Chapter 20
Non-conceptive Sexual Interactions in Monkeys, Apes, and Dolphins

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Abstract Primates and dolphins exhibit comparable examples of all categories of non-conceptive sexual behaviors, including sexual interactions involving immature individuals, those involving individuals of the same sex, and copulation during the non-conceptive period. Although mammals of other taxa also perform non-conceptive sexual behaviors, the fact that there are so many reports of non-conceptive sexual interactions among higher primates and dolphins suggest a link between the nonreproductive use of sexual behaviors and high intelligence. This link might be because the greater role of learning in sexual behavior expands the possibility for sex to be incorporated into a variety of non-conceptive functions. Non-conceptive sexual behaviors seem to reflect or be influenced by important social factors, including affiliative relations and alliance between individuals of the same or different sex, high social status of females, within-group or between-group tension resolution, mate selection, and infanticide prevention. Animals may employ non-conceptive sexual behaviors to control various important aspects of their relationships with others which they cannot control with other social behaviors, which suggests that instances of non-conceptive sexual behaviors may serve as keys to understanding important aspects of the social relationships or social structure of the species.

Keywords Bonobo • Bottlenose dolphin • Estrus • Homosexual • Non-conceptive • Sexual behavior

20.1 Introduction

An interesting area of convergence between primates and cetaceans is the extent to which sexual behavior occurs in nonreproductive contexts. An overview of these interactions and their possible roles may lead to a better understanding of the evolution of sexual behaviors in mammals, with special reference to the relationship between the use of sexual behaviors and large brains.

Non-conceptive sexual behavior in primates occurs in a variety of contexts and may satisfy proximate functions such as self-satisfaction and greeting, and ultimate functions including the formation or maintenance of relationships, strengthening or confusing paternity, and female control of female–female and male–male competition (Dixson 1998; Sommer and Vasey 2006). Sexual behavior is clearly non-conceptive when it occurs between individuals whose age and sex present no possibility of conception, such as male–male, female–female, adult–immature, or immature–immature interactions. Especially, homosexual behaviors have been observed in many primate species, and researchers have identified and examined the proximate and ultimate roles of such behaviors (Vasey 1995; Dixson 1998; Sommer and Vasey 2006). Even between mature males and females, sexual behaviors may sometimes be used for nonreproductive purposes without involvement of obvious sexual arousal (Furuichi 1987; Dixson 1998). Copulation involving sexual arousal and ejaculation may also be performed for nonreproductive purposes, especially when performed during non-conceptive periods such as during pregnancy and postpartum amenorrhea (chimpanzee (*Pan troglodytes schweinfurthii*): Tutin and McGinnis 1981; bonobo (*Pan paniscus*): Furuichi 1987; Kano 1992; gorilla (*Gorilla beringei beringei*): Harcourt and Stewart 2007; Japanese macaque (*Macaca fuscata*): Takahata 1982; Fujita et al. 2001; Fujita et al. 2004; rhesus macaque (*Macaca mulatta*); capuchin (*Cebus* spp.): Fragaszy et al. 2004). Furthermore, for copulation performed during conceptive periods, we may need to consider nonreproductive explanations, such as infanticide avoidance by paternity confusion, if large numbers of copulations are performed with very low probability of conception (Matsumoto-Oda 1999; Wrangham 2002; Hashimoto and Furuichi 2006a, 2006b).

Non-conceptive sexual behavior has been observed in a range of cetaceans (reviewed in Bagemihl 1999), from river dolphins (*Inia geoffrensis*) to killer whales (*Orcinus orca*) to grey whales (*Eschrichtius robustus*), but here we derive our comparisons almost entirely from observations of bottlenose dolphins (*Tursiops* spp.) in Shark Bay, Western Australia, where the social and mating-system contexts of non-conceptive sexual behavior are better known than for other cetacean populations (Connor et al. 2000).

Life history parameters of the bottlenose dolphins in Shark Bay, including age of weaning, age of first reproduction, interbirth interval, and the duration of postpartum amenorrhea, are similar to values reported in chimpanzees (Connor and Volmer 2009). As we see here, non-conceptive sexual behavior in bottlenose dolphins is used, as it is in primates, in both social (e.g., dominance, bond formation) and reproductive strategies (e.g., confusion of paternity). The mating system of the Shark Bay bottlenose dolphins is characterized by a diffuse mating season in which alliances of two or three males consort with individual females for multiple periods that are thought to correspond to multiple estrous cycles and ovulations (Connor et al. 1996). The dolphin consortships are often initiated and maintained by aggressive herding (Connor et al. 1992a, 1992b, 1996, 2000; Connor and Volmer 2009), which is costly to females (Watson-Capps 2005). These costs, viewed in the context of multiple estrus cycles, led Connor et al. (1996) to predict that infanticide played an important role in the evolution of the bottlenose dolphin mating system. Evidence for infanticide was discovered subsequently in at least two other populations (Patterson et al. 1998; Dunn et al. 2002) but has yet to be confirmed in Shark Bay. Thus paternity confusion, a common strategy females use to reduce the risk of infanticide, stands as an important explanation for some forms of non-conceptive sexual behavior in bottlenose dolphins, as it does in some primates.

Here we focus our discussion mainly on chimpanzees, bonobos, Japanese macaques rhesus macaques, and bottlenose dolphins because their sexual behavior is well studied in this area under natural conditions.

