenorrhoea and cross hatches pregnant females.

Mean glucocorticoid excretion per individual and reproductive status varied considerably (Fig. 3.25). As already mentioned in chapter 3.4.3.2, in each study group iDOA levels collected during pregnancy were higher than any other value.

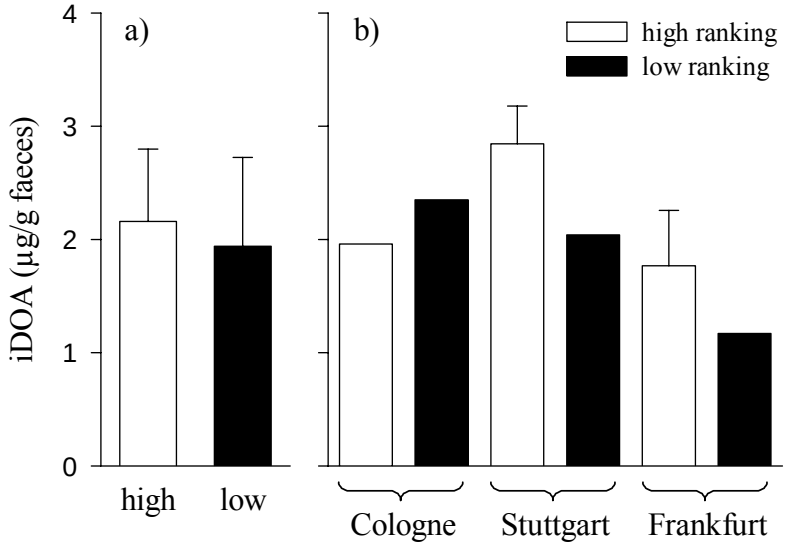

Fig. 3.26 Mean glucocorticoid levels of high and low ranking females. Mean levels (± SD) over (a) all groups and (b) per group. Data collected during pregnancy are excluded.

The comparison of glucocorticoid levels of high and low ranking individuals (excluding pregnancy) did not reveal a difference (Fig. 3.26). No status-dependent difference was found either when mean glucocorticoid levels of all females with menstrual cycles were compared (T-test, df = 7, $n_{low} = 4$, $n_{high} = 5$, t = -0,237, $p > 0.80$). This result did not change when females in lactational amenorrhoea were included to the analysis (T-test, df = 8, $n_{low} = 5$, $n_{high} = 6$, $t = 0.116$, $p > 0.90$). Focussing on group level, high ranking females appear to have higher adrenocortical activity than low ranking animals in the groups of Stuttgart and Frankfurt, whereas the opposite effect was found in the Cologne females (Fig. 3.26b).

Table 3.15 Results of the ANOVA analysing the relationship between mean individual glucocorticoid level, reproductive status (excl. pregnancy) and social status and between mean individual glucocorticoid level, group and social status.

	F (1,7), F(1,4)	P
reprod. Status	0.040	> 0.80
social status	3.294	> 0.10
reprod. status * social status	4.148	> 0.08
Group	5.947	> 0.06
social status	1.399	> 0.30
group * social status	1.268	> 0.30

However, integrating the reproductive status (menstrual cycles or amenorrhoea) in the analysis as a cofactor, analysis of variance after log-transformation of the data revealed a tendency of mean glucocorticoid levels to differ between high ranking and low ranking females (Table 3.15). When the social group instead of the reproductive status was considered as a cofactor, the tendentious difference between low and high ranking females disappeared whereas an influence of the study group was found (Table 3.15).

4 Discussion

4.1 Variability of menstrual cycles and swelling patterns

This study confirmed that the pattern of faecal immunoreactive pregnandiol excretion is a valuable tool for determining ovulation and the respective phases of the menstrual cycle in bonobos. Contrastingly, the high day-to-day variability in faecal oestrogen excretion did not allow an objective determination of the pre-ovulatory oestrogen peak and therefore this metabolite was not useful in dating ovulation. The data presented here also show that the reproductive status influences patterns of menstrual cycles. While parity was not found to influence menstrual cycle duration, i.e. cycle duration did not differ between nulliparous and parous females, lactation significantly extended the duration of menstrual cycles. Parity was still not found to influence duration of menstrual cycles when only young adult nulliparous females (i.e. adolescent females) were included in the analysis. In addition, the results indicate that mainly the duration of the follicular phase determines the length of intermenstrual interval. In contrast to this, the duration of the luteal phase was much less variable and was not found to correlate with the duration of the menstrual cycle. Moreover, with increasing length of the menstrual cycle, the duration of maximum tumescence was increasing as well.

Also other bobobo studies had difficulties in determining ovulation from the excretion pattern of oestrogens because of a lack of distinctive cyclic peaks (Jurke *et al.*, 2000; Möhle, 1995). It was suggested that this problem of high day-to-day variability could be a consequence of oestrogen metabolites being mainly excreted via urine (Jurke *et al.*, 1998; Jurke *et al.*, 2000). Although this is well possible, detailed radiometabolism studies that could prove this explanation are lacking. Non-invasive analyses of faecal oestrogen excretion patterns have proven to yield difficulties for the determination of ovulation in several other primate species as well. For example, faecal oestradiol levels were successfully used for determining ovulation in captive hanuman langurs (Heistermann *et al.*, 1995) but not in wild specimens (M. Heistermann, pers. communication). The same was reported for part of the ovulatory cycles in capuchin monkeys (Carosi *et al.*, 1999), muriquis (Strier & Ziegler, 1997) and Japanese macaques (Fujita *et al.*, 2001).

Consequently, the day of ovulation was determined solely based on the excretion pattern of faecal progestins in those studies (Heistermann *et al.*, 2001; Strier & Ziegler, 1997) as well

as in the present study. This methodology is also applied to time ovulation in a number of non-primate mammalian species (Schwarzenberger *et al.*, 1997).

Similar to common chimpanzees, the reproductive history was found to influence the duration of menstrual cycles to a certain extent in bonobos. In contrast to chimpanzees, nulliparous bonobos do not differ in their menstrual cycle duration from parous females. Similarly, a previous study on one captive bonobo could not find differences in cycle duration when cycles while the female was nulliparous were compared to later cycles when the female was multiparous (Vervaecke *et al.*, 1999). In chimpanzees and several other non-human primate species, however, nulliparous females often have longer cycles than parous females (reviewed in Butler, 1974). For example, it was reported that adolescent female bonobos have longer cycles than middle-aged, parous females (Thompson-Handler, 1990). These longer cycles were only shown during the first year following menarche. In the subsequent years prior to first birth cycles were very similar to those of prime adult females (Thompson-Handler, 1990). Assuming that this division of early / late adolescence may be a general pattern, the young females of the present data set - who had passed menarche most probably more than a year ago - were now of an age when bonobos typically give birth to their first offspring in captivity (Neugebauer, 1980; Parish, 1996). The age of menarche can be as early as six years in captivity (own observation, Vervaecke *et al.*, 1999). Thus, the young females of this study might not be the typical representatives of young females in early adolescent sterility. It is noteworthy that the number of cycles per individual varied enormously in Thompson-Handler's data set (1990) and was not accounted for. Therefore, some of her results might be heavily influenced by individual females and should be interpreted with caution.

Menstrual cycles of parous, non-lactating female bonobos are similar to those of chimpanzees (bonobos: 35.4 days (this study), chimpanzees: 33.2 days (Wallis, 1997)). And like in chimpanzees, menstrual cycles are significantly extended when females are lactating. In contrast, Vervaecke *et al.* (1999) could not find an effect of lactation on cycle duration (but see Heistermann *et al.*, 1996). A possible reason for this might be that the study analysed data of only one female. Furthermore, lactation may extend intermenstrual intervals only during the first cycles postpartum, with the effect gradually diminishing over time (Wallis, 1997). This influence of lactation on cycle duration is also common in lion-tailed macaques and baboons (Clarke *et al.*, 1993).

