DEVELOPMENT AND SEXUAL SELECTION IN PRIMATES

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Revised manuscript for Kappeler PM & van Schaik CP (editors). Sexual Selection In Primates: New and Comparative Perspectives. Cambridge: Cambridge University Press.

INTRODUCTION

Studies of sexual selection in primates or other animals tend to focus on outcomes – sexual dimorphism, differential mating and reproductive success for adult males and females. However, adult sex differences represent the end-points of complex and interrelated developmental processes, and arise from differences in behaviour and physiology between males and females. In most vertebrates, including primates, the sexes are nearly identical in size and shape during early development and adult differences are thus the product of divergent growth strategies (Badyaev, 2002). Sex differences in growth and development arise as a result of the different roles played by the two sexes in reproduction and the corresponding determinants of reproductive success for males and females, which are intricately linked to social organisation and mating system (Kappeler & van Schaik, 2002). Evolution shapes processes throughout the life cycle, and the mechanisms for partitioning resources among growth, reproduction and survival are to a large part established during development, while consequences may not be observed until the end of the lifespan. A developmental perspective is therefore fundamental to studies of the action of sexual selection (see also Pereira & Leigh, 2003).

For mammals in general, and primates in particular, past work on sexual selection and development has concentrated on the influence of growth on sexual dimorphism (e.g. ungulates: Jarman, 1983; Georgiadis, 1985; Clutton-Brock et al., 1992; seals: Trillmich, 1996; primates: Leigh, 1995; Pereira & Leigh, 2003) or growth and life history traits such as rates of reproduction (e.g. Gordon, 1989; Pontier et al., 1989; Lee & Kappeler, 2003). However, integration in the context of sexual selection of these elements – growth and development, attained adult sexual dimorphism and reproductive output –is generally lacking. In this chapter we explore inter-relations between development and sexual selection, and, in so doing, highlight the paucity of available data for testing hypotheses concerning sexual selection and development in primates.

Primates are characterised by a lengthy pre-reproductive period relative to their body size (Brody, 1945; Schultz, 1956; 1969). This is a period of high risk from extrinsic sources of mortality (predation, infanticide, environmental stochasticity leading to starvation or catastrophic death), as well as death due to growth faltering, disease or stress (Small & Smith, 1986; Janson & van Schaik, 1993; Lee, 1997; Altmann, 1998; Ross & Jones, 1999). Selection acting on the immature phase of the life history is therefore evolutionarily extremely important (Pereira & Fairbanks, 1993). Individuals who survive either were born in favourable times, or have specific genetic, maternal or learned characteristics ~~(genetic, maternal or learned)~~ advantageous for survival. Mortality during the pre-reproductive period is the pacemaker of life history evolution (Promislow & Harvey, 1990), and life history underlies the maintenance of sexually dimorphic traits (Pereira & Leigh, 2003). The study of primate development from a perspective of sexual selection is particularly interesting because primate growth and development strategies differ from those of many other animals, and they attain sexual size dimorphism (where it occurs) differently. Mammals often show maximum growth rates shortly after birth, and in sexually dimorphic species dimorphism is achieved by faster postnatal growth rates from birth onwards (e.g. Jarman, 1983; Clutton-Brock et al., 1992; Lee & Moss, 1995). In primates growth rates are rapid shortly after birth, then decline until puberty, at which point males (and in some species females) experience a peak in growth rate (the "adolescent growth spurt": e.g. Watts, 1985; 1986; Leigh, 1992).

Investigations of sexual selection from a developmental perspective in primates have focussed on sex differences in the duration of growth (bimaturism) and rates of development, and differences in costs and benefits of early or late maturation have been demonstrated by sex (e.g. Leigh, 1995; Leigh & Shea, 1995; Leigh & Terranova, 1998; Bercovitch, 2000; 2001). A further interesting question with regard to sexual selection is whether heterochrony explains some of the differences between species in the extent of sexual dimorphism, with selection acting to displace the timing of developmental events relative to an ancestral condition, and thus promoting or constraining sexual dimorphism as a function of patterns of development (Shea, 1983; 2000).

Development can be regarded as both a continuous process, from conception to old age, and as a series of events (discontinuities, e.g. Bateson, 1981) separating different stages, each with continuity. Underlying physiological systems can undergo abrupt changes; for example, lactase production terminates at nutritional weaning, and the sudden onset of the GnRH pulse generator determines puberty. By contrast, somatic growth processes are continuous; for example long bone growth until epiphysiseal closure (e.g. Hamada & Udono, 2002). The distinction between discontinuities and continuous processes is fundamental to assessing sex-specific vs phase-specific selective pressures. The simultaneous occurrence of gradual and discontinuous processes during development suggests that an exploration of rates of processes and the timing of events will contribute~~d~~ towards understanding the mechanisms and outcomes of sexual selection (e.g. Watts, 1985; Leigh, 1992; 1995; Setchell & Dixson, 2002; Pereira & Leigh, 2003). Developmental phases are made up of a combination of physical traits, behavioural characteristics and mortality risks that can be compared between the sexes, and sexual selection may be a determinant of differences in either rate or timing or both.

MATURATIONAL “STAGES”

We are not the first to highlight confusion and lack of consensus in the primatological literature concerning the definition of developmental phases (see also Pereira & Altmann, 1985; Altmann & Alberts, 1987; Caine, 1987; Altmann et al., 1981; Bernstein et al., 1991; Bercovitch, 2000). Lack of clarity or consistency in terminology means that concepts crucial to understanding development may reflect different stages or events to different authors, despite being particularly important for comparative studies of sexual selection. In this section we therefore examine developmental terms and definitions, associated maturational changes for the two sexes, and sex differences in mortality at each life history stage. For each stage we attempt to assess the potential for the action of sexual selection on development, and show how sexual selection theory leads to different predictions for males and females growing up in specific social or reproductive contexts. The examples of sex differences in traits are selective rather than exhaustive. In many cases there are few data available for primates, and we thus use representative examples from the literature on other mammal species to make predictions for primates.

Infancy

Definition

It is relatively easy to define a primate “infant” (e.g. Altmann, 1980). Infancy begins at birth, continues while the individual is directly dependent on the mother for survival, and ends when the animal attains the capacity to provide its own nutrition and survive maternal death (Pereira & Altmann, 1985). Infants also rely on caretakers for transport and~~,~~ protection from elements, infanticide and predation (Pereira & Altmann, 1985). Weaning is a process of transition to general self-sufficiency, rather than a sharp cut-off, and includes the gradual nutritional shift from mother’s milk to solid foods (Martin, 1984). Both suckling and time in contact with the mother (or caretaker) decline with age, as independence increases and infants explore their environment and learn to obtain sold food (reviewed in Pereira & Altmann, 1985; Janson & van Schaik, 1993; Lee, 1997).

~~Sex ratio at birth~~

~~Just a few sentences to emphasize that the number of male and female infants born may already reflect the action of sexual selection? Cross-reference to Silk & Brown (this volume) will take care of all details.~~

Physical sex differences

Physical sex differences during infancy obviously include the primary sexual characteristics, but there can also be slight, but consistent, sex differences in body mass, with males being heavier than females in species with sexual dimorphism in adult mass (Smith & Leigh, 1998). Little is known about sex differences in growth and development during infancy (but see Leigh, 1992; 1995; Bowman & Lee, 1995; Setchell et al., 2001). Mass growth rates are highest soon after birth and gains in body mass decelerate as infancy progresses (Leigh, 1992; 1995). The deciduous dentition erupts during infancy – effectively a discontinuity in development as well as a process. The appearance of deciduous and then permanent teeth are often used as markers of life history stages (e.g. Smith, 1992; Smith et al., 1994; Godfrey et al., 2001), and there appears to be less variation in the sequence of dental development than there is in infant mass growth (Lee, 1999), suggesting that the two phenomena may not be directly linked as life history processes. Again, there are few data on sex differences in non-human primate dental development.

Sex differences in behaviour

In cercopithecid species where females remain in their natal group for life, associating in matrilines, but males disperse during adolescence, infant males and females both receive and exhibit differential interest towards adults of both sexes, and they differ in the patterns of interactions with peers (Berman 1980; Brown & Dixson, 2000). Sex-differentiation of infantile behaviour or attractivity may be expected to be less marked or even non-existent in ~~nongregarious~~non-gregarious and monogamous taxa. However, adult behaviour is sexually differentiated in all primate species, and Nash (1993) has shown sex-differentiated sociosexual behaviour in pre-reproductive galagos, a non-gregarious species.