In this chapter, we include for discussion any interactions involving genital contact or genital manipulation in sexual behaviors, irrespective of the involvement of sexual arousal. In fact, it is very difficult to observe sexual arousal of participants by facial, vocal, and physical expressions. Although penile erection can be regarded as a sign of sexual arousal in males, it is sometimes difficult to confirm penile erection during field observations. Furthermore, penile erection is sometimes observed in apparently nonreproductive interactions such as agonistic interactions, display, and play. Sexual arousal of females may sometimes be expressed by estrous calls, approaches, and presenting behavior, but copulation between adult males and females is not always preceded by these behaviors. It seems that sexual arousal is not an essential criterion for the use of sexual behaviors for nonreproductive purposes.

20.2 Sexual Interactions Between Non-conceptive Participants

20.2.1 Interactions Involving Immature Individuals

Although copulation-like behaviors are rather widely seen in immature mammals, bonobos are unusual among primates in that they start exhibiting such behaviors before weaning (Fig. 20.1) (Kano 1992; Furuichi et al. 1998). Although bonobos usually are nursed until they are 3 to 4 years old, bonobo infants start showing sexual behaviors as early as 1 year of age. Three types of sexual behaviors are observed in immature bonobos, and these types reveal sex-based developmental differences (Hashimoto and Furuichi 1994; Hashimoto 1997).

The first type, performed more frequently by males, is sexual behavior during play. While hugging in the ventro-ventral position during play, participants make mutual genital contact. This kind of sexual behavior is also found in chimpanzees (Tutin and McGinnis 1981; Plooij 1984; Goodall 1986) and gorillas (Harcourt et al. 1981; Nadler 1986). Immature bonobos also have sexual interactions while playing with adult males. For example, adult males sometimes hold an infant on their lap in the ventro-ventral position while sitting, and shake the body of the infant with a foot so that their genitals rub with each other. In most cases, the adult male does not have an erection, so this type of sexual behavior seems to be performed without sexual arousal (Hashimoto 1997).

The second category includes copulation-like sexual behaviors, which are observed between immature males and mature females, but not between immature females and mature males. Adult females usually do not resist when infant or juvenile males with erections perform penile insertions. This behavior increases in frequency with age, peaking when males are young juveniles, then declines as attempts at penile insertion by old juvenile and young adolescent males are met with resistance by females and aggression by adult males. Thus, this tolerated copulation-like behavior is a unique sexual behavior found in infant and juvenile males.

Copulation-like sexual behavior is sometimes seen between immature males and their mothers, but the context of such interactions seems to be somewhat different from those between immature males and mature females other than the mother. Although immature males usually take the lead of the interaction in the latter case, mothers may also initiate sexual behavior with their male offspring, using sex to soothe the temper

Fig. 20.1 Two infant bonobos performing ventro-ventral copulation-like behavior on the back of a mother

of frustrated or excited infants. The frequency of the mother–offspring copulation-like sexual behavior decreases with the increasing age of the offspring and almost completely vanishes before they reach adolescence. Copulation-like sexual behavior between immature males and their mothers is also observed in chimpanzees, where the ages of participating males, as well as the context of the interactions, are similar to bonobos (Hashimoto, unpublished data).

The third category is sexual behaviors that are used to control social relationships. This behavior is absent among infants. However, immature males start engaging in sexual behaviors with adult males with increasing frequency as they approach adulthood. Most of these behaviors are mounting or rump–rump contact that is usually performed among adult males (see following). They occur during agonistic interactions or when party members are excited at the beginning of a feeding session. In contrast, female juveniles are rarely involved in this kind of sexual interaction with adult males or females. It seems that immature females do not commit to social relationships in the group until they emigrate from their natal group and enter a new one as adolescents. Upon entering a new group, immigrant adolescent females frequently perform sexual behaviors with one another and with senior adult females. Thus, the development of sexual behaviors during the immature period in this male-philopatric species seems to reflect sex differences in social status and life history. Another type of sexual behavior in this category, unique to bonobos, occurs when adult females hold their infant ventro-ventrally while standing quadruped and rub their genitals against the genitals of the infant. As is the case for genito-genital rubbing among adult females (see following), this seems to be a kind of tension-reducing behavior by mothers that follows aggression received from other bonobos.

Bottlenose dolphins might be called “aquatic bonobos” when it comes to the frequency and variety of non-conceptive sexual behavior, and in the category of immature sex it is clear that they exceed bonobos by a considerable margin. Although immature bonobos may exhibit sexual behavior by the time they are 1 year old (Furuichi et al. 1998; Kano 1992), male bottlenose dolphins only 2 days old have been observed engaging in sexual behavior with their mothers. Mann (2006) examined sexual behavior among infant Indian Ocean bottlenose dolphins in Shark Bay (average weaning age = 4 years). Sexual behavior included mounting, probing the genital slit with the rostrum (= “goosing”), pressing the head into another dolphin’s genital area to push them up, and contact between the pectoral fin and genital area. Approximately half the observations were same-sex interactions. Homosexual interactions were observed much more often among male than female infants, and those among males tended to involve pairs and trios whereas female infant homosexual behavior was limited to pairs. Male infants were also observed to engage in sexual behavior with their mothers more often than female infants (Mann 2006). The rate that male dolphin calves engage in sexual behavior is extraordinarily high: some 40 times that of adult female bonobos, who have a reputation for frequent sexual behavior. Even female dolphin infants exceed the bonobo rate by a considerable margin (Mann 2006).