In summary, the present data suggest that bonobos and chimpanzees share similar reproductive patterns with the exception that bonobo cycles seem not to be influenced by parity. The differences found in some previous studies (e.g. Dahl *et al.*, 1991) can be explained by influences of different reproductive histories and the small sample size bonobo data usually relied on.

In humans, menstrual cycle length depends primarily on the rate and quality of follicular growth (Speroff *et al.,* 1994 cited in (Harlow *et al.*, 2000)), i.e. the duration of the follicular phase determines the length of the menstrual cycle. Exactly this was found to be the case in bonobos as well. For example, in non-lactating females, intermenstrual intervals varied between 26 and 40 days, with the respective follicular phase ranging from 16 to 30 days. The correlation between duration of follicular phase and intermenstrual interval was highly significant (mean $r_s = 0.966$), whereas no correlation between luteal phase and intermenstrual interval could be detected (mean $r_s = -0.214$). Similar observations are reported for chimpanzees (Nadler *et al.*, 1985). Chimpanzee follicular phases vary between 15 and 25 days (mean 20.4 ± 1 day) and luteal phases between 13 and 18 days (mean 15.0 ± 0.5 days), with the length of follicular phase being more highly correlated with cycle duration than length of luteal phase.

In humans, long menstrual cycles with an extended follicular phase of > 24 days were found to be due to extended oestrogen peaks or the demise and replacement of a dominant follicle (Harlow *et al.*, 2000). Since not only the duration of follicular phase but also the duration of maximum tumescence correlated positively with cycle duration in this study, this might hint to a slow and extended follicular maturation in long menstrual cycles in bonobos. If follicular maturation was simply delayed in long menstrual cycles, the duration of maximum tumescence should not correlate positively with cycle duration. Rather, the onset of maximum tumescence should be delayed under these circumstances. Thus, slow follicular growth would be the most obvious explanation for extended phases of sexual swelling in long cycles. Naturally, the prerequisite for this is the stimulating effect of oestrogens on the degree of tumescence of the sexual swelling as it has been previously shown for bonobos (Heistermann *et al.*, 1996) and other primates (Ozasa & Gould, 1982, 1984 for other primates). Cycles with extended follicular phase are not necessarily infertile. For example, one female (Salonga) conceived after a follicular phase of 38 days and gave birth to a son 230 days later. As well, it is shown for humans that extended cycle

patterns are quite frequent and do not differ from “normal” cycles in terms of oestrogen concentrations around ovulation (Harlow *et al.*, 2000).

However, more exhaustive studies are necessary to establish the precise relationship between follicular maturation and sexual swellings in bonobos so as to explain the physiological background of long menstrual cycles. Especially, the collection of urinary samples should be preferred over faecal samples as they might reflect oestrogen secretion more reliably. Above all, it has to be evaluated whether non-invasive methods will be useful at all to answer such specific and detailed questions.

Even if long intermenstrual intervals during lactation might be a physiological consequence of ongoing suckling that slows follicular growth, their exclusion from the data set still leaves a range of 26-40 days for intermenstrual intervals. This variability raises the question whether it is the by-product of inherent variations of ovarian folliculogenesis or whether it serves an adaptive function. A recent paper on ovarian cycles and paternity confusion suggested that there should be a selection for variability in the duration of the follicular phase if females benefit from confusing ovulation (van Schaik *et al.*, 2000). According to this scenario, the best way for a female to hide the exact timing of ovulation from males is to make ovulation unpredictable (van Schaik *et al.*, 2000). This could be achieved by variation in the duration of follicular phase whereas the same variability in the luteal phase would not be advantageous. Variation in the duration of maximum swelling would be an alternative tool. This idea could explain why there is much more variability in the duration of the follicular than in the luteal phase in females of primate species living in multi- male groups. It could also give explanation why the duration of the follicular phase correlates with that of the intermenstrual interval. Naturally, this only works when males do not rely on other cues of pending ovulation. This issue was addressed in the second part of the study.

In conclusion, the results of this study suggest that relationship between menstrual cycles and reproductive history is similar in chimpanzees and bonobos. However, more data are needed, especially from bonobos to elucidate the physiological background that determines the great variability in cycle and swelling patterns. This is of special value to further evaluate the adaptive significance of variability of menstrual cycles.

4.2 Reliability of sexual swellings as a signal of ovulation

The aims of the second part of the study were (1) to investigate whether the pattern of sexual swelling of bonobos is a reliable signal of ovulation, (2) to determine whether mating activity and other sexual interactions are solely influenced by the stage of female sexual swelling or also by her reproductive status, specifically the fertile phase of the cycle, and (3) to examine whether sexual interactions differ in frequency between the follicular and the luteal phase of the cycle.

The pattern of sexual swelling was shown to be a poor predictor of ovulation in bonobos. The results further indicate that female attractivity and receptivity were significantly influenced by the stage of the sexual swelling but not by the fertile phase. Female proceptivity changed neither with advancing degree of sexual swelling nor during the fertile phase. Finally, sexual interactions were not found to differ between the follicular and the luteal phase of the ovarian cycle.

As the data show, the phase of maximum tumescence in the bonobo is markedly long, covering on average a period of 31.2 % of the menstrual cycle. In addition, the duration of the swelling stages shows high variation both within and between individuals. These findings are in line with other data on wild and captive bonobos (Dahl, 1986; Furuichi, 1992; Heistermann *et al.*, 1996) as well as with reports of other primate species (maximum tumescence in macaques: 3 to 37 days, baboons: 3 to 20 days, chimpanzees: 7 to 17 days (Lindburg & Harvey, 1996; Shaikh *et al.*, 1982; Tutin, 1979)).

The timing of ovulation in relation to the onset as well as the end of maximum tumescence of the sexual swelling is highly variable in bonobos. One third of ovulations took place when the swelling had already started to deflate (but see Heistermann *et al.*, 1996). This phenomenon was observed in several of the study females and did not seem to indicate infertile cycles, as one individual conceived during such a cycle and gave birth after a normal gestation length of 230 days (Dahl, 1986; Heistermann *et al.*, 1996). This suggests that detumescence in bonobos is not as reliable as in other primate species in indicating that ovulation has occurred (Heistermann *et al.*, 1996; Nadler *et al.*, 1985; Shaikh *et al.*, 1982). The fact that only 56.5 % of ovulations (13 of 23) actually occurred during the last four days of maximum tumescence (baboons 93 %, (Shaikh *et al.*, 1982)), a period which has been suggested to represent the fertile phase in chimpanzees (Goodall, 1986 p. 444; Hasegawa & Hiraiwa-Hasegawa, 1983; Nishida, 1997; Wallis, 1992), indicates that

inferring ovulation retrospectively from the onset of detumescence may lead to wrong conclusions for bonobos. Additionally, it underscores the importance of hormonal information for an accurate timing of the ovulatory event (see also sooty mangabeys: Whitten & Russell, 1996).

Apart from the sexual swelling, males could use other cues to detect ovulation, e.g. olfactory cues from genital inspections or urine sniffing. However, data on pheromones in Old World primates are rare and inconclusive (Dixson, 1998; Fox, 1982; Gould & Martin, 1981; reviews: Hrdy & Whitten, 1986; Zeller, 1987). Although olfactory communication has not yet been investigated in bonobos specifically, the fact that the rates of sexual interactions were not found to differ between the non-fertile and the fertile phase in this study suggests that male bonobos do not use other, non-morphological cues of ovulation successfully. The results did not change, when only those copulations with a high probability of ejaculation were considered.

These findings are in line with previous data on wild bonobos that report that copulation rates are highest at stages of maximum tumescence (Furuichi, 1987) and that copulations are more often initiated by males than by females (Takahata *et al.*, 1996). In contrast to bonobos, the degree of sexual swelling as well as the presumed fertile phase are suggested to influence copulation frequency in chimpanzees (Deschner *et al.*, 2004; Goodall, 1986). Mean copulation duration in this study of 11.8 ± 7.1 s was similar or slightly shorter than it is reported for wild bonobos with also the range being comparable (Kano, 1989; Thompson-Handler, 1990; Thompson-Handler *et al.*, 1984). The difference in mean duration of copulation could be partly due to the much smaller sample size for the wild specimens.