Sex differences in mortality

Infancy appears to include periods of sensitivity to environmental constraints, which can influence subsequent development (Worthman, 1993). Sex differences in body mass and size, and in the rate and duration of post-natal growth, although small, may be biologically significant if associated with either mortality risk or attained adult mass. If males in sexually dimorphic species grow faster, under conditions of limited nutrition they may suffer higher mortality than females. Support for this "fragile male" hypothesis (van Schaik & de Visser, 1990), that males are more susceptible to mortality during development, is found in some dimorphic mammal species (Lee & Moss, 1986; Clutton-Brock, 1991; Trillmich, 1996). As yet, very few data exist on primates to assess whether males are more vulnerable to early mortality*~~ in primates~~, or whether differential early mortality is linked to the degree of sexual dimorphism or to a species' social system (which are, of course, all inter-related!). While male infants do have higher mortality among captive strepsirhines (Debyser, 1995), Fedigan & Zohar (1997) found no sex difference in infant mortality in Japanese macaques. The lack of a sex difference in mortality for a relatively sexually dimorphic species may be explained by the fact that growth rates in primates diverge later in life than do those of other mammals (Leigh, 1995), or by hypotheses predicting excess female mortality (e.g. van Schaik and de Visser, 1990).

~~(*captive infant male prosimians have higher mortality rates: Debyser, I. 1995. Prosimian juvenile mortality in zoos and primate centers. *Int J Primatol* **16**, 889-907.)~~

Sexual selection and infancy

The major influence on infant development is that of the mother or caretaker. Differences between individuals in maternal style (a function of dominance rank, parity, and experience) have significant consequences for the behavioural development of both male and female infant primates (e.g. Altmann, 1980), with impacts on growth processes. Maternal age and status (Setchell et al., 2001), mass (Bowman & Lee, 1995) and maternal condition (Johnson & Kapsalis, 1995) have been related to infant mass in cercopithcid primates. Sex and individual differences in neonate mass and growth rate relate to gestation costs, and raise interesting questions about maternal expenditure (see Brown, 2001; Bercovitch 2002). It can be suggested that a skew in sex ratio at birth might represent either differential vulnerability to mortality in utero, or differential investment in the production of one sex, both of which are consequences of sexual selection (see Silk & Brown, this volume). Postnatal growth is clearly a function of maternal investment, which has the potential to vary by sex. If an infant must attain a certain threshold mass (weaning mass) before it is able to nutritionally sustain itself at weaning, then growth to weaning is under a metabolic constraint (Lee et al., 1991). The rate of attainment of weaning mass, and the time taken to grow, is thus available for selection acting on the proximate control mechanisms of growth (hormones and growth factors). Unfortunately, almost no data exist to relate weaning mass (early growth) to weaning age for male and female infants (Lee, 1999).

While mothers respond protectively to infants as a function of mortality risks, which can potentially differ between the sexes, they do not show consistent sex biases in their treatment of infants or in care allocation (see Fairbanks, 1996). Weaning is later for sons in some primates (e.g. chimpanzees; Boesch, 1997), while it is later for daughters of subordinate mothers in rhesus macaques (Gomendio, 1990). Despite numerous analyses (e.g. van Schaik & Hrdy, 1991), no consistent sex differences in weaning age have been described. Factors such as maternal dominance, size and composition of matrilines, predation, and local food abundance interact to obscure any clear trends in sex-specific care allocation.

A further potential influence on the survival of primate infants is sexually selected infanticide by males (see van Schaik & Janson, 2000; van Schaik et al., this volume). This mortality risk can be expected to select for the evolution of traits in infants that counter the threat of infanticide. For example, Treves (1997) has shown that natal coat contrast is significantly associated with adult testes weight, suggesting a link between mating system and infant colouration, and that the natal coats found in many species of primate may serve as an infanticide avoidance strategy.

The juvenile period

Definition

A juvenile is defined as a weaned individual, capable of surviving the death of its mother (or other caretaker), but that has not yet entered puberty (Pereira & Altmann, 1985). Juveniles thus obtain their own food, travel independently, and avoid danger unaided, although case studies suggest that they may still be psychologically dependent on their mother (Pereira & Altmann, 1985). The infant-juvenile transition can be defined using various markers, including tooth eruption, lactational weaning, interbirth interval, and percentages of maternal mass. As these developmental markers do not necessarily co-occur, the "boundaries" of this stage are difficult to determine, while the stage itself is relatively distinctive.

Physical sex differences

The rate of mass gain decreases during the juvenile period and although sex differences in mass remain slight, the velocity of mass growth may already differ between the sexes in sexually dimorphic species, with males growing faster than females (Leigh, 1992; 1995). This difference has implications for both foraging behaviour (i.e., energetics) and mortality risks. The deciduous dentition is completed during the juvenile period, and subsequently replaced by the eruption of the permanent dentition. A study of squirrel monkeys has shown that there are no sex differences in the eruption of the deciduous dentition, but that females are more precocious in the appearance of the permanent teeth (Galliari & Colillas, 1985).

Sex differences in behaviour

Juvenile physical and behavioural development underlies, at least in part, sex differences in adult reproductive strategies. Despite an edited volume synthesising knowledge of juvenile primate life history, development and behaviour (Pereira & Fairbanks, 1993), juveniles remain the least studied life history stage in primates (Pereira & Leigh, 2003). Behavioural sex differences occur in socialisation processes, interactions and competition with conspecifics, and foraging behaviour (Lee & Johnson, 1992; Nikolei & Borries, 1997) as a function of species social system (Pereira & Altmann, 1985). In sexually dimorphic species, sex differences in foraging behaviour are predicted: juvenile males should compete more for food because they are growing faster than their female counterparts and need additional energy (e.g. Pereira, 1988).

Sex differences in mortality

Juvenile mortality rates are lower than those during infancy, but are still approximately double those of adults. A recent summary of mortality for 20 strepsirrhine, New and Old World monkeys and apes found ~~on average~~ that, on average, 15% of juveniles die annually (Ross & Jones, 1999). Both avoiding predation (e.g. Stanford, 1998) and maximising energy intake (e.g. S. Altmann, 1998) are specific problems faced by juveniles, where survival probability can be directly linked to behaviour in the juvenile period. As with infants, few data on sex-differentiated mortality exist for juvenile primates. The "fragile male" hypothesis (see above) predicts that juvenile mortality should be biased towards males in sexually dimorphic species because higher growth rates and consequently lower levels of fat reserves in males make them more vulnerable to nutritional stress than females. However, this hypothesis is not supported in analyses of the few data available for juvenile primates (van Schaik & de Visser, 1990; Hauser & Harcourt, 1992; van Schaik, 1992; Fedigan & Zohar, 1997).

Sexual selection and the juvenile period

Juveniles are, by definition, non-reproductive, and a juvenile's "task" is to survive predation and starvation, in such a way as to maximise its chances of reaching the required age and / or size for reproductive maturation and thus ensure its future reproductive success. If adult size is a consequence of either compromised or enhanced growth during the juvenile stage (due to status and differential resource acquisition; e.g. S. Altmann, 1991, or environmental factors; e.g. Bercovitch & Strum, 1993), then this period underlies adult social status, morphology, reproductive tactics and reproductive success. In particular, negative energy balance during the juvenile stage may affect health and limit growth, delaying the age at reproductive maturation (Hamilton & Bulger, 1990), or altering the adult career (Pereira, 1995), and thus influencing lifetime reproductive success.

Adolescence

Definition

The transition between pre-reproductive juvenile to full adult has been termed "puberty", "subadulthood", "young adulthood", and "adolescence", depending to some extent on the definition of "adult" used. The use of these terms is by no means standardised between species, between studies (Caine, 1987) or even between the two sexes in the same study (see references in Bernstein et al., 1991).

Puberty is a suite of physiological changes that culminate in reproductive maturity (a process, not an event: Bernstein et al., 1991), initiated by increases in gonadotrophic hormones and sex steroid production during sleep, and induced by the onset of activity in the hypothalamic-pituitary axis, and increased secretion of luteinising hormone-releasing hormone (Plant, 1994). The internal process can typically be assessed only in terms of visible outcomes (e.g. first swelling in females, first ejaculation of semen in males), which occur some time after the increase in sex steroid levels (faecal hormone analyses – e.g. Whitten et al. ~~,~~ (1998) – may allow for more accurate determination of hormonal events during puberty).