Juvenile sexual behavior in Shark Bay sometimes mimics adult consortship behavior as two dolphins will temporarily “herd” another, with mounting and goosing. These bouts are distinguished from true adult consortship behavior by three characteristics: (1) role switches, as the identity of the “herded” dolphin changes, (2) the “herded” dolphin is often male, and (3) the herding behavior ends when the social bout ends and the dolphins return to nonsocial activities such as resting, traveling or foraging (Connor et al. 2000). Such observations support practice, dominance, and male–male bonding functions for juvenile sexual behavior.

20.2.2 Interactions Involving Mature Participants of the Same Sex

Sexual behavior between mature individuals of the same sex is widely seen in many kinds of mammals (Vasey 1995; Sommer and Vasey 2006). Although the mounting behaviors between males are well recognized, mainly as ritualized dominance interactions, sexual behaviors between females are also observed in many primate species, and a variety of functions have been proposed for them (Vasey 1995). Female

Japanese macaques and rhesus macaques show mounting behaviors similar to male–female copulation (Kapsalis and Johnson 2006; Vasey 2006). Females will mount estrous females and even show thrusting movements. Kapsalis and Johnson (2006) suggested that rhesus females perform the sexual behaviors to establish new affiliative relationships and alliances, because such behavior was frequently observed following the loss of alliance partners through artificial trapping or mortality. On the other hand, Vasey (2006) performed quantitative analyses on the probable functions of female–female mounting in Japanese macaques, including alliance formation, dominance demonstration, acquisition of alloparental care, acquisition of opposite-sex mates, reconciliation, and regulation of social tension, but none of these functions was statistically supported. The author speculated that females perform homosexual behavior in pursuit of the proximate benefit of pleasure, and that such behavior is a by-product of female–male mounting that females employ to prompt sexually disinterested or sluggish males to copulate with them.

Bonobos exhibit various other types of same-sex sexual behaviors. Among these, genito-genital rubbing behavior, in which two females hug each other ventro-ventrally and rub their genitals repeatedly in a rapid lateral motion of their hip, has received considerable attention with respect to its social roles. Similar to chimpanzees, bonobos form male-philopatric groups. Although males stay in their natal group throughout their life, females usually transfer between groups in early adolescence (Kano 1982, 1992; Furuichi 1989; Gerloff et al. 1999; Hashimoto et al. 2008). Therefore, most females found in a group are thought to be unrelated, except for the case in which some related females immigrate from the same group. Compared to males, female chimpanzees do not often participate in large mixed-sex parties or have social interactions with each other. This tendency may be partly explained by the lack of kin-relations among females and by forging constraints as they range and feed alone or in small parties (Wrangham 1979; Pusey and Packer 1987; Furuichi 2006). However, bonobo females are found in mixed parties even more frequently than males and have various social interactions with each other, including grooming, food sharing, cofeeding, and genito-genital rubbing (Kuroda 1980; White 1988; Furuichi 1989; Kano 1992; Mulavwa et al. 2008).

Females usually perform genito-genital rubbing in two contexts. First, they perform genito-genital rubbing in tense situations when they are excited upon arriving at feeding sites, when they hear vocalizations of different groups, and when they are involved in agonistic interactions. Genito-genital rubbing in these contexts seems to regulate tension, because after genito-genital rubbing females usually continue feeding or resting in a more relaxed state (de Waal 1987; Furuichi 1989; Kano 1992; Hohmann and Fruth 2000). Second, genito-genital rubbing promotes the establishment or maintenance of affiliative social relationships. When adolescent females immigrate into a new group, they have no relatives or other close female associates. In such circumstances, immigrant females tend to choose a specific senior female with whom to associate, and solicit her for various social interactions, including genito-genital rubbing, food sharing, and cofeeding. When these immigrants find the senior female feeding in a certain position, they approach and solicit a bout of genito-genital rubbing, after which they beg for food or cofeed beside her, even when food is abundant elsewhere. When two or more adolescent females immigrate into a group around the same time, they tend to associate closely and frequently perform genito-genital rubbing with each other (Furuichi 1989; Idani 1991).

Male–male sexual interactions are common in bonobos, including mounting and rump–rump contact (two males bring their rumps together and hit their genitals against each other repeatedly in a quick forward-and-back motion) (Kuroda 1980; de Waal 1987; Kano 1992). In contrast to sexual behaviors between adult females, those between adult males are almost exclusively performed in tense situations. Sexual behaviors may appease an excited male showing display behaviors or may be used to reconcile immediately after agonistic interactions (Furuichi and Ihobe 1994). Interestingly, bonobo males rarely show behaviors such as hugging, touching, embracing, kissing, or pant-grunting that are well developed in chimpanzees for greeting, conflict resolution, reconciliation, or reassurance. In these contexts, male bonobos usually employ sexual behaviors. Also, although chimpanzee males use pant-grunts and other behaviors to express or confirm dominance relationships, bonobo males rarely show such behaviors. The typical rump–rump contact is a symmetrical behavior, and even when they use mounting, males alternate roles as if they are avoiding the expression of a dominance relationship. Thus the use of sexual behaviors by bonobo males seems to reflect social relationships that are egalitarian compared to chimpanzees.