Regarding the function of sexual swellings in bonobos, the unreliability of the sexual swelling as a signal of ovulation and the lack of increased mating activity during the fertile phase suggest that the ‘obvious ovulation’-hypothesis (Hamilton, 1984) cannot explain the function of sexual swellings in *Pan paniscus*. As the number of males in my study groups was limited, it is more difficult to rule out or support alternative hypotheses on the function of sexual swellings that interpret the sexual swelling as a signal with varying degree of reliability in advertising the timing of ovulation.

Taking already published data into account, female bonobos are known to mate promiscuously during the menstrual cycle in captivity (as far as possible) and in the wild (de Waal, 1988b; Furuichi, 1992; Takahata *et al.*, 1999; Vervaecke & van Elsacker, 2000).

This would favour the 'many males'- rather than the 'best male'-hypothesis (Clutton-Brock & Harvey, 1976; Hrdy, 1979, 1981) to explain the function of sexual swellings in bonobos. Additionally, by not advertising the fertile phase reliably, as has been shown in this study, females should have more chances to mate with multiple males than when advertising more reliably. In the latter case, increased intra-sexual competition among males could limit female choice.

Turke (1984) hypothesised that concealed and synchronised ovulation together with extended sexual receptivity forced protohominid males into extended consortships. While the unreliability of the swelling as a signal of ovulation and the mating pattern across the swelling cycle observed in this study could support Turke's idea, no trend towards ovulatory or swelling synchrony was detected (data not shown). Moreover, despite being one of three possible male mating strategies in chimpanzees (Goodall, 1986; Tutin, 1979), consortships have not been reported to play a significant role in bonobos (Kano, 1992; Takahata *et al.*, 1999).

It has recently been proposed that sexual swellings allow female primates to follow a mixed strategy of confusing and biasing paternity (Nunn, 1999; van Schaik *et al.*, 2000). The adaptive advantage for a female hiding the precise timing of ovulation is suggested to be paternity confusion. As males are not expected to kill offspring they potentially sired this should protect prospective offspring from infanticide (Hrdy, 1979, 1981; Soltis *et al.*, 2000; van Schaik *et al.*, 2000; van Schaik *et al.*, 1999). Assuming that the swelling is a graded signal that advertises the probability of ovulation (Martin, 1992), females could mate promiscuously during stages of moderate swelling to protect their offspring (Wolff & Macdonald, 2004), but mate more selectively during the fertile period of the cycle. Recent data on chimpanzees support this hypothesis (Deschner *et al.*, 2004; Stumpf & Boesch, 2005). The model also fits for bonobos. As already mentioned above, 56.6 % of ovulations occurred during the last four days of maximum tumescence. Since the probability of ovulation decreased with increasing temporal distance from the onset of detumescence, this could be interpreted as a probability distribution of the likelihood of ovulation *sensu* Martin (1992) and Nunn (1999). Although the similar gestation / lactation ratio for chimpanzees and bonobos suggests a comparable intrinsic infanticide risk, infanticide has not been observed in bonobos in contrast to chimpanzees (Goodall, 1986; Stanford, 1998). Therefore it was suggested that female bonobos benefit less from paternity concentration and thus from male protection because male infanticide risk is reduced compared to the

closely related common chimpanzee (van Schaik *et al.*, 2000). The findings that mating activity did not peak during the fertile phase in bonobos in contrast to reports on chimpanzees (Deschner *et al.*, 2004; Goodall, 1986; but see Klinkova *et al.*, 2005) and that mating activity did not differ between follicular and luteal phase would fit into this scenario. In common chimpanzees, preference for mating partners was found to change during the periovulatory phase of the menstrual cycle as compared to the non-fertile phase of the maximum swelling (Stumpf & Boesch, 2005) as is expected from the 'bias and confuse'-hypothesis. To further evaluate the 'bias and confuse'-hypothesis for bonobos, it remains to be investigated in greater detail, firstly, whether infanticide risk is really reduced in this species as compared to chimpanzees, and secondly, whether female mating preferences in bonobos actually change during the swelling and the ovarian cycle.

Apart from being a more or less precise signal of ovulation, sexual swellings have also been suggested to serve as a reliable indicator of female quality upon which males can decide how much to compete for a female (Pagel, 1994). This idea builds on the hypothesis of honest signalling (Zahavi, 1977) that postulates that signals remain honest over time only when a certain cost is implied. Although some correlation between swelling size and female lifetime reproductive value was recently found in wild baboons (Domb & Pagel, 2001), it still remains to be shown that a male actually prefers the female with the bigger swelling if he can chose between two females of equal stage of tumescence. The results of Domb's study could not be confirmed by observations on other baboon groups (Zinner *et al.*, 2002). A comparative test using interspecific data of various catharrhine species could not support the reliable indicator hypothesis either (Nunn *et al.*, 2001). Even more important, however, the cost, which is necessary to keep an honest signal evolutionarily stable, has not been shown yet convincingly for sexual swellings (Hamilton, 1984) or for other sexual traits in general (Kotiaho, 2001). Conceivable costs of sexual swellings could be an increase in travel costs caused by increased body weight due to water retention during maximum tumescence and susceptibility of the hairless skin patch to blood sucking parasites (see citations in Nunn *et al.*, 2001).

In summary, the present data suggest that sexual swellings of bonobos do not reliably advertise the fertile phase. Female behavioural cues do not advertise this phase either and males are therefore not able to detect impending ovulation. As a conclusion, the 'obvious ovulation'-hypothesis cannot explain the function of sexual swellings in bonobos. Nevertheless, sexual swellings of bonobos appear to be "honest enough" to stimulate male

arousal and mating, but leave room for females to manipulate the males by not being a precise signal of ovulation. Further studies are needed to assess mate choice of female bonobos during the menstrual cycle and to test whether other hypotheses better explain the function of sexual swellings in this species.

4.3 Context and function of sexual interactions between females

The present study indicates that the alliance formation-, competition reduction- and reconciliation-hypothesis cannot explain the occurrence of genital rubbing in female bonobos. The data support the tension regulation- and partly the status display hypothesis. The results of the specific tests are summarised in Table 4.1.

Table 4.1 Summary of hypotheses on genital rubbing and predictions. ++: prediction statistically supported, ?: prediction not testable, --: prediction not supported. For content of the predictions see Table 3.3.

Hypothesis	Prediction 1	Prediction 2	Prediction 3	Prediction 4
Alliance formation	++°	--	--	--
Competition reduction	--	--	--	
Reconciliation	++°	--	?	
Display of status	++°	++	--	
Tension regulation	++	++	?	

° same prediction: frequency of genital rubbing should differ between kin and non-kin.

4.3.1 Alliance formation

In the observed groups, genital rubbing occurred less often among related than among unrelated females. This is in line with data on wild bonobos (Hohmann & Fruth, 2000b) and Japanese macaques (Vasey, 1996). Although the fulfilment of this first prediction supports the alliance formation - as well as other hypotheses - it remains problematic, since the presence of adult female relatives in the group might not be typical for an adult female bonobo. There are no records of the presence of mothers of adult females in the wild bonobo communities of Lomako and Wamba, suggesting female emigration during adolescence and male philopatry (Gerloff *et al.*, 1999; Hashimoto *et al.*, 1996). However, avoidance of genital rubbing between mothers and their adolescent or young adult daughters is common both in captivity (this study) and in the wild (Hohmann & Fruth, 2000b). Although female emigration is the typical pattern for chimpanzees as well, the fact

that sometimes females return to their natal community in Gombe suggests that permanent dispersal is not absolutely obligatory (Pusey, 1979; Tutin & Mc Ginnis, 1981).

