

Chapter 1:

GENERAL INTRODUCTION

Sexual selection, reproductive strategies and the conflict between the sexes

After Darwin (1859) had developed his theory of evolution by natural selection, he noticed not only apparent differences in reproductive strategies between males and females, but also sex differences in the occurrence of conspicuous morphological traits (e.g. bright colors, horns and other weapons). As an explanation for these differences he developed his theory of sexual selection (Darwin, 1871) in which he proposed that sexual selection functions by two mechanisms: i) selection that results from competition between members of one sex for members of the opposite sex (intra-sexual selection) and ii) selection that results from differential choice by members of one sex for members of the opposite sex (inter-sexual selection). These mechanisms could potentially appear as i) male-male competition, female-female competition or ii) male mate choice, female mate choice. Yet, Darwin mainly discussed two ways through which sexual selection occurred: male-male competition and female choice. The reason why sexual selection might be biased towards inter-male competition and female choice was later explained by Trivers (1972) in terms of an asymmetry in parental investment. Males produce a large number of sperm cells and thus can sire a potentially high number of offspring. In the majority of cases their parental investment does not go beyond the contribution of their gametes, however (Clutton-Brock, 1991; Woodroffe & Vincent, 1994). Since male reproductive success is limited by the number of females a male can fertilize, males should compete for access to as many fertile females as possible to maximize their reproductive success. Females, on the other hand, produce only few egg cells and, compared to males, are more limited in the number of offspring they can produce, while investing far more in each than do males. Therefore females should carefully select their mating partners, in order to enhance the fitness of their offspring and thereby their own reproductive success (Maynard Smith, 1991).

In most mammals, females provide more parental investment and parental care (e.g. internal fertilization, long gestation, lactation) than males (Clutton-Brock, 1991). In some species of other vertebrate taxa, however, the roles are reversed and males are responsible for all parental care (the majority of teleost fishes, anurans, urodeles, and some birds; reviewed in Clutton-Brock & Vincent, 1991). The fact that in these species, other than expected, sometimes males and sometimes females compete for mates, has led to a replacement of the primary parental investment theory by a theory about the potential reproductive rate of males

and females (Clutton-Brock & Parker, 1992). According to this new theory, the sex with the lower potential reproductive rate will be less available for mating, which results in a skewed operational sex ratio (OSR, the ratio of receptive females to fertile males, Emlen & Oring, 1977). The identity of the competitive sex and the choosy sex is then finally determined by the skew of the OSR.

Concerning sexual selection, competition for mates and mate choice have attracted most interest, nevertheless there are also other important mechanisms of sexual selection (reviewed in Andersson & Iwasa, 1996). Among those are sexual coercion and sperm competition. Sexual coercion was first recognized by Smuts & Smuts (1993) and described as a behavioral expression of inter-sexual mating conflict in primates, where a male uses threat or force (e.g. harassment, intimidation and forced copulations) to increase the chances that a female will mate with him and not with other males (Clutton-Brock & Parker, 1995). An extreme form of sexual coercion that occurs post-mating is infanticide (Kappeler & van Schaik, 2004), which makes the infant's mother sooner receptive to a new male as if her infant had survived (Hrdy, 1979; Packer & Pusey, 1983; Hausfater & Hrdy, 1984).

Competition between males may still continue after copulation and insemination (post-copulatory) which was first recognized by Parker (1970) and referred to as sperm competition. Sperm competition which is defined as "competition between the sperm from two or more males for the fertilization of a given set of ova" (Parker, 1998) occurs, when a female mates with multiple males within the fertile phase of her ovarian cycle. Testes size across mammal species has been shown to be positively correlated with the occurrence of sperm competition (e.g. Harvey & Harcourt, 1984; Kenagy & Trombulak, 1986; Ginsberg & Huck, 1989; Ginsberg & Rubenstein, 1990; Stockley & Purvis, 1993). While the definition reflects that sexual competition was seen as a mainly male-driven phenomenon (Hrdy & Williams, 1983) and females were noticed as more passive, more recently sperm competition has been viewed from both, a female and male perspective (Birkhead, 1995). The term now comprises all the morphology, physiology and behaviors associated with multiple mating by females (Birkhead & Møller, 1992; Birkhead, 1994), including the view that females might exert some physiological control over the paternity of their offspring. This mechanism is referred to as cryptic female choice (Thornhill, 1983; Eberhard, 1996).