The male–male sexual behaviors in bonobos do not necessarily involve sexual arousal. The participants do not usually show penile erection, and even when they do, we cannot know whether it is caused by sexual arousal or excitement. In fact, male bonobos often show penile erection in various situations that may not involve sexual arousal, including during display, agonistic interactions, play, and when they find preferred foods. One of the authors, Furuichi, observed only one case of male–male mounting that involved ejaculation during his 28 months of field studies. By contrast, male–male mounting in gorillas is usually performed in a manner similar to male–female copulation in terms of the behavioral pattern and vocalizations, and ejaculation was confirmed in 2 of 97 cases, which hints at a higher frequency than bonobos (Yamagiwa 2006).

Homosexual behavior in adult bottlenose dolphins is much more commonly observed in males than females (Fig. 20.2). The same sexual behaviors employed by infants, mounting and goosing, are used frequently by adults. The review by Connor et al. (2000) concluded that sexual behavior, including mounting with erections, is used in both affiliative and agonistic contexts. At one extreme, one adult alliance herded a maturing male pair for more than an hour, even using aggressive vocal signals typical of herding (Connor and Smolker 1996). The mounting and goosing were conducted in an energetic, almost violent manner. On another occasion mounting between two allied males was clearly nonaggressive, occurring in a slow relaxed manner. Occasionally, older larger males permit smaller male calves and juveniles to mount them as well (Connor et al. 2000).

To examine the sexual interactions of male dolphins, one of the authors, Connor, extracted observations of the two most unambiguous and easily detected types of sexual behaviors, mounting and goosing, from 155 focal follows (552 hours) on

Fig. 20.2 Mounting behavior between adult male bottlenose dolphins

alliance-forming males. Two of the alliances were categorized as young (one trio of two immature and one mature male and one pair of maturing males), three alliances were mature (one pair and two trios), and two alliances (a pair and a trio) were considered "old" mature based on extensive ventral speckling (Connor et al. 2000). Other males were occasionally present during follows.

Sexual behavior (goosing or mounting) was observed in 54 of the 155 follows. There were interesting differences in the sexual behavior of older and younger males as well as in heterosexual versus homosexual interactions. Following Mann (2006), any sexual behavior that followed another within 5 min was considered to be part of the same bout. Considering first the recipients of sexual behavior, an individual was scored as a recipient only once per alliance per follow, regardless of the number of mounts or gooses he or she received during the follow. Young males targeted males (23) more than females (15) for sexual interactions whereas mature and old mature males targeted females (24) more than males (14) ($\chi^2=4.266$, $p=0.039$). Eighteen females were recipients of sexual behavior from mature males but the 15 bouts by young males were distributed among only 7 females. Of the 13 males targeted by young males, 9 were also in the young (juvenile or maturing) category while 4 were mature males. Of the 7 males targeted by mature males, 5 were young and 2 were mature.

Some bouts included only goosing or mounting while other bouts included both. Scoring a bout based on the first sexual behavior in the bout, the 15 males (9 young and 6 mature) targeted for sex by males were more often mounted (22) than goosed (15), while the 24 female targets were more often goosed (30) than mounted (17) ($\chi^2=4.515$, $p=0.037$). The higher proportion of mounting to goosing in male–male compared to male–female interactions may seem surprising, but our surprise likely reflects the fact that we understand the normal reproductive function of mounting, but not goosing. If, for example, goosing, conducted in the appropriate manner, serves to enhance female receptivity, then the high proportion of goosing in male–female interactions makes sense. Regardless, a key result is that homosexual interactions constitute a significant proportion of male dolphin sexual interactions for both young and mature individuals.

20.3 Copulation Involving Mature Males and Females During the Non-conceptive Period

20.3.1 Adolescent Infertility

There is a significant gap between first estrus and first birth in Japanese macaques. For example, on Yakushima Island where wild Japanese macaques have been observed without artificial provisioning for more than 30 years, females tend to show first estrus in the mating season at the age of 3 to 4 years. However, they seldom give birth in the next breeding season when they are 4 years old, but usually give birth at the age of 5 or 6 years (Takahata et al. 1998). There are no detailed reports on adolescent infertility in other macaque species, which may be partly because of difficulties in detecting a short gap between first estrus and first conception in nonseasonal-breeding species living in warmer environments. In Japanese macaques, which mate seasonally in autumn, the delay of conception by a few months results in a delay of first delivery by a year.

Adolescent infertility is also reported for female chimpanzees. In Mahale Mountains in Tanzania, females usually show first estrus during late adolescence at the age of 10 years (128 months), and they emigrate from their natal groups at the age of 11.27 years. The mean number of months elapsing from immigration into a new group and first birth was 32 months (Nishida et al. 1990, 2003). Thus, females have a period of adolescent infertility of about 4 years if we assume that females immigrate into a new group immediately after emigrating from their natal group. More detailed, but atypical, data obtained from four females who did not transfer groups until their first birth showed that females experienced adolescent infertility for 1 year 2 months to 4 years 1 month (Nishida et al. 2003).

It is more difficult to estimate the duration of adolescent infertility in bonobos because there has been no observed case in which females stayed in their natal group until the first birth. Female bonobos do not usually start estrus or copulation until they leave their natal group at the age of 6 to 10 years. Females who temporarily joined the study groups at the estimated age of 7 to 9 years did not show estrus, but females who joined the study group at the estimated age of 10 years performed copulation from the beginning and gave first birth at the age of 13 to 15 years. Thus, although there may be some error in the age estimates, there seems to be a period of adolescent infertility of 2 years or more (Hashimoto et al. 2008; Furuichi et al. 2012).