Furthermore, females did not prefer the same partner for genital rubbing and grooming in this study, as it has been reported for wild bonobos (Fruth & Hohmann, 1998). Thus, while grooming and frequent association are suggested to be an expression of affiliation, genital rubbing may not have the same meaning. In the present study, females supported each other only rarely in female-female conflicts but more often in conflicts with males. This occurred independent of rates of genital rubbing. In contrast, same-sex consortships correlate with support during agonistic encounters in female macaques, but only during the period of consort (Vasey, 1996). Vasey (1996) postulated that despite the correlation between same-sex sexual behaviour and agonistic support, female Japanese macaques do not form same-sex consorts to mediate alliances. In newly formed groups of captive and semi-free ranging rhesus monkeys, however, female same-sex sexual behaviour was suggested to mediate the formation of alliances between females (Fairbanks *et al.*, 1977). In this species, formation of new groups leads to increased levels of aggression and of hetero- and same-sex sexual interactions which decline over time. Yet a similar formation of new groups does not occur under natural situations, as rhesus monkeys are a female-bonded species. In line with the later (Fairbanks *et al.*, 1977), Parish (1994; 1996) postulated that co-operation allows female bonobos to have priority of access to food in situations when food is not accessible to everyone. In contrast to her own conclusions drawn from the study of an artificial termite-fishing site at the Stuttgart zoo, Parish (1994) reports that females are able to possess monopolisable food sources alone. The present study also indicates that females can monopolise food sources alone, without the help of an ally. Also in the wild, access to resources like meat or large fruits is often controlled by single females (Wood & White, 1996). Parish (1994) and Hohmann & Fruth (2000b) report that solicitations for genital rubbing in the feeding context are mainly directed towards the food owner - opposite to the findings of this study. Yet, in the present study, the same animals were responsible for the initiation of genital rubbing in the feeding experiment and in contexts not related to food. Therefore, I suggest that the direction of solicitation may be not influenced by the ownership of a valuable resource. This is supported by the finding that Kombote, still the highest ranking female in Stuttgart a couple of years after Parish's experiments, was solicited more often for genital rubbing by other females than she solicited them. Both during the termite fishing experiments and

outside this competitive feeding context, Kombote was solicited by other females (target of adult and adolescent females in approx. 60 % of genital rubbing during termite fishing (Parish, 1994) versus 69.6 % during routine observation (this study)). Thus, before concluding that solicitations towards the food owner serve to mediate food sharing, it has to be shown that the direction of solicitation is actually influenced by resource ownership by comparing events during feeding with events outside the feeding context. Although feeding at the artificial termite site still occurred in the Stuttgart group when I observed the group there, co-feeding was hardly ever seen and the excitement over this food source appeared to be much reduced compared to Parish's descriptions. Parish (1994) emphasises the higher female success in bonobos compared to chimpanzees in obtaining access to the artificial termite fishing site. Yet the male bonobo was as successful in her study as the females during the first five minutes of feeding at the fishing site, when competition for food is expected to be highest. No difference in duration of feeding bouts between chimpanzees and bonobos became obvious either (Parish, 1994, Fig. 3). However, her study showed clearly that the two *Pan* species differed in the frequency of co-feeding, which was much more common in bonobos. No correlation between genital rubbing and food sharing was found in the present study nor earlier by Parish (1994). In summary, there is no convincing proof that the formation or maintenance of alliances among females depends on the occurrence of genital rubbing.

4.3.2 Competition reduction

No evidence was found to support the competition reduction-hypothesis (Takahata *et al.*, 1996). Genital rubbing did not occur more frequently at maximum swelling than at lower swelling stages. This is consistent with results on wild animals (Takahata *et al.*, 1996). Additionally, one of the participants in dyads performing genital rubbing was often found to be detumescent in Wamba (Kuroda, 1980). In Lomako bonobos, however, genital rubbing is reported to occur more often at maximum tumescence than would be expected by chance, while no differences during other stages of tumescence were found (Hohmann & Fruth, 2000b). It appears therefore, that the influence of sexual swelling on the occurrence of genital rubbing is very weak if existing at all. This is further strengthened by the result of this study that solicitations for genital rubbing were not influenced by differences in the stage of genital swelling of the interacting females. Same-sex sexual behaviour has not been found to be restricted to the period of oestrus in other mammal

species either (but see Srivastava *et al.*, 1991; reviewed in Vasey, 1995). Although mutual sexual attraction and gratification is suggested to be the proximate motivation for the formation of same-sex consortships in macaques (Vasey, 1996; Vasey *et al.*, 1998), scientific evidence that females are sexually aroused when they engage in same-sex sexual behaviour is very weak. While subordinate Japanese macaques profit from sexual consortships in terms of reduced aggression and a temporary rise in rank (Vasey, 1996), the results of this study do not show that bonobo females actually are less often victim of female aggression during advanced stages of tumescence.

4.3.3 Reconciliation

Also reconciliation does not explain the occurrence of genital rubbing. The frequency of genital rubbing by far exceeded the frequency of conflicts between females. Only some dyads were observed to perform genital rubbing after a conflict. While this resulted in genital rubbing not being more frequent after a conflict than before in the present study, Hohmann & Fruth (2000b) reported that rates of genital rubbing increased after a conflict in wild specimen. The difference could be due to the fact that Hohmann & Fruth (2000b) considered not only dyadic but also triadic interactions, i.e. genital rubbing that included one former opponent and a third individual that had not been involved in the conflict. Of 26 cases of post-conflict genital rubbing, 15 actually were reported to occurr between former opponents in their study. While a female approaching a third individual who was not involved in the previous conflict might indeed search "substitute reconciliation" with relatives or allies of the opponent (reviewed in Kappeler & van Schaik, 1992), she might also seek consolation, i.e. appeasement, from a third party (de Waal & van Roosmalen, 1979). Alternatively, she might try to gain an alliance partner and thus wish to proceed with the aggressive interaction rather than to terminate it (de Waal & Aureli, 1996). In order to decide upon the function of such a triadic interaction, detailed knowledge of the relationships of all three participants and of further interactions would be needed. Thus, to avoid confusion of the possible functions of post-conflict interactions, I decided not to combine dyadic and triadic interactions in the present study but rather to focus on 'direct', i.e. dyadic reconciliation. Hohmann & Fruth (2000b) also state that dyads involved in genital rubbing were usually not identical with those performing agonistic interactions in a given context. This is consistent with the present results and confirms that genital rubbing is highly unlikely to be a tool of direct reconciliation in bonobos. The idea that socio-

sexual behaviour may serve to reconcile former opponents after a conflict was first postulated by de Waal (1987), with genital rubbing being one of many suggested behavioural elements. De Waal's study, however, has several caveats. First, half of his study subjects were subadolescent, and thus of an age where practice sex still may play a role. Additionally, females did not have adult members of the same sex for interaction. Second, and even more important, data on same-sex and hetero-sexual mounting and other interactions involving genital manipulation of at least one participant were pooled with data on affiliative behaviours (e.g. touching, embracing) to investigate the influence of feeding or aggression on their frequency. Thus, although in total these behavioural elements were increasing upon arrival of food or after aggression (de Waal, 1987), it can not be concluded from that study that genital rubbing itself is a tool of reconciliation.

In general, the concurrent increase of agonistic and sexual interactions in the presence of food can lead to false positive results if agonism during feeding is included into the testing of the reconciliation hypothesis, especially when analyses are not done pair-wise. If the arrival of food stimulates both competition and mounting, then the probability that genital rubbing falls into a post-conflict period is higher in the food than in the non-food context. Thus, tension and reconciliation might be difficult to distinguish. In summary, although limited, the data obtained here do not support the reconciliation-hypothesis.