Puberty ends when an individual attains reproductive competence – i.e. when a female can bear an infant to term, and a male can impregnate a female. Some authors (e.g. Pereira & Altmann, 1985) have used this criterion of reproductive maturity to define the beginning of adulthood. However, the end of puberty generally occurs prior to the attainment of adult size and the cessation of growth in primates (Watts, 1985; Bercovitch, 2000), and individuals therefore continue to invest in their own growth as well as in reproduction once they have attained reproductive maturity (see Table 1).

There is no doubt that reproductive maturity is an important milestone in an individual’s life history, but should it be termed adulthood? A 4 year old female mandrill suckling her first infant has reproduced successfully, but she is only 2/3 of her final adult body mass and has a further five years to grow in mass and size (Setchell et al., 2001). She is unlikely to have her full permanent dentition (Setchell, unpublished observations). Similarly rhesus mothers first give birth at 2/3 of adult body mass, and many still have some deciduous teeth at this stage (Bernstein et al., 1991). Are these mothers adult? A male human, aged 15 years, with large testes, a deep voice, and a beard is reproductively capable, but will not attain his full adult height for another 5 years (Bogin, 1999). Male baboons of 6 years are reproductively competent, but may be too physically and socially inferior to other males to copulate with a fertile female (Alberts & Altmann, 1985a). Unflanged male orang-utans aged 23 years can (and do) reproduce, but have arrested secondary sexual development, and show none of the typical adult male secondary sexual traits of the species (Utami et al., 2002; van Hooff & Utami, this volume). Can we term these males adult?

Caine (1987) defines reproductively capable, but non-reproducing individuals as adolescent, and we concur, defining “adolescence” as the period from the onset of puberty to the attainment of full adult size (see also Watts, 1985). Puberty and adolescence thus have the same onset, but while puberty ends at reproductive maturity, adolescence continues until adult size and appearance are attained, and somatic growth is complete. If the term “adolescence” is ambiguous, then “subadult” is even more loosely applied in the literature (Caine, 1987), and is usually only used for males. We question the use of this term, finding it more useful to consider the chronological age and developmental stage of individuals studied.

Adolescence is thus a period of rapid morphological, physiological and behavioural development, leading to the cessation of physical growth, endocrine stability, and social competence. By the end of adolescence, female primates are sexually mature, fully grown, and have begun their reproductive career. Males have attained sexual maturity, adult dominance rank (in group-living species), and may have sired offspring. In males this last milestone is dependent on proximate, often stochastic variables; for example, the age at which a male baboon first consorts with a female depends on the number of sexually cycling females in the group and his relative rank (Alberts & Altmann, 1995a).

Physical sex differences

During puberty and adolescence physical sex differences become pronounced in sexually dimorphic primates. However, relatively little is known about physical development in pubertal and adolescent primates, particularly for strepsi~~r~~rhines (reviewed in Caine, 1987). As well as initiating sexual maturation, pubertal hormones lead to events and new processes in physical growth and development. The skeletal system matures, with fusion of the epiphyses. Males, and females of some species, show a growth spurt in mass (Leigh, 1992; 1995). Complete adult dentition is attained with the eruption ~~of last~~ of the last permanent teeth (Watts, 1985). In strepsi~~r~~rhines, puberty is indicated by the advent of particular kinds of scent-marking (e.g. genital scent-marking in ring-tail lemurs: Pereira 1995). The relationships between hormones and aspects of growth and development remain unclear, as do inter-relationships between developmental markers (Watts, 1985).

In female primates, the release of luteinising hormone leads to the maturation of ovarian tissues during puberty. Females of many species show tumescence, with changes in facial or perineal coloration during this period (Caine, 1987). Pubertal sexual swellings may occur even in species where adults do not show sexual swellings (Dixson, 1998). However, although first sexual swelling, or first menstruation, are often used as an indicator of puberty, neither are signs of full sexual maturity in females. Both can occur prior to first ovulation, which is a late event in female puberty (Tanner, 1962). First ovulation itself can only be determined hormonally, and does not indicate capacity to carry a pregnancy to term. The first several menstrual cycles are often irregular and anovulatory, while complete maturation of luteal function, necessary to maintain embryo implantation, occurs last (Hobson et al., 1980). Female reproductive maturity is attained when the hormonal cycle is regular, and is not achieved until about 5 years after menarche in human females (Bogin, 1999). It is difficult to estimate the age at onset of puberty from external signals in females, and occurrence of the various proxies used is not necessarily simultaneous or inter-correlated (Bercovitch, 2000). Once physiologically mature, female primates start to reproduce, perhaps the most major change in a primate's life since her own birth. However, even after the first birth, adolescent females may not be as fertile as adult females, with longer interbirth intervals than fully-grown females, most likely because they still investing in their own growth or body condition to some extent (e.g. Paul & Thommen, 1984; Itoigawa et al., 1992; Setchell et al., 2002; see below).

In males, the first visible sign of puberty is descent or rapid enlargement of the testes, and this is often used as a marker for the onset of male puberty (Rowell & Dixson, 1975; Nigi et al., 1980; Altmann et al., 1981; Pereira & Altmann, 1985; Watts, 1985). This is more useful than the visible markers used for females, as testicular development occurs fairly early in puberty (e.g. Nieuwenhuijsen et al., 1987a). As the testes develop, the Leydig cells produce increasing quantities of testosterone, although there is a time lag of several months before circulating levels of testosterone begin to increase (Glick, 1979; Nigi et al., 1980; Kraemer et al., 1982). The tubules and cellular elements involved in sperm production proliferate, leading ultimately to the production of mature sperm (Dang & Meussy-Dessolle, 1984). Male primates are fertile before testes reach full "adult" dimensions (e.g. Nielson et al., 1986; Wickings & Dixson, 1992) and the testes reach adult dimensions at approximately the same age as does the body (Kraemer et al., 1982, Setchell & Dixson, 2002; Nieuwenhuijsen et al., 1987a). Testosterone levels continue to increase, and secondary sex characters mature under the influence of the increased production of gonadal steroid hormones. Males of some species develop sexual ornamentation. Although the development (and individual variation in development) of these characteristics is rarely documented (but see Tanner, 1962; Watts, 1985; Liang et al., 2000; Setchell & Dixson, 2002), it is linked to dominance rank in some species (reviewed in Setchell, in press). For example, only dominant male mandrills develop full adult male traits, and subordinate status has been linked to failure to develop secondary sexual traits in male orang-utans (van Hooff & Utami, this volume). The maturational process takes time, and changes may occur over a period of years (e.g. 4 years in male rhesus: Bernstein et al., 1991; and mandrills: Setchell & Dixson, 2002).

Sex differences in behaviour

As hormonal and physical maturation proceed during adolescence, changes in behaviour also occur. This process of behavioural development is somewhat better understood than physical development and has been comprehensively reviewed elsewhere (Kraemer et al., 1982; Pereira & Altmann, 1985; Caine, 1987; Pusey, 1990), although adolescence remains under-represented in the primate literature. During this period, individuals continue to make the transition from maternal association to integration into the adult community, or dispersal, and adult behaviour develops. Natal dispersal is often sexually differentiated, with consequences for sexual selection (Pusey & Packer, 1987; van Noordwijk & van Schaik, 2001; this volume). The relationships between physiological maturation and behavioural development are not well understood (but see Kraemer et al., 1982; Pusey, 1990; Setchell, 1999; Table 1). Pusey (1990) has shown that stage of genital development is more closely correlated with a decline in association with the mother in male chimpanzees than are chronological age or body mass. In mandrills, male peripheralisation is more related to morphological development than to age (Setchell & Dixson, 2002). Behavioural changes, for example in male aggression and hierarchical behaviour (Nadler et al., 1987; Kraemer et al., 1982), appear to be associated with adult hormone production and function and adult size, rather than linked to the onset or event marking the increase in hormone levels.