Given the different strategies that males and females follow to maximize their reproductive success, it is obvious that there is a conflict between the sexes over reproduction. How this conflict is expressed in the different species depends on the strategies followed, which in turn is influenced by the ecological and social factors under which an animal lives (Emlen & Oring, 1977; Cheney et al., 1987; Clutton-Brock, 1989; Shuster & Wade, 2003).

Male and female reproductive strategies in primate groups

The diversity of the primate order is also reflected in its varying social- and mating systems ranging from solitary (e.g. mouse lemurs, aye-aye) to multimale-multifemale groups with up to hundreds of individuals (e.g. capuchins, macaques, baboons, mandrills) (Dunbar, 1988; Dixon, 1998), and from monogamy (e.g. indris, aotus monkeys, titi monkeys) to promiscuity (e.g. chimpanzees, mandrills, brown capuchins, rhesus macaques, long-tailed macaques) (see Dixon for review, 1998). However, the vast majority of primate species live in complex social groups (multimale-multifemale groups) whose members stay together all year round (Dixon, 1998). A typical primate group contains individuals of different ages, sexes, dominance ranks and kinship. The members of such groups sometimes form temporary alliances, subgroups or long-term associations which result in i) a complex network of interactions, with many alternative strategies for survival and reproduction and ii) social groups in which individuals are likely to pursue a number of different strategies during their lifetimes (Cheney et al., 1987).

Male strategies

Male primates, just as other mammal males, are mainly limited in their reproductive success by the number of females they can fertilize. Therefore it is expected that selection has favored morphological traits as well as behavioral strategies that help them to maximize their mating success and thereby increase their reproductive success. Among primates, numerous examples of conspicuous morphological traits (e.g. large body and canine size) that are signs of contest competition between males over females can be found, and are, as expected, more common in species with a polygynous and promiscuous mating system (Clutton-Brock, 1984; Plavcan & van Schaik, 1992; Dixon, 1998). Contest competition among males can occur in different ways (summarized in Dixon, 1998). Physical exclusion of all other males from a group of females leads to a one male social structure (e.g. geladas, hamadryas baboons, gorillas) in which the strongest male gains exclusive access to fertile females (priority of access to females; Altmann, 1962). In multimale-multifemale groups (e.g. mandrills, chimpanzees, macaques; Dixon, 1998), males form dominance hierarchies, and rank often correlates with priority of access to females (Altmann, 1962). This mechanism of reproductive competition is often manifested as mate guarding or consortship (Kappeler & van Schaik, 2004). Such consortships are temporary and the duration varies enormously between species (reviewed in Dixon, 1998). High-ranking males are often more successful in the formation of consortships (Bercovitch, 1991; Cowlshaw & Dunbar, 1991; Weingrill et

al., 2000, 2003; Setchell et al., 2005), but some females are not exclusively in consort with the dominant male, but with several males in succession (Hrdy & Whitten, 1987; Hrdy, 2000). Nevertheless in many primate species, dominance seems to be an important factor in influencing a male's reproductive success (e.g. long-tailed macaques: de Ruiter et al., 1994; Engelhardt et al., 2006; drills: Dixson et al., 1993; hanuman langurs: Launhardt et al., 2001; sooty mangabeys: Gust et al., 1998; stump-tailed macaques: Bauers & Hearn, 1994; savanna baboons: Altmann et al., 1996). However, the fact that in some species, significant numbers of offspring are fathered by subordinate or extra-group males (e.g. Japanese macaques: Inoue et al., 1993; Soltis et al., 2001; yellow baboons: Alberts et al., 2003; rhesus macaques: Berard et al., 1993, 1994; Widdig et al., 2004) suggests that factors in addition to rank are also involved in determining male reproductive success.