4.3.4 Display of social status

However, genital rubbing might serve as a display of social status. In a dyad that performed genital rubbing in the study groups, the dominant female took the mounter's position more often than the subordinate female. This corresponds to data on wild bonobos from Lomako (Hohmann & Fruth, 2000b). Hohmann & Fruth (2000b) and Parish (1994) also found rank-related asymmetries in the initiation of genital rubbing whereas no asymmetry was found in the present study and for macaques (Vasey *et al.*, 1998). In the two earlier bonobo studies, genital rubbing was not analysed per dyad as was done in the present study. Instead, all data were pooled. If solicitations observed during this study were analysed in the same way as in the study on wild bonobos (Hohmann & Fruth, 2000b), dominant captive female bonobos would solicit genital rubbing more often than subordinate ones (186 versus 44 solicitations). This finding would be exactly the opposite of Hohmann & Fruth (2000b)'s study. Because of the enormous differences in the frequency of genital rubbing between dyads, however, I performed dyadic analyses rather

than pooling of all data, as the latter would result in certain dyads having more weight than others.

In Hanuman langurs, mounters are usually higher ranking than mountees and mother-daughter dyads are underrepresented in dyads that perform female-female mounting (Srivastava *et al.*, 1991). Contrastingly, no rank-related asymmetries were found in solicitations or in the position during female mounting in Japanese macaques (Vasey *et al.*, 1998). Thus, while genital rubbing might be a display of social dominance in bonobos, in general, the connection between dominance and female-female mounting is unclear in primates (Tyler, 1984; Wallen & Parsons, 1997).

4.3.5 Tension regulation

The results of the present study confirm the tension regulation-hypothesis. The presence of food incited male sexual arousal as well as heterosexual mounting, sexual interactions between females and agonistic interactions. In this context, aggression between two females tended to occur when no genital rubbing was observed at the same occasion, but this was not statistically testable. A party's arrival at a new food source has been shown to stimulate social excitement and sexual arousal in wild chimpanzees as well as in captive bonobos and often leads to increased frequency of mating behaviour (de Waal, 1995b; Goodall, 1986; Tutin & Mc Ginnis, 1981). As predicted, the quality of the food sources (i.e. dispersed or clumped distribution) and the resulting potential for monopolisation influenced the level of excitement and of food competition. In wild bonobos, food patch size was found to correlate with the rate of genital rubbing (White & Thompson-Handler, 1989) and genital rubbing is more frequent when a food source is monopolisable than when food is accessible to all party members (Hohmann & Fruth, 2000b). These publications in line with the present data support the hypothesis that genital rubbing serves as a mechanism of tension regulation (de Waal, 1987; Kano, 1982; Kuroda, 1980).

Tension regulation would not only explain the occurrence of genital rubbing in the feeding context but could also explain its occurrence during immigration and inter-group encounters. When young adolescent bonobo females immigrate into a new group, they tend to initiate affiliative interactions and genital rubbing with specific senior resident females. The frequency of these interactions decreases with time following the immigration event (Idani, 1991). This could be explained most directly by the young female trying to reduce the tension resulting from her immigration into the new group. An alternative

interpretation would be that the immigrating female initiates genital rubbing to establish an alliance with this high ranking female. While the young female would clearly profit immediately from such an alliance, its advantage for the high ranking female is questionable, as the new immigrant will be of low rank and of unknown quality as an ally. Therefore, the tension regulation-hypothesis can explain this observation better than the alliance formation-hypothesis. A hint for the successful regulation of tension by genital rubbing could be the much lower incidence of female aggression during immigration in bonobos as compared to chimpanzees, who lack this behaviour (Idani, 1991; Pfalzer & Ehret, 1995). Furthermore, the occurrence of genital rubbing during inter-group encounters (Idani, 1990 G. Hohmann & J. Eriksson pers. comm.) can be interpreted as well by the mechanism of tension reduction but not of alliance formation.

In conclusion, while many different hypotheses have been developed to explain the functional significance of genital rubbing, most do not stand a closer examination. The available data do not support the 'reconciliation'-, the 'female attraction'- and the 'alliance formation'-hypotheses. Genital rubbing might have a function as a dominance display. However, the present data and also most previously published studies most strongly support the 'tension regulation'-hypothesis. Genital rubbing may help in the formation or maintenance of close proximity between females by not only bringing individuals closely together but also engaging in non-aggressive body contact. Thus, the occurrence of genital rubbing during feeding and other socially tense situations and also occasionally after a conflict or during inter-group encounters can be explained most parsimoniously by this hypothesis.

4.4 Behavioural and endocrine parameters of female social status

In this study I showed that the 11-ketoetiocholanolone (DOA) assay is a valid tool to assess adrenocortical activity in chimpanzees and bonobos. As expected, application of ACTH significantly increased the level of excreted faecal iDOA in the chimpanzee. A significant increase in faecal iDOA was also found in bonobos after anaesthesia. Furthermore, the excretion of glucocorticoids was significantly elevated during pregnancy when compared to other reproductive stages, whereas a period of social excitement in the Frankfurt group (group re-unification) did not influence excretion patterns of glucocorticoid levels. I also demonstrated that females profit from high social status when

access to resources is limited and food is monopolisable. However, no clear relationship existed between social rank and glucocorticoid excretion in captive female bonobos.

4.4.1 Assay validation

In several mammalian species, non-invasive techniques proved to be an important tool for the assessment of adrenocortical activity, since this method does not disturb animals and therefore allows long-term data collection. Thus, non-invasive methods have been successfully applied to investigate glucocorticoid excretion patterns of ruminants (Dehnhard *et al.*, 2001; Palme & Möstl, 1997), elephants (Foley *et al.*, 2001), hyenas (Goymann *et al.*, 1999), big cats (Wasser *et al.*, 2000), guinea pigs (Sachser *et al.*, 1998), rabbits (von Holst, 1986) and many primate species (Cavigelli, 1999; Robbins & Czekala, 1997; Saltzman *et al.*, 1994). Apart from not distressing the study objects during data collection, faecal samples offer the advantage of representing a cumulative secretion over several hours. Thus, the potential for mistakes by the confounding variable of diurnal secretion patterns is minimised (Whitten *et al.*, 1998a). At the same time, this renders the detection of short term changes in adrenocortical activity by faecal hormone analysis impossible.

To prove that the glucocorticoid metabolite excreted into urine or faeces and measured with a given antibody shows the appropriate physiological significance, i.e. is a measure for adrenocortical activity, ACTH challenges are usually the first step of validation (Goymann *et al.*, 1999; Wasser *et al.*, 2000). The ACTH challenge of a chimpanzee as analysed here showed that faecal iDOA truly reflects adrenocortical activity in this species. The same approach was not possible for bonobos, because their endangered status and rare presence in captive settings does not allow invasive procedures. However, since a stressful event, anaesthesia, could be used for validation, an ACTH challenge was not necessary. In chimpanzees and olive baboons, anaesthesia has been shown to be an acute stressor that leads to elevated glucocorticoid levels (Sapolsky, 1982; Whitten *et al.*, 1998b). Also in bonobos, glucocorticoid excretion increased significantly one to two days after anaesthesia in all study females where sample frequency was high enough to allow analysis of phases before, during and after intervention. Furthermore, glucocorticoid levels were significantly elevated during pregnancy when compared to other reproductive stages. This increased adrenocortical activity is a consequence of the positive influence of oestrogens on the pituitary-adrenocortical function in primates, resulting in a continuous increase of

glucocorticoid levels during gestation (see also elephants Foley *et al.*, 2001; Giussani *et al.*, 2000). However, when analysing a period of presumable social excitement and tension, i.e. the re-unification of a group that had been separated for several months, no consistent pattern of glucocorticoid excretion could be found. A reason for this could be that the reunification was not perceived as a stressful event by the females. This is supported by the finding that the frequency of genital rubbing which has been shown to increase during phases of social tension was not elevated either above baseline values during the reunification period (see chapter 3.4.3.2).

Taken together, analysing faecal excretion patterns of iDOA proved to be a valid tool to investigate adrenocortical activity in bonobos.