Morphological maturation also elicits a change in the responses of other individuals. Adult male baboons (Scott, 1984) and mandrills (Setchell, 1999) show interest in adolescent female cycles, although this is less than that for full adults. Young cycling (tumescent) females often appear nervous in baboons (Scott, 1984) and mandrills (Setchell, unpublished observations), suggesting that proceptive and receptive behaviour have major learned components. Dominant males cease to tolerate sexual behaviour from what are now reproductively competent males, and therefore potential rivals. Juvenile male stump-tailed macaques copulate “publicly”, but post-pubertal males do so surreptitiously (Nieuwenhuijsen et al., 1987b), while 5-6 year old sooty mangabeys receive more aggression and chases from dominants when they mount females than do younger males (Gust & Gordon, 1991). Males developing conspicuous secondary sex characters may also receive increased aggression (e.g. Rowell, 1977). Thus the frequency of copulation may decline in adolescent males, although adult behaviour, such as consortships, begin and successful consortships may be achieved as males approach adult size (e.g. Pusey, 1990). For species where relationships and integration into group of adult males are of paramount importance to male reproductive success, males cultivate relationships with other males (Pusey, 1990). Little is known about the reproductive success of adolescent male primates. Adolescent males are generally subordinate and physically inferior (less powerful or skilled in contests) to ‘prime’ males, and mate opportunistically, with less attractive females (e.g. Kuester & Paul, 1999; Setchell, 1999). Ejaculate volume and sperm number have implications for fertility (~~Kappeler &~~ Birkhead & Kappeler~~,~~ this volume), but are unknown for most species.

Sex differences in mortality

Where variation in reproductive success is higher in males than in females, male reproductive strategies are expected to involve a higher mortality risk, but a higher potential reproductive gain than those of females (Trivers, 1985). In sexually active primates, males may range over larger areas than females in search of mates or while dispersing, and thus have a higher risk of death from predation or starvation (Alberts & Altmann, 1995b; Isbell et al., 1990). Males also risk serious injury or death along with energetic costs of male-male competition for access to receptive females. For example, Fedigan & Zohar (1997) found that adolescent and adult Japanese macaque males have higher mortality than females and juvenile males, and males remain at greater risk than females until old age. In addition, high levels of circulating androgens can suppress immunity (Folstad & Karter, 1992); simply being male involves costs that are not incurred by females. The high risk, high benefit strategies employed by males are ultimately responsible for female-biased sex ratios in polygynous species (Clutton-Brock et al., 1977; Clutton-Brock, 1991; Kappeler, 1999).

The extent of sexual dimorphism is generally related to the extent of male-male competition (Plavcan, 1999; this volume) but also appears to be associated with which sex disperses from the natal unit. Using a measure of adult sexual dimorphism based on the residual of the regression of female mass against male mass (where the regression was calculated separately for strepsir~~r~~hines and anthropoids), species with male dispersal have significantly smaller females for male body size (ANOVA, hierarchical model, removing subfamily on step 1 to control for phylogenetic similarity, $F = 5.09$, $df = 2, 89$, $p = 0.009$, post hoc, all $p < 0.05$; methods and dataset in Lee & Kappeler, 2003). It can thus be suggested that increased costs of ranging, exposure to predation, and risks of injury due to contest competition tend to be associated with male dispersal and that attaining large male size relative to that of females may be advantageous in this context. As dispersal is often initiated in adolescence, a relationship could be predicted between the timing of the male growth spurt and which sex disperses, but such data are not currently available.

Sexual selection and adolescence

Individuals experience the same **sequence** of events during adolescence, but can vary considerably~~e~~ in the rate of changes and when these occur during the process (e.g. Tanner, 1962; Watts, 1985; Setchell & Dixson, 2002). Differences in the age at first reproduction, in attained mass or size, in the development of coloration or other signals, weaponry, and behaviour associated with reproduction, all influence reproductive success. Thus, all are the product of sexual selection, while the variation between individuals is the focus of selection.

The effect of nutrition or energy balance on the age at which female primates reach menarche suggests that a minimum investment in growth and body condition is required before reproduction occurs (e.g. Schwaltz et al., 1988; Surbey, 1990; Bercovitch & Strum, 1993; Bercovitch, 2000; Setchell et al., 2002). Early maternal influences on growth and individual success as a juvenile thus are factors which may pace processes in adolescence. Social factors are also important in the regulation of puberty (e.g. Vandenbergh et al., 1972; Vandenbergh & Coppola, 1986; Surbey, 1990; Worthman 1993), and intrasexual competition influences age at maturity in female strepsir~~r~~hines (Izard, 1990), Old World monkeys (Bercovitch & Goy, 1990), New World monkeys (Abbot et al., 1990; Ziegler et al., 1990) and apes (Graham & Nadler, 1990). In tamarins and common marmosets, males contribute to infant care and reproductive skew is high amongst females, producing intense female-female competition. Reproductive function and puberty are physiologically suppressed in subordinate females in the presence of dominants, and high-ranking females interrupt the copulations of other females (Abbott et al., 1990; Dixson, 1998; Ziegler et al., 1990).

The timing of puberty in males is influenced by neonatal testosterone (Mann et al., 1989; 1998; Eisler et al., 1993, Lunn et al., 1994), and conditions during the infant stage thus have consequences for pubertal development. The timing of sexual maturation may also be affected by the social environment. For example, the onset of puberty occurs earlier in higher-ranking male rhesus macaques (Bercovitch, 1993) and baboons (Alberts & Altmann, 1995a). High-ranking male mandrills have larger testes for their age than do lower ranking males (Setchell & Dixson, 2002). There may be a mass threshold that is necessary, but not sufficient, for reproductive maturation in males (Bercovitch, 2000; Setchell et al., 2001), although age at puberty onset in male stump-tailed macaques is not significantly correlated with mass, rank or maternal rank (Nieuwenhuijsen et al., 1987a). Maternal rank affects adolescent social and physical development (see also Colvin, 1983): male rhesus macaques born to high-ranking mothers have higher levels of circulating testosterone and larger testes during adolescence (Dixson & Nevison, 1997), and adolescent sons of high-ranking female mandrills are heavier for their age than are the sons of low-ranking females (Setchell et al., 2001). Prepubertal differences in body mass are likely to determine the dominance rank of age-mates in adolescence, with heavier males continuing to dominate lighter age-mates (Lee & Johnson, 1992; Pereira, 1995). Dominant males have higher testosterone levels, and hence develop more conspicuous secondary sexual traits more quickly, although in captive primates, high levels of testosterone are a result of, rather than a predictor of, high dominance rank (Sapolsky, 1993). Low testosterone levels in subordinate males may be due to stress-induced suppression of testicular function (Sapolsky, 1985; Graham & Nadler, 1990), while differences in the hormone responsiveness of tissues, feeding competition, and / or metabolic efficiency may play a part in constraining the rate and extent of development for subordinate males (Bercovitch, 2000).

The timing of full reproductive maturation represents an opportunity for the action of sexual selection, but this is not clear-cut. In general, primate species with relatively high male-biased sexual dimorphism tend to be those where females reproduce relatively early (Figure 1), suggesting that dimorphism has costs for both sexes. Early maturation may represent a trade-off ~~of~~ between decreased investment in growth against early reproduction, or it may be a consequence of higher risks taken early in life, thus attaining a threshold mass at a younger age. Individuals who delay reproduction face increased mortality risks as well as a loss of reproductive time. We need far more data on individual growth patterns up to sexual maturity to be able to relate sexual selection to strategies for growth and dispersal at adolescence.

Adulthood

Definition

The problem of what constitutes an adult primate is probably the most important one for comparative studies of selection pressures (c.f. Bernstein et al., 1991; Bercovitch, 2000). As with all developmental stages, the characteristics used to define adults are neither uniform nor necessarily linked to one another. Comparative studies of "adult" characteristics across mating systems, be they body size, mass, or differential reproductive success, are severely limited by differing usage of the term "adult". Furthermore, greater attention is needed to the several adult life-history stages that are usually classed together as one ("adulthood") or two ("adolescence" and "adulthood") stages. For example, Pereira & Altmann (1985) have suggested that "adulthood" be divided into "young", "mature", and "aged" stages. From their perspective, "adolescent" primates are gametogenic but not yet reproductive, young adult primates grow and reproduce (here termed adolescent), mature adults reproduce but have ceased to grow, and senescent adults are past their prime, show signs of old age, and have reduced reproductive rates. We consider adults as socially integrated, reproductive individuals that have ceased physical growth and attained endocrine stability.

"Adulthood" itself does not represent an end-point. Rather, maturation is a life-long process that does not cease at the onset of adulthood. Age-graded changes in physical parameters, in fertility, in reproductive strategies, and in reproductive experience have all been widely discussed in relation to sexual selection. As such we will simply highlight some areas where patterns in early development lead to predictions about reproductive tactics used by the two sexes.