The function of adolescent infertility in Japanese macaques is unknown. Because they live in female-philopatric troops where females have stable social relationships with related females, there is no urgent need for females to form social relationships with males via copulation. The length of adolescent infertility in Japanese macaques is rather short and variable because of nutritional conditions. In fact, in an artificially provisioned group in Arashiyama, 3.9 % of females gave birth at the age of 4 years during the breeding season following the mating season in which they showed first estrus (Koyama et al. 1992), while the age of first birth was delayed under poor nutritional conditions (Watanabe et al. 1992). By contrast, the long adolescent infertility in chimpanzees and bonobos may confer a benefit on adolescent females, because copulation with males in the new group to which they immigrate may help establish stable social bonds and reduce the risk of infanticide. Although immigrant adolescent female bonobos do not attract much sexual attention from males, they show prolonged estrus, approach males, try to have various interactions, and copulate with a higher frequency than older adult females (Furuichi 1989, 1992; Idani 1991; Kano 1992; Furuichi and Hashimoto 2004). Adolescent female chimpanzees also show irregular and long-lasting sexual swelling, but the frequency of copulation is not as high as that of adult females (Goodall 1986; Pusey 1990; Hashimoto unpublished data).

In Shark Bay, some pre-parturient females may be consorted by adult males during more than one season before they conceive. However, this has not been quantitatively distinguished from the same phenomenon in females that have previously given birth, as they may also be consorted for two or more consecutive seasons before giving birth again.

20.3.2 Estrus During Non-conceptive Periods of Adult Females

Estrus and copulation during pregnancy are seen in many primate species including capuchins (Fragaszy, et al. 2004), Japanese macaques (Takahata 1982; Fujita et al. 2004), chimpanzees(Tutin and McGinnis 1981), bonobos (Furuichi 1987; Kano 1992), and gorillas (Harcourt and Stewart 2007). Non-conceptive periods of adult females occur during postpartum amenorrhea, pregnancy and during parts of the estrous cycle that are far from ovulation.

In capuchins, copulations occur frequently outside the females' periovulatory phase, including during pregnancy and postpartum amenorrhea. Copulations occur frequently in socially tense situations, during play, and during group formation in captivity (Dixson 1998; Fragaszy et al. 2004). Thus, capuchins seem to use copulation for social purposes such as forming affiliative relationships or resolving tensions.

Although the period differs from site to site because of climate differences, Japanese macaques have a mating season of 4–5 months around autumn, and females show cyclic estrus during this period (Takahata 1980). It is quite interesting, however, that many females conceived during the first estrous period but still continued showing cyclic estrus and copulated after conception (Takahata 1982; Fujita et al. 2004). In an extreme report for a wild group in Kinkazan Island, as many as 80 % of females conceived during the first estrous cycle but still continued showing cyclic estrus (Fujita et al. 2004).

There are two main hypotheses for the role of estrus during pregnancy in Japanese macaques. Females sometimes form specific relationships with certain males through repeated copulation during the mating season, and such a relationship may provide benefits such as support during agonistic interactions and competition over food (Takahata 1982). In this case, females may benefit from repeated copulations after conception. Another possibility concerns intergroup competition. In Japanese macaques, males seeking better mating opportunities transfer among female-philopatric troops (Suzuki, et al. 1998). When two troops meet at the boundary area of their home ranges, females confront each other in “frontlines,” and males actively fight for the troops to which they belong at that moment (Saito et al. 1998). Thus, troops having more males may enjoy a competitive advantage. Males tend to appear around troops that have more females in estrus during the mating season, and some of these males continue to reside in the troop afterward (Furuichi 1985; Sprague 1989). Therefore, repeated estrus by females during pregnancy may aid in the recruitment of males.

Female chimpanzees and bonobos show cyclic estrus (Furuichi 1987; Nishida, et al. 1990; Wallis 1997). Even after conception, female chimpanzees may have a further two estrous cycles (Tutin and McGinnis 1981). Female bonobos also continue showing cyclic estrus until 1 month before giving birth, although the cycles are not as regular as before conception (Furuichi 1987; Kano 1992).

Female bonobos also show estrus during postpartum amenorrhea. Although female chimpanzees do not exhibit estrus until the weaning of offspring at about 4 years of age (Nishida et al. 1990; Wallis 1997), female bonobos start showing estrus about 1 year after giving birth while nursing their offspring (Kano 1992; Furuichi and Hashimoto 2002). The interbirth interval for bonobos with a surviving offspring is 4.8 years. If we deduct 1 year of postpartum amenorrhea and 7.6 months of gestation, the period for female bonobos to show estrus before conception is as long as 3 years (Furuichi et al. 1998; Furuichi and Hashimoto 2002). Why do female bonobos resume estrus so early during lactation when there is no possibility of conception?