4.4.2 Social status and its impact on access to resources

In all four study groups, dyadic dominance relationships based on displacement activities could be established. In all but one group, these relationships resulted in linear hierarchies which corresponded to reports of the animal keepers. The Frankfurt group was the only exception. Here, the dominance hierarchy was not linear, the elderly former alpha-female Margrit had lost her clear dominance status (C. Knott, pers. obs.). Rather, she was often observed to avoid the group and seemed to prefer resting alone. She sometimes appeared to keep away from the infants when those were playing. Thus, when Margrit was leaving upon approach of either Salonga or Ukela, she in fact might have avoided their association because of the accompanying infants and the resulting disturbance (see also Furuichi, 1997). There are yet not enough data to show if female dominance hierarchies are typically linear in bonobos although two studies on a wild and a captive group suggest so (Furuichi, 1997; Vervaecke *et al.*, 2000). Congruent with data from Wamba is the low occurrence of agonistic interactions among females, mostly consisting of displacements without any overt aggression (Furuichi, 1997). Thus, most researchers group females in different rank classes as was done for this study as well (c.f.Hohmann & Fruth, 2000b; Kano, 1982).

Although the advantage of high social status in an egalitarian society might be limited in situations when food is more or less evenly distributed, it nevertheless should influence the accessibility of restricted resources. In captive situations that could be either the accessibility of preferred parts of the enclosure, e.g. for resting, or of preferred food items that are given rarely and are monopolisable. Indeed, it could be shown in the Frankfurt group that the high ranking bonobo females were able to monopolise a clumped food item

more often than the low ranking female. The elderly female Margrit was most successful in obtaining this resource. This confirms that she is still be the top ranking female although she retreats upon approach of some females. As well, previous observations of an artificial termite fishing site in another captive group reported that the lowest ranking adult female was least successful in obtaining monopolisable food (Parish, 1996). In summary, high social status in bonobos may pay off in situations of contest competition that are accompanied by increased frequencies of agonistic interactions (see also chapter 3.3.6).

4.4.3 Physiological correlates of social status

The priority of access to rare yet valuable resources has often been suggested to result in a better physical condition and finally in higher reproductive success of high ranking females as was shown for baboons (Packer *et al.*, 1995) and chimpanzees (Pusey *et al.*, 1997). Apart from physical condition, harassment by high ranking animals was suggested to reduce the fertility of subordinate females (Abbott, 1987; Chapais, 1992; Dunbar, 1980; Dunbar & Dunbar, 1977). While the influence of social status on bonobo reproductive success has not yet been evaluated due to the relatively short time this species has been studied, harassment of high ranking females towards low ranking ones was shown to be common in wild and captive groups (Hohmann & Fruth, 2000a; Vervaecke & van Elsacker, 2000). It was not observed in the four study groups, though. If female harassment developed as a strategy of high ranking females to maximise their own reproductive success, it could enhance adrenocortical activity and thus decrease fertility of subordinate females. The question whether female status influences reproductive parameters, e.g. duration of menstrual cycles and incidence of anovulatory cycles could not be answered in this study due to the limited sample size and the confounding influence of lactation on the duration of intermenstrual intervals (see also chapter 3.1.1). However, no significant difference in faecal glucocorticoid excretion was detected between high ranking and low ranking females in this study. As well, a preliminary study on a bonobo group at Planckendael zoo, Belgium, could not find a correlation between glucocorticoid levels and rank although a linear, mixed-sex hierarchy was described (Meulemann *et al.*, 2000). This finding can be interpreted in different ways.

(1) The lack of status-dependent difference in iDOA levels might be caused by the setting of the study as well as the limited sample size. It can be argued that the limited space in captivity and the lack of possibilities to avoid confrontations and conspecifics may result in

a general increase of adrenocortical activity which masks the effect of status-dependent differences in corticoid secretion. While it is difficult to totally rule out this possibility, the animals studied for this project had access to more than one enclosure during most of the day and therefore victims could avoid the aggressor after a conflict. In addition, status-dependent differences in basal cortisol levels have been detected in captive studies (e.g. Alexander & Irvine, 1998; e.g. Saltzman *et al.*, 1996; Stefanski, 2000), so that the findings of this study are unlikely to be merely a consequence of captivity.

(2) Females might not differ in their glucocorticoid status because their levels of perceived stress do not differ. The bonobo society is described as dispersal-egalitarian and within-group contest between females has been reported to be relatively low (Sterck *et al.*, 1997). Consequently, the profit of high social status in terms of access to resources should be smaller than when living in nepotistic-despotic societies. While the low ranking female Ukela was least successful in monopolising food during the feeding experiment, she was the most successful adult in terms of obtaining food from the food owner (see chapter 3.3.2.4, note however, that only very small amounts of food were exchanged during food sharing). Observed levels of aggression between adult females were very low and thus might not result in chronic adrenocortical stimulation in low ranking females. Agonistic encounters between females were found not only to be very rare but also to be bidirectional. Accordingly, aggression might not be frequent and severe enough to change basal glucocorticoid levels of subordinates, contrasting to some macaque species (Aureli & van Schaik, 1991; Smucny *et al.*, 1996). In addition, social support in form of affiliative interactions or physical support during conflicts has been shown to minimise the effect of stress (Sachser *et al.*, 1998; von Holst, 1998; Waples & Gales, 2002). The frequent non-agonistic interactions of low ranking bonobos females with group members may therefore help to attenuate the effect of social stress. Furthermore, as tension reduction is suggested to play an important role in the regulation of aggression in bonobos (de Waal, 1987, 1995a, 1995b; Furuichi, 1989, 1997; Hashimoto & Furuichi, 1994; Hohmann & Fruth, 2000b), these mechanism should further alleviate social stress (see also chapter 3.3.6).

In general, the relationship between social status and glucocorticoids proves to be more complex than it is often assumed. As already mentioned in the introduction, results so far have been very inconclusive. While in some cooperative breeders glucocorticoids are elevated in subordinates (review in Creel, 2001), in others, dominant individuals have higher basal glucocorticoid levels than subordinates (Creel, 2001; Creel *et al.*, 1997). For

example, cortisol levels in dominant female marmosets are higher than in subordinates (Saltzman *et al.*, 1994). Yet the inhibitory effect of chronically elevated glucocorticoid levels on reproductive function appears to be circumvented in this New Wold monkey, as only the dominant female breeds while subordinates are anovulatory. As has been already mentioned above, positive correlations between social status and glucocorticoid levels can result from low ranking individuals experiencing higher rates of aggression and lacking opportunities to fight back or redirect aggression (Sapolsky, 1982). However, if the position of high ranking individuals is permanently challenged, they have to fight more than low ranking individuals to keep their position and consequently might face higher levels of social stress that would then result in higher glucocorticoid levels (African wild dogs: Creel *et al.*, 1997). Alternatively, status-dependent differences in HPA activity might not exist at all in stable social situations but only become obvious under conditions of instability (Sapolsky, 1992a). It would be advantageous to activate the HPA system only when necessary since chronic stimulation may lead to patho-physiological effects like suppressed immune function, hypertension, etc. (Mc Ewen *et al.*, 1997; Ottenweller *et al.*, 1992; von Holst, 1998). In baboons, for example, instability of the social system leads to enhanced adrenocortical activity only in those individuals whose social position is at stake (Sapolsky, 1992a, 1993; see also review in von Holst, 1998). The dominance hierarchies in the bonobo study groups were described as being stable since several years by the animal keepers, no sign of a rank turnover was obvious during the observation period either. Furthermore, mode and degree of the physiological answer to an unstable social situation also depend on the coping pattern of an individual (Johnson *et al.*, 1992; Sachser *et al.*, 1998).