Physical sex differences

Although statural growth ceases at epiphyseal closure, growth in body mass does not stop abruptly, but declines gradually (Leigh, 1992) and gradual changes in fertility, bone mass and body mass occur throughout an individual's lifetime (e.g. Schwartz & Kemnitz, 1992; Johnson & Kapsalis, 1998). Captive male orang-utans continue to increase in body mass throughout their adult life (Leigh & Shea, 1995). Dentition becomes worn further, affecting body mass (e.g. Phillips-Conroy et al., 2000). Secondary sexual characters may change during the adult phase. For example, male mandrill coloration can both increase and fade during adulthood (Setchell & Dixson, 2001b), and cheek flanges in orang-utans develop relatively late in the lifespan of a male (see van Hooff & Utami, this volume).

Sex differences in behaviour

Sex differences in the behaviour of adult primates are well known and need not be reiterated here. Of interest here are those elements of behaviour which relate to sexual selection acting earlier in the developmental stages, and as there have been so few long-term studies on different primate species, much is speculation. For example, we know very little about the consequences of early reproduction in females and later mortality. Does, as has been suggested for humans (Lycett et al., 2000), fruitflies (Partridge, 1988) and captive elephants (Clubb & Mason, 2002), early reproduction lead to earlier death? Does investing heavily in one offspring to ensure its growth and survival lead to depletion of maternal resources and thus lowered investment in subsequent offspring?

Primiparous females have longer inter-birth intervals than do experienced females (e.g. Bercovitch et al., 1998; Setchell et al., 2002), suggesting that they have fewer resources to invest in offspring. Inter-birth intervals increase again in old females (Strum & Western, 1982). As fertility declines, females may invest more in each individual offspring or litter, more in one sex of offspring than in another, or employ more costly tactics to ensure fertility. However, convincing tests of hypotheses as to the extent and nature of sex biases in maternal investment are difficult to carry out (Brown & Silk, 2002; Silk & Brown, this volume).

As with females, male reproductive success is age-graded, related to experience, and associated with different behavioural tactics (e.g. Dunbar, 1984; Sommer & Rajpurohit, 1989; Altmann & Alberts, 1995b; van Noordwijk & van Schaik 2001; this volume; van Hoof & Utami, this volume). Changes in reproductive potential and fighting ability over a lifetime should affect mate choice criteria and competitive tactics. While prime males may rely on competition to gain access to fertile females and guard them from other males' mating attempts, younger males, or senescent males, may employ sneaky tactics to obtain matings. Other examples of tactical decisions in group living species which depend on age and condition include: when to transfer from one group to another; whether to associate with a group of females, with an all-male band, or to live alone; and whether to challenge higher-ranking or harem males for access to fertile females. In non-gregarious species, decisions also include dispersal and ranging tactics, such as whether to challenge for possession of a territory, and attempt to exclude other males from access to females, or to range as a "floating" male and sneak copulations (e.g. galagos: Charles-Dominique, 1977; Bearder, 1987; orang-utans: van Hooff & Utami, this volume). Again, more detailed information is required from long-term studies to determine the stability and reproductive payoffs of alternative reproductive tactics over the lifespan in male primates, and specifically how these relate to early physical and social development.

CONSEQUENCES OF SEXUAL SELECTION FOR DEVELOPMENT

Sexual dimorphism and development

While it is relatively easy to measure sexual dimorphism, understanding the impact of sexual selection on dimorphism is more problematic (Plavcan, 1999; this volume). However, selection may be inferred from patterns and processes of growth and maturation. With the exception of growth in body mass (notably Leigh, 1992; 1995) and studies of humans (e.g. Tanner, 1962; Malina, 1978), detailed studies of growth to maturity are extremely rare for primates, particularly for wild populations (but see Altmann & Alberts 1987; Strum, 1991; Cheverud et al., 1992).

Leigh (1992; 1995) investigated how mass growth rates diverge between male and female primates, and sex differences in the length of the growth period. Using mixed longitudinal and cross-sectional body mass data for 37 species of captive primate, he showed that, as predicted from patterns of adult size dimorphism, species with low levels of inter-male competition do not show sex differences in development (monogamous / polyandrous mating systems). Where it occurs, adult sexual size dimorphism can arise via sex differences in the duration of growth (sexual bimaturism), by differential growth rates in the two sexes, or by a combination of the two (Gavan & Swindler, 1966; Shea, 1986). These different ontogenetic trajectories, bimaturism (male time hypermorphosis) and differential growth rates (male rate hypermorphosis), can none the less produce similar levels of adult dimorphism observed in relatively closely-~~-~~related species (Leigh, 1992). Species with a multi-male, multi-female mating system develop sexual size dimorphism through bimaturism, with minimal sex differences in growth rate, and males attain adult mass later than do females. By contrast, in species where a single male monopolises a group of females, dimorphism is attained through males growing faster than females, with less input from increased duration of growth. Leigh (1995) relates these ontogenetic differences to the distribution of risks during a male's development, suggesting that growth rate differences occur in taxa where the lifetime distribution of risks changes rapidly (uni-male, multi-female groups), whereas bimaturism occurs in species that have a relatively uniformly changing or stable risk distribution (multi-male, multi-female groups).

In addition to linking mortality risks, patterns of development and sexual dimorphism, Leigh's data suggest independence between adult morphology and the specific pathway to attaining that morphology; developmental trajectories can vary in pattern but yield similar adult morphologies. Rather than selection targeting a particular degree of adult dimorphism, it may be targeting development and adult dimorphism thus is not constrained by the pattern of development. Leigh (2001) has recently highlighted this flexibility of developmental stages in primates, demonstrating a lack of correlation in the relative duration of the infant, juvenile, and adolescent growth periods. This has important implications for selection, which can alter these periods independently. The degree to which patterns of development and adult morphology are linked and constrained, however, remains an open question.

Sex differences in timing of reproductive maturation

Differential selection for enhanced male size and competitive ability, in combination with a divergence between the reproductive strategies of males and females (e.g. Wilner & Martin, 1985), has led to sex differences in reproductive development and maturity. Bercovitch (2000) collated data on age at puberty, first parturition, and full size for males and females of polygynous c~~C~~ercopithecid species, showing that females enter puberty significantly earlier, and reach adult body size significantly earlier than do males. He also makes the important distinction between the onset of reproductive capacity (which occurs around the same age in males and females), and the observed onset of reproduction (on average later in males than females). As a result, the interval between potential and actual reproduction is shorter for females than for males. However, male reproduction can occur earlier in the final growth phase than it does for females. This is most likely because gametogenesis is relatively cheap for males and thus not in conflict with growth. By attaining physiological maturity early, the potential age at first reproduction can be reduced for males who employ surreptitious mating tactics.

Investment in growth versus investment in reproduction

All else being equal, individuals should mature and reproduce as early as possible, since the risk of mortality increases with any delay to onset of reproduction. Only when the benefits of delayed reproduction outweigh the mortality costs associated with delay should reproduction be postponed. There is the potential for conflict between the allocation of resources to growth rather than reproduction and investment in progeny if females are still growing when they reproduce for the first time. This conflict may be accentuated when there are energetic limitations (Martin et al., 1994; Strum, 1991). At the point where the advantages of extra growth (either for neonate or individual survival) are outweighed by the advantages of earlier reproduction, females allocate resources to maintenance, growth **and** reproduction, with consequences for reproductive outcomes in primiparous mothers (Wilner & Martin, 1985; Martin et al., 1994; Strum, 1991).

Male reproductive effort depends on gaining access to fertile females. Where male mating opportunities are related to contest ability, and males compete directly for access to females, they achieve only occasional successful matings before they attain full adult size (e.g. mandrills - Figure 2), although they reach sexual maturity long before this point. Males of such species therefore invest in traits that will lead to mating success: dominance rank, skills in assessment, large body size, weaponry and displays where contest competition is important (Wickings & Dixson, 1992; Setchell & Dixson, 2001a;b); fat reserves where endurance rivalry is important (e.g. Bercovitch, 1983; Alberts et al., 1996). Sexual dimorphism has important costs for males in terms of time and energy. Males grow for longer (bimaturism) and / or invest more resources in growth during the growth period (rate dimorphism) than females, and the associated postponement of reproduction increases the risk of mortality before males begin their reproductive career. Thus the fitness benefits of large body size, in terms of high rank and access to females, must offset these costs. Large body size in males reduces vulnerability to predators, is energetically advantageous during dispersal, reduces susceptibility to disease (Scanlan et al., 1987; Raleigh & McGuire, 1990), and females may prefer to mate with larger ~~bodied~~ males.