Furuichi and Hashimoto (2002) showed that the variation in interbirth interval is significantly larger for bonobos than for chimpanzees. With this finding, they suggested that the restriction for the timing of conception is less for bonobos than for chimpanzees. The cost of travel between distant food patches prohibits female chimpanzees from having two dependent offspring at the same time. Therefore, female chimpanzees need to wait for the weaning and independence of one offspring before having the next. However, in bonobo habitats key food patches are larger and many small food patches exist among those large food patches (White and Wrangham 1988; Wrangham 2000; Furuichi, unpublished data), so the daily range required for obtaining adequate nutrition is reduced (Furuichi et al. 2008; Furuichi 2009). Therefore, female bonobos, traveling more slowly, may not suffer

Fig. 20.3 A female bonobo carrying two infants. Such females have been observed both in a provisioned group (this photograph) and unprovisioned groups

the debilitating costs that two dependent offspring would impose on chimpanzees. In fact, female bonobos sometimes give birth before their previous offspring achieves independence, and will carry one infant on her back and the other on her chest (Fig. 20.3). This difference may partly explain why female bonobos can resume estrus earlier, with a possibility, although not high, of a short interbirth interval.

The estrous period in bonobos, because it occurs during gestation and postpartum amenorrhea, is considerably prolonged. Considering various reproductive parameters, Furuichi and Hashimoto (2002) calculated that female chimpanzees show estrus for only about 5 % of the adult life, even if we include estrus during the early stage of gestation. Thus, only 1 of 20 females show estrus at a time, and estrous sex ratio (or operational sex ratio), which is the proportion of adult males to a female showing estrus at one time, is as great as 20 if there are the same number of males and females in a group. Because the actual number of males is smaller than that of females, probably because of mortality from severe sexual competition, the estrous sex ratio was lower than 20, but still as high as 4.2 for chimpanzees in Mahale, and 12.3 for Gombe (Furuichi and Hashimoto 2002). Such a high estrous sex ratio may have produced severe sexual competition among males that, in turn, imposes significant costs on females. In contrast, owing to a much longer estrous period during gestation and a long estrous period in postpartum amenorrhea, female bonobos show estrus for as much as 27 % of their adult life. Therefore, the estrous sex ratio was as low as 2.8 for bonobos at Wamba, even though there were similar numbers of males and females in a group.

Male sexual competition is reduced in bonobos compared to chimpanzees. In bonobos at Wamba, the frequency of male–male aggression over estrous females is very low. Because of the high percentage of the females in estrus, there are a number of estrous females in a group of bonobos at a given time, which reduces the ability of high-ranking males to monopolize females and allows for female mate choice (Furuichi 1997; Furuichi and Hashimoto 2002). Compared with chimpanzees, bonobos form more stable mixed-sex parties. Females join such parties more frequently than do males; female social status is almost equivalent to that of males, females have priority of access to food, and females can control group movements and ranging. All these advantages for females might be related to the reduced male–male competition and female mate choice (Kano 1982, 1992; White 1988; Furuichi 1989, 1997, 2011; Furuichi et al. 2008; Mulavwa et al. 2008; Stevens et al. 2008).

The Shark Bay bottlenose dolphins have a diffuse mating season that extends from the austral spring though early summer. However, females that conceive during the mating season (September–December) were often herded during the late winter period (July–August), before the mating season. Although this pre-mating season behavior may simply reflect additional ovulations that fail to produce pregnancy (bottlenose dolphins are known to have two to seven ovulations during the year they conceive), it may also reflect anovulatory cycles, a phenomenon also known from captive studies (Connor et al. 1996). The evolutionary reason for anovulatory cycles in bottlenose dolphins may be the same as that for multiple ovulatory cycles: confusion of paternity associated with reducing the risk of infanticide (Connor et al. 1996).

Consortships with pregnant female bottlenose dolphins have been documented in Shark Bay, but it is not clear how common this phenomenon is (Connor et al. 1996). Also, we must be cautious about interpreting such behavior in terms of female tactics because some consortship behavior may relate more to male–male alliance bonds than male and female mating tactics. For several years three mature males were among a group of dolphins that were provisioned with dead fish each day (Connor and Smolker 1995). Relationships among these three males were highly unstable with respect to the formation of consortships with females (Connor and Smolker 1996), and they consorted with more females in a nonfertile reproductive state (e.g., females with newborn calves) than was typical of nonprovisioned males in the area (Connor et al. 1996). Non-conceptive herding by the provisioned males suggests that some cases of herding have more to do with maintaining fragile male–male bonds than conception, but the behavior may have simply been a maladaptive effect of the provisioning itself. However, a male-bonding function is supported by observations following the formation of a new alliance between two nonprovisioned adult males in 1994; each of the first 8 days they were observed in the new alliance they herded a different female, including one that was unlikely to be receptive as she had a 1.5-year-old calf (cycling typically resumes when a calf is 2.5 years old), was not herded again that year by other males, and did not conceive until the following year (Connor and Mann 2006).

20.4 Excessive Number of Copulations with Low Probability of Conception

Although it is difficult to know the probability of conception of wild animals, female chimpanzees present a good example of copulation with a low probability of conception. Female chimpanzees usually resume cycling after weaning an infant, show estrus for about 12 days before monthly ovulation, and typically exhibit five to nine cycles before conception (Hasegawa and Hiraiwa-Hasegawa 1983; Nishida et al. 1990; Wallis 1997). They show high proceptivity during estrus, especially during the periovulatory periods when the frequency of copulation is very high (Tutin 1979; Wrangham 2002; Hashimoto and Furuichi 2006a, 2006b). In an extreme case in the Kalinzu Forest, Uganda, when high-ranking males failed to herd an estrous female, the female copulated more than 60 times with 12 males in a day (Furuichi, personal observation). Although female bonobos show estrus during a larger proportion of their adult life than do chimpanzees, the frequency of copulation during the estrous period is much higher for female chimpanzees than for female bonobos (Furuichi and Hashimoto 2002). It is estimated that female chimpanzees sometimes copulate several hundred or even more than a thousand times from the initiation of estrus to conception (Matsumoto-Oda 1999; Wrangham 2002; Hashimoto and Furuichi 2006a, 2006b; Watts 2007). If the possibility of conceiving during a given copulation is extremely low, we may need to consider such copulation as a kind of non-conceptive sexual behavior and to seek to understand the benefit for females. Why do female chimpanzees need to perform such a large number of copulations? Why do not female chimpanzees conceive on the first ovulation even if they copulate numerous times with many males during the periovulatory period?