Such alternative male strategies could be, for example, i) the formation of coalitions (e.g. yellow baboons: Bercovitch, 1988, 1995) or alliances (e.g. chimpanzees: de Waal, 1992) of subordinate males in order to break up consortships between high-ranking males and fertile females, ii) the occurrence of sneaked copulations by subordinate males (e.g. Barbary macaques: Küster & Paul, 1989) or extra-group males (e.g. Japanese macaques: Sprague, 1991; Soltis et al., 2001) without the notice of other males or iii) sexual coercion of females in the form of forced copulations and interruption of copulations (reviewed in Smuts & Smuts, 1993; see also Dixson, 1998) or in its most extreme in the form of infanticide (Hrdy, 1979; Kappeler & van Schaik, 2004). Infanticide has nowadays been reported for many populations of wild primates (e.g. hanuman langurs: Sommer, 1994; Borries & König, 2000; wedge-capped capuchins: Valderrama et al., 1990; savannah baboons: Collins et al., 1984; chacma baboons: Weingrill, 2000; hamadryas baboons: Swedell & Tesfaye, 2003).

Whereas all male strategies mentioned above function on the pre-copulatory level, strategies may operate on the post-copulatory level as well. Competition between primate males can also continue post-copulatory. Even though primates exhibit a great diversity of social systems (Dunbar, 1988; Dixson, 1998, see above), females in the vast majority of species mate with more than one male during a single reproductive cycle (see below), so that sperm competition should be intense in primates (Birkhead & Kappeler, 2004). The finding that primate males living in multimale-multifemale groups have higher testis to body weight ratios, and a higher volume of the sperm midpiece (which provides energy for motility) in comparison to those living in one-male groups or in monogamous mating systems, has been interpreted as a result of sperm competition (Harcourt et al., 1981; Anderson & Dixson, 2002).

While males are more seen as the competitive sex and females as the choosy sex (see above), the occurrence of conspicuous morphological traits (apart from aiding in male-male competition) as well as secondary adornments, signaling male quality (Folstad & Karter, 1992; Waite et al., 2003) may be part of a male strategy to attract females and thus raise the chance to be chosen. The most striking examples of masculine secondary sexual adornments are to be found in Old World monkeys and apes (catharrines) (Dixon, 1998). Among those adornments are the paranasal swellings in mandrills and drills, the red chest patch of the geladas as well as the manes of the geladas and the hamadryas baboons (Dixon, 1998), which have been suggested to have evolved through sexual selection by female choice (Jolly, 1963).

Finally, although primate males, just as other males, are not assumed to be selective in their choice of mates, male mate choice does occur in primates (Kappeler & van Schaik, 2004). Male vervet monkeys and macaques, for instance, sometimes prefer higher-ranking over lower-ranking females (Keddy, 1986; Samuels et al., 1984) and male anubis baboons seem to prefer females with larger sexual swellings (Domb & Pagel, 2001). Constraints, such as physiological costs of sperm production, which appear much more significant than previously thought (Dewsbury, 1982; Wedell et al., 2002), and sperm delivery, which can be limited by consecutive ejaculations (Dixon, 1995, 1998), might drive the evolution of mate selectivity in males (Kappeler & van Schaik, 2004).

Summarized it can be said that primate males employ numerous strategies to get access to fertile females and although mate choice does occur, male-male competition seems to play a more important role for male reproductive success. However, according to the theory of sexual selection, reproduction is always an interaction between male and female strategies.

Female strategies

Within the primate order, sexual selection has for a long time been envisioned as operating principally among males (Goss-Custard et al., 1972). Primate mating systems have thus usually been described as being male dominated or controlled, whereas the females were envisioned as passive recipients of “male choice”. Due to their limited reproductive potential (Lee, 1996; Ross, 1998) and the little or no direct infant care provided by males (Kappeler & van Schaik, 2004), female primates should select their mating partners carefully, in order to enhance the fitness of their offspring and thereby their own reproductive success (Andersson, 1994). Nowadays there is increasing evidence, that female primates do show preferences for certain males as mating partners (Loy, 1970; Taub, 1980; Small, 1989, 1990) and that, at least

in some species, females are more active in soliciting males than previously thought. Female primates have been reported to choose mates based on different attributes such as dominance rank, novelty, color and access to resources (e.g. brown capuchins: Janson, 1984; Welker et al., 1990; vervet monkeys: Keddy, 1986; savannah baboons: Bercovitch, 1991; ringtailed lemurs: Pereira & Weis, 1991; Japanese macaques: Huffman, 1992; rhesus macaques: Manson & Perry, 1993, mandrills: Setchell, 2005; chimpanzees: Stumpf & Boesch, 2006). Instead of actively choosing males, females may also refuse to mate with males (e.g. blue monkeys: Cords et al., 1986; vervet monkeys: Andelman, 1987; ringtailed lemurs: Pereira & Weis, 1991; Japanese macaques: Huffman, 1987, 1991) or choose their mating partners in a more indirect way by influencing the availability of mates. Female participation in male-male aggressive interactions, for example, can influence group memberships (indirect female choice; Smuts, 1987).