(4) When discussing the lack of status-dependent glucocorticoid excretion it is of great importance not to equate stress with adrenocortical function. Levels of social stress might vary dependent on social status, but this might be expressed by other means than the basal adrenocortical activity. Before stating that individuals of different rank do not differ in their levels of “stress”, more parameters apart from basal adrenocortical function need to be evaluated. For example, animals might show differences in the degree of their physiological reaction to stressors, like in their adrenocortical capacity. This has been found in baboons, where dominant males showed a bigger stress reaction in terms of plasma cortisol increase than subordinate individuals (Sapolsky, 1982). Further, stress may act not only on the hypothalamo-pituitary-adrenocortical axis but also on the sympathetico-

adrenomedullary axis. Acute stress has been shown to activate the sympathetico-adrenomedullary axis which results in an increased secretion of the catecholamines adrenalin and noradrenalin within a few minutes (Sapolsky, 1992b). However, direct measurement of catecholamines proved to be difficult. Firstly, their secretion rate is modulated quickly upon disturbance which would render invasive assessment of individual catecholamine levels problematic. And secondly, they are rapidly metabolised and degraded which makes their non-invasive detection in urine difficult. Therefore, an indirect assessment of the sympathetico-adrenomedullary activity, like the measurement of heart rate would be easier to realise (Smucny *et al.*, 1996; Stöhr, 1986). It has also been shown that chronic stress suppresses immune function (Ader & Cohen, 1984; Johnson *et al.*, 1992; Mc Ewen *et al.*, 1997; Stefanski, 1998, 2000; von Holst *et al.*, 1999). Because of the complexity of the immune system, it would be required to assess different immunological parameters in blood to obtain an informative picture of an individual's immune status.

In conclusion, the present study shows that social status influences access to restricted resources in bonobos whereas no status dependent influence on cortisol excretion was found. This finding would be in line with behavioural patterns like genital rubbing that are suggested to decrease social tension among females. More data are necessary to further evaluate whether animals of different status differ in their levels of social stress, though. Especially, other physiological indicators of social stress apart from activity of the adrenal cortex, like adreno-medullary activity and immune function would be of great value to complete the picture. This would also allow assessing the existence of different coping strategies of the animals. In order to obtain this set of information, the collection of long-term data (life history) on wild bonobos would be as important as the development of a fast and effective method of collecting blood samples that allows a broad assessment of physiological stress parameters. Experiments under controlled conditions in captivity would further be a valuable tool to address very specific questions concerning short term effects of social status. In addition, long-term data from the wild would allow assessing the influence of social status on parameters of reproductive success, like duration of intermenstrual intervals and lactational amenorrhoea, length of inter-birth intervals, age at menarche and first parturition, and survival of offspring.

4.5 Outlook

Taken together, although many publications were published on bonobos during the past years, especially long-term data and experimental data are missing that allow to explain the functional significance of the species‘ behaviour and to shed light on the reproductive biology of this species against the background of its natural habitat.

For example, to assess the function of unpredictable ovulation in bonobos, it still needs to be established whether infanticide risk is actually lower for bonobos than for chimpanzees. Furthermore, long-term data from the wild could establish whether females of different social status also differ in terms of reproductive parameters, like duration of menstrual cycles, frequency of infertile cycles, inter-birth intervals, duration of lactation, etc. As well, experiments both in the wild and in captivity would be helpful in explaining the importance of social status for this species. Long-term data on relationships between females could also help to further establish the function of genital rubbing. For example, it is of importance to assess how changes in the relationship between two females, e.g. changes in status or in time spent together in a party, are reflected in the pattern of genital rubbing.

It is also of high importance to collect more physiological data that may help to answer many open questions for this species. How can the big temporal variability between sexual swelling and ovulation be explained on a physiological level? Do females of different social status differ in their immunological parameters or in the activity of their sympathico-adrenomedulary stress axis? How do they differ in their reaction to external stressors that influence the group? To give valid answers to these questions on the physiology of the species, non-invasive methods need to be accompanied by invasive methods.

5 Summary

The present study investigates sexual behaviour and the importance of dominance in female bonobos. Detailed behavioural studies were carried out on four mixed-sex captive groups of bonobos together with the collection of morphological data and faecal samples to allow the non-invasive assessment of physiological parameters.

First, I addressed the background for the great variability in patterns of menstrual and swelling cycles in bonobos. The reproductive history was found to influence the duration of menstrual intervals. Menstrual cycles and phases of maximum tumescence of the sexual swelling lasted longer when females were still lactating. No influence of parity on cycle patterns was detected. The results show further that the variability of the duration of intermenstrual intervals is mainly caused by variability in the length of the follicular phase. The luteal phase, contrastingly, was found to be much less variable and not to influence the length of intermenstrual intervals.

The question resulting from this is whether the sexual swelling serves as a reliable indicator of ovulation in bonobos. Hormone analyses showed that the day of ovulation could not be predicted from the onset of maximum tumescence. Detumescence of the swelling was no clear sign that ovulation had occurred either. Nonetheless, sexual interactions were found to vary according to the degree of tumescence, being most frequent at maximum tumescence. No further change in frequency of sexual interactions was found in the peri-ovulatory phase nor was there a difference between follicular and luteal phase.

These results indicate that sexual swellings are not a reliable signal of ovulation. Rather, sexual swellings could be a graded signal that advertises the probability of ovulation thus allowing females to follow a mixed strategy of confusing and biasing paternity.

Next, the context and function of same-sex sexual interactions among female bonobos were investigated. Genital rubbing took place more often between non-related females than between related females. Females were able to get hold of and defend monopolisable food items without the help of other females in feeding experiments. No relationship between genital rubbing and food sharing was found and no female-female coalitions were formed during these experiments. Interventions in conflicts outside the feeding experiments were observed - most often in heterosexual conflicts - but females supported each other irrespective of preferences for genital rubbing. The frequency of genital rubbing did not

vary in dependence of the degree of genital swelling nor was the solicitation of genital rubbing asymmetric in dependence of the relative degree of swelling of the two partners. Above that, the degree of tumescence did not influence the frequency of received or overall aggression for a female. Although most female dyads were involved in same-sex conflicts, genital rubbing was observed in less than half of the dyads after the conflict. Comparing time windows of 15 minutes before and after a conflict did not reveal an increase of genital rubbing after the conflict. High-ranking females took the male position during genital rubbing significantly more often than low ranking ones. The direction of initiation of genital rubbing was not influenced by social status.

The data do no support the hypothesis that genial rubbing serves to form or maintain alliances, to reduce competition among females or to reconcile former opponents. However, genital rubbing may be a display of social status or may serve to reduce tension.

Finally, the correlation of physiological parameters and social status in female bonobos was studied. I investigated whether females differ in their excretion pattern of the glucocorticoid 11-ketoetiocholanolone (DOA) in dependence of their social status. Based on displacements, females were categorised to either high or low social status. During the feeding experiments carried out on one group, high social status transferred in access to monopolisable food, the low ranking female was not successful in monopolising the food item. However, female social status was not reflected in the faecal excretion pattern of glucocorticoid metabolites in any of the three groups analysed. In two groups the high-ranking individuals had higher levels of iDOA than low-ranking individuals, in the other group it was vice versa. The fourth group did not allow this investigation as the high ranking individual was pregnant and pregnancy was found to result in elevated glucocorticoid levels.

The results indicate that also in bonobo females, high social status translates into better access to monopolizable resources. Status dependent differences in cortisol excretion may not exist in bonobos or may become obvious only during periods of social instability. Alternatively, social status may not influence adrenocortical function but other physiological parameters of the so-called stress axes.

Taken together, this study provides an interdisciplinary view on bonobo female behaviour and physiology helping to better understand the adaptive significance of a species' social and mating system.

6 Zusammenfassung

Die vorliegende Studie untersucht das Sexualverhalten und die Bedeutung des sozialen Ranges bei weiblichen Bonobos. Detaillierte Verhaltensbeobachtungen in Kombination mit dem Sammeln morphologischer Daten und Kotproben wurden an vier gemischten zoolebenden Bonobogruppen durchgeführt, um die nicht-invasive Untersuchung physiologischer Parameter zu ermöglichen.