As we note above, early female reproduction (for body mass) is associated with higher sexual dimorphism, not just among the c~~C~~ercopithecids, suggesting some causal or selective relationship between the pace of growth and reproductive strategies of males and females. This observation lends additional support to the proposal that one mechanism for enhancing dimorphism is for females to start reproduction earlier and at a smaller size and thus divert resources away from growth (Wilner & Martin, 1985). Interestingly sexual dimorphism is also associated with relative reproductive rates, with shorter interbirth intervals (for female mass) found in species with higher dimorphism (Figure 3). More dimorphic species tend to lead more rapid reproductive lives, and we expect that early mortality should underlie at least some of these patterns. All in all, males of highly sexually dimorphic species appear to gain additional advantages for their reproductive potential – their females begin reproduction relatively early and they reproduce relatively frequently for their mass. This suggests to us that over and above the energy, time and mortality cost inherent in growing rapidly and/or for longer, dimorphism contributes to the “average” male’s reproductive success. As dominant males in highly dimorphic species may also gain priority of access paternity (e.g. Altmann et al., 1996), the advantages of enhanced male size appear to be significant.

CONSEQUENCES OF DEVELOPMENT FOR SEXUAL SELECTION

Developmental trajectories have potentially far-reaching consequences for the action of sexual selection (Leigh & Pereira, 2003). Ecological and social conditions during neo-natal and pre-reproductive development influence adult reproductive potential and behavioural strategies (Harcourt & Stewart, 1981; Draper & Harpending, 1982; Altmann, 1998, Pereira & Leigh, 2003). Development is modulated by maternal factors, nutrition, disease, and psychological stress, all of which impact on adult outcomes. Furthermore, the reproductive tactics employed by individuals to maximise fitness are influenced by environmental conditions, age, physical or reproductive condition, population density or structure (Brockman, 2001), which may act at any point from infancy onwards. Different ontogenetic pathways may be set early in life, as hypothesised for orang-utans (Maggioncalda et al., 1999). It is therefore important to include ontogeny in studies of alternative mating tactics (Caro & Bateson, 1986), and to relate differences in ontogeny to differences during adulthood. Maternal and allomaternal care have major consequences for infant survival and mortality in primates, which again interact with the potential for selection on female size, contest ability and reproductive strategies. Moreover, sexual selection may vary in action or intensity over the course of an individual's lifetime. For example, adolescent or subordinate adult males, faced with a competitive disadvantage and potentially increased mortality, will pursue alternative mating tactics, which should lead to a shifting pattern of sexual selection over time (e.g. Setchell & Dixson, 2001a;b; Utami et al., 2002; van Hooff & Utami ~~et al.,~~, this volume).

Furthermore, developmental rates and patterns of mortality may constrain the potential for the evolution of sexual dimorphism. In the interspecific comparisons attempted here, relative birth mass was positively correlated with sexual dimorphism – the larger the male relative to the female, the greater the relative size of the neonate (Figure 4). However, this relationship varies as a function of mortality risks due to predation. For species with little risk of predation, neonates are relatively smaller (and cheaper to produce) when dimorphism is greater, while the opposite is true for neonates born to species where predation risk is high. Predation may be driving both male mass and birth mass to increase and thus enhancing the ability of individuals to escape predation, but when predation risks are low, sexual dimorphism arises from male competition and females may be producing cheaper infants when infanticide risks due to this competition are be high. A similar trend is found in age at weaning (Figure 5). Relatively highly d~~`~~imorphic species wean early when the risks of mortality due to predation are low (and possibly the risks of infanticide are high), but wean late when the predation risks are high. Strategies to ensure infant survival in risky environments (e.g. Janson & van Schaik, 1993) interact with sexual selection, and impact on growth patterns for different species. This is further emphasised when environmental risks are nutritional. The relatively low levels of mass dimorphism amongst neotropical primates may reflect the limited energy availability from patchy fruit supplies (e.g. Ford, 1994), which again constrains the potential for rapid or prolonged growth during the developmental period. Similarly Leigh & Terranova (1998) suggest that extreme seasonality, reduced growth periods, and relatively early male maturation in lemurs when compared with anthropoid primates of similar body sizes, preclude the evolution of sexual dimorphism through bimaturism, despite high levels of inter-male competition.

Examination of relationships among the timing of events during development, fecundity, mortality and reproductive tactics in primates requires long-term studies, following the fate of individuals and cohorts from birth to death. Clearly, studies linking experiences during development to reproductive tactics and fitness, such as those on red deer (Kruuk et al., 1999) and yellow baboons (Altmann, 1991) are required to identify ontogenetic strategies. Studies of sexual selection will benefit greatly from the application of a developmental and life history perspective.

SUMMARY & CONCLUSIONS

Our aim in this chapter has been to explore how sexual selection relates to development over the lifespan, and how patterns of sexual selection change over the course of an individual's lifetime. Sexual dimorphism in body size, behaviour and physiology results from selection pressures acting on male and female characters independently, and in different ways, during development. Within-species, sex-specific growth rates and developmental trajectories evolve when age-dependent expenditure~~s~~ on reproductive effort~~s~~ differs by sex (Wiley, 1974). While we currently have insufficient longitudinal data on development and its consequences to specify mechanisms for either sex, some patterns are clear. Female primates are time-limited, needing to attain the minimum mass required to conceive and support the costs of pregnancy and lactation during maturation. Energetic and time constraints thus suppress female growth in favour of allocating resources to reproduction (Demment, 1983; Strum, 1991; Martin et al., 1994). Mortality risks also influence the life history strategies of females, enhancing opportunities for sexual selection and specifically acting on sexual size dimorphism. By contrast, where male reproductive success depends on fighting ability and body size, male maturation is delayed to achieve larger size and competitive ability. This delay, which involves greater expenditure and risk prior to first reproduction, may be profitable for male mating effort, especially as highly dimorphic species also appear to have rapid reproductive rates.

Before we can fully understand how sexual selection operates on development and how development constrains or facilitates sexual selection, we need more data on primate patterns of development (see also Pereira & Leigh, 2003), and in particular to be able to link discontinuities with the gradual processes of development. Individual variation in rates of growth, age at reproductive maturation, social contexts, and paternity need to be brought together to gain a synthetic perspective on the reproductive outcomes of alternative ontogenetic pathways. Finally, sexual selection in the context of development may be represented most clearly by heterochronic changes in timing of developmental events and states between ancestors and descendents.

ACKNOWLEDGEMENTS

We are grateful to Peter Kappeler & Carel van Schaik for their invitation to contribute to this volume. Michael Pereira provided detailed criticism of an earlier draft of the manuscript; an anonymous reviewer and the editors also provided helpful comments and encouragement during the process of gestation.~~.~~

Table 1. Stages of development defined by physiological signals, with approximate age of occurrence for chimpanzees (*Pan troglodytes*) from Kraemer et al. (1982), and mandrills from Setchell & Wickings (in prep.)

Period	Development			Chimpanzees age range (mo)		Mandrills age range (mo)	
	Males	Males and Females	Females	Males	Females	Males	Females
Infant	-	Mass gain decelerates	-	0-24		0-8	
		Deciduous dentition erupts					
Juvenile	Low testosterone (T) and luteinising hormone (LH) levels	Mass gain accelerates		24-60		8-46	8-43
	Testes grow slowly	Deciduous dentition complete					
Puberty	Testes growth accelerates	Rise in LH results in increased gonadotrophic hormones and sex steroid production	First, irregular, sexual swellings	60-84	60-96	46-?	43-48
	Production of sperm	Loss of deciduous dentition and eruption of adult dentition	Menarche First ovulation				
	Secondary sex characters (SSCs) begin to develop	Reproductive maturity attained					
Adolescence (includes puberty)	Mass growth spurt	All deciduous dentition lost	Continued investment in own growth as well as reproduction	84-132	96-144	46-120	43-84
	T peaks	Adult dentition completed					
	SSCs continue to develop	Epiphyseal union					
Adult	Adult levels of T	Full size attained		132+	144+	120+	84+
	Adult SSCs						

~~Table 1. Stages of development defined by physiological signals, with approximate age of occurrence~~

~~for chimpanzees (*Pan troglodytes*) from Kraemer et al. 1982~~

FIGURE LEGENDS

Figure 1: The correlation between relative sexual dimorphism and relative female age at first birth for primate species. Sexual dimorphism is expressed as the unstandardised residual of male mass to female mass and age at first birth has been expressed as the unstandardised residual of age for female body mass. Life history data from Lee & Kappeler (2003); sexual dimorphism from Smith & Jungers (1997).