To date, a number of hypotheses have been proposed for the role of such an excessive number of copulations. Females may choose a desirable father of the offspring through sperm competition (best male hypothesis), females may copulate with many males to form or maintain familiar relationships with males (many males hypothesis), females may use such a high frequency of copulation as a social passport, or females may copulate with many males to avoid infanticide by confusing paternity (Boesch and Boesch-Achermann 2000; Furuichi and Hashimoto 2002; Wrangham 2002).

To distinguish among these hypotheses, it would be useful to have a better understanding of the proximate factors involved, including the hormonal and genetic mechanisms underlying the low probability of conception. Studies on human females showed that there is a graded continuum from fully fecund ovarian cycles through follicular and luteal suppression, anovulation, oligomenorrhea, to amenorrhea, and that ovulation is strongly impacted by nutritional condition (Ellison et al. 1993). If females show fecund ovarian cycles from the beginning but do not achieve successful conception for 5 to 9 months, we may need to consider whether there exists a threshold for the combination of genotypes, such as complementary major histocompatibility complex (MHC) types. In this case the "best" male is not an absolute standard but is relative to the female's genotype. On the other hand, if females show estrus without fecund ovarian cycles, we may need to consider possible social factors that favored the evolution of a female pseudo-estrus.

During the year they conceive, female bottlenose dolphins in Shark Bay are consorted by male alliances for varying periods of time that may span several months or longer (Connor et al. 1996). Such extended attractive periods may correspond to the multiple ovulations and, as we noted, even anovulatory cycles. Evidence that consortships are coerced is observed in about half the cases (Connor et al. 1996; Watson-Capps 2005) and, given the difficulty of observing the brief episodes of consortship aggression, the actual percentage is likely much higher (see Connor and Volmer 2009). The costs of enduring aggressively maintained consortships (see Watson-Capps 2005) focuses our attention on the nature of the benefits to multiple cycling that would outweigh such costs. Connor et al. (1996) suggested that paternity confusion to reduce infanticide risk was the likely answer, and infanticide was soon discovered in European and North American populations (Patterson et al. 1998; Dunn et al. 2002). To a large extent dolphin infanticide is "cryptic," because the lethal wounds from blows are internal and an infant victim that strands may not exhibit obvious injury.

20.5 Conclusion

When we enumerate non-conceptive sexual interactions in nonhuman primates and dolphins, we realize that such behavior covers a range of phenomena with an equally impressive variety of possible explanations. It was surprising that primates and dolphins exhibit comparable examples of all categories of non-conceptive sexual behaviors (Table 20.1). There are many more reports on non-conceptive sexual behaviors in other mammal species (Dixson 1998; Sommer and Vasey 2006). Furthermore, because it is difficult to know the periods of pregnancy, postpartum amenorrhea, and cases of low probability of conception of wild animal populations, many more instances of non-conceptive copulation will be found when we carry out long-term detailed observation of animals. Nevertheless, the fact that there are so many reports of non-conceptive sexual interactions among primates and dolphins may tell us something important about the evolution of the nonreproductive use of sexual behaviors and high intelligence. An important role for learning in sexual behavior, for at least some primates, is clear. Some higher primates have difficulties in performing copulation if they are raised in isolation. The implication that learning plays a role in sexual behavior likely expands the possibility for sex to be incorporated into a greater variety of nonreproductive functions.

Each example of non-conceptive sexual behavior that we discussed in this chapter seems to reflect or be influenced by important social factors. Copulation during the postconception periods in Japanese macaques may provide important roles for female social status or intergroup conflict. Homosexual behaviors among female macaques seem to contribute to the formation of affiliative relationships under