Zuerst untersuchte ich den Hintergrund für die große Variabilität in den Menstruations- und Schwellungszyklen der Bonobos. Es wurde gezeigt, dass die reproduktive Vorgeschichte eines Weibchens die Dauer der Menstruationszyklen beeinflusst. Menstruationszyklen und die Phase der Maximalschwellung der Genitalschwellung dauerten bei laktierenden Weibchen länger als bei nicht-laktierenden. Es wurde aber kein Einfluss der Parität auf Zyklusmuster gefunden. Die Ergebnisse zeigen weiterhin, dass die Variabilität der Dauer der Intermenstruationsintervalle vor allem durch die Variabilität der Follikelphase bedingt ist. Im Gegensatz dazu ist die Dauer der Lutealphase wesentlich weniger variabel und beeinflusst die Dauer der Intermenstruationsintervalle nicht.

Daraus resultierte die Frage, ob Genitalschwellungen bei Bonobos als verlässlicher Ovulationsindikator dienen. Wie Hormonanalysen zeigten, konnte der Tag der Ovulation nicht mit dem Beginn der maximalen Tumeszenz der Genitalschwellung vorhergesagt werden. Auch war Detumeszenz kein klares Signal, dass die Ovulation bereits eingetreten war. Dennoch wurde gefunden, dass sexuelle Interaktionen mit dem Grad der Tumeszenz variierten, sie waren bei maximaler Tumeszenz am häufigsten. In der peri-ovulatorischen Phase wurde keine weitere Veränderung in der Häufigkeit sexueller Interaktionen gefunden. Zudem gab es keinen Unterschied in ihrer Häufigkeit zwischen Follikel- und Lutealphase.

Diese Ergebnisse deuten darauf hin, dass die Genitalschwellung kein verlässliches Ovulationssignal bei Bonobos ist. Stattdessen könnten Genitalschwellungen ein graduiertes Signal darstellen, das die Wahrscheinlichkeit der Ovulation anzeigt, so dass Weibchen einer gemischten Strategie von Verschleierung und Suggerierung von Vaterschaften folgen könnten.

Als nächstes wurden Kontext und Funktion gleichgeschlechtlicher sexueller Interaktionen zwischen Bonoboweibchen untersucht. Genitalreiben fand häufiger zwischen nicht-

verwandten als zwischen verwandten Weibchen statt. Weibchen konnten in Futterexperimenten monopolisierbare Futterstücke ohne Unterstützung anderer Weibchen in Besitz nehmen und verteidigen. Während dieser Experimente wurde kein Zusammenhang zwischen Genitalreiben und Futterteilen gefunden und es wurden keine Koalitionen zwischen Weibchen gebildet. Interventionen in Konflikte außerhalb der Futterexperimente wurden beobachtet – am öftesten bei heterosexuellen Konflikten – aber Weibchen unterstützten einander unabhängig von ihrer Präferenz beim Genitalreiben. Die Häufigkeit des Genitalreibens variierte nicht in Abhängigkeit des Grades der Genitalschwellung. Auch die Aufforderung zum Genitalreiben fand nicht asymmetrisch statt in Abhängigkeit des relativen Grades der Genitalschwellung der beiden Partnerinnen. Darüber hinaus hatte der Grad der Genitalschwellung keinen Einfluss auf die Häufigkeit, mit der ein Weibchen attackiert wurde oder mit der es generell in Konflikte involviert war. Verglich man die 15 Minuten-Zeitfenster vor und nach einem Konflikt, so fand sich kein Anstieg des Genitalreibens nach einem Konflikt. Hochrangige Weibchen nahmen beim Genitalreiben signifikant häufiger als rangniedere Weibchen die Männchenposition ein. Die Richtung der Initiation des Genitalreibens wurde nicht vom sozialen Rang beeinflusst.

Diese Daten unterstützen die Hypothesen nicht, die postulieren, dass Gentialreiben der Bildung oder dem Erhalt weiblicher Allianzen, der Reduktion der Konkurrenz zwischen den Weibchen oder der Versöhnung ehemaliger Kontrahentinnen dient. Genitalreiben könnte dagegen als Indikator des sozialen Ranges oder zur Spannungsregulierung dienen.

Schließlich wurde der Zusammenhang zwischen physiologischen Parametern und sozialem Status betrachtet. Ich untersuchte, ob sich Weibchen in Abhängigkeit von ihrem sozialen Rang in ihren Exkretionsmustern des Glucocorticoids 11-Ketoetiocholanolon (DOA) unterscheiden. Basierend auf Ausweich-Interaktionen wurden Weibchen einem hohen oder niederen sozialen Rang zugeordnet. Während der Futterexperimente, die an einer Gruppe durchgeführt wurden, resultierte hoher Rang im Zugang zu monopolisierbaren Futterstücken, während das niederrangige Weibchen Futter nicht monopolisieren konnte. Der soziale Status der Weibchen spiegelte sich jedoch in keiner der drei untersuchten Gruppen in den fäkalen Exkretionsmustern des Glucocorticoid-Metaboliten wider. In zwei Gruppen hatten ranghohe höhere iDOA-Werte als rangniedere Individuen, in der anderen Gruppe war es umgekehrt. In der vierten Gruppe konnte diese Analyse nicht durchgeführt werden, da das ranghohe Weibchen trächtig war und Trächtigkeit zu erhöhten Glucocorticoid-Titern führt.

Die Ergebnisse weisen darauf hin, dass auch bei Bonoboweibchen hoher sozialer Rang in besseren Zugang zu monopolisierbaren Resourcen resultiert. Status-abhängige Unterschiede in der Corticoidausscheidung scheinen nicht zu existieren oder nur während Phasen sozialer Instabilität offensichtlich zu werden. Alternativ könnte der soziale Rang nicht die Nebennierenrinden-Funktion, sondern andere physiologische Parameter der sog. Stress-Achse beeinflussen.

Zusammenfassend liefert diese Arbeit eine interdisziplinäre Darstellung des Verhaltens und der Physiologie von Bonoboweibchen und trägt zum besseren Verständnis der Bedeutung von Sozial- und Paarungssystem einer Art bei.

7 Abbreviations

ACTH	adrenocorticotrophic hormone
BSA	bovine serum albumin
cpm	count per minute
DDI	dyadic displacement index
DOA	dioxoandrostane = 11-ketoetiocholanolone
E1C	oestrone-3-glucoronide
E_2	oestradiol
HPA	hyphtholamo-pituitary-adrenocortical (axis)
IMI	intermenstrual interval
Pd	pregnandiol
rpm	rotations per minute
SD	standard deviation
TDI	total dominance index

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9 Acknowledgements

My deepest thanks go to the many supervisors who encouraged and supported this study:

- Prof. von Holst for giving me the chance to do this external thesis and for his interest in this project;
- Dr. Gottfried Hohmann for initiating and supporting this work, for introducing me into bonobos and and primates;
- Prof. Keith Hodges for his continuing support and input;
- Prof. Christophe Boesch for financial support and for many fruitful discussions;

Without the cooperation of the zoos this project would not have been feasible. I thank Prof. Nogge & Dr. Rumpf of The Cologne zoo, Miss Badham of the Twycross zoo, Dr. Jauch & Dr. Holtkoetter of the Wilhelma in Stuttgart and finally, Dr. Schmidt & Dr. Dmoch of the Frankfurt zoo to give me the opportunity to study their bonobo groups.

Even more important, I want to express my deepest thanks to the zoo keepers for their willingness to cooperate and for sharing their longterm experience with me: M. Ebert, B. Walsh, H. Stumpf and C Knott and their teams.

Special thanks to Dr. Michael Heistermann for his support during the hormone analyses.

Thanks to Dr. Urike Möhle for introducing me into the methodology of the enzyme immunoassays.

Thanks to the members of the department of Reproductive Biologyhe German Primate Centre, Göttingen and the department Primatology of the MPI for Evolutionary Anthropology, Leipzig for stimulating discussions and their input on this project.

Very special thanks to Dr. Julia Lehmann and Dr. Andreas Reichert for valuable comments on this work.

Thanks to Dr. Daniel Stahl for statistical advice.

Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.

Ferner erkläre ich, dass ich nicht diese oder eine gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden habe.

Bayreuth, den 7. Oktober 2005

Karin Reichert