Figure 2: Reproduction vs age in mandrills. Top: probability that a female mandrill gives birth vs age. Bottom: successful copulations (ejaculation) observed for males vs age. Open circles are adults of unknown age.

Figure 3: The relationship between relative interbirth intervals and relative sexual dimorphism (F = 4.54, df= 1, 81, p = 0.037, controlling for phylogeny at the subfamily level) for primate species. Data as Fig. 1.

Figure 4: The correlation between relative neonate mass and relative sexual dimorphism (r = 0.256, n = 86, p = 0.017 overall), shown separately for those primate species where predation risk categories were assigned (n = 80). High and Low risk categories differ (p<0.05 post hoc), controlling for phylogeny at the subfamily level. Data as Fig. 1.

Figure 5: The relationships between relative age at weaning and sexual dimorphism as a function of predation risk category for 65 primate species. The correlations for High (r = 0.493, n = 19, p = 0.032) and Low risk (r = -0.490, n = 23, p = 0.025) are significant. Data as Fig. 1.

Figure 1

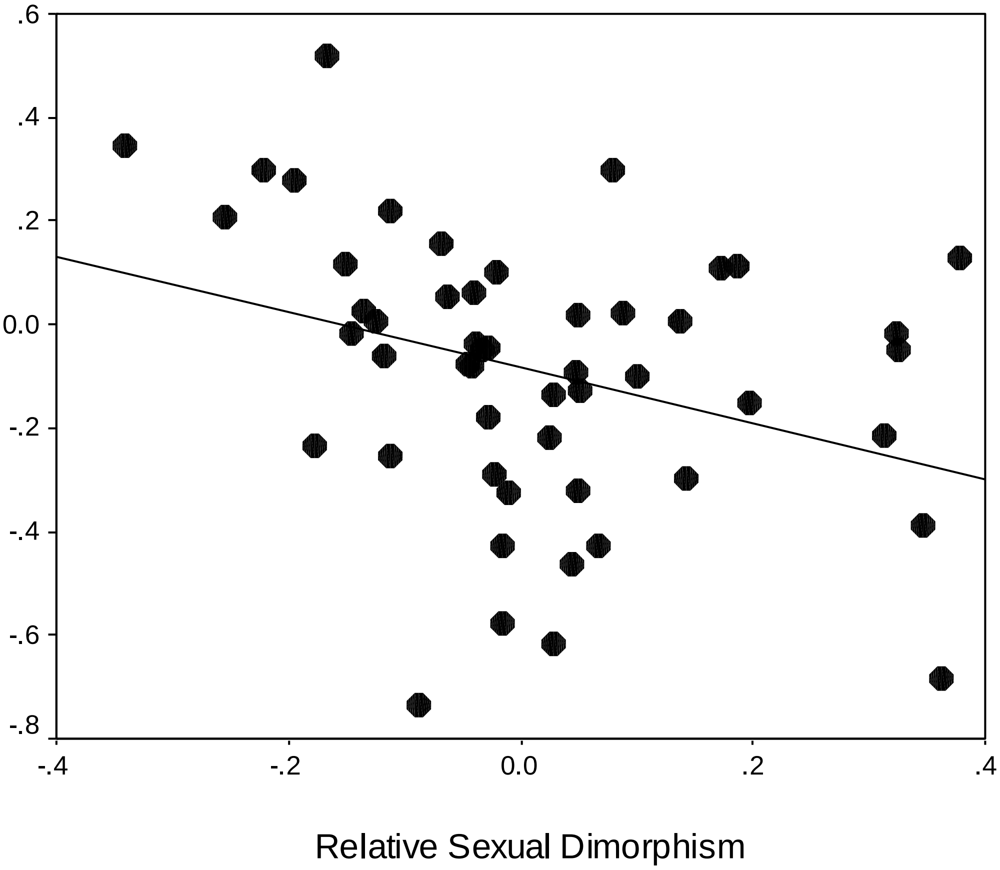

Figure 2

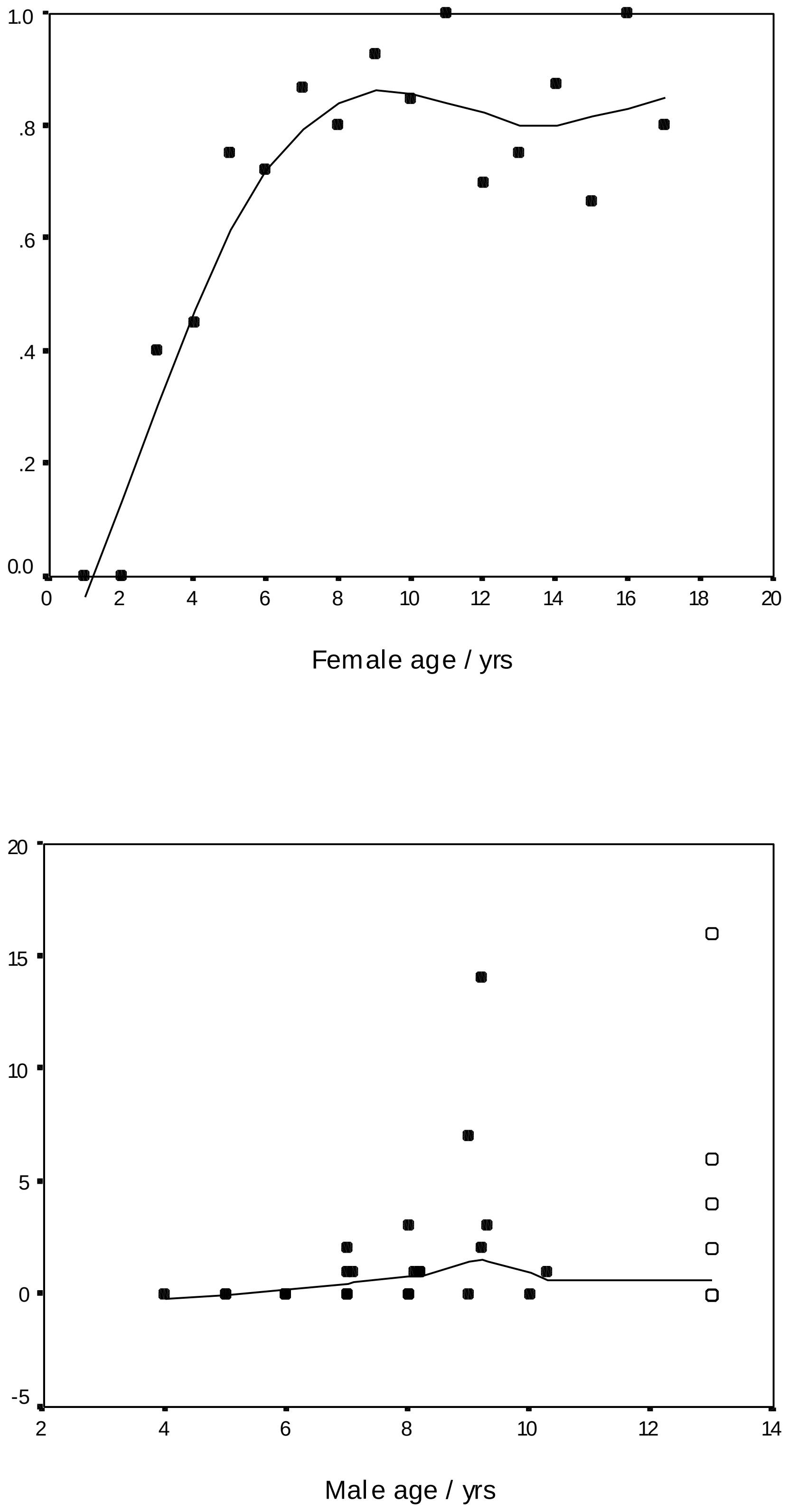
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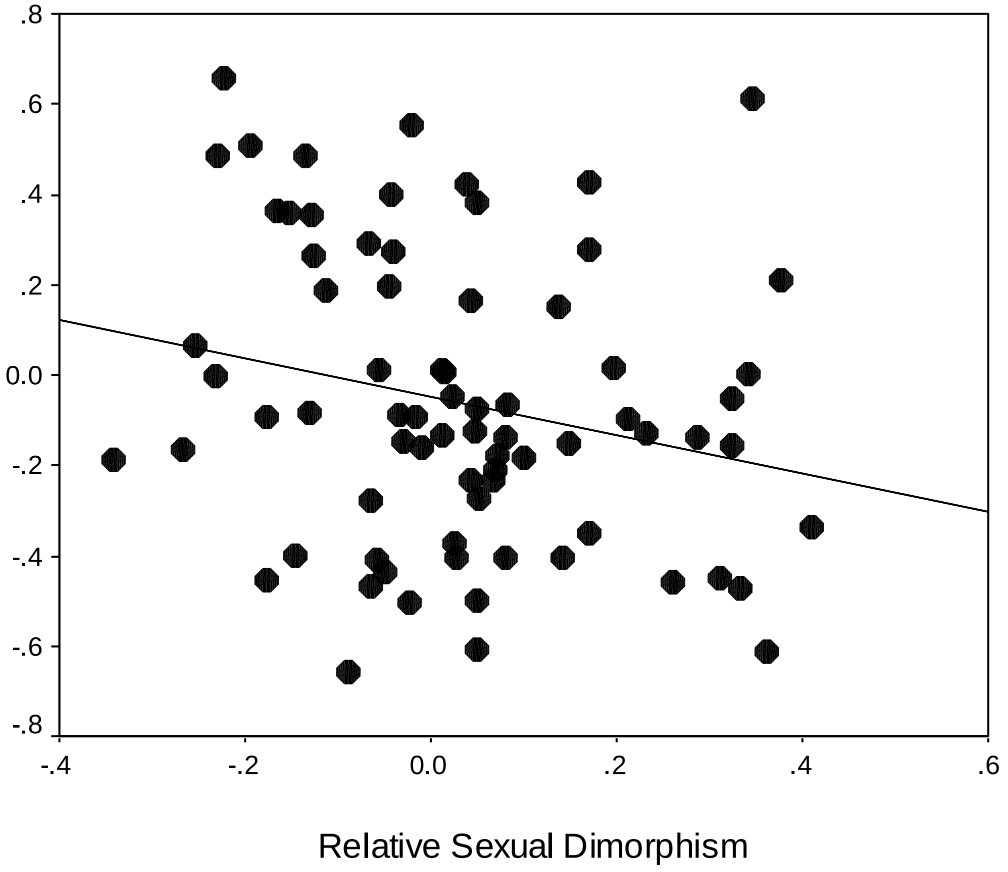
Figure 3:



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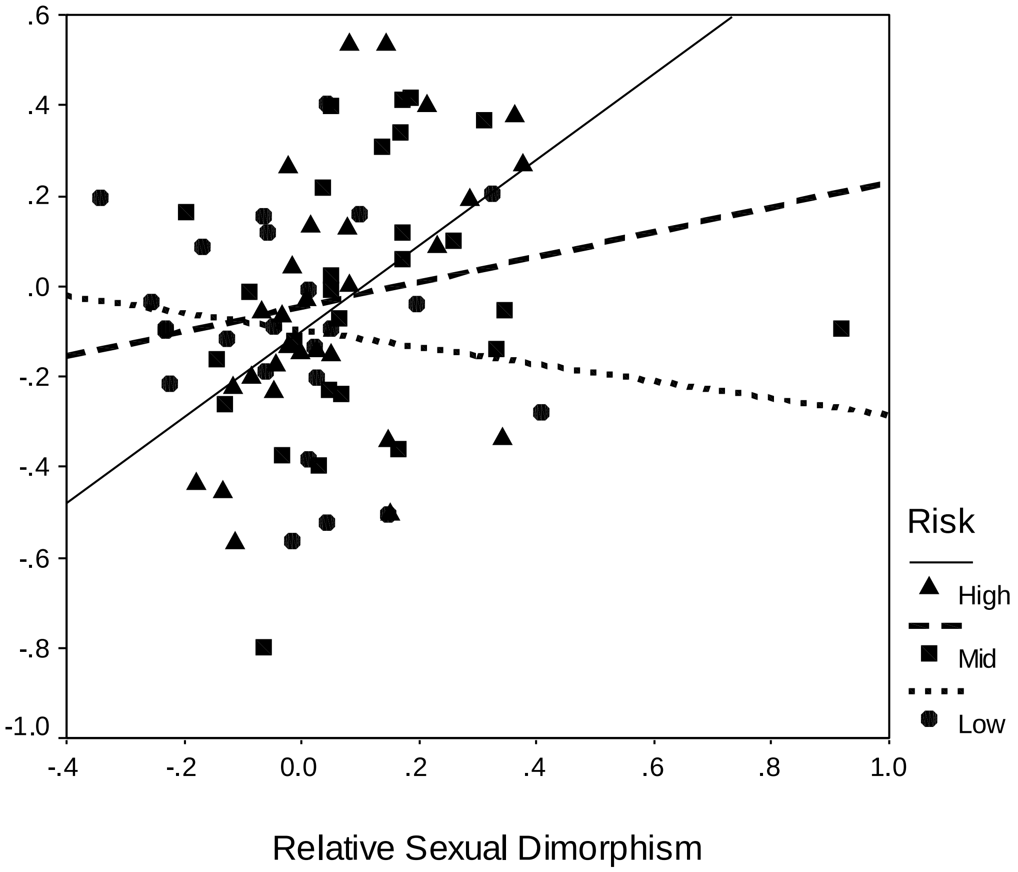
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Relative Sexual Dimorphism
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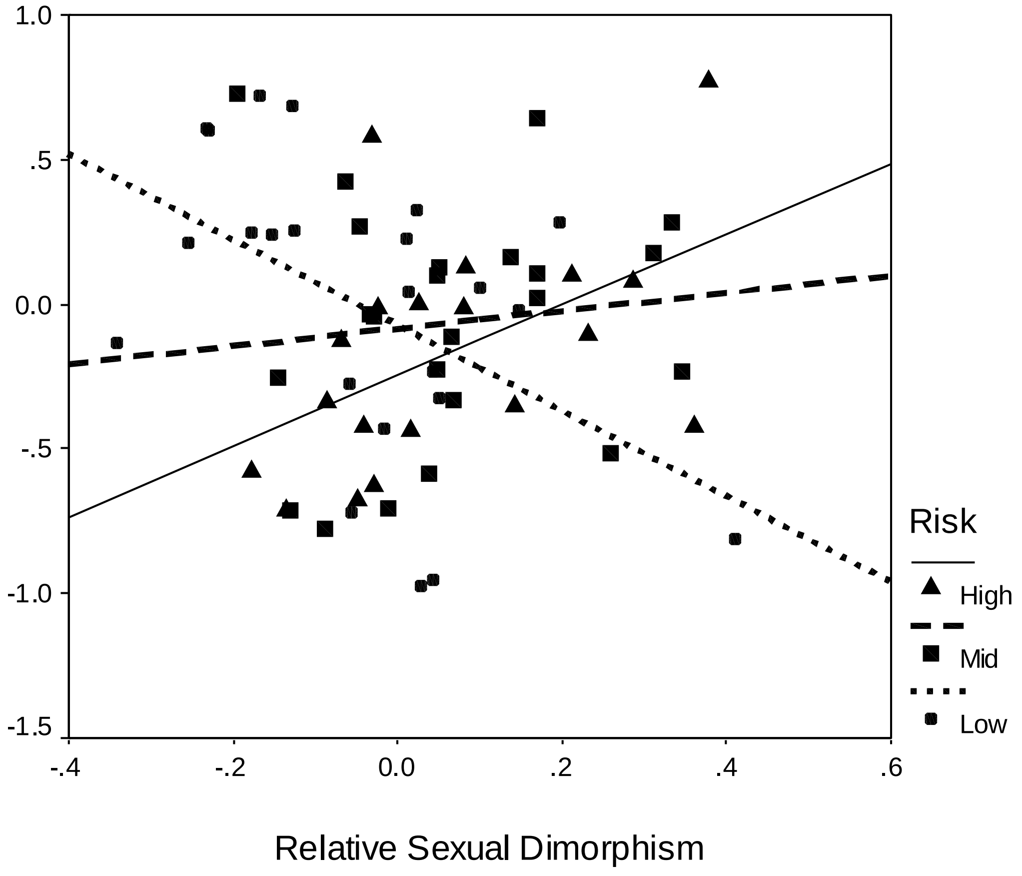
Figure 5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Relative Sexual Dimorphism
Risk
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Mid
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