Similarly, their reproductive physiology provides female primates with several mechanisms to manipulate the number and identity of available mates (Wiley & Poston, 1996). One of these mechanisms is the synchronization of ovarian cycles, a factor that seems to affect male monopolization (Kappeler & van Schaik, 2004). If more than one female is receptive at the same time, the ability for a single male to monopolize access to all of them decreases (Paul, 1997; Nunn, 1999a; Dunbar, 2000; Eberle & Kappeler, 2002), which on the other hand may increase the females' opportunity to mate with additional males (Kappeler & van Schaik, 2004). Other possibilities to influence the number and identity of mating partners are to i) advertise the fertile phase which can incite male-male competition (Pagel, 1994) or ii) conceal the fertile phase and thereby reduce male monopolization (Hrdy, 1979, 1981). Concealment might also serve to confuse paternity and thereby reduce the risk of infanticide (since males are not expected to kill infants they might have sired, Borries & König, 2000), or enhance the share of paternal care (Alexander & Noonan, 1979).

Female primates often mate with multiple males within a single reproductive cycle or even within a single day (Taub, 1980; Hrdy & Whitten, 1987; Small, 1993; van Schaik et al., 1999; see also Birkhead & Kappeler, 2004). Both, polyandrous mating and female choice may be strategies to ensure that the female i) gets the "best male" to father her offspring (Small, 1989), ii) avoids costs of inbreeding or genetic incompatibilities (Newcomer et al., 1999; Zeh & Zeh, 2001), iii) increases paternal care (Taub, 1980), iv) guarantees high-quality sperm through sperm competition (Yasui, 1997; Dixson, 1998) or v) reduces the risk of infanticide (van Schaik et al., 2000).

As in males, female strategies are not restricted to the pre-copulatory level. While male competition can still occur on the post-copulatory level (sperm competition, see above), a variety of mechanisms might allow females to continue choice as well after copulation (female cryptic choice, Eberhard, 1996; reviewed in Reeder, 2003). Females may discard or destroy sperm of unfavored males, hinder sperm transportation to the fertilization sites, choose among the sperm that have reached the egg or abort zygotes (Reeder, 2003). Cryptic female choice might be an adaptation to situations where females cannot prevent males from mating or where they have other reasons to mate with multiple males (Gowaty, 1997; Tregenza & Wedell, 2002; Zeh & Zeh, 2001).

Although competition has been studied traditionally in male rather than in female primates, researchers recently have begun to concentrate on female-female competition and factors that affect differential reproductive success among females. Variance in male reproductive success has been assumed to be greater than that in females, but many studies have concluded that variance in female reproductive success is indeed higher than previously thought (Hrdy, 1981; Fedigan, 1983; Wasser, 1983; Small, 1984, 1993; Harcourt, 1987). Female primates may for instance compete over access to food resources, mates or social partners (e.g. Whitten, 1983a, 1984; Barton, 1993) using strategies, such as harassment during the reproductive cycle (e.g. Dunbar & Dunbar, 1977; Wasser, 1983) to lower other females' fertility. In several studies correlations between dominance rank and fertility, access to resources or access to mates have been found, indicating that female-female competition enhances fitness. (e.g. Silk et al., 1980, 1981; Small, 1981; Whitten, 1983b; Linn et al., 1991).

Summarized it can be said that female primates are far from being "passive" and seem to have a greater influence on their own and male reproductive success than primarily thought. Since female interests are, however, compromised by male reproductive strategies and their ability to override female strategies, it still remains poorly understood to which degree female choice affects male mating success and thereby also male reproductive success. Female primates may use different strategies to overcome restrictions caused by male reproductive strategies, to gain more freedom to pursue their own reproductive interests and to choose between their possible mates.

The relative importance of male and female reproductive strategies upon paternity outcome in primates is still poorly understood. For studies addressing this question, it is important to investigate sexual behavior and mating patterns in relation to the female reproductive status because females are only fertile during a short period surrounding the time of ovulation (fertile phase) and it is only during this period when reproductive strategies can lead to successful fertilization (Gomendio et al., 1998).