Table 20.1 Non-conceptive sexual behaviors and proposed functions

	Nonhuman primates	Bottlenose dolphins
1. Sexual interactions between non-conceptive participants		
(a) Involving immature individuals	*Sexual behavior performed during play* – Observed among immatures in chimpanzees, bonobos, gorillas, etc. – More frequently performed by males (bonobos) – Also observed between immatures and adult males *Copulation-like behaviors* – Observed between immature males and non-kin adult females, but not between immature females and adult males, in bonobos and chimpanzees – Adult females show great tolerance – Decreases in older juvenile years or early adolescence because of increased intolerance of adult males and females *Copulation-like behavior with mother* – Observed in chimpanzees and bonobos – Immature males usually take the lead with sexual arousal – Mothers sometimes take the lead for soothing the temper of frustrated or excited infants – Almost completely disappears before sexual maturity *Sexual behavior for the control of social relationships* – Observed in many primate species (mounting) and in bonobos (rump–rump contact) – Mostly observed between immature males with increasing frequency as they approach adulthood (bonobos) – Immature females rarely perform this behavior, but begin performing it frequently (genito-genital rubbing) after immigration to other groups (bonobos) – Mothers sometime perform sexual behavior with their infant to control their own tension (bonobos)	*Sexual behavior with nonidentified purposes* – Including mounting, probing the genital slit with the rostrum, pressing the head into another's genital area, and contact between the pectoral fin and genital area – Extremely frequent as compared with those in bonobos, and more frequent for males – Performed both between same-sex and opposite-sex individuals – Those among males sometimes involve more than two individuals – Male infants engage in sexual behavior with their mothers more often than female infants *Sexual behavior that mimics adult consortship behavior* – Two immatures herd another with mounting and rostro-genital contact (goosing) – Distinguished from those by adults by (1) role switches, (2) males are often herded, (3) herding ends when social bout ends – For practice of herding and male–male bonding

(continued)

Table 20.1 (continued)

	Nonhuman primates	Bottlenose dolphins
(b) Involving mature participants of the same sex	*Japanese macaque* – Females show mounting behavior similar to male–female copulation – Quantitative analysis did not support any functions, including alliance formation, dominance demonstration, acquisition of alloparental care, acquisition of opposite-sex mates, reconciliation, and regulation of social tension: just for fun? – By-product of female–male mounting that females employ to solicit sexually disinterested or sluggish males *Rhesus macaque* – Females show mounting behavior similar to male–female copulation. – Establishment of new affiliative relationships and alliances, following the loss of alliance patterns through artificial trapping or mortality *Bonobo* – Female–female sexual interactions for formation or maintenance of new affiliative relationships, soothing tension, and resolution of agonistic interaction – Male–male sexual interactions for soothing tension and resolution of agonistic interactions – In contrast to male–male mounting in other mammals, dominance is rarely expressed in the male–male sexual interactions	– Same suite of sexual behaviors employed by calves are used frequently by adults – Much more commonly observed among males – Mounting is used in both affiliative and agonistic contexts – For male-bonding and dominance
2. Copulation involving mature males and females during non-conceptive period		
(a) During adolescent infertility	*Japanese macaque* – First estrus at 3 or 4 years old but usually give birth at the age of 5 or 6 years (Yakushima) – Variable and short period of infertility and unspecified benefit *Chimpanzee and bonobo* – Chimpanzees in Mahale: First estrus at 10 years old and emigrate from natal group at 11.27 years old. First delivery in 32 months from immigration into a new group; thus more than 3 years of infertility	– Males herd prepartum females for more than one season before conception, but same may also occur for adult females

	– Bonobos at Wamba: First estrus occurs at immigration into a new group at around 10 years old and first delivery occurs at 13–15 years old; thus more than 2 years of infertility – Adolescent females sometimes show noncyclic continuous estrus – Helps immigrant females establish stable social bonds and reduces risk of infanticide	
(b) During non-conceptive periods of adult females	*Capuchin* – Frequent copulation outside the periovulatory phase including during pregnancy and postpartum amenorrhea – Occurring frequently in socially tense situation, during play, and during group formation in captivity *Japanese macaque* – Cyclic estrus during 4–5 months of mating season, but many females conceive during the first estrus – Formation of affiliative relationships with troop males – Recruitment of non-troop males *Chimpanzee* – Two estrous cycles after conception, probably because of estrogen secreted from the placenta *Bonobo* – Continuous estrus until 1 month before giving birth – Estrus during postpartum amenorrhea – Paternity confusion – Controls intermale aggression by reducing estrous (operational) sex ratio – Leads to high social status of females	– Males sometimes are attracted to females for periods exceeding the duration of rising estrogen levels – Males occasionally herd females in late pregnancy, during first 2 weeks after parturition, and the day after the loss of a nursing infant – Consortships with nonfertile females is observed more frequently in captivity – Herding nonfertile females for a male-bonding function
3. Excessive number of copulations with low probability of conception	*Chimpanzee* – Very high frequency of copulation with many males during the estrous periods – Hundreds or even more than a thousand copulations during 6–9 months from resumption of estrus to successful conception – Various hypotheses including many male hypothesis, best male hypothesis, paternity confusion hypothesis, and high genetic threshold hypothesis	– Females are consorted by multiple male alliances for several months or longer, including multiple ovulations and anovulatory periods – Coerced consortships are observed in half of cases – Paternity confusion (infanticide observed in some populations)

some unstable conditions. Capuchins perform copulation during the non-conceptive periods to help form affiliative relations or to resolve tensions. The difference in the sexual behaviors between immature males and females in bonobos may reflect the life history of each sex. Prolonged estrus of female bonobos during postpartum amenorrhea and gestation may be related to the high social status of females in their male-philopatric groups. The excessive number of copulations with a low probability of conception of female chimpanzees may be understood as playing roles in mate selection, formation of a familiar relationship with males, and infanticide prevention, and the homosexual behaviors and cooperative herding of females in non-conceptive period in bottlenose dolphins may contribute to male–male bonding. Thus, animals may employ sexual behaviors to control various important aspects of their relationships with others that they cannot control with other ordinary social behaviors such as grooming, following, cofeeding, fighting, or displaying dominance or subordinance. This study suggests to us that studies of non-conceptive sexual behavior may inform us about key aspects of social relationships and social structure in other species